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# UNIVERSITÀ DEGLI STUDI DI TORINO

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14 Rise of the generalists: evidence for climate driven homogenization in avian communities

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25

26

27 **ABSTRACT**

28 **Aims** Biogeographical evidence suggests a strong link between climate and patterns of  
29 species diversity, and climate change is known to cause range shifts. However, there is little  
30 understanding of how these relate to community composition and we lack empirical evidence  
31 of recent climate change impacts on the diversity of vertebrates. Using a long-term  
32 comprehensive dataset on bird abundance, we explore recent patterns of change in different  
33 components of species diversity and avian communities, and postulate a process to explain  
34 the observed changes in diversity and specialization.

35 **Location** Britain

36 **Methods** We used Breeding Bird Survey data for Britain from 1994 - 2006 to calculate site-  
37 specific diversity and community specialization indices. We modeled these indices using  
38 Generalized Additive Models to examine the relationship between local climate and spatial  
39 and temporal trends in community metrics and the relationship between changes in diversity  
40 and specialization.

41 **Results** Local temperature was positively associated with alpha diversity, which increased  
42 over the study period, supporting empirical and theoretical predictions of the effect of climate  
43 warming. Diversity increased in all habitats, but the rate of increase was greatest in upland  
44 areas. However, temperature was negatively associated with community specialization  
45 indices, which declined over the same period. Our modeling revealed a non-linear relationship  
46 between community specialization and species diversity.

47 **Main conclusions** Our models of diversity and specialization provide stark empirical evidence  
48 for a link between warming climate and community homogenization. Over a thirteen-year  
49 period of warming temperatures, diversity indices increased while average community  
50 specialization decreased. We suggest that the observed diversity increases were most likely  
51 driven by range expansion of generalist species and that future warming is likely to increase  
52 homogenization of community structure. When assessed in combination, diversity and  
53 specialization measures provide a powerful index for monitoring climate change impacts.

54

55 **Keywords:** climate change, birds, species diversity, richness, homogenization, specialization

56

## 57 INTRODUCTION

58 Global changes in climate have had significant impacts not just on individual species but on  
59 the fundamental composition of ecological communities (Sax & Gaines, 2003). In Britain  
60 observed responses of bird species to warming climate include: northward expansion of  
61 ranges (Thomas & Lennon, 1999); changes in migrant (Sparks *et al.*, 2007) and resident  
62 phenology (Crick & Sparks, 1999) and the establishment of introduced species outside of their  
63 endemic climatic ranges (Dudley *et al.*, 2006). Many studies have linked the specificity of  
64 these climate impacts to species traits such as mobility and niche space (e.g. Warren *et al.*  
65 2001, Pöyry *et al.* 2001). However, despite a multitude of studies documenting climate impacts  
66 on individual avian species, there is a paucity of information available on the impact these  
67 species' specific responses have had on the greater community as measured by changes in  
68 local (alpha) diversity, beta diversity and regional (gamma) diversity.

69 Several macroecological studies have demonstrated a relationship between climate  
70 and observed variation in taxonomic richness (Hawkins *et al.*, 2003; Currie *et al.*, 2004).  
71 Avifaunal species richness has been shown to decrease with increasing latitude and lower  
72 temperatures (Turner *et al.*, 1988; Lennon *et al.*, 2000) and in northern-temperate regions  
73 energy is expected to be the limiting factor for species (Hawkins *et al.*, 2003). Cool to  
74 temperate regions, such as Britain, that experience warming are therefore expected to show  
75 increases in species richness (Lennon *et al.*, 2000; Hawkins *et al.*, 2003). Despite evidence of  
76 these biogeographical patterns, the mechanism linking climate and species diversity remains  
77 elusive (Clarke & Gaston, 2006). In particular, there is a paucity of empirical evidence showing  
78 a link between changing climate and species richness of terrestrial vertebrates. One recent  
79 North American study found that species richness of winter bird communities was positively  
80 correlated with annual temperatures that increased during the study period of 1975 – 2001 (La  
81 Sorte *et al.*, 2009). Within other taxonomic groups there is greater evidence of the relationship  
82 between climate change and community metrics. A number of studies have now shown links

83 between warming temperatures and localised increases in species richness in plant, butterfly  
84 and fish communities (Klanderund & Birks, 2003; Menéndez *et al.*, 2006; Wilson *et al.*, 2007;  
85 Hiddink & ter Hofstede, 2008; Britton *et al.*, 2009). However, these increases were often  
86 localised and associated with range expansion in generalists and range contractions in  
87 specialists (Warren *et al.*, 2001; Wilson *et al.*, 2007; Britton *et al.*, 2009). Specialist species  
88 with small range-restricted populations are thought to be particularly vulnerable to extinction  
89 as a result of environmental change (McKinney, 1997; McKinney & Lockwood, 1999; Gaston &  
90 Blackburn 2002; Julliard *et al.* 2003). In contrast, generalists are expected to be less  
91 susceptible to, and may even benefit from, environmental disturbance (McKinney & Lockwood,  
92 1999). Increases in the prevalence of generalists under climate change have already been  
93 documented (Menéndez *et al.*, 2006; Britton *et al.*, 2009) and warming temperatures have  
94 been shown to increase species turnover in communities (Hillebrand *et al.*, 2010).

95         Although high alpha diversity is often used as a measure of ecosystem health and  
96 functioning (Balvanera *et al.*, 2006), increases due to colonisation by common generalist  
97 species are likely to reduce beta diversity and eventually gamma diversity as widespread  
98 species dominate and communities become homogenized (Van Turnhout *et al.*, 2007).  
99 Several recent studies have highlighted the importance of monitoring homogenization in  
100 conjunction with other diversity metrics (Devictor *et al.*, 2008; Devictor & Robert, 2009; Filippi-  
101 Codaccioni *et al.*, 2010a,b). These studies all demonstrated that increases in alpha diversity in  
102 disturbed habitats were directly associated with a loss of community specialization. Therefore,  
103 to obtain a more comprehensive overview of community dynamics, functional diversity should  
104 be monitored in conjunction with alpha diversity. As no reference state exists for 'ideal'  
105 diversity and specialization, to assess the impacts of environmental change on communities  
106 we need to use datasets that allow us to monitor how indices have changed through space  
107 and time.

