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Assessing taxonomic and functional change in British breeding bird assemblages over time

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- 1 i. Title: Assessing taxonomic and functional change in British breeding bird assemblages
- 2 over time

3 ii. Running Title (less than 40 characters): Temporal diversity change in British birds

- 4 iii. Abstract and Keywords
- 5 <u>Aim</u>
- 6 To identify the primary drivers of compositional change in breeding bird assemblages over a
- 7 40-year period.
- 8 *Location*
- 9 Britain
- 10 <u>*Time Period</u>*</u>
- 11 1970 to 2010
- 12 <u>Major Taxa Studied</u>
- 13 Birds

14 <u>Methods</u>

15 Using morphological trait measurements and a dataset of presence-absence data for British

16 breeding birds surveyed in 10×10 km hectads across two time periods, we calculated

17 temporal taxonomic and functional beta diversity for each hectad alongside species richness

18 change, mean nearest taxon distance (MNTD), and mean pairwise distance (MPD). We also

- 19 estimated potential drivers of beta diversity, including climatic and land-use and land cover
- 20 (LULC) change variables, elevation, and assemblage species richness in 1970. We used
- 21 random forest regressions to test which variables best explained compositional change in the

assemblages. We also assessed spatial taxonomic and functional change by analysing
multiple-site beta-diversity and pairwise dissimilarities between time periods.

24 <u>Results</u>

Initial (1970) species richness was the most important predictor (highest importance score)
across all models, with areas characterised by higher initial richness experiencing less
assemblage change overall. Coordinates included to capture spatial autocorrelation in the data
were also important predictors of change. Most climate and LULC variables had relatively
low explanatory power; elevation and average temperature were the most influential. All
metrics increased slightly with increasing elevation, except for species richness change and
MPD, which decreased.

32 <u>Main Conclusions</u>

The composition of British breeding bird assemblages changed substantially between 1970 and 2010. Spatial heterogeneity increased, both functionally and taxonomically. We show evidence that hectads with larger assemblages have been buffered from temporal diversity change and that those at higher elevations changed more in composition than those at lower elevations. Overall, coarse resolution climate and LULC only explained small to moderate amounts of variation, suggesting that stochastic assembly change or finer scale drivers may be drivers of temporal changes in assemblage composition.

Keywords (6-10 arranged alphabetically): beta diversity, British birds, climate change,
community ecology, LULC, macroecology.

42 iv. Main Text

43 1 Introduction

Recently there has been an increasing focus in ecology on analysing biodiversity change 44 through time and identifying the drivers of that change (Dornelas et al. 2014; Antão et al. 45 2020; Blowes et al. 2019; Pilotto et al. 2020). Climate and land use and land cover (LULC) 46 change have both been identified as predictors of biodiversity change globally and linked, 47 either directly or indirectly, to increased extinction risk in many taxa in the coming decades 48 (Newbold, 2018; Thomas et al., 2004; Urban, 2015; Wieczynski et al., 2019). Of the two, 49 50 land-use change is generally acknowledged as the largest current driver of biodiversity loss (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Seto, Güneralp, & Hutyra, 51 52 2012; Sohl, 2014; Tratalos et al., 2007; Zabel et al., 2019). However, warming temperatures are impacting species through range alterations/niche tracking (Batt, Morley, Selden, Tingley, 53 & Pinsky, 2017; Fox et al., 2014; Tayleur et al., 2015) and shifting phenologies (Bell et al., 54 2019). These impacts will likely intensify and climate change is expected to match or exceed 55 land-use change as the leading biodiversity change driver this century (Newbold, 2018). 56 While deterministic processes (e.g., LULC and climate change) can drive assemblage change, 57 non-deterministic processes (e.g., stochastic change) have also been identified as drivers 58 (Baselga, Bonthoux & Balent, 2015; Stegen et al., 2013). Indeed, many biodiversity models 59 (e.g., the equilibrium theory of island biogeography and neutral models; Hubbell, 2001; 60 MacArthur & Wilson, 1967) predict the temporal turnover of species in a community as a 61 theoretically stochastic process. 62

Two main factors hinder many biodiversity change studies. First, appropriate time-series data covering species composition from sites at two or more time points are required (Antão et al., 2020; Dornelas et al., 2018). However, due to the resources required to collect time-series data, most studies analysing assemblage diversity change use a space-for-time substitution, analysing dissimilarity between sites within the same study system and time period (e.g.

Swenson, Anglada-Cordero, & Barone, 2011). Whilst space-for-time analyses assume that
communities are at equilibrium, temporal analyses do not (Damgaard, 2019).
Second, many studies examining temporal change in assemblages in response to
anthropogenic drivers use only taxonomic diversity (quantifying changes in species
composition in each locality over time); this ignores species-specific differences in functional
traits that provide ecological information regarding individual species' roles in their
community (Sekercioğlu, 2006).

