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

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

cathdavey@yahoo.com

^Current address: Dipartemento di Biologia Animale e dell'Uomo, Universita di Torino, Via Accademia Albertina 13, 10123 Torino, Italy.

ABSTRACT

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

Location Britain

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

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

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

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

INTRODUCTION

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

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

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

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

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

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

METHODS

Survey data

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

Bird detectability

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

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

Measures of community diversity

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

Community specialization index (CSI)

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

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

Land cover and climate data

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

Statistical analysis

Diversity and CSI

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

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

Where $g(\mu)$ is the link function, β_0 is the intercept and s is a thin plate spline. We used a three way interaction of latitude, longitude and year to allow us to model all the spatial and temporal variation in our dataset without constraints Habitat was a categorical variable based on LCM2000 classification. We also included a weighting to account for the original square stratification, which was the reciprocal of the survey density in different regions. The GAM fits a smooth two-dimensional surface to the data which optimizes a fit to peaks and troughs in the response variable, which have no support from the environmental data, thus controlling for unmeasured variables which may be affecting the response variable. This surface also implicitly fits spatial autocorrelation in the data, because it optimizes the degrees of freedom used in the surface to describe the patterns of the response variable. In doing so, it controls for similarities in the response variable at nearby points, and thus the climate variables describe relationships which are not described by the smooth GAM surface. In this way, spatial autocorrelation is partially controlled for by the two-dimensional smooth. The model parameters were determined *a priori* as potentially important determinants of species diversity so no model selection was undertaken (e.g. Habitat: Devictor *et al*., 2008; Filippi-Codaccioni *et al*., 2010; Temperature: Lennon *et al*., 2000; La Sorte *et al*., 2009; Rainfall: Allbright *et al*.,

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

Relationship between CSI and other community metrics

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

RESULTS

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

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

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

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

Mean modeled diversity increased across all habitats from 1994-2006, with upland showing the greatest mean percentage gain in diversity (36.85 ± s.e 0.18), richness (23.05 ± s.e 0.21), evenness (6.66 ± s.e 0.01) and temperature (15.57± s.e 0.03) (Fig. 3). Mean modeled CSI decreased across all habitats from 1994-2006, with agricultural habitats showing the greatest mean percentage loss in CSI (Fig. 3b).

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

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

DISCUSSION

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

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

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

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

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

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

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

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

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

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

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

Conclusions

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

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

Appendix S2 Additional modeling results and graphs.

BIOSKETCH

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

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

TABLE AND FIGURE CAPTIONS

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

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

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

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

percentage change in mean breeding season temperatures (˚C) plotted with solid circles. Habitats are abbreviated as follows: Arable (AR), Improved Grassland (IG), Mixed Farmland (MF), Mixed (MI), Natural Grassland (NG), Urban (UR), Woodland (WO). Standard error bars are shown but are small in relation to the means.

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

	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

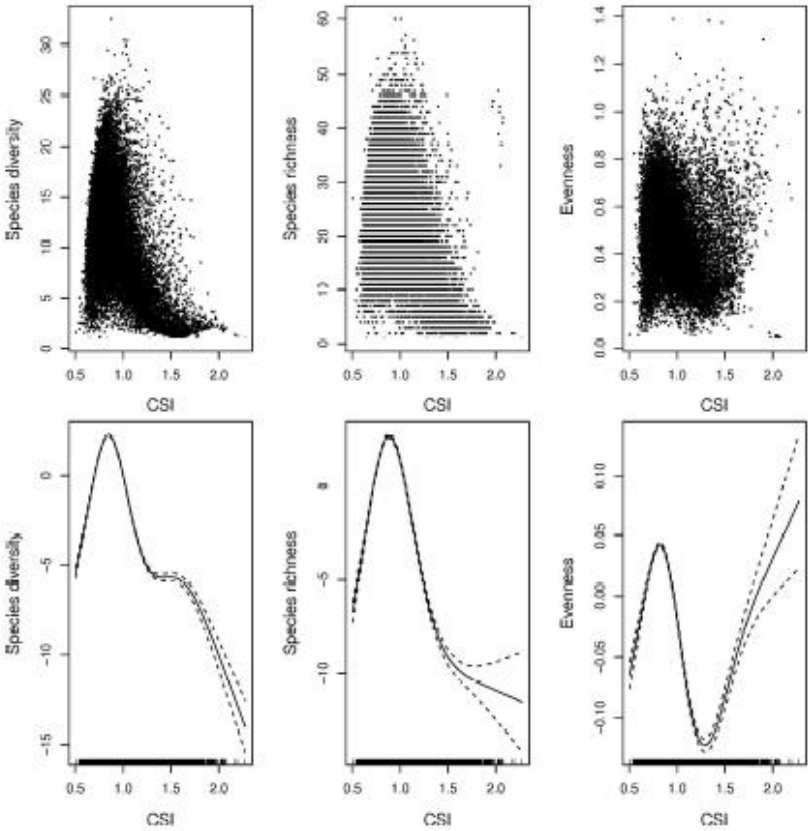
Species diversity
Species richness
Evenness
CSI
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Figure 1.