108         The BTO/JNCC/RSPB Breeding Bird Survey (BBS), is an annual extensive monitoring  
109 scheme that began in 1994 and covers around 3000 1km squares in Britain each year. One of  
110 the strengths of the BBS dataset is that it allows geographical and temporal trends in bird

111 populations to be examined. The BBS has shown that British bird populations continue to  
112 show long-term declines for several species groups, with climate and land-use change the  
113 likely drivers (Newton, 2004; Hewson & Noble 2009; Baillie *et al.*, 2010). Here we use BBS  
114 data to investigate how climate has affected measures of community diversity and  
115 specialization over a 13 year time period throughout Britain.

116

## 117 **METHODS**

### 118 **Survey data**

119 In this study we use BBS data from Britain only, for the period 1994-2006 during which about  
120 3,000 1-km squares were surveyed annually. This period matches the public availability of  
121 British climate data. This survey employs a stratified random sampling design, based on  
122 randomly-selected 1-km squares within regional strata that differ slightly in survey intensity.  
123 Surveys are conducted annually, usually by the same observer, and require two visits, one  
124 from April to mid-May and a second from mid-May to the end of June. During the survey, each  
125 observer records birds along two 1 km transect routes through each 1-km square. All birds  
126 seen and heard are recorded in three distance bands (0-25m, 25-100m, >100m) (Risely, *et al.*  
127 2009). Birds recorded in flight were discarded from the dataset as they were less likely to be  
128 associated with the square for breeding. Observers also record habitat for each 200m transect  
129 section using a hierarchical coding system (Crick, 1992).

130

### 131 *Bird detectability*

132 To correct for differences in detectability between species, we used a distance-sampling  
133 approach (Buckland *et al.*, 2001). For each species, we fitted half-normal distributions to data  
134 from the first two distance bands only (see Newson *et al.*, 2008) using the Mark-Recapture  
135 Distance Sampling (MRDS) package (Thomas *et al.*, 2010) for R (R Development Core Team,  
136 2009). A global model using data from across the BBS dataset (1994-2008), was used to  
137 maximise the number of observations available for each species. An estimate of species-

138 specific detection probability ( $\hat{p}$ ), was calculated for all species for which there were 10 or  
139 more observations, 209 species in total. 51 species with fewer than 10 observations, were  
140 excluded from the analyses here. The excluded records comprised less than 0.003% of the  
141 total bird observations, and were mainly rare vagrants or escapees from captivity. Distance  
142 models failed to produce estimates for 16 species, for which the detection probability from a  
143 similar surrogate species was used, chosen on the basis of expert opinion. A full list of  
144 species, along with sample sizes, and surrogates where applicable, is provided online in  
145 Appendix S1.

146

#### 147 *Measures of community diversity*

148 The density of each bird species was calculated as the maximum count per surveyed square,  
149 summed over the first two distance bands and divided by the detection probability. For each  
150 square/year combination, the reciprocal Simpson's index ( $1/D$ ) and Simpson's measure of  
151 evenness ( $E_{1/D}$ ) were calculated using the detectability-adjusted abundance data, while  
152 species richness ( $S$ ) was calculated as the number of species. We used Simpson's index, and  
153 the associated evenness measure, as it is considered to be robust and easy to interpret (see  
154 Magurran 2004 for review). While Simpson's index is correlated with both species richness  
155 and Simpson's measure of evenness we included both these measures, so as to help  
156 determine the mechanism by which climate affects diversity. Simpson's measure of evenness  
157 is not sensitive to species richness (Magurran, 2004).

158

#### 159 *Community specialization index (CSI)*

160 To obtain a measure of community specialization we followed the methods of Julliard *et al.*  
161 (2006) and Devictor *et al.* (2008). We first calculated species specialization indices (SSI) for  
162 species with greater than ten observations, using the coefficient of variation (standard  
163 deviation/mean) of the species' density across habitats. SSI values are provided online in  
164 Appendix S1. We calculated species' habitat-specific density using data from the first two



165 distance bands from all years of the BBS (1994-2008). We defined habitat using the primary  
166 habitat category from the BBS data using the classification system of Newson *et al.* (2009)  
167 which identified 12 broad habitat classes. The community specialization index (CSI) was  
168 calculated for each square/year combination as the average SSI weighted for species  
169 abundance (Julliard *et al.* 2006; Devictor *et al.* 2008). We used abundance data corrected for  
170 detectability in the weighting to account for differences in detection probability across species.

171

### 172 **Land cover and climate data**

173 For estimating changes in the diversity metrics across habitat types, habitat classification per  
174 BBS square was based on CEH Land Cover Map 2000 (LCM2000) Aggregate Classes (AC),  
175 which are classified at 25m resolution and summarized at the 1km scale (Jackson, 2000).  
176 Habitat categories were defined as follows: Woodland (AC 1,2); Sea (AC 10); Coastal (AC 9) ;  
177 Improved Grassland (AC 4); Natural Grassland (AC 5); Arable (AC 3); Urban (AC 7) ; Upland  
178 (AC 6). Squares were categorized using the dominant class (>50% cover) within the 1km  
179 square. Squares containing a mixture of grassland and arable classes but no dominant class  
180 were defined as 'Mixed Farmland'. Squares with no dominant aggregate class were defined as  
181 'Mixed'. Those squares categorized as 'Sea' and 'Coastal' were removed from the analyses as  
182 they were unlikely to contain terrestrial breeding birds. Climate variables were obtained from  
183 the UKCIP02 dataset at 5km square resolution for the period of publically available data 1994  
184 – 2006, a full description of the methods used to create the weather variable surface is  
185 provided in Perry & Hollis (2005). BBS survey squares and UKCIP data are both based on the  
186 GB National Grid and therefore BBS squares fell wholly within the boundary of each 5km  
187 climate square. To examine the associations with climate we calculated mean breeding  
188 season temperature (°C) and rainfall (mm) measures for each 1km square. The 'breeding  
189 season' was defined as April to the end of July. We also examined the influence of winter  
190 climate variables, measured from December to February.

