

1 **Title: Attributing changes in the distribution of species abundance to weather variables**
2 **using the example of British breeding birds**

3

4 **Short Running Title: Attributing abundance changes to weather variables**

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21

22 **Summary**

23 **1.** Modelling spatio-temporal changes in species abundance and attributing those
24 changes to potential drivers such as climate, is an important but difficult problem. The
25 standard approach for incorporating climatic variables into such models is to include each
26 weather variable as a single covariate whose effect is expressed through a low-order
27 polynomial or smoother in an additive model. This, however, confounds the spatial and
28 temporal effects of the covariates.

29 **2.** We developed a novel approach to distinguish between three types of change in any
30 particular weather covariate. We decomposed the weather covariate into three new covariates
31 by separating out temporal variation in weather (averaging over space), spatial variation in
32 weather (averaging over years) and a space-time anomaly term (residual variation). These
33 three covariates were each fitted separately in the models. We illustrate the approach using
34 generalized additive models applied to count data for a selection of species from the UK's
35 Breeding Bird Survey, 1994-2013. The weather covariates considered were the mean
36 temperatures during the preceding winter and temperatures and rainfall during the preceding
37 breeding season. We compare models that include these covariates directly with models
38 including decomposed components of the same covariates, considering both linear and
39 smooth relationships.

40 **3.** The lowest QAIC values were always associated with a decomposed weather
41 covariate model. Different relationships between counts and the three new covariates
42 provided strong evidence that the effects of changes in covariate values depended on whether
43 changes took place in space, in time, or in the space-time anomaly. These results promote
44 caution in predicting species distribution and abundance in future climate, based on
45 relationships that are largely determined by environmental variation over space.

46 **4.** Our methods estimate the effect of temporal changes in weather, whilst accounting for
47 spatial effects of long-term climate, improving inference on overall and/or localised effects of
48 climate change. With increasing availability of large-scale data sets, need is growing for
49 appropriate analytical tools. The proposed decomposition of the weather variables represents
50 an important advance by eliminating the confounding issue often inherent in large-scale data
51 sets.

52

53 **Key words:** *climate change; decomposition of spatial, temporal and anomaly effects;*
54 *generalized additive models; generalized linear models; spatio-temporal modelling; species*
55 *abundance; UKCP09 climate projections.*

56

57 **1. Introduction**

58 It has been demonstrated for a wide range of taxa that climate change has an effect on
59 abundance and distribution of individual species as well as community measures of
60 biodiversity (e.g. Talley, Coley & Kursar 2002; Schummer et al. 2010; WallisDeVries,
61 Baxter & Van Vliet 2011). In order to detect or predict the impacts of climate change on
62 biodiversity, many studies either analyse spatial variation in species' abundance or
63 occurrence as a function of spatial variation in climate (e.g. Beale et al. 2013, Renwick et al.
64 2012, Johnston et al. 2013), or temporal variation in abundance in relation to temporal
65 changes in weather variables (e.g. Davey et al. 2012, Devictor et al. 2012, Pearce-Higgins et
66 al. 2015). However, the potential to improve inference from combined spatio-temporal
67 variation in both biological and climate/weather variables has rarely been considered. The
68 standard approach currently available for this is to include either a single covariate in a
69 generalized linear model, or a single smoothing term in a generalized additive model (GAM)
70 (e.g. Araújo et al. 2005). However, this approach confounds the spatial and temporal effects

71 of the covariates. This confounding means, e.g., that a change in temperature in one location
72 from 12°C to 13°C would have the same effect as the difference between two locations at one
73 point in time: one location at 12°C and one at 13°C.

74 We developed a method with more flexibility in attributing patterns in abundance
75 which disentangles the temporal and spatial effects of the weather covariates via
76 decomposition into three components. The temporal term is the average of observed covariate
77 values over space for a given time; the spatial term is the average over time for a given
78 location; the space-time anomaly term is the residual variation for a given location and time.
79 When using these decomposed covariates, a difference in the original covariate can be
80 associated with the temporal, spatial or residual variation component or a combination of the
81 components. This method allows the fitted models to differentiate between spatial, temporal
82 and spatio-temporal variation in the original weather covariate on abundance, thus alleviating
83 the confounding issue.

84 To investigate changes in species abundances over space and time, data are required
85 from well-designed long-term surveys such as the UK Breeding Bird Survey (BBS). The UK
86 BBS is a large-scale biodiversity monitoring programme with a protocol that allows spatio-
87 temporal correlation in animal abundances *and* differences in detectability to be accounted
88 for (Yoccoz, Nichols & Boulinier 2001; Risely et al. 2013), both of which can cause serious
89 biases in analyses of biodiversity or abundance trends (Buckland et al. 2012). To
90 accommodate imperfect detectability in observed counts, sites are surveyed using line-
91 transect methods, an example of distance sampling (Buckland et al. 2001). We accounted for
92 spatial and temporal autocorrelation in the observed counts using modelling techniques for
93 abundance estimation that smooth across space and time (Harrison et al. 2014). Besides
94 climate, the spatial distribution and abundance of bird species are affected by other factors
95 defining habitat suitability (Gregory & Baillie 1998); hence, we also included land class and

96 elevation as covariates. To illustrate our methods, we selected three weather covariates for
97 our models based on Eglinton & Pearce-Higgins (2012): the centred means of temperatures
98 during the preceding winter and temperatures and rainfall in the preceding breeding season.

99 We describe the decomposition of the weather covariates as well as the modelling
100 approach for the BBS data (Section 2) and compare models that include these covariates
101 directly with models including decomposed components of the same covariates. We consider
102 linear (Section 3.1) and smooth terms (flexible, nonlinear model components, Sections 3.2,
103 3.4) for these covariates to assess the need for fitting smooth terms for weather covariates
104 rather than linear terms. We further investigate the necessity of a space-time smooth in the
105 model after fitting the weather covariates as smooth effects (Section 3.3). The best model is
106 used to predict abundances for each species (Section 3.5). Lastly, we discuss the benefits of
107 our approach for biological interpretations of the models (Section 4).

108

109 **2. Methods**

110 2.1 DATA

111 We begin by describing the data for the response variable of the models, the BBS bird counts,
112 which determines the spatial and temporal resolution required for the weather data. We then
113 describe our newly proposed method of decomposing the weather variables in Section 2.1.2.

114 *2.1.1 BBS data*

115 Sampling sites for the BBS are randomly selected 1km squares; the number of sites surveyed
116 each year has increased since the survey began, from ~1500 in 1994 to 3350 in 2013. Sites
117 were visited twice per year (April to early-May and late-May to June), during which
118 volunteers walked two parallel 1km transect lines and assigned each detected bird to one of
119 four categories (0-25m from the line, 25-100m, >100m, flying). We only considered data
120 from the first two distance intervals for which detection probabilities were adequate (>0.1)

121 for model fitting and estimating average detection probabilities (the proportion of birds
122 detected within the surveyed area, Buckland et al. 2001). We minimised the possibility of
123 including juvenile birds by using data only from the early visit for most species, and the later
124 visit for late breeding birds such as summer migrants (Table 1).

125 We analysed the BBS data collected in 1994-2013, excluding 2001 when an outbreak
126 of foot-and-mouth disease restricted access to many areas (Risely et al. 2013), and present
127 results for five species of birds that are likely to show a range of sensitivities to changes in
128 climate, namely goldcrest (*Regulus regulus*), song thrush (*Turdus philomelos*), linnet
129 (*Carduelis cannabina*), cuckoo (*Cuculus canorus*) and willow warbler (*Phylloscopus*
130 *trochilus*). This choice of species included residents whose populations may have increased
131 in response to recent warming (goldcrest, song thrush and linnet, Pearce-Higgins et al. 2015),
132 and declining long-distance migrants whose populations may be affected by conditions in the
133 UK, during migration or in Africa (cuckoo and willow warbler, Ockendon, Johnston &
134 Baillie 2014).

