THE INFLUENCE OF RIVER FLOW ON THE DISTRIBUTION AND COMMUNITY ORGANISATION OF RIVER BIRDS

by

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Abstract

River flow is a major driver of community dynamics in riverine-floodplain ecosystems. Flow-induced disturbance can have large impacts on taxonomic groups at higher trophic levels such as birds. However, our understanding of river flow-avian relationships is constrained by a failure to focus on multiple species' responses to hydrological variables across large geographical areas. The aims of this thesis are to combine a national-scale dataset of river bird surveys with river flow archives to: (i) understand *how* hydrological disturbance affects the distribution of river birds, and (ii) evaluate the potential *impacts* of climate change-induced shifts in river flow on such species' distributions. Species have complex, but biologically interpretable, associations with hydrological variables. Variation in river flow acts as an environmental filter that influences community assembly processes. Specialist river birds are most vulnerable to climate-induced shifts in river flow and their distributions may shift in response to future changes in river habitat suitability. The success of relating hydrological variables to the distributions of river birds demonstrates that variability in river flow has consequences for ecological structure at high trophic levels and that climate-induced shifts in river flow may represent a previously unidentified mechanism by which climate change mediates range shifts in birds.

Acknowledgements

I would like to thank the British Trust for Ornithology for access to datasets and the numerous volunteers who collected Waterways Breeding Bird Survey data between 1998 and 2012. I am also grateful to the Centre for Ecology & Hydrology, in particular Christel Prudhomme, for providing National River Flow Archive and Future Flow Hydrology data. I would also like to extend gratitude to my supervisors, James Reynolds, David Hannah, David Noble and Jonathan Sadler, for the direction and advice they provided throughout the development of this thesis. Finally, I would like to say thank you to Emily Burge for her invaluable support throughout my PhD research. This research was made possible by financial support from a National Environment Research Council (NERC) studentship (NE/J500240/1).

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List of abbreviations

AIC - Akaike Information Criterion

AUC - Area under the curve of a receiver operating characteristic plot

BEM – Bioclimatic Envelope Model

BIC – Bayesian Information Criterion

BTO – British Trust for Ornithology

FD – Functional Diversity

FDiv – Functional Divergence

FEve – Functional Evenness

FFH – Future Flow Hydrology dataset

FRic – Functional Richness

GAM – Generalized Additive Model

GEEs – Generalized Estimating Equations

GLM – Generalized Linear Model

JSDM - Joint Species' Distribution Model

K – Cohen's Kappa

NRFA – National River Flow Archives

P(x) - Probability of Occurrence

REML – Restricted Maximum Likelihood

SDM – Species Distribution Model

SES – Standard Effect Size

SPs - Selection Probabilities

SR – Species Richness

SVI – Species Vulnerability Index

WBBS – Waterways Breeding Bird Survey

1. Introduction

Animal populations have spatially heterogeneous distributions with discrete patch boundaries (Sousa 1984). Spatial and temporal variation in the distributions and abundances of species may be explained by biological filters (e.g. competition and facilitation) but also by species' tolerances to physical gradients in the environment (Sousa 1984). Abiotic disturbance plays a key role in maintaining natural heterogeneity in environmental conditions, and the influence of disturbances on species' distributions and the composition of animal communities has gained increased recognition (Brawn et al. 2001, Jetz 2006, Melo et al. 2009, Baselga et al. 2012, Belmaker et al. 2012).

Disturbances may be biotic or abiotic in nature and, while they may be destructive on a local scale, they create habitat heterogeneity and facilitate niche diversity (Jentsch and Beierkuhnlein 2003). Disturbances act as an environmental filter that selects for species best adapted to living in a dynamic environment. They are, therefore, an evolutionary force for the development of life-history attributes and functional traits (Petchey and Gaston 2002, Devictor et al. 2008). Disturbances affect ecosystem-level processes, including primary and secondary production, biomass accumulation, energetics and nutrient cycling (Woodward 2009), and their impacts can cascade through a food web to affect other trophic levels (Parmesan et al. 2000). Disturbances vary from having negligible to extreme effects on population survival. Less extreme disturbance events, which include biological interactions such as predation or grazing (MacArthur and Levins 1967, Cody 1974), may change competitive interactions between species and lead to re-balanced costs and benefits (e.g. optimal foraging niche) (Gutschick and BassiriRad 2003). However, the most extreme, catastrophic events, such as droughts and floods, may result in the major alteration of habitats and associated biota (McKechnie and Wolf 2010, Woodward et al. 2012).

As climate warms, the frequency of extreme hydrological events is expected to increase, even if the climatic means do not change substantially (IPCC 2012) (Figure 1.1). Changes in the variance of the frequency distribution of climatic variables will alter the frequency of extreme events at either end of the distribution (Easterling et al. 2000, Meehl et al. 2000). Floods and droughts are expected to increase in frequency, magnitude and duration in temperate zones (Pall et al. 2011, Prudhomme et al. 2012b, Prudhomme et al. 2013). There is, therefore, a need for greater understanding of the impacts of hydrological disturbance on the ecology of species that are responding to climate change. This requirement is of considerable significance for communities inhabiting riparian systems because they sit at the interface between terrestrial and aquatic habitats and so encompass steep environmental gradients in climate, inundation, soil moisture, disturbance and nutrients (Poff et al. 1997, Ward et al. 2002).

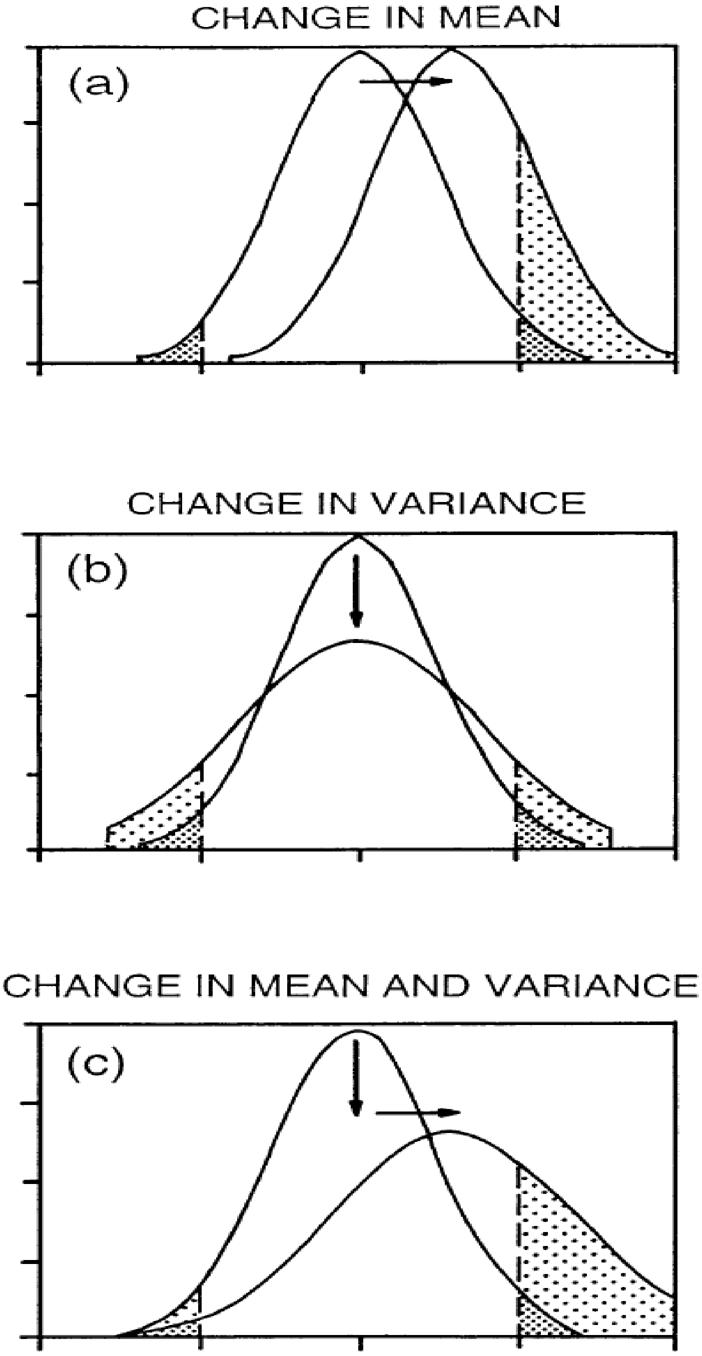

Figure 1.1 *Schematic from Meehl et al. (2000) illustrating how changes in mean (a), variance (b), and mean and variance (c) can affect extreme weather events. Dotted areas represent the frequency in the occurrence of extremes.*

Variability in river flow regime is the most significant disturbance in riverine systems (Poff et al. 1997) and causes a shifting mosaic of habitats, both aquatic and terrestrial, that creates a series of habitat patches in differential stages of succession (Tockner et al. 2000). Structurally diverse riverine habitats with variability in hydrological conditions generally support high species richness (Bunn and Arthington 2002, Ward et al. 2002, Ormerod et al. 2010). Several studies have explored the effects of episodic flow disturbances, such as floods, on the numbers (Olsen and Townsend 2005, Suren and Jowett 2006, Gerisch et al. 2012b, Buendia et al. 2014) and dynamics (e.g. dispersal and species interaction) (Lancaster 2000, Bates et al. 2006, Ledger et al. 2006, Gibbins et al. 2007, Lambeets et al. 2008, Gibbins et al. 2010, O'Callaghan et al. 2013) of aquatic or riparian invertebrates, whilst river flow regime parameters have been identified as valuable predictors of hydro-ecological associations (Monk et al. 2007, 2008). Flow disturbances may have a direct impact on invertebrates as they may lead to increased dispersal, while the indirect impacts from substrate turnover, uprooted macrophytes and seed dispersal via hydrochory create a mosaic of habitat patches (Bates et al. 2006, Ledger et al. 2006). Remnant invertebrates from the local species pool colonise suitable habitat patches, with the surviving species composition influencing the subsequent development of the invertebrate community (Ledger et al. 2006).

As it is acknowledged that the variation and persistence of in-stream communities are linked to hydrological variability, it is ecologically relevant to suggest that other taxonomic groups may be influenced by hydrological variables. This is especially pertinent given that flow-induced disturbance can have disproportionately large impacts on taxonomic groups at higher trophic levels (Ledger et al. 2012). River birds typically sit at the top of aquatic-riparian food webs (Buckton and Ormerod 2002) and so may be affected by knock-on bottom-up processes resulting from changes in the abundance and richness of prey species (Bures 1995, Chiu et al. 2008, Jonsson et al. 2012, Chiu et al. 2013). Additionally, river birds may be affected by physical changes in habitat conditions following hydrological disturbances because of disruption to the prevalence or quality of foraging or breeding habitats (Reiley et al. 2013, Jankowiak and Ławicki 2014) (

Figure 1.2). Variation in flows can influence the habitat occupancy (Reiley et al. 2013, Jankowiak and Ławicki 2014), abundance (Chiu et al. 2008), foraging behaviour (Taylor and O'Halloran 2001, Cumming et al. 2012, Wood et al. 2013), timing of breeding (Arthur et al. 2012, van Turnhout et al. 2012), reproductive success (Strasevicius et al. 2013) and survival (Chiu et al. 2013) of river birds. Extreme flows such as flooding may have positive effects on some species, such as piscivores (Knutson and Klaas 1997) as, in areas of normally low productivity, floods may lead to pulses in productivity and the creation of different habitats, resulting in a proliferation of prey species and an increase in the numbers of birds (Roshier et al. 2002, Kajtoch and Figarski 2013). However, extreme flows can also have negative impacts on river bird species, for instance by reducing the prevalence of prey (Wilson and Peach 2006), limiting the opportunity for foraging (Taylor and O'Halloran 2001) and by flooding nests and causing nestling mortality (Kirsch 1996, Chiu et al. 2013).

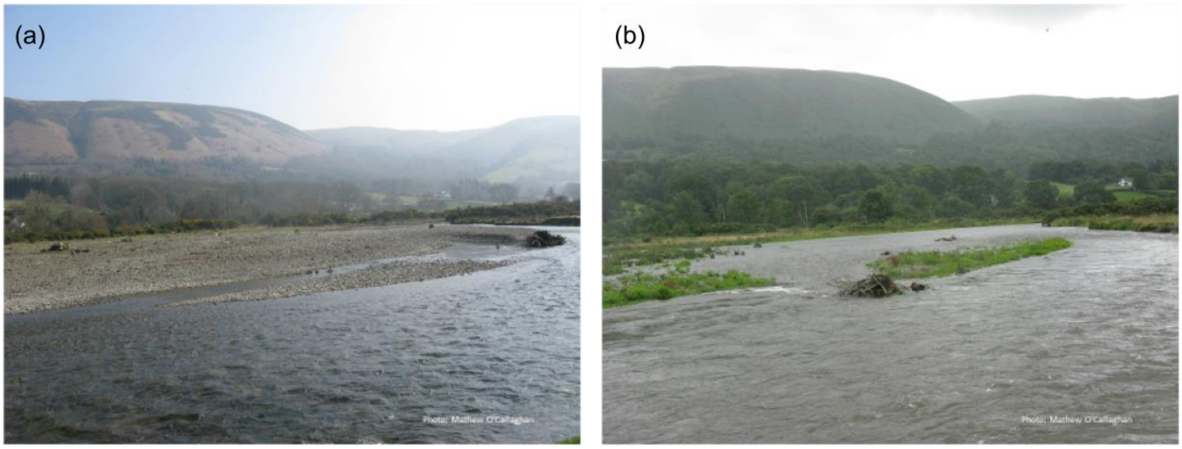

***Figure 1.2** Images illustrating the changes in habitat following an extreme high flow event on the River Wye, North Wales. The shingle bars at the river margin (a) are an important foraging habitat for river birds, such as common sandpiper (*Actitis hypoleucos*), grey wagtail (*Motacilla cinerea*), little ringed plover (*Charadrius dubius*) and western yellow wagtail (*Motacilla flava*), but becomes submerged during extreme high flows (b). Photo credit: Matt O'Callaghan.*

However, our understanding of river flow-avian relationships is limited because of our interpretation is typically limited to a few single species studies. In addition, due to the unpredictable nature of hydrological disturbances and the rarity of long-term ecological time-series datasets, there is a lack of long-term studies investigating the relationship between hydrological variability and ecology. Previous studies of the influence of river flow on bird populations are typically spatially and temporally constrained, with most focusing on a single watershed after a specific flood event. This poses a problem when trying to predict how a climate change-induced shift in river flow regimes may impact on river bird populations due to changes in the suitability of flow conditions in river habitat (Jenouvrier 2013). Changes in the timing of flows from climate change may adversely impact on river birds via a phenological mismatch in the timing of foraging behaviour with peaks in prey abundance (Visser et al. 2012) or habitat availability (Whitehouse et al. 2013), leading to range shifts (Renwick et al. 2012) or changes in phenology (Carey 2009) related to breeding (Ockendon et al. 2013) and migration (Gill et al. 2014), for example.

1.1. Aims and thesis outline

The aims of this thesis are to (i) understand how hydrological disturbance affects the distribution of river birds and (ii) evaluate the potential impacts of climate change-induced shifts in river flow on such species' distributions. **Figure 1.3** provides a diagrammatic representation of the thesis' structure.

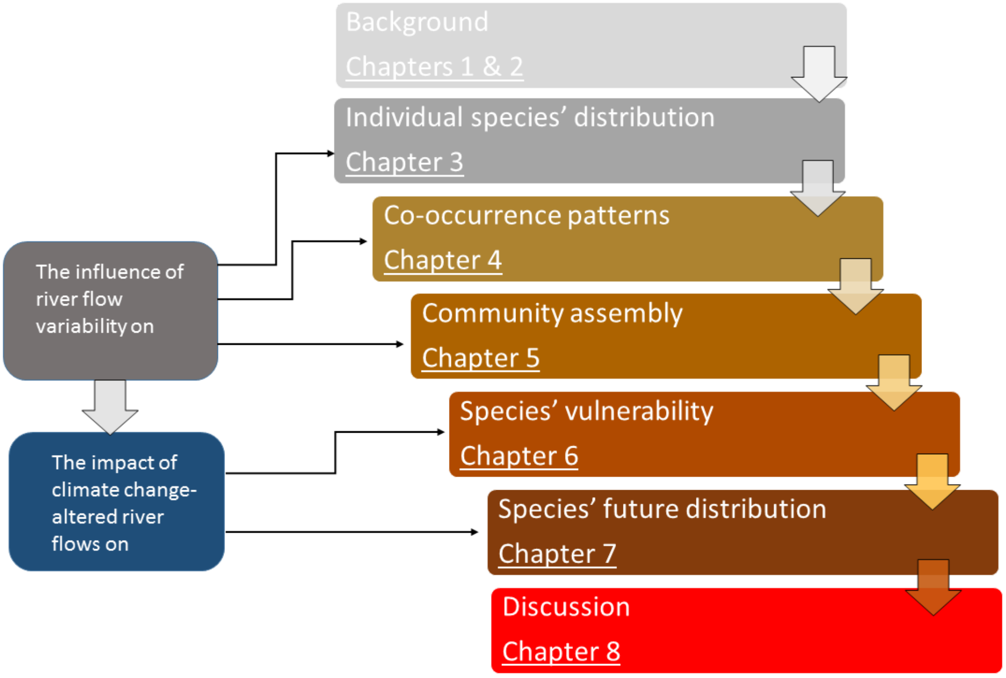

Figure 1.3 *Flow diagram displaying an outline of the thesis structure and the content of each of the eight chapters.*

This thesis comprises a sequence of five quantitative chapters, each of which has been published (Chapter Three [(Royan et al. 2013)]; Chapter Four [Royan et al. (2015)] Chapter Six [(Royan et al. 2014)]), accepted for publication (Chapter Seven [(Royan et al. In press)]) or recently submitted (Chapter Five). Initially, an overview of the scientific context (see above in Chapter One) of each chapter is provided, followed by the general methodology and data analysis procedures (Chapter Two). Across the main empirical chapters the thesis will provide a holistic overview of how variability in river flows influences the structure of river bird populations and how climate change-induced shifts in river flow impact species' distributions. Chapters Three to Five will address the first aim of the thesis, investigating how river flow influences the distribution of individual species (Chapter Three), as well as patterns of co-occurrence (Chapter Four) and the diversity of functional traits and community structure (Chapter Five). Additionally, Chapters Four and Five will assess the role of river flow variability as an environmental driver of community structure and compare this to the role of other environmental variables (e.g. climate and habitat) and other community assembly mechanisms (e.g. biotic interactions and neutral models).

Chapters Six and Seven will address the second aim of the thesis. First, the functional relationships between river bird distributions and variables of river flow identified in Chapters Three to Five will be used to develop an index of river bird species' vulnerability to a climate change-induced shift in the frequency, duration and magnitude of hydrological extremes (floods and droughts) (Chapter Six). Finally, Chapter Seven will use projections of river flows throughout the 21st century to predict how the distribution of a riverine-specialist bird may change in response to climate change-induced contemporaneous perturbations in river flows. **Figure 1.4** provides a visual representation of the key themes in the thesis.

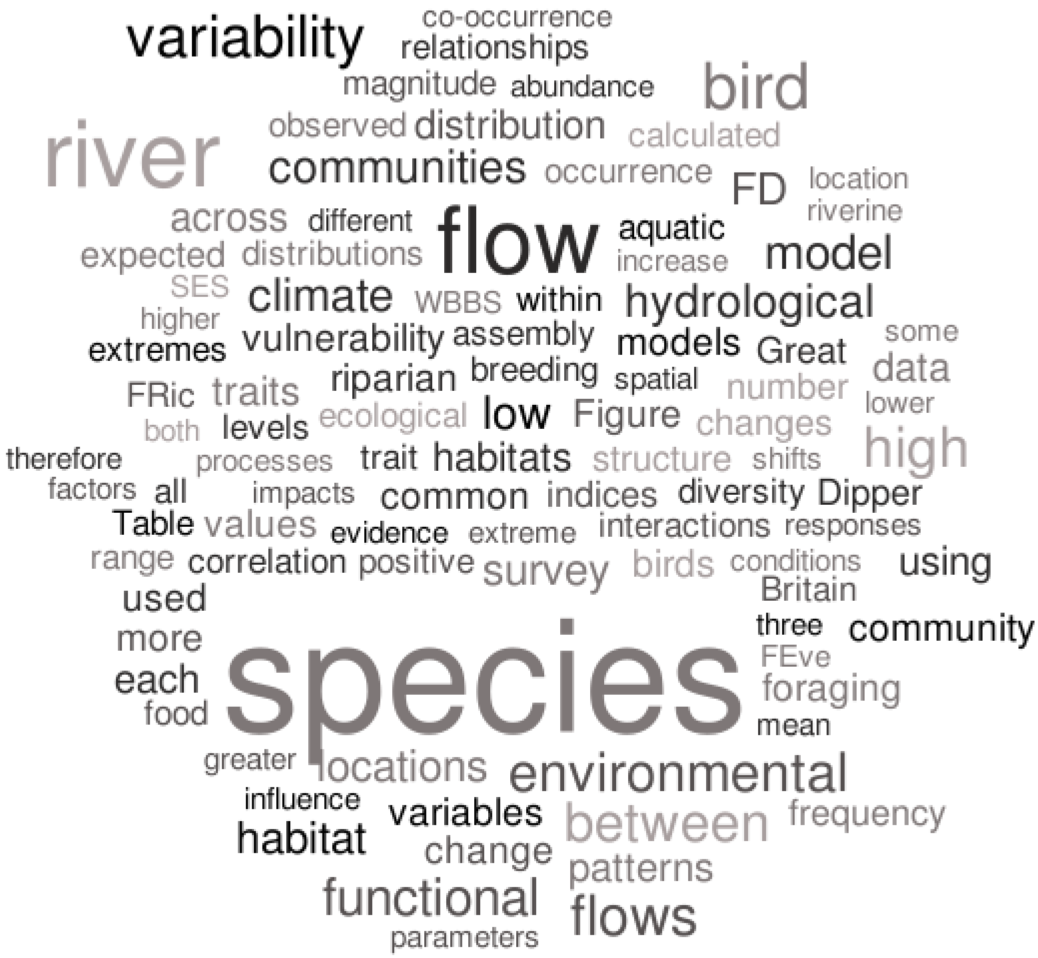

Figure 1.4 *A word cloud showing the relative prevalence (based on frequency of occurrence) of key words throughout Chapters Three to Seven (inclusive). The font size of text of each term is directly proportional to its frequency of occurrence.*

2. Methods

To understand how variability in river flow variables affects the distribution of river birds, two datasets were coupled to: (i) capture the distribution of river birds across mainland Great Britain and (ii) quantify long-term variability in river flows. An overview of the two datasets – the Waterways Breeding Bird Survey (WBBS) and the National River Flow Archive (NRFA) – is provided below.

2.1. Waterways Breeding Bird Survey (WBBS)

The WBBS is an annual census of birds on rivers and canals in Great Britain organised by the British Trust for Ornithology (BTO). The aim of the WBBS is to monitor changes in the breeding populations of bird species along waterways in Great Britain. The WBBS started in 1998 and was developed as a successor to the Waterways Bird Survey (WBS), which had been running since 1974 (Marchant 1999). It was also designed to complement the Breeding Bird Survey (BBS) as the BBS tends to have a low survey effort on waterways (Newson 2003). Consequently, the methodology of WBBS is similar to that of the BBS, being only adjusted slightly to account for linearity of habitat (with transects positioned parallel to the waterway rather than dissecting a 1 km square as in BBS (Marchant 1999)).

Waterway locations for the WBBS are randomly selected according to a stratification procedure (Marchant 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 (Marchant 2002). A single waterway within each square is then randomly selected, with the start and end points of the survey location determined by the observer. Maps with the survey locations are distributed to regional BTO representatives who then match the survey sites with suitably qualified observers.

Each year two visits are made to WBBS survey locations, one in the first half of the breeding season (typically April) and one in the second half (typically late June) (Marchant 2002). 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 (Marchant 2002). Observers count 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 (Marchant 2002).

A list of the bird species included in this thesis, with details of their breeding season habitats and key references, are provided in Table 2.1.

Table 2.1 List of species included in the thesis. Breeding season distribution and habitat based on Sharrock (2010), Newson (2003) and Cramp and Simmons (1977-1996).

Species	**Breeding season habitats**	**Additional references**
Common kingfisher Alcedo atthis	Slow flowing streams and rivers with vegetated banks for nesting.	(Marchant and Hayde 1980, Ormerod et al. 1988)
Common merganser Mergus merganser	Upland, fast flowing rivers.	(Meek and Little 1977, Gregory et al. 1997, Vaughan et al. 2007)
Common moorhen Gallinula chloropus	Widespread on wetland habitat, such as lakes, rivers, streams and ponds, including farmland and urban areas.	(Marchant and Hayde 1980)
Common redshank Tringa totanus	Saltmarshes, lakes and exposed mudflats of lowland rivers.	(Marchant and Hayde 1980)
Common reed bunting Emberiza schoeniclus	Wet vegetation surrounding wetlands and farmland.	(Marchant and Hayde 1980)
Common sandpiper Actitis hypoleucos	Fast flowing rivers and lakes.	(Marchant and Hayde 1980, Vaughan et al. 2007)
Eurasian coot Fulica atra	Lakes, reservoirs, ponds and rivers.	(Marchant and Hayde 1980)
Eurasian oystercatcher Haematopus ostralegus	Lowland rivers with exposed mudflats.	(Marchant and Hayde 1980, Vaughan et al. 2007)
Eurasian reed warbler Acrocephalus scirpaceus	Reedbeds surrounding lowland, slow flowing rivers and lakes.	(Vaughan et al. 2007)
Great cormorant Phalacrocorax carbo	Large lowland rivers.	(Vaughan et al. 2007)
Great crested grebe Podiceps cristatus	Lowland lakes, estuaries and slow flowing rivers.	
Grey heron Ardea cinerea	Most wetland and water types.	(Vaughan et al. 2007)
Grey wagtail Motacilla cinerea	Fast flowing rivers and streams in upland areas.	(Marchant and Hayde 1980,

		Ormerod et al. 1988)
Mallard Anas platyrhynchos	Widespread on wetland habitat, such as lakes, rivers, streams and ponds, including urban areas.	(Marchant and Hayde 1980, Vaughan et al. 2007)
Mute swan Cygnus olor	Lowland lakes and slow flowing rivers, and urban wetlands.	(Marchant and Hayde 1980, O'Hare et al. 2007, Vaughan et al. 2007)
Northern lapwing Vanellus vanellus	Farmlands and wetlands with short grass, often bordering large rivers.	(Wilson et al. 2001, Gillings et al. 2005, Vaughan et al. 2007)
Sand martin Riparia riparia	Rivers and gravel pits with steep banks for nesting.	
Sedge warbler Acrocephalus schoenobaenus	Reedbeds and damp wetlands next to rivers and farmland.	(Marchant and Hayde 1980, Vaughan et al. 2007)
Western yellow wagtail Motacilla flava	Fast flowing rivers and streams.	(Marchant and Hayde 1980, Bradbury and Bradter 2004)
White wagtail Motacilla alba	Most habitats near rivers and wetland, including urban areas.	(Marchant and Hayde 1980)
White-throated dipper Cinclus cinclus	Fast flowing rivers and streams in upland areas and some lowland rivers in SW England.	(Marchant and Hayde 1980, O'Halloran et al. 1990, Ohalloran et al. 1990, Tyler and Ormerod 1994, Vaughan et al. 2007)

2.2. National River Flow Archive (NRFA)

The NRFA is the UK's repository for a variety of hydrometric datasets collated from a network of approximately 1,500 gauging stations. Managed by the Centre for Ecology & Hydrology (CEH), it applies quality controls and archives data from gauging stations operated by the Environment Agency (England), Natural Resources Wales, the Scottish Environment Protection Agency, and the Rivers Agency (Northern Ireland) (Fry and Swain 2010). The primary database held by the NRFA is a database of daily mean flow (gauged daily flows) data. These data are archived and made available for free via a comprehensive retrieval service on the NRFA website (http://www.ceh.ac.uk/data/nrfa/index.html).

River flow data in the NRFA are accompanied by a number of additional spatial datasets that provide historical and contemporary catchment-level metadata (e.g. grid references, bankfull flow, catchment sensitivity statistics such as Base Flow Index, rainfall, land cover, elevation and hydro-geology, exceedance percentile flows) (Fry and Swain 2010). These metadata assist users of NRFA data to understand the hydrological context of observations (Fry and Swain 2010). It should be noted however that the NRFA data set may be less accurate for extreme high flows due to the technical limitations imposed by gauging equipment.

2.3. Coupling of WBBS and NRFA data

WBBS survey locations were coupled with NRFA data according to the following procedure. All WBBS survey locations were mapped on Google Earth using the grid reference of the start points of the first 500 m transect. The gauging stations associated with NRFA flow data were then mapped and the Euclidian distance between the WBBS survey location and the closest gauging station was calculated using Google Earth measuring tools. In total 742 NRFA gauging stations were mapped (Figure 2.1). WBBS locations within 10 km of a gauging station were then selected, with those over 10 km away from a gauging station discarded, thus ensuring a closer fit of flow variables to WBBS survey data.

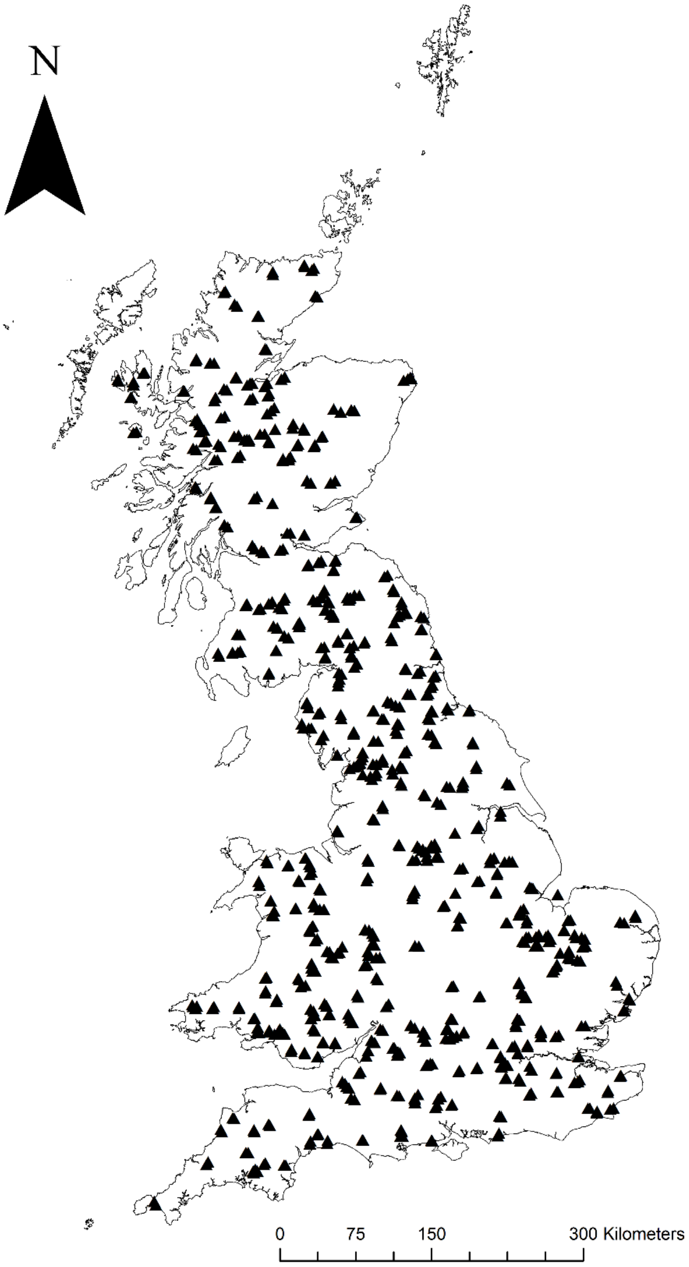

Figure 2.1 Map showing the locations of 742 Waterways Breeding Bird Survey (WBBS) locations which were plotted and coupled with National River Flow Archive (NRFA) locations by calculating the Euclidian distance between the WBBS and NRFA locations.

River flow data for WBBS-gauging station pairings were then subject to a data quality protocol to assess the extent of missing data points. Following Monk et al. (2007), gauging stations where > 10% of annual daily mean flow values were missing were excluded from all further analyses. Where ≤ 10% of annual daily mean flow values were missing, missing values were interpolated using long-term daily means. As the hydrological year runs approximately between October and September in the UK (Bower et al. 2004), annual river flow variables used as predictors in statistical models were calculated according to this timeframe. Flow variables based on long-term averages however were calculated using the full length of river flow time series data. The decision process for coupling NRFA and WBBS data are illustrated in Figure 2.2.

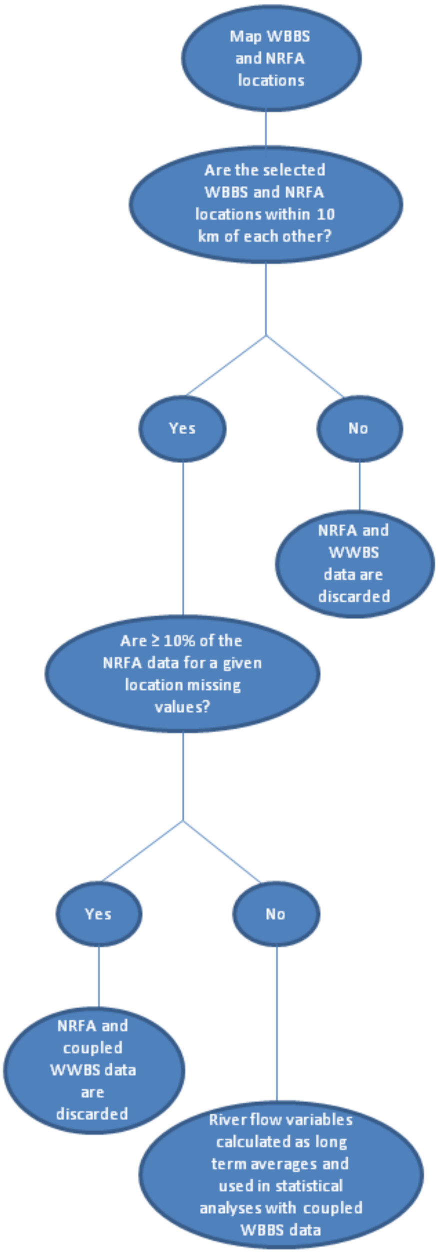

Figure 2.2 *A flow diagram illustrating the decision process used to couple National River Flow Archive (NRFA) and Waterways Breeding Bird Survey (WBBS) locations.*

2.4. Statistical procedure

In the following chapters a number of statistical modelling techniques are used to quantify, visualise and interpret functional relationships between river birds and variables of river flow. This includes a suite of frequentist methods, such as multiple linear regression and the generalized regression extensions for linear (generalized linear models) and non-linear (generalized additive models) predictor-response relationships, and correlated outcomes (generalized estimating equations) (Zuur et al. 2009), as well as Bayesian approaches (La Sorte and Jetz 2010). The models used herein were selected in relation to the specific research questions and how relationships between response and predictor variables should be characterised (e.g. linear or non-linear, null hypothesis testing or Bayes inference), given the data structure.