191

### 192 **Statistical analysis**

193 *Diversity and CSI*

194 Generalized additive models (GAMs) were used to examine the effects of year, location,  
195 habitat, temperature and rainfall on bird diversity, evenness, richness and CSI at the 1km  
196 scale. The GAMs were constructed using version 1.6–1 of the mgcv package (Wood, 2006) in  
197 the statistical package R (R Core Development Team 2009). We used generalized cross  
198 validation (GCV) optimization to select the degrees of freedom for each term automatically and  
199 included a gamma penalty of 1.4 to reduce the likelihood of over fitting the data (Wood, 2006).  
200 All indices were normally distributed, so the identity link function was used. The model took  
201 the form:

202

$$203 \quad g(\text{diversity}) = \beta_0 + s(\text{lat, long, year}) + \text{habitat} + \text{mean temperature} + \text{mean rainfall}.$$

204

205 Where  $g(\mu)$  is the link function,  $\beta_0$  is the intercept and  $s$  is a thin plate spline. We used a three  
206 way interaction of latitude, longitude and year to allow us to model all the spatial and temporal  
207 variation in our dataset without constraints. Habitat was a categorical variable based on  
208 LCM2000 classification. We also included a weighting to account for the original square  
209 stratification, which was the reciprocal of the survey density in different regions. The GAM fits  
210 a smooth two-dimensional surface to the data which optimizes a fit to peaks and troughs in the  
211 response variable, which have no support from the environmental data, thus controlling for  
212 unmeasured variables which may be affecting the response variable. This surface also  
213 implicitly fits spatial autocorrelation in the data, because it optimizes the degrees of freedom  
214 used in the surface to describe the patterns of the response variable. In doing so, it controls  
215 for similarities in the response variable at nearby points, and thus the climate variables  
216 describe relationships which are not described by the smooth GAM surface. In this way,  
217 spatial autocorrelation is partially controlled for by the two-dimensional smooth. The model  
218 parameters were determined *a priori* as potentially important determinants of species diversity  
219 so no model selection was undertaken (e.g. Habitat: Devictor *et al.*, 2008; Filippi-Codaccioni *et*  
220 *al.*, 2010; Temperature: Lennon *et al.*, 2000; La Sorte *et al.*, 2009; Rainfall: Allbright *et al.*,

221 2010). Our observed diversity and CSI values were used to fit the model and then national  
222 habitat and climate data were used to predict modeled values for each 1-km square in Britain  
223 over the same period as our sample. To test our model validity we also examined the fit of the  
224 final model to a random selection of 50% of our observed data, which showed a good fit to the  
225 unmodeled section of the data (Appendix S2).

226

### 227 *Relationship between CSI and other community metrics*

228 To examine the relationship between CSI and species diversity, richness and evenness we  
229 first plotted the data. These plots indicated that a non-linear, unimodal relationship existed  
230 between CSI and species diversity and also between CSI and richness (Fig. 4). There was  
231 less evidence of a clear relationship between CSI and evenness (Fig. 4). We modeled these  
232 relationships by fitting GAMs with a smooth of CSI and parametric year and habitat variables.  
233 We used GCV optimization and an identity link function for diversity and evenness and a log  
234 link for richness. We constrained the degrees of freedom to 5 to prevent overfitting.

235

## 236 **RESULTS**

237 Between 1994-2006, 4,782 1km squares were surveyed at least once; within the first two  
238 distance bands a total of 6,897,246 individuals of 260 species were counted. Over the study  
239 period, mean breeding season temperatures were variable but showed a general upward  
240 trend with a mean increase between 1994-2006 of  $1.39\text{ }^{\circ}\text{C} \pm \text{s.e } 0.004$  (Fig. 1). There was no  
241 consistent trend in rainfall patterns. The GAMs of species diversity, species richness, species  
242 evenness and community specialization accounted for 45.9%, 55.1%, 12.7% and 64.2% of the  
243 total deviance respectively (Table 1).

244 Upland followed by urban habitats were the least diverse while the three agricultural  
245 habitats (arable, improved grassland and mixed farming) were the most diverse (Table 1).  
246 Modeled values showed that increases in diversity between 1994-2006 were almost  
247 ubiquitous (Fig. 2(a-c)). There was a clear latitudinal gradient in diversity, which decreased  
248 with latitude (Fig. 2 (a,b)). Patterns in species richness were similar to diversity, with the

249 lowest numbers of species found in upland habitats and the highest in agricultural habitats  
250 (arable, improved grassland and mixed farmland) (Table 1). The habitat coefficients for the  
251 evenness measure showed a different pattern to richness and diversity with the lowest values  
252 seen in urban habitats and the highest in arable and woodland habitats, although the model  
253 predictors explained the variance in the evenness measure poorly (Table 1). Modeled values  
254 of CSI showed a decline in all regions of Britain (Fig. 2 (d-f)) with a decreasing trend across  
255 years (Fig. 1(b)). Habitat-specific patterns in CSI were generally opposite to those for diversity,  
256 with upland having the highest CSI, and agricultural habitats the lowest. Again a latitudinal  
257 gradient was clear, with CSI higher in northern areas, likely reflecting the distribution of upland  
258 habitat (Table 1, Fig. 2 (d,e)).

