Avian diversity, homogenization and warming climate

UNIVERSITÀ DEGLI STUDI DI TORINO

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

15

16

17 Catherine M. Davey, Dan E. Chamberlain^, Stuart E. Newson, David G. Noble, Alison

18 Johnston

19

20

21 British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU

22 cathdavey@yahoo.com

23 ^Current address: Dipartemento di Biologia Animale e dell'Uomo, Universita di Torino, Via

24 Accademia Albertina 13, 10123 Torino, Italy.

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   g(diversity) = β_0 + s(lat, long, year) + habitat + mean temperature + mean rainfall.

204

205   Where $g(\mu)$ is the link function, β_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 $^{\circ}$C $\pm$ 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 ± s.e 0.18), richness (23.05 ±

271 s.e 0.21), evenness (6.66 ± s.e 0.01) and temperature (15.57± 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*

314   *al.,* (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 21st 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). Asides from competition, the climate-

376   mediated spread of generalists could have secondary effects on avian communities though

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

413

414   **REFERENCES**

415   Allbright, T.P., Pidgeon, A.M., Rittenhouse, C.D., Clayton, M.K., Flather, C.H., Culbert, P.D.,

416   Wardlows, B.D. & Radeloff, V.C. (2010) Effects of drought on avian community

417   structure. *Global Change Biology*, **16**, 2158-2170.

418   Baillie, S.R., Marchant, J.H., Leech, D.I., Joys, A.C., Noble, D.G., Barimore, C., Downie, I.S.,

419   Grantham, M.J., Risely, K. & Robinson, R.A. (2010) *Breeding Birds in the Wider*

420   *Countryside: their conservation status 2009*. BTO Research Report No. 541. British

421   Trust for Ornithology, Thetford. (http://www.bto.org/birdtrends)

422   Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D. &

423   Schmid, B. (2006) Quantifying the evidence for biodiversity effects on ecosystem

424   functioning and services. *Ecology Letters,* **9**, 1146–1156.

425   Britton, A. J., Beale, C. M., Towers, W. & Hewison, R. L. (2009). Biodiversity gains and losses:

426   evidence for homogenization of Scottish alpine vegetation. *Biological Conservation*,

427   **142**, 1728-1739.

428   Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L.

429   (2001) *Introduction to distance sampling: estimating abundance of biological*

430   *populations*. Oxford University Press, Oxford.

431   Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubb, M. (2000) Changes

432   in the abundance of farmland birds in relation to the timing of agricultural intensification

433   in England and Wales. *Journal of Applied Ecology*, **37**, 771–788.

434

435 Clarke, A., & Gaston, K.J. (2006) Climate, energy and diversity. *Proceedings of the Royal*
436   *Society B*, **273**, 2257-2266.

437 Clavero, M. & Brotons, L. (2010) Functional homogenization of bird communities along habitat
438   gradients: accounting for niche multidimensionality. *Global Ecology and Biogeography*,
439   **19**, 684-696.

440 Crick, H.Q.P. (1992) A bird-habitat coding system for use in Britain and Ireland incorporating
441   aspects of land-management and human activity. *Bird Study*, **39**, 1-12.

442 Crick, H.Q.P. & Sparks, T.H. (1999) Climate change explains bird egg-laying trends. *Nature,*
443   **399**, 423–424.

444 Crick, H.Q. (2004) The impact of climate change on birds. *Ibis,* **146**, 48–56.

445 Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J., Hawkins, B.A., Kaufman,
446   D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turner, J.R.G. (2004) Predictions and
447   tests of climate-based hypotheses of broad-scale variation in taxonomic richness.
448   *Ecology Letters,* **7**, 1121–1131.

449 Devictor, V., Julliard, R., Couvet, D., Lee, A& Jiguet, F. (2007) Functional homogenization
450   effect of urbanization on bird communities. *Conservation Biology*. **21**, 741-751.

451 Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A., & Couvet, D. (2008) Functional biotic
452   homogenization of bird communities in disturbed landscapes. *Global Ecology and*
453   *Biogeography*, **17**, 252-261.

454 Devictor, V. & Robert, A. (2009) Measuring community responses to large-scale disturbance in
455   conservation biogeography. *Diversity and Distributions*, **15**, 122-130.