Throughout this thesis data were prepared for analyses using a consistent and robust data exploration protocol (Zuur et al. 2010). These included checking for outliers in non-binary outcomes using boxplots, the calculation of leverage statistics (e.g. hat scores) and outliers tests (e.g. the Bonferroni outlier test) (Fox 2011). Homogeneity of variance was checked by plotting model residuals against fitted values and each covariate (Zuur et al. 2010). Where necessary, homogeneity was achieved by stabilising the response variable through transformation techniques such as the logarithmic transformation. Normality assumptions were also checked using histograms and quantile-quantile plots (Fox 2011). Alternative probability distribution functions (e.g. Poisson or quasi-Poisson for over-dispersed count data) were fitted to models where appropriate (Zuur et al. 2009). Correlation between covariates was tested using multi-panel scatterplots with correlation coefficients (Zuur et al. 2010) and by calculating variance inflation factor (VIF) scores (Graham 2003). Finally, violation of the independence of data points assumption due to spatial and/or temporal correlation was investigated by plotting auto-correlation functions, which calculates the Pearson correlation between a time series and the same time series shifted by *k* time units (Zuur et al. 2010), and partial Mantel tests (Dormann et al. 2007). Where necessary, models were adapted to incorporate spatially and temporally correlated parameters (e.g. using generalized estimating equations).

Further details on statistical analyses and the rationale for their application are provided in each chapter.

3. Avian community responses to variability in river hydrology

Royan, A., D. M. Hannah, S.K. Reynolds, D. G. Noble, and J. P. Sadler. 2013. Avian community responses to variability in river hydrology. Plos One **8**:e83221.

3.1. Abstract

River flow is a major driver of morphological structure and community dynamics in riverine-floodplain ecosystems. Flow influences in-stream communities through changes in water velocity, depth, temperature, turbidity and nutrient fluxes, and perturbations in the organisation of lower trophic levels are cascaded through the food web, resulting in shifts in food availability for consumer species. River birds are sensitive to spatial and phenological mismatches with aquatic prey following flow disturbances; however, the role of flow as a determinant of riparian ecological structure remains poorly known. This knowledge is crucial to help to predict if, and how, riparian bird communities will be influenced by climate-induced changes in river flow characterised by more extreme high (i.e. flood) and/or low (i.e. drought) flow events. Here, we combine national-scale datasets of river bird surveys and river flow archives to understand how hydrological disturbance has affected the distribution of riparian species at higher trophic levels. Data were analysed for 71 river locations using a Generalized Additive Model framework and a model averaging procedure. Species had complex but biologically interpretable associations with hydrological indices, with species' responses consistent with their ecology, indicating that hydrological disturbance has implications for higher trophic levels in riparian food webs. This quantitative analysis of river flow-bird

relationships demonstrates the potential vulnerability of riparian species to the impacts of changing flow variability and represents an important contribution in helping to understand how bird communities might respond to a climate change-induced increase in the intensity of floods and droughts. Moreover, the success in relating parameters of river flow variability to species' distributions illustrates both the need and potential to include river flow data in climate change impact models of species' distributions.

3.2. Introduction

The physical and ecological structures of riverine-floodplain ecosystems are controlled by variability in river flows (Junk et al. 1989, Poff et al. 1997). River flow influences in-stream ecological communities through changes in factors such as velocity, depth, water temperature, turbidity, channel stability and nutrient fluxes (Junk et al. 1989, Poff et al. 1997). River flows connect in-channel, riparian and floodplain habitats to create an ecologically dynamic system (Junk et al. 1989) whereby flooding (inundation) has consequences for invertebrate communities and creates greater diversity and variability in functional traits (Lambeets et al. 2008, Lambeets et al. 2009). The ability of invertebrates to tolerate high levels of inundation-driven pressure is determined by their resilience (i.e. ability to recover) and resistance (ability to withstand) to flow-induced disturbances (Palmer et al. 1996), and by their ability to utilise habitat patches as refugia during high flows (Palmer et al. 2009). Disturbance in the organisation of lower trophic levels (e.g. primary producers such as phytoplankton) is conveyed through the food web and can result in reduced food availability for consumer species (Woodward et al. 2010, Ledger et al. 2012, Woodward et al. 2012).

Climate change poses a severe threat to freshwater biodiversity as river flows are coupled closely to atmospheric drivers; thus, climate change will lead to changes to key processes in the global water cycle such as precipitation, runoff and evaporation, and shifts in drought and flood events (Min et al. 2011, Durack et al. 2012). Moreover, observations and models indicate that hydroclimatological variability is outside of ‘natural’ ranges already and consistent with anthropogenically-enhanced global warming (Pall et al. 2011). More extreme and/or more frequent high and low flows will threaten aquatic communities by removing vulnerable taxa, and can result in a significant increase in the proportion of small-sized species (Daufresne et al. 2009) and a reconfiguration of biomass fluxes and food web structure (Ledger et al. 2012). Whilst this can lead to greater extinction for some predators, others may benefit from short-term increases in *r*-selected focal prey species that are able to exploit disturbance (Ledger et al. 2012).

Although much less is known about riparian compared with in-stream dynamics, a few studies have shown that flow disturbances affect riparian invertebrate assemblages and determine interactions between trophic levels in food webs (e.g. (Bates et al. 2006, Henshall et al. 2011, O'Callaghan et al. 2013). As with in-stream environments, one might hypothesise that riparian communities are influenced by river flows sensitive to climate change. However, our understanding of how variability of the flow regimes (e.g. flow magnitude, high and low flow variability, timing, frequency) shapes riparian species’ distribution and ecological structure is limited, particularly at higher trophic levels (e.g. tertiary consumers such as birds). Therefore, quantification of the relationships between river flow variability and riparian ecology is an urgent and important research challenge in the context of unravelling and projecting the impacts of climate change-induced flow alteration.

River birds represent an excellent focal taxon because river flow is a key predictor of patterns of species' occurrence (Vaughan et al. 2007). These species are often at the top of food chains and so are sensitive to disturbance at lower trophic levels, including spatial and temporal mismatches in the availability of their prey (Chiu et al. 2008, Chiu et al. 2013); consequently pulses in flow may determine the timing of foraging (Cumming et al. 2012) and breeding (Arthur et al. 2012) behaviours. Regulation of river flows may influence the abundance (Jonsson et al. 2012), breeding success and survival (Strasevicius et al. 2013) of river birds through modification of aquatic insect emergence and consequent prey availability (Jonsson et al. 2013). Moreover, seasonal fluctuations in invertebrate prey fluxes from aquatic to terrestrial habitats subsidise the diets of river birds, resulting in dramatic shifts in aquatic prey use and foraging behaviour according to species-specific foraging tactics (Murakami and Nakano 2001). This may include a shift in species' seasonal distributions whereby species move to higher elevations to take advantage of the post-breeding increase in terrestrial prey relative to lower elevations (Nakano and Murakami 2001, Jonsson et al. 2013). However, previous investigations of river flow-avian relationships are spatially and temporally constrained, with most focusing on a single watershed after a specific flood event. The influence of low flows (i.e. drought) on river birds is also not well researched (but see (Smith 1982).

This study uses data from a long-term bird monitoring scheme and river flow archives to investigate the relationship between avian species' occurrence and river flow regime attributes across Great Britain. Hydrological shifts were selected *a priori* and are consistent with those anticipated under climate change (Pall et al. 2011) to investigate the hypotheses that the probability of bird species' occurrence is reduced for rivers characterised by greater hydrological fluctuations, including:

I. larger variability around high and low flows;
II. higher frequency of extreme flow events;
III. higher flow variability during species' breeding seasons;
IV. extreme high or low flow magnitude.

The present thesis deals with how species' responses to these key attributes of river flow are mediated by life-history traits that influence their distribution in river-floodplain ecosystems. Presence/absence data for 17 river bird species were conditions from the WBBS for 71 river locations, which captured a wide range of the hydrological variability across Great Britain (Figure 3.1). Bird data were paired with mean daily river flows from the NRFA. The relationships between river bird occurrence and river hydrology were characterised using parameters that each quantified one of five hydrological facets: magnitude, frequency, high flow variability, low flow variability and timing (Table 3.1), within a Generalized Additive Model (GAM) framework. The relative importance of each hydrological parameter was assessed using an information-theoretic model averaging approach (Burnham and Anderson 2002).

3.3. Methods

Waterways Breeding Bird Survey (WBBS) data between 1998 and 2010 (inclusive) were used, although data from 2001 were excluded from analyses as a very small proportion of locations was surveyed due to the foot-and-mouth outbreak; this required large-scale quarantine measures to limit the spread of disease and thereby restricted access to the countryside. Each location was surveyed during at least three years during the survey period and at least once since 2008. The number of species used in the analysis was constrained by their occurrence across the sample sites as, to reduce model instability, only species for which records comprised no less than 10% of the response values were analysed; the least prevalent species was the western yellow wagtail which occurred in 10.3% of site-year combinations (mean prevalence of all species used was 37.7%). Individual years at each site were treated separately, totalling 574 separate site-year combinations.

Presence/absence data per stretch of river were extracted for each year separately. The hydrological year in the UK runs from October to September (Bower et al. 2004) and bird data were paired with hydrological data from the associated hydrological year (e.g. bird data from spring 2010 were paired with hydrological indices calculated from daily flow data between 1st October 2009 and 30th September 2010). Thus, hydrological variability was measured before, during and after the birds' breeding seasons.

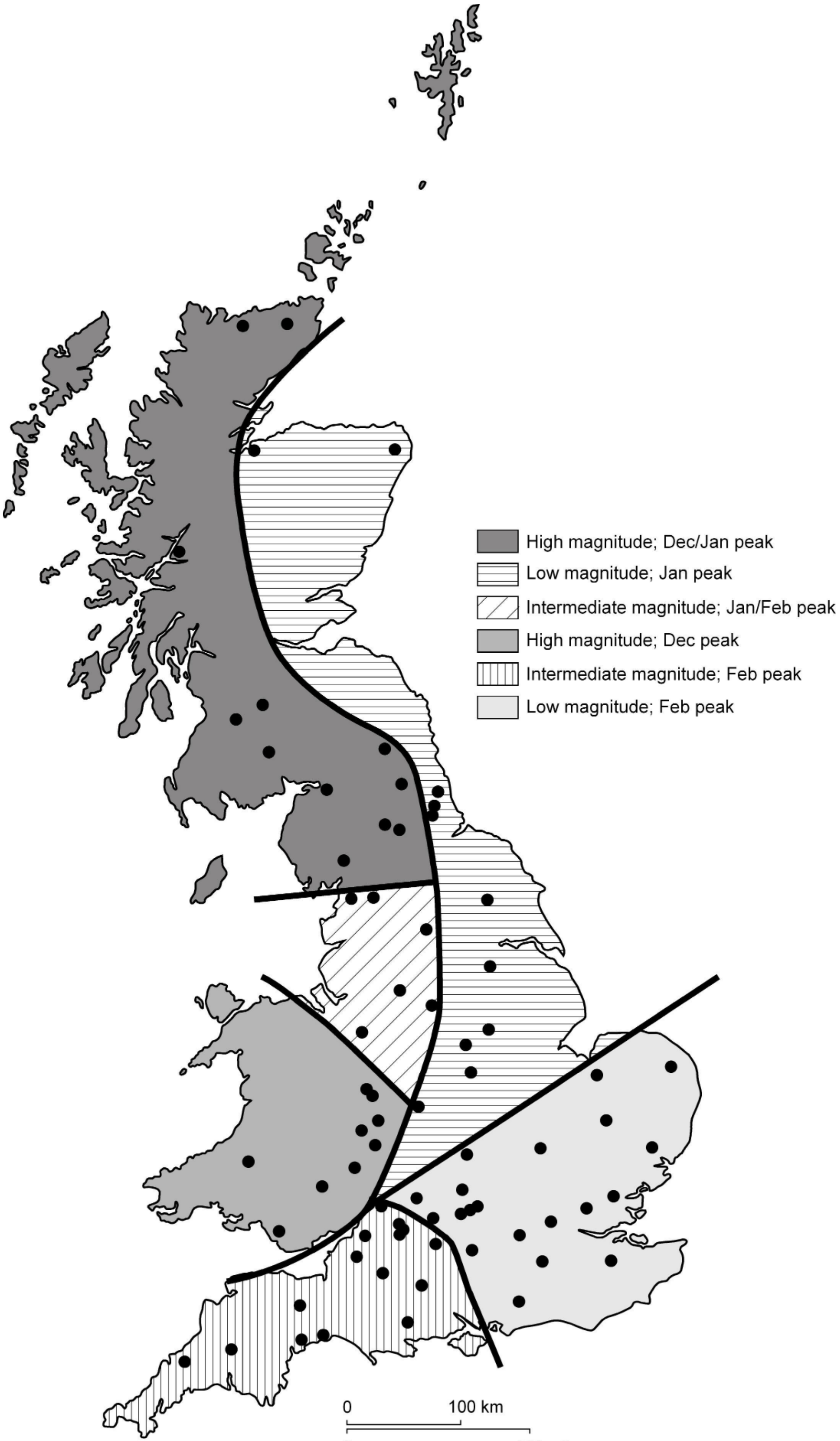

Figure 3.1 *Distribution map of the 71 Waterways Breeding Bird Survey (WBBS) locations. Shaded areas on the map are indicative of the hydrological regions within which each survey site is located. Hydrological regions were determined on the basis of flow regime shape*

(based on timing of major runoff peaks) and flow regime magnitude (based on the mean, maximum, minimum, and standard deviation of average monthly flows (Bower et al. 2004)]).

As there is concern that considerable multi-collinearity exists amongst many widely used hydrological indices (Olden and Poff 2003, Monk et al. 2007), model parameters were considered *a priori*, whilst ensuring that each one was statistically independent, by producing multi-panel scatterplots (Zuur et al. 2010), and had Variance Inflation Factor (VIF) scores below two (Graham 2003). Separate binomial GAMs were created, specifying a logarithmic link function, for all 17 species to quantify the relationship between the hydrological indices and species' *P(x)*. GAMs are a particularly useful regression method for species' distribution modelling (Austin 2002) as they do not force a parametric relationship between the response and predictor, and smoothers can be used to model complex non-linear relationships that are frequently observed in ecology. Where non-linear relationships were observed, a cubic smoothing spline was fitted to the predictor, with a fixed degree of smoothing (two degrees of freedom) so as to capture the trends in the data with the least number of degrees of freedom whilst preventing over-fitting (Wood 2006). GAMs were fitted using version 1.7-24 of the mgcv package for R (Wood 2006).

Table 3.1 *Description of five hydrological indices used as predictors of the presence or absence of river bird species in Great Britain.*

Predictor	Range	Description
High flow variability		
Three Day Maximum (m^3)	1.549 – 83.607	Average annual 3-day maximum divided by median annual discharge. A measure of annual variability around high flows and the deviation of high flows from the median. High values imply greater variability in the magnitude of high flows and water depth while low values imply stability in high flows
Low flow variability		
Three Day Minimum (m^3)	0.009 – 0.645	Average annual 3-day minimum divided by median annual discharge. A measure of annual variability around low flows and the deviation of low flows from the median. High values imply greater stability in the magnitude of low flows and water depth while low values imply variability in low flows
Frequency		
High Flow Frequency	0 – 124	Number of high flow days per year above three times the median. A measure of the number of extreme high flow days on a river during the UK hydrological year (October–September)
Timing		
April Flow Variation (m^3)	0.011 – 73.657	Standard deviation of April discharge. A measure of flow variability during birds' breeding seasons. High values imply greater flow variability while low values imply stability in flows during birds' breeding seasons
Magnitude		
Mean Daily Flow (m^3)	0.223 – 117.812	Mean value of daily discharge divided by median of daily discharge. A measure of flow magnitude providing an estimate of river size

The response variable was defined as the presence or absence (i.e. non-detection) of a species during the survey in any one year, as specified by WBBS methodology (i.e. two visits per breeding season). To account for correlation between survey years and variation in the geographic coverage of WBBS sites, a three-way interaction between year, latitude and longitude was included as a fixed effect in all models. This approach controls for: (i) similarities in the response variable at nearby points by fitting a smooth two-dimensional surface to these data and (ii) unmeasured variables that may affect the response by fitting to response peaks and troughs, thereby fitting spatial autocorrelation in the dataset by optimising the degrees of freedom (Davey et al. 2012). Additionally, the number of transects completed at each location was included as an offset to account for variation in survey effort and corresponding probability of species' detection.

The Information-Theoretic (IT) model averaging approach was used for data analysis (Burnham and Anderson 2002) as it corrects for potential model selection bias and error associated with parameter estimation and presents the results in the context of strength of evidence (Burnham and Anderson 2002, Burnham and Anderson 2004, Stephens et al. 2005). A model was produced for every permutation of predictors, resulting in 31 models per species, and the fit of each model was assessed using the Akaike Information Criterion (AIC). Akaike weights (AIC w_i s) were calculated for all models as follows:

$$\omega_i = \frac{\exp(-\frac{1}{2}\Delta AIC_i)}{\sum_{r=1}^{n}\exp(-\frac{1}{2}\Delta AIC_r)}$$

(Equation 3.1)

where w_i is the probability that model *i* would again be selected as the model of best fit if the data were collected again under the same circumstances (Burnham and Anderson 2002). For all models w_i sums to 1, and selection probabilities (*Sp*s) for each predictor were calculated by summing w_is for every model containing each predictor. Poor predictors do not always have *Sp*s close to zero so an approximate, yet conservative, w_i interval was provided to evlauate the importance of individual predictors (Whittingham et al. 2005). One hundred randomly generated predictors with a distribution between zero and one were produced and every model was run in turn with each of these. *Sp*s were calculated for each null predictor and a 95% confidence null interval computed. Rather than use the *Sp*s from all null predictors to produce the null interval (e.g. (Whittingham et al. 2005)), the 10 largest values were selected as this produced a more conservative and robust interval against which *Sp*s for the hydrological parameters could be compared. Only strong predictors of species' occurrence should have *Sp*s larger than this null interval.

3.4. Results

All 17 focal bird species had a strong association with at least one of the five hydrological indices, with *Sp*s well above that of the null predictor interval (Table 3.2). Model performance was assessed using the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (an indicator of the goodness-of-fit of the model that is independent of the threshold probability at which the presence of the target organism is accepted) and Cohen's Kappa (*K*) (measures the level of agreement between observed occurrences and absences with those predicted by the model after accounting for chance effects). According to AUC, nine species' model sets had 'high accuracy' (i.e. AUCs > 0.9) and seven were 'useful' (i.e. 0.7 <

AUCs ≤ 0.9) (Swets 1988) (Table 3.2). According to *K*, the strength of agreement between model predicted values (values set as: absences < 0.5 < presences) and observed response values varied from ‘almost perfect’ (0.81 < *K*s ≤ 1) (common sandpiper, Eurasian oystercatcher [*Haematopus ostralegus*], white-throated dipper) to ‘slight’ (0 < *K*s ≤ 0.2) (grey heron [*Ardea cinerea*], western yellow wagtail) (Landis and Koch 1977). Species’ models broadly support hypotheses 1-4, but with important and clear differences in hydrological associations observed between species (

Figure **3.2** and Figure 3.3) that were consistent with their respective life-history traits.

*Table 3.2 Selection probabilities (*Sps*) of five hydrological indices for 17 river bird species in Great Britain.*

Species	**Three Day Maximum**	**Three Day Minimum**	**High Flow Frequency**	**April Flow Variation**	**Mean Daily Flow**	**Null**	**Models < ΔAIC 2**	***K***	**AUC**
Common kingfisher *Alcedo atthis*	0.535(±)	0.402	0.391	0.998(+)	0.312	0.345-0.382	7	0.261	0.738
Common merganser *Mergus merganser*	0.533(±)	0.318	0.467(±)	0.858(+)	0.415	0.272-0.341	9	0.499	0.910
Common moorhen *Gallinula chloropus*	0.285	0.999(+)	0.295	0.377	0.915(-)	0.393-0.426	4	0.591	0.890
Common reed bunting *Emberiza schoeniclus*	0.669(-)	0.303	0.731(-)	0.860(+)	0.819(+)	0.342-0.405	4	0.507	0.875
Common sandpiper *Actitis hypoleucos*	0.995(±)	0.439	0.982(±)	0.999(±)	0.360	0.499-0.500	4	0.891	0.994
Eurasian coot *Fulica atra*	0.369	0.945(+)	0.718(-)	0.361	0.469	0.378-0.427	6	0.582	0.904
Eurasian oystercatcher *Haematopus ostralegus*	0.491	0.932(-)	0.999(-)	0.019	0.992(-)	0.366-0.429	2	0.963	0.998
Eurasian reed warbler *Acrocephalus scirpaceus*	0.289	0.625(+)	0.180	0.453	0.423	0.379-0.454	7	0.496	0.916
Great cormorant *Phalacrocorax carbo*	0.693(+)	0.949(+)	0.285	0.999(+)	0.546(-)	0.366-0.432	4	0.377	0.822
Great crested grebe *Podiceps cristatus*	0.295	0.330	0.307	0.999(±)	0.360	0.337-0.429	5	0.533	0.945
Grey heron *Ardea cinerea*	0.299	0.997(+)	0.378	0.440	0.410	0.334-0.382	7	0.162	0.694

Grey wagtail *Motacilla cinerea*	0.568(+)	0.408	0.800(±)	0.354	0.652(+)	0.385-0.441	10	0.488	0.838
Mute swan *Cygnus olor*	0.286	0.999(+)	0.551(-)	0.999(±)	0.327	0.331-0.430	5	0.617	0.918
Northern lapwing *Vanellus vanellus*	0.319	0.989(-)	0.347	0.303	0.828(-)	0.372-0.443	3	0.581	0.901
Sand martin *Riparia riparia*	0.341	0.320	0.386	0.999(±)	0.353	0.336-0.412	5	0.526	0.891
Western yellow wagtail *Motacilla flava*	0.549(-)	0.801(+)	0.960(-)	0.385	0.706(-)	0.330-0.429	5	0.213	0.877
White-throated dipper *Cinclus cinclus*	0.947(+)	0.620(-)	0.967(±)	0.596(±)	0.999(-)	0.425-0.465	3	0.868	0.986

*Sp*s were calculated by summing Akaike weights (AICw_i) of all model permutations containing each predictor. Parameters included in a greater proportion of the best-supported models have larger selection probabilities (*Sp*s), considerably above the null predictor, thereby demonstrating strong support for their inclusion in the best approximating model. The inclusion of parameters with lower S*p*s is less important for obtaining good model fit. The null interval was calculated from simulations of 100 randomly generated predictors, summing AICw_is of all models containing each null predictor and then using the highest 10 values to calculate 95% confidence intervals. For high *Sp*s, (+) indicates a positive relationship, (-) a negative relationship and (±) a quadratic relationship (see Figures 2 and 3 for graphical representation). The number of models with Akaike Information Criteria (AICs) within two of the best fitting model is also given to provide an estimate of uncertainty around specification of the best approximating model. The average *K* and AUC for this reduced model set are provided as measures of model performance.

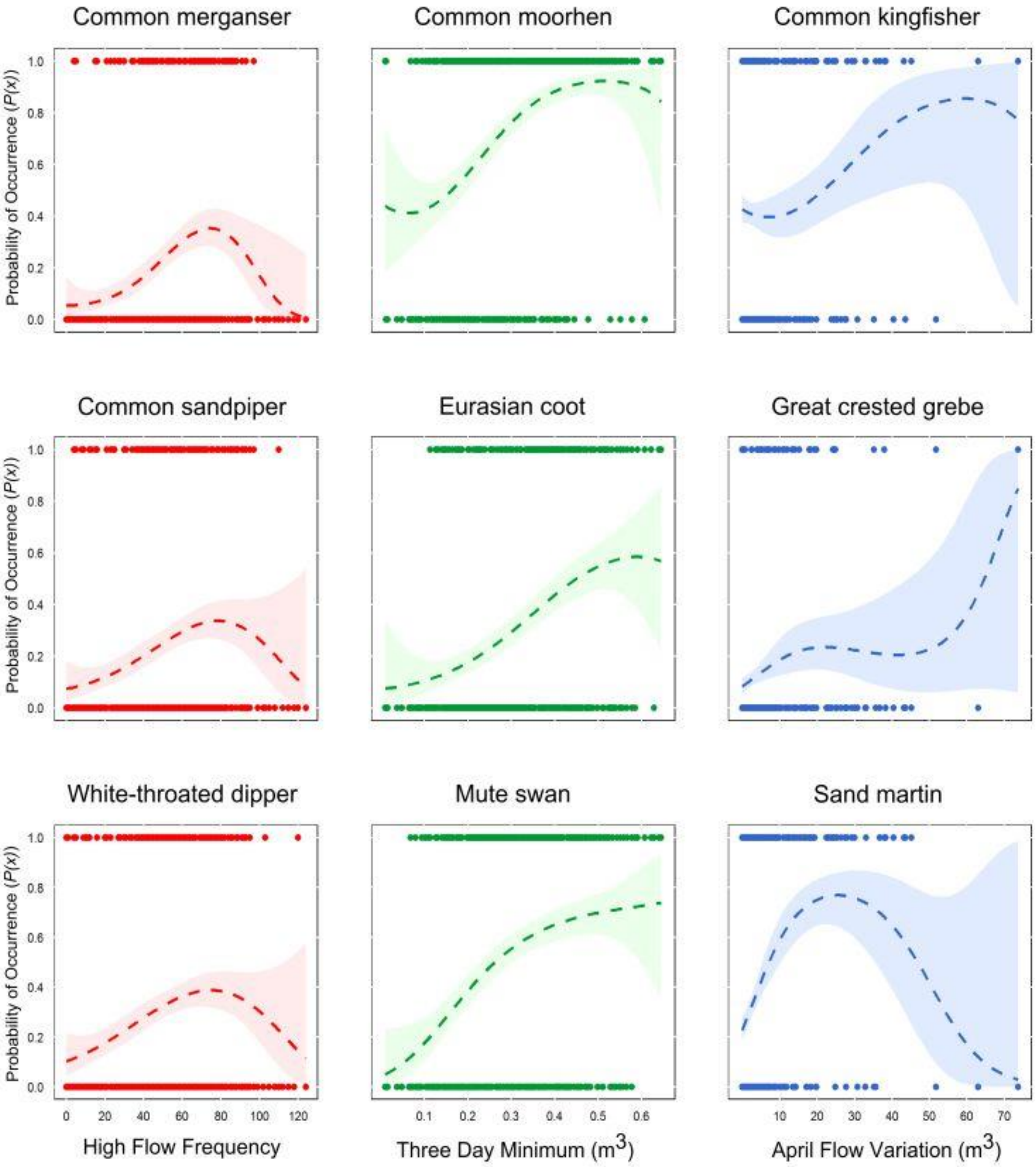

Figure 3.2 *Examples of non-linear relationships from models between species'* P(x) *and three measures of hydrological variability. High Flow Frequency (red), a measure of the number of extreme high flow days; Three Day Minimum (green), a measure of low flow variability and the deviation of low flows from the median; and April Flow Variation (blue), a measure of flow variability during the species' breeding seasons. Dashed lines give the probability curve from a GAM with a cubic regression spline and two degrees of freedom. Shaded regions represent 95% confidence limit for the spline fit.*

Species associated with upland environments (e.g. common merganser [*Mergus merganser*], common sandpiper, grey wagtail, white-throated dipper) displayed positive and quadratic relationships with Three Day Maximum, which suggests their probability of occurrence (*P(x)*) increases with higher flows. For these same upland species, quadratic associations were observed with High Flow Frequency, indicating increased *P(x)* under more high flow disturbance (
Figure **3.2**). Ten species had either positive or negative associations with Three Day Minimum; species that forage typically within aquatic macrophytes (e.g. common moorhen [*Gallinula chloropus*], Eurasian coot [*Fulica atra*], grey heron and mute swan [*Cygnus olor*]) preferred stability around low flows (
Figure **3.2**), whereas some species that forage predominantly at terrestrial river margins (e.g. Eurasian oystercatcher, northern lapwing [*Vanellus vanellus*]) benefited from increased low flow variability. White-throated dipper, which typically feeds in the river channel, also favoured increased low flow variability which may indicate a propensity for this species to forage opportunistically outside breeding territories when marginal habitats are exposed.

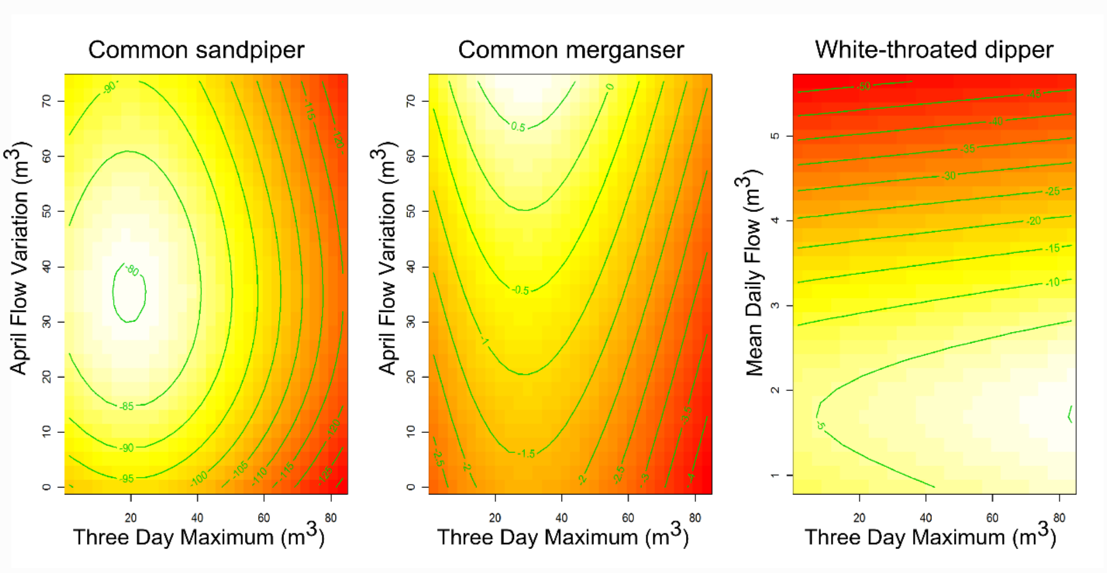

Figure 3.3 *Example response surfaces showing the relationship between species’* P(x) *and two hydrological indices. Surface plots show the interactive effects of two hydrological indices on species’* P(x), *where lighter areas of shading illustrate a stronger influence on* P(x). *When considered independently, the indices have limited effects on P(x) compared to the combined effect of both indices.*

Flow timing was an important predictor of occurrence for nine species. In particular, April Flow Variation was the most important predictor of occurrence for the three diving species (i.e. common merganser, great cormorant [*Phalacrocorax carbo*], great crested grebe [*Podiceps cristatus*]) and the two bank-nesting species (i.e. common kingfisher [*Alcedo atthis*], sand martin [*Riparia riparia*],

Figure **3.2**). Interpretation of species’ relationships with this parameter, however, is somewhat hindered by a lack of data at higher discharges, which is reflected by the larger confidence intervals around the smoothed line in

Figure **3.2**. Species displayed largely negative associations with Mean Daily Flow, although both common reed bunting (*Emberiza schoeniclus*) and grey wagtail had positive associations.

3.5. Discussion

This study has demonstrated that the occurrence of river birds is influenced strongly by elements of river flow regimes. By quantifying the different facets of flow regime, species' distributions were shown to be characterised by complex responses to: (i) variability around extremes of high and low flows, (ii) flow frequency, (iii) the timing of flow events, and (iv) flow magnitude. It is well established that river flows and hydrological variability influence the distribution and trajectories of the life history of aquatic and, to a lesser extent, riparian invertebrates; however, this quantitative study provides evidence of the influence of river flows on species' distributions extending beyond lower trophic levels to tertiary consumers at the top of aquatic/riparian food webs. Fluctuations in flow conditions may impact these species primarily by: (a) causing disturbances in aquatic food webs, which decrease prey abundance or shift prey composition, and (b) temporarily altering the availability of foraging and breeding habitats.

Altered river flow regimes may impact riparian species at higher trophic levels through the removal of prey adapted to life in aquatic habitats under specific flow conditions, which may lead to a breakdown in energy fluxes, removal of trophic pathways and compromised food web resilience (Palmer et al. 2009, Woodward et al. 2010, Ledger et al. 2012, Woodward et al. 2012). Variability in high flows causes large fluctuations in water velocity and depth, which can determine the availability of foraging habitats for birds (Cumming et al. 2012) and influence foraging efficiency and net energy gain (Taylor and O'Halloran 2001). Clear positive quadratic associations between the distribution of some species and measures of high flow variability and high flow frequency suggest that some species require a range of variability around high flows. Intermediate measures of high flow may provide optimal foraging habitat for some riparian fauna whereas floods may decrease prey abundance and shift prey composition (Chiu et al. 2008, Chiu et al. 2013), perhaps resulting in increased consumer competition or broadening of foraging niches, while exceptionally large or prolonged extreme flow events may lead to marked increases in adult and juvenile mortality for the most sedentary of species (Chiu et al. 2013).

Fluctuation of low flows increases heterogeneity in the spatial and temporal extent of river marginal habitat (Junk et al. 1989, Poff et al. 1997). Strong positive associations exist between the occurrence of some species that forage predominantly at river margins and measures of low flow variability. This suggests low flow variability positively influences the availability or prevalence of foraging habitats for these riparian consumer species. However, species that forage or breed within macrophytes in-stream or at river margins preferred stability around low flows, perhaps because substrates remain undisturbed promoting greater diversity and growth of these plants (Bunn and Arthington 2002).

Changes in the timing of flows may be attributed to climate change (Pall et al. 2011). Riparian species can be adversely affected by increased flow variability during sensitive periods of their annual cycles such as during breeding, resulting in reproductive failure (Wilson and Peach 2006, Strasevicius et al. 2013), increased dispersal (Roche et al. 2012) or increased adult mortality (Chiu et al. 2013). The occurrence of bank-nesting species (i.e. common kingfisher, sand martin) was sensitive to flow timing. Bank-nesting species may be particularly vulnerable to flow variability during breeding seasons as nest sites on marginal habitats are prone to inundation (e.g. (Roche et al. 2012). Both species nest in exposed river sediment banks that are formed during scouring high flows, suggesting annual variability in high flows across seasons is required for the creation of breeding habitat. The greater tolerance of breeding season flow variability exhibited by the common kingfisher models may reflect a propensity for this solitary bank-nester to nest more frequently on tributaries, where it is buffered from the impact of the highest flows on the main channel. As such, the vulnerability of riparian species to flow variability during sensitive periods of their annual cycle may be determined by a combination of the sensitivity and plasticity of intrinsic behavioral traits, such as nest site selection (Williams et al. 2008b).

River systems are vulnerable to climate change, with current hydrological simulations in regional climate models for the UK predicting that by 2050 river flows will have changed considerably; most models broadly predicting decreases in summer flows and increases in winter flows (Prudhomme et al. 2012b). The current results indicate that future ecological consequences of changes in river flow are not restricted to aquatic communities but may have profound effects on other riparian biota such as birds. It is well established that climate change may increase extinction risk and strongly influence the phenology and dynamics of bird populations (Jenouvrier 2013, Warren et al. 2013). Climate models can be used to predict future changes in bird species' ranges based on air temperature shifts; however, such models for bird species' distribution do not take into consideration river flow variability (Huntley et al. 2007) and rarely even account for changes in habitat. Our findings have implications for climate change impact models as they emphasise the need to include the effects of hydrological change on riparian biota, as well as the value of using long-term, spatially-extensive datasets to understand flow variability, including the importance of extreme events.