An effective and widely used tool for analysing change in composition is temporal beta-75 76 diversity (Baselga et al., 2015; Shimadzu, Dornelas, & Magurran, 2015; Matthews, Sadler, Carvalho, Nunes, & Borges, 2019). Temporal beta-diversity metrics capture changes in the 77 78 size and composition of a single assemblage over two or more time points. Those studies that have analysed time-series data show mixed outcomes, variously indicating increases 79 (Christian, Isabelle, Frédéric, & Vincent, 2009; Jarzyna & Jetz, 2017; Schipper et al., 2016), 80 81 decreases (Konvicka, Fric, & Benes, 2006; Tingley & Beissinger, 2013; Wilson, Gutiérrez, 82 Gutiérrez & Monserrat, 2007), or no systematic change (Dornelas et al., 2014; Petchey, Evans, Fishburn, & Gaston, 2007) in diversity. Further evidence of temporal biodiversity 83 change and any drivers of that change is thus needed. 84

Here, we use measures of temporal taxonomic and functional beta diversity to analyse 85 patterns of assemblage change in British breeding bird assemblages. To assess how 86 assemblage diversity changed spatially, we used two complementary analyses to identify 87 changes in the spatial dissimilarity structure and overall heterogeneity. Based on previous 88 89 work on temporal diversity change, we expected average temperature change to be selected 90 as an important variable (defined by the importance score in the random forest modelling) in driving diversity patterns (Davey, Chamberlain, Newson, Noble & Johnston, 2012; Lennon, 91 Greenwood, & Turner, 2000), and we expected turnover to be the main component of both 92

loss (Baselga et al., 2015; Blowes et al., 2019; Dornelas et al., 2014; Pilotto et al., 2020;
Stegen et al., 2013). The effect of LULC change was more difficult to predict. Previous
studies indicated correlations between compositional change and LULC change variables, but
LULC change variables generally had low explanatory power (Jung, Scharlemann &
Rowhani, 2020).

functional and taxonomic compositional change, with no overall pattern of consistent species

99 2 Materials and Methods

100 Data collection

93

101 Species Composition Data

Data on the summer (breeding) distributions of the British avifauna recorded over two 102 103 separate periods (Gillings et al., 2019) were collected during April-July 1968-1972 (BA1970) and 2008-2011 (BA2010) by volunteers on behalf of the British Trust of Ornithology (BTO) 104 and the Scottish Ornithologists' Club (SOC). Each atlas (the data collected over each 105 sampling period) consists of data on presence or absence of British bird species within 10km 106 x 10km (100km²) hectads covering the British Isles on a continuous grid (Fig. S1.1). We 107 108 prepared the data by removing some species (e.g. marine species and vagrants), and removing hectads that were calculated to have potentially low sample completeness (defined as the 109 difference in the proportion of benchmark species found in each hectad in each sampling 110 period) or had less than 50% land or comprised offshore islands (see Appendix S1 in the 111 Supporting Information for more details). 112

113 Trait data

We selected nine continuous traits (eight morphometric traits and body mass) measured from museum specimens or extracted from the literature to characterise the functional diversity of each assemblage (all species present in a hectad) (Pigot et al., 2020). All traits selected (two estimates of beak length (culmen from tip-to-skull and tip-to-nares), beak width, beak depth,
secondary length, tarsus length, wing chord length, tail length, and body mass) provide
information about dietary niche, locomotion, and ecological function (Pigot et al., 2020;
Tobias & Pigot, 2019; Trisos, Petchey, & Tobias, 2014).

We log-transformed measures of all traits then standardised them to a mean of zero and a standard deviation of one. We then entered measures of all traits into a principal component analysis (PCA), and extracted all axes, as all axes, including the minor axes, have been shown to provide useful information with regard to these trait data (Pigot et al., 2020).

125 *Climate Data*

We downloaded monthly temperature and precipitation data for 1960 to 2011 (ten years 126 before the first Atlas period to capture lag effects) from the UK Met Office, which provides 127 climate data interpolated from local weather stations onto a 1km x 1km grid across the UK 128 (Hollis, McCarthy, Kendon, Legg, & Simpson, 2019). For each hectad, we calculated change 129 in several climate variables for the breeding season (defined as the start of March to the end 130 of July), selected *a priori*. We calculated average temperature (°C) as the mean monthly 131 temperature across the breeding months for each year (1960 - 2011). We selected this 132 variable because it impacts species' metabolic loads and temperature increases are thought to 133 reduce this load and allow more energy for reproduction (Lennon et al., 2000), and 134 temperature has been found to be a predictor of avian occurrence and abundance in the 135 breeding season (Jarzyna, Zuckerberg, Porter, Finley, & Maurer, 2015; Jiguet et al., 2010; 136 McDonald, McClure, Rolek & Hill, 2012). We summed precipitation (mm) for each hectad 137 over the breeding season for each year. We calculated range in temperature as the mean 138 139 maximum temperature over the breeding season minus the mean minimum temperature for each year. We also calculated the mean temperature in the warmest and coldest month for 140 each year. To assess the effect of unusually cold or warm periods, we calculated the "fat-tail" 141

142	for the coldest and warmest months across the 40 year period ($Cold_{FAT}$ and $Warm_{FAT}$). The
143	fat tail is the duration of the period in the tails of the distribution relative to that in the central
144	mass, calculated as $(Q \ 0.975 - Q \ 0.025)/(Q \ 0.875 - Q \ 0.125)$, where Q is the quantile
145	function (Brys, Hubert & Struyf, 2006).
146	To calculate climatic change, we averaged each of the climate variables over two periods to
147	match each atlas $(1960 - 1970 \text{ and } 2001 - 2011)$ and also calculated the standard deviation
148	for each. We then subtracted the earlier mean from the later one to give the change in average
149	temperature (Tavg), change in the range of temperature (Range), change in precipiation
150	(Prec), change in average temperature of the coldest month (Cold), and change in the average
151	temperature of the warmest month (Warm). We repeated this for the standard deviation to
152	measure how variation around the mean changed across time (Tav g_{SD} , Range $_{SD}$, Prec $_{SD}$,