456 Dudley, S.P., Gee, M., Kehoe, C. & Melling, T.M. (2006) The British list: a checklist of birds of
457   Britain. *Ibis,* **148**, 526–563.

458 Evans, K. L., Greenwood, J. J. D. & Gaston, K. J. (2005a) Dissecting the species–energy
459   relationship. *Proceedings of the Royal Society B,* **272**, 2155–2163.

460 Evans, K. L., Greenwood, J. J. D. & Gaston, K. J. (2005b) Relative contribution of abundant
461   and rare species to species–energy relationships. *Biology Letters,* **1**, 87–90.

462 Filippi-Codaccioni, O., Devictor, V., Bas, Y., Clobert, J., & Julliard, R. (2010b) Specialist
463   response to proportion of arable land and pesticide input in agricultural landscapes.
464   *Biological Conservation*, **143**, 883-890.

465 Filippi-Codaccioni, O., Devictor, V., Bas, Y. & Julliard, R. (2010b) Toward more concern for
466   specialization and less for species diversity in conserving farmland biodiversity.
467   *Biological Conservation*, **143**, 1493-1500.

468 Gaston, K.J. & Blackburn, T.M. (2002) Large-scale dynamics in colonization and extinction for
469   breeding birds in Britain. *Journal of Animal Ecology,* **71**, 390-399.

470 Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M., Kerr, J.T.,
471   Mittelbach, G.G., Oberdorff, T., O'Brien, E.M, Porter E.E, Turner R.G. (2003) Energy,
472   water, and broad-scale geographic patterns of species richness. *Ecology,* **84**, 3105–
473   3117.)

474 Hewson, C.M. & Noble, D.G. (2009) Population trends of breeding birds in British woodlands
475   over a 32-year period: relationships with food, habitat use and migratory behaviour. *Ibis*,
476   **151**, 464-486.

477 Hiddink, J.G. & ter Hofstede, R. (2008) Climate induced increases in species richness of
478   marine fishes. *Global Change Biology*, **14**, 453-460.

479 Hillebrand, H., Soininen, J. & Snoeijs, P. (2010) Warming leads to higher species turnover in a
480   coastal ecosystem. *Global Change Biology*, **16**, 1181-1193.

481 Huntley, B., Green, R.E., Collingham, Y.C. & Willis, S.G. (2007) *A climatic atlas of European*
482   *breeding birds.* Lynx Edicions, Barcelona.

483 Jackson, D.L. (2000) *Guidance on the interpretation of the Biodiversity Broad Habitat*
484   *Classification (terrestrial and freshwater types): definitions and the relationships with*
485   *other habitat classifications.* JNCC Report No. 307. Joint Nature Conservation
486   Committee, Peterborough.

487 Julliard, R., Jiguet, J. & Couvet, D. (2003) Common birds facing global changes: what makes a
488   species at risk? *Global Change Biology*, **10,** 148-154.

489 Julliard, R., Clavel, J., Devictor, V., Jiguet, J. & Couvet, D. (2006) Spatial segregation of

490   specialists and generalists in bird communities. *Ecology Letters*, **9**, 1237-1244.

491   Klanderud, K. & Birks, H. J. B. (2003). Recent increases in species richness and shifts in

492   altitudinal distributions of Norwegian mountain plants. *Holocene*, **13**, 1-6.

493   La Sorte, F. A., Lee, T. M., Wilman, H. & Jetz, W. (2009). Disparities between observed and

494   predicted impacts of climate change on winter bird assemblages. *Proceedings of the*

495   *Royal Society B,* **276**, 3167-3174.

496   Lennon, J.J., Greenwood, J.J.D. & Turner, J.R.G. (2000) Bird diversity and environmental

497   gradients in Britain: a test of the species-energy hypothesis. *Journal of Animal Ecology,*

498   **69**, 581–598.

499   Lemoine, N. & Böhning-Gaese, K. (2003) Potential impact of global climate change on species

500   richness of long-distance migrants. *Conservation Biology*, **17**, 577-586.

501   Magurran, A.E. (2004) *Measuring biological diversity*. Blackwell Publishing, Malden.

502   McKinney, M. L. (1997). Extinction vulnerability and selectivity: Combining ecological and

503   paleontological views. Annual Review of Ecology and Systematics, **28**, 495-516

504   McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many

505   losers in the next mass extinction. *Trends in Ecology and Evolution,* **14**, 450–453.