621

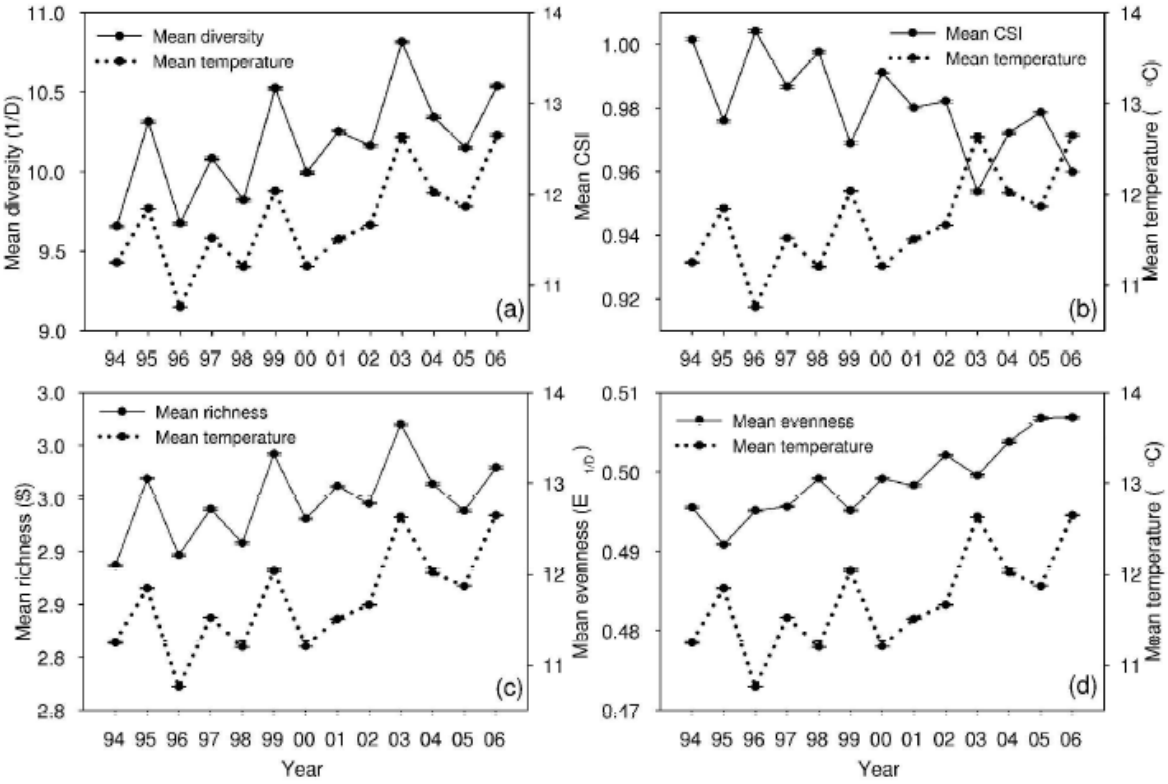
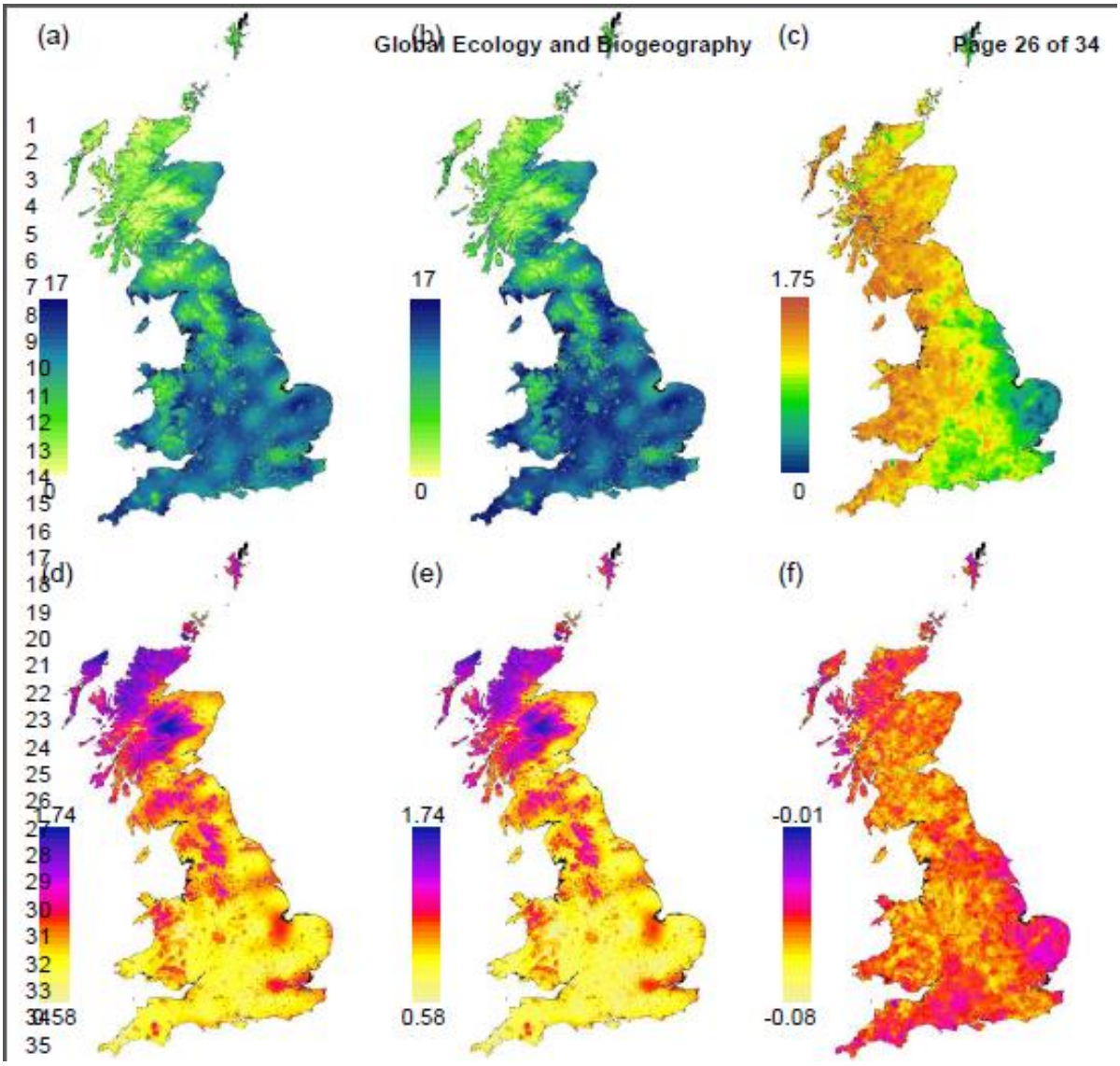