153 Cold_{SD}, and Warm_{SD}).

154 Land Use Data

We obtained data for land-use change from the Historic Land Dynamics Assessment 155 (HILDA, Version 2.0) model (Fuchs, Herold, Verburg, & Clevers, 2012). The HILDA model 156 uses multiple data streams of land cover to reconstruct historic LULC change, including 157 where transitions have occurred (e.g. from forest to settlement). We obtained land cover data 158 on the basis of dominant, gross LULC changes for 1970 and 2010 (Fuchs et al., 2012; Fuchs, 159 Herold, Verburg, Clevers, & Eberle, 2015). From these data, we calculated the number of 160 1km² grid cells within each hectad classed as settlements (hereafter urban land-use), cropland, 161 and forest in 1970. We repeated this process with the 2010 data and subtracted the number of 162 grid cells present in each land-use class in 1970 from the number of grid cells present in the 163 same class in 2010. This provided a measure of the land-use change (converted to % change) 164 within the hectads over the 1970-2010 period (Urbanchange, Cropchange, and Forestchange). 165

166 HILDA also provides the number of times a 1km x 1km grid cell transitioned (changed

167 primarily from one LULC class to another) between 1970 to 2010. We summed all transitions

168 within each hectad to give a measure of total LULC change (Total_{change}). We calculated

169 Shannon's diversity index for each hectad to capture the amount and variability in land cover

types, then subtracted the earlier measure from the latter to give a measure of difference

171 (Shan).

172 *Elevation Data*

173 We obtained elevation data from the shuttle radar topography mission (SRTM). For each

hectad, we used 400 equally spaced points to extract data. We then calculated the average and

standard deviation from these data (Elevation and SD_{elev}, respectively).

176 We used Pearson's correlations to test for multicollinearity between the predictor variables.

177 Mean_{elev} and SD_{elev} had an absolute correlation above 0.70 (-0.78), as did Tavg and Warm

178 (0.84). Therefore, we removed SD_{elev} and Warm.

179 <u>Measuring compositional change through time</u>

180 Temporal Taxonomic and Functional Beta-Diversity

181 We calculated taxonomic dissimilarity between 1970 and 2010 for each hectad with the

182 function *beta.temp* from the R package 'betapart' (Baselga & Orme, 2012). This function

183 computes the beta-diversity (i.e., the compositional dissimilarity) between the earlier

assemblage and the later assemblage within the same hectad. We used Sørensen's

dissimilarity index (BD_{TOTAL}; Baselga, 2010; Koleff, Gaston, & Lennon, 2003).

186 We partitioned total beta-diversity (BD_{TOTAL}) into its two constituent components, turnover

and nestedness resultant dissimilarity. Turnover (hereafter, BD_{TURN}) is the proportion of

- 188 dissimilarity due to species replacement between the two time periods, whereas nestedness
- 189 (hereafter, BD_{NEST}) is the proportion of the dissimilarity due to the earlier or later assemblage

being a nested subset of the other through either species loss or gain (Baselga, 2010). We also
calculated a simple measure of taxonomic change (2010 species richness – 1970 species
richness) (SP_{change}).

We then calculated functional beta-diversity using Sørensen's dissimilarity index and 193 Baselga's partitioning framework (Phylosor). For this approach, we first used the 194 agglomerative hierarchical clustering method (UPGMA) to create a global functional 195 dendrogram containing all the species included in the study. This method produces a rooted 196 tree where the distance between the root to all tips is equal (Petchey & Gaston, 2002). We 197 used the phylo.sor function in the 'betapart' package (Baselga & Orme, 2012) to calculate 198 functional dissimilarity on the basis of the shared branch length of the functional dendrogram 199 between 1970 and 2010 (hereafter called FD_{TOTAL}). Although this method is usually applied 200 to phylogenies, we applied it to a functional dendrogram to give a functional measure 201 202 analogous to taxonomic beta-diversity, allowing for a straightforward comparison. We also used this method due to the large number of sites and therefore the substantial computing 203 time required to use convex hull approaches. We partitioned FD_{TOTAL} into nestedness 204 resultant dissimilarity (FD_{NEST}) and turnover (FD_{TURN}). 205

We performed a Pearson's correlation between the Euclidean distances in the distance matrix and the cophenetic distances in the dendrogram to test whether the functional distances were representative of the actual distances between the species. The correlation was high (Pearson's r = 0.80), showing that the dendrogram provided a good measure of the functional distances between species.

211 MNTD (Mean Nearest Neighbour Distance) and MPD (Mean Pairwise Distance)

As an alternative to Baselga's temporal functional beta-diversity framework, we calculated

the beta-diversity versions of mean nearest taxon distance (MNTD) and mean pairwise

214 distance (MPD) (see Appendix S3 for more details regarding these metrics).

215 We calculated MPD and MNTD with the *comdist* and *comdistnt* functions, respectively, in

the R package 'picante' (Kembel et al., 2010; Webb, Ackerly & Kembel, 2008). We plotted

values of all metrics to identify any spatial clustering of areas of high or low change.