135 A complication for spatial modelling is that some species are rare or absent in parts of
136 Britain; if we extrapolated our predictions for such species to those areas, the predictions
137 might be unstable and not meaningful. Therefore, we created a grid of 100km squares
138 throughout Britain and restricted our modelling for each species to those 100km squares for
139 which there were a total of over three positive observations of the species during the years of
140 the study (Harrison et al. 2014; “propM” from Table 1 gives the proportion of Britain
141 included in the models by species).

142

143 2.1.2 Weather data and decomposition method

144 For the weather data 1993-2013 we used UKCP09 5x5km gridded observation data compiled
145 by the Met Office (www.metoffice.gov.uk). To model abundance in a given breeding season,

146 we included three weather variables for the preceding winter and preceding breeding season.
 147 To reduce correlations between parameter estimates we used their centred values which for a
 148 given location and time point is equal to the original value minus the mean over all locations
 149 across Britain and time points for the respective covariate. We indexed the values according
 150 to the year of the corresponding response variable:

151 $W_{i,t}$ = centred monthly means of the daily minimum temperature during the preceding winter
 152 (Dec-Feb) in year $t - 1$ (Dec) and t (Jan-Feb) at location i ;

153 $B_{i,t}$ = centred monthly means of the daily mean temperature during the preceding breeding
 154 season (April-July in year $t - 1$) at location i ;

155 $P_{i,t}$ = centred square root of the monthly means of the total rainfall during the preceding
 156 breeding season (April-July in year $t - 1$) at location i . We use the square root to reduce the
 157 effect of very large rainfall values.

158 We note that the 5km resolution weather variable values get applied to each 1km
 159 square within them. We refer to the centred weather covariates as W , B and P (short for
 160 winter, breeding and precipitation) for brevity and decompose each of them into three
 161 components: the average over space for a given time (year); the average over time for a given
 162 spatial location and; the residual variation term. For example, for winter minimum
 163 temperature we define the first component, the *average over space for a given time* (temporal
 164 component), as:

165
$$W_{time}: W_{\cdot,t} = \frac{\sum_i W_{i,t}}{N}$$

166 where N is the number of 5km grids across Britain. The second component, the *average over*
 167 *time for a given spatial location* (spatial component) is given by:

168
$$W_{space}: W_{i,\cdot} = \frac{\sum_t W_{i,t}}{T}$$

169 where T gives the number of time points. Finally the third component, the *residual variation*
170 *term* (or *space-time anomaly*), which can be thought of as the difference between the original
171 value and what is expected given the overall yearly and overall spatial effect, is defined as:

$$172 W_{resid}: W'_{i,t} = W_{i,t} - W_{.,t} - W_{i.}$$

173 For any of the three centred covariates W , B and P , we distinguish between the three
174 corresponding decomposed variables using the subscripts *time*, *space* or *resid*, e.g., where
175 W_{time} denotes the average over space for a given time for the preceding winter temperatures
176 (W).

177 Figures 1-3 graphically depict the decomposed variables for W , B and P , showing the
178 patterns of variation between years averaging over space, between grid cells averaging over
179 years, and the residual variation.

180

181 2.1.3 Land class and elevation data

182 In addition to terms describing the weather variables of interest, it is beneficial to include
183 other terms in the model to remove some aspects of broad-scale variation related to other
184 factors. Following Harrison et al. (2016), we include elevation and habitat information.

185 Habitat information was obtained from the 2007 land cover map compiled by the Centre for
186 Ecology and Hydrology (CEH). This gives the percentages of 10 aggregate land classes
187 (broadleaf woodland, coniferous woodland, arable, improved grassland, semi-natural
188 grassland, mountain/heath/bog, saltwater, freshwater, coastal and built-up areas/gardens) for
189 all 1km squares across Britain(<https://catalogue.ceh.ac.uk/documents/c3723adb-1a8c-4b57-958b-1d610d2c37fe>, Morton et al. 2011).

191

192 2.2 DATA ANALYSES

193 2.2.1 Models for the relationships between weather and species abundance

194 For each of the five species, we fitted GAMs assuming a quasi-Poisson distribution (Section
195 2.2.2) with a log-link function to the count data from each recorded site and year. All models
196 contained elevation and land class covariates, plus a selection amongst a space-time smoother
197 and the weather covariates which were of particular interest. See below and Table 2 for
198 model summaries and explanation of model terms.

199 Overall, these models can be expressed as:

$$200 \quad E[Y_{s,i,t}] = \exp(\alpha_s + \beta_{e,s}elev_i + \sum_{l=1}^L \beta_{l,s}pac_{l,i} + f_s(east_i, north_i, t) + \mathcal{M}_{s,i,t}) \quad (1),$$

201 where $E[Y_{s,i,t}]$ gives the expected count for species s on 1km square i in year t ; $elev$ the
202 mean elevation; pac_l the percentage of each of the L ($= 10$) land classes; f_s is a space-time
203 smooth and $\mathcal{M}_{s,i,t}$ pertains to the weather covariates and varied between models. The location
204 of squares was given by eastings ($east$) and northings ($north$). GAMs were fitted using
205 package `mgcv` (version 1.8-4, Wood 2006) in the statistical software R (R core development
206 team 2011).

207 For the space-time smooth, f_s , we used a tensor product of a thin plate regression
208 spline (TPRS) of $east$ and $north$ and a TPRS of t (Wood 2006, p. 225). Models thus
209 incorporate interactions between space and time and the spatial component captures, along
210 with any spatial autocorrelation, differences in the character of the land cover across Britain
211 (Renwick et al. 2012). The amount of smoothing is described by the effective degrees of
212 freedom (EDF). In accordance with our previous analysis of biodiversity trends in breeding
213 birds (Harrison et al. 2014) we set an upper limit of five for the EDF of the temporal TPRS,
214 with the actual value being determined by in-built cross-validation. By trial and error we
215 found 25 to be a suitable upper limit for the EDF of the spatial TPRS. If, however, some of
216 the 100km grids had been removed for the species (Section 2.1.1), the maximum EDF for the
217 spatial TPRS was scaled according to the proportion of Britain remaining (“propM”, Table
218 1). To minimise unwanted edge effects (unrealistic relationships for smooth terms in extreme

219 regions of the covariate) when modelling the cuckoo, for which 96% of counts were zero, we
220 divided the upper limits of both EDFs by two.

221 We used the model without any weather covariates, i.e. the term from eqn (1)
222 pertaining to the weather covariates, $\mathcal{M}_{s,i,t}$ equals zero, as a baseline model *mSTS*. We
223 investigated the effects of the weather variables firstly by considering them as linear
224 covariates, with the further aim of disentangling their spatial, temporal and residual
225 components. Building on *mSTS*, we fitted seven models with at least one linear effect of the
226 weather covariates (Table 2A). In these models, $\mathcal{M}_{s,i,t}$ contained linear functions of either
227 only a single centred weather covariate (i.e. not decomposed into three components), all three
228 centred weather covariates or two centred and one decomposed weather covariate. We
229 refrained from decomposing more than one weather covariate in a single model to avoid
230 overfitting and complexity of model interpretation.

231 As linear effects may not capture the relationship sufficiently, we replaced these with
232 smooth functions of the centred and decomposed weather covariates to create seven further
233 models, each corresponding to a smooth equivalent of one of the models with linear weather
234 terms (Table 2B). Smooth functions allow capturing nonlinear relationships between counts
235 and covariates (on the linear predictor scale) using the flexibility of splines.

236 We investigated the consequences of removing the space-time smooth from the model
237 because the need for this term may be reduced by including covariates that are varying in
238 space and time and because the presence of this term may be influencing the estimated form
239 of the weather variable effects. Here we used the seven models with the smooth functions for
240 the weather covariates and fitted the corresponding models without the space-time smooth for
241 comparison, i.e. omitting f_s from the model (Table 2C). Model m_- corresponds to *mSTS*
242 without the space-time smooth.

243 For each species, the overall best model was used to predict abundances throughout
244 Britain (excluding areas not part of the analysis for that species) using the 1km squares from
245 Section 2.1.3. Here, we used the estimates of average detection probability for each species
246 (Section 2.1.1) to scale up from predicted counts to predicted abundance within the 1km
247 squares.