506   Menéndez R, Megías A.G, Hill J.K, Braschler B, Willis S.G, Collingham Y, Fox R, Roy D.B,

507   Thomas C.D. (2006) Species richness changes lag behind climate change. *Proceedings*

508   *of the Royal Society B,* **273**, 1465–1470.

509   Menéndez, R., González-Megías, A., Collingham, Y., Fox, R., Roy, D.B., Ohlemüller, R. &

510   Thomas, C.D. (2007) Direct and indirect effects of climate and habitat factors on

511   butterfly diversity. *Ecology*, **88**, 605-611.

512   Newson, S.E., Evans, K.L., Noble, D.G., Greenwood, J.J. & Gaston, K.J. (2008) Use of

513   distance sampling to improve estimates of national population sizes for common and

514   widespread breeding birds in the UK. *Journal of Ecology,* **45**, 1330–1338.

515   Newton, I. (2004) The recent declines of farmland bird populations in Britain: an appraisal of

516   causal factors and conservation actions. *Ibis,* **146**, 579-600.

517   Perry, M. & Hollis, D. (2005) The generation of monthly gridded datasets for a range of climatic

518   variables over the UK. *International Journal of Climatology, 25*, 1041-1054.

519   Pöyry, J., Luoto, M., Heikkinen, R. K., Kuussaari, M. & Saarinen, K. (2009). Species

520   traits explain recent range shifts of Finnish butterflies. *Global Change Biology*, **15**,

521   732-743.

522   R Development Core Team (2009) *R: A language and environment for statistical computing.* R

523   Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

524   Risely, K., Noble, D.G. & Baillie, S.R (2009) *The Breeding Bird Survey 2008*. BTO Research

525   Report, 537. British Trust for Ornithology, Thetford.

526   Robinson, R.A., Learmonth, J.A., Hutson, A.M., Macleod, C.D., Sparks, T.H., Leech, D.I.,

527   Pierce, G.J., Rehfisch, M.M. & Crick, H.Q.P. (2005) *Climate change and migratory*

528   *species.* BTO Research Report, 414, 85–88. British Trust for Ornithology, Thetford.

529   Sax, D.F. & Gaines, S.D. (2003) Species diversity: from global decreases to local increases.

530   *Trends in Ecology and Evolution,* **18**, 561–566.

531   Sparks, T.H., Huber, K., Bland, R.L., Crick, H.Q., Croxton, P.J., Flood, J., Loxton, R.G.,

532   Mason, C.F., Newnham, J.A. & Tryjanowski, P. (2007) How consistent are trends in

533   arrival (and departure) dates of migrant birds in the UK? *Journal of Ornithology,* **148**,

534   503–511.

535   Thomas, C.D. & Lennon, J.J. (1999) Birds extend their ranges northwards. *Nature,* **399**, 213.

536   Thomas, C.D., Franco, A.M.A. & Hill, J.K. (2006) Range retractions and extinction in the face

537   of climate warming. *Trends in Ecology and Evolution*, **21**, 415-416.

538   Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop,

539   J.R., Marques, T.A. & Burnham, K.P. (2010) Distance software: design and analysis of

540   distance sampling surveys for estimating population size. *Journal of Applied Ecology*,

541   **47**, 5-14.

542   Turner, J.R., Lennon, J.J. & Lawrenson, J.A. (1988) British bird species distributions and the

543   energy theory. *Nature*, **335**, 539-541.

544 Van Turnhout, C.A., Foppen, R.P., Leuven, R.S., Siepel, H. & Esselink, H. (2007) Scale-
545   dependent homogenization: Changes in breeding bird diversity in the Netherlands over
546   a 25-year period. *Biological Conservation,* **134**, 505–516.

547 Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.M.,
548   Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate
549   change. *Natur*e, **416,** 389–395.

550 Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., Roy, D. B., Telfer, M.
551   G., Jeffcoate, S., Harding, P. *et al.* (2001). Rapid responses of British butterflies to
552   opposing forces of climate and habitat change. Nature, **414**, 65-69.