218 Change in spatial taxonomic and functional beta-diversity

We performed two complementary analyses to test whether different aspects of spatial beta-219 diversity changed. Changes in the spatial dissimilarity structure (i.e., similar sites becoming 220 dissimilar and vice-versa) can be detected as low-level correlations between the dissimilarity 221 between sites in the earlier period and the dissimilarity between sites in the later period 222 (Baselga et al., 2015). We calculated pairwise dissimilarities between each hectad and every 223 other hectad during both time periods. We then used Mantel tests (Mantel, 1967) to assess the 224 significance of the correlation of the turnover (PBD_{TURN}, i.e., pairwise beta-diversity 225 turnover) and nestedness (PBD_{NEST}) dissimilarities between sites across the two time periods. 226 We repeated this process for functional turnover (PFD_{TURN}) and nestedness (PFD_{NEST}). 227 228 In contrast to pairwise dissimilarities, multiple site beta-diversity provides information about the overall spatial heterogeneity of assemblages (Baselga et al., 2015; Baselga & Orme, 229 230 2012). Multiple site beta-diversity (here referred to as MBD_{TOTAL}, i.e., total multiple site 231 beta-diversity) can also be partitioned into its constituent components, nestedness (MBD_{NEST}) and turnover (MBD_{TURN}). To test for increases or decreases in heterogeneity, we used the 232 233 beta.sample function in the package 'betapart' to generate 1000 multiple site functional and taxonomic beta-diversity values for both time periods from a random sample of 1/5 of the 234 sites (Baselga et al., 2015; Baselga & Orme, 2012). We compared the distributions for both 235

the turnover and nestedness resultant dissimilarity portions for each period with the function

- 237 *mded* (in the package 'mded'; Aizaki, 2014; Poe, Giraud & Loomis, 2005; Poe, Welsh &
- 238 Champ, 1997), which quantifies the difference between two non-independent empirical
- 239 distributions. We repeated this process for multiple site functional beta-diversity (MFD_{TOTAL})
- 240 and its constituent components (nestedness: MFD_{NEST}, and turnover: MFD_{TURN}).

241 Modelling variation in temporal beta-diversity

242 Random Forest Regression

243 We used random forest regression to explore whether our explanatory variables influenced

the temporal beta-diversity metrics. We tuned the forests with combinations of three

245 hyperparameters (see Appendix S3 for further details) with the function *rf_tuning* in the

246 package 'spatialRF' (Benito, 2021). We selected the combination that best fit the data

247 (evaluated with the R^2 of the fit to the out-of-the-bag [OOB] data).

We included coordinates of hectad centres as predictor variables (latitude [Y] and longitude 248 [X] (Georganos et al., 2021; Hengl, Nussbaum, Wright, Heuvelink & Gräler, 2018)). We then 249 assessed spatial autocorrelation of the residuals from the random forest models with Moran's 250 251 I index (Anselin 2010; Moran 1948). We used a Euclidean distance matrix between all sites with model residuals in Moran's I tests, implemented as standard in the functions utilised to 252 run the models in the package 'spatialRF' (Benito, 2021; Wright & Ziegler 2017). 253 254 Because random forest is a stochastic algorithm, we ran twenty replicates for each of the 255 response metrics, yielding 20 models for each metric. We calculated variable importance (defined as the increase in mean square error with a random variable instead of the original) 256 with permutations within each forest (Breiman, 2001). We recorded the median and SD of 257 258 variable importance across the 20 models.

We assessed the predictive performance of the models through spatial cross-validation. We split the data into 20 sets of spatially distinct training (75%) and testing (25%) data. Reported here are the median variable importance and mean R^2 (OOB) values across the 20 models for each response metric and the mean performance (R^2 and root mean squared error [RMSE]) across the 20 evaluation models for each of the response metrics. Because variation in climate and other predictors may be spatially structured, we repeated the above with the spatial coordinates omitted from the model.

We assessed relationships between the explanatory variables and the response variables by calculating the marginal effect of each variable across the 20 models for each response. We plotted the mean marginal effect and the standard deviation.

269 **3 Results**

270 Climate change between 1960 and 2010

Precipitation and range in temperature increased across most of Britain, and all changes in 271 average temperature and mean temperature in the coldest month were positive (Fig. S4.1). 272 However, precipitation and range in temperature decreased in some areas over the period 273 274 (977 [43.6%] and 12 [0.5%] of the hectads, respectively), (Fig. S4.1). The standard deviations of precipitation, range in temperature, and temperature in the warmest month increased in 275 most areas, whereas the standard deviation of average temperature decreased, and the 276 277 standard deviation of the average temperature in the coldest month increased in some areas and decreased in others. Average Cold_{FAT} (1.62 ± 0.15) and Warm_{FAT} (1.57 ± 0.16) were 278 similar. 279

280 Land-use change

The area of forest and urban land cover both increased on average but variation was high ($4.4\% \pm 6\%$ and $0.6\% \pm 2.5\%$, respectively) and cover of these classes decreased in some areas (167 and 54 grid cells, respectively). Forest increases were scattered throughout Britain

in clusters, whereas increases in urban land were largely congruent with already built-up

areas (Fig. S4.2). Cropland decreased on average but with large variation (- $4.9\% \pm 16.7\%$)

(Fig. S4.2). All but 69 hectads had some form of LULC change over the 40 years between the

atlases, and the average number of transitions between LULC types was 19.8 ± 19.1 .