Mean diversity
Mean temperature
Mean diversity (1/D)
(a)
Mean CSI
Mean temperature
Mean CSI
Mean temperature (°C)
(b)
Mean richness
Mean temperature
Mean richness (S)
(c)
Mean evenness
Mean temperature
Mean evenness (E1/D)
Mean temperature (°C)
(d)
94 95 96 97 98 99 00 01 02 03 04 05 06
Year

Figure 2.


(a)
(b)
(c)
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17
0
17
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1.75
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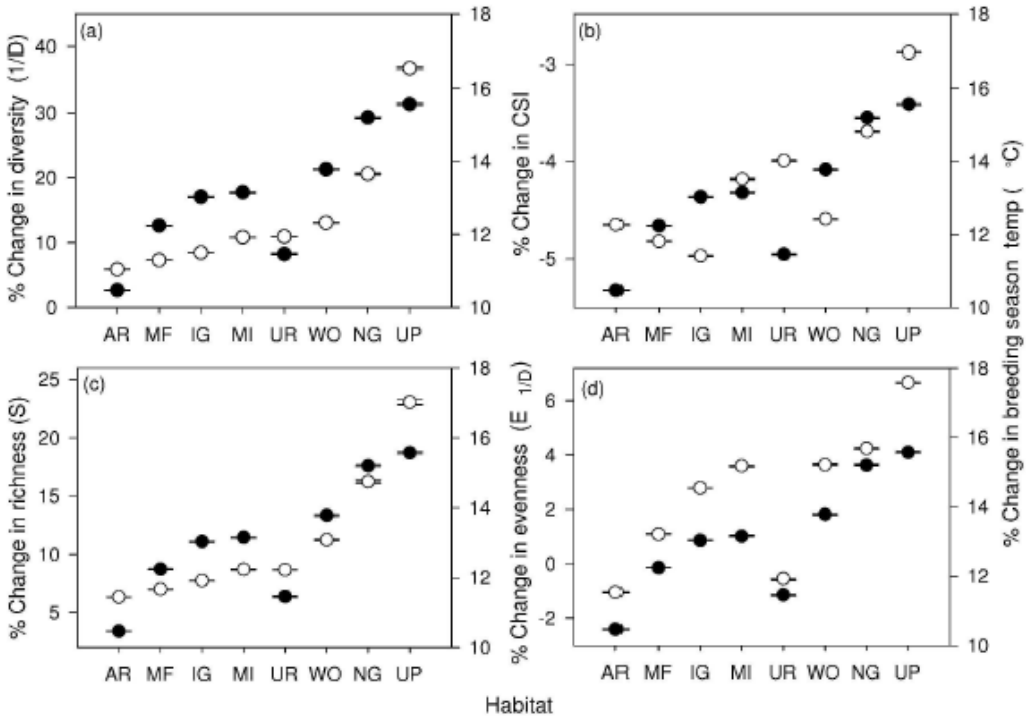
(d)
(e)
(f)
1.74
0.58
1.74
0.58
-0.01
-0.08

Figure 3.



168x126mm (600 x 600 DPI)

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Figure 4.