553 Wilson, R. J., Gutiérrez, D., Gutiérrez, J. and Monserrat, V. J. (2007). An elevational shift in
554   butterfly species richness and composition accompanying recent climate change.
555   Global Change Biology, **13**, 1873-1887.

556 Wood, S.N. (2006) *Generalized Additive Models: an introduction with R*. Chapman & Hall /
557   CRC, Boca Raton.

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 (˚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 (˚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	$3.02E^{-04}$	$5.55E^{-05}$	<0.001
Model term	edf		*P*	edf		*P*
s(lat,long,year)	187		<0.001	192		<0.001

|	Species Richness (S)			Species Evenness ($E_{1/D}$)		
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	$1.37E^{-04}$	$5.31E^{-05}$	0.010
Model term	edf		*P*	edf		*P*
s(lat,long,year)	186.6		<0.0001	176.1		<0.0001

619

620
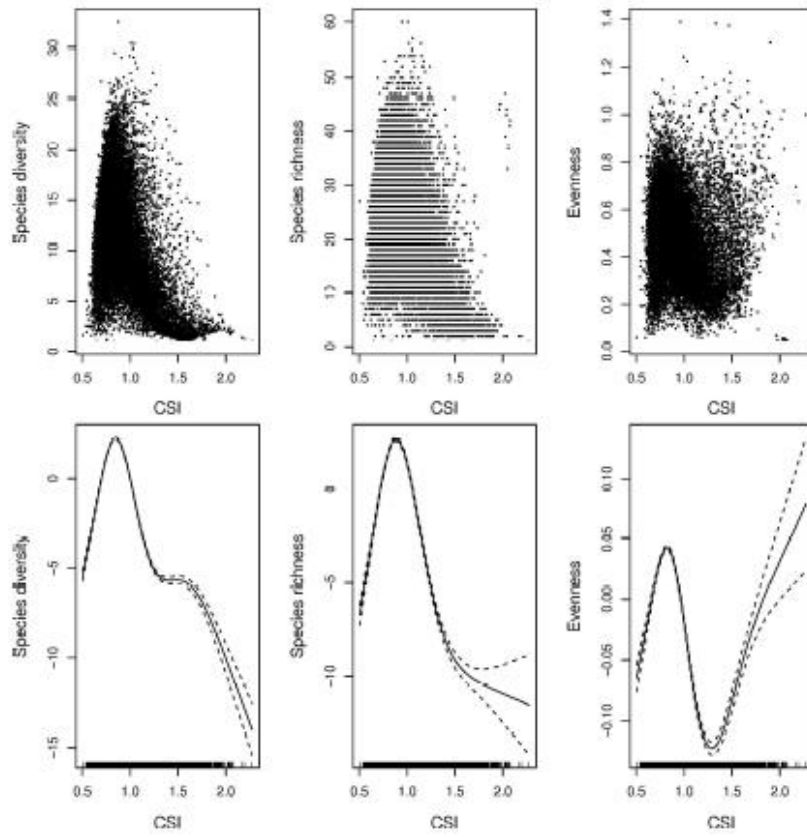
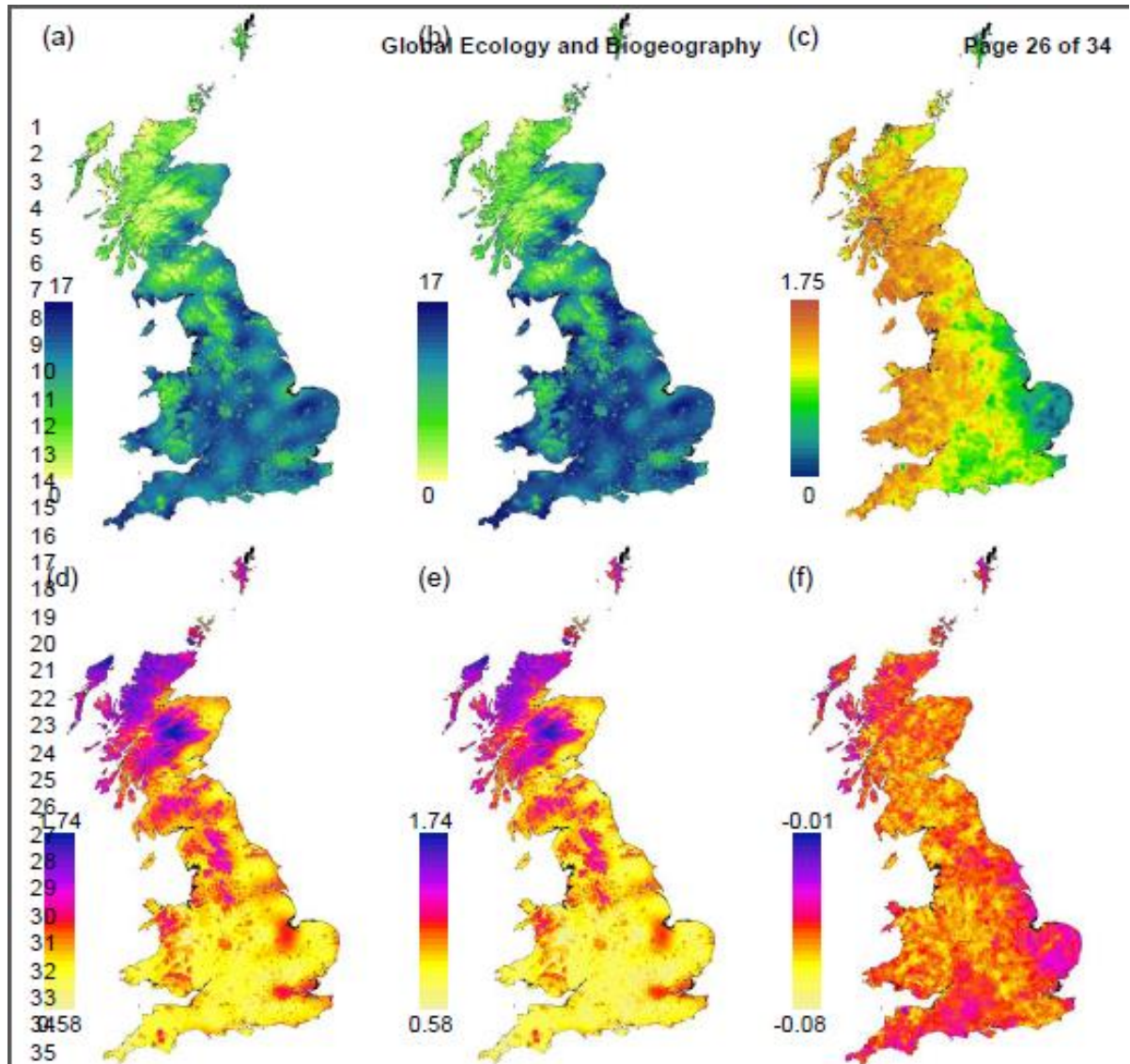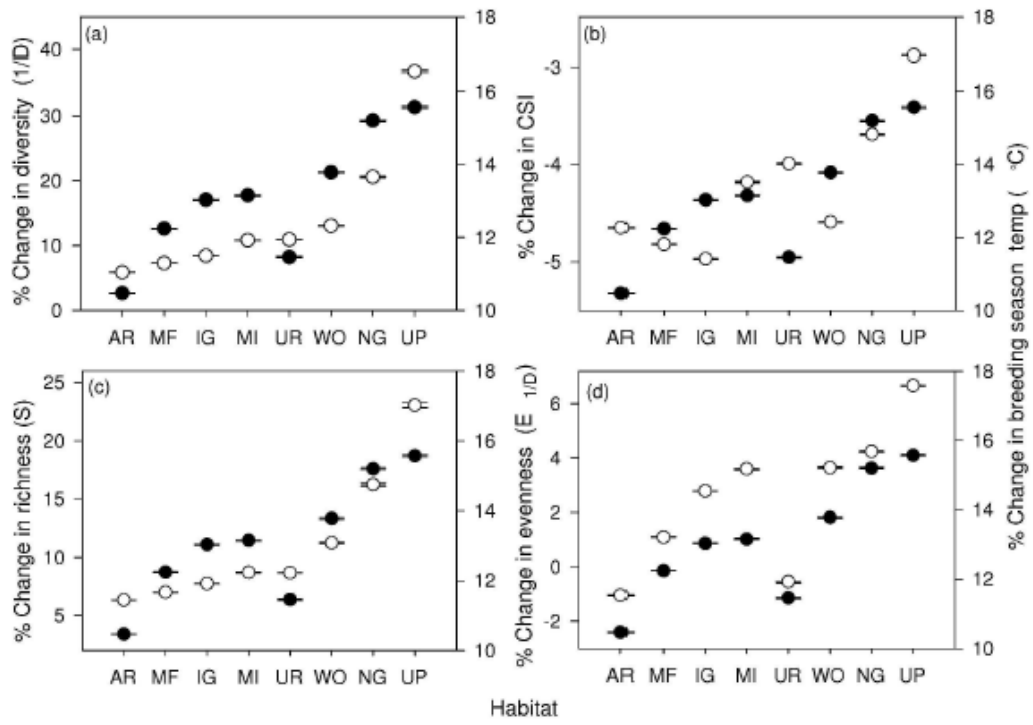177x177mm (600 x 600 DPI)