Shannon's index increased in 1654 grid cells and decreased in 447 (average change 0.1 ± 0.2)

289 (Fig. S4.2).

290 *Changes in taxonomic assemblage composition through time*

291 Change in all taxonomic measures was relatively uniform across Britain, but with a clear

spatial pattern found in species richness change (SP_{change}; Fig. 1). There appeared to be

clustering of areas with increases or decreases in species richness, although there was no

strong latitudinal or longitudinal divide (Fig. 1). Mean SP_{change} was slightly negative across

the hectads but with large variation $(-0.21 \pm 10.95, \text{ range} = -39 \text{ to } 41)$ and a median of zero.

Slightly more assemblages had a net loss of species than a net gain (1095 and 1054

assemblages, respectively).

For taxonomic beta diversity, mean total taxonomic beta-diversity (BD_{TOTAL}) was 0.20 ± 0.06

(range = 0.08 - 0.54). BD_{TOTAL} was mainly driven by turnover (BD_{TURN}, 0.15 ± 0.06 , range =

0 - 0.46, mean % of BD_{TOTAL} = 75%) with nestedness responsible for a lower portion on

301 average (BD_{NEST}, 0.05 ± 0.05 , range = 0 – 0.29, mean % of BD_{TOTAL} = 25%). There was no

strong signal of species loss or gain at the hectad level over the period (Fig. 1).

303 *Changes in functional assemblage composition through time*

304 The pattern of temporal functional beta-diversity across the assemblages was similar to

taxonomic beta-diversity, with higher average turnover than nestedness (FD_{TURN}, 0.13 ± 0.05

306 (mean % of $FD_{TOTAL} = 72\%$) and 0.05 ± 0.04 (mean % of $FD_{TOTAL} = 28\%$), respectively),

307 highlighting no systematic loss of functional diversity. However, mean total functional beta-

diversity (FD_{TOTAL}) was 0.18 ± 0.05 (range = 0.08 - 0.42), lower than mean BD_{TOTAL} (Fig.

1). In addition, change in FD_{TOTAL} was greater in upland areas than in the lowlands (Fig. 1).

By contrast, mean pairwise distance (MPD) was higher in lowland areas (mainly the south-

east) than in uplands (Fig. 1.). Average MPD across the hectads was 3.64 ± 0.11 (range =

 $312 \quad 3.15 - 3.94$) and average mean nearest neighbour distance (MNTD) was 0.36 ± 0.11 (range =

313 0.15 – 1.10) (Fig. 1).

314 Spatial taxonomic and functional beta-diversity change

The spatial structure of dissimilarities changed between 1970 and 2010, as shown by the low 315 correlations between pairwise taxonomic nestedness (PBD_{NEST}; $R^2 = 0.18$, Mantel *p*<0.001) 316 and pairwise functional nestedness (PFD_{NEST}; $R^2 = 0.19$, Mantel p < 0.001), in the two time 317 periods. Therefore, overall, pairs of sites became less nested (Fig. 2). There was no low-level 318 correlation observed for either pairwise taxonomic turnover or pairwise functional turnover 319 (Fig. 2). Heterogeneity across the region changed significantly, as evidenced by significantly 320 higher turnover in the sampled multiple taxonomic turnover (MBD_{TURN}) and multiple 321 functional turnover (MFD_{TURN}) values for 2010 compared to 1970 (both p < 0.05) (Fig. 2). 322 The sampled values of multiple taxonomic nestedness (MBD_{NEST}) and multiple functional 323 nestedness (MFD_{NEST}) in 1970 and 2010 overlapped considerably (Fig. 2). 324

325 Random forest models

The random forest models explained between 13% (FD_{NEST}) and 60% (MPD) of the variation

327 in the temporal beta-diversity metrics based on average OOB R^2 values (across 20 random

328 forest models) (Fig. 3). Models trained on 75% of the data explained, on average, between

 $4\% \pm 3\%$ (BD_{NEST}) and $50\% \pm 16\%$ (MPD) of variation across the 20 training sets containing

330 25% of the data (Tables. S5.1 & S5.2, respectively).

331 Across all the models, the order of variable importance was similar. For all metrics except 332 MPD, species richness in 1970 was the most important variable by a relatively large margin 333 (Fig. 3). The variable importance for species richness and elevation in the MPD models was 334 similar. Coordinates were also ranked highly across the models, with latitude more important 335 than longitude for all metrics except for SP_{change} (Fig. 3). Changes in the standard deviation of 336 the climatic variables were consistently ranked higher than the mean equivalent in all models 337 except nestedness, MPD and SP_{change} (Fig. 3). LULC predictors were consistently poor 338 predictors across the response metrics, although the difference in importance between these 339 and most other variables was low (Fig. 3). Partial plots for the three most important variables 340 (calculated using variable importance scores; see Appendix S6 for plots displaying all the 341 variables) showed that all taxonomic and functional Baselga beta-diversity measures 342 decreased with increasing species richness in 1970 and increased slightly with change in the 343 standard deviation of average temperature (Tavg_{SD}; although the lines were largely stable, 344 with functional nestedness and taxonomic nestedness flat) (Figs. 4 - 5). SP_{change} also 345 decreased with increasing species richness in 1970 and elevation, but increased slightly with 346 increasing change in average temperature (Tavg; Fig. 4). 347 MPD and MNTD had opposite relationships with 1970_{rich} (MPD increasing, MNTD 348 decreasing) (Fig. 5). In addition, MPD decreased with elevation and increased slightly with 349 Tavg (Fig. 5), whereas MNTD increased slightly with Tavg_{SD} and decreased slightly with 350 change in standard deviation of precipitation (Prec_{SD}). Other variables had a limited effect 351 (Fig. 5).