248

249 *2.2.2 Model comparisons*

250 In all the models we assumed a quasi-Poisson error structure for the $Y_{s,i,t}$ (observed counts) to
251 allow for over- or underdispersion. Overdispersion is a common feature when simple
252 statistical models are fitted to count data due to heterogeneity that the models have failed to
253 account for. Underdispersion can occur if birds are territorial and hence self-organising in a
254 manner that can lead to less-than-random variation. In the standard Poisson model the
255 residual variance equals the mean. For the quasi-Poisson model, we relax this constraint to
256 proportionality, thus moving from “*variance=mean*” to “*variance= θ ×mean*” in which the
257 scale parameter θ determining the variance-mean relationship is estimated during the model
258 fitting ($\hat{\theta} > 1$ corresponding to overdispersion, $\hat{\theta} < 1$ to underdispersion) We used deviance
259 residuals for estimating θ for more reliable variance estimation compared to the default
260 Pearson residuals (Harrison et al. 2016). Standard errors for parameters of a quasi-Poisson
261 model are adjusted by multiplying the standard errors of the equivalent Poisson model with
262 $\sqrt{\hat{\theta}}$.

263 We used QAIC values (Richards 2008) for model comparison. QAIC differs from
264 AIC in that the log-likelihood component is divided by $\hat{\theta}_c$ which is the $\hat{\theta}$ from the most
265 complex of the candidate models. Three models were equally complex – those with the
266 space-time smoother and three weather covariates of which one was decomposed. For a given
267 species, we used the smallest $\hat{\theta}$ from these three models as $\hat{\theta}_c$ for all models (which also

268 happened to be the smallest $\hat{\theta}$ between all candidate models). For cuckoo where $\hat{\theta} < 1$ for all
269 models, we set $\hat{\theta}_c = 1$. We describe differences between QAIC values as δ -QAIC, which
270 represent differences from the model with the smallest QAIC value for each species.

271

272 **3. Results**

273 In the following, we compare the linear and smooth functions of the weather variables from
274 the different models by illustrating the coefficients and smooth functions for the respective
275 covariate. Model definitions and δ -QAIC values are given in Table 2.

276

277 *3.1 Including weather covariates as linear effects in the models*

278 For all species except cuckoo, the best of the models with linear covariates used a
279 decomposed covariate, W for goldcrest, song thrush, linnet; P for willow warbler.
280 Inspection of the regression coefficients (Figure 4) showed that those for the three
281 decomposed covariates corresponding to a single weather variable can be of very different
282 magnitude and, most notably for goldcrest $mSTS_lWPBd$, of different signs. Where one of the
283 decomposed covariate values differed substantially from the others, it was always the spatial
284 decomposition that stood apart from the temporal and anomaly coefficients.

285

286 *3.2 Replacing linear terms with smooth effects*

287 Using smooth instead of linear effects generally led to moderate or substantial improvement
288 of model fit (compare e.g. Table 2B row $mSTS_sW$ vs the corresponding entry in Table 2A
289 rows $mSTS_lW$ or 2B row $mSTS_sWBPD$ vs 2A row $mSTS_lWBPD$).

290 The smoothers associated with each model for each species are shown in Appendix 1; we
291 show a selection of smoothers in Figure 5. For these models with the space-time smoother,
292 the influence of any weather variable on any given bird species depended very little on

293 whether the other weather covariates were included in the model or not (e.g. for goldcrest,
294 compare the W smoothers for models $mSTS_sW$ and $mSTS_sWBP$. Furthermore, when any
295 one weather variable was decomposed, the estimated effects of the other weather variables
296 changed little (e.g. for goldcrest, compare the smoothers for W between the models
297 $mSTS_sWBP$, $mSTS_sWBPd$ and $mSTS_sWPBd$).

298

299 *3.3 Dropping the space-time smoother*

300 Dropping the space-time smooth, either from the models without any weather covariates, or
301 the models with smooth weather covariates, led to enormous increases in QAIC (Table 2, $m_$
302 vs $mSTS$ and Table 2C vs the corresponding elements of Table 2B). However, whether the
303 space-time smoother was included in the model had little effect on conclusions regarding
304 weather covariates apart from a few instances (e.g. willow warbler, B).

305

306 *3.4 Descriptions of best models, all containing decomposed smoothed terms*

307 For goldcrest, the best model $mSTS_sBPWd$ suggests abundance was higher in colder
308 locations (W_{space}) and in warmer winters (W_{time}) and when and where there were positive
309 anomalies (W_{resid}) (Figure 5). All three of these smoothers differed markedly in shape from
310 the single smoother for W prior to decomposition in model $mSTS_sWBP$, demonstrating the
311 decomposition is able to describe different functional responses when separated.

312 For song thrush, the best model $mSTS_sWPBd$ suggests little effect on abundances of
313 temperature in the preceding breeding season (B_{time}) or the anomalies (B_{resid}) (Figure 5). The
314 smoother for B_{space} (the spatial covariate) is similar in shape to the smoother for B prior to
315 decomposition, but with a more marked effect.

316 For linnet, the best model $mSTS_sBPWd$ indicates little effects of W_{time} or W_{resid} but
317 lower abundances in locations with cold winters (W_{space}) (Figure 5). Thus the mostly positive

318 relationship of the single covariate W is almost entirely due to spatial variation in mean
319 winter temperatures (as opposed to variation over time or the anomaly).

320 For cuckoo the best model $mSTS_sWBPd$ indicates higher abundance in locations
321 which generally have drier breeding seasons (P_{space}) and less residual variation in
322 precipitation (P_{resid}) while the temporal covariate (P_{time}) showed little effect (Figure 5). This
323 pattern was only evident when decomposing covariate P .

324 For willow warbler, the best model $mSTS_sWPBd$ revealed higher abundances for
325 locations with moderate breeding season temperatures (B_{space}) and negligible effects of the
326 temporal and anomaly components (B_{time} and B_{resid}) (Figure 5). The pattern from the
327 undecomposed B was similar to the spatial effect and therefore largely represents the spatial
328 component of breeding season temperature.

329

330 *3.4 Abundance predictions*

331 We used the best model for each species to construct maps of predicted abundances
332 throughout Britain for each year 1994-2013 (Appendix 2 shows all years); we present four
333 selected years, roughly equally separated: 1994, 2000, 2006 and 2013 (Figure 6). For each
334 species, the best model contained a decomposed weather covariate for which the spatial
335 component showed the strongest pattern (Figure 5). The relationship between abundance and
336 elevation was negative for all species, whereas the relationships between numbers and the ten
337 land classes varied between species.

338

339 **4. Discussion**

340 There is an increasing recognition of the potential to analyse long-term biodiversity
341 monitoring data sets to document the impacts of long-term environmental changes upon
342 species' distributions, abundances and communities. Interest in the consequences of climate

343 change has resulted in a significant increase in the number and types of these studies. These
344 often either collate data from multiple locations to identify temporal trends and analyse those
345 in relation to climate change (e.g. Davey et al. 2012, Devictor et al. 2012, Pearce-Higgins et
346 al. 2015), or model spatial variation in abundance or occurrence as a function of climate to
347 describe changes in distribution (e.g. Beale et al. 2013, Renwick et al. 2012, Johnston et al.
348 2013). Often sufficient resolution in time and space is not available in a dataset, so spatial
349 variation is used implicitly or explicitly as a proxy for temporal variation (e.g. Chen et al.
350 2011, Bellard et al. 2012 and Warren et al. 2013), where, e.g. the estimated species response
351 between cold and warm locations is used to estimate the species response in cold locations
352 that warm under climatic change. We proposed a novel way of including weather variables in
353 spatio-temporal models of abundance that involves decomposing each weather variable into a
354 spatial component, a temporal component and anomalies. Even after fitting a space-time
355 smoother alongside land class and elevation covariates in our models, we found that for all
356 five species the best models involved the decomposed covariates. This may have been due to
357 the divergence of spatial and temporal responses to the covariates.

