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

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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 the ecology of 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, we construct a Bioclimatic Envelope Model (BEM) ensemble 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 (*Cinclus cinclus*). 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.

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INTRODUCTION

Climate warming and associated changes in precipitation patterns are predicted to modify river flows (Pall et al. 2011, Prudhomme et al. 2013*a*). 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 are 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 organization (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 macroinvertebrates (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.

Here, we use predictions of climate-driven changes in the flow regimes of British rivers (Prudhomme et al. 2013b) to model shifts in the probability of occurrence ($P(x)$) of the White-throated Dipper (*Cinclus cinclus*) (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 behaviors also mean the Dipper occupies a unique niche among passerine birds in Great Britain and these behaviors are likely to reduce its adaptive capacity to climate change.

The modelling procedure was a two-part process: (1) develop a correlative model to relate Dipper distribution to variables of river flow, and (2) construction of a Bioclimatic Envelope Model (BEM) ensemble using future flow predictor variables. The models were constructed using an extensive bird survey dataset from the British Trust for Ornithology's (BTO's) Waterways Breeding Bird Survey (WBBS) and river flow archive data. By using flow parameters to describe climate-driven changes in species' habitat our 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.

METHODS

Data and model structure

We defined the structure of the BEMs 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. Our response variable was defined as the presence or absence of birds at a survey location across the entirety of the time series. We reduced the likelihood of incorporating false zeros into the data set by only using WBBS survey locations surveyed at least three times, as multiple site visits provides 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 multicollinearity exists among them (Olden and Poff 2003). Therefore, we identified a priori model parameters that characterize key facets of the hydrological regime on rivers in Great Britain (e.g., variation in flow magnitude, frequency, and duration). In Royan et al. 2013, the importance of river flow predictor variables in describing Dipper distribution was tested using a model averaging approach, comparing the performance of 31 plausible model structures. Here we constructed our models using the four hydrological variables (Table 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 utilized. 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).

We found strong evidence of non-linear relationships so the bivariate relationship and functional form between hydrological predictors and Dipper distribution were modelled using Gener-

Table 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	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.

alized 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). 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.

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. 2012*a*). 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, our 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
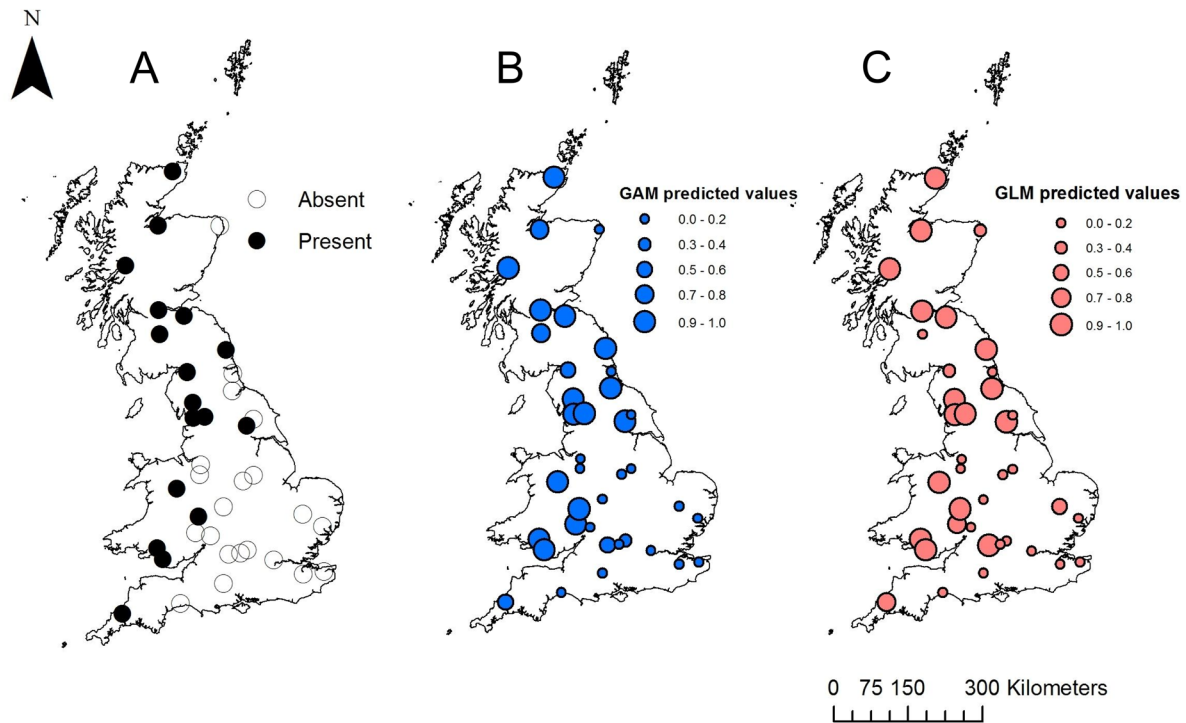
Fig. 1. Maps showing (A) the survey records of Dipper presence/absence for 38 locations, (B) the Generalized Additive Model (GAM) predicted values (Cohen's Kappa = 0.843), and (C) the Generalized Linear Model (GLM) predicted values (Cohen's Kappa = 0.684).