All relationships between the composition change metrics and the predictors strengthened in
 the absence of spatial coordinates, but none of the relationships changed to any great extent
 (see Appendix S7).

355 4 Discussion

356 Assemblage change

357 Individual assemblages changed, often substantially, between 1970 and 2010, mainly driven by the turnover of species and functional diversity. This suggests that species in local 358 assemblages were replaced rather than lost systematically, consistent with previous work on 359 temporal patterns of community change (Antão et al. 2020; Blowes et al. 2019; Dornelas et 360 361 al. 2014; Dornelas et al. 2018; Nunes et al. 2020; Petchey et al. 2007; Tinoco et al. 2021; Tsianou, Touloumis & Kallimanis 2021). Functional change was slightly lower on average 362 than taxonomic change across the assemblages, highlighting that the assemblages were less 363 functionally disturbed despite the taxonomic change (see also Tsianou et al., 2021). However, 364 365 these results do not necessarily imply that functional redundancy was high in all assemblages. Species that were replaced or were lost from or gained by an assemblage seemingly often had 366 distinct traits, as shown by nearly proportional changes in both taxonomic and functional 367 368 nestedness (Petchey et al. 2007).

Observed composition changes were mainly influenced by the number of species present in 369 the assemblage in the earlier period, with larger assemblages changing relatively less than 370 smaller ones. Because taxonomic nestedness, and therefore total taxonomic beta-diversity, 371 are not independent of species richness gradients, we cannot make assumptions on the basis 372 373 of these results. Taxonomic turnover, however, did not depend on these gradients. Comparatively lower turnover in sites with greater species richness may mean that more 374 diverse assemblages may be protected to an extent against temporal disturbance, perhaps 375 because they have a wider array of traits (and therefore functions) leading to a better 376 functioning system and therefore more resilience (Jarzyna & Jetz, 2017; Weeks, Naeem, 377 Lasky, & Tobias, 2020 PREPRINT). The hectads with higher initial species richness could 378 379 also have been located in areas that were less disturbed (for example, in conservation reserves), although we found little evidence for less disturbance using coarse-resolution 380

LULC and climate change variables. Alternatively, the lower observed change in species richer sites could be due to facilitation between species, with negative relationships between turnover and diversity expected when communities are characterised by strong interspecific facilitative interactions (Shurin, 2007; Pandit & Kolasa, 2012).

Although species richness changes were centred around zero, the variation around the average indicates that many assemblages did change, in some cases quite substantially. Large losses from some areas were nearly equally balanced by large gains in others, similar to results found for changes in plant communities at local scales globally (Vellend et al., 2013). This could relate to species ranges increasing or decreasing, or alternatively to factors such as conservation and biodiversity-focused land management efforts (Rittenhouse et al. 2012; Reif 2013; Inger et al. 2015).

392 The spatial structure of breeding bird assemblages also changed, as evidenced by a significant increase in spatial heterogeneity (measured by comparing the distributions of multiple site 393 394 beta-diversity in each time period) through time for both taxonomic and functional turnover. Pairs of sites also became less functionally and taxonomically nested. Given that the number 395 of sites that gained or lost species was roughly even, and the functional pattern matched the 396 taxonomic, the decrease in nestedness may be driven by the loss or gain of functionally 397 unique or rare species. For example, the range of the common buzzard (*Buteo buteo*) 398 increased from 940 to 2130 hectads (226% increase), and the range of the cuckoo (Cuculus 399 canorus) decreased from 2107 to 1258 hectads (60% decrease). All things being equal, these 400 changes in distribution would decrease nestedness between areas in which buzzards were 401 absent and those in which buzzards were present, or, in the case of the cuckoo, between areas 402 in which cuckoos were present and those in which cuckoos were absent. 403

In comparison, Baselga et al. (2015) found no change in heterogeneity of bird assemblages in 404 south-west France, although their study region was much smaller than ours. However, they 405 found the same reduction in nestedness between pairs of sites. Because changes in the spatial 406 structure of dissimilarities in our study were driven by both losses and gains in species 407 richness, and those were not driven by LULC or climate changes to any great extent (see 408 below), it appears that some of this assemblage change may be stochastic (Baselga et al., 409 410 2015; O'Sullivan, Terry & Rossberg, 2021; Stegen et al. 2013; Terry & Rossberg, 2021), or perhaps inappropriate or missing covariates. For example, the increases in distribution of the 411 412 buzzard likely are due to enhanced protection. Declines in the distribution of the cuckoo have been attributed to grassland degradation, phenological changes in hosts, and conditions along 413 migratory routes (Hewson, Thorup, Pearce-Higgins, & Atkinson, 2016). Such factors, and 414 likely those affecting other species, were not considered in our modelling. 415