358 Our methods enabled us to obtain improved understanding of how these effects of
359 climate and weather combine to drive spatial and temporal variation in species abundance.
360 Model results showed that the direction of relationships between a variable and abundance
361 could vary depending on whether temporal or spatial variation was modelled separately
362 (Plummer et al. 2015). It also provided more detailed information about how annual
363 fluctuations in weather affected the spatial variation in population trends of five exemplar
364 bird species in Britain, and therefore may be used to infer additional responses to climate
365 change.

366 Responses to increasing winter and breeding season temperature in Britain have
367 generally been found to be positive, at least amongst resident species (Greenwood & Baillie

1991, Pearce-Higgins et al. 2015). These may be operating over multiple time-frames: from immediate responses to direct extreme events, impacts of prey availability operating over timescales of weeks to years, to long-term impacts of habitat change. Spatial variation in climate may affect the long-term equilibrium of species abundances by impacting the average habitat, food resources and indirectly the biotic competition. Temporal variation in weather may be more likely to have immediate effects, such as changing survival or productivity, through physiology, food availability, or breeding conditions (e.g. Robinson, Baillie & Crick 2007, Pearce-Higgins et al. 2015). Our proposed methods have the potential to assist in disentangling these multiple processes in a single analysis, as illustrated by our responses for five exemplar bird species, which we consider here in two groups.

Populations of the resident species, goldcrest, linnet and song thrush, would generally be expected to have increased during our study period due to warmer temperatures leading to increases in overwinter survival and reproductive success (Eglington & Pearce-Higgins 2012, Pearce-Higgins et al. 2015). As expected, positive effects of preceding winter temperature (W) were generally apparent for goldcrest and linnet across most of the linear models (Figure 4). However, in *mSTS_IBPWd* goldcrest and song thrush both showed large negative effects of W_{space} , highlighting the potential divergence of spatial and temporal responses to temperature. Linnet showed a large positive effect of W_{space} suggesting lower abundance in locations with colder average winters (Swann et al. 2014).

For the migratory species considered, cuckoo and willow warbler, models predicted strong population declines in the south and increases in the north (Figure 6) which concur with previous studies (Ockendon et al. 2012; Morrison et al. 2013). Variation in these populations may be partly influenced by conditions on migration (Hewson et al. 2016) or on their African wintering grounds (Johnston et al. 2016). However, we found strong spatial trends in abundance which suggests there was likely also a strong impact of breeding season

393 environmental variables for these species, including summer temperature, which is
394 quadratically associated with spatial variation in willow warbler productivity (Eglington et al.
395 2015), and rainfall. Positive effects of temporal variation in breeding season temperature B_{time}
396 and negative effects of spatial variation B_{space} – as shown for willow warbler – add weight to
397 previous suggestions for poleward shift in distribution and negative impacts of warming on
398 the breeding grounds in the south. This may be affecting at least some long-distance migrant
399 species, potentially through more lagged effects (e.g. Pearce-Higgins et al. 2015).

400 Overall, the spatial terms indicated larger effects than the temporal and residual terms
401 in the models for most species and effects. If this was due to the generally wider range of
402 values for the spatial term compared to the corresponding temporal or residual terms (see x-
403 axes in Fig. 5), we would expect the pattern of, e.g., the smooth for the temporal component
404 to resemble the smooth for the spatial component for the equivalent range of values. This was
405 not generally the case (see Appendix 1, Figure A1.2). Given that spatial variation in
406 environmental variables are here found to be most important, this may suggest limited
407 evidence for local adaptation in these populations and environmental covariates. It does
408 suggest that spatial variation in environment cannot be reliably used as a proxy for temporal
409 variation in environment. This finding promotes further caution in predicting species
410 distribution and abundance in future climate, based on relationships that are largely
411 determined by environmental variation over space. In some cases the direction or shape of
412 effect differed across the decomposed variables, suggesting that different ecological
413 processes govern spatial and temporal patterns in abundance.

414 The potential user of our methods should consider if the quasi-Poisson is the
415 appropriate error structure for fitting models to their data. Alternatives are the Poisson (if data
416 are not over/underdispersed) or the negative binomial. The advantage of the Poisson or
417 negative binomial over the quasi-Poisson is that they are standard distributions and allow

418 using, e.g., AIC for model selection. For the BBS data, we chose quasi-Poisson as it
419 accommodates overdispersion and, in contrast to the negative binomial, the underdispersion
420 encountered for cuckoo (and several other species in the BBS data not presented here). It also
421 provided a better fit to the data compared to the negative binomial (as evidenced by smaller
422 mean-squared errors and lower cross-validation scores; Appendix 3).

423 A remaining potential issue for fitting complex models like ours is overfitting, i.e. that
424 unnecessarily complex models might appear to be preferred over simpler models regardless
425 of whether the additional level of complexity reflects the underlying truth. Where this issue
426 appears to be a substantive concern, it should be addressed in the usual way via testing
427 existing model selection tools in simulation studies and, where necessary, trialling potential
428 new model selection tools.

429 Given the multi-dimensional nature of climate change, developing tools for
430 incorporating multiple climatic factors will ultimately be required to more fully model the
431 overall impact of climate change on species' populations. The general increase in well-
432 designed species recording schemes will provide a greater range of response variables; the
433 expansion of land-based and aerial earth observation has potential to provide covariate data
434 with fine temporal and spatial resolution. Hence, it is reasonable to expect these methods to
435 become increasingly applicable in future. Our methods can be extended in many ways, e.g.
436 by introducing some spatial averaging into the covariates since it is unlikely that only the
437 values at a location affect the species there. Hence, whilst the methods introduced in this
438 paper are a substantial advance, there is further development to be undertaken to extract
439 further information from spatio-temporal species-environment data sets.

440

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545

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551 (www.climatexchange.org.uk).

552

553 Data accessibility

554 The weather data used in this manuscript can be obtained from the Met Office website
555 <http://www.metoffice.gov.uk/climate/uk/datasets/>. The bird data used as an example in this
556 manuscript are available through the BTO's standard data request procedure
557 (<http://www.bto.org/research-data-services/data-services/data-and-information-policy>).

558

559 **Table 1.** For the analysed species, “L” indicates species for which late visit records were
 560 used; “propM” gives the proportion of Britain included in the models; “prop0” gives the
 561 proportion of zero counts in the data; “p.hat” gives the estimated detection probabilities and
 562 $\hat{\theta}_{m1}$ and $\hat{\theta}_c$ give the estimated quasi-Poisson dispersion parameters for the baseline model
 563 (*mSTS*, Table 2) and the most complex model used for calculating QAIC, respectively.

ID	species name	visit	propM	prop0	p.hat	$\hat{\theta}_{m1}$	$\hat{\theta}_c$
1	goldcrest		0.99	0.80	0.27	1.45	1.43
2	song thrush		0.99	0.48	0.50	2.01	1.99
3	linnet		0.97	0.73	0.31	3.58	3.54
4	cuckoo	L	0.94	0.96	0.76	0.31	1.00
5	willow warbler	L	1.00	0.67	0.44	2.48	2.46

564

565 **Table 2.** Summaries and δ -QAIC values of the models fitted to the counts of five species of breeding birds. Models are compared in three
566 sections given in bold. Models beginning with ‘*mSTS*’ contain the space-time smooth, models beginning with ‘*m_*’ do not; ‘*l*’ refers to linear
567 effects of the weather covariates, e.g. ‘*lWBPd*’ contains the linear effects of *W* and *B* and of the decomposed covariate *P*, i.e. P_{time} , P_{space} , P_{resid} ;
568 ‘*l*’ is replaced with ‘*s*’ for models containing smooth functions of the weather covariates. All models contain the land class and elevation
569 covariates from eqn (1) (Section 2.2.1). The δ -QAIC values were obtained by subtracting the minimum QAIC value across all models for a
570 species from each model’s QAIC value. Smallest δ -QAIC for each section are in bold font.