Incorporating flow variables into such models has the potential to improve future projections beyond those based on climate alone as they may identify areas that will become unsuitable owing to non-climatic factors and prevent over-prediction of climate change impacts (Brook et al. 2009). Moreover, the incorporation of flow parameters into models to describe climate-driven changes in species' habitat represents a more biologically realistic approach because they include small-scale habitat attributes overlooked by coarse large-scale climate models (Bellard et al. 2012). Interpreting the future distributions of river birds requires new research to assess the ecological consequences of climate and hydrological extremes on aquatic and riparian ecosystems. More fundamentally, conservation assessments are reliant on longitudinal long-term surveys, which facilitate the detection and monitoring of temporal and spatial patterns in river bird populations.

The success in relating hydrological indices to the distributions of river birds in this study demonstrates that variability in river flow regime has consequences for the distribution of riparian species and ecological structure at high trophic levels in aquatic-riparian food networks. By using national-level, long-term datasets, it was possible to identify spatial and temporal patterns in species' relationships with the hydrological indices. Species' occurrence changed with variability in both high and low flows, including the frequency of extreme flow events, as well as with variability in both the timings and magnitude of flows. These relationships were complex but could be explained by ecological traits that characterise species within aquatic-riparian ecosystems. This chapter represents an important contribution in helping to understand how bird communities might respond to a climate change-induced shift in river flow and also highlights a potential vulnerability of species to an increase in the intensity of floods and droughts. This approach not only generates new insights as reported here but also establishes foundations for further work on modelling of the impact of river flow variability on both avian and non-avian water-dependent taxa.

In this chapter, data from a long-term bird monitoring scheme and river flow archives were used to investigate the relationship between avian species' occurrence and river flow regime attributes across Great Britain. Now, Chapter 4 will examine how patterns of co-occurrences in river birds might be influenced by river flows and how variability in hydrological regimes might act as an environmental filter on avian community organisation.

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

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4.1. 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 two complementary modelling methodologies are applied - 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 conspecifics, and (ii) examine the strength of evidence for four alternative models of community structure. Species co-occurred more often than would be expected according to 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. Limited evidence for behaviour-driven assemblage patterns in bird communities was found 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; thus if shared environmental responses are not quantified, studies of co-occurrence may overestimate the role of species interactions in shaping community structure.

4.2. Introduction

Species' distributions are determined by a range of factors, including climate, land cover, landscape barriers, dispersal ability and species interactions (MacArthur 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 and Jetz 2013). Environmental filters restrict community membership to species possessing a particular set of functional traits (Petchey 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 and Rozenfeld 2013). Such interactions may leave imprints on species' distributions that are detectable at large spatial scales (Heikkinen et al. 2007, Gotelli et al. 2010, Baselga et al. 2012); both positive and negative interactions can be discernible across scales of hundreds of kilometres (Araújo and Rozenfeld 2013). However, positive/negative associations can result from species having similar/dissimilar habitat requirements as well as from direct or indirect interactions (Ovaskainen et al. 2010), meaning that similarity in habitat preference (or lack of) 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 debated issue in ecology (Macarthur 1958, MacArthur and Levins 1964, Barnagaud et al. 2014, Kraft et al. 2014, Peron and Altwegg 2015).

Interactions between species have particularly pervasive impacts on bird populations, where interspecific competition may influence the distribution, habitat choice, abundance and reproduction of species (Cody 1974) and interactions amongst interspecifics have been detected in the distributions of species at large scales (Heikkinen et al. 2007, Gotelli et al. 2010, Robertson 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 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 (Gotelli et al. 1997, Mattsson et al. 2013, Börger and Nudds 2014, Kroll et al. 2014).

Considering the impact of both environmental and biotic effects, there are four prevalent hypotheses that explain the distribution of heterospecifics (Mattsson 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 conspecifics (Hubbell 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 1958). Community membership will therefore be restricted to those species possessing a particular set of functional traits (Petchey et al. 2007) and one might expect species occurrences to be highly correlated with environmental variables; (3) the conspecific interaction hypothesis, where species distributions are primarily influenced by the occurrence of conspecifics and species either aggregate in patches occupied by conspecifics or segregate to occupy empty patches. Individuals may cluster with conspecifics because of the benefits of group membership in terms of increased vigilance, reduced predation risk and enhanced assessment of habitat quality (Ward and Zahavi 1973). Conversely, segregation may occur due to mechanisms such as competitive exclusion (MacArthur and Levins 1967). In this conspecific interaction hypothesis one 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 conspecifics 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 and Luoto 2007) and provide a strong analytical framework in macro-ecological studies where the manipulation of experimental conditions is not possible (Gotelli and McGill 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 et al. 1997, Gotelli et al. 2010, Ulrich and Gotelli 2010). 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 (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 et al. 2010). However, the abundance of conspecifics could act as a surrogate for absent important environmental variables (Araujo and Luoto 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 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 et al. 2014) but has less applicability to macro-ecological studies of multiple species' distributions.

This study 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. Two complementary models were applied 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 the probabilistic model of species' co-occurrence developed by Veech (2013) was used to calculate significant positive, negative or random associations between species, which represent all of the ways in which species can co-occur (Veech 2014). The output of the probabilistic model was then compared to that of a joint species distribution model (JSDM) (Pollock 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.

Three specific objectives were addressed, 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.

4.3. Methods

4.3.1. River bird data

WBBS survey locations with a minimum of four repeated visits between 1998 and 2011 (inclusive) were selected. In total, 100 WBBS locations were used, achieving wide coverage across mainland Great Britain (**Figure 4.1**). Data for 19 bird species were used. They were selected because they are largely ubiquitous across riverine landscapes in Great Britain and sufficiently characterised diversity in river bird communities (Royan et al. 2013, Royan 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 conspecifics (Vandewalle et al. 2010, Newbold et al. 2014), whilst the relationship between their distribution in Great Britain and key environmental variables is well characterised (Vaughan et al. 2007, Royan et al. 2013). 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 et al. 2013), river bird occurrence data could potentially be influenced by the date of survey. 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.

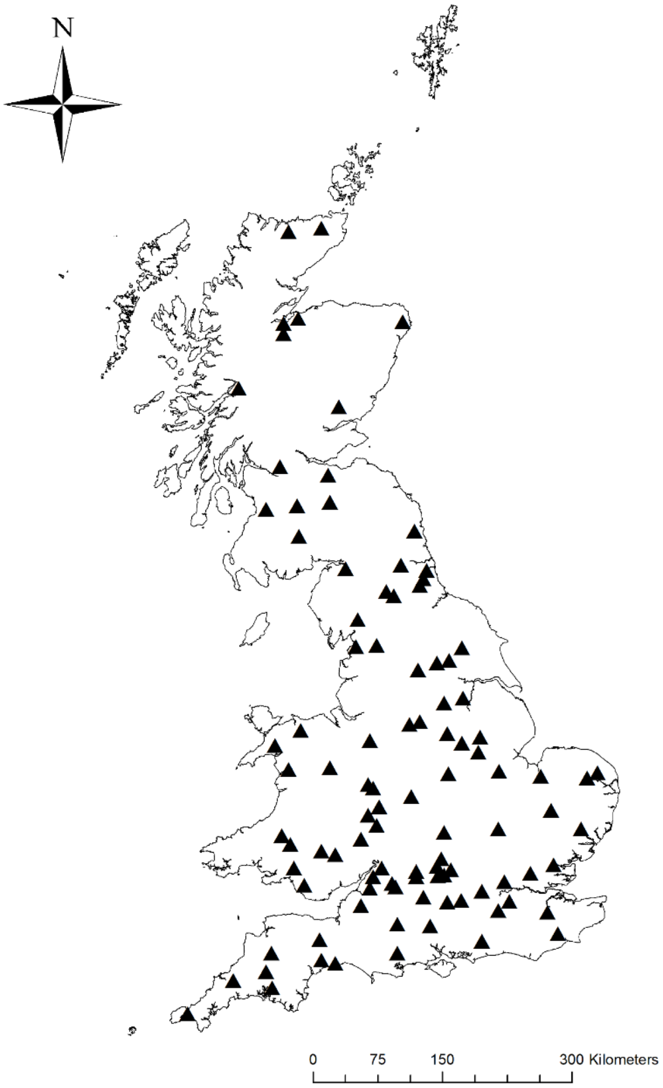


Figure 4.1 *Map showing the distribution of the 100 Waterways Breeding Bird Survey (WBBS) survey locations used to derive presence/absence data for 19 river bird species.*

4.3.2. Environmental data

Bird distributions can be influenced by a range of environmental factors, including hetereogeneity in land use and habitat (Luck et al. 2013), variability in climate (Renwick et al.

2012) and, in the case of river birds, variability in river flows (Royan et al. 2013). Therefore, river bird occurrence data were paired with variables that quantify each of these environmental factors (

Table 4.1).

Table 4.1 *Description of the 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 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
Climate variables		
Total Breeding Season Rainfall (mm)	Sum of April to July (inclusive) rainfall between 1998 and 2011 (inclusive)	A measure of total rainfall during birds' breeding season.
Mean Breeding Season Temperature (°C)	Mean value of April to July (inclusive) temperature between 1998 and 2011 (inclusive)	A measure of average temperature during birds' breeding season.
Land use variables		

Area of woodland (%)	Broadleaved/mixed woodland Coniferous woodland	Percentage area of the catchment that is woodland habitat
Area of arable land (%)	Arable cereals Arable horticulture Arable non-rotational	Percentage area of the catchment that is arable habitat
Area of grassland (%)	Improved grassland Set-aside grass Neutral grass Calcareous grass Acid grassland Bracken Fen, marsh, swamp	Percentage area of the catchment that is grassland habitat
Area of heathland (%)	Montane habitats Dense dwarf shrub heath Open dwarf shrub heath Bog (deep peat)	Percentage area of the 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 and Davies 2003)	Percentage area of urban extent within the catchment boundary.

River flow variables

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

Annual river flow data for the period 1998 to 2011 were obtained from the NRFA. 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 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 on an unregulated river. It was 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 each 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). Mean breeding season temperature (°C) and total breeding season rainfall (mm), with the breeding season defined as April to July (inclusive), were calculated. Climate variables calculated during the breeding season rather than annual or winter variables were chosen as they have been shown to be better predictors of breeding bird distributions in Great Britain (Renwick et al. 2012).

4.3.3. Modelling procedure

Initially, the probabilistic modelling approach developed by Veech (2013) was used 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.

Co-occurrence patterns were further analysed using the JSDM developed by Pollock 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 conspecific interaction hypothesis, although one cannot completely discount the possibility of some influence of unmeasured habitat relationships (Börger and Nudds 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 are detected.

Full details of the JSDM can be found in Pollock et al. (2014) but below this approach is summarised 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. If the latent variable for one species is independent of the others in the model then a bivariate normal distribution is used. Otherwise, a multivariate normal distribution is assumed. Probabilities of occurrence are modelled by changing the locations of the latent normal distribution and probabilities of co-occurrence by changing the correlations of the latent 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 re-scaling 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 2014). Five chains for 100,000 iterations were run 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. Vague normal priors were used for all model parameters (mean = 0, standard deviation = 1).

The composition of river bird communities was characterised 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.

4.4. 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 (**Figure 4.2**). 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.

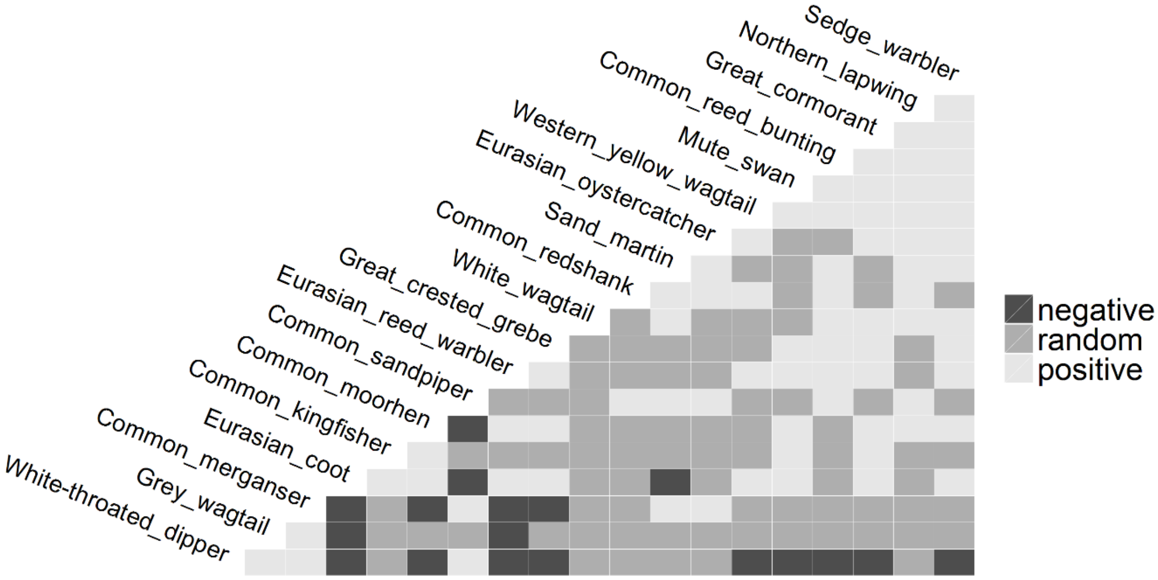


Figure 4.2 *Heatmap visualisation showing pairwise associations between 19 river bird species calculated according to the probability model of species' co-occurrence (Griffith In press). Significant positive (negative) associations are displayed where species co-occurred more (less) frequently than by chance, with an alpha threshold of 0.05.*

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 (**Figure 4.**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 (**Figure 4.4**).

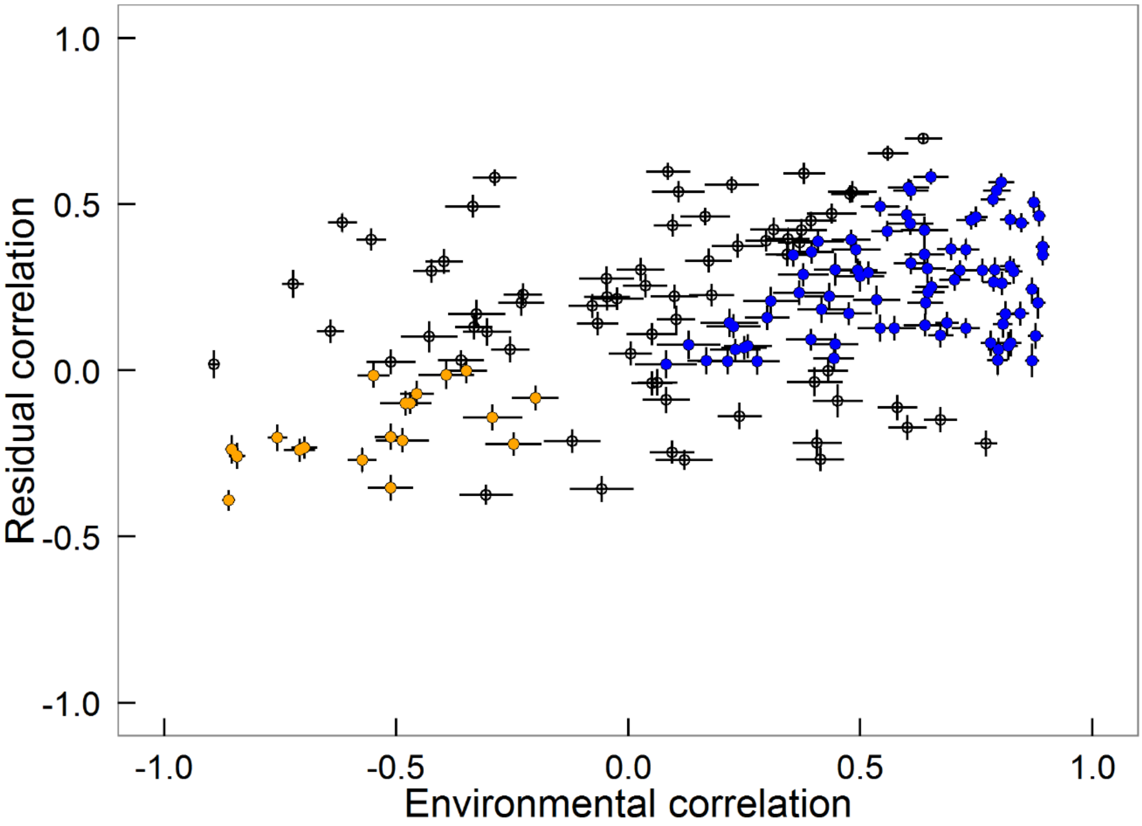


Figure 4.*3 Modelled environmental and residual correlations between pairs of all 19 river bird species (i.e. 171 pairs) averaged across all 100 WBBS locations. The error bars display 95% confidence intervals for the mean modelled environmental and residual correlations. The points are coloured blue 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.*

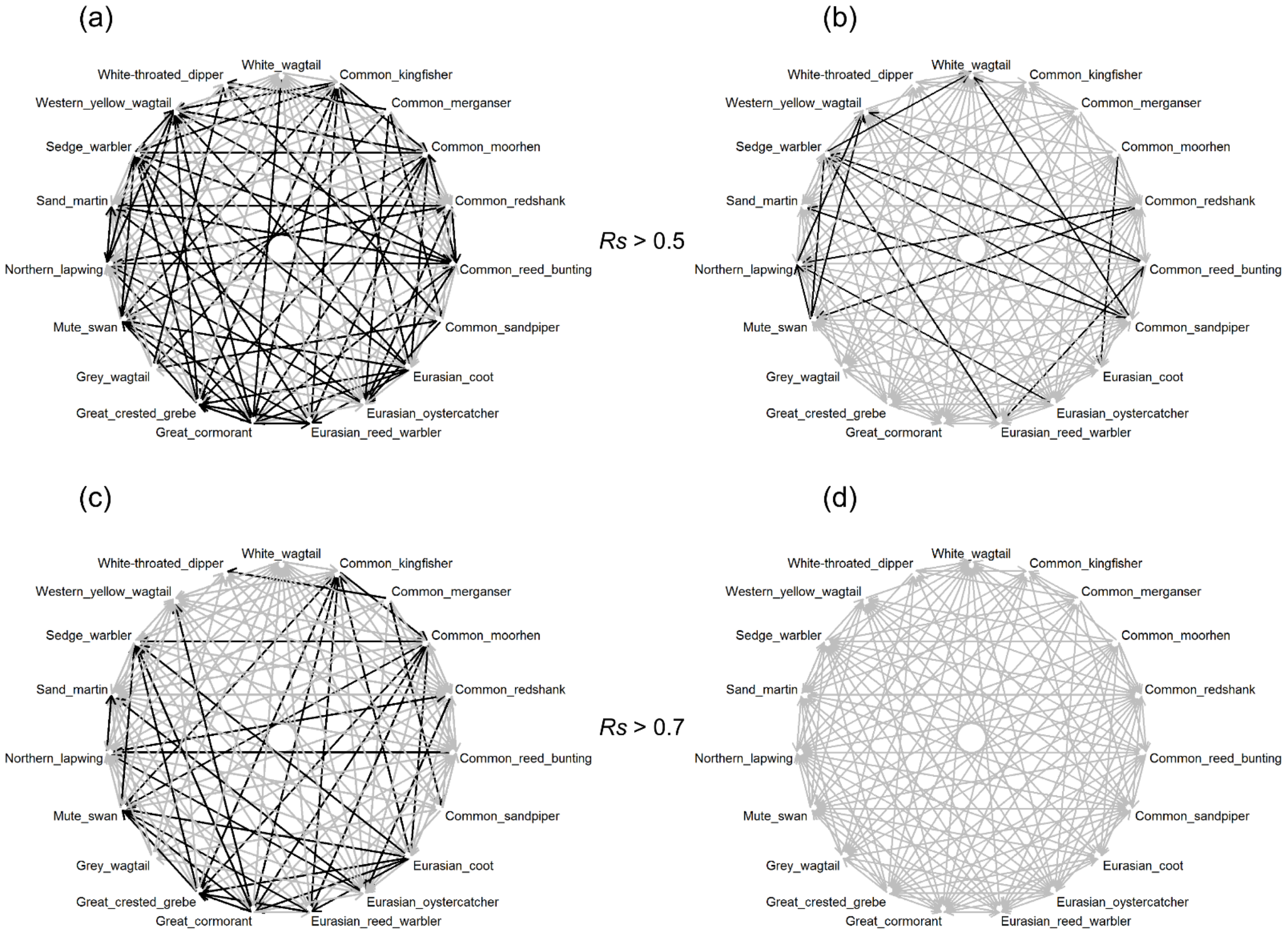


Figure 4.4 *Network diagrams showing modelled environmental correlation (a & c) and residual correlation (b & d) between 19 river bird species, where the black lines represent positive correlations at Rs > 0.5 and Rs > 0.7.*

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 (**Figure 4.5**). Species within each guild displayed similar characteristics for habitat and resource acquisition as well as range. 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: $\chi^2 = 15.70$, $p < 0.001$) (**Figure 4.**6).

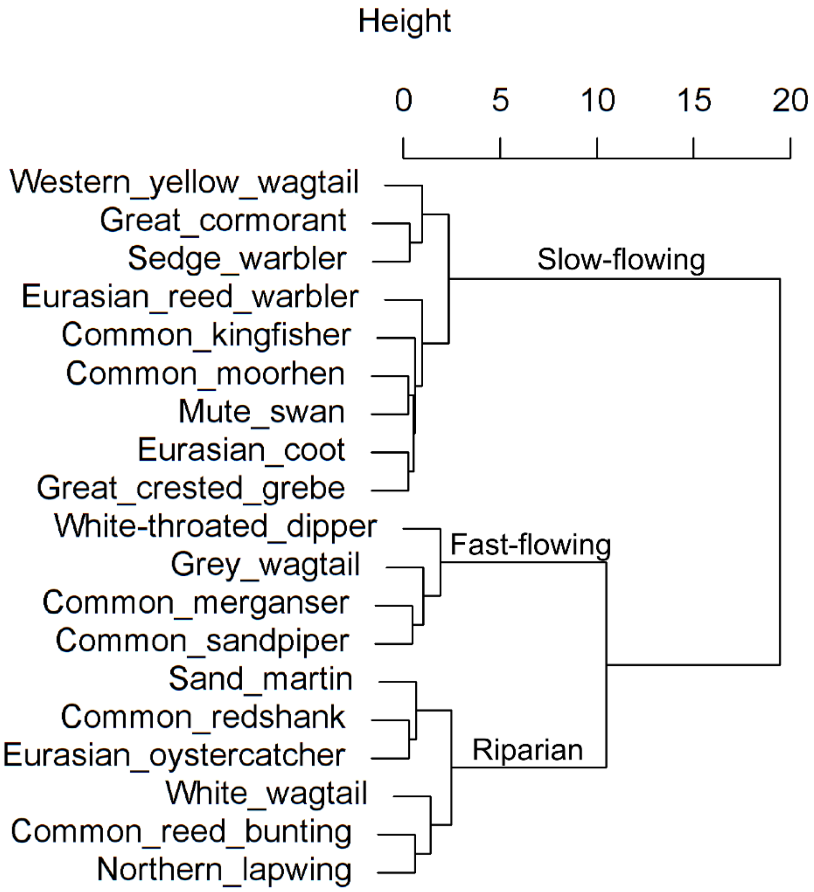


Figure 4.5 *A dendrogram, created by converting the matrix of species' occurrences across the 100 river locations into a binary dissimilarity matrix and by then using hierarchical cluster analysis, to show how species' occurrences cluster in a manner consistent with three guilds based on foraging habitat and resource acquisition: slow-flowing species, fast-flowing species, and riparian species.*

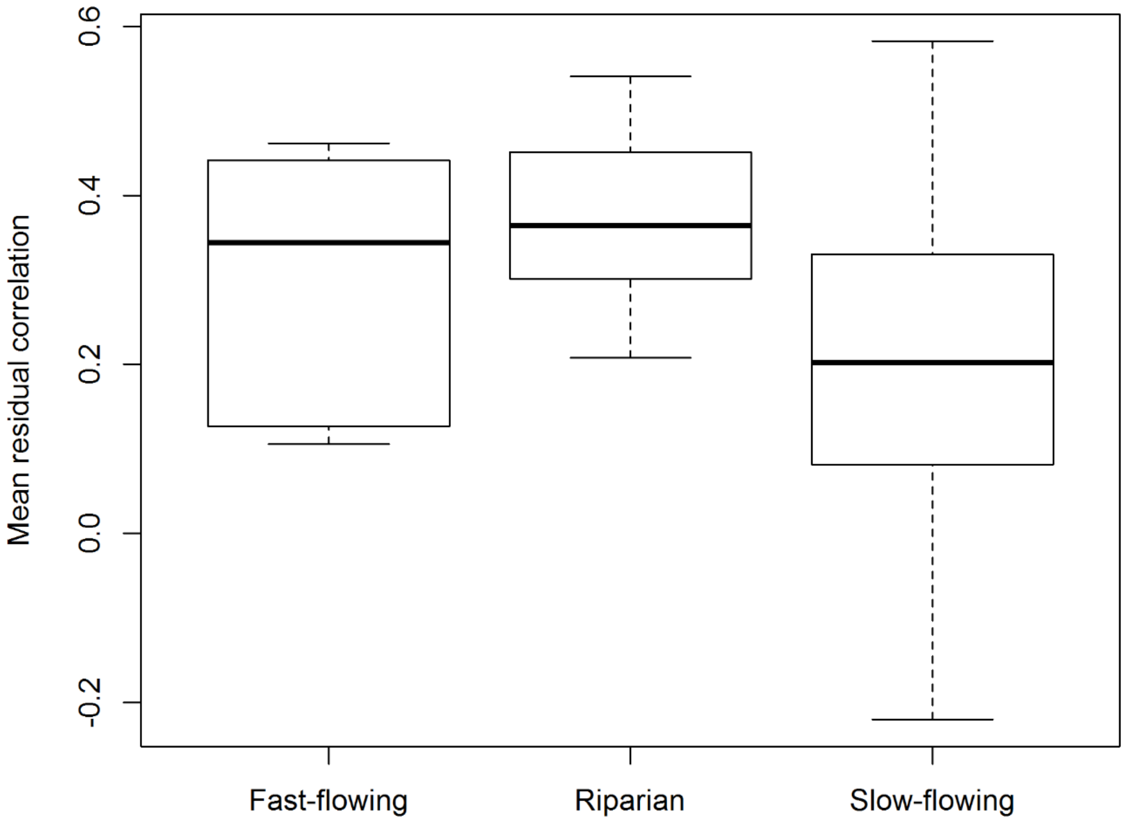


Figure 4.*6 Box-and-whisker plots of the mean residual correlation between species within three guilds based on foraging habitat and resource acquisition: fast-flowing, riparian, and slow-flowing (see Results section for the species composition of guilds). In each box the thick black line represents the median average residual correlation between species and the limits illustrate the interquantile 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.*

4.5. 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 et al. 2010) and the testing of surrogate hypotheses (Araujo and Luoto 2007). Species' interactions affect the distribution of many bird species (Cody 1974) and their inclusion in some SDMs can improve model performance (Meier et al. 2010). However, the importance of interactions between species in structuring bird communities at macro-ecological scales is hotly debated in the ecological literature (Araujo and Luoto 2007, Heikkinen et al. 2007, Gotelli et al. 2010, Meier et al. 2010, Ovaskainen et al. 2010, Araújo and Rozenfeld 2013, Kroll et al. 2014).

Here, co-occurrence patterns in river bird communities across Great Britain were analysed and the degree to which patterns could be attributed to shared environmental responses was assessed. This allowed the testing of alternative community assembly hypotheses: a null hypothesis of random assembly, environmental filtering, conspecific interaction, and a pluralistic model of assembly. However, the discussion is not limited to mechanistic models of community assembly and the influence of the filtering of species from regional species pools on community structure is also considered. It was 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 conspecific interaction is reduced to an ancillary role.

Whilst these results corroborate the findings of some studies in suggesting that species interactions are of secondary importance relative to habitat structure and resource availability (Gotelli et al. 1997, Petchey et al. 2007, Mattsson et al. 2013, Börger and Nudds 2014, Kroll et al. 2014), they contrast markedly with others (Heikkinen et al. 2007, Gotelli et al. 2010, Sebastian-Gonzalez et al. 2010, Robertson et al. 2013). One reason for this might be that here the focus was 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 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 et al. 2002). Perturbations in aquatic-riparian food webs also cause irregularity in ecological processes such as production and biotic interactions (Ledger 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 et al. 2007, Mattsson et al. 2013, Robertson 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. 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 et al. 2012).

However, the predictive performance of the JSDM varied between bird foraging guilds, with residual correlation highest amongst riparian species. 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 to hypothesise that competition amongst these functionally similar species for transitory food resources is likely and that this would lead to segregation (MacArthur and Levins 1967). However, co-occurrence between these species was observed to be positive, suggesting the operation of an alternative model of conspecific interaction such as heterospecific attraction.

Hetereospecific 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 et al. 1990). Such patterns have previously been observed in some waterbird species including riparian waders (Sebastian-Gonzalez 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 and Martorell 2009). However, this requires intraspecific competition to be stronger than interspecific competition, allowing for niche partitioning (MacArthur and Levins 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 (Leyequien et al. 2007). Temporal niche separation, for instance through nocturnal foraging in northern lapwing, 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. Firstly, random patterns of co-occurrence may point towards a strong influence of the random filtering of species from the regional species pool. The filtering of species from regional pools into communities may be greatest at locations with lower productivity and reduced competitive exclusion (Houseman and Gross 2006). Variability in river flows exerts a strong disturbance regime that can limit productivity in aquatic-riparian environments which, in turn, prevents competitive exclusion (Poff et al. 1997, Bunn and Arthington 2002, Ledger et al. 2012). 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 and Crujeiras 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 et al. 2004). However, here the potential for bias caused by species' detection probability was minimised by only using survey locations that were visited on several occasions.

In summary, co-occurrence patterns were primarily driven by shared environmental responses. Limited evidence was found 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, this study also demonstrates 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, the results of this study 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 heterospecific attraction may operate to promote positive associations amongst some species. The 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.

In this chapter, pairwise patterns in species' co-occurrence were partitioned into correlative responses to environmental variables or potential species' interactions to evaluate the evidence for the operation of different community assembly processes. Now, Chapter 5 will provide a quantitative analysis of the environmental processes that structure spatial patterns of functional traits in river bird assemblages. This will facilitate further investigation of the environmental processes and assembly mechanisms that determine structural patterns in river bird communities, as well as characterise shifts in the functional composition of bird communities across environmental gradients.

5. Analyses of functional traits reveal shifts in river bird community structure across land uses and environmental gradients

5.1. Abstract

The distinctiveness of local and regional biotic assemblages is declining and wide-ranging habitat generalists are replacing habitat specialists. An evaluation of the important environmental drivers of this variation in community structure is therefore required to determine how rapid global environmental change might alter community assembly processes. The community structure of river bird assemblages in Great Britain were analysed using indices of functional diversity (FD) to examine how shifts in response to different land-uses and gradients of climate and river flow. A standardised metric for the deviation of observed FD from expected FD (Standard Effect Size) was calculated to reveal the operation of different assembly mechanisms and functional groups of species were identified using a dendrogram method. FD tended to be lower than expected, indicating that species in bird communities typically display a degree of similarity in functional traits and low levels of functional redundancy. Environmental filtering strongly influence community assembly, but different mechanisms may operate depending on the environmental conditions at each specific river location. Natural habitats supported greater FD, while modified habitats and a loss of river flow variability were associated with shifts in community structure consistent with 'functional homogenisation'. Natural environmental variability and disturbance regimes have a crucial role in sustaining functionally diverse river bird assemblages. Loss of natural habitats and an

alteration of river flow regimes through anthropogenic modification or climate change may have profound impacts on river bird communities.

5.2. Introduction

The distinctiveness of local and regional biotic assemblages is declining and wide-ranging habitat generalists are replacing habitat specialists (McKinney and Lockwood 1999, Rooney et al. 2007). The increase in the functional similarity in biotas over time is typically characterised by the loss of species possessing unique functional traits (a process termed ‘functional homogenisation’) (Olden and Rooney 2006). Understanding the drivers that structure ecological assemblages is of paramount importance in the conservation and restoration of communities that have been impacted by changes in environmental conditions. As a result, this has become a central theme in recent research in community and macro-ecology (Belmaker et al. 2012).

Biodiversity studies have traditionally focused on measures of taxonomic diversity such as species richness (SR). Trait-based measures, however, have found favour as they provide mechanistic links between ecosystems and organisms and, thus, reveal the operation of stochastic and deterministic community assembly rules (Petchey and Gaston 2006, Cornwell and Ackerly 2009, Cadotte et al. 2011). Non-randomness in the distribution of species functional traits indicates where species co-existence’ and different assembly processes shape community structure (Mouchet et al. 2010). For instance, environmental filtering assumes that randomly distributed environmental factors filter traits and only allows a subset of viable traits from the species pool to persist. Niche models (e.g. competitive exclusion and limiting dissimilarity) assume the displacement of species with similar traits, resulting in communities composed of functionally dissimilar species. Alternatively, neutral theory (Hubbell 2001) implies that biodiversity patterns occur randomly and differences between individual species are ‘neutral’ and, thus, independent of interspecific interaction.

Functional diversity (hereafter termed ‘FD’) metrics have been refined since early studies that used measures such as the number of functional groups in a community, which ignored differences between species within groups. These measures have now been supplanted by methods that continuously quantify measures of functional traits in a multi-dimensional and dynamic space (Petchey and Gaston 2002, Mason et al. 2005, Villéger et al. 2008, Mouchet et al. 2010). Negative departures of FD from random community assembly suggest that the dominant assembly mechanism is environmental filtering in which habitat variability filters traits suited to particular environments. A positive departure suggests the operation of competition or limiting similarity processes whereby the co-existence of species with dissimilar traits is promoted through competitive exclusion and niche overlap.

The FD of some bird communities in Great Britain is lower than expected by chance (Petchey et al. 2007, Mendez et al. 2012). This suggests that competition and limiting similarity processes are of secondary importance with the effects of species’ interactions strongest at finer, local scales and environmental conditions structuring diversity at coarser, regional scales. However, the environmental drivers of spatial variation in the FD of bird communities have yet to be quantified. Measuring the magnitude of importance of assembly mechanisms across environmental gradients is required to determine how rapid global environmental change and associated shifts in habitat, resource availability and climatic conditions might alter community assembly processes (Mouchet et al. 2010, Mendez et al. 2012). Moreover, environmental variation can also differentially influence groups of functional species (e.g. habitat specialists or generalists) with the favourability of particular traits shifting across the gradient of environmental conditions (Flynn et al. 2009).