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 analyzed 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 (Appendix B). 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.

RESULTS

Both the GAM (K = 0.843) and GLM (K = 0.684) approaches successfully captured species' current distribution (Fig. 1).There was considerable overlap in predicted trends between GAM and GLM models, indicating strong convergence of findings (Fig. 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 (Tables 2 and 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 (Fig. 2). Changes in the east of Great Britain were considerably smaller than in western regions, with $P(x)$s estimated to show a
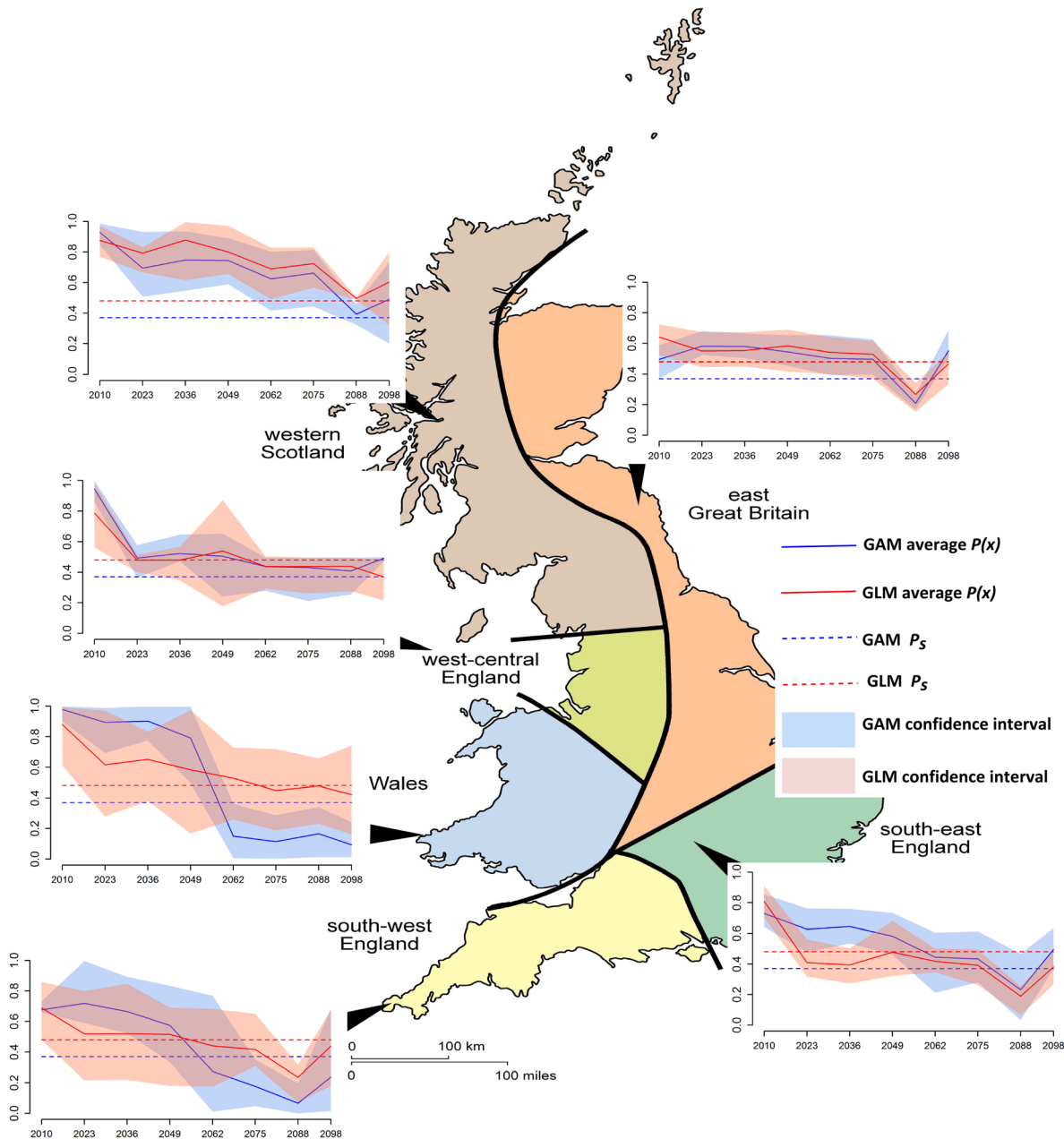
Fig. 2. GAM (blue line) and GLM (red line) predicted trends in the regionalized average $P(x)$ of Dipper (y axes), between a baseline period through seven future periods (x axes), with shaded regions illustrating the range between 5th and 95th percentiles as an indication of the uncertainty in climate predictions across the 11 plausible scenarios. Dashed lines represent P_s for both the GAM and GLM models, whereby values above and below the lines represent a likelihood of occurrence and absence, respectively.