571
572

Model	Weather covariates	Space-time smooth	Goldcrest	Song thrush	Linnet	Cuckoo	Willow warbler
Baseline model							
<i>mSTS</i>	none	Yes	652	304	529	44	409
A: Weather included as linear covariates							
<i>mSTS_lW</i>	linear <i>W</i>	Yes	642	300	491	44	394
<i>mSTS_lB</i>	linear <i>B</i>	Yes	645	298	395	45	411
<i>mSTS_lP</i>	linear <i>P</i>	Yes	653	295	437	36	411
<i>mSTS_lWB</i>	linear <i>W</i> , <i>B</i> , <i>P</i>	Yes	608	293	364	38	388
<i>mSTS_lWBPd</i>	linear <i>W</i> , <i>B</i> , P_{space} , P_{time} , P_{resid}	Yes	574	290	336	41	363
<i>mSTS_lWPBd</i>	linear <i>W</i> , <i>P</i> , B_{space} , B_{time} , B_{resid}	Yes	403	264	320	41	384
<i>mSTS_lwBPWd</i>	linear <i>B</i> , <i>P</i> , W_{space} , W_{time} , W_{resid}	Yes	206	224	199	39	374
B: Weather included as smooth effects							
<i>mSTS_sW</i>	smooth of <i>W</i>	Yes	621	248	467	42	374
<i>mSTS_sB</i>	smooth of <i>B</i>	Yes	626	182	361	41	214
<i>mSTS_sP</i>	smooth of <i>P</i>	Yes	652	293	412	32	357
<i>mSTS_sWBP</i>	smooths of <i>W</i> , <i>B</i> , <i>P</i>	Yes	569	160	299	30	174

<i>mSTS_sWBPd</i>	smooths of $W, B, P_{space}, P_{time}, P_{resid}$	Yes	429	118	119	0	45
<i>mSTS_sWPBd</i>	smooths of $W, P, B_{space}, B_{time}, B_{resid}$	Yes	218	0	110	22	0
<i>mSTS_sBPWd</i>	smooths of $B, P, W_{space}, W_{time}, W_{resid}$	Yes	0	28	0	30	49
C: Models without the space-time smooth							
<i>m_</i>	none	No	3621	2189	2583	672	8763
<i>m_sW</i>	smooth of W	No	3448	2116	2502	650	8456
<i>m_sB</i>	smooth of B	No	3603	1924	2322	596	4681
<i>m_sP</i>	smooth of P	No	3592	2139	2433	546	8013
<i>m_sWBP</i>	smooths of W, B, P	No	3405	1795	2094	496	4375
<i>m_sWBPd</i>	smooths of $W, B, P_{space}, P_{time}, P_{resid}$	No	3095	1622	1871	339	3526
<i>m_sWPBd</i>	smooths of $W, P, B_{space}, B_{time}, B_{resid}$	No	3170	1656	1859	311	3330
<i>m_sBPWd</i>	smooths of $B, P, W_{space}, W_{time}, W_{resid}$	No	2974	1742	1825	441	4135

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577 **Figure 1.** Weather variable W (centred monthly means of the daily minimum temperature
578 during the preceding winter) decomposed into the temporal (top left), spatial (right) and
579 residual variation components (bottom left panel). What is shown e.g. for 1994 entails the
580 temperatures from December 1993 and January-February 1994.

581

582 **Figure 2.** Weather variable B (centred monthly means of the daily mean temperature during
583 the preceding breeding season) decomposed into the temporal (top left), spatial (right) and
584 residual variation components (bottom left panel). What is shown e.g. for 1994 entails the
585 temperatures April-July in 1993.

586

587 **Figure 3.** Weather variable P (centred square root of the monthly means of the total rainfall
588 during the preceding breeding season) decomposed into the temporal (top left), spatial (right)
589 and residual variation components (bottom left panel). What is shown e.g. for 1994 entails
590 the rainfall from April-July in 1993.

591

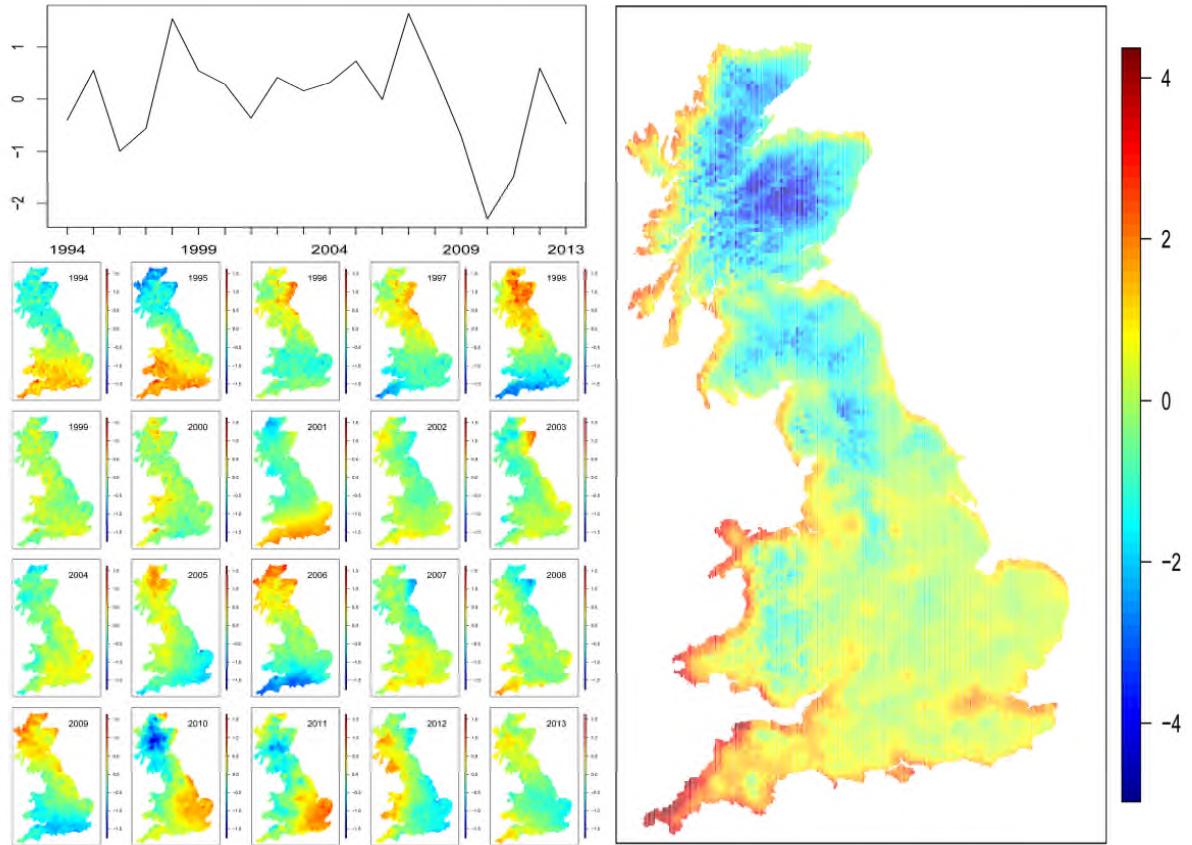
592 **Figure 4.** Regression coefficients (and 95% confidence intervals) corresponding to linear
593 effects of the weather covariates after standardisation (multiplying with the standard
594 deviation of the covariate), presented as one panel for each species, with model names
595 defined in Table 2. Dotted lines separate different models, dots give the estimates and
596 horizontal lines represent the uncertainty of the estimates (the endpoints being the
597 $\text{estimate} \pm (\text{SE} \times 1.96)$). Coefficients for W or its decomposed version (time top, space middle
598 and anomaly bottom) are represented in green, for B in blue and for P in red. In the figure,
599 estimates and interval endpoints are multiplied by the standard deviation of the respective
600 covariate to allow the relative effects of the covariates to be assessed.

601 **Figure 5.** Comparison of smooths between centred and decomposed weather variables. For
602 each species, the smooths for the decomposed covariates from the best fitting model are
603 compared with the smooth of the corresponding centred covariate from model *mSTS_sWBP*.