The limits of bird species' ranges often match combinations of broad-scale climatic variables (Huntley et al. 2007, Jenouvrier 2013), but turnover among assemblages may be best explained by variation in climate at more localised scales (La Sorte and Boecklen 2005, Araújo et al. 2013, Ockendon et al. 2013, Whitehouse et al. 2013). Bird community structure is also strongly influenced by heterogeneity in land-cover characteristics (Mattsson et al. 2013); assemblages are sensitive to shifts in land use which alter competitive interactions that can result in the loss of specialist species (Robertson et al. 2013). Furthermore, urbanisation (Devictor et al. 2007) and fragmentation (Cintra et al. 2013, Ding et al. 2013) of natural habitats and the associated loss of habitat complexity (Evans et al. 2009) can further degrade assemblages, resulting in levels of functional redundancy higher than expected by chance (Luck et al. 2013), as well as homogenization through the increased dominance of generalist species (Devictor et al. 2007).

For bird species associated with rivers and riparian habitats the influence of river flow is also a key determinant of their ecology and the distribution of river bird species is influenced by variability in flows (Royan et al. 2013) and by the occurrence of extremes, including both floods and droughts (Royan et al. 2014). Variability in flows creates heterogeneity in riparian habitats that affects the prevalence and quality of foraging habitats for birds (Jonsson et al. 2012), which, in turn, can increase the diversity and abundance of birds (Chiu et al. 2008, Kajtoch and Figarski 2013). Conversely, river regulation and associated reduced flow variability lead to a loss of species' diversity (Kingsford et al. 2004), with species' loss greatest amongst riverine-specialists (Jonsson et al. 2012).

This chapter provides a quantitative analysis of the environmental processes that structure patterns of functional traits in river bird assemblages at 101 river locations in Great Britain. The specific objectives were to: (i) characterise spatial and temporal patterns in the distribution of bird functional traits using complementary indices of FD (e.g. functional richness, evenness and divergence); (ii) investigate the environmental processes and assembly mechanisms that determine structural patterns in river bird communities; and (iii) characterise shifts in the functional composition of bird communities across environmental gradients.

The following four hypotheses were tested:

1. The FD of bird communities will be typically lower than expected, indicating low levels of functional redundancy and a strong influence of environmental filtering.
2. Functional redundancy will be highest in bird communities in landscapes with a predominance of modified habitats (e.g. farmland and urban habitats), with associated decreases in the richness, evenness and divergence of functional traits.
3. As variation in river flows creates complexity in habitats across the riverine-floodplain interface, greater river flow variability will increase the functional richness, evenness and divergence of traits in bird communities.
4. The contribution of functionally rare species will be lower in riverine landscapes bordered by modified land uses (e.g. urban and farmland) compared to natural land uses (e.g. natural semi-natural grassland) in a manner consistent with ‘functional homogenisation’.

5.3. Methods

5.3.1. Bird survey data

This study employed distributional data on resident breeding birds on British rivers derived from the WBBS. Bird assemblages were quantified for 21 species (Figure B1) that are characteristic of British riverine communities (Royan et al. 2013). In total, bird data were obtained for 101 river locations (Figure B2) using WBBS data from 1998 to 2011 (inclusive). Only a single survey location was used per watershed so as to maintain the statistical independence of survey sites. River locations were surveyed on at least four separate occasions and at least once since 2010 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 et al. 2012). In total 956 survey years were included in the analyses.

During the surveys, recorders made two visits to each survey location, noting the number of each species of bird seen or heard on each occasion. For bird abundances, count data were used from either the first or second survey visit depending on which was higher so as to avoid double counting individual birds (Davey et al. 2012).

5.3.2. Land cover, river flow and climate data

During WBBS surveys observers also recorded land cover for each 500 m transect using a hierarchical recording system. Land-cover categories were broadly defined as follows: woodland; scrubland; semi-natural grassland; heathland and bogs; farmland; human sites (urban); water-bodies; coastal; and inland-rock. However, only woodland, semi-natural grassland, farmland and urban categories occurred sufficiently frequently to ensure homogeneity of variances between categories and, thus, be included in analyses. Survey locations were categorised using the dominant habitat category (i.e. > 50% of transects). A number of major habitat types occurred within each of these land-cover categories (e.g. both reed beds and salt marshes are contained within the semi-natural grassland category), with details of these habitat types provided in Table B1. A fifth land cover category ('mixed') was used for survey locations with no dominant habitats.

Annual river flow data for the period 1998 to 2011 (inclusive) were obtained from the NRFA. Bird data were paired with flow data where a gauging station was situated within 10 km of the start or end point of the WBBS transects. The sample avoided locations where major tributaries existed between the gauging station and WBBS transect, or where anthropogenic modifications (e.g. flow regulation structures) of the river were present. In addition, data were not used where > 10% of flow records were missing for any particular year. Missing data were otherwise interpolated using long-term daily mean flow values. To ensure that flow variables were representative of long-term variability in hydrological regime, flow variables were calculated across the hydrological year in Great Britain (October to September) (Bower et al. 2004). Two flow variables were calculated to examine the relationship between variability in river flow regimes and bird communities: mean daily flow – the mean value of daily discharge divided by median of daily discharge – and the standard deviation of daily flow. River flow variables were determined *a priori* (c.f Royan et al. (2013)).

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). To examine the relationships between climate and river bird communities mean breeding season temperature (°C) and total breeding season rainfall (mm) was determined, with the breeding season defined as April to July (inclusive). The influence of winter climate temperature and rainfall variables was also examined, both measured with data from December to February (inclusive) (Table B2).

5.3.3. Functional diversity indices

Functional variation in the river bird species was assessed using five trait categories that characterised their ability to exploit different food resources (Table 5.1). Four of the categories, which concerned diet, foraging behaviour and habitat use, were split into binary traits as the characteristics may not be mutually exclusive. Body mass was also included as a continuous variable as it is known to be an informative parameter in functional diversity studies (Ding et al. 2013). This was calculated, using Dunning (2008), as average male or female weight depending on which was greater. In common with other bird FD studies (Mendez et al. 2012, Ding et al. 2013, Luck et al. 2013), trait values of birds were obtained from the *Handbooks of the Birds of Europe, the Middle East and North Africa* (BirdGuides Ltd 2006).

Table 5.1 *Traits used for calculation of FD indices.*

Functional trait	Type	Values	Units/Categories
Body mass	Continuous	Mean	G
Diet	Binary	9 levels	Aerial insects, amphibians, aquatic invertebrates, aquatic plant material, fish, riparian/terrestrial invertebrates, terrestrial plant material, worms, and others
Sensory modality to detect prey	Binary	2 levels	Sight and touch
Main foraging strategy	Binary	8 levels	Diving, flycatching, gleaning, grazing, jabbing, pecking, probing, and upending
Foraging habitat	Binary	3 levels	Aquatic, riparian, and terrestrial

A suite of complementary indices proposed by Villéger et al. (2008) and reviewed by Mouchet et al. (2010) were used to quantify FD; functional richness (FRic), evenness (FEve) and divergence (FDiv). FRic measures the proportion of a convex hull volume of functional space occupied by a community. This index was used as a measure of functional richness as it has high power to detect community assembly rules and performs well when the number of species is relatively low (i.e. < 30) (Mouchet et al. 2010). FEve is constrained between 0 and 1 and measures the evenness in the distribution of abundances of species in functional trait space. Low values indicate that abundances are less evenly distributed across the axes of functional trait space whereby abundances are concentrated in a small compartment of trait space. Conversely, higher values represent a more even spread in the distribution of species' abundances and greater similarity in the distances amongst the nearest neighbouring species (Villéger et al. 2008). FDiv is also constrained between 0 and 1 and measures the divergence of species' abundances from the centre of trait space that is actually occupied. Both FEve and FDiv were weighted by the abundance of species. According to Mouchet et al. (2010), these indices each performed best in measuring their respective aspects of FD.

It is important to consider the relationship between SR (i.e. the number of species in the community) and indices of FD to determine if they are independent (Mouchet et al. 2010). The strength of the relationships between each of the FD indices and SR was assessed using linear regression with the former fitted as the dependent variable. Both linear and quadratic relationships were investigated with the latter accepted if it improved model fit, as assessed by Akaike's Information Criterion (AIC) corrected for smaller sample sizes (AICc) (Burnham and Anderson 2004).

Deviations in observed from expected FD reveal the operation of different assembly mechanisms (Mouchet et al. 2010). To test if the observed values of the FD indices differed from expected values, simulated communities were constructed to generate a distribution of expected values. For each river location, 999 communities were simulated by selecting species from the observed species pool and randomly assigning them to a location without replacement. This maintains patterns of SR. The expected values for FD indices were calculated as the mean of 999 simulations for each location. Measures of the observed FD indices were deemed significantly different if they were ranked higher or lower than the 5th or 95th percentiles from the distribution of expected values (Luck et al. 2013). For each river location, observed values were tested against expected values using paired two-tailed Wilcoxon signed-rank tests (Pakeman 2011).

For each location, a standardized measure of the difference between observed and expected FD values was then calculated as the standard effect size (SES) index:

SES FD = (Observed FD – Expected FD)/Standard deviation of the expected FD

(Equation 5.1)

SES FD values: > 0 indicate that community assembly tends towards random and highlight the increasing importance of niche differentiation assembly mechanisms; and < 0 indicate a stronger overall effect of environmental filtering. To test how these assembly mechanisms might shift across environmental gradients, each SES FD index was regressed against the environmental variables.

5.3.4. Statistical analyses

Variation in the FD and SES FD indices was modelled using Generalized Additive Models (GAMs), using version 1.8-1 of the ‘mgcv’ package for R (Wood 2006). River flow and climate variables were fitted with a cubic regression spine with the degrees of freedom determine automatically using Restricted Maximum Likelihood (REML). REML offered a reliable and high-performing method of parameter estimation (Wood 2011), thus ensuring that the modelled functional relationships were described with minimal degrees of freedom (Fewster et al. 2000). This also allowed us to test for non-linear relationships between the FD indices and the explanatory variables (Gerisch et al. 2012a). Land cover was fitted as a categorical variable. Models included a gamma penalty of 1.4 to reduce the likelihood of overfitting the data (Wood 2006) and were fitted with an identity link function, with explanatory variables log-transformed to satisfy normality assumptions where necessary. Models were also weighted by the inverse of the total survey effort at each river location (the total number of 500 m transects surveyed) so as to account for spatial variation in the coverage of surveys and to ensure that river locations with a greater survey effort had a greater contribution to the calculation of coefficients. To account for correlation between survey years and variation in the geographic coverage of WBBS sites, a three-way interaction between year, latitude and longitude was included as a fixed effect. This controls for: (i) similarities in the response variable at nearby points by fitting a smooth two-dimensional surface to these data; and (ii) unmeasured variables that may affect the response by fitting to response peaks and troughs, thereby fitting spatial autocorrelation in the dataset by optimising the degrees of freedom (Davey et al. 2012).

5.3.5. Functional groups

Groups of functionally similar species were classified using the dendrogram method to characterise shifts in bird community structure across environmental gradients (see Petchey and Gaston (2002)). The trait matrix was then converted into a distance matrix, using Gower distance, and a functional dendrogram was produced to describe the functional relationship between species. UPGMA clustering was used as it gave the highest cophenetic correlation (c = 0.84) compared to single or Ward’s methods. Functional groups were identified according to the position of species within the dendrogram (Laliberte et al. 2010). The relationship between the percentage composition of bird assemblages that comprised each functional group and the three FD indices was then modelled using GAMs (Wood 2006). Models were specified with a quasi-binomial distribution and included a gamma penalty of 1.4. The FD indices were fitted with cubic regression splines, with the optimal amount of smoothing defined using REML.

5.4. Results

Correlation analysis showed that FRic, FEve and FDiv were independent of each other (

Table B3) and so provided different information on the FD of bird communities. The three FD indices also had markedly different relationships with SR; the relationship between SR and FRic was best explained with a second order polynomial (R^2 = 0.71) (Figure B3), while the relationships of SR with FEve and FDiv were comparatively weaker and were best explained by second (R^2 = 0.11) and third (R^2 = 0.06) order polynomials respectively.

5.4.1. Observed and expected FD

Two-tailed Wilcoxon signed-rank tests showed that the median of expected FD values for all three indices (calculated as the average expected FD for all simulations for each year at each location) was significantly different from that of observed values at an alpha level of 0.001. Observed FRic values were significantly higher than expected (i.e. above the 2.5th percentile from the distribution of expected values) in nine (0.9%) survey years and significantly lower than expected (i.e. lower than the 97.5th percentile from the distribution of expected values) in 41 (4.3%) survey years (Figure 5.1); FEve was higher than expected in five (0.5%) survey years and lower in 131 (13.7%), and FDiv higher in 194 (20.3%) survey years, and lower in 113 (11.8%). A negative departure from zero in SES FRic was observed in 657 (68.7%) survey years and in 791 (82.7%) and 336 (35.1%) survey years for SES FEve and SES FDiv, respectively.

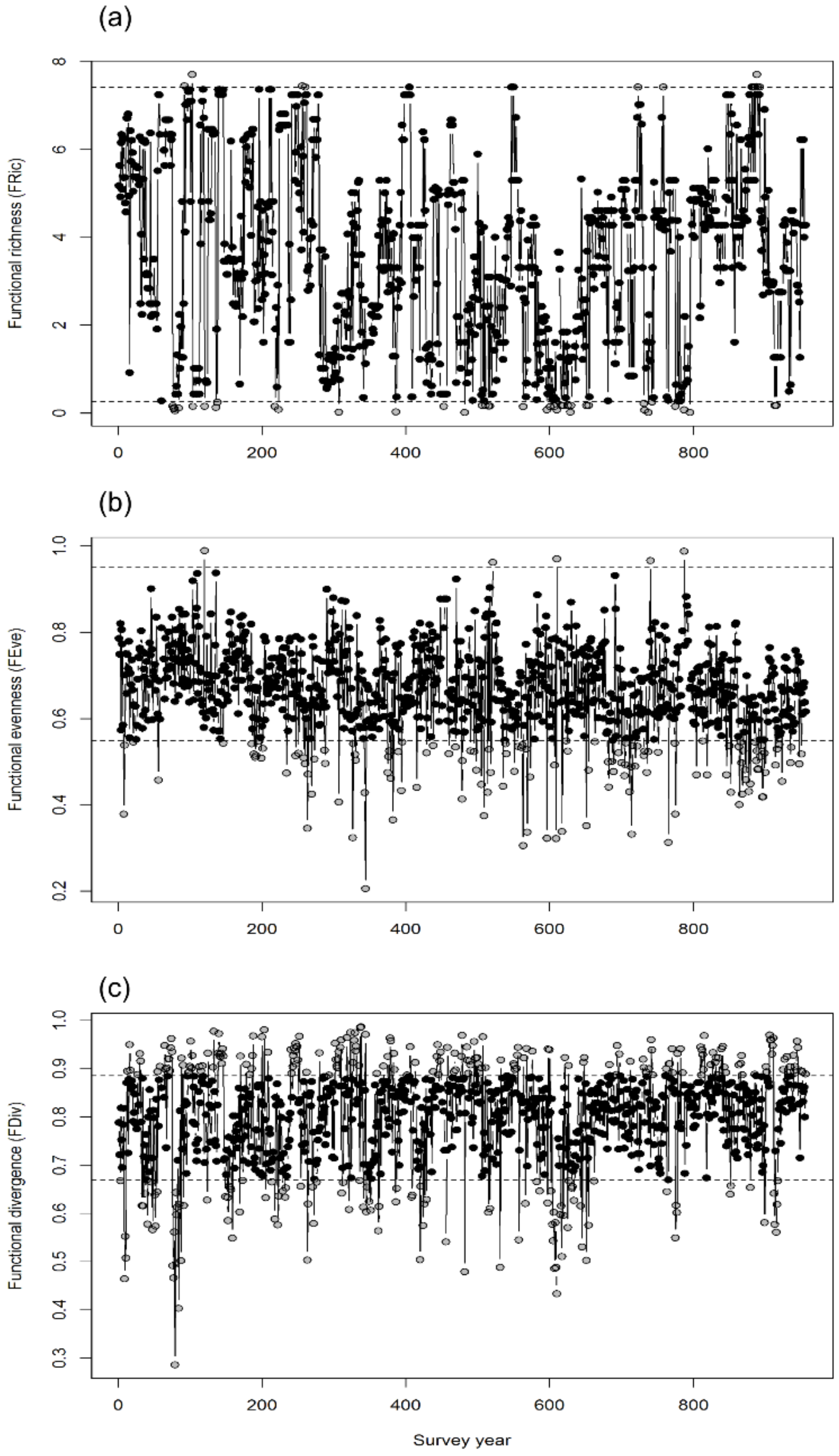


Figure 5.1 *Plots showing how (a) functional richness (FRic), (b) evenness (FEve) and (c) divergence (FEve) changed over the 956 survey years across 101 river locations. The dashed lines represent the 2.5th and 97.5th percentiles from the distribution of expected values with values above or below (grey-filled points) the dashed lines deemed significantly different from expected.*

5.4.2. Relationships between FD and environmental variables

*The GAMs of FRic, FEve and FDiv accounted for 48.8%, 17.6% and 18.2% of the total deviance, respectively. Modelled coefficients (**Table 5.2**) showed that river locations bordered by woodland land cover had the lowest FRic, followed by those with urban. The highest FRic was recorded at river locations bordered by farmland, semi-natural grassland and mixed land cover (* **Figure 5.2**). FRic was also significantly related to the standard deviation of annual daily flows and increased non-linearly with this variable. FEve was highest at river locations bordered by woodland and farmland and lowest at those with mixed land cover. Conversely, FDiv was highest at river locations bordered by mixed and lowest at those with woodland land cover.

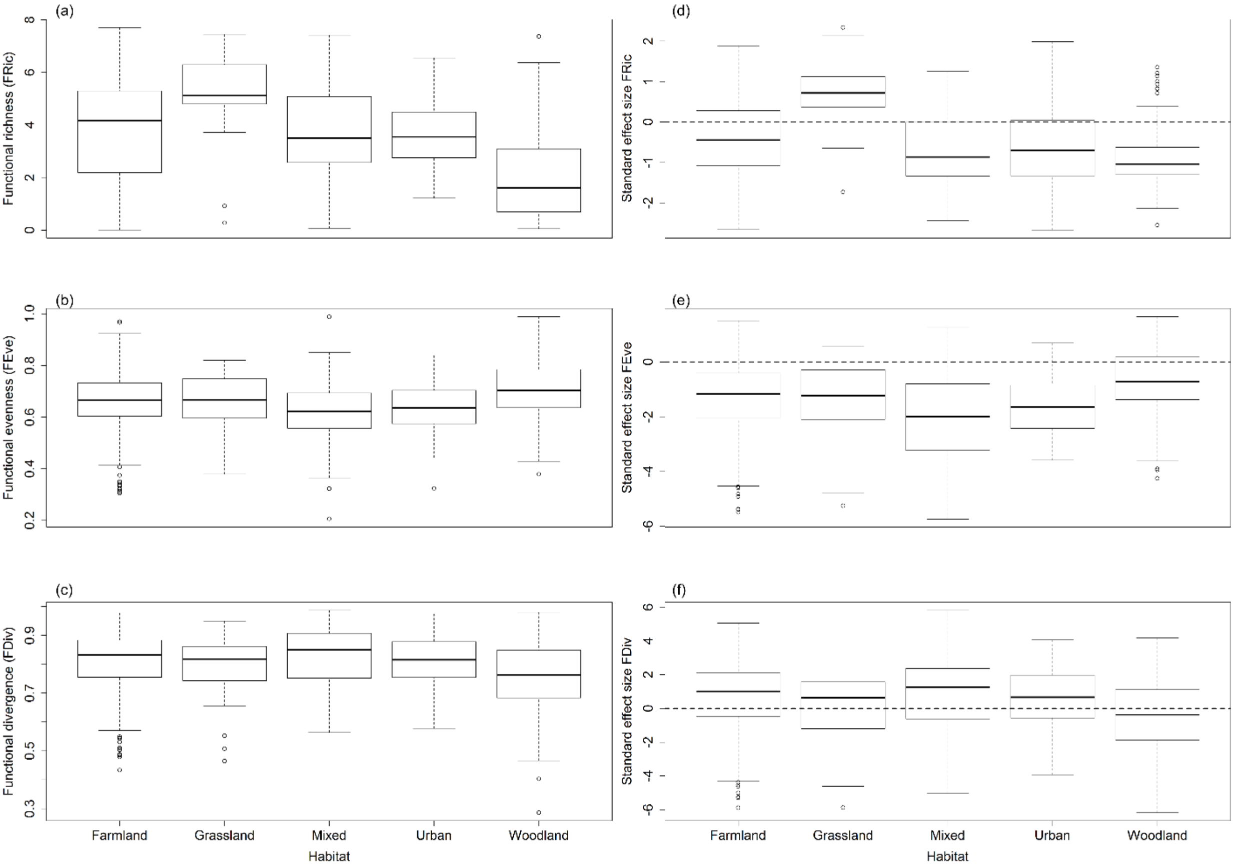


***Table 5.2** Results of the generalized additive models (GAMs) used to examine the association of habitat, river flow, climate, year and location with observed and standard effect size (SES) measures of three indices of functional diversity (FD): functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). Parameter estimates, standard errors and P values are shown for the parametric terms along with the P values for the smoothed terms. Habitat coefficients are in reference to woodland habitat, which had the lowest FRic . 'Edf' is the equivalent degrees of freedom.*

	Model term (Parametric terms)	**(Intercept)**	**Farmland**	**Semi-natural grassland**	**Mixed**	**Urban**	**Model term (Smoothed terms)**	**Mean daily flow (m^3-sec)**	**Standard deviation of daily flow (m^3-sec)**	**Mean temperature (°C)**	**Mean rainfall (mm)**	**s(lat, long, year)**	**Deviance explained (%)**
Functional richness (FRic)	**Coefficient**	2.388	1.455	1.706	1.376	0.353	**Edf**	4.133	3.551	5.05	1.001	41.069	48.8
	SE	0.338	0.393	0.993	0.533	0.855	***F***	0.881	4.543	0.671	0.006	0.655	
	***P* value**	< 0.001	< 0.001	0.086	0.033	0.68	***P* value**	0.494	< 0.001	0.677	0.938	0.975	
Functional evenness (FEve)	**Coefficient**	0.704	-0.04	-0.055	-0.084	-0.044	**Edf**	1	2.304	1	1	24.288	17.6
	SE	0.021	0.024	0.06	0.033	0.051	***F***	0.049	0.201	0.028	1.176	0.225	
	***P* value**	< 0.001	0.092	0.356	0.011	0.387	***P* value**	0.825	0.894	0.866	0.279	1	

Functional divergence (FDiv)	**Coefficient**	0.77	0.045	0.009	0.048	0.022	**Edf**	4.347	3.859	2.045	3.481	25.443	18.2
	SE	0.02	0.024	0.059	0.033	0.053	***F***	0.325	1.436	0.283	0.282	0.274	
	***P* value**	< 0.001	0.057	0.877	0.14	0.68	***P* value**	0.91	0.21	0.811	0.905	1	
SES Functional richness (SES FRic)	**Coefficient**	-0.892	0.566	1.042	0.204	0.072	**Edf**	1.187	5.608	5.345	2.401	31.919	32.2
	SE	0.162	0.188	0.471	0.258	0.419	***F***	0.289	0.562	0.441	0.218	0.42	
	***P* value**	< 0.001	0.003	0.027	0.428	0.863	***P* value**	0.66	0.781	0.865	0.888	1	
SES Functional evenness (SES FEvE)	**Coefficient**	-0.851	-0.424	-0.575	-1.022	-0.123	**Edf**	3.2	3.525	1	1.003	18.031	23.4
	SE	0.245	0.284	0.698	0.389	0.627	***F***	0.285	0.754	0.123	0.578	0.361	

	***P* value**	< 0.001	0.136	0.411	0.009	0.845	***P* value**	0.891	0.568	0.726	0.448	0.998	
SES Functional divergence (SES FDiv)	**Coefficient**	-0.02	0.797	-0.174	0.785	0.073	**Edf**	4.574	3.769	1.003	2.485	23.388	17.5
	SE	0.388	0.449	1.115	0.617	0.997	***F***	0.371	1.61	0.423	0.174	0.268	
	***P* value**	0.96	0.077	0.876	0.203	0.942	***P* value**	0.889	0.158	0.517	0.923	1	

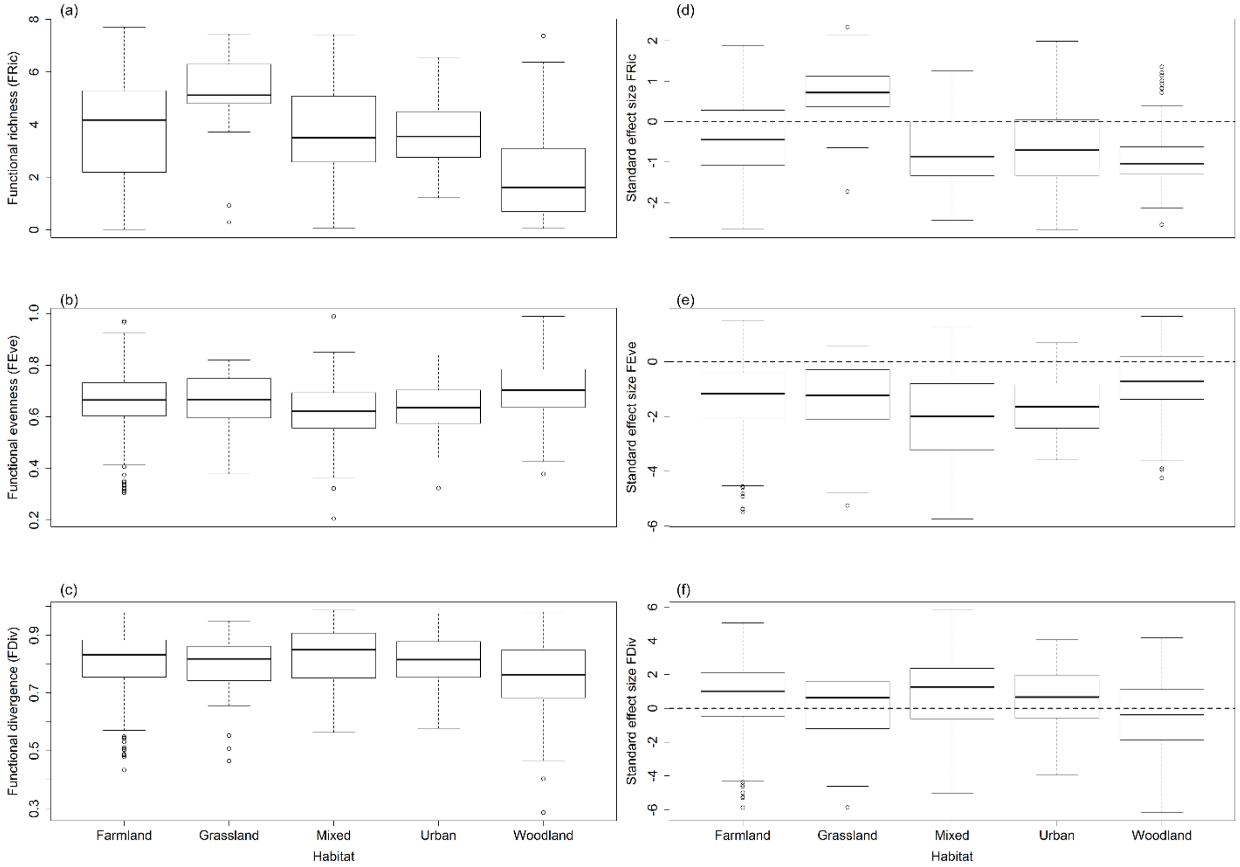
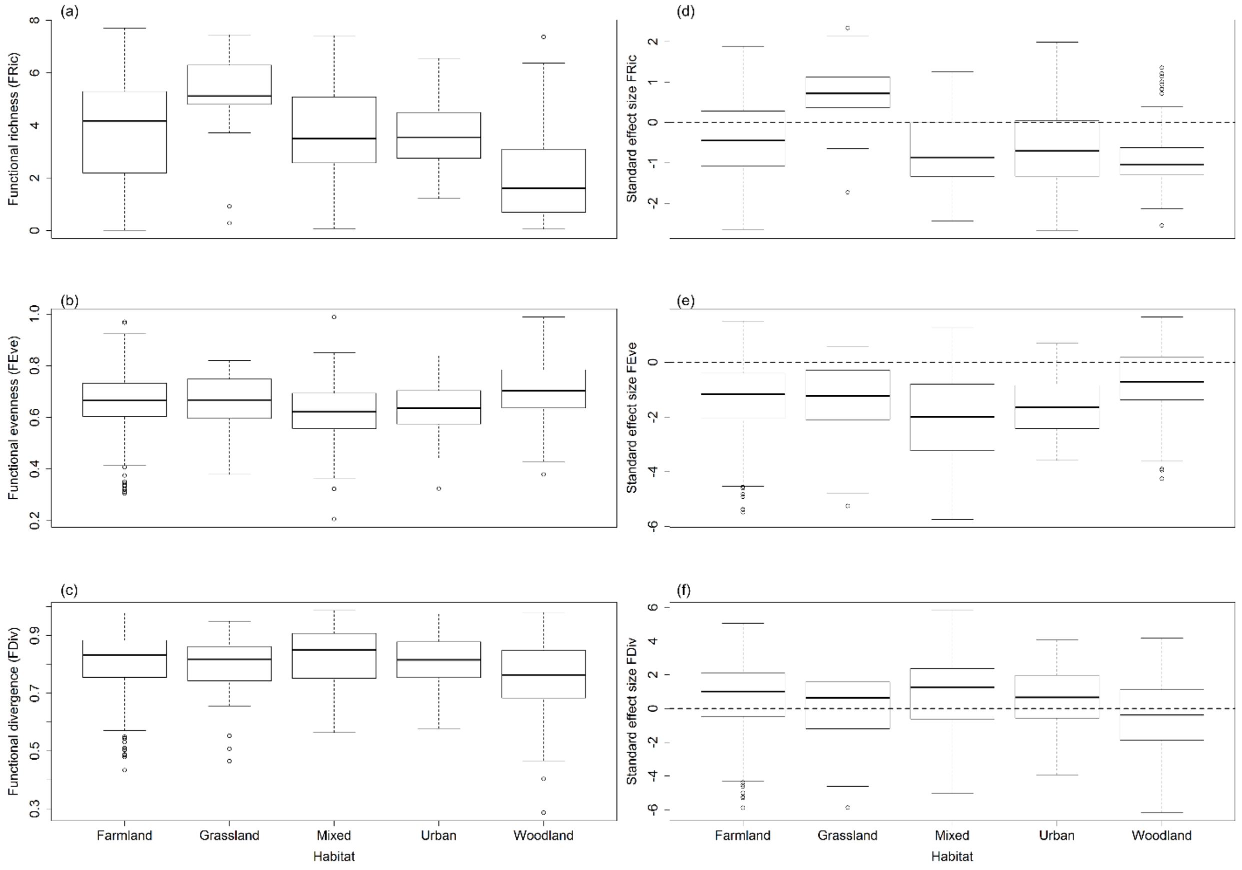


***Figure 5.2** Box-and-whisker plots of three indices of functional diversity (FD): (a) functional richness (FRic), (b) evenness (FEve) and (c) divergence (FEve); and three standard effect size (SES) indices of FD: (d) functional richness (SES FRic), (e) evenness (SES FEve) and (f) divergence (SES FEve), across five habitat categories at 101 river locations. In each box the thick black line represents the median FD index value and the limits illustrate the interquantile 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.*

The GAMs of SES FRic, SES FEve and SES FDiv accounted for 32.3%, 23.4% and 17.5% of the total deviance, respectively. The lowest SES FRic was recorded at river bordered by woodland and urban land cover and the highest values at locations bordered by semi-natural grassland and farmland (***Table 5.2;*** **Figure 5.2**). SES FEve was highest at river locations bordered by woodland and urban land cover and lowest at those with mixed land cover. SES FDiv was highest at river locations bordered by farmland and mixed land cover and lowest at those with semi-natural grassland and woodland. None of the observed FD or SES FD indices displayed significant relationships with the climate variables.



5.4.3. Functional groups

As bird communities were not random, a dendrogram clustering method was used to classify bird assemblages into five groups with functionally similar species (Figure 5.3). These were the following functional groups: A – waterfowl that forage primarily on aquatic and/or riparian macrophytes (e.g. mute swan, mallard [*Anas platyrhynchos*]); B – diving species that forage on submerged aquatic prey (e.g. white-throated dipper, common merganser); C – wader species that forage at riparian margins (e.g. common redshank, common sandpiper); D – reed bed species (e.g. common reed bunting, Eurasian reed warbler) and more terrestrial species (e.g. sedge warbler); and E – riparian insectivores that forage on aerial (e.g. sand martin) or terrestrial insects (e.g. grey wagtail, western yellow wagtail). Both groups B and E largely comprise species typically regarded as riverine specialists.

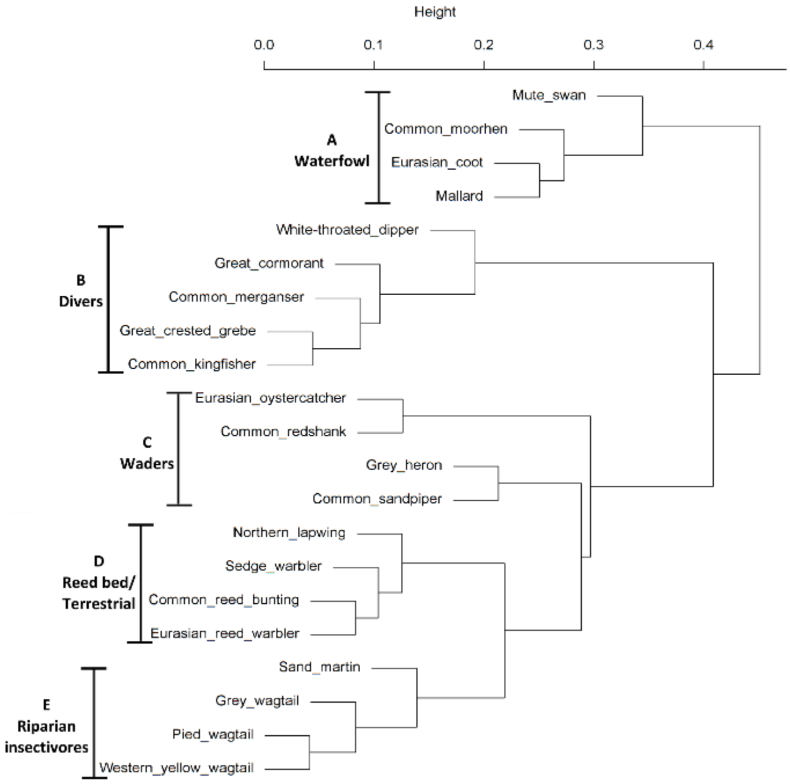


Figure 5.3 *Functional dendrogram describing the functional relationship between 21 river bird species from 101 river locations produced using UPGMA clustering with Gower distances; the tree height refers to the distance linkage between clusters. The position of species within the dendrogram was used to identify five functional groups.*

The percentage composition of each functional group within bird communities was modelled across gradients of the three FD indices (**Table 5.3**; **Figure 5.4**). The percentage composition of reed bed/terrestrial and, to a lesser extent, insectivore species increased significantly as the FRic of bird communities increased. Conversely, the percentage composition of divers and waterfowl decreased. As the FEve of bird communities increased, so did the percentage composition of waders, but the percentage composition of waterfowl decreased. The percentage composition of waterfowl also decreased as FDiv increased, while the percentage composition of insectivores increased with FDiv.