Figure 1.
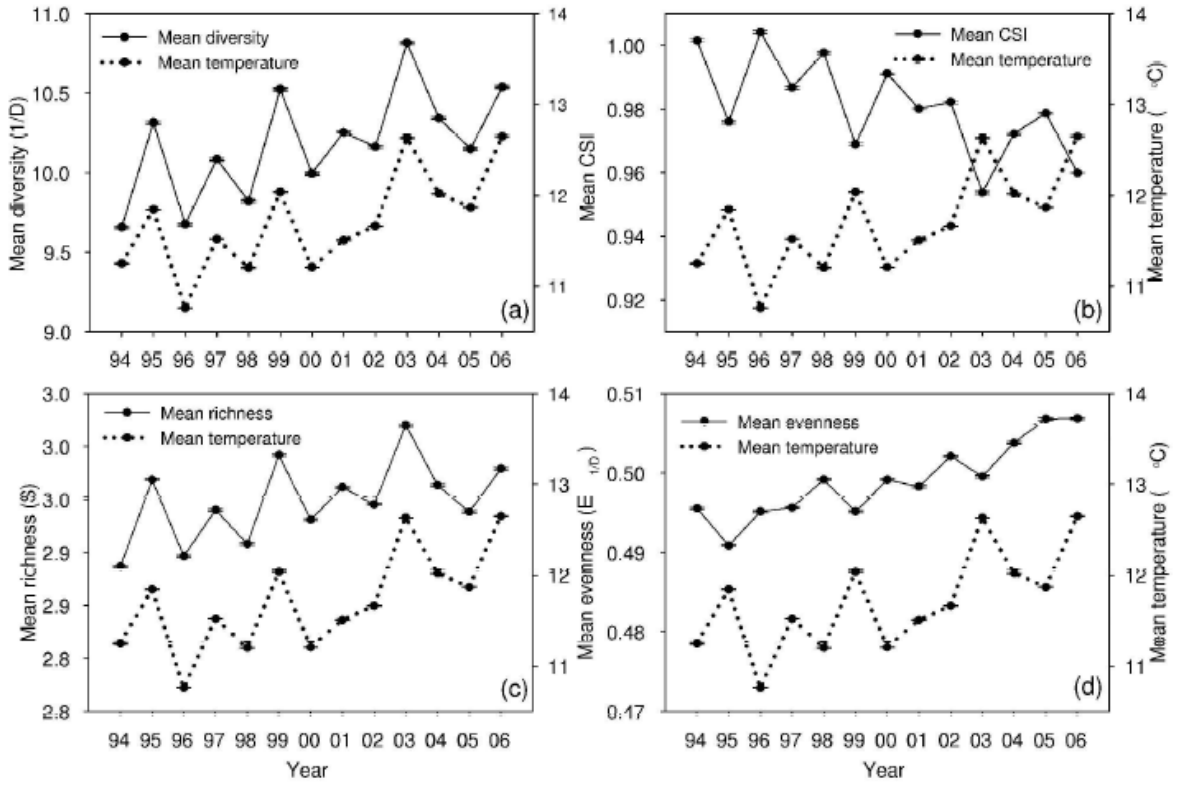
Figure 2.

622

Figure 3.

168x126mm (600 x 600 DPI)

623

Figure 4.