604

605 **Figure 6.** Log-abundance estimates for the five bird species predicted for four selected years
606 using the best fitting model. Predictions were made only for areas included in the analysis
607 (see Section 2.1.1 and Table 1).

608

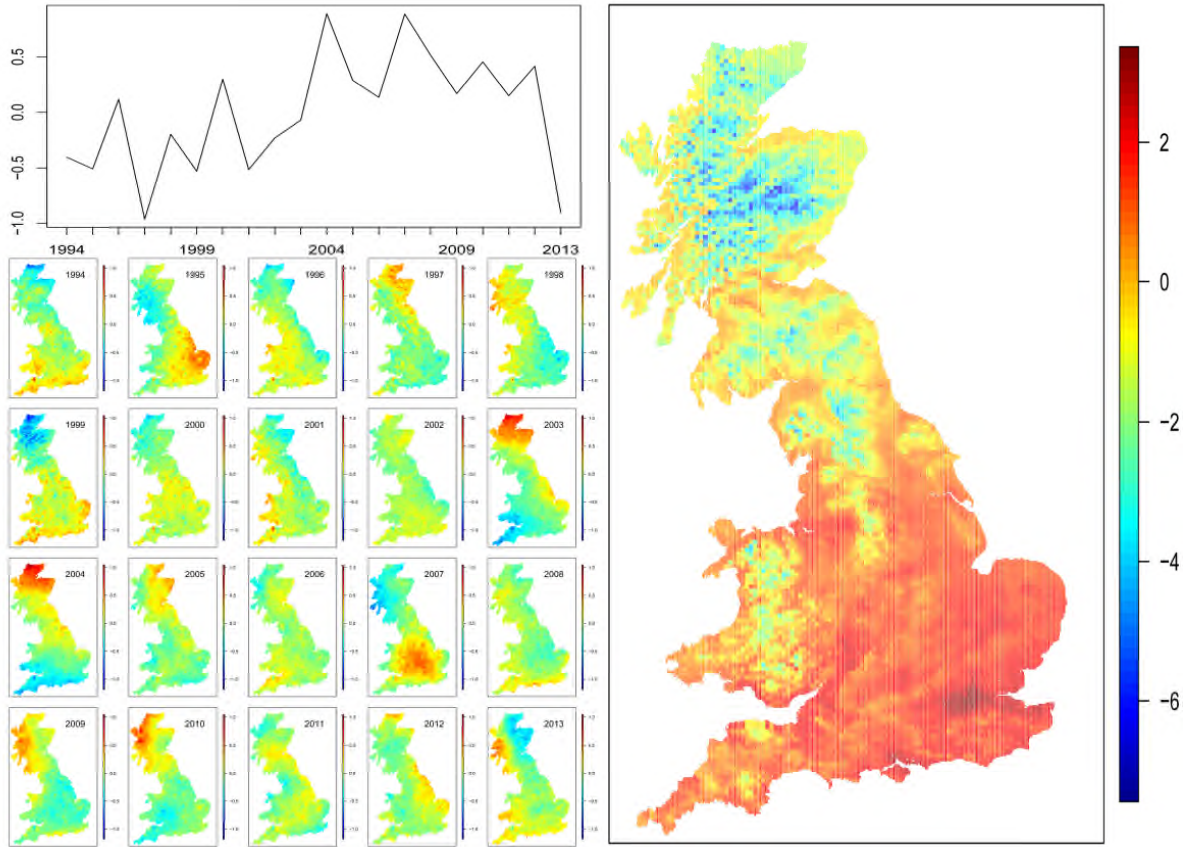


609

610 **Figure 1.** Weather variable W (centred monthly means of the daily minimum temperature
 611 during the preceding winter) decomposed into the temporal (top left), spatial (right) and
 612 residual variation components (bottom left panel). What is shown e.g. for 1994 entails the
 613 temperatures from December 1993 and January-February 1994.

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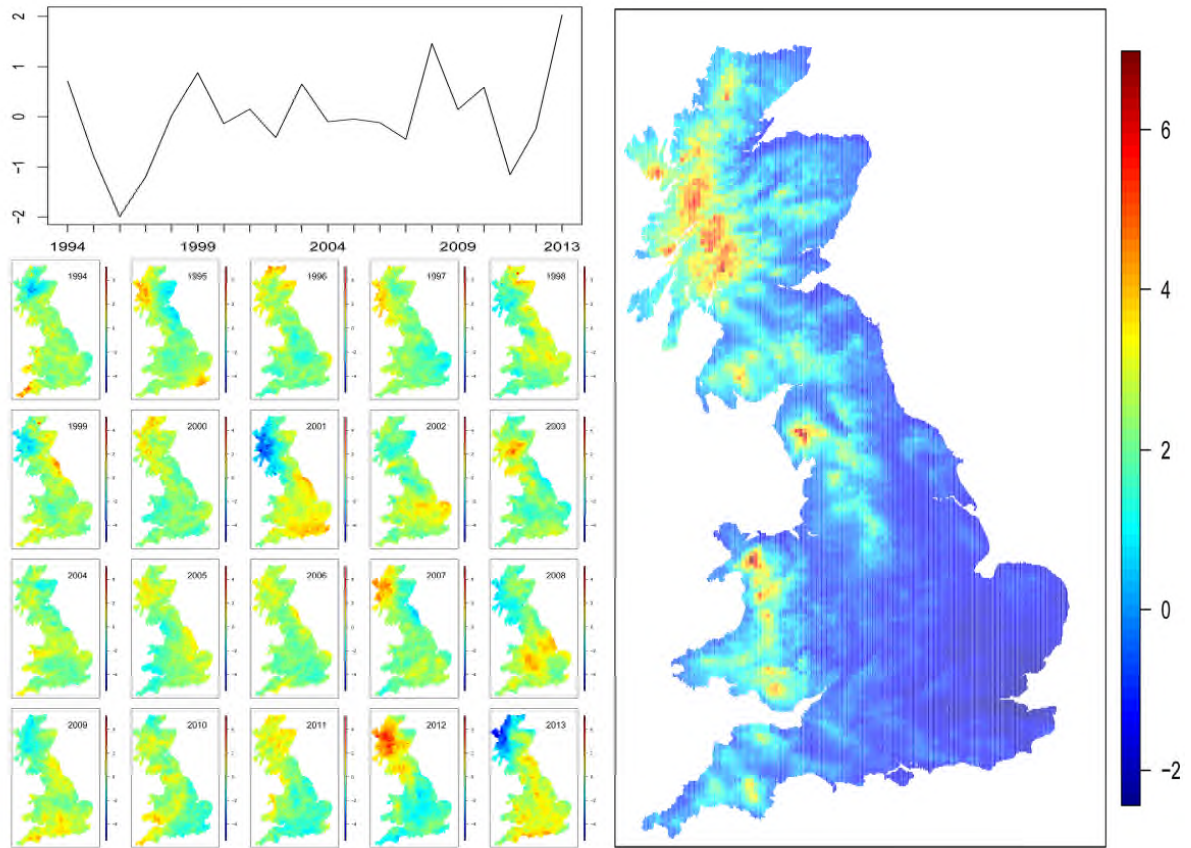


616

617 **Figure 2.** Weather variable B (centred monthly means of the daily mean temperature during
 618 the preceding breeding season) decomposed into the temporal (top left), spatial (right) and
 619 residual variation components (bottom left panel). What is shown e.g. for 1994 entails the
 620 temperatures April-July in 1993.