416 <u>Elevation, climate change, and LULC change</u>

Assemblage composition changed more in upland areas in Britain than in lowland regions. 417 Species richness increased slightly in the lowlands and decreased in the uplands, which may 418 indicate that upland species (such as those in the Scottish Highlands) are more at risk of local 419 extirpation. These losses could result from either increased competition (as species' ranges 420 421 shift up-slope) or environmental filtering in upland areas through time. Alternatively, the 422 observed elevation effect could be an effect of species richness itself, given that we observed that more species-rich communities changed less than less species-rich communities, and 423 species richness is known to often decrease with elevation (Guo et al., 2013). 424

425 Climate change variables had higher importance scores in the models than LULC change
426 variables but less so than species richness in 1970 and elevation; change in average
427 temperature and change in the standard devation of average temperature were the most

428	important. These findings generally are consistent with work that used data from earlier
429	periods and highlighted that change in average temperature drove compositional change of
430	British birds, although we found a weaker effect of climate than these studies in general
431	(Davey et al., 2012; Davey, Devictor, Jonzén, Lindström, & Smith, 2013; White,
432	Montgomery, Storchová, Hořák, & Lennon, 2018). The importance scores of climate relative
433	to both spatial coordinates and species richness in 1970 was generally low. This may be due
434	to the resolution at which the assemblages were sampled. Climatic conditions were more
435	relevant to avian temporal assemblage dissimilarity at finer (5km x 5km) compared to coarser
436	resolutions (up to 80km x 80km) in New York State, although this resolution dependence was
437	not as strong for temporal turnover in the same study (Jarzyna et al., 2015).
438	When considering the impact, or lack thereof, of LULC variables within the models, there are
439	several potential factors. As can be seen from the 90% central range lines in the partial plots
440	(red lines; Figs. S6.1 – S6.9), Urbanchange was heavily zero-inflated. Low recorded land-use
441	change may be due to the measure of land change. The base LULC data used here was the
442	dominant LULC type on a 1km ² grid. Therefore, for urban land to be classified as increasing
443	or decreasing in a 1km ² grid cell within the larger 100km ² hectad, that 1km ² grid cell must
444	have changed from mainly urban to another land-use, or from another land-use to mainly
445	urban. Such change is uncommon in an extensively urbanised country such as the UK. The
446	UK can be described as a post-perturbation system where considerable LULC change has
447	already occurred, and the pace, range, and intensity of LULC change has slowed in recent
448	decades. Different results are expected for other countries, particularly many tropical
449	countries, where LULC change is more prominent (e.g., Rurangwa et al., 2021). Our LULC
450	data also do not account for fragmentation, small changes in LULC within each 1km ² , and
451	agricultural intensification, all of which are potentially drive assemblage change (Boulinier et
452	al., 1998; Hendershot et al., 2020).

453 **Limitations and considerations**

454 A potentially confounding factor is the impact of wintering grounds or hazards during the 455 passage to Britain for the migratory species included in this study. British migratory species 456 have different responses to differences in temperature, with long-distance migrants preferring 457 colder springs and resident species preferring warmer springs (Wittwer, O'Hara, Caplat, 458 Hickler, & Smith, 2015). Hunting along the migratory route and abiotic and biotic variables 459 within wintering grounds can impact populations, potentially causing fewer migrants to reach 460 Britain and therefore not utilising the maximum available areas (Lormée et al., 2019; Vickery 461 et al., 2014).

462 Sampling effects can have impacts on analyses of assemblage composition (Neate-Clegg, 463 Horns, Adler, Kemahlı Aytekin, & Şekercioğlu, 2020). While the use of citizen scientists has 464 some drawbacks, including the over or under-sampling of some areas (Neate-Clegg et al., 465 2020), citizen scientists can collect good-quality data that are valuable for detecting trends in 466 assemblages and populations (Horns, Adler, & Şekercioğlu, 2018; Mccaffrey, 2005). We 467 accounted for potential sampling bias by removing the grid cells that considerably changed in 468 the number of benchmark species detected (Gillings et al., 2019; Appendix S1). In addition, 469 the atlases censuses are conducted over four years, so they should provide a more accurate 470 picture of species colonisations and extirpations than a singular year of sampling. 471 Notwithstanding, sampling effects are possible, particularly in regions that are difficult to 472 sample. Another potential factor is the selection of tetrads for surveying. Although this 473 information is not available in the published data (Gillings et al., 2019), if the selection of 474 tetrads was biased towards public lands (where development is often restricted) in one or both 475 of the atlases, then results could be misleading (Mentges, Blowes, Hodapp, Hillebrand & 476 Chase, 2021). A potential avenue could be to incorporate the percentage of public and private

⁴⁷⁷ land into future work. Future work could also investigate the differences between sampling
⁴⁷⁸ years within the Atlases, as the data were not available to explore that here.

Species traits are not stationary in time and space and likely vary spatially and temporally across study regions according to local adaptation (Weeks, Willard, et al. 2020). Therefore, functional diversity could have changed across the study region without any composition change within or between assemblages. However, the extent of this variation appears to be negligible in relation to interspecific variation (see Tobias et al. 2021), suggesting that our application of species trait averages, and the assumption that trait values are constant across the region, were justified.