259 Mean breeding season temperature had a significant ( $P < 0.05$ ) positive association with  
260 species diversity and species richness, but a significant negative association with CSI and  
261 evenness (Table 1, Fig 1(a-d)). Mean breeding season rainfall had a significant negative  
262 association with species diversity and richness, but a small positive association with species  
263 evenness and CSI (Table 1). Because the trend in diversity and richness remained positive,  
264 we can assume that temperature had a greater influence on these variables than rainfall.  
265 These results also suggest that temperature-related increases in species diversity are driven  
266 by changes in the number of species present, rather than the evenness component of the  
267 index. Winter climate variables had a similar influence on our dependent variables, although  
268 explained less overall variance (Appendix S2).

269 Mean modeled diversity increased across all habitats from 1994-2006, with upland  
270 showing the greatest mean percentage gain in diversity ( $36.85 \pm \text{s.e } 0.18$ ), richness ( $23.05 \pm$   
271  $\text{s.e } 0.21$ ), evenness ( $6.66 \pm \text{s.e } 0.01$ ) and temperature ( $15.57 \pm \text{s.e } 0.03$ ) (Fig. 3). Mean  
272 modeled CSI decreased across all habitats from 1994-2006, with agricultural habitats showing  
273 the greatest mean percentage loss in CSI (Fig. 3b).

274 The above results imply that increasing alpha diversity and decreasing specialization  
275 are related processes. Plots of the relationship between CSI and the three diversity metrics  
276 suggest a non-linear relationship (Fig. 4). GAMs using a smooth of CSI appeared to confirm

277 this and explained 42.5% of the deviance of species diversity and 39.0% of the deviance of  
278 species richness. The smooth CSI term was significant ( $P < 0.0001$ ). Evenness was not well  
279 explained by the model with only 14.2% of the deviance accounted for (Appendix S2). The full  
280 GAM results are provided in Appendix S2. Both diversity and richness exhibited a unimodal  
281 relationship with CSI. The models suggest that at very low values of richness and diversity  
282 further increases in species will increase CSI, after the turning point this relationship is  
283 reversed (Fig. 4). Upland habitats were represented towards the right hand side of the curve  
284 (Appendix S2), showing that they typically had higher CSI values, but also that further  
285 increases in species richness in these habitats tend to decrease CSI.

286

## 287 **DISCUSSION**

288 This is the first study to examine trends in diversity and homogenization of British bird  
289 assemblages utilising extensive national monitoring data from 1994-2006. Against the  
290 backdrop of variable population trends (Baillie *et al.*, 2010), the alpha diversity of British bird  
291 assemblages, as measured using Simpson's index and species richness, has shown a  
292 positive trend over thirteen years of climate warming (Fig. 1,2). However, increases in diversity  
293 and richness have been concurrent with declines in community specialization (Fig. 1,2)  
294 suggesting that, although local diversity and species richness are increasing, these gains are  
295 likely to be at the expense of specialists in the community. Therefore, although our results  
296 show increases in alpha diversity, the increasing levels of homogenization suggest that a loss  
297 of beta and gamma diversity is likely to occur due to the localized distribution of our highly  
298 specialized communities (Fig. 1 d,e). Filippi-Codaccioni *et al.* (2010b) quantified a significant  
299 negative linear relationship between species richness and CSI. However, with our extensive  
300 dataset we found a non-linear relationship between CSI and richness (Fig 4). Our model  
301 demonstrated that there is a short increase period during which richness and CSI are  
302 positively correlated, but that a turning point exists after which this relationship reverses. By  
303 looking at where particular habitats fall on this curve, we can see that the most 'specialized'  
304 habitats such as upland and urban fall to the right of the turning point (Appendix S2), indicating

305 that any further increases in species in these habitats are likely to decrease community  
306 specialization. These results suggest that climate change has already had a significant impact  
307 on the composition of British bird communities and that some habitats are more vulnerable  
308 than others.

309 Our findings contribute to the growing number of empirical studies that have  
310 demonstrated climate impacts on diversity indices (e.g. Klanderund & Birks, 2003; Menéndez  
311 *et al.*, 2006; Wilson *et al.*, 2007; Hiddink & ter Hofstede, 2008; Britton *et al.*, 2009) and add to  
312 the relatively sparse literature documenting impacts on terrestrial vertebrates (e.g. Lemoine &  
313 Böhning-Gaese, 2003; La Sorte *et al.*, 2009). Our results support the predictions of Lennon *et al.*,  
314 (2000) who hypothesised that warmer summers would increase bird diversity, and the  
315 magnitude would vary geographically dependent on the sensitivity of the resident avifauna.  
316 Previous studies indicate changes in species richness often reflect an increased prevalence of  
317 generalists (e.g. Menéndez *et al.*, 2006; Britton *et al.*, 2009). Our analysis indicates that  
318 increases in generalists have concurrent, negative implications for community specialists. This  
319 suggests a detrimental impact of climate change on specialist species, corroborating recent  
320 studies that demonstrate decreases in community specialization due to environmental  
321 disturbance (Devictor *et al.*, 2007, 2008; Devictor & Robert, 2009; Filippi-Codaccioni *et al.*,  
322 2010a,b).

323 As a result of future climate change, European resident species are predicted to  
324 advance by 550 km north-east on average by the end of the 21<sup>st</sup> century (Huntley *et al.*, 2007).  
325 Within Britain, we would expect elevational and latitudinal shifts in species' distributions to  
326 have the greatest impact on communities in northern and upland habitats. Some of the  
327 observed increases in alpha diversity may be due to recent colonists. For example, Black  
328 Redstart (*Phoenicurus ochruros*), Cetti's Warbler (*Cettia cetti*) and Little Egret (*Egretta*  
329 *garzetta*) are thought to have colonized Britain from the continent during this period,  
330 movements likely to have been facilitated by warming temperatures (Robinson *et al.*, 2005).  
331 Species introduced outside of their endemic climate range have also become established, for  
332 example the Ring-necked Parakeet (*Psittacula krameri*) has seen a 600% increase in

333 population size between 1995 and 2007 (Risely *et al.*, 2009). However, the ubiquitous nature  
334 of diversity increases suggest that range expansion of resident species is the most likely factor  
335 driving the observed variation in our indices.