***Table 5.3** Results of the generalized additive models (GAMs) used to examine the association of the percentage contribution (percentage of total number of species) of five functional groups of species with three indices of functional diversity (FD): functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). P values are shown for the smoothed terms; ‘Edf’ is the equivalent degrees of freedom.*

	S(FRic)			S(FEve)			S(FDiv)		
Model term	Edf	*F*	*P* value	Edf	*F*	*P* value	Edf	*F*	*P* value
Divers	5.486	3.732	< 0.001	1.126	1.371	0.238	5.370	1.253	0.273
Insectivores	6.273	1.818	0.077	5.111	0.492	0.822	1.637	15.142	< 0.001
Reed bed/Terrestrial	8.404	4.163	< 0.001	2.810	3.594	0.933	5.738	0.598	0.755
Waders	2.399	1.696	0.166	2.755	4.158	0.004	4.956	1.659	0.127
Waterfowl	5.025	4.293	< 0.001	1	5.236	0.022	3.498	2.324	0.049

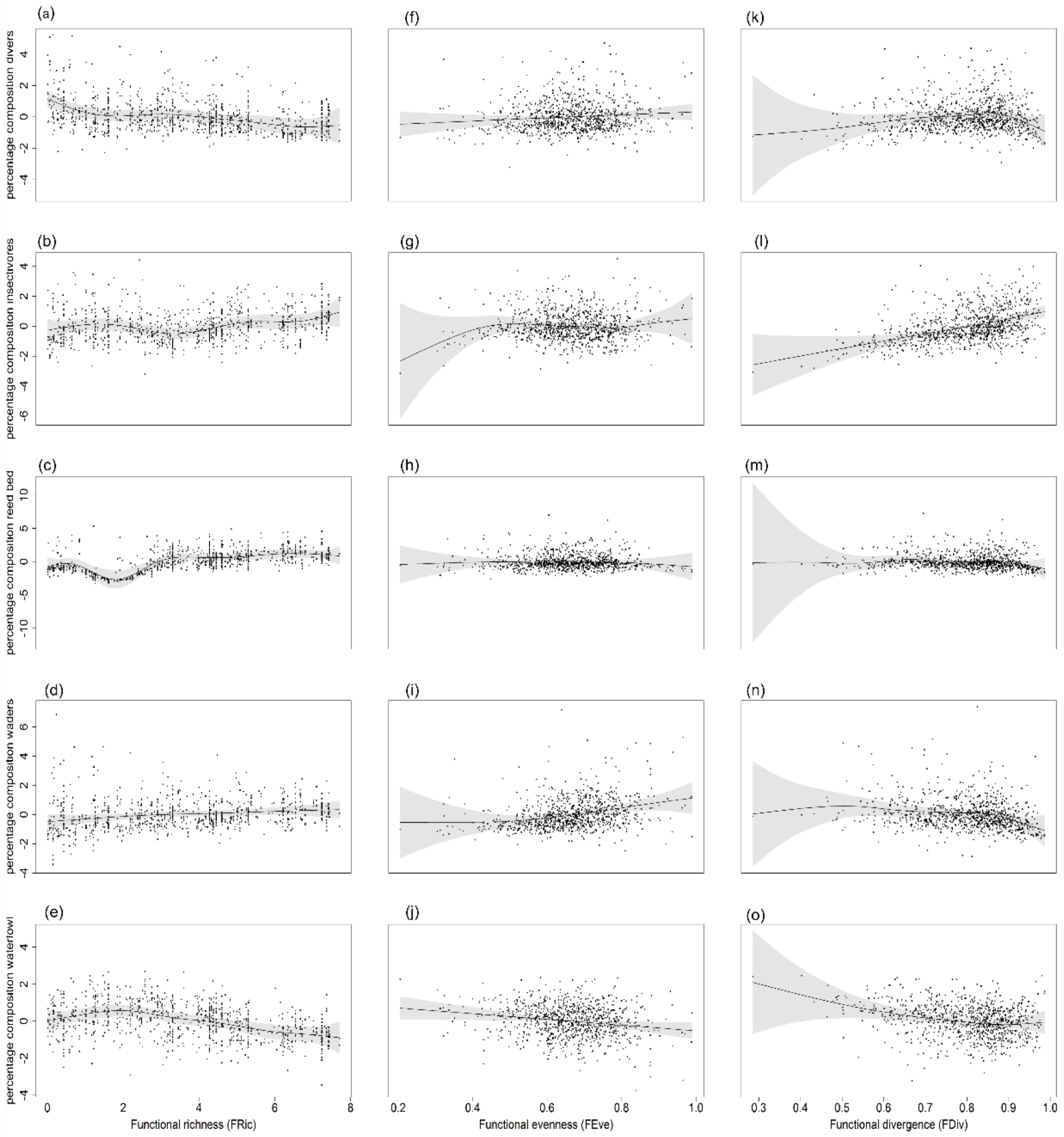


Figure 5.4 *Generalized Additive Model (GAM) partial regression plots showing the relationships between the percentage contributions (percentage of total number of species) of five functional groups of species with three indices of functional diversity (FD): (a-e) functional richness (FRic), (f-j) functional evenness (FEve), and (k-o) functional divergence (FDiv). The shaded regions show the confidence bands for a smoothed FD index term with parametric location and year terms.*

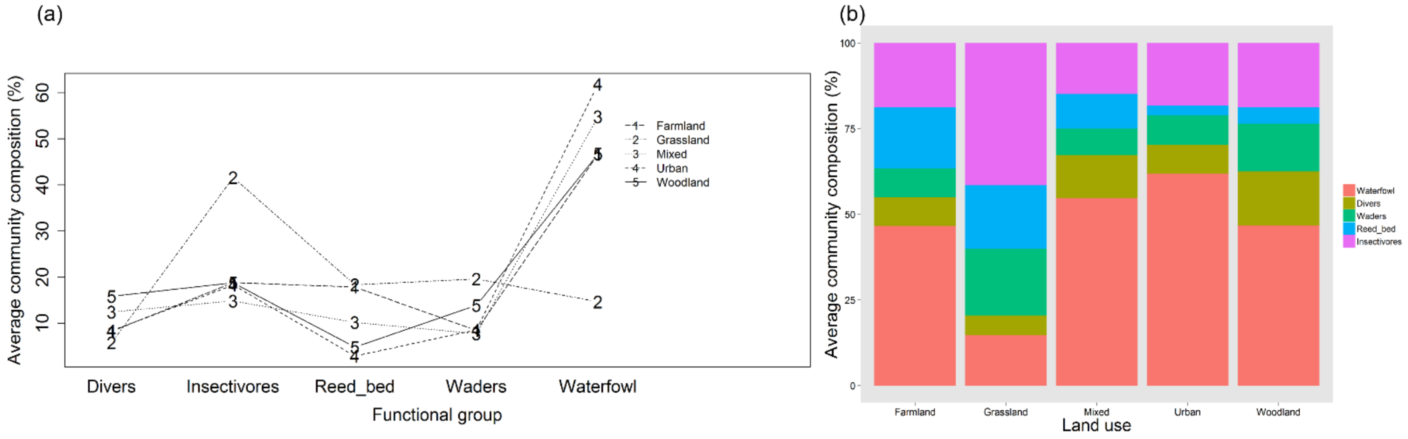


Figure 5.5 *Interaction plot (a) and stacked barchart (b) showing how the average percentage of community composition for five functional groups changes across five land-use categories.*

5.5. Discussion

Evidence suggests that local and regional biotic assemblages are increasing in their functional similarity, with species possessing unique functional traits increasingly lost from assemblages and replaced by wide-ranging habitat generalists (McKinney and Lockwood 1999, Rooney et al. 2007). It is therefore vital to understand the environmental drivers of the ecological structure of communities to determine how rapid global environmental change might alter community assembly processes (Mouchet et al. 2010, Mendez et al. 2012). Here, a quantitative analysis of the environmental processes that structure patterns of functional traits in river bird assemblages was provided. By characterising the spatial and temporal patterns in the distribution of bird functional traits using complementary indices of FD, it was possible to indirectly investigate the environmental processes and assembly mechanisms that determine structural patterns in river bird communities, as well as characterise shifts in the functional composition of bird communities across different land uses and environmental gradients.

5.5.1. Deviation from expectation and community assembly processes

This study initially hypothesised that the FD of bird communities would be typically lower than expected as an indication of low levels of functional redundancy and a strong influence of environmental filtering. In support of this, FD was typically lower than expected, although for the most part measurements of FD did not depart significantly from the range of expectation. Nevertheless, these results corroborate previous research on the FD of UK avian populations (Petchey et al. 2007, Mendez et al. 2012) suggesting that species in bird communities typically display a degree of similarity in functional traits and low levels of functional redundancy. In particular, it was found that FEve was significantly lower than expected in 13.7% of survey years and FDiv significantly higher in 20.3% of survey years. FEve is an indicator of the evenness of functional space within a community and decreases with less regularly spaced species' abundances in trait space (Villéger et al. 2008). FDiv measures the divergence of species' abundances and increases if abundant species are close to the margins of occupied trait space (Villéger et al. 2008). Consequently, species in bird communities were more ecologically similar than expected by chance, as indicated by an uneven spread of species' abundances and for unique traits at the edge of trait space to be more abundant than expected. This suggests that some communities have non-random structural patterns in which certain functional traits are favoured over others and species' abundances are skewed according to possession of these traits. Explaining FD patterns and disentangling the roles of different assembly mechanisms (e.g. environmental filtering and limiting similarity) is challenging as they may operate simultaneously to structure bird communities and their relative contribution may depend upon the spatial scale considered (Lavergne et al. 2010). However, one potential explanation for these patterns is that there is a strong influence of environmental filtering which reduces river bird communities to a subset of the riverine species pool which is dominated by species with traits that most benefit fitness. That FDiv was typically higher than expected and SES FDiv largely departed positively from zero provide further evidence for this as those species at the margins of functional trait space could be expected to experience lower competition due to their divergent trait characteristics.

5.5.2. Functional redundancy and habitat

The FD and SES FD indices displayed strong relationships with some of the land-use and river flow variables, suggesting the level of functional redundancy is dependent on landscape characteristics. SES FRic was typically higher than expected in semi-natural grassland. This provides some support for hypothesis two in suggesting that levels of functional redundancy are greater in more natural habitats; the semi-natural grassland category enveloped a range of natural habitats found in Great Britain, including reed swamp, saltmarsh, machair, water-meadow and grass moor (Table B1). Consequently, a degradation of natural habitats to modified land uses may act as a pervasive environmental filter that causes a reduction in the diversity of functional traits. However, the impact of urban or agricultural land use was of secondary importance to the patterns of the FD and SES FD indices relative to woodland; FRic, FDiv, SES FRic and SES FDiv were lowest and FEve and SES FEve highest in locations surrounded by woodland. These results suggest that in some landscapes, particularly those with a predominance of woodland but also farmland and urban habitats, functional redundancy is higher, as expressed by low functional richness and a rarity of species with unique traits at the edge of trait space. This reinforces the expectation that functional redundancy will be lower at locations with a predominant matrix of natural habitats. This finding is consistent with that of Flynn et al. (2009), who found functional richness to be lower than expected in 25% of bird communities in farmland. Luck et al. (2013) also found functional richness to decrease across a gradient of low to high land-use intensity.

However, evenness in species’ abundances was highest at locations with a prevalence of woodland and grassland habitats. This suggests that in functionally rich or functionally impoverished communities there is less numerical dominance amongst species. One potential explanation for this is that competitive interactions play an increased role in natural habitats (e.g. semi-natural grassland) and in habitats where environmental filtering has reduced the diversity of functional traits (e.g. woodland and farmland), thereby facilitating considerable differentiation between the traits of co-existing species (MacArthur and Levins 1967). Consequently, the importance of different assembly mechanisms may be contingent on the environmental conditions at each specific site and both environmental filtering and competition processes may operate to structure bird communities.

The similarity of species amongst bird communities may be higher in less complex landscapes and habitat heterogeneity is important in the preservation of avian functional diversity (Tscharntke et al. 2008). However, FEve was lowest and FDiv highest in mixed habitat land uses, suggesting that the dominant species were similar in trait value and sat at the outer edges of trait space (i.e. at greater distances from the 'average' functional trait composition). One potential explanation is that the 'mixed' land-use category is dominated by modified land uses such as urban and farmland and so also quantified the degree to which the landscape is fragmented. Additionally, the mixed land-use category was dominated by habitat-generalist waterfowl species (Figure 5.5), some of which (e.g. mute swan and Eurasian coot) may have sat at the outer edges of occupied trait space (Figure B1). This interpretation is supported by Devictor et al. (2008) who found habitat fragmentation to have disproportionate impacts on specialist species. However, the models explaining variation in FEve and FDiv were weak (explaining 17.6% and 18.2% of deviance, respectively) compared to the model for FRic.

5.5.3. River flow and climate as drivers of functional diversity

Variability in river flows increases the complexity of the habitat matrix across the riverine-floodplain interface and creates conditions that promote greater biodiversity (Poff et al. 1997, Bunn and Arthington 2002). As a consequence, it is possible to hypotheses that functional richness, evenness and divergence of bird communities increases with greater variability in river flows. In support of this, FRic increased with variability in river flows, suggesting that a loss of flow variability causes a reduction in the diversity of traits represented in the bird community. Since river flows strongly influence the distribution, abundance, and diversity of river organisms by simultaneously destroying and generating new habitats (Ward et al. 2002), a loss of flow variability may lead to the loss of key foraging habitats and food. A reduction in flow variability can have disproportionate impacts on some bird foraging guilds (Kingsford et al. 2004), including those that forage primarily on exposed aquatic insects in transient habitats (e.g. waders and riparian insectivores) (Jonsson et al. 2012). An increase in FRic with increased variability in river flows may, therefore, indicate that flow variability creates environmental conditions that promote the occupancy of less common species with rarer trait values and unique foraging trait characteristics, such as the common merganser (Figure B1). Such patterns would be supported by an increase in FEve with an increase in river flow variability; however, no significant relationships were observed between this index and the river flow variables.

The degree to which climatic and non-climatic factors (e.g. biotic interactions) influence community structure at different spatial scales is the focus of considerable debate (Araújo and Rozenfeld 2013). This may partly be explained by the fact that the relative contribution of difference environmental and limiting similar processes to community structure is likely to be highly dependent on the spatial scale considered (Lavergne et al. 2010). Relationships between the FD indices and the climate variables were weak and non-significant, suggesting that variation in the structure of river bird communities is better explained by environmental variation acting on community structure and environmental processes at the local scale (linear survey transects ranged from 500 m to 5 km in length). It is therefore plausible that habitat variability, disturbance regimes and food availability structure river bird communities at finer spatial scales, with climatic envelopes becoming more important in determining neighbourhood associations at coarser scales (Börger and Nudds 2014, Kroll et al. 2014).

5.5.4. Contribution of functional groups to communities

Diversity in the responses of species to environmental variation sustains community resilience and is crucial for the re-organisation of communities following disturbances (Elmqvist et al. 2003, Laliberte et al. 2010). Termed ‘response diversity’, this important facet of community assembly can provide insight into functional redundancy by identifying the relationship between groups of functionally similar species and environmental gradients (Laliberte et al. 2010). Spatial variation in the FD of river birds revealed different levels of trait dispersion amongst communities and differences in the resilience of species to shifts in the environmental drivers of community structure.

The contribution (percentage of total number of species) of reed bed/terrestrial species (e.g. common reed bunting, sedge warbler) and riverine-specialist riparian insectivores (e.g. grey wagtail, western yellow wagtail) increased with the FRic of bird communities. This suggests that these species possess a number of unique foraging traits that increase the volume of trait space occupied by a community. However, the contribution of waterfowl (e.g. common moorhen, Eurasian coot, mute swan) was greatest in bird communities characterised by lower measures of functional richness, evenness and divergence. Consequently, these species tend to dominate river bird communities with low SR and a concentration of less divergent traits. The contribution of insectivore and reed bed species was also highly dependent on the availability of natural semi-natural grassland habitat (note reed bed is a sub-category of natural semi-natural grassland) (Table B1), whereas waterfowl dominated bird communities surrounded by all other land uses, but especially urban land uses. The loss of functionally specialist species from more modified land uses (e.g. urban) and an increased dominance of habitat generalists is consistent with hypothesis four: ‘functional homogenisation’ (Olden and Rooney 2006). It is likely that functionally unique species which have specific requirements are most vulnerable to changes in landscape structure, such as habitat loss, because they cannot utilise food resources from the modified food production matrix (Jonsson et al. 2012, Robertson et al. 2013).

The observation that particular foraging guilds of birds can decline disproportionately in response to shifts in certain land uses and environmental gradients conflicts with Luck et al. (2013) but concurs with Flynn et al. (2009), who found waterfowl and raptors most likely to be excluded from agricultural habitats, possibly because of a decline in the prey base caused by grassland improvement (Butet and Leroux 2001, Barnett et al. 2004). This has conservation implications for bird communities in highly modified landscapes as the alteration of natural habitats could result in a degradation of the FD of assemblages and an associated shift towards dominance by species with common traits. The relationship between FRic and river flow also suggests that bird communities on highly regulated rivers where flow regimes are closely controlled, which typically dampens seasonal and inter-annual flow variability (Poff et al. 2007), may lose functionally unique species, such as white-throated dipper (Chiu et al. 2008), with specific foraging techniques that allow them to occupy disturbed heterogeneous landscapes. Such an impact could occur through a decline in food resource availability caused by a simplification of aquatic-terrestrial linkages and a decline in aquatic insect emergence

(Jonsson et al. 2012), as well as the loss of shallow water and riparian margin habitats (Cumming et al. 2012, Royan et al. 2013).

5.5.5. Methodological considerations

A major challenge in understanding patterns in FD is the choice of metrics to quantify FD (Luck et al. 2013). The suite of FD indices used here was developed by Villéger et al. (2008) and selected because, when compared to alternative statistics, they performed best in measuring their respective aspects of FD (Mouchet et al. 2010). The FRic index was used as it has high power to detect assembly rules, particularly for communities smaller than 30 species (Mouchet et al. 2010) but the dendrogram-based functional richness index of Petchey and Gaston (2002) was discarded as it was more influenced by SR ($R > 0.9$). Nevertheless, both indices were strongly correlated ($R = 0.86$), suggesting that each index would have produced comparable results. FRic itself can be inflated by rare species with extreme trait values. However, rare species were retained in the trait matrix as they can have disproportionately high influence on the functional characteristics of a community (O'Gorman et al. 2011). FD indices were also weighted by species' abundances. Because interspecific variation in local abundances will vary systematically with the prevalence of the traits considered, the number of individuals possessing a particular trait may be more important than the number of species when assessing community contribution to ecosystem function and resilience to environmental change (Newbold et al. 2012). In addition, the inclusion of abundance information increases the slope of the relationship between SR and FD, which decreases the likelihood for simulated FD values to be lower than observed FD values and so increases confidence in inferences of habitat filtering (Calba et al. 2014). The suite of FD indices used here might also be complemented by further analysis using a parameter that quantifies phylogenetic diversity – the amount of evolutionary history represented in the species of a particular community (Mouquet et al. 2012). Phylogenetic diversity may display markedly different relationships to SR compared to that between FD and SR (Calba et al. 2014). Consequently, phylogenetic diversity may therefore provide additional information on how evolutionary processes create complex trait patterns.

The likelihood for simulated FD to be lower than expected is also affected by the choice of null model randomisation procedure (Calba et al. 2014). Here, a matrix-swap randomisation procedure was adopted in which species were drawn randomly from the species' list and replaced with an abundance from the list of abundances for that species at the particular site (Pakeman 2011). The relative rarity or commonness of species was therefore perturbed but species' diversity is maintained. Alternative approaches would have been to draw species from a regional or even national species pool; however, by not preserving local-scale habitat filters, these methods allow the co-existence of species with markedly different traits, which can lead to high simulated FD values (Calba et al. 2014). Moreover, given that the environmental variables in this study were calculated at the local scale, it was appropriate to use the local regional species pool to define patterns of rarity and commonness.

A further methodological consideration is the choice of traits used to quantify FD. The number of traits, as well as correlations between traits, is important as this will affect the dimensionality of trait space (Petchey and Gaston 2002) and the relationship between FD and SR (Calba et al. 2014). It is, therefore, necessary to focus on functionally important traits. Traits that are widely recognised as characterising foraging behaviour and resource use were identified *a priori*, as they provide insight into how species' behaviours respond to environmental change (Mendez et al. 2012, Ding et al. 2013, Luck et al. 2013). Ideally, the significance of each trait should be tested through experimentation; however, the logistical challenges presented by in-field testing of several traits across multiple communities restrict trait selection to informed *a priori* decisions (Petchey and Gaston 2002).

Here, changes in FRic were approximately proportional to changes in SR. This is to be expected as the addition of new species will bring functionally new or uncommon traits, causing phylogenetic differences to accumulate and the amount of trait space occupied to increase (Calba et al. 2014). Where SR is greater, the FD of communities will tend towards saturation with the addition of new species. Functional redundancy, therefore, appears to be relatively low in avian riparian communities and the selection of traits introduced an effective number of trait dimensions to investigate functional redundancy effectively (Petchey and Gaston 2002). However, only a small number of FRic values were significantly different from expected. Due to its positive association with SR, patterns in FRic may partly be the product of species-area relationships and so are also representative of the diversity of the local species pool (Petchey et al. 2007).

5.5.6. Conclusions

This study has highlighted the importance of traits in the structuring of riverine bird communities. Communities differed from what would be expected if assemblages were just random sets of species, revealing the operation of different assembly mechanisms. Shifts in the magnitude of importance of these mechanisms were observed across different habitat landscapes. These results are consistent with a strong influence of environmental filtering on bird populations, although different assembly mechanisms may interact where particular environmental conditions occur. In particular, this study emphasises the crucial role of natural habitats and variability in river flows for sustaining functionally rich river bird assemblages. A loss of variability in land cover and flow disturbance was characterised by a decline in functionally unique or specialist species (e.g. insectivores) and an increased dominance of species with common traits (e.g. waterfowl). Alterations to natural riparian habitats and river flow regimes through anthropogenic regulation or climate change may, therefore, have profound impacts on river bird communities.

In this chapter, a quantitative analysis of the environmental processes that structure spatial patterns of functional traits in river bird assemblages was provided. The environmental processes and assembly mechanisms that determine structural patterns in river bird communities and shifts in the functional composition of bird communities across environmental gradients were revealed. Now, through the development of a species vulnerability index (SVI), Chapter Six will aim to identify the river bird species most vulnerable to climate change-induced alterations in the variability of high (flood) and low (drought) river flows.

6. River birds’ response to hydrological extremes: new vulnerability index and conservation implications

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6.1. Abstract

There is growing evidence that as a consequence of climate change the frequency of extreme hydrological events will increase. Predicting the impacts of these extreme events on ecological systems is a major research challenge. It is predicted that change in future river flows, characterised by greater occurrence of floods and droughts, will have profound impacts on aquatic invertebrate communities by removing sensitive species and restructuring food networks. However, it remains unclear how an increase in these hydrological extremes will impact riparian communities and species at higher trophic levels. Here, a new method that facilitates the integration of quantitative outputs of species’ distribution models with the expert knowledge of conservation practitioners to produce a species’ vulnerability index (SVI) is described. Using the SVI framework, the vulnerability of 16 river bird species to a potential climate-induced shift in the frequency, duration and magnitude of flood and drought events is assessed and ranked. Vulnerability was associated primarily with ecological traits that restrict species to in-channel riverine habitat. Whilst the SVI was developed to assess species’ vulnerability to hydrological extremes on rivers, it is equally applicable to other environmental

domains as well as a range of avian and non-avian taxa. Furthermore, this original methodological approach provides researchers and managers with a valuable conservation tool that allows them to identify the species most vulnerable to climate change impacts and plan mitigation and adaptation strategies.

6.2. Introduction

There is increasingly robust evidence that global warming and the associated increase in climatic variability will lead to more extreme climatic events (Min et al. 2011, Hansen et al. 2012, Seneviratne et al. 2014). Given their potentially profound impacts, understanding the role of extremes in shaping ecological systems has gained increasing importance and momentum (Smith 2011b, a). Climate change is predicted to result in the intensification of key processes in the water cycle such as precipitation, evaporation and runoff (Durack et al. 2012). As river flows are coupled closely to atmospheric drivers (Laizé and Hannah 2010), shifts in the distribution of precipitation will result in modified hydrological regimes characterised by increasing trends in the frequency, duration and magnitude of hydrological extremes, including floods and droughts (Pall et al. 2011, Prudhomme et al. 2013).

River flow is regarded as the ‘master variable’ (Power et al. 1995) in riverine environments as flow not only structures physical habitats (e.g. channel width and stability), but also determines the physicochemical properties (e.g. water temperature, dissolved oxygen concentrations) of in-channel habitats which, in turn, regulate a range of environmental processes (e.g. production, nutrient retention) (Ward et al. 2002). Subtle changes in the spatio-temporal heterogeneity of river flows can determine the distribution and abundance of certain taxa (e.g. aquatic invertebrates, fish) (Bunn and Arthington 2002), while extreme high and low flows can exclude sensitive species and restructure food webs by simplifying the network architecture and reducing species' richness at higher trophic levels (Ledger et al. 2012). Thus, an increase in climate-induced hydrological extremes is likely to have dramatic impacts on riverine biodiversity. Yet, incorporating extreme events into the experimental design of ecological studies remains a considerable challenge (Thompson et al. 2013).

Variability in river flows influences the spatio-temporal distribution of riparian consumers such as river birds (Royan et al. 2013). Flooding influences the habitat occupancy (Reiley et al. 2013), abundance (Chiu et al. 2008), breeding success (Strasevicius et al. 2013), breeding timing (Arthur et al. 2012), and survival (Chiu et al. 2013) of river birds. Moreover, changes in the quality of foraging habitat can determine the timing of foraging activities (Cumming et al. 2012). The maintenance of unregulated (near-natural) riverine hydrological variability, including the occurrence of flooding and drought events, can be beneficial to river birds, with both diversity and abundance declining on rivers where anthropogenically-regulated, stable flow regimes exist (Kingsford et al. 2004). The impact of river regulation can be highest for those bird species (e.g. European pied flycatchers [*Ficedula hypoleuca*]) adapted to feeding on emergent aquatic invertebrates (Jonsson et al. 2012, Strasevicius et al. 2013). However, extreme flow events can also have dramatic negative impacts on river-obligate birds through marked shifts in surface flows (Hinojosa-Huerta et al. 2013).

Understanding of the vulnerability of river bird communities to hydrological extremes is limited because of a failure to focus on multiple species' responses to a range of hydrological extremes across large geographical areas. This may partly be explained by the low probability of occurrence of hydrological extremes but also by the lack of conceptual frameworks for studying extremes, given that the description of an event as "extreme" is catchment-specific and depends on previous flow conditions (Smith 2011b, a). Consequently, a study of this type may be best achieved using long-term, large-scale, multi-species data as these will facilitate the investigation of species' ecological responses to hydrological parameters across a range of 'extremes' (e.g. statistical quantiles) and across a range of ecosystems which vary in their sensitivity to hydrological extremes.

Two tools used regularly to evaluate the effects of climate change on biodiversity are: (1) species' distribution models (SDMs), which relate data on species' occurrence (Jones et al. 2013) or abundance (Renwick et al. 2012) to environmental drivers, and (2) assessments of species' sensitivity and exposure to climate change effects to determine the vulnerability of species to climate change (Davison et al. 2012). Aspects of both of these approaches were combined to produce a species' vulnerability index (SVI) for assessing the ecological effects of hydrological extremes. River bird data from the WBBS were combined with mean daily river flow data from the NRFA to investigate the vulnerability of 16 river bird species to a potential climate-induced increase in the frequency, duration and magnitude of hydrological extremes (floods and droughts) across 117 river locations. The IPCC (2012) define an "extreme" as being a statistically rare event (i.e. events outside a defined percentile under current climate conditions). This was adopted here to investigate the relationship between species' abundance and flow parameters measured across a range of extremes (e.g. 95th, 90th and 75th percentiles for low flows and 5th, 10th and 25th percentiles for high flows).

Vulnerability to climate change impacts is comprised of two separate facets: sensitivity and exposure (Williams et al. 2008b). Sensitivity is mediated by the resilience and adaptive capacity of the species, as determined by factors such as specific ecological traits (Williams et al. 2008b). Exposure depends on the degree of buffering offered by species' occupied habitat and species' behaviour that reduce future exposure to the specific climate effects (Williams et al. 2008b). Following the methodology of other SVIs (Furness and Tasker 2000, Garthe and

Huppop 2004, Williams et al. 2008a, Furness et al. 2012), exposure scores were created by providing relative numerical scores to a set of key qualitative questions. These scores were then combined with quantitative outputs from an ensemble of SDMs to provide a framework for assessing species' vulnerability. SVIs offer researchers and managers a valuable conservation tool that allows them to identify priority species for conservation action (Davison et al. 2012).

The specific objectives of this study were to:

1. identify species of river birds most sensitive to changes in high (flood) and low (drought) river flows;
2. combine quantitative analyses of species' sensitivity with assessments of species' exposure to a potential future increase in hydrological extremes in order to develop an index of species' vulnerability;
3. identify priority riverine locations that support greater abundances of species of high vulnerability.

6.3. Methods

6.3.1. Data

River bird data were obtained from the BTO's WBBS. To determine the response variable (relative abundance), species' counts were pooled across all transects in the sample year and either the sum of counts for the first or second visit were then used depending on which was higher. This count was then divided by the number of transects to ensure that that variability in abundance was not confounded by heterogeneity in sampling effort.

The procedure used to select WBBS survey locations for analyses was as follows. Survey locations with a minimum of four repeated visits were selected as datasets that involve multiple visits to sample sites provide more reasonable estimations of species' occupancy and abundance by reducing bias associated with detection probability (Royle and Nichols 2003). Survey data between 1998 and 2011 (inclusive) were used but data from 2001 were excluded as few sites were surveyed due to the foot-and-mouth outbreak when access to rural areas was restricted by the UK Government. Lastly, survey locations were selected where a species was recorded in at least 80% of survey years. This reduced the likelihood of including sites that had been newly colonised or sites where populations were extirpated during the survey time series in the analyses (Oliver et al. 2012). This final criterion also served to remove false zeros, caused by sampling outside species' habitat range, from datasets as well as limiting overdispersion and associated model parameter and standard error bias (Zuur et al. 2012). In total, 117 WBBS survey locations were used (Figure 6.1), although the number of sites varied between species.

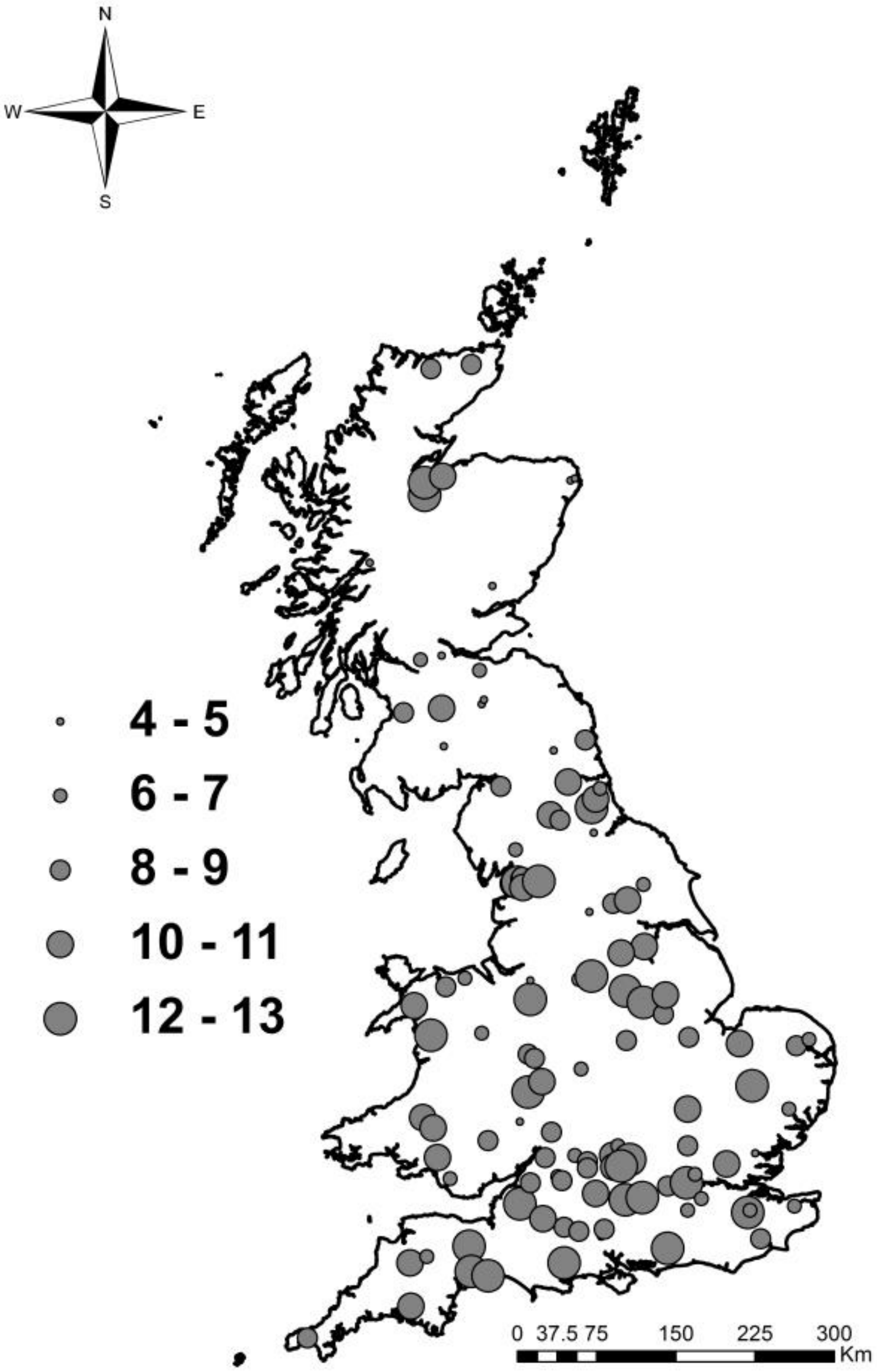

Figure 6.1 *Distribution of the 117 Waterways Breeding Bird Survey (WBBS) locations across Great Britain. Circles illustrate differences in sampling effort (total number of visits to survey locations).*

The hydrological year in Great Britain runs from October to September (Bower et al. 2004) and bird data were paired with hydrological data from the associated hydrological year (e.g. bird data from spring 2010 were paired with hydrological indices calculated from daily flow data between 1st October 2009 and 30th September 2010). This meant flow variability was measured before, during and after the breeding seasons of focal avian taxa. This was preferable to calculating flow variables from a snapshot of the flow data (e.g. during the respective species' breeding seasons) as it allowed species' abundances to be related to long-term flow variability and its impact on the fluvial processes that create river habitats. See Figure 6. 2 for four example hydrographs.