change between the baseline period and last time period of between +12% and −27%, although models were in less agreement.

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 (Fig. 2), presumably because such regions form the core of this species' range

Table 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; SE = 0.324; T = −0.304; P = 0.762.

Table 3. Generalized Linear Model (GLM) coefficients for hydrological indices.

Hydrological index	Coefficient	SE	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; SE = 0.933; T = 3.772; P < 0.001.

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 southwest England, and between 2023 and 2088 in southeast 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 (Appendix C).

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 = −2.390, P = 0.03, +0.984° ± 0.357°; GLM: t = −2.511, P = 0.02, +0.798° ± 0.257°). There was no significant shift in the latitude of modelled occurrences (GAM: t = 0.293, P = 0.77; GLM: t = 0.300, P = 0.77).

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). Our BEMs 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 Rozenfeld 2013). 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 we were able 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 et al. 1997) 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.

Our results 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.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Supplementary methods

Waterways Breeding Bird Survey (WBBS) locations consisted of a single stretch of river averaging 3 km in length (range: 0.5–5 km) that overlapped a focal randomly selected 2×2 km tetrad. Each location was surveyed at least three times during the survey time series. Bird survey data were paired with flow data collected at gauging stations within 10 km of each WBBS sample location. However, paired data were not analyzed where a major tributary inflow occurred between the gauging station and survey location. This was to ensure flow metrics calculated at gauging station sites were representative of flow at survey locations and to avoid inconsistencies caused by flow influxes at large tributaries. Furthermore, for gauging stations with <10% missing values for any one year, we interpolated data gaps using long-term mean daily flows; however, gauging stations with ≥10% missing values were excluded from the analyses (Monk et al. 2007). Flow data were extracted from the UK National River Flow Archive (NRFA).

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, we

decided to adopt a statistic, *K*, which 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. *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, we optimized the predictive power of the models 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).