336 Common British birds and those with broader niches exhibit stronger species-energy  
337 relationships than rare ones (Evans *et al.*, 2005a,b) and are therefore more likely to show  
338 positive population responses to warming temperature. We found that upland communities  
339 were the most specialized (Table 1) and as predicted, these habitats incurred losses of  
340 specialization concurrently with the greatest increases in alpha diversity and temperature. We  
341 hypothesize that diversity gains in upland habitats are likely to have been driven by altitudinal  
342 and latitudinal shifts by generalists. Range-restricted and specialist species are unlikely to  
343 have the phenotypic plasticity required to adapt rapidly to novel climatic conditions and  
344 habitats (Crick, 2004) and will come under increasing pressure from loss of habitat and the  
345 shifting ranges of more generalist species. Extinctions of some species and distribution  
346 expansion of others will likely lead to a homogenization of assemblages (McKinney &  
347 Lockwood 1999) as demonstrated for birds in the Netherlands and France (Van Turnhout *et*  
348 *al.*, 2007; Devictor *et al.* 2008). Our results support the hypothesis that widespread  
349 homogenization is also occurring in British bird communities. We saw a significant national  
350 decrease in CSI during our study period, suggesting that the prevalence of generalists within  
351 assemblages is on the increase (Fig 1f). Further work is needed to quantify the impact of  
352 generalist expansion on specialists at the species level.

353 While temperature appears to be the predominant driver of these processes, rainfall  
354 had a significant negative association with species diversity and richness and a positive  
355 association with CSI (Table 1). Lemoine & Böhning-Gaese (2003) found that changes in  
356 rainfall had different impacts on long and short distance migrants suggesting that future shifts  
357 in precipitation would also have implications for the composition of communities.

358 We must consider that our results could reflect a spurious correlation between  
359 two increasing variables (alpha diversity and temperature). For example, whilst climate  
360 appears to have an important role in the homogenization process, a number of factors such as

361 land-use change have also been associated with profound changes in UK bird populations  
362 (e.g. Chamberlain *et al.* 2000), and specialist bird species have been shown to be more  
363 susceptible to farming intensification than generalists in France (Filippi-Codaccioni *et al.*  
364 2010a,b). However, habitat changes and climate are intrinsically linked; several studies have  
365 highlighted the importance of habitat as a factor affecting distribution changes in response to  
366 climate change (Pöyry *et al.*, 2001; Warren *et al.*, 2001; Menéndez *et al.*, 2007), although  
367 separating cause and effect between climate and habitat induced changes in vertebrates is  
368 complex. While this study did not examine the contribution of land-use or habitat change to  
369 patterns in diversity, what we have shown is that changes in climate explain almost half of the  
370 observed variation in diversity trends over this 13 year period (Table 1). Furthermore, the size  
371 of our dataset and the fine spatial scale at which the bird and climate data were collected  
372 would have greatly reduced the likelihood of spurious correlations arising. Our analysis also  
373 accounted for differences in detection probability between species, reducing much of the  
374 potential bias from creating indices using multiple species. Ultimately, most local extinctions  
375 result from multiple factors (Thomas *et al.*, 2006). Besides from competition, the climate-  
376 mediated spread of generalists could have secondary effects on avian communities through  
377 alteration of predator-prey interactions and the introduction of novel diseases and parasites.  
378 Future work should attempt to synthesize the relative contributions of these different factors to  
379 diversity change.

380           Quantifying the impact of environmental change on communities by measuring  
381 declines in species diversity has been common practice for some time. However, as  
382 demonstrated here, levels of alpha diversity often remain stable or increase as a result of  
383 environmental change (Sax & Gaines, 2003). Studies that have used measures of both alpha  
384 diversity and specialization have found these indices tend to have contrasting trends as a  
385 result of environmental disturbance (Devictor & Robert, 2009; Calvero & Brotons, 2010; Filippi-  
386 Codaccioni *et al.*, 2010b). However, all community metrics have strengths and limitations and  
387 we must be careful not to consider the presence of specialists as a *de facto* measure of  
388 ecosystem quality. It is rarely feasible to assess diversity and specialization values against



389 those of a pristine system (Devictor *et al.*, 2008). The strength of extensive long-term datasets  
390 such as the BBS, is that we can use temporal and spatial changes in metrics to inform our  
391 interpretation.

392

### 393 **Conclusions**

394 As long as species have differential abilities to adapt, disperse and compete, the  
395 impact of climate change will vary on a species-specific basis. There is now excellent evidence  
396 in place to describe climate impacts based on species traits but the implications for  
397 communities are less certain. Using an extensive long-term dataset we provide stark evidence  
398 for a link between warming climate and perturbation of British bird assemblages. Although  
399 species diversity and richness were shown to increase with rising temperatures, these gains  
400 were concurrent with increased homogenization and were likely the result of generalists' range  
401 expansion. As such, our observed increase in diversity over a period of recent warming is  
402 likely to be transient (Walther *et al.*, 2002; Devictor & Robert, 2009). Future climate change is  
403 likely to expedite further assemblage perturbation, with the UK likely to suffer permanent  
404 losses of specialist and range-restricted species. These results highlight the importance of  
405 considering measures of specialization in conjunction with more common diversity metrics.

406

407 **Acknowledgements**

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409 the collection of field data. The BBS is funded funded jointly by the British Trust for  
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413

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558

559 **Appendix S1** File containing species sample sizes and species specialization index (SSI)  
560 values.

561 **Appendix S2** Additional modeling results and graphs.

562

563

564

## 565 **BIOSKETCH**

566 **Catherine Davey** has recently completed a postdoctoral position at the British Trust for  
567 Ornithology where she worked on a variety of applied conservation issues. Prior to her work  
568 on patterns in avian diversity she completed an evaluation of the efficacy of environmental  
569 schemes for reversing farmland bird declines in England. She will soon take up a position at  
570 Lund University to study Swedish bird populations and climate change.