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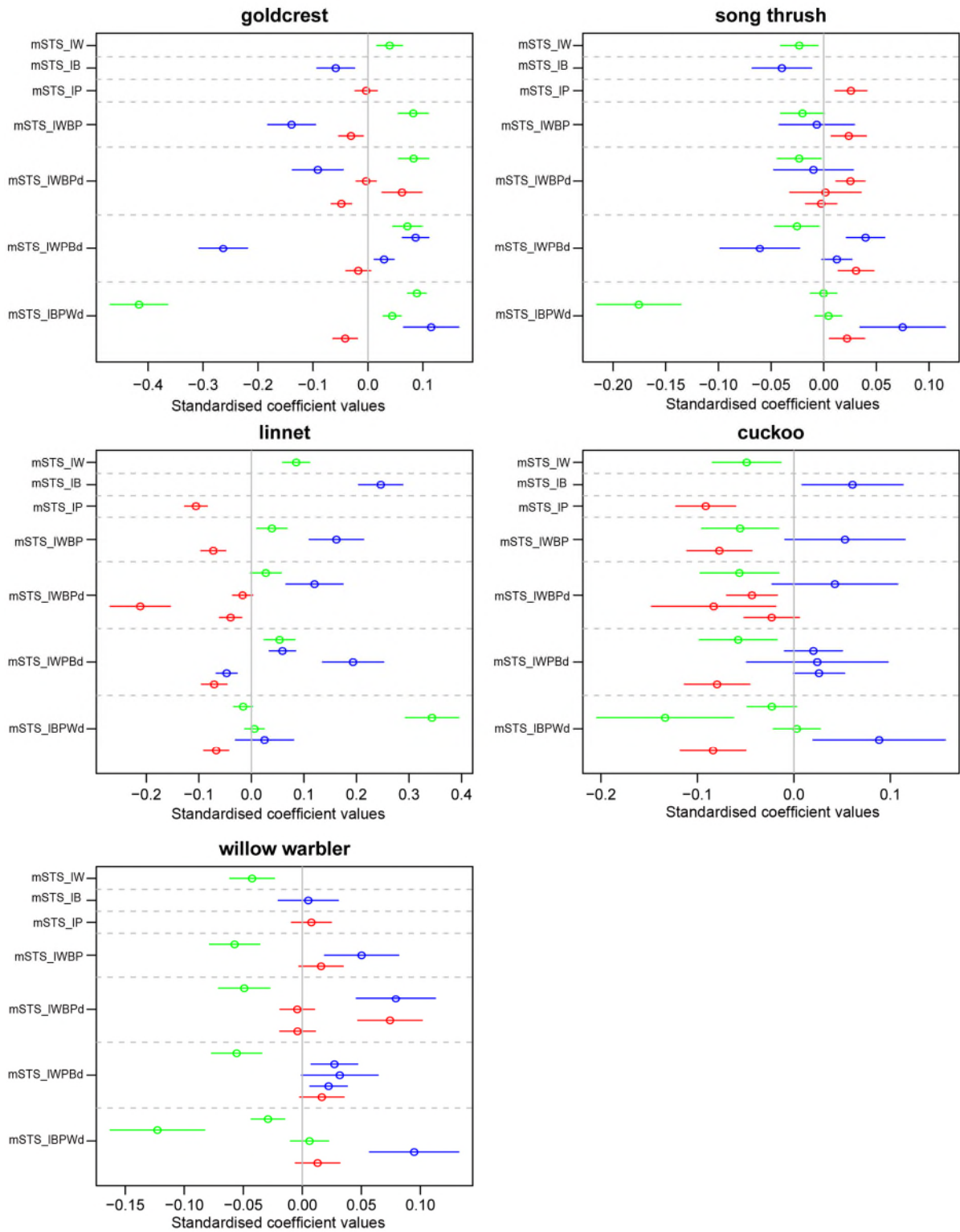


623

624 **Figure 3.** Weather variable P (centred square root of the monthly means of the total rainfall
 625 during the preceding breeding season) decomposed into the temporal (top left), spatial (right)
 626 and residual variation components (bottom left panel). What is shown e.g. for 1994 entails
 627 the rainfall from April-July in 1993.

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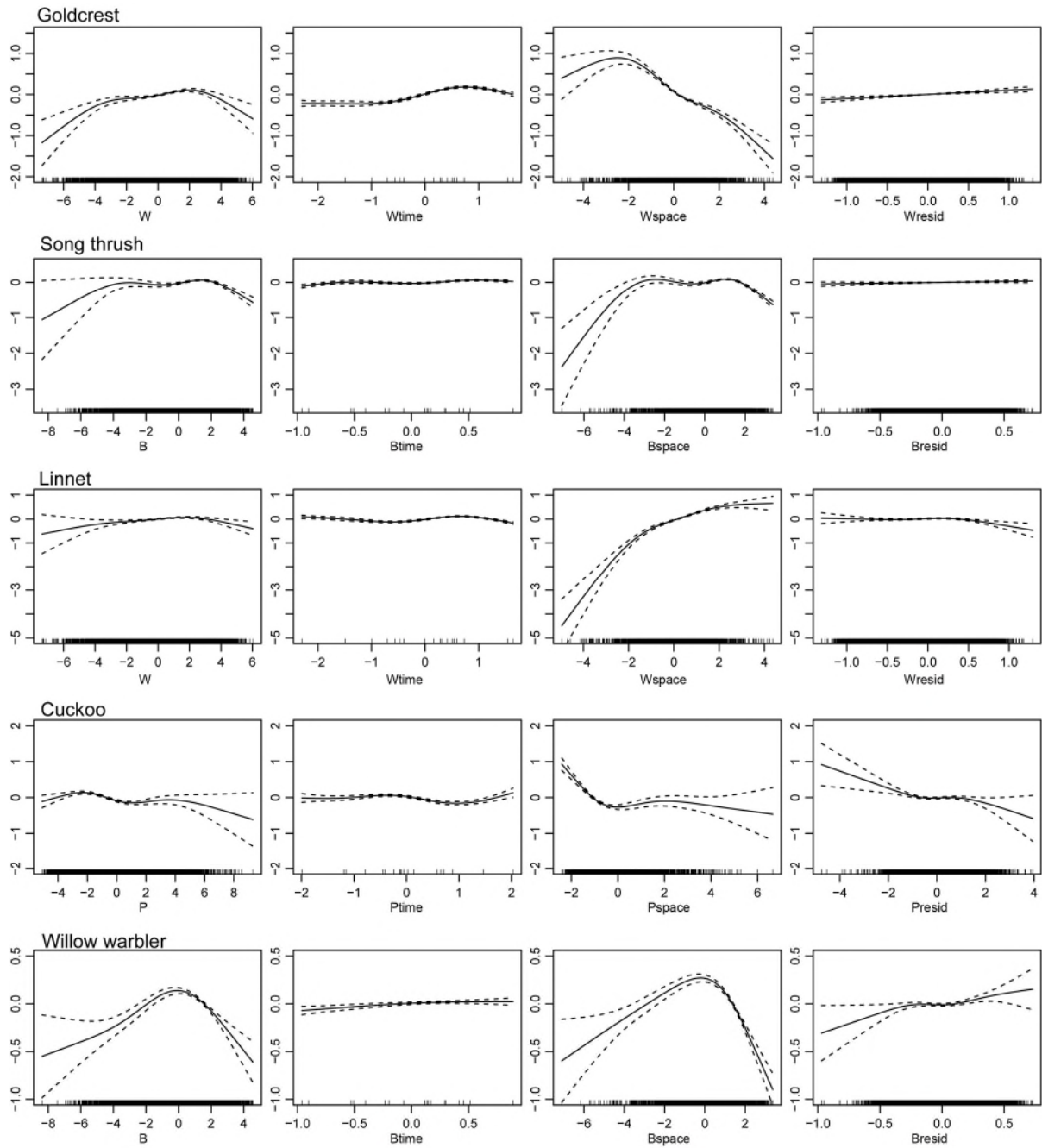
631 **Figure 4.** Regression coefficients (and 95% confidence intervals) corresponding to linear

632 effects of the weather covariates after standardisation (multiplying with the standard

633 deviation of the covariate), presented as one panel for each species, with model names

634 defined in Table 2. Dotted lines separate different models, dots give the estimates and

635 horizontal lines represent the uncertainty of the estimates (the endpoints being the
636 estimate \pm (SE \times 1.96)). Coefficients for *W* or its decomposed version (time top, space middle
637 and anomaly bottom) are represented in green, for *B* in blue and for *P* in red. In the figure,
638 estimates and interval endpoints are multiplied by the standard deviation of the respective
639 covariate to allow the relative effects of the covariates to be assessed.
640