APPENDIX B

Table B1. Description of dates used to create seven 12-year time slices (including a baseline period) and one 10-year time slice.

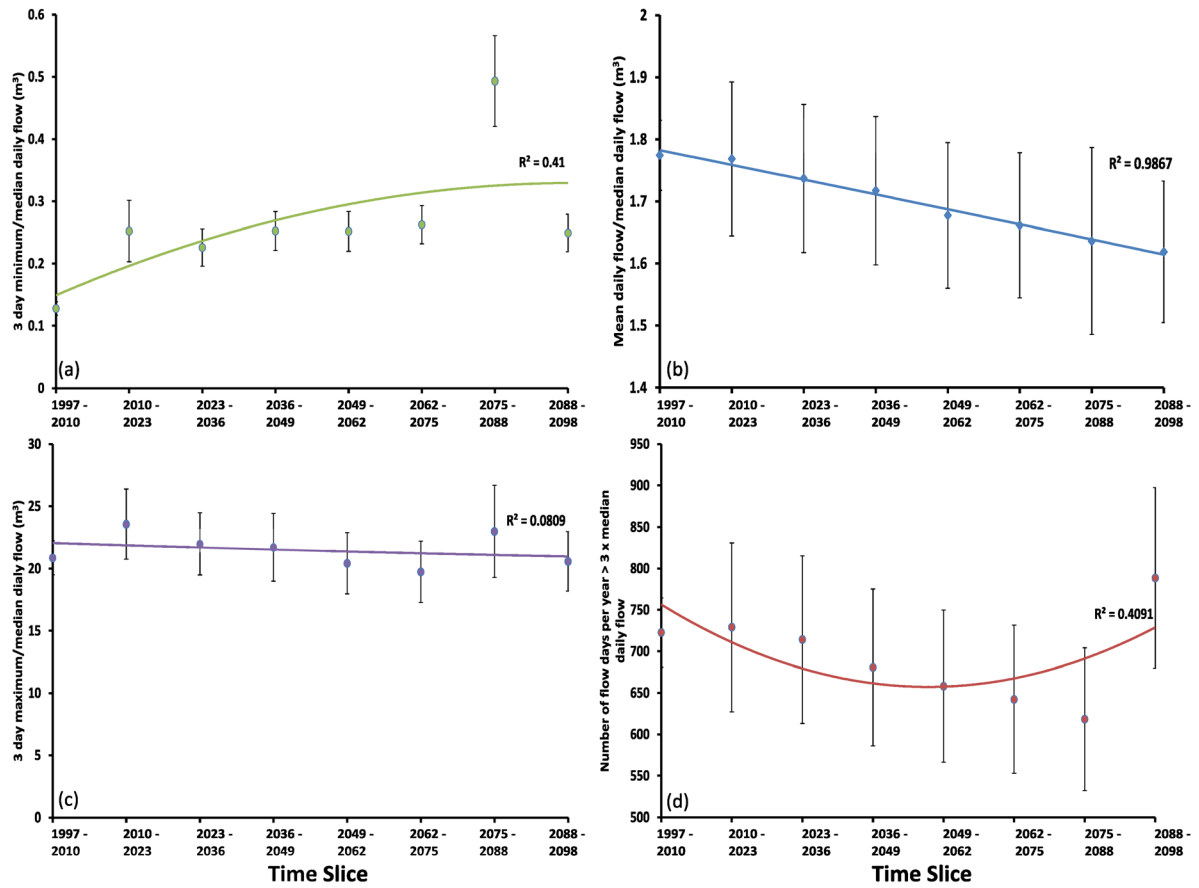| Period	Time slice
Baseline	1 October 1997 to 30 September 2010
1	1 October 2010 to 30 September 2023
2	1 October 2023 to 30 September 2036
3	1 October 2036 to 30 September 2049
4	1 October 2049 to 30 September 2062
5	1 October 2062 to 30 September 2075
6	1 October 2075 to 30 September 2088
7	1 October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

Appendix C

Fig. C1. 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.