571

572 **Alison Johnston** is the Ecological Statistician at the British Trust for Ornithology where she is  
573 responsible for statistical advice across the organization and contributes to a wide variety of  
574 scientific projects. She is interested in the dynamics of wild bird populations, and the  
575 demographic processes which contribute to changing populations and how statistical  
576 techniques can reduce the bias in surveys.

577



578

579 **TABLE AND FIGURE CAPTIONS**

580

581 **Table 1** Results of the Generalized additive models (GAMs) used to examine the association  
 582 of year, location, habitat, breeding season temperature and rainfall with bird diversity, the  
 583 community specialization index (CSI), richness (S) and evenness ( $E_{1/D}$ ) of British bird  
 584 assemblages as measured at the 1km scale. Parameter estimates, standard errors and *P*-  
 585 values are shown for the parametric terms along with the *P*-values for the smoothed terms.  
 586 Habitat coefficients are in reference to 'upland' habitat (UP), which had the lowest overall  
 587 diversity and highest CSI.

588

589 **Figure 1** Mean modeled Simpson diversity values ( $1/D$ ) (a); mean modeled community  
 590 specialization indices (CSI) (b); mean modeled species richness (S) (c); and mean modeled  
 591 species evenness ( $E_{1/D}$ ) (d); all shown using a solid line and plotted with mean breeding  
 592 season temperatures ( $^{\circ}\text{C}$ ) plotted with a dotted line. Standard error bars are shown but are  
 593 small in relation to the means.

594

595 **Figure 2** (a-c) Map of the modeled Simpson diversity values ( $1/D$ ) for Britain in (a) 1994 and  
 596 (b) 2006; darker squares represent greater diversity. The absolute change in diversity  
 597 between 1994 and 2006 is shown in (c) with colours tending towards orange representing a  
 598 greater increase in diversity across the study period. (d-f) Map of the modeled community  
 599 specialization indices (CSI) for Britain in (d) 1994 and (e) 2006; darker squares represent  
 600 greater community specialization. The absolute change in CSI between 1994 and 2006 is  
 601 shown in (f) with lighter values representing a greater decrease in CSI across the study  
 602 period.

603

604 **Figure 3** Mean modeled percentage change over the study period of 1994 – 2006 for each  
 605 habitat type in Simpson diversity ( $1/D$ ) (a); community specialization index (CSI) (b); species  
 606 richness (S) (c); and species evenness ( $E_{1/D}$ ) (d), all plotted with open circles, shown with

607 percentage change in mean breeding season temperatures ( $^{\circ}\text{C}$ ) plotted with solid circles.  
608 Habitats are abbreviated as follows: Arable (AR), Improved Grassland (IG), Mixed Farmland  
609 (MF), Mixed (MI), Natural Grassland (NG), Urban (UR), Woodland (WO). Standard error bars  
610 are shown but are small in relation to the means.

611

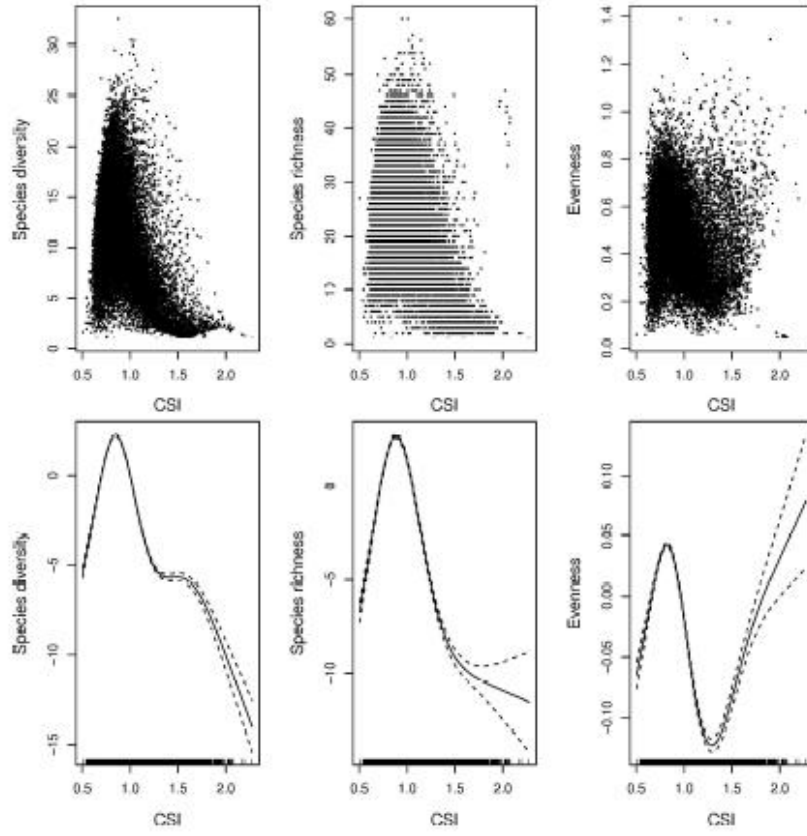
612 **Figure 4** Plots showing the relationships between the Community Specialization Index (CSI)  
613 and species diversity ( $1/D$ ), species richness ( $S$ ) and evenness ( $E_{1/D}$ ). The top row contains  
614 the plots of observed values using data from all years. The bottom row shows the modeled  
615 relationship created using a Generalized Additive Model (GAM) with a smooth CSI term (solid  
616 line); 95% confidence intervals are shown using broken lines.