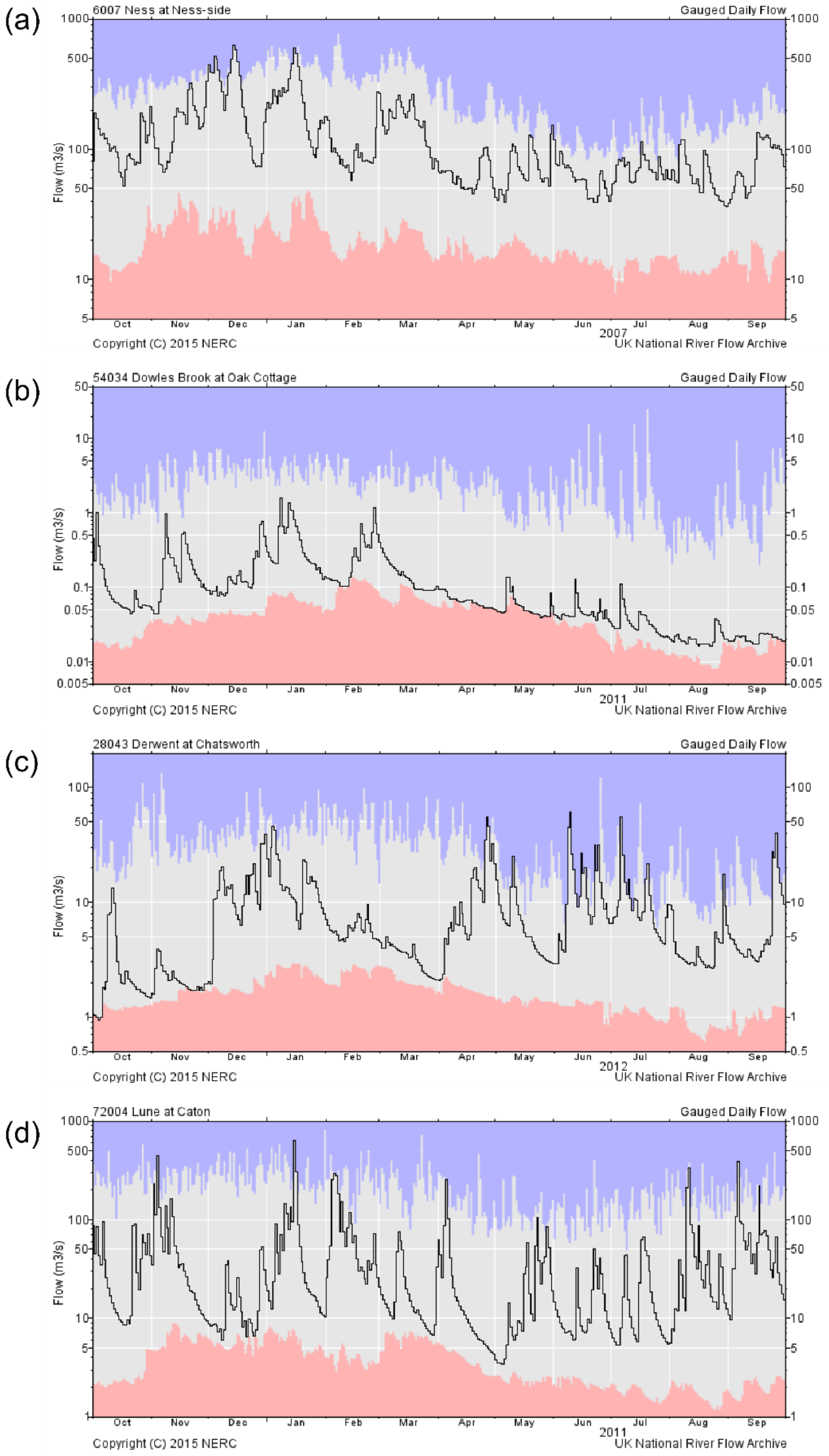

Figure 6. 2 *Hydrographs for gauging locations with (a) a high frequency of high flows (River Ness, 2007), (b) a low frequency of low flows (Dowless Brook, 2011), (c) a high frequency of low flows (River Derwent, 2012), and (d) a low frequency of low flows (River Lune, 2011). Copyright NERC.*

6.3.2. Modelling Approach

To provide a quantitative measure of the sensitivity of river birds to hydrological conditions for 16 river bird species, the relationship between species' relative abundance and a range of hydrological parameters that quantify the three important facets of river flow variability (flow frequency, duration and magnitude) (Monk et al. 2007) for high (flood) and low (drought) flow conditions (**Table 6.1**) was modelled. As significant collinearity existed between these flow parameters (typically Rs > 0.7), each parameter was modelled independently, resulting in an ensemble of 14 independent models for each species.

***Table 6.1** Hydrological parameters used to characterise the main facets of flow regimes (frequency, duration and magnitude) in species distribution models for 16 river bird species. Frequency and duration were characterised across a range of extremes defined using statistical percentiles (e.g. Q1 = 1^{st} percentile).*

Flow condition	Hydrological parameter
High flows	
Frequency	Number of flow events > Q1, Q10, Q25
Duration	Number of consecutive flow days > Q1, Q10, Q25
Magnitude	Maximum flow value/Q50
Low flows	
Frequency	Number of flow events < Q99, Q90, Q75
Duration	Number of consecutive flow days < Q99, Q90, Q75
Magnitude	Minimum flow value/Q50

The hierarchical nature of the WBBS dataset, involving repeated visits to the survey location, represents a considerable statistical challenge due to the lack of temporal independence between species' counts. Individual survey years will not contribute an entire degree of freedom to the analysis and conventional regression techniques under-estimate the variance and standard errors (Vaughan et al. 2007). Generalized Estimating Equations (GEEs) (Liang and Zeger 1986) were used to correct for this. GEEs accommodate correlated data by treating inter-cluster correlation as a problem parameter and by adjusting the confidence limits around regression parameters (Liang and Zeger 1986). GEEs utilise a marginal model approach and, thus, model the expectation of the dependent variable as a function of the covariates by adjusting the covariance matrix of the estimated parameters to account for non-independence (Liang and Zeger 1986). The marginal model approach is ideally suited to this study as it accounts for collinearity in inter-annual river flow variability (Bower et al. 2004), which is considered as a 'nuisance parameter' that introduces undesirable noise into the dataset.

Models were fitted in version 1.1-6 of ‘geepack’ (Halekoh et al. 2006) in the statistical package R, specifying a Poisson error structure and a logarithmic link function. A fully iterated jackknife variance estimator was used as the number of survey locations in the datasets was small (i.e. < 30) (Halekoh et al. 2006), thereby reducing error in parameter estimation. As the inter-year correlation could be expected to decrease as time increases (Zorn 2001), a first order autoregressive correlation structure was applied to all models. Where appropriate, square-root and logarithmic transformations were applied to parameters to satisfy assumptions of linearity.

6.3.3. Sensitivity Scoring

For each independent model relating species’ relative abundance to the flow parameters, the Wald statistic (z^2) was extracted and a Bayesian Information Criterion (BIC) value was calculated using the following equation (Raftery 1995):

$$BIC = z^2 – \log(n)$$

(Equation 6.1)

where n = number of clusters (i.e. survey locations) and BIC values signify: no evidence to reject the null hypothesis (< 0); a ‘weak relationship’ (0–2); a ‘positive relationship’ (2–6); and a ‘strong relationship’ (> 6). Each BIC value was assigned a sensitivity score as follows:

$BIC = 0 – 2$

$BIC = 2.01 – 6.0$

$BIC > 6.0$

As the frequency and distribution parameters were measured across a range of statistical extremes (Table 6.1), the sensitivity scores assigned to these parameters were corrected to account for the parameter's likelihood of occurrence. This was achieved by dividing the sensitivity scores by the deviation from the mean, given a normal probability distribution, of the quantile associated with the parameter (i.e. sensitivity scores for: Q1 and Q99 parameters divided by 2.33 standard deviations [SDs]; Q10 and Q90 parameters divided by 1.28 SDs; and for Q25 and Q75 parameters divided by 0.67 SDs). Total sensitivity scores were calculated for high (Shigh) and low (Slow) flow conditions by summing the sensitivity scores for all parameters that quantify either high or low flow conditions, respectively. A total sensitivity score to a change in all flow conditions (Stotal) was also calculated by summing sensitivity scores for both high and low flow conditions.

6.3.4. Exposure Factors

Four factors were derived from species' traits which all provided measures of species' relative exposure to climate change-driven flow alterations (**Table 6.2**). For instance, a species may be buffered from the full magnitude of flow alterations if it has little association with aquatic habitats for foraging or breeding and occurs across a broad range of habitats, if it has a broad foraging niche that enables it to take advantage of the increase in r-selected species that follows disturbance events (Ledger et al. 2012), or if it is highly dispersive and is at reduced risk of flow-induced mortality (O'Callaghan et al. 2013). All four factors were arranged on an exposure scale of 1 (i.e. low) to 3 (i.e. high) according to criteria detailed in **Table 6.2**. Initial factor scores were generated using comprehensive data published in del Hoyo et al. (1992-

2013) and Cramp and Simmons (1977-1996), and were then independently moderated using the Delphi technique whereby scores were evaluated by a panel of six experts (expert profiles and scoring are in the appendices: Table C3) chosen according to their experience. When systematic and quantitative data are not readily available or easily applied to a methodological framework, this method has been favoured in many ecological studies (Furness and Tasker 2000, Garthe and Huppop 2004, Davison et al. 2012, Furness et al. 2012). Changes to the scores were made where three or more members of the panel suggested adjustments to the original scoring.

Table 6.2 *Criteria used to assign scores to exposure scores for four factors.*

Exposure factor	Exposure score		
	1	2	3
Foraging habitat (A)	Tend to forage across a variety of aquatic, marine or terrestrial habitats with little association with specific aquatic/riparian habitats	Tend to forage in aquatic or riparian habitats	Tend to forage in specific aquatic habitats
Breeding habitat (B)	Tend to breed across a variety of aquatic, marine or terrestrial habitats with little association with specific aquatic/riparian habitats	Tend to breed in aquatic or riparian habitats	Tend to breed in specific aquatic habitats
Food specialisation (C)	Tend to forage across a variety of aquatic, marine or terrestrial habitats with little association with specific aquatic/riparian habitats	Tend to forage on aquatic taxa or taxa on marginal aquatic habitats such as gravel beds or mudflats	Tend to forage on aquatic taxa (e.g. fish, aquatic invertebrates and macrophytes)
Dispersal potential (D)	Nomadic or migratory	Non-migratory but can move large distances between habitat patches	Non-migratory, largely sedentary species with relatively small home ranges

6.3.5. Vulnerability Index

An index for species' vulnerability to high flows (VIhigh), low flows (VIlow) and a change in all flow conditions (VItotal) was created adapting a methodology similar to that of Garthe and Huppop (2004). First, the natural logarithm of the species' total sensitivity score (Stotal), adding 1 to avoid undefined values, was multiplied by the average score for the four factors A to D. Each individual species' VItotal score was then expressed as a percentage of the maximum (11.49) and then divided into designated categories of vulnerability that ranged from low vulnerability to very high vulnerability. This yielded the following equation:

$$VI = \sum_{species}(\ln(S_{total}+1)*((\frac{A*B*C*D}{4})))$$

(Equation 6.2)

6.3.6. Species' vulnerability maps

Priority areas for species placed in the very high and high vulnerability categories were identified by plotting the relative abundances of species across Great Britain using 509 WBBS survey locations. A surface of abundances was created using kriging, specifying a Gaussian semi-variogram structure. Kriging assigns values to un-surveyed locations using a weighted moving average technique, with the statistical relationship between spatially correlated points specified using the semi-variogram model (de Smith et al. 2013).

6.4. Results

6.4.1. Sensitivity scoring

Total sensitivity (S_{total}) ranged from 0 (grey heron) to 16.6 (common sandpiper), with high scores also for common merganser and mute swan (**Table 6.3**; **Figure 6.3**). The species that exhibited the most sensitivity to high flows (S_{high}) and low flows (S_{low}) were common merganser, common sandpiper and mute swan (Table 6.3).

Species displayed very different responses to the hydrological parameters. It is indicated in the appendices (Table C1) where a specific increase in either the variability of high or low flows resulted in either a positive or negative shift in species' relative abundances. Some species displayed a positive relationship around either high or low flows. Typically, however, this was tempered by an aversion to an increase in variability at the other end of the flow spectrum. For instance, common sandpiper, great cormorant, mute swan, common reed bunting and Eurasian reed warbler all showed an affinity to variability in low flows but an aversion to variability in high flows. However, some species showed an aversion to variability in both high and low flows (e.g. great crested grebe and sand martin).

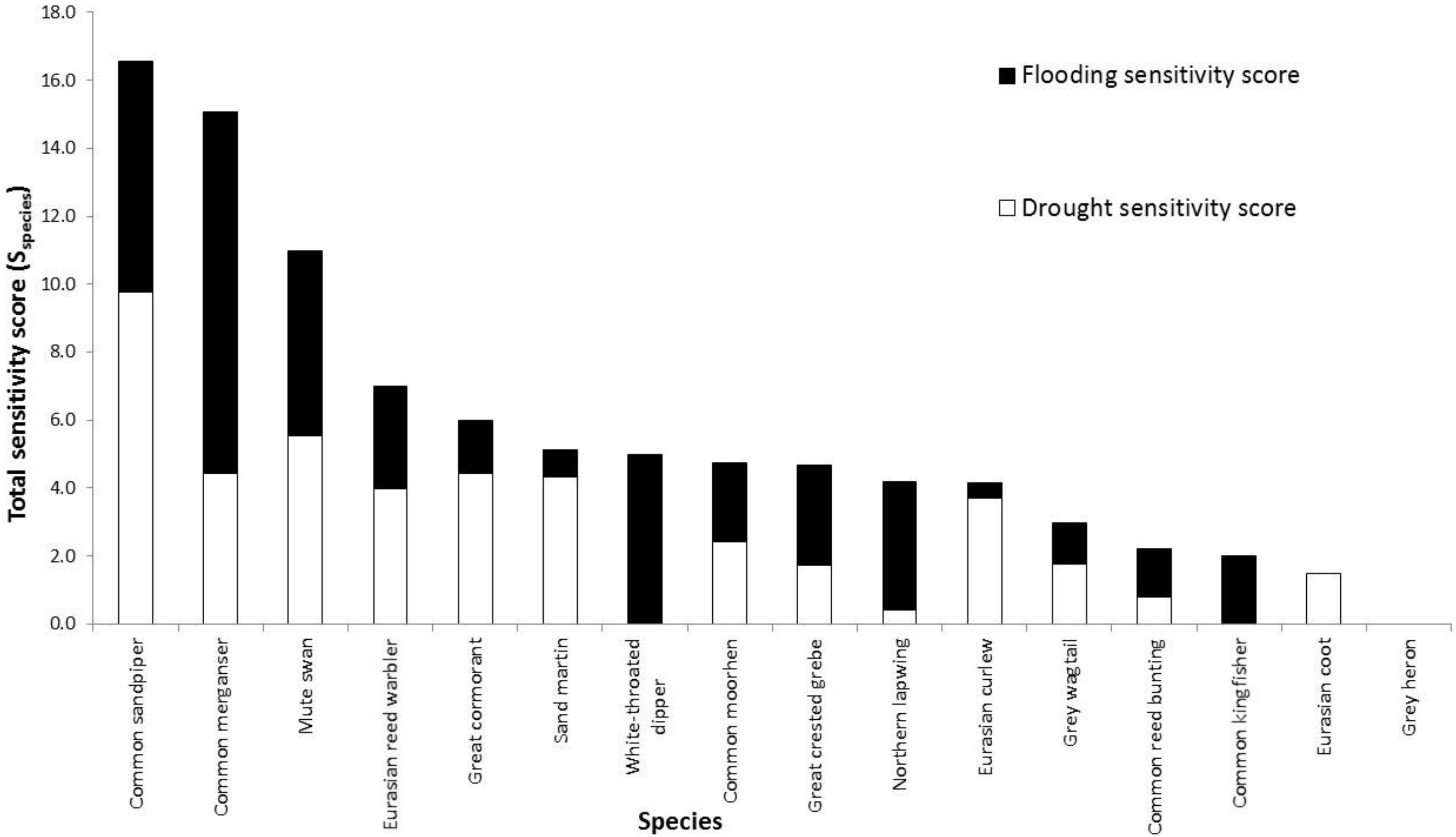

Figure 6.3 *Plot showing total sensitivity scores (Stotal) for 16 species and the contribution to this by sensitivity to floods (Shigh) and droughts (Slow).*

Table 6.3 *Species vulnerability index to a shift in flood and drought flow conditions for 16 river bird species.*

Species	Locations	S_{high}	S_{low}	S_{total}	Foraging habitat	Breeding habitat	Food specialisation	Dispersal	$Exposure_{total}$	VI_{low}	VI_{high}	VI_{total}	$\%VI_{total}$	Vulnerability
Common merganser *Mergus merganser*	15	10.6	4.4	15	3	1	3	2	9	5.5	3.8	6.2	54.4	**Very high**
White-throated dipper *Cinclus cinclus*	28	5	0	5	3	3	3	3	12	5.4	0	5.4	46.7	**High**
Common sandpiper *Actitis hypoleucos*	12	6.8	9.8	16.6	2	2	2	1	7	3.6	4.2	5	43.6	**High**
Mute swan *Cygnus olor*	51	5.4	5.5	10.9	2	2	2	2	8	3.7	3.8	5	43.2	**High**
Great crested grebe *Podiceps cristatus*	10	3	1.7	4.7	3	3	3	2	11	3.8	2.8	4.8	41.6	**High**
Great cormorant *Phalacrocorax carbo*	18	1.6	4.4	6	3	1	3	2	9	2.1	3.8	4.4	38.1	**Moderate**
Eurasian reed warbler *Acrocephalus scirpaceus*	16	3	4	7	2	3	2	1	8	2.8	3.2	4.2	36.2	**Moderate**
Common moorhen *Gallinula chloropus*	64	2.3	2.4	4.7	1	2	1	3	7	2.1	2.2	3.1	26.7	**Moderate**
Common kingfisher *Alcedo atthis*	18	2	0	2	3	2	3	3	11	3	0	3	26.3	**Moderate**
Grey wagtail *Motacilla cinerea*	44	1.2	1.8	3	2	2	2	2	8	1.6	2	2.8	24.1	**Moderate**
Sand martin *Riparia riparia*	13	0.8	4.3	5.1	2	2	1	1	6	0.9	2.5	2.7	23.6	**Moderate**
Common reed bunting *Emberiza schoeniclus*	39	1.4	0.8	2.2	1	2	1	3	7	1.6	1	2	17.8	**Low**
Eurasian curlew *Numenius arquata*	21	0.4	3.7	4.1	1	1	1	1	4	0.4	1.6	1.6	14.3	**Low**
Northern lapwing *Vanellus vanellus*	21	3.7	0.4	4.1	1	1	1	1	4	1.6	0.4	1.6	14.3	**Low**
Eurasian coot *Fulica atra*	25	0	1.5	1.5	2	2	1	2	7	0	1.6	1.6	13.9	**Low**
Grey heron *Ardea cinerea*	65	0	0	0	1	1	3	2	7	0	0	0	0	**Low**

Vulnerability was described according to $\%VI_{total}$: 0 > 19.9 – Low; 20.0 - 39.9 – Moderate ; 40.0 - 49.9 – High: ≥ 50 – Very high.

6.4.2. Exposure and vulnerability scoring

The species judged to have the highest exposure to shifts in river flow ($\text{Exposure}_{\text{total}}$) were white-throated dipper, common kingfisher and great crested grebe, while common merganser and cormorant also scored highly (Table 6.3). The species exhibiting the lowest exposure were Eurasian curlew (*Numenius arquata*) and northern lapwing.

The species with the overall highest total vulnerability (VItotal) was common merganser, solely occupying the very high vulnerability category, with white-throated dipper, common sandpiper, mute swan and great crested grebe were categorised as having high vulnerability (Table 6.3). The least vulnerable species was grey heron. The species with the highest vulnerability to flooding (VIhigh) were common merganser and white-throated dipper and the species with the highest vulnerability to drought (VIlow) were common sandpiper, cormorant, common merganser and mute swan (Table 6.3).

6.4.3. Species' vulnerability maps

Priority regions for very high and high vulnerability species were identified by mapping species' abundances across Great Britain (**Figure 6.4**). Relative abundances of common merganser, white-throated dipper and common sandpiper were highest at riverine locations in upland regions of northern England, southern and northern Scotland and Wales, whereas those of mute swan and great crested grebe were highest at lowland riverine locations in south-east England.

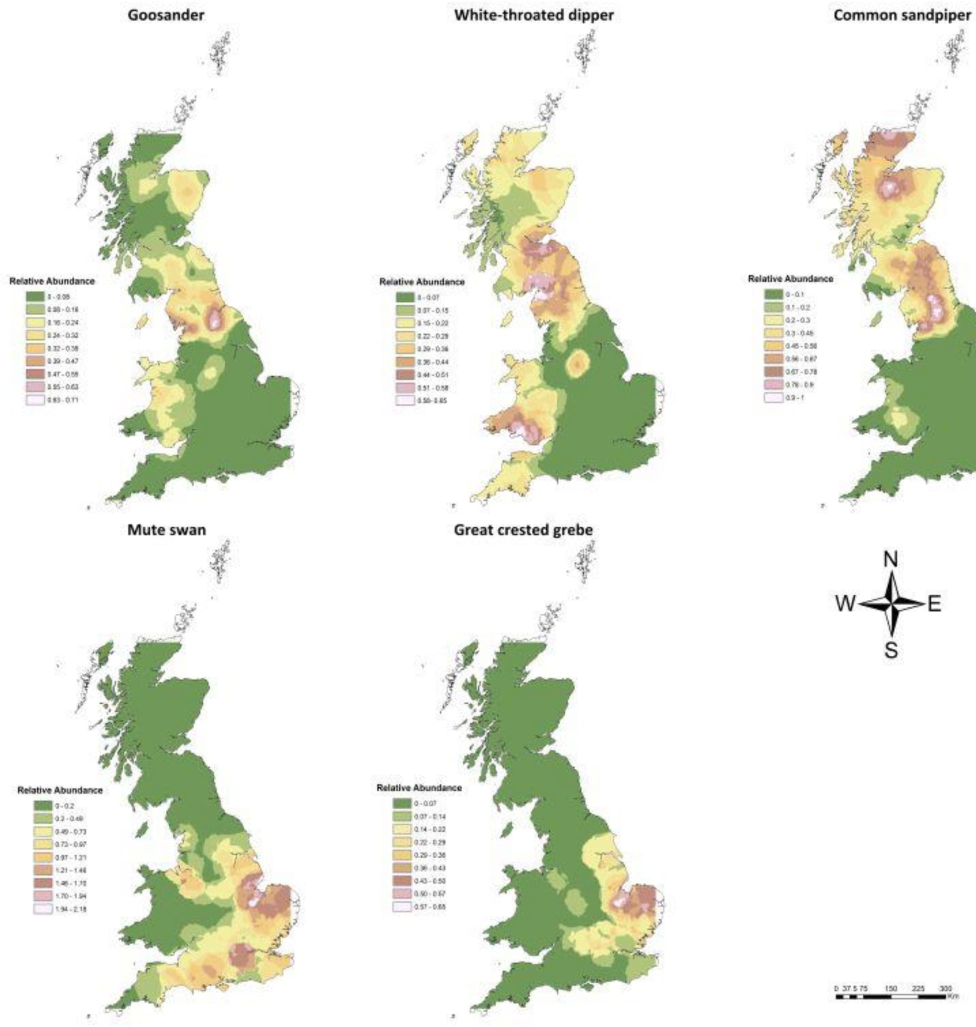

Figure 6.4 *Variation in the relative abundances of species identified as of very high and high vulnerability by the SVI (see* ***Table 6.3*** *for further details) across Great Britain. Relative abundance was calculated as total counts divided by survey effort.*

6.5. Discussion

Ecologists have started to examine how climate extremes shape ecosystems (Smith 2011b, a). This has been driven by an expectation that climate change will increase the intensity of extremes events (Min et al. 2011, Hansen et al. 2012, Seneviratne et al. 2014). Changes in climate extremes will have profound impacts on aquatic-riparian systems through shifts in flood and drought frequency, duration and magnitude (Pall et al. 2011, Prudhomme et al.

2013), creating novel flow regimes that will remove sensitive species and simplify the architecture of food web networks (Ledger et al. 2012). Whilst there is some evidence to suggest that this may have elevated impacts on species at higher trophic levels (Ledger et al. 2012), our understanding of the relationship between species' distributions and hydrological extremes is limited by a scarcity of large-scale studies that encapsulate both temporal and spatial variability in species' relationships with river flow. Here, the vulnerability of river bird species to a potential climate-driven shift in hydrological extremes was quantified by combining datasets from long-term national river bird surveys with river flow archives. This study demonstrates that the abundance of river birds is influenced by the occurrence of extreme river flows and that species are vulnerable to a potential future increase in occurrence of floods and droughts. Moreover, it highlights the importance of incorporating variability in extremes in climate change impact studies of ecological communities.

6.5.1. Vulnerable taxa

By developing a methodology in which the outputs of correlative SDMs are combined with expert assessments of species' future exposure to climate change impacts, it was possible to quantify species' vulnerability to flow change in mainland Britain.

While some species such as common merganser and white-throated dipper demonstrated an affinity to high flows and common sandpiper to low flows, no species demonstrated an affinity to variability in both. As climate change is expected to alter the mean and variance of both high and low flows (Pall et al. 2011), this implies that all of the studied species with an association with one or more of the hydrological variables are vulnerable to some degree to climate-driven perturbations in river flow regimes. An opinion-based scheme was used to designate taxa into one of four vulnerability criteria, ranging from low vulnerability to very high vulnerability, based on final VI_{total} scores. Whilst the linear numerical criteria used to identify category cut-off points were simple, this ranking scheme facilitated the identification of priority species – this was one of the key aims of the chapter.

Using this approach, five species were identified as of high or very high vulnerability. These included species such as common sandpiper, common merganser and white-throated dipper that are commonly associated with fast-flowing, upland rivers and streams in Great Britain (Figure 6.3). Common mergansers are found mainly on the wider stretches of the upper reaches of rivers during the breeding season (Gregory et al. 1997), while dippers are adapted to clear, fast-flowing upland streams where they feed on benthic macro-invertebrates and fish in riffles and pools (Tyler and Ormerod 1994). It may have been expected that the positive relationship would exist between the abundance of these species and the parameters for high flow frequency and duration as observed. However, the strength of this relationship decreased as the high flow parameter became more extreme, suggesting that whilst some degree of variability in high flows is beneficial it is lost at higher flow events. This supports findings from studies of dipper activity budgets which demonstrated that time spent diving increases with rising flow discharge to a point but then dropped off as flow increases (D'amico and Hémery 2007). This may be because the prevalence of favoured foraging microhabitats, such as riffles, is reduced at extreme levels of high flow, but also because extreme high flows lead to mortality or increased dispersal amongst species at lower trophic levels in aquatic food webs, impacting the river birds' prey base (Chiu et al. 2008, Chiu et al. 2013).

In Great Britain, the common sandpiper breeds alongside fast-flowing, mainly upland rivers and typically forages at the water's edge on exposed riparian mudflats and gravel bars (Cramp and Simmons 1977-1996, del Hoyo et al. 1992-2013). Abundance of this species was found to decrease with an increase in the frequency and duration of high flows whilst it increased with the frequency and duration of low flows. It is likely that increased variability in low flows increases the prevalence of exposed riparian foraging; however, in a similar manner to the white-throated dipper, the benefit of the increased variability in low flows decreased with the magnitude of the low flow event. Given that species' diversity in aquatic food webs and the contribution of larger-sized species to overall biomass decreases as the intensity of drought increases (Ledger et al. 2012), the abundance of riparian consumers may be negatively affected by this degradation of food web networks. This may have a greater impact on species such as the common sandpiper through a decline in aquatic-riparian food subsidies (Jonsson et al. 2012, Strasevicius et al. 2013) than species such as the white-throated dipper that forages primarily on submerged aquatic prey.

A climate-induced increase in the frequency and duration of flooding may affect the foraging behaviour of these species, whereby birds will have to feed on a broader range of prey species or move to habitats peripheral to the main channel, such as smaller tributaries, where they are buffered from the full impacts of the flood, to find preferred prey species. This broadening of foraging niches would also increase the likelihood of intra- and inter-specific competition and perhaps impact foraging efficiency through patch depletion and decreased food handling time. If flooding were to occur during a sensitive period of the annual cycle, a shortage of prey could also limit breeding performance, for example, through phenological mismatch (Whitehouse et al. 2013) or carry-over effects (Harrison et al. 2011). These effects may be most profound for species with limited capacity for adaptive plasticity, which, in the short-term, might allow foraging and breeding efforts to be aligned with the locations and timings of peaks in resource availability (Charmantier et al. 2008). In the long-term, the costs on offspring productivity incurred from a mismatch between species' breeding behaviour and their prey will lower population viability (Visser et al. 2012). Whilst there is evidence from some species that genetic changes which alter the timings of seasonal events, such as breeding, have evolved in response to recent, rapid climate change (Bradshaw and Holzapfel 2006), there is currently no consensus on how adaptive capacity can be best assessed quantitatively.

For lowland species, vulnerability was also associated commonly with species (such as the great cormorant, great crested grebe and mute swan) that feed from the water surface on submerged prey or macrophytes. Species displayed negative relationships with high flow frequency and duration, suggesting that stability around high flows is favoured and they are negatively affected by flood events. Diving and surface swimming are likely to be the most energetically expensive activities for these species (Wood et al. 2013) which may not forage during extreme high flows when energetic investment in feeding may outweigh energy gain from ingested food (Taylor and O'Halloran 2001, Wood et al. 2013). Foraging efficiency is likely to be severely compromised under conditions of elevated water velocity, depth and turbidity (Vilches et al. 2013).

Limited vulnerability was observed amongst species such as the Eurasian coot and grey heron that occupy a range of foraging and breeding habitats across the aquatic, riparian and terrestrial landscapes. The generalist foraging behaviour of some river bird species potentially buffers these species from the full impact of the predicted future change in floods and droughts. As predicted, low vulnerability was also observed amongst species associated with habitats at greater distance from the main river channel.

Priority riverine locations which support greater relative abundances of very high and high vulnerability species were identified in upland regions of the north of England, southern and northern Scotland and Wales. Worryingly, these priority areas correspond with those regions predicted to have the largest percentage changes in river flow from climate change

(Prudhomme et al. 2012), with large decreases in spring and summer flows and more variable autumn and winter flows predicted by a number of regional climate model scenarios. Given that previous investigations of climate change impacts on these species (e.g. common merganser, white-throated dipper, common sandpiper) predict a gradual northward shift in range (Huntley et al. 2007), these species could increasingly become restricted to sub-optimal habitats where prey availability is reduced or more variable. It should be noted, however, that the application of kriging to identify priority river locations does not take into account river catchment boundaries or other physical patterns and involves interpolation across terrestrial features. Yet, this facilitates a valuable visual interpretation of how areas of high species' abundances correspond to the boundaries of river flow regimes (Bower et al. 2004) where climate change is predicted to have considerable impact on river flows.

6.5.2. Suitability of the Vulnerability Index

The species' vulnerability index presented here represents a novel and dynamic approach for assessing the impacts of potential future shifts in climate extremes. By combining long-term, national datasets on river bird distribution with river flow archives, the methodological framework presents robust quantitative assessments of species' relationships with hydrological extremes. However, by combining the outputs of SDMs with scores from expert judgements, the methodology also represents a very pragmatic approach to making rapid assessments and ranking the relative vulnerability of a range of species to potential climate change impacts. This approach will offer a potent conservation tool in the face of increased floods and droughts as predicted by climate modellers. Given the rapid rate at which climate change is occurring, conservation managers will have increasingly stretched resources which will necessitate targeted conservation action focused on priority species and in priority geographical areas (Khamis et al. 2013). Thus, a methodology that identifies hierarchical levels of vulnerability may allow conservationists to allocate management effort more effectively to the most vulnerable species.

The usefulness of an index is contingent upon the appropriate selection of the factors upon which it is constructed. Ideally, an index should be based on a combination of factors that explain the extent of species' distributions and regulate species' exposure to climate change impacts at microhabitat scales (Williams et al. 2008b). In addition to the outputs of modelled distributions, here four factors were used which were assessed using subjective expert scoring. Whilst these four factors were qualitative in structure, ranking species relative to their perceived exposure, assessing these scores objectively and consistently using collected field data would have been inappropriate given the large variance within ecological traits across species. While it is possible that the SVI might have been improved by considering additional factors, this would have increased the amount of collinearity between factors which would have exaggerated the dichotomy in scoring between vulnerable and non-vulnerable species. The SVI also does not consider the size of species' range or species' conservation status, although the impacts of an increase in the intensity of floods and droughts may be more severe for species with small population size. However, the SVI was designed to assess the vulnerability of river birds that are, for the most part, ubiquitous across the British landscape. Moreover, it was possible that the inclusion of conservation status as an additional factor might decrease the reliability of the results given that the parameters used to assess species' status (e.g. Birds of Conservation Concern 3 2009; (Eaton et al. 2009) are not restricted to the riverine environment.

A further important consideration for any future application of this SVI is that the z-score, used in the calculation of the BIC, will be greater where *n* is large as the standard error of the parameter is reduced. There is, therefore, the potential in this study that the VI_{total} score of species recorded at a large number of survey sites (e.g. for mute swan) will be inflated. However, this is an unavoidable problem caused by converting coefficient values, which vary around the associated error, into a dimensionless index. In addition, the choice of *n* in calculating the z-score is also important. Raftery (1995) used the number of observations, but the number of survey locations as the observations within each location were not independent.

The SVI appears well-suited for assessing the vulnerability of river birds to hydrological extremes because the outputs showed clear differences between species and the vulnerability classifications were in broad agreement with knowledge on species' ecological traits – vulnerability was associated with traits that restrict species to in-channel riverine habitats and non-vulnerability was associated with more generalist strategies. Such findings are supported by other studies which have demonstrated clear relationships between the abundance and diversity of river birds and hydrological variability (Kingsford et al. 2004, Chiu et al. 2008). Secondly, sensitivity analyses showed that the SVI outputs were robust to small changes in both the sensitivity and exposure scores. Thirdly, the relative final vulnerability rankings assessed using the GEE approach were comparable to those of an alternative generalized linear mixed-effect model approach (see Table C2 for a comparison of model outputs), indicating that the SVI framework is robust to the choice of modelling methodology used.

6.5.3. Concluding remarks: conservation implications

River bird populations have close relationships with river flows whereby natural variability and the occurrence of extreme high and low flows promotes species' diversity and regulates key life-history stages such as breeding and survival (Kingsford et al. 2004, Arthur et al. 2012, Cumming et al. 2012, Jonsson et al. 2012, Royan et al. 2013, Strasevicius et al. 2013). Species' responses to river flow parameters illustrate their vulnerability to a climate-induced shift in the frequency, duration and magnitude of hydrological extremes. Conservation efforts in an era of climatic uncertainty will increasingly rely on the careful targeting of valuable resources at priority species and regions (Khamis et al. 2013). Therefore, practical methodological frameworks such as this will become increasingly valuable to applied conservation. Moreover, this chapter was made feasible by the availability of long-term and spatially broad annual bird survey data and daily river flow data, allowing species' distributions to be related to measures of hydrological extremes that are typically difficult to study due to their rarity and unpredictability. These data also allowed species' relationships to be placed in the context of previous exposure to the investigated parameter. This is extremely important given that the precise definition of an "extreme event" can be highly dependent upon the magnitude of previous flow events within a particular focal system (Smith 2011a). The results discussed here emphasise the value and applicability of WBBS data and other repeated survey methodologies in the investigation of the impact of extreme events on ecological systems.