641

642 **Figure 5.** Comparison of smooths between centred and decomposed weather variables. For

643 each species, the smooths for the decomposed covariates from the best fitting model are

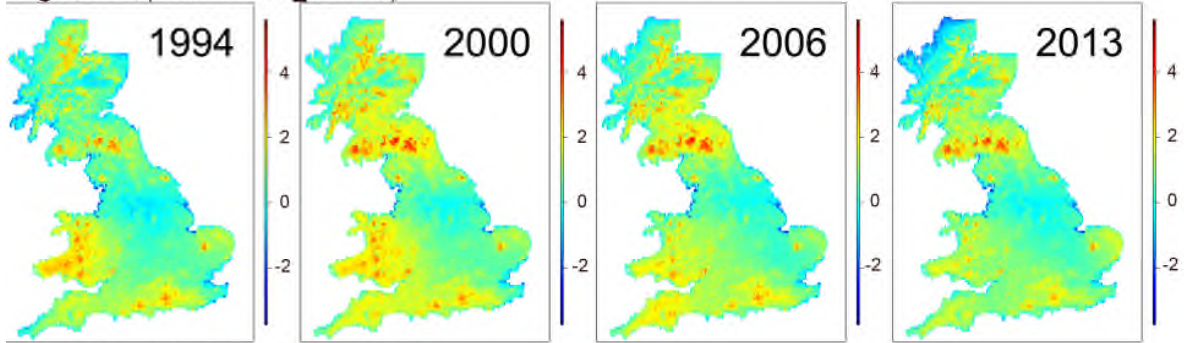
644 compared with the smooth of the corresponding centred covariate from model *mSTS_sWBP*.

645

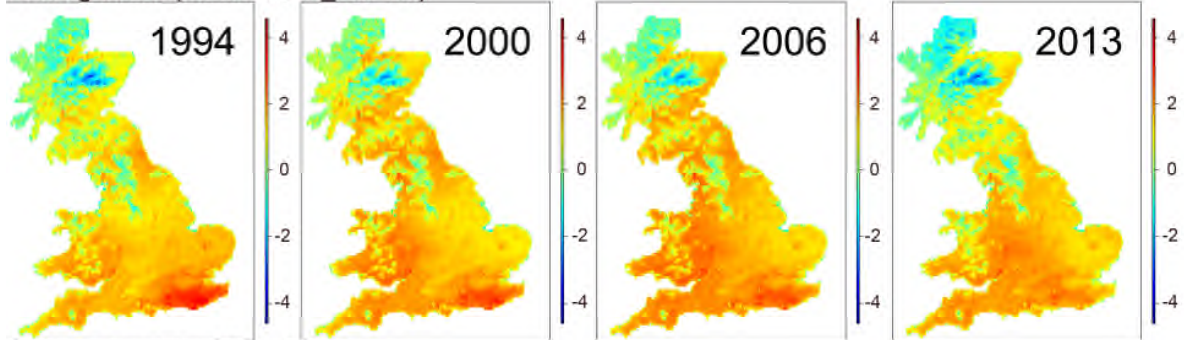
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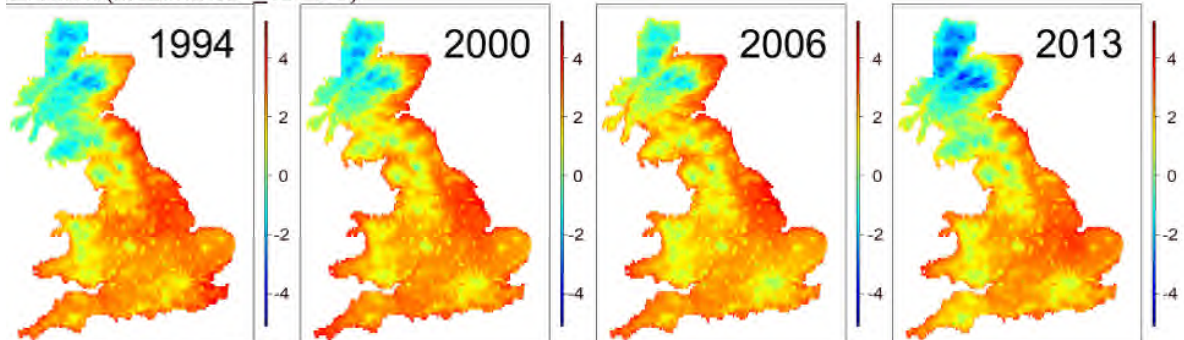
A: goldcrest (model $mSTS_sBPWd$)



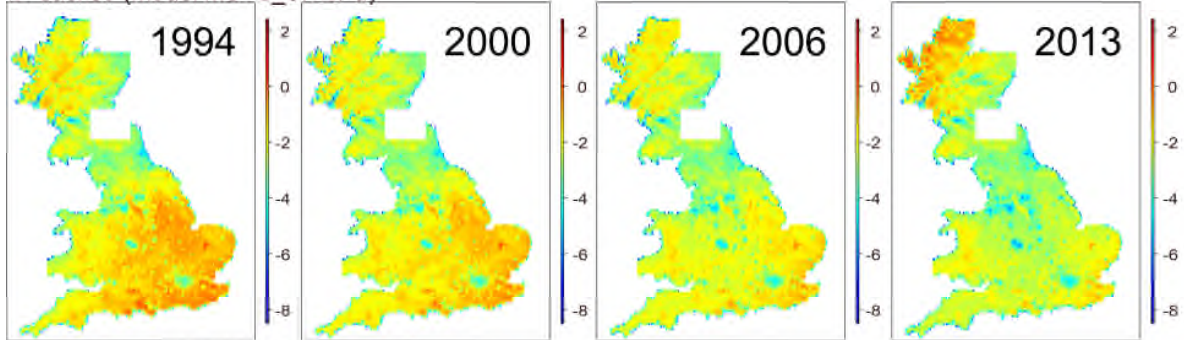
B: song thrush (model $mSTS_sWPBd$)



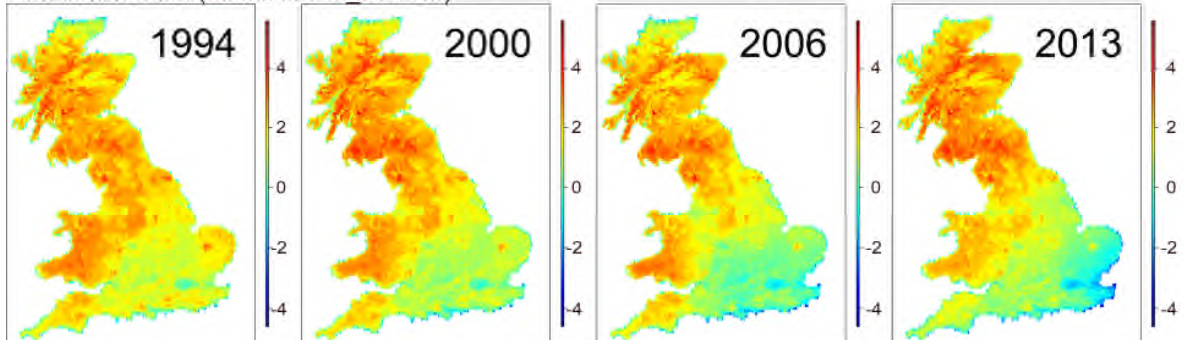
C: linnet (model $mSTS_sBPWd$)



D: cuckoo (model $mSTS_sWPBd$)



E: willow warbler (model $mSTS_sWPBd$)



649 **Figure 6.** Log-abundance estimates for the five bird species predicted for four selected years
650 using the best fitting model. Predictions were made only for areas included in the analysis
651 (see Section 2.1.1 and Table 1).

652

653 **Authors' contribution statement**

654 All authors contributed to developing the methodology of covariate decomposition; CSO lead
655 the analyses and writing of the manuscript. Major parts of the R code were first developed by
656 PJH. Species were selected by SF, DAE, MKB, AJ and SB. Data were provided by AJ and
657 JWPH. All authors contributed critically to the drafts and gave final approval for publication.