617

618

	Species Diversity (1/D)			Community Specialization Index (CSI)		
n = 26105	deviance explained = 45.9%			deviance explained = 64.2%		
Model term	Coefficient	S.E	P	Coefficient	S.E	P
(Intercept)	-0.441	0.469	0.347	1.494	0.020	<0.001
Arable (AR)	5.565	0.136	<0.001	-0.337	0.006	<0.001
Improved Grassland (IG)	5.676	0.134	<0.001	-0.337	0.006	<0.001
Mixed Farmland (MF)	5.980	0.123	<0.001	-0.306	0.005	<0.001
Mixed (MI)	4.548	0.133	<0.001	-0.231	0.006	<0.001
Natural Grassland (NG)	1.826	0.135	<0.001	-0.108	0.006	<0.001
Urban (UR)	0.842	0.172	<0.001	-0.097	0.007	<0.001
Woodland (WO)	3.606	0.141	<0.001	-0.322	0.006	<0.001
Mean temperature (°C)	0.617	0.035	<0.001	-0.026	0.001	<0.001
Mean rainfall (mm)	-0.008	0.001	<0.001	3.02E <sup>-04</sup>	5.55E <sup>-05</sup>	<0.001
Model term	edf		P	edf		P
s(lat,long,year)	187		<0.001	192		<0.001
	Species Richness (S)			Species Evenness (E <sub>1/D</sub> )		
n = 26105	deviance explained = 55.1%			deviance explained = 12.7%		
Model term	Coefficient	S.E	P	Coefficient	S.E	P
(Intercept)	1.897	0.788	0.016	0.497	0.019	<0.001
Arable (AR)	8.675	0.228	<0.001	0.049	0.005	<0.001
Improved Grassland (IG)	10.082	0.225	<0.001	0.027	0.005	<0.001
Mixed Farmland (MF)	10.561	0.206	<0.001	0.025	0.005	<0.001
Mixed (MI)	8.731	0.223	<0.001	-0.004	0.005	0.451
Natural Grassland (NG)	2.820	0.227	<0.001	0.008	0.005	0.160
Urban (UR)	4.421	0.290	<0.001	-0.085	0.007	<0.001
Woodland (WO)	5.299	0.238	<0.001	0.048	0.006	<0.001
Mean temperature (°C)	1.213	0.059	<0.001	-0.003	0.001	0.044
Mean rainfall (mm)	-0.021	0.002	<0.001	1.37E <sup>-04</sup>	5.31E <sup>-05</sup>	0.010
Model term	edf		P	edf		P
s(lat,long,year)	186.6		<0.0001	176.1		<0.0001

619



177x177mm (600 x 600 DPI)

Figure 1.

621

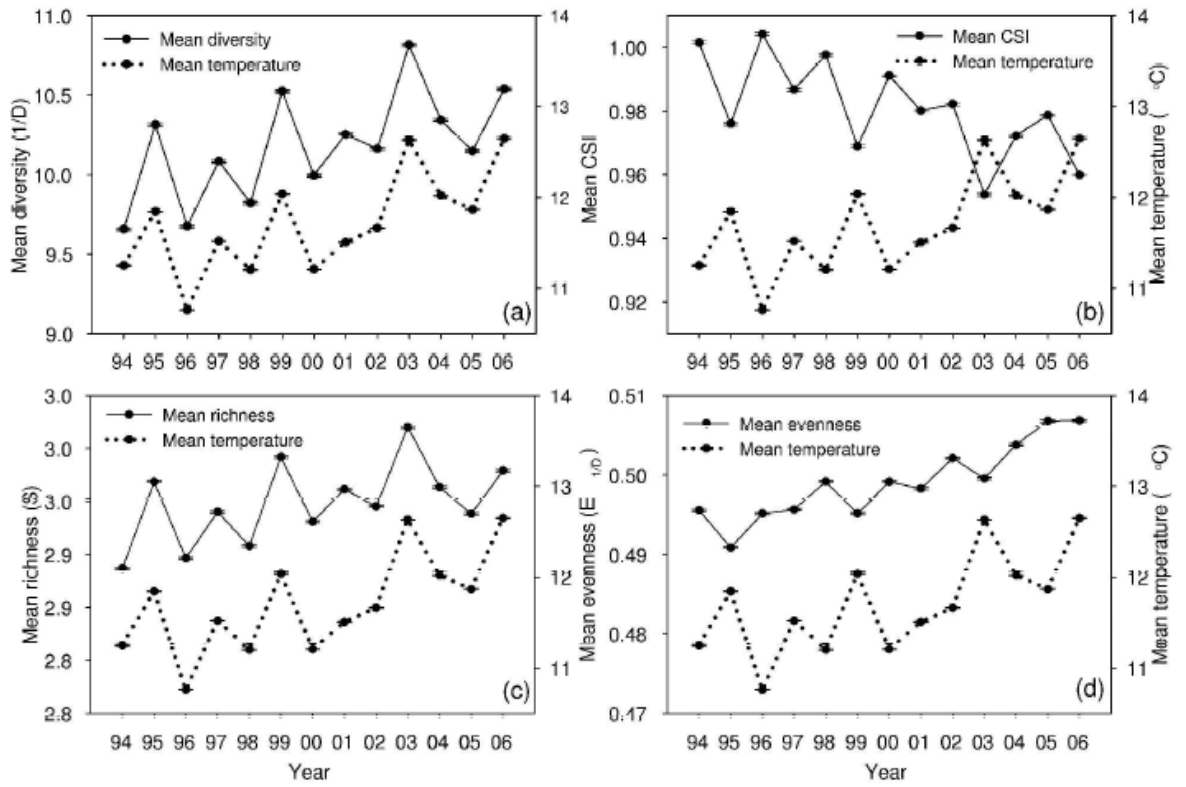


Figure 2.