In this chapter, a Species Vulnerability Index (SVI) was developed to identify the river bird species most vulnerable to climate change-induced alterations in the variability of high (flood) and low (drought) river flows. This allowed the identification of priority species which are most vulnerability to future climate change impacts on riverine systems. Now, Chapter Seven will use predictions of climate-driven changes in the flow regimes of British rivers

(Prudhomme et al. 2012a) to model shifts in the probability of occurrence (*P(x)*) of a riverine specialist bird, the white-throated dipper.

7. Climate-induced changes in river flow regimes will alter future bird distributions

Royan, A., C. Prudhomme, D. M. Hannah, S. J. Reynolds, D. G. Noble, and J. P. Sadler. In press. Climate-induced changes in river flow regimes will alter future bird distributions. Ecosphere.

7.1. Abstract

Anthropogenic forcing of the climate is causing an intensification of the global water cycle, leading to an increase in the frequency and magnitude of floods and droughts. River flow shapes riverine ecosystems and climate-driven changes in river flows are predicted to have severe consequences for riverine species, across all levels of trophic organization. However, understanding species' responses to variation in flow is limited through a lack of quantitative modelling of hydroecological interactions. Here, a Bioclimatic Envelope Model (BEM) ensemble is constructed that is based on a suite of plausible future flow scenarios to show how predicted alterations in flow regimes may alter the distribution of a predatory riverine species, the white-throated dipper. Models predicted a gradual diminution of dipper probability of occurrence between present day and 2098. This decline was most rapid in western areas of Great Britain and was principally driven by a projected decrease in flow magnitude and variability around low flows. Climate-induced changes in river flow may, therefore, represent a previously unidentified mechanism by which climate change may mediate range shifts in birds and other riverine biota.

7.2. Introduction

Climate warming and associated changes in precipitation patterns are predicted to modify river flows (Pall et al. 2011, Prudhomme et al. 2013). Because patterns of flow regimes, including extreme high and low flows, structure the morphology and regulate the physico-chemical and biotic properties of rivers, variability in river flows is a major driver of community dynamics in riverine-floodplain ecosystems (Bunn and Arthington 2002). Flow variability drives productivity and species' demographics and altered flows can have severe consequences for species' populations and assemblages across all levels of trophic organisation (Ledger et al. 2012). Therefore, climate-driven shifts in river flows are likely to result in major changes in the structuring of riverine ecological communities.

River birds are vulnerable to spatial and phenological mismatches with prey caused by shifting flows, as both species' distribution (Royan et al. 2013) and abundance (Royan et al. 2014) are closely linked to variability around high (flood) and low (drought) flow conditions. High flows reduce river bird prey abundance and biomass, such as aquatic macro-invertebrates (Chiu et al. 2013), impacting, in turn, on the timing and location of avian foraging (Cumming et al. 2012), territory occupancy (Reiley et al. 2013), and survival and breeding success (Strasevicius et al. 2013). Despite this, the impacts of climate-driven flow alterations on river birds remain unexplored.

Predictions of climate-driven changes in the flow regimes of British rivers (Prudhomme et al. 2012a) were used to model shifts in the probability of occurrence ($P(x)$) of the white-throated dipper (hereafter termed the 'dipper'). The dipper has highly specific habitat requirements, concentrating foraging on rivers with a high degree of flow variability where riffles and pools of deep water are found (Tyler and Ormerod 1994). Foraging frequency decreases at high flow rates (O'Halloran et al. 1990) and birds become less selective when foraging during periods of high flows (Taylor and O'Halloran 2001). The creation of key dipper habitats is, therefore, conditional upon variability in river flows. Such behaviours also mean the dipper occupies a unique niche among passerine birds in Great Britain and these behaviours are likely to reduce its adaptive capacity to climate change.

The modelling procedure was a two-part process: (i) develop a correlative model to relate dipper distribution to variables of river flow, and (ii) construction of a Bioclimatic Envelope Model (BEM) ensemble using future flow predictor variables. The models were constructed using the BTO’s WBBS and river flow archive data. By using flow parameters to describe climate-driven changes in species’ habitat these BEMs have the potential to provide more biologically realistic scenarios than those built on climatic predictors alone and provide new perspectives on how climate change may impact on riverine species.

7.3. Methods

7.3.1. Data and model structure

The structure of the BEMs was defined by initially relating the presence of the dipper at 103 river locations to indices of hydrological variability using river flow archives and the BTO’s WBBS data between 1998 and 2010 (inclusive). However, data from year 2001 were excluded from analyses as a very small proportion of locations were surveyed due to the foot-and-mouth outbreak. The response variable was the presence or absence of birds at a survey location across the entirety of the time series. The likelihood of incorporating false zeros into the dataset was minimised by only using WBBS survey locations surveyed at least three times, as multiple site visits provide more realistic estimates of species' occupancy by reducing bias associated with species' detection probability (Royle and Nichols 2003).

A large number of hydrological indices exist in the literature and there are concerns that a high degree of multi-collinearity exists among them (Olden and Poff 2003). Therefore, model parameters were identified *a priori* that characterize key facets of the hydrological regime on rivers in Great Britain (e.g. variation in flow magnitude, frequency, and duration). Royan et al. (2013) showed that river flow predictor variables were important in describing dipper distribution when tested using a model averaging approach, comparing the performance of 31 plausible model structures. Here, models were constructed using the four hydrological variables (Table 7.1) that best characterized dipper distribution in Royan et al. (2013). These variables capture variability around flow magnitude, frequency, and duration around both high and low flows, which are predicted to be significantly altered as a result of climate change (Prudhomme et al. 2012b). No further model selection procedure was utilised. The option to use all four predictor variables is preferable to building a more 'parsimonious' model as the use of a wider range of predictor variables ensures better transferability of model outputs across time (Rapacciuolo et al. 2012).

Table 7.1 Description of river flow predictor variables.

Hydrological Index	**Description**
Flow magnitude	A measure of the magnitude of daily flows. Calculated as the mean daily discharge divided by the median daily discharge (m^3/sec).
Low flow variability	A measure of low flow variability and deviation of low flows from the median. Low values imply greater variability in the magnitude of low flows while high values imply greater stability. Calculated as the average annual 3-day minimum divided by the median annual discharge (m^3/sec).
High flow variability (m^3/sec)	A measure of high flow variability and the deviation of high flows from the median. High values imply greater variability in the magnitude of high flows while low values imply greater stability. Calculated as average annual 3-day maximum divided by the median annual discharge (m^3/sec).
High flow frequency	A measure of the number of extreme high flow days on a river. Calculated as the total number of high flow days during time series above three times the median.

Strong evidence of non-linear relationships exist so the bivariate relationship and functional form between hydrological predictors and dipper distribution were modelled using Generalized Additive Models (GAMs) and Generalized Linear Models (GLMs) with quadratic terms. Both regression methods have high accuracy and transferability across time periods and perform well under small sample sizes when using presence/absence data (Guisan and Thuiller 2005). Models were defined with a quasi-binomial error structure and logarithmic link function. Models were also weighted by the inverse of the total survey effort within each BTO region so that locations with lower survey effort receive greater weight in their contribution to the calculation of model coefficients. This accounts for spatial variation in the coverage of WBBS squares and prevents the results being biased towards well-surveyed locations (Renwick et al. 2012). GAMs were defined with cubic smoothing splines, as automatic selection criteria such as Generalized Cross Validation have the potential to over fit short times series, with a fixed two degrees of freedom (Wood 2006). This sufficiently captured trends in the data whilst limiting the penalized least squares criterion (Fewster et al. 2000). The GAMs were constructed using version 1.7-11 of the mgcv package in the statistical package R, version 2.13.2 (Wood 2006).

Model predictive power was assessed using Cohen’s Kappa (K) as it is more robust to threshold selection than other commonly used methods (e.g. TSS, ROC) (Nenzén and Araújo 2011). K assesses model performance by comparing it to the performance expected by chance (Cohen 1960). It is a widely used measure for assessing the accuracy of presence-absence predictions, in part because of its tolerance of zero values. Additionally, the critical threshold $P(x)$ (P_s) at which K is maximized was optimized by testing P_s values from 0.0 to 1.0 in 100 steps and selecting the P_s value that maximizes model prediction accuracy (Huntley et al. 2012). When Dipper $P(x)$ is projected to drop below P_s, it can be interpreted that the probability of species’ absence is greater than species’ presence.

7.3.2. Bioclimatic Envelope Model (BEM) ensemble

The BEM ensemble was constructed using future flow predictor variables obtained by applying change factors to observed local flow statistics (Prudhomme et al. 2010). The changes were derived from the Future Flow Hydrology (FFH) dataset. This comprised an ensemble of transient daily river flow simulations up to the end of year 2098 calculated by driving the semi-distributed conceptual hydrological CERF model (Young 2006) with the Future Flows Climate (Prudhomme et al. 2012a). The ensemble of flow factors include uncertainty in future climate signal and can be associated with large variations in the projections of species' $P(x)$s (Prudhomme et al. 2010). The climatic ensemble was based on the UK Met Office Regional Climate Model (RCM) 11-member perturbed physics ensemble HadRM3-PPE (Murphy et al. 2007) simulations of the 20th and 21st century for historical and medium anthropogenic forcing (SRESA1B emissions scenario (IPCC 2000)]). Such ensemble forecasting frameworks are necessary to capture uncertainty in regional climate model projections (Murphy et al. 2007). Due to the spatial coverage of these data and the ability to pair with bird data, BEMs were restricted to 38 river locations. The spatial spread of these locations successfully captured the full range of variability in river flows across the environmental and geographical range of the dipper in Great Britain, thus preventing predictions of presence in uninhabitable locations (Chefaoui and Lobo 2008).

For consistency with the length of dipper survey data, FFH time series were analysed for 12-year separate time periods to describe short-, medium- and long-term implications of climatic change, with the 1997-2010 period defining the baseline (Table D1). Regionalized curves were derived by averaging $P(x)$s across all survey locations within the hydrological region for each of the 11-member climate scenarios. Hydrological regions were classified using a previously described method (Bower et al. 2004) based on long-term spatial and temporal trends in flow magnitude and the timing of flow peaks. Riverine catchments that exhibit similar inter-annual hydroclimatic responses are identified, allowing the hydrological sensitivity of each region to be separately evaluated. This involves a two-stage clustering procedure (hierarchical cluster analysis using Ward's method followed by non-hierarchical k means clustering) followed by discriminant function analysis.

7.4. Results

Both the GAM (*K* = 0.843) and GLM (*K* = 0.684) approaches successfully captured species' current distribution (**Figure 7.1**).There was considerable overlap in predicted trends between GAM and GLM models, indicating strong convergence of findings (**Figure 7.2**). Dipper *P(x)* was primarily driven by changes in low flow variability, although flow magnitude and high flow frequency were also important predictors in the GAM model (Table 7.2 and Table 7.3). The largest changes in *P(x)* averaged across the 11 climate scenarios are estimated for the west of Great Britain, particularly Wales and western Scotland where *P(x)* between the baseline period and 2088-2098 are projected to decline by 52-91% and 31-47% respectively (**Figure 7.2**). Changes in the east of Great Britain were considerably smaller than in western regions, with *P(x)*s estimated to show a change between the baseline period and last time period of between +12 and -27%, although models were in less agreement.

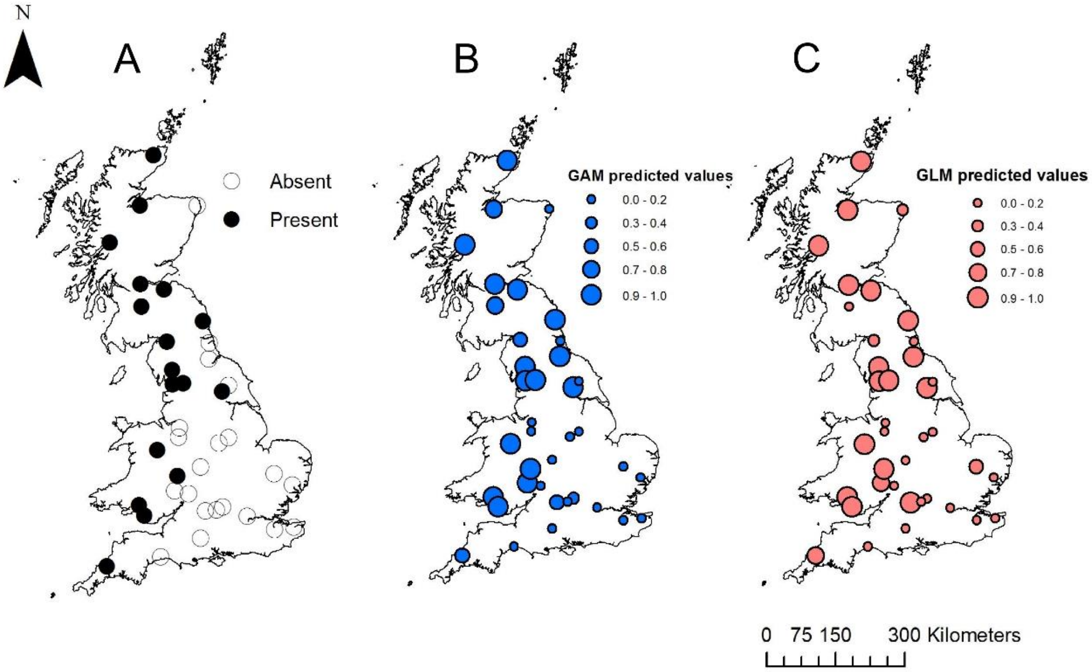

Figure 7.1 *Maps showing (a) the survey records of dipper presence/absence for 38 locations, (b) the Generalized Additive Model (GAM) predicted values (Cohen's Kappa = 0.843), and (c) the Generalized Linear Model (GLM) predicted values (Cohen's Kappa = 0.684).*

***Table 7.2** Generalized Additive Model (GAM) coefficients for smoothed hydrological indices; 'edf' refers to equivalent degrees of freedom.*

Smoothed hydrological indices	**edf**	***F***	***P***
Flow magnitude	2	7.056	0.001
High Flow Frequency	2	6.137	0.003
Low Flow Variability	2	9.849	< 0.001
High Flow Frequency	2	1.513	0.226

Notes: Coefficients for parametric terms: intercept coefficient = -0.099; standard error = 0.324; T = -0.304; P = 0.762.

***Table 7.3** Generalized Linear Model (GLM) coefficients for hydrological indices.*

Hydrological indices	**Coefficient**	**Standard Error**	***T***	***P***
Flow magnitude	-0.072	7.056	-0.057	0.9545
High Flow Frequency	-0.036	6.137	-1.033	0.3043
Low Flow Variability	-12.91	9.849	-4.400	< 0.001
High Flow Frequency	-2.127e-05	1.513	-0.931	0.3539

Notes: Coefficients for intercept: coefficient =3.520; standard error = 0.933; T = 3.772; P < 0.001.

Both models estimated average $P(x)$ to drop below P_s within the total timeframe for all regions, except western Scotland and west-central England (**Figure 7.2**), presumably because such regions form the core of this species' range in Great Britain and, thus, population densities are higher. Average $P(x)$ dropped below P_s between 2062 and 2075 in Wales, around 2062 in south-west England, and between 2023 and 2088 in south-east England. This means that across time the model predictions tended more towards a probability of absence rather than a probability of presence in western and northern parts of Great Britain. Changes in *P(x)* were principally driven by a projected decrease in flow magnitude and variability around low flows (Figure D1).

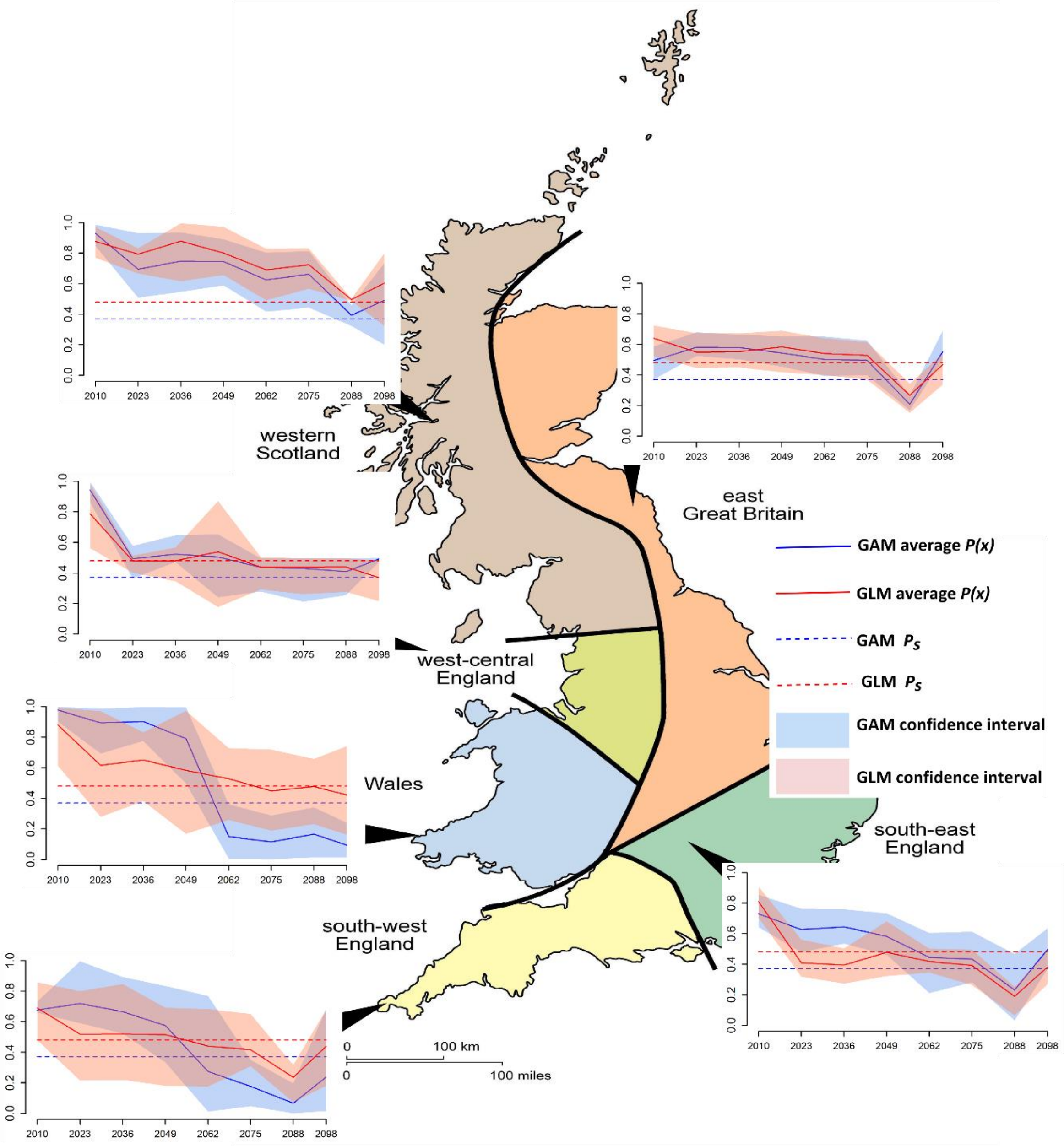

Figure 7.2 Generalized Additive Model (GAM) (blue line) and Generalized Linear Model (GLM) (red line) predicted trends in the regionalized average P(x) of white-throated dippers (Cinclus cinclus*)(y axes), between a baseline period through seven future periods (x axes), with shaded regions illustrating the range between 5th and 95th percentiles as an indication of the uncertainty in climate predictions across the 11 plausible scenarios. Dashed lines represent Ps for both the GAM and GLM models, whereby values above and below the lines represent a likelihood of occurrence and absence, respectively.*

A geographic shift in species' occurrences between the baseline period and 2088-2098 was tested using paired t-tests (for the future time period, modelled predictions were averaged across the 11-ensemble members). Locations of dipper occurrences were predicted to shift significantly eastwards within the timeframe (GAM: t = -2.39, P = 0.03, +0.984° ± 0.357°; GLM: t = -2.51, P = 0.02, +0.798° ± 0.257°). There was no significant shift in the latitude of modelled occurrences (GAM: t = 0.29, P = 0.77; GLM: t = 0.30, P = 0.77).

7.5. Discussion

The models indicate how a riverine-specialist consumer in Great Britain is potentially vulnerable to future climate-driven changes in river flows. Changes in climate may mediate shifts in the abundance (Huntley et al. 2012) or range (Huntley et al. 2007) of birds; however, shifts in distribution from climate-driven alterations to river flows may be a widespread, yet previously unidentified, potential mechanism by which climate change may impact birds dependent on riverine habitats.

BEMs are based upon a number of statistical and theoretical assumptions and, thus, must be discussed with caveats. BEMs were built on relationships fixed in space and time which are assumed to be transferable to environmental domains outside of those upon which the models were built. Nonetheless, validation has shown BEMs to have considerable predictive power (Araújo et al. 2005) and can be useful in guiding conservation action (Guisan et al. 2013). The BEMs here produce predictions of changes in suitable flow habitat conditions and thus can be used to show how dipper *P(x)* might change in the future due to changes in flow across hydrological regions. This informs about possible changes in species' distributions based on the suitability of dipper habitat.

Most avian-focused models, including those for dipper, that assess the impact of climate change on species' distributions have been constructed using climatic predictors alone and predict poleward shifts in species' ranges (e.g. (Huntley et al. 2007)). This limits the biological relevance of BEMs as non-climatic impacts tend to dominate local, short-term biological changes (Araújo and New 2007). In fact, dynamic studies which model how species' distributions may change as a direct result of climate change-induced perturbations in habitat suitability are rare. This is in part a consequence of climatic variables often being only available at regional-scale resolution (Domisch et al. 2013). However, by coupling the WBBS and FFH datasets it was possible to measure how species' presence at localized spatial scales changes in response to climate-induced alterations in habitat suitability.

The model ensemble predicted a significant eastward shift in species' occurrences but no significant shift in latitude. This was likely caused by the modelled prediction that flow conditions on rivers in the east of Great Britain would become more variable and, therefore, increase habitat suitability for dipper through the creation of critical foraging habitats. Average $P(x)$ was also projected to drop below P_s within the total timeframe for all regions, except western Scotland and west-central England, suggesting the viability of some dipper populations could be threatened by climate-induced changes in river flow suitability. River flow is the dominant driver of morphological structure in riverine habitats (Poff and Zimmerman 2010) and determines the availability and prevalence of key dipper foraging and breeding habitats (O'Halloran et al. 1990, Taylor and O'Halloran 2001). Shifts in Dipper $P(x)$ over time are, therefore, driven by changes in habitat suitability, which is altered as a direct consequence of the climate change signal and climate variability.

By incorporating measures of river flow into the modelling framework, the BEMs have suggested a climate impact on future habitat suitability due to regional variation in future river flows. A focus solely on climatic predictors may well under-estimate the full impact of climate change on species' distributions. Incorporating predictor variables into climate impact models that assess the suitability of areas using non-climatic (e.g. habitat) factors will prevent the over- or under-estimation of climate change impacts whilst simultaneously expanding the range of environmental conditions under which models are calibrated, thereby improving predictive performance (Thuiller et al. 2004). This would also have the additional benefit of adding more biological 'realism' to, often coarse, large-scale climate models, which is especially important for species that respond primarily to multiple local scale factors, as aquatic-riparian species do to habitat structure, water quality and abiotic or biotic processes (Ormerod et al. 2010). This is especially pertinent for the dipper since it occupies highly dynamic, disturbance-prone systems.

The results of this study suggest that subtle shifts in future flows may result in considerable changes in the occurrence of a riverine specialist consumer. Changes in flow may thus present a previously unidentified threat to species in riverine environments wholly or largely dependent on aquatic food resources. These findings have important implications for how we interpret current predictions of species' ranges under climate change scenarios as climate-driven alterations to habitat may lead to multi-directional shifts in range. It also highlights the importance of incorporating local non-climatic factors into climate impacts models.

8. General discussion, synthesis and conclusions

Variability in river flows is a major force shaping the morphology and ecological structure of riverine-floodplain ecosystems (Poff et al. 1997). By influencing factors such as water velocity, depth, water temperature, turbidity, channel stability and nutrient fluxes, river flow variability causes disturbance in the organisation of lower trophic levels (e.g. primary producers such as phytoplankton) in aquatic ecological communities (Bunn and Arthington 2002, Poff and Zimmerman 2010). Perturbations in the lower trophic levels are conveyed through the food web, resulting in deflated food availability for consumer species such as river birds (Ledger et al. 2012, Strasevicius et al. 2013). Additionally, physical changes in habitat following hydrological disturbances, such as the submersion of breeding or foraging habitats, can influence the habitat occupancy (Reiley et al. 2013, Jankowiak and Ławicki 2014), abundance (Chiu et al. 2008), foraging behaviour (Taylor and O'Halloran 2001, Cumming et al. 2012, Wood et al. 2013), timing of breeding (Arthur et al. 2012, van Turnhout et al. 2012), breeding success (Strasevicius et al. 2013) and survival (Chiu et al. 2013) of river birds. However, by largely focusing on a single watershed after a specific flood event, previous investigations of river flow-avian relationships are spatially and temporally constrained, and this has limited our understanding of how river flow influences the distribution and community organisation of river birds. This has also restricted our ability to predict how climate change-induced shifts in river flow regimes might impact river birds.

This thesis sought to resolve some of the shortcomings that are prevalent in the scientific literature on avian-flow interactions by using river flow archives and data from a long-term bird monitoring scheme across Great Britain to investigate the relationship between river bird distributions and hydrological variables over large spatial and temporal scales and at different levels of community organisation. The overall aims of this thesis were to: (i) understand how hydrological disturbance affects the distribution of river birds, and (ii) evaluate the potential impacts of climate change-induced shifts in river flow on species' distributions. Chapters Three, Four and Five addressed the first aim. By synthesizing individual studies that investigated different levels of community organisation in river bird assemblages, from the distribution of individual species (Chapter Three) to patterns of co-occurrence (Chapter Four) and the diversity of functional traits and community structure (Chapter Five), these three chapters provided a holistic overview of how variability in river flows influences the structure of river bird populations. Chapters Six and Seven addressed the second aim by, first, assessing river bird species' vulnerability to a climate change-induced shift in the frequency, duration and magnitude of hydrological extremes (floods and droughts) (Chapter Six) and, secondly, by predicting how a riverine specialist bird species may shift in distribution as climate change alters river flow regimes (Chapter Seven).

8.1 Synthesis

Quantification of the relationships between river flow variability and riparian ecology is an urgent and important research challenge in the context of unravelling and projecting the impacts of hydrological variability on ecological systems (Markovic et al. 2014). An understanding of ecological responses to flow is imperative for the development of effective environmental flow management programmes (Poff and Zimmerman 2010). However, the availability of large-scale ecological datasets is often a limiting factor in attempts to assess ecological responses to environmental change (Huntley et al. 2012). Using river bird occurrence data for 71 river locations, Chapter Three demonstrated that the occurrence of river birds is influenced strongly by elements of river flow variability. Species' distributions are characterized by complex responses to: (i) variability around extremes of high and low flows, (ii) flow frequency, (iii) the timing of flow events, and (iv) flow magnitude. This provides evidence that the influence of river flows on species' distributions extends beyond lower trophic levels to tertiary consumers at the top of aquatic/riparian food webs (Woodward et al. 2010, Ledger et al. 2012). Fluctuations in flow conditions likely impacts on these bird species primarily by: (a) causing disturbances in aquatic food webs, which decrease prey abundance or shift prey composition (Wilson and Peach 2006, Chiu et al. 2008), which, in turn, alters foraging decisions (Wood et al. 2013) and net energy gain (Taylor and O'Halloran 2001); and (b) altering the availability of foraging and breeding habitats (Cumming et al. 2012, Reiley et al. 2013, Jankowiak and Ławicki 2014). Quadratic responses to variables characterizing high flows suggest that intermediate measures of high flow provide optimal foraging habitat for some riparian fauna, such as white-throated dipper, whereas floods may decrease prey abundance and shift prey composition (Chiu et al. 2008), perhaps resulting in increased consumer competition or broadening of foraging niches (Korňan et al. 2013). Exceptionally large or prolonged extreme flow events may lead to marked increases in adult and juvenile mortality for the most sedentary of species (Chiu et al. 2013). Analyses also revealed that low flow variability may positively influence the availability or prevalence of foraging habitats for riparian consumer species such as waders, possibly through the creation of riparian foraging habitat and refugia (Jankowiak and Ławicki 2014). However, species that forage or breed within macrophytes in-stream or at river margins, such as mute swan and common moorhen, prefer stability around low flows, perhaps because substrates remain undisturbed promoting greater diversity and growth of these plants (Bunn and Arthington 2002).

Analyses in Chapter Four provided further evidence that variability in river flow influences the basic structure of river bird communities. Co-occurrence patterns in river bird assemblages are primarily explained by shared environmental responses to river flow variables. Mechanistic models of community assembly predicate that the impacts of 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 and Jetz 2013). Environmental filters restrict community membership to species possessing a particular set of functional traits, causing them to cluster relative to the prevalence of traits in the regional pool (Petchey et al. 2007). In addition, 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 and such interactions may leave imprints on species' distributions that are detectable at large spatial scales (e.g. species' clustering or segregation) (MacArthur 1972, Hubbell 2001, Gotelli et al. 2010).

Analyses in Chapter Four showed that river bird species co-occur more often than random with co-occurrence patterns primarily explained by shared responses to river flow variables. The evidence for an influence of biotic interaction in shaping community structure is comparatively weak. This is significant as the importance of interactions between species in structuring bird communities at macro-ecological scales is hotly debated in the ecological literature (Araujo and Luoto 2007, Gotelli et al. 2010, Belmaker et al. 2012, Cortes-Avizanda et al. 2012, Korňan et al. 2013, Börger and Nudds 2014). That an environmental filtering model of community assembly was found to be the dominant mechanism shaping river bird community structure corroborates the findings of some studies in suggesting that species' interactions are of secondary importance relative to habitat structure and resource availability in structuring avian assemblages (Gotelli et al. 1997, Petchey et al. 2007, Mattsson et al. 2013, Börger and Nudds 2014, Kroll et al. 2014). However, it contrasts markedly with others (Heikkinen et al. 2007, Gotelli et al. 2010, Sebastian-Gonzalez et al. 2010, Robertson et al. 2013), perhaps because this study focussed on bird communities on riverine systems which are highly dynamic, disturbance-prone environments in which high levels of environmental disturbance exert strong formative pressure on ecological communities (Junk et al. 1989). As the dominant driver of ecosystem structure in riverine-floodplain ecosystems (Junk et al. 1989), the influence of river flow variability on community organisation appears to exceed the influence of alternative models of community assembly (e.g. biotic interaction). These findings have further implications for macro-ecological studies of species' distributions as they show that the prevalence of shared environmental responses should not be under-estimated and should be incorporated into JSDMs so as not to over-state the influence of species' interactions on community structure. These findings also suggest that it is possible that studies based solely on analyses of null model matrices (Gotelli and McGill 2006) or probabilistic models (Veech 2013) may exaggerate the pervasiveness of species' interactions in community assembly processes.

Further evidence of an important role of environmental filtering was observed in Chapter Five whereby the FD of river bird assemblages was found to be typically lower than expected, suggesting that species in river bird communities typically display a degree of similarity in functional traits and low levels of functional redundancy. This corroborates previous research on the FD of avian populations in Great Britain (Petchey et al. 2007, Mendez et al. 2012). Species in bird communities were more ecologically similar than expected by chance, as indicated by an uneven spread of species' abundances. Non-randomness in the distribution of species' functional traits indicates where species' co-existence and different assembly processes shape community structure (Mouchet et al. 2010). Disentangling the roles of different assembly mechanisms (e.g. environmental filtering and limiting similarity) is challenging as they may operate simultaneously to structure bird communities and their relative contribution may depend upon the spatial scale considered (Lavergne et al. 2010). However, one potential explanation for the patterns observed in Chapter Five is that there is a strong influence of environmental filtering which reduces river bird communities to a subset of the species pool which is dominated by species with traits that most benefit fitness (Lebrija-Trejos et al. 2010, Kraft et al. 2014).

Whilst previous research on the FD of bird communities in Great Britain has revealed the operation of environmental filtering mechanisms impinging on avian community structure (Petchey et al. 2007, Mendez et al. 2012), the principle environmental drivers of community change have not been measured. In Chapter Five, the FD of river bird assemblages increased with variability in river flows, suggesting that a loss of flow variability causes a reduction in the diversity of traits represented in the bird community. Consequently, greater flow variability appears to create environmental conditions that promote the occupancy of less common species with rarer trait values and unique foraging trait characteristics, such as the common merganser. This is likely driven by variability in river flows increasing the complexity of the habitat matrix across the riverine-floodplain interface and creating conditions that promote greater avian biodiversity (Poff et al. 1997, Bunn and Arthington 2002), in part by increasing the flow of aquatic invertebrate subsidies for riparian foraging birds (Jonsson et al. 2013).

In addition, levels of functional redundancy were lower at locations with a predominant matrix of natural habitats. One potential explanation for this is that competitive interactions play an increased role in natural habitats (e.g. semi-natural grassland) and in habitats where environmental filtering has reduced the diversity of functional traits (e.g. woodland and farmland), thereby facilitating considerable differentiation between the traits of co-existing species (MacArthur and Levins 1967). Consequently, the importance of different assembly mechanisms may be contingent on the environmental conditions at each specific site and both environmental filtering and competition processes may operate to structure bird communities. Changes in the FD of avian communities across different land uses (Flynn et al. 2009, Luck et al. 2013) and habitat heterogeneity gradients have been observed (Tscharntke et al. 2008); however, observations of shifts in the magnitude of importance of alternative assembly mechanisms across different habitat landscapes represent a new development in the study of avian community organisation.

The results of Chapter Five also emphasise the crucial role of natural habitats and variability in river flows for sustaining functionally rich river bird assemblages. River flow variability, including the occurrence of hydrological extremes (Kajtoch and Figarski 2013), and the maintenance of a natural habitat matrix are important for sustaining biodiverse ecological communities on rivers (Jonsson et al. 2012, Leigh et al. 2012, Catford et al. 2014). In Chapter Five, a loss of variability in land cover and flow disturbance was characterized by a decline in functionally unique or specialist species (e.g. insectivores) and an increased dominance of species with common traits (e.g. waterfowl) in a manner consistent with functional homogenization (Olden and Rooney 2006, Rooney et al. 2007). Consequently, this shows that alterations to natural riparian habitats and river flow regimes through anthropogenic regulation or climate change may have profound impacts on river bird communities. Studies such as this provide valuable evidence that illustrates the conservation value of maintaining heterogeneous riverine landscapes with natural variability in river flows whilst contributing to the multi-disciplinary evidence required for the effective management of riverine landscapes in a changing climate (Heino et al. 2009, Palmer et al. 2009, Wilby et al. 2010).