Although British breeding bird assemblages changed in both time and space between 1970 486 and 2010, that change does not appear to be driven by coarse-resolution LULC change. 487 Climate change played a relatively larger role, although its impact was still limited in general. 488 This could indicate that stochastic processes, or perhaps finer-resolution factors not included 489 490 here, are driving temporal dissimilarity. The observed change was relatively greater for less 491 species-rich assemblages at higher elevations than more species-rich assemblages at lower elevations, and indeed, larger assemblages appeared somewhat buffered to change. Although 492 no consistent signal of species loss or gains was found, these presence-absence data do not 493 incorporate abundance. Indeed, across a similar time period (1970 - 2017), the estimated 494 drop in the abundance of North American birds was 2.9 billion (Rosenberg et al. 2019). Work 495 incorporating abundance, or looking at how individual species or functional groups may have 496 497 been impacted by LULC or climate change, should therefore be a priority to assess further 498 how the composition of British breeding bird assemblages has changed. Further studies in other post perturbation systems are required to confirm the generality of these findings. 499

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787 vi. Conflict of interest

788 The authors declare no conflict of interest.

789 vii. Data availability statement

- 790 The data table with variables has been made available along with scripts to run the analyses.
- 791 See Gillings et al. (2019) for how to access original atlas data.
- vii. Tables embedded in the text (each table complete with title and footnotes)
- viii. Figures embedded in the text (each with a figure legend)



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Fig. 1. Temporal change observed in breeding bird communities in Britain between 1970 and 2010 within 10km x 10km hectads for different taxonomic and functional metrics: the temporal taxonomic beta diversity (BD_{TOTAL}), taxonomic turnover (BD_{TURN}), taxonomic nestedness resultant dissimilarity (BD_{NEST}), temporal functional beta diversity (FD_{TOTAL}), functional turnover (FD_{TURN}), functional nestedness resultant dissimilarity (FD_{NEST}), species richness change (SP_{change}), and two additional measures of functional change: mean pairwise distance

(MPD) and mean nearest taxon distance (MNTD). The values represent the change within each
hectad between the 1970 and 2010 periods, as derived from two atlases produced by the British
Trust of Ornithology (BTO). Grey areas indicate where grids were removed due to a large
difference in the number of benchmark species detected during the 1970 atlas and the 2010
atlas (these areas were mainly within Scotland). Because the scale varies among measures, they
are not directly comparable to one another.



Fig. 2. Spatial change in taxonomic and functional beta-diversity of British bird breeding 808 809 assemblages between 1970 and 2010. The density plots on the left show the turnover and nestedness components for both taxonomic (MBD_{TURN} and MBD_{NEST}) and functional 810 811 (MFD_{TURN} and MFD_{NEST}) beta-diversity. The dashed grey lines show the mean value of the metric across the sampled distribution, with p-values from empirical tests shown in the top left 812 corner. The plots to the right show the correlations between pairwise dissimilarities calculated 813 in 1970 and 2010 for both taxonomic (PBD_{TURN} and PBD_{NEST}) and functional (PFD_{TURN} and 814 PFD_{NEST}) beta-diversity. The solid grey lines show the relationship between the metrics using 815 OLS linear regression. Fit (R^2) from the regression is shown in the bottom right-hand corner. 816



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Fig. 3. Variable importance scores from spatial random forest models for different measures of 818 temporal change in assemblages (100km² hectads) of British birds from 1970 to 2010. The 819 mean model explanatory power (R^2) is in the lower right of each plot. The metrics of 820 assemblage composition change are: temporal taxonomic beta diversity (BD_{TOTAL}), taxonomic 821 turnover (BD_{TURN}), taxonomic nestedness resultant dissimilarity (BD_{NEST}), temporal functional 822 beta diversity (FD_{TOTAL}), functional turnover (FD_{TURN}), and functional nestedness resultant 823 dissimilarity (FD_{NEST}), species richness change (SP_{change}), mean pairwise distance (MPD), and 824 mean nearest taxon distance (MNTD). Variables are ranked in descending order of importance 825

(most important first), with the values on the x-axis showing the variable importance of each
predictor. For each variable in each plot, the vertical line is the median importance across the
20 models, and the box indicates the inter-quartile range (IQR). Points highlight outliers, and
the whiskers show data 1.5 times the IQR.



Fig. 4. Partial plots of the marginal effect of each of the top three most important predictor variables (calculated from median random forest importance scores) on the temporal taxonomic beta-diversity (BD_{TOTAL}) of British breeding bird communities from 1970 – 2010, and its component parts, turnover (BD_{TURN}) and nestedness resultant dissimilarity (BD_{NEST}). Also

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shown are the partial plots for species richness change (SP_{change}). Each partial plot shows the
mean marginal effect of the predictor variable across 20 random forest models for each metric.
Effects of the predictor variables were assessed across the central 90% of the predictor variables
value (the red section of the lines). Variables are ordered according to median importance
across the models (left to right).



Fig. 5. Partial plots of the marginal effect of each of the top three most important predictor
variables (calculated from median random forest importance scores) had on the temporal
functional beta-diversity (FD_{TOTAL}) of British breeding bird communities from 1970 – 2010,
and its component parts, turnover (FD_{TURN}), nestedness resultant dissimilarity (FD_{NEST}), and

- ⁸⁴⁵ mean nearest taxon distance (MNTD) and mean pairwise distance (MPD). Each partial plot
- shows the mean marginal effect of the predictor variable across 20 random forest models for
- ⁸⁴⁷ each metric. Effects of the predictor variables were assessed across the central 90% of the
- ⁸⁴⁸ predictor variables value (the red section of the lines). Variables are ordered according to
- 849 median importance across the models (left to right).