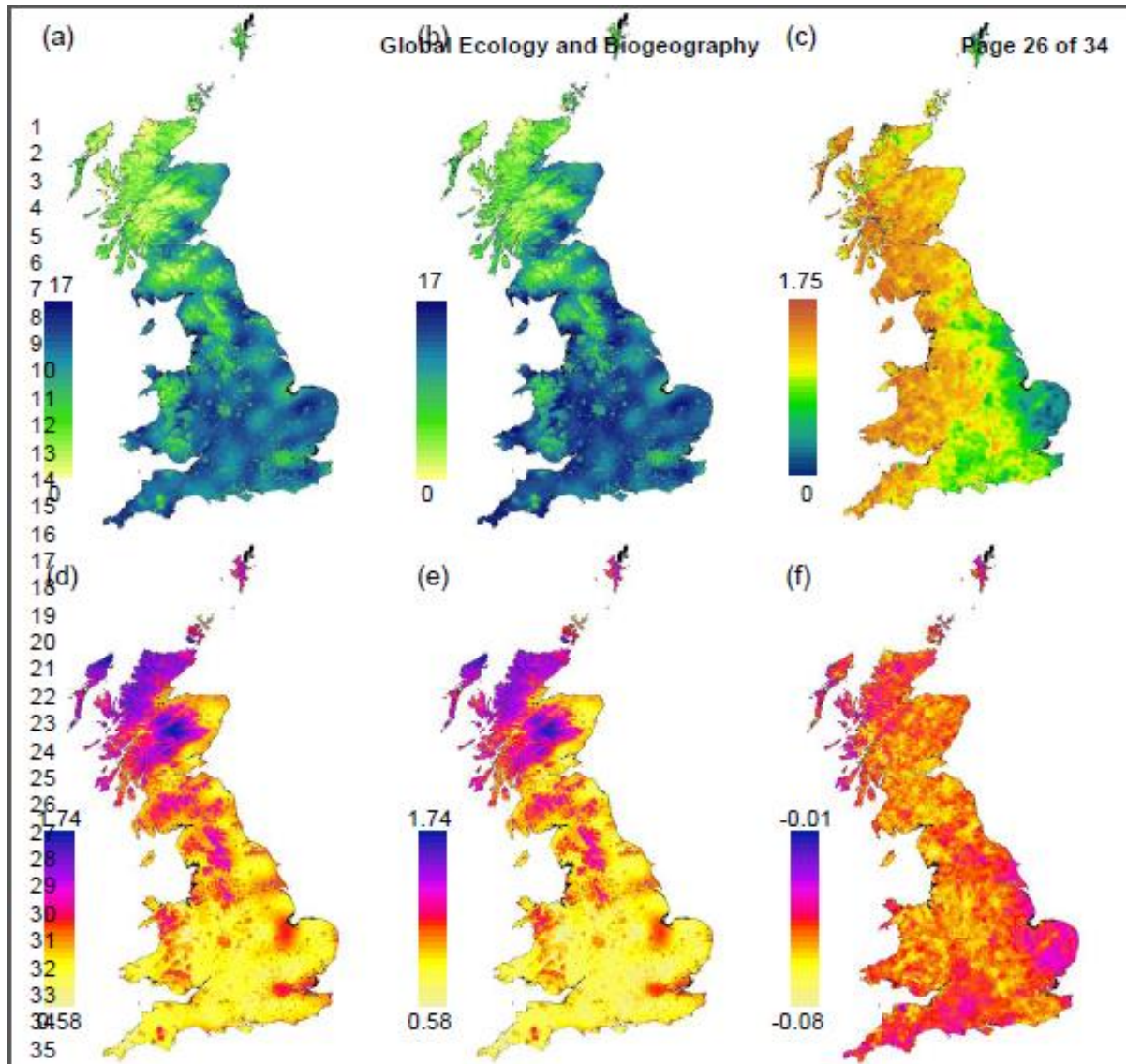
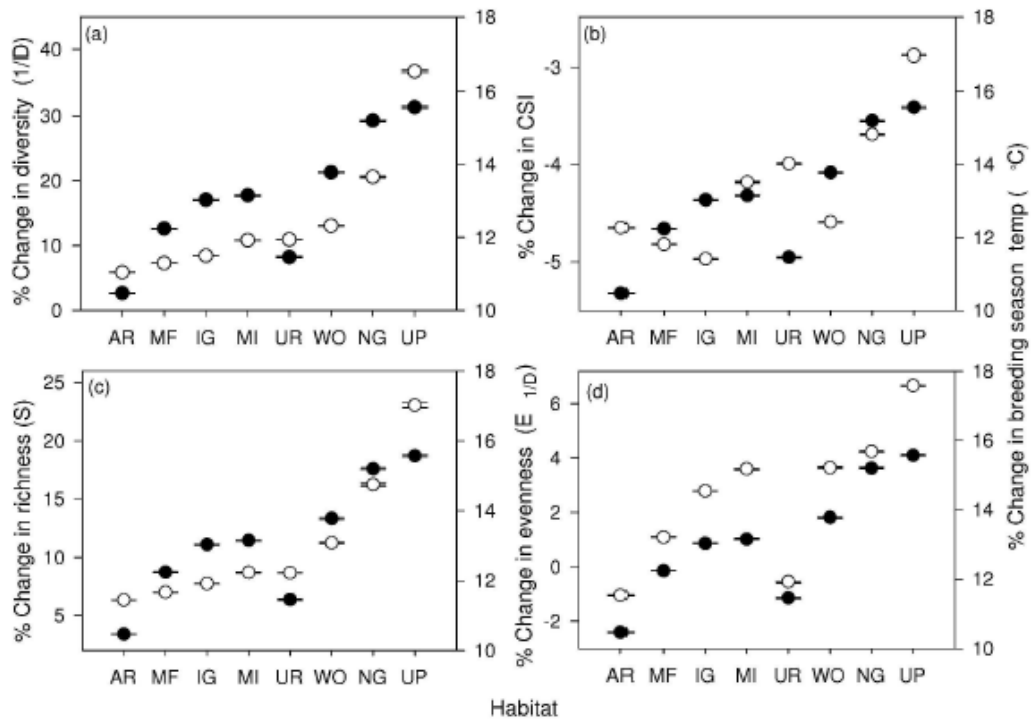


Figure 3.



168x126mm (600 x 600 DPI)

623

Figure 4.