Global warming and the associated increase in climatic variability is predicted to intensify key processes in the water cycle such as precipitation, evaporation and runoff (Durack et al. 2012). As river flows are coupled closely to atmospheric drivers (Laizé and Hannah 2010), shifts in the distribution of precipitation will result in modified hydrological regimes characterised by increasing trends in the frequency, duration and magnitude of hydrological extremes, including floods and droughts (Pall et al. 2011, Prudhomme et al. 2013). Understanding of the relationship between species' distributions and hydrological extremes is limited by a scarcity of large-scale studies that encapsulate both temporal and spatial variability in species' relationships with river flow (Smith 2011b, a). However, in Chapter Six, it was possible to combine the WBBS and NRFA data to quantify the vulnerability of river bird species to a potential climate-driven shift in hydrological extremes and highlight the importance of incorporating variability in extremes in climate change impact studies of ecological communities. The intimate association between river birds and river flow variability revealed in Chapters Three to Five shows that river bird species are vulnerable to shifts in hydrology associated with global climate change. Chapter Six therefore aimed to investigate the vulnerability of river bird species to a potential climate-induced increase in the frequency, duration and magnitude of floods and droughts, by combining SDM methodology and estimates of species' exposure to future climate change impacts to develop a SVI to floods and droughts.

Five species were identified as of high or very high vulnerability. The species most vulnerable to an increase in floods and droughts were those with ecological traits that restrict their foraging or breeding behaviour to in-channel river habitat. This included species that are commonly associated with fast-flowing, upland rivers and streams in Great Britain (e.g. common sandpiper, white-throated dipper). It is likely that this vulnerability manifests through extreme high flows limiting the time birds can spend foraging (D'amico and Hémery 2007) or extreme high flows reducing the prevalence of favoured foraging microhabitats (Benson and Bednarz 2010). In addition, extreme high flows may cause mortality or increased dispersal amongst species at lower trophic levels in aquatic food webs (Bates et al. 2006, Ledger et al. 2012, O'Callaghan et al. 2013), impacting the river birds' prey base (Chiu et al. 2008, Chiu et al. 2013). As a consequence, it is possible that a climate-induced increase in the frequency and duration of flooding will affect the foraging behaviour of these species (Wood et al. 2013), whereby birds broaden their foraging niches by moving to habitats peripheral to the main channel to find preferred prey species (La Sorte and Jetz 2010). However, a negative consequence of this might be an increase the likelihood of intra- and inter-specific competition which could perhaps impact foraging efficiency through patch depletion and decreased food handling time (Tylianakis et al. 2008). Moreover, if flooding were to occur during a sensitive period of the annual cycle, a shortage of prey could also limit breeding performance, for example, through phenological mismatch (Whitehouse et al. 2013) or carry-over effects (Harrison et al. 2011). These effects may be most profound for species with limited capacity for adaptive plasticity, which, in the short-term, might allow foraging and breeding efforts to be aligned with the locations and timings of peaks in resource availability (Charmantier et al. 2008). Limited vulnerability was observed amongst species such as the Eurasian coot and grey heron that occupy a range of foraging and breeding habitats across the aquatic, riparian and terrestrial landscapes. The generalist foraging behaviour of some river bird species likely buffers these species from the full impact of the predicted future change in floods and droughts (Menéndez et al. 2006).

In Chapter Six, species' responses to river flow variables illustrate their vulnerability to a climate-induced shift in the frequency, duration and magnitude of hydrological extremes. A potential response to climate change impacts might be a shift in species' ranges (Thomas et al. 2006, Huntley et al. 2007, Lavergne et al. 2010). The objective of Chapter Seven was to investigate the potential for range shifts in a specialist river bird species which was identified as of 'High Vulnerability' to climate-induced shifts in river flows in Chapter Six, the white-throated dipper. This species has highly specific habitat requirements whereby it concentrates foraging on rivers where riffles and pools of deep water are found (Tyler and Ormerod 1994). Its foraging frequency decreases at high flow rates (O'Halloran et al. 1990) and birds become less selective when foraging during periods of high flows (Taylor and O'Halloran 2001). These behaviours mean that its distribution is highly conditional upon specific river flow regimes but also reduce its adaptive capacity to climate change.

The BEM ensemble, which was based on a suite of plausible future flow scenarios, predicted a gradual diminution of dipper $P(x)$ between present day and 2098, with this decline most rapid in western areas of Great Britain. This was principally driven by a projected decrease in flow magnitude and variability around low flows. The model ensemble also predicted a significant eastward shift in species' occurrences but no significant shift in latitude. This contrasts with previous studies of dippers which suggest a northward shift in range in response to climate change (Huntley et al. 2007). However, most avian-focussed models, including those for dipper, that assess the impact of climate change on species' distributions have been constructed using climatic predictors alone, which may be poor predictors of species' distributions (Thuiller et al. 2004, Araújo et al. 2005, Baselga et al. 2012). However, in Chapter Seven, by incorporating river flow, which is an important factor in dipper habitat suitability (Tyler and Ormerod 1994), into the climate impact models, an element of biological 'realism' that is often absent from models constructed using climatic predictors alone was included in the model predictions. This is crucial for riverine species as non-climatic impacts tend to dominate local, short-term biological changes (Ormerod et al. 2010, Araújo and Rozenfeld 2013).

The predictions of future dipper distribution in Chapter Seven suggest that climate-induced changes in river flow may represent a previously unidentified mechanism by which climate change may mediate range shifts in species in riverine environments wholly or largely dependent on aquatic food resources. Moreover, they reveal that a focus solely on climatic predictors in BEM-type models may well under-estimate the full impact of climate change on species' distributions. The addition of habitat factors into BEM models will increase their value and appropriateness through the inclusion of data that adds more biological 'realism' to, often coarse, large-scale climate models (Araújo and Peterson 2012). Moreover, the inclusion of habitat factors will expand the range of environmental conditions under which models are calibrated (Thuiller et al. 2004) and this will help to improve the predictive performance of climate impacts models of aquatic and riparian species' distributions (Domisch et al. 2013).

8.2 Conclusions

The success in relating hydrological indices to the distributions of river birds demonstrates that variability in river flow regime has consequences for the distribution of riparian species and ecological structure at high trophic levels in aquatic-riparian food networks. By using national-level, long-term datasets, it was possible to identify spatial and temporal patterns in species' relationships with river flow variability. These relationships are complex but can be explained by ecological traits that characterize species within aquatic-riparian ecosystems. This thesis has also demonstrated that variability in river flow acts not only on individual species' distributions but is a pervasive environmental filter that influences the structure of river bird assemblages, with evidence suggesting that other alternative assembly mechanisms (e.g. biotic interaction) are reduced to an ancillary role relative to environmental filtering. This highlights the importance for macro-ecological studies of species' interaction to consider shared environmental responses, especially in environments where gradients of disturbance exist such as estuarine landscapes with intertidal habitats or floodplains. Further research that investigates the interaction between the operation of assembly rules and changes in key environmental drivers will add great insight into the future impacts of environmental change on riverine systems. In particular, this might further our understanding of the impacts of environmental change on specialist or functionally unique riverine species from a range of taxa.

This thesis also showed that the influence of river flow on community structure is contingent on the traits present in river bird assemblages. For instance, a loss of river flow variability has disproportionate impacts on species with rare or specialist functional traits. Consequently, the maintenance of 'natural' river flow regimes will be important to sustain functionally rich river bird assemblages. It is also plausible that the impacts of alterations to river flows might be greatest for particular taxonomic groups that share particular traits or that occur at low abundances. Such patterns will be best tested through experimental work on different faunal groups across multiple trophic levels. Species' vulnerability to climate change and a climate-induced shift in the frequency, intensity and magnitude of hydrological extremes are also determined by ecological traits. The phenomenon of trait-mediated vulnerability to climate change impacts deserves further research such that the riverine species most likely to be threatened by future climate change may be identified.

Conservation efforts in an era of climatic uncertainty will increasingly rely on the careful targeting of valuable resources at priority species and priority regions. Therefore, practical methodological frameworks such as the SVI in this thesis that develop hierarchical levels of vulnerability across a range of avian and non-avian taxa will become increasingly valuable to applied conservation. Conservation efforts will also need to take into consideration the potential for shifts in species' range as this thesis has also demonstrated the potential for a riverine specialist river bird species to alter its distribution in responses to changes in river flow habitat suitability. Climate change-induced shifts in flow may therefore present a previously unidentified threat to species in riverine environments wholly or largely dependent on aquatic food resources. The application of BEM-type ensemble modelling approaches clearly has value in projecting climate change impacts whilst capturing uncertainty in predictions.

This thesis also emphasises the value and applicability of long-term and spatially broad annual bird survey data and daily river flow data. In particular, this allowed species' distributions to be related to measures of hydrological extremes that are typically difficult to study due to their rarity and unpredictability. These data allowed species' relationships to be placed in the context of previous exposure to the investigated parameter. This is extremely important given that the precise definition of an 'extreme event' can be highly dependent upon the magnitude of previous flow events within a particular focal system. The application of these long-term data in this thesis therefore validates large-scale ornithological surveys currently being conducted by organisations such as the BTO or the European Bird Census Council (EBCC) (Hagermeijer 1997). Without the accumulation of decades of data that were utilized here the opportunity to study phenomena such as hydrological extremes might not have been possible. Long-term monitoring data can therefore yield high quality ecological studies and are vital in identifying new research problems.

This thesis represents an important contribution in helping to understand how river flow influences the distribution of riparian species and how bird communities might respond to a climate change-induced shift in river flow. It also highlights a potential vulnerability of riparian species to an increase in the intensity of floods and droughts resulting from climate change. By combining two large-scale, national-level datasets, the approach utilised in this thesis not only generates new insights into hydroecological interactions, but also establishes foundations for further work on modelling of the impact of river flow variability on both avian and non-avian water-dependent taxa.

9. Appendices

9.1. Appendix A – Appendices for Chapter Four

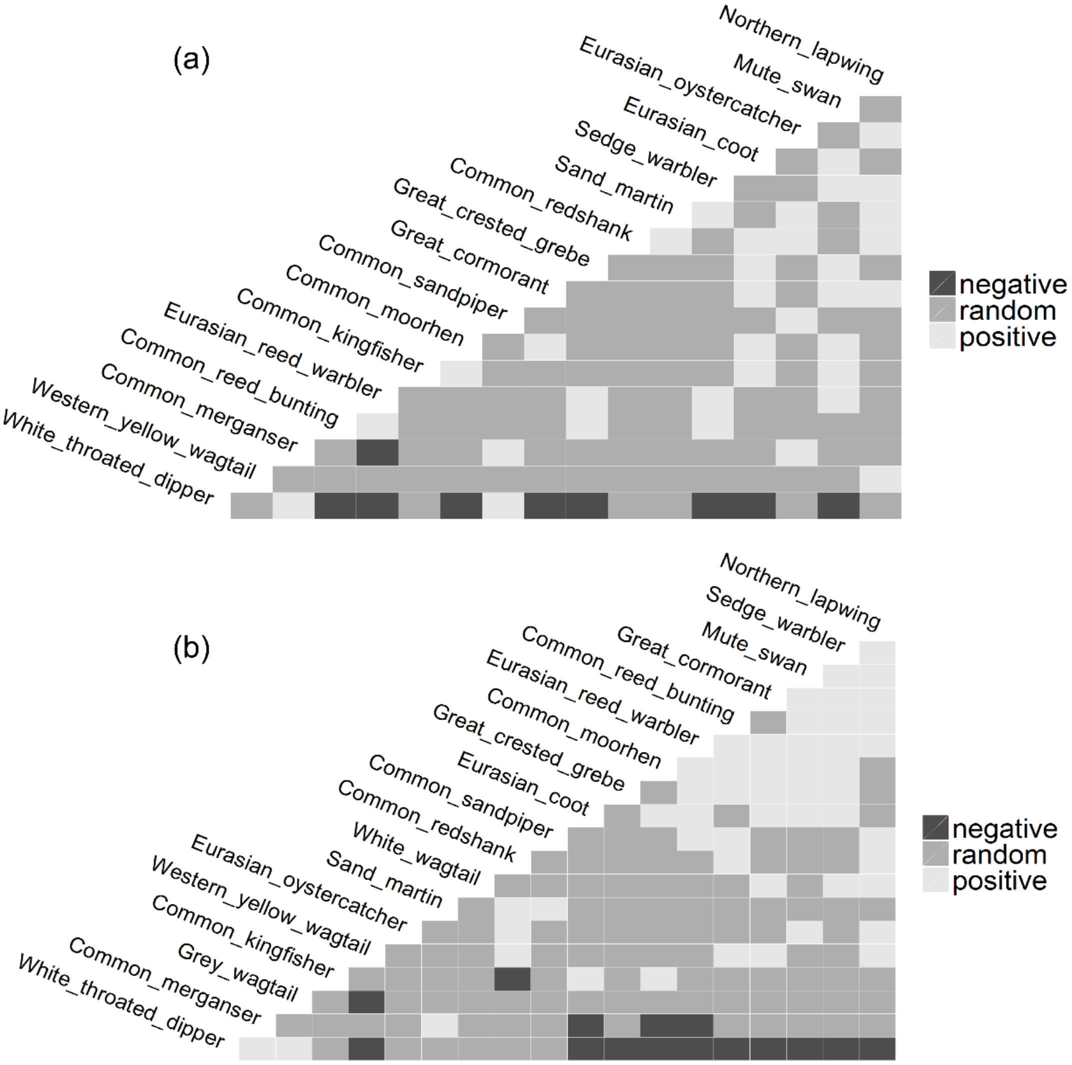

Figure A1 Heatmap visualisations showing pairwise associations between 19 river bird species calculated according to the probability model of species co-occurrence for locations with high (a) and low (b) river flow disturbance (Griffith In press). The 100 Waterways Breeding Bird Survey (WBBS) locations were ranked by the standard deviation of annual flows, calculated between 1998 and 2011 (inclusive). The locations with the 50 highest standard deviation of annual flows values were categorised as of high disturbance (plot a) *and the 50 locations with the lowest values as of low disturbance (plot b). Significant positive (negative) associations are displayed where species co-occurred more (less) frequently than by chance, with an alpha threshold of 0.05. For the high disturbance locations (a), 20% of species' associations were positive, 5% were negative, and 75% were random. For the low disturbance locations (b), 30% of species' associations were positive, 9% were negative, and 61% were random.*

9.2. Appendix B – Appendices for Chapter Five

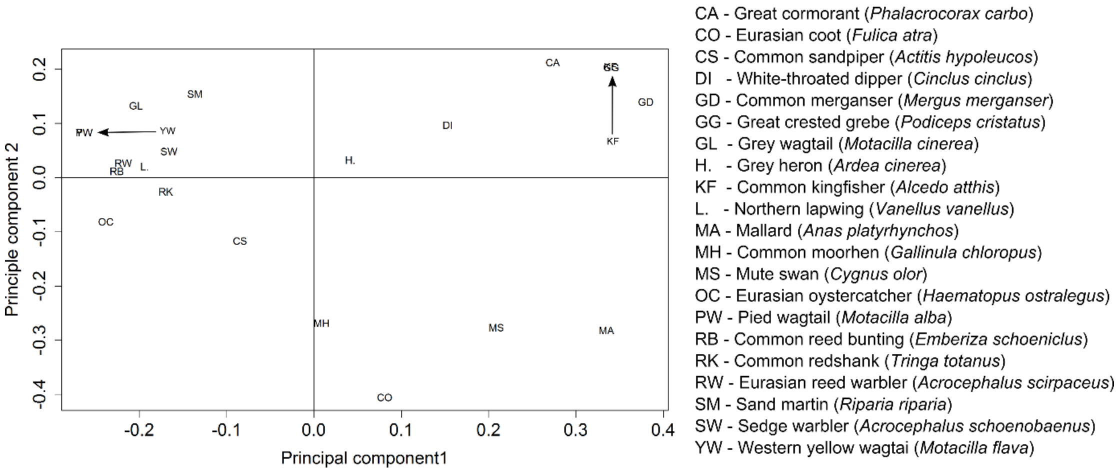

Figure B1 List of river bird species used in analyses and a PCA biplot showing the position of each species in trait space.

Figure B2 Figure of the geographical distribution of the 101 Waterways Breeding Bird Survey (WBBS) locations used to collate bird survey data.

Table B1 Table of the major habitat types recorded within the four WBBS habitat land cover categories. The prevalence (%) of each habitat within the land use categories is also indicated in parenthesis. A fifth category ('mixed') was included in analyses to account for survey locations with no dominant habitats.

Farmland	**Semi-natural Grassland**	**Urban**	**Woodland**
Improved grassland (48%)	Chalk downland (0.1%)	Urban (18%)	Broadleaved (65%)
Unimproved grassland (21%)	Grass moor (36%)	Suburban (48%)	Coniferous (7%)
Mixed grass/tilled land (12%)	Grass moor mixed with heather (12%)	Rural (34%)	Mixed (>10% of each) (22%)
Tiled land (18%)	Machair (0.1%)		Broadleaved waterlogged (4%)
Orchard (0.1%)	Other dry grassland (10%)		Coniferous waterlogged (0%)
Other farming (0.3%)	Water-meadow/grazing marsh (30%)		Mixed waterlogged (1%)
	Reed swamp (7%)		
	Other open marsh (4%)		
	Saltmarsh (0.3%)		

Table B2 Results of the generalized additive models (GAMs) used to examine the association of winter climate with observed and standard effect size (SES) measures of three indices of functional diversity (FD): functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). The coefficients for the winter climate variables are displayed. 'Edf' is the equivalent degrees of freedom.

	Functional richness FRic			Standard Effect Size FRic		
	Deviance explained = 48.7%			Deviance explained = 31.7%		
Model term	Edf	*F*	*P* value	Edf	*F*	*P* value
Mean winter temperature (°C)	5.605	0.351	0.927	5.649	0.387	0.908
Mean winter rainfall (mm)	2.081	0.282	0.813	2.255	0.177	0.904

	Functional evenness FEve			Standard Effect Size FEve		
	Deviance explained = 16.5%			Deviance explained = 22.9%		
Model term	Edf	*F*	*P* value	Edf	*F*	*P* value
Mean winter temperature (°C)	1	0.076	0.784	1	0.147	0.702
Mean winter rainfall (mm)	1.615	0.523	0.517	1	0.919	0.338

	Functional divergence FDiv			Standard Effect Size FDiv		
	Deviance explained = 15%			Deviance explained = 14.8%		
Model term	Edf	*F*	*P* value	Edf	*F*	*P* value
Mean winter temperature (°C)	1.332	0.047	0.922	1.001	0.294	0.588
Mean winter rainfall (mm)	1.603	0.160	0.853	1.444	0.033	0.955

Table B3 Table of the correlation coefficients from Pearson correlation analysis between species richness and the three FD indices.

	Species richness SR	Functional richness FRic	Functional evenness FEve	Functional divergence FDiv
Species richness SR	---	0.71	0.11	0.06
Functional richness FRic	---	---	-0.11	0.24
Functional evenness FEve	---	---	---	-0.06
Functional divergence FDiv	---	---	---	---

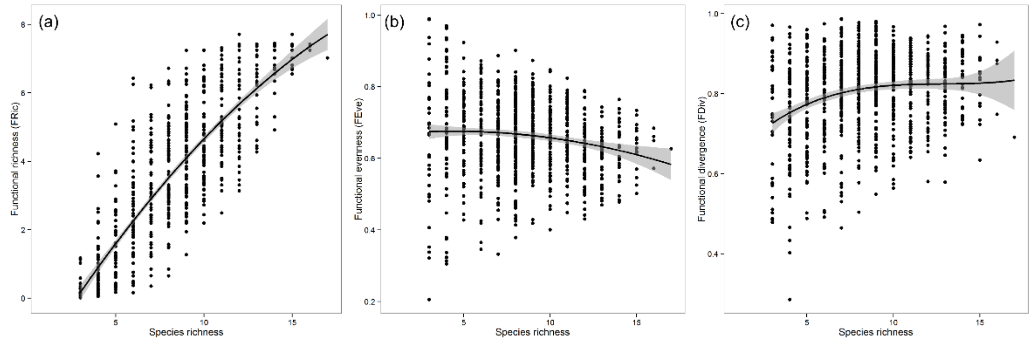

Figure B3 Relationship between species richness (SR) and the three functional diversity (FD) indices; (a) functional richness (FRic), (b) functional evenness (FEve), and (c) functional divergence (FDiv). The solid line is the predicted relationship from a linear regression model with a second order polynomial ([a] and [b]) and a third order polynomial (c). Shaded regions represent 95% confidence intervals.

9.3. Appendix C - Appendices for Chapter Six

9.3.1. Appendix C1- Further notes on Generalized Estimating Equations (GEEs)

In hierarchical datasets where multiple visits are made to survey locations, the independence assumption is violated due to potential inter-cluster autocorrelation. Ignoring this dependence structure in a conventional regression would under-estimate the variance and standard errors, resulting in spurious correlations and associated Type I errors. GEEs, first introduced by (Liang and Zeger 1986), are a statistical tool that extends Generalized Linear Models (GLMs) with quasi-likelihood estimation to correct for correlated data by adjusting the confidence limits around the parameter estimates to take account of the autocorrelation. The estimates of the regression coefficients tend to be similar to those of a conventional GLM and can be interpreted in the same way. Generalized linear mixed models (GLMMs) can also be used to account for within-subject correlation but they do not make allowance for particular correlation structures (e.g. where temporal dependence occurs). GEEs have the advantage in allowing a ‘working correlation’ structure to be specified for the covariance matrix prior to fitting the model, thereby allowing for the incorporation of prior knowledge of the nature of the within-cluster dependency (Zorn 2001). This is made possible by the adoption of a marginal model approach whereby the mean response only depends on covariates and not on random effects. Conventional random effects models on the other hand model the probability distribution of the dependent variable as a function of the covariates as well as a parameter specific to each cluster, allowing the within-cluster dependency on the covariance matrix to vary between observations (Zorn 2001). The accuracy of GEEs is maximised where there is some prior knowledge of the correlation structure, although estimates from GEEs are thought to be robust to mis-specification of the correlation structure (Zorn 2001, Diggle 2002).

9.3.2. Appendix C2 – Expert profiles

Dr Greg Conway, British Trust for Ornithology (BTO) - Research ecologist responsible for the organisation of single species surveys in Great Britain for the BTO.

John Marchant, British Trust for Ornithology - Projects coordinator for the BTO monitoring team, organising long-term BTO surveys including Waterways Breeding Bird Survey (WBBS).

Prof. John O'Halloran, University College Cork - Applied ecologist with particular interests in how land use and habitat changes influence the distribution and abundance of avian species. He has a specific interest in the white-throated dipper.

Dr John Quinn, University College Cork - Evolutionary ecologist with particular interests in avian cognitive ability and personality, seabird ecology, predator-prey interactions and group living, applied ecology, and wetland and waterbird ecology.

Dr Ian Hartley, Lancaster University - Behavioural ecologist with particular emphasis on family interactions, including mate choice and parental care, in birds.

Dr Will Cresswell, University of St Andrews - Behavioural and conservation ecologist with particular research interests in predation risk, and foraging behaviour and the conservation of migrant bird species.

9.3.1. Appendix C3 - Sensitivity and uncertainty analyses

Table C1 BIC scores assigned to 16 species for 14 hydrological parameters and sensitivity scores for high flows (S_{high}) and low flows (S_{low}) and total sensitivity scores (S_{total}). Parameters for frequency and duration were measured across a range of extremes defined using quantiles (e.g. Q1 = 1st quantile). Number of survey locations varied between species. Superscript indicates the direction of species' responses to the respective parameter.

Species	**High flows**							**Low flows**							S_{high}	S_{low}	S_{total}
	Frequency			**Duration**			**Magnitude**	**Frequency**			**Duration**			**Magnitude**			
	Q1	**Q10**	**Q25**	**Q1**	**Q10**	**Q25**	**Max/Q50**	**Q99**	**Q90**	**Q75**	**Q99**	**Q90**	**Q75**	**Min/Q50**			
Common kingfisher *Alcedo atthis*	0	0	0	0	0	0	2^-	0	0	0	0	0	0	0	2	0	2
Common moorhen *Gallinula chloropus*	0	1.56^+	0	0	0.78^+	0	0	0.43^-	0	0	0.43^-	1.56^-	0	0	2.3	2.4	4.7
Common sandpiper *Actitis hypoleucos*	0	0.78^-	1.48^-	0	1.56^-	2.97^-	0	0	0.78^+	2.97^+	0	1.56^+	4.45^+	0	6.8	9.8	16.6
Cormorant *Phalacrocorax carbo*	0	0.78^-	0	0	0.78^-	0	0	0	0	1.48^+	0	0	2.97^+	0	1.6	4.4	6
Eurasian coot *Fulica atra*	0	0	0	0	0	0	0	0	0	0	0	0	1.48^-	0	0	1.5	1.5
Eurasian curlew *Numenius arquata*	0	0	0	0.43^+	0	0	0	0.86^+	0	0	0.86^+	0	0	2^-	0.4	3.7	4.1
Common merganser *Mergus merganser*	0	2.34^+	4.45^+	0	2.34^+	1.48^+	0	0	0	0	0	0	4.45^-	0	10.6	4.4	15
Great crested grebe *Podiceps cristatus*	0	0	1.48^-	0	0	1.48^-	0	0.86^-	0	0	0.86^-	0	0	0	3	1.7	4.7
Grey heron *Ardea cinerea*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grey wagtail *Motacilla cinerea*	0.43^+	0	0	0	0.78^-	0	0	0	0	0	0	0.78^-	0	1	1.2	1.8	3
Mute swan *Cygnus olor*	0	0	2.97^-	0	0	1.48^-	1^-	0	1.56^+	2.97^+	0	0	0	1^+	5.4	5.5	10.9
Northern lapwing *Vanellus vanellus*	0	0	1.48^+	0	0.78^+	1.48^+	0	0	0	0	0.43^-	0	0	0	3.7	0.4	4.1
Reed bunting *Emberiza schoeniclus*	0.43^-	0	0	0	0	0	1^-	0	0	0	0	0.78^+	0	0	1.4	0.8	2.2
Reed warbler *Acrocephalus scirpaceus*	0	0.78^-	0	0	0.78^-	1.48^-	0	0	0	0	0	0	2.97^+	1^+	3	4	7
Sand martin *Riparia riparia*	0	0	0	0	0.78^-	0	0	0.43^-	0.78^-	1.48^-	0.86^-	0.78^-	0	0	0.8	4.3	5.1
White-throated dipper *Cinclus cinclus*	0.43^+	1.56^+	0	0.43^+	1.56^+	0	1^+	0	0	0	0	0	0	0	5	0	5

An uncertainty analysis was carried out to investigate how the results of the SVI might be influenced by inaccuracies in the sensitivity or exposure scoring. Following Garthe and Huppop (2004), one species from each category of vulnerability was randomly selected and the sensitivity score and a randomly selected exposure score were manipulated by the addition of 1 where possible (maximum exposure scores of 3 cannot be increased) and the deviation of manipulated VI scores from the original scores calculated. Furthermore, the sensitivity and robustness of the GEE approach was assessed by comparing the final SVI rankings using GEEs with those from a generalized linear mixed-effects model approach. This specified a random intercept for survey location to account for variation between locations, and a first-order autoregressive temporal correlation structure. One species from each vulnerability ranking was randomly selected and species' relative abundances were modelled with the hydrological parameters using the lme4 package in R (Bates et al. 2011).

For the four randomly selected species analysed, the final VItotal rankings were identical for both the GEEs and mixed-effects modelling approaches suggesting that the SVI methodology was robust to choice of modelling approach. When sensitivity scores were manipulated by 1, the deviation in VItotal was reasonable: 0.1 for common merganser, 0.1 for common sandpiper, 0.2 for sand martin and 0.6 for Eurasian coot. The deviation in VItotal was similarly moderate when an exposure factor was manipulated: 0.6 for common merganser, 0.7 for common sandpiper, 0.5 for sand martin and 0.2 for Eurasian coot (*Fulica atra*). The deviations between perturbed and original VItotal scores were comparable to those of other published studies (Garthe and Huppop 2004).

Table C2 Comparison of total sensitivity scores (S_{total}) and total vulnerability (VI_{total}) calculations for four randomly selected avian species using a generalized estimating equation and a generalized liner mixed-effects model approach.

	Generalized Estimating Equations		**Generalized Linear Mixed-Effects Model**	
Species	$\mathbf{S_{total}}$	$\mathbf{VI_{total}}$	$\mathbf{S_{total}}$	$\mathbf{VI_{total}}$
Common merganser	15.11	6.25	4.68	3.92
Common sandpiper	16.64	5.01	8.19	3.88
Sand martin	5.11	2.72	1.56	1.43
Eurasian coot	1.48	1.59	1.00	1.21

9.3.2. Appendix C4 – Experts' scoring

Table C3 Experts' scoring of exposure factors relating to avian species' vulnerability.

	Foraging habitat						Breeding habitat						Food specialisation						Dispersal potential					
Expert	A	B	C	D	E	F	A	B	C	D	E	F	A	B	C	D	E	F	A	B	C	D	E	F
Common kingfisher *Alcedo atthis*	3	3	3	3	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	2	2	2	3	3
Common moorhen *Gallinula chloropus*	3	1	2	1	2	1	3	1	2	1	2	2	2	1	3	1	2	1	2	3	3	3	3	3
Common sandpiper *Actitis hypoleucos*	3	2	3	2	3	2	2	2	3	2	3	3	2	2	3	2	2	2	3	1	1	1	1	1
Cormorant *Phalacrocorax carbo*	3	3	1	3	1	2	1	3	1	1	1	2	3	3	3	3	3	3	3	2	2	2	2	2
Eurasian coot *Fulica atra*	2	2	2	2	2	2	1	3	2	2	2	2	1	2	1	1	2	1	2	3	1	1	2	2
Eurasian curlew *Numenius arquata*	1	2	1	1	1	1	1	1	3	1	3	1	1	2	1	1	2	1	1	1	1	1	2	1
Common merganser *Mergus merganser*	3	3	3	3	2	2	1	2	3	1	3	1	3	3	3	3	3	3	1	2	1	2	2	1
Great crested grebe *Podiceps cristatus*	3	3	3	3	3	2	3	3	3	3	3	2	3	3	3	3	3	3	2	2	1	2	2	2
Grey heron *Ardea cinerea*	2	2	1	1	1	2	1	1	1	1	2	2	3	3	1	1	3	3	2	2	2	3	2	2
Grey wagtail *Motacilla cinerea*	2	2	2	2	2	2	2	3	2	2	3	3	2	2	2	1	3	2	3	2	2	2	2	2
Mute swan *Cygnus olor*	3	2	1	2	1	2	2	3	2	2	1	2	2	2	1	2	1	3	2	3	2	2	2	3
Northern lapwing *Vanellus vanellus*	1	1	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1
Reed bunting *Emberiza schoeniclus*	1	1	2	1	2	1	1	2	2	1	2	1	1	1	2	1	1	1	2	2	3	3	2	3
Reed warbler *Acrocephalus scirpaceus*	1	2	2	2	3	3	3	2	2	2	3	3	1	2	2	2	2	1	1	1	1	1	1	1
Sand martin *Riparia riparia*	2	2	1	1	2	2	2	2	1	2	3	2	1	2	2	1	2	1	1	1	1	1	1	1
White-throated dipper *Cinclus cinclus*	2	3	3	2	3	3	2	3	3	2	3	3	2	3	3	2	3	3	3	3	3	3	3	3
Common kingfisher *Alcedo atthis*	3	3	3	3	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	2	2	2	3	3

9.4. Appendix D - Appendices for Chapter Seven

9.4.1. Appendix D1 – Supplementary methods

The choice of threshold selection method in building binary models is a key step because this can have large impacts on modelled predictions and, consequently, may result in considerable differences in projected alterations to species' ranges (Nenzén and Araújo 2011). Therefore, a statistic, K, which is more robust to threshold selection than other commonly used methods (e.g. TSS, ROC) was adopted (Nenzén and Araújo 2011). K assesses model performance by comparing it to the performance expected by chance (Cohen 1960). It is a widely used measure for assessing the accuracy of presence-absence predictions, in part because of its tolerance of zero values. K values < 0.40 indicate poor model performance, 0.40 - 0.75 good performance, and > 0.75 excellent performance (Landis and Koch 1977). Furthermore, rather than use a simple arbitrary P_s value of 0.5, the predictive power of the models was optimised by testing P_s values from 0.0 to 1.0 in 100 steps and selecting the P_s value that maximises model prediction accuracy (Huntley et al. 2012).

Table D1 Description of dates used to create seven 12 year time slices (including a baseline period) and one 10 year time slice.

Period	**Time slice**
Baseline	1st October 1997 – 30th September 2010
1	1st October 2010 – 30th September 2023
2	1st October 2023 – 30th September 2036
3	1st October 2036 – 30th September 2049
4	1st October 2049 – 30th September 2062
5	1st October 2062 – 30th September 2075
6	1st October 2075 – 30th September 2088
7	1st October 2088 – 31st December 2098

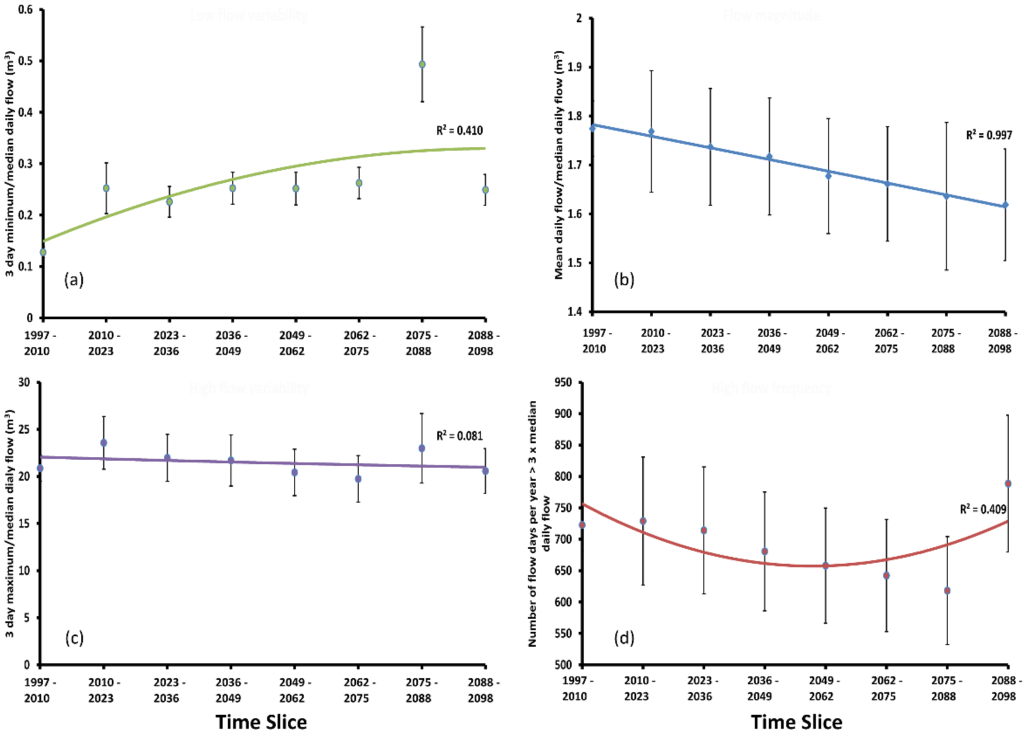

Figure D1 Plots showing the predicted trends in the four model predictor variables: (a) low flow variability, (b) flow magnitude, (c) high flow variability, and (d) high flow frequency. The standard error bars represent variation in the 11 model scenarios, between a baseline period through seven future periods. Changes in Dipper occurrence were primarily driven by variation in low flow variability and a long-term decline in flow magnitude.

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