

## 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 *Aim*

6 To identify the primary drivers of compositional change in breeding bird assemblages over a  
7 40-year period.

8 *Location*

9 Britain

10 *Time Period*

11 1970 to 2010

12 *Major Taxa Studied*

13 Birds

14 *Methods*

15 Using morphological trait measurements and a dataset of presence-absence data for British  
16 breeding birds surveyed in 10 x 10km 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

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

#### 24 Results

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

#### 32 Main Conclusions

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

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

#### 42 **iv. Main Text**

#### 43 **1 Introduction**

44 Recently there has been an increasing focus in ecology on analysing biodiversity change  
45 through time and identifying the drivers of that change (Dornelas et al. 2014; Antão et al.  
46 2020; Blowes et al. 2019; Pilotto et al. 2020). Climate and land use and land cover (LULC)  
47 change have both been identified as predictors of biodiversity change globally and linked,  
48 either directly or indirectly, to increased extinction risk in many taxa in the coming decades  
49 (Newbold, 2018; Thomas et al., 2004; Urban, 2015; Wieczynski et al., 2019). Of the two,  
50 land-use change is generally acknowledged as the largest current driver of biodiversity loss  
51 (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Seto, Güneralp, & Hutyra,  
52 2012; Sohl, 2014; Tratalos et al., 2007; Zabel et al., 2019). However, warming temperatures  
53 are impacting species through range alterations/niche tracking (Batt, Morley, Selden, Tingley,  
54 & Pinsky, 2017; Fox et al., 2014; Tayleur et al., 2015) and shifting phenologies (Bell et al.,  
55 2019). These impacts will likely intensify and climate change is expected to match or exceed  
56 land-use change as the leading biodiversity change driver this century (Newbold, 2018).

57 While deterministic processes (e.g., LULC and climate change) can drive assemblage change,  
58 non-deterministic processes (e.g., stochastic change) have also been identified as drivers  
59 (Baselga, Bonthoux & Balent, 2015; Stegen et al., 2013). Indeed, many biodiversity models  
60 (e.g., the equilibrium theory of island biogeography and neutral models; Hubbell, 2001;  
61 MacArthur & Wilson, 1967) predict the temporal turnover of species in a community as a  
62 theoretically stochastic process.

63 Two main factors hinder many biodiversity change studies. First, appropriate time-series data  
64 covering species composition from sites at two or more time points are required (Antão et al.,  
65 2020; Dornelas et al., 2018). However, due to the resources required to collect time-series  
66 data, most studies analysing assemblage diversity change use a space-for-time substitution,  
67 analysing dissimilarity between sites within the same study system and time period (e.g.

68 Swenson, Anglada-Cordero, & Barone, 2011). Whilst space-for-time analyses assume that  
69 communities are at equilibrium, temporal analyses do not (Damgaard, 2019).

70 Second, many studies examining temporal change in assemblages in response to  
71 anthropogenic drivers use only taxonomic diversity (quantifying changes in species  
72 composition in each locality over time); this ignores species-specific differences in functional  
73 traits that provide ecological information regarding individual species' roles in their  
74 community (Şekercioğlu, 2006).

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

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

93 functional and taxonomic compositional change, with no overall pattern of consistent species  
94 loss (Baselga et al., 2015; Blowes et al., 2019; Dornelas et al., 2014; Pilotto et al., 2020;  
95 Stegen et al., 2013). The effect of LULC change was more difficult to predict. Previous  
96 studies indicated correlations between compositional change and LULC change variables, but  
97 LULC change variables generally had low explanatory power (Jung, Scharlemann &  
98 Rowhani, 2020).

## 99 **2 Materials and Methods**

### 100 **Data collection**

#### 101 *Species Composition Data*

102 Data on the summer (breeding) distributions of the British avifauna recorded over two  
103 separate periods (Gillings et al., 2019) were collected during April-July 1968-1972 (BA1970)  
104 and 2008-2011 (BA2010) by volunteers on behalf of the British Trust of Ornithology (BTO)  
105 and the Scottish Ornithologists' Club (SOC). Each atlas (the data collected over each  
106 sampling period) consists of data on presence or absence of British bird species within 10km  
107 x 10km (100km<sup>2</sup>) hectads covering the British Isles on a continuous grid (Fig. S1.1). We  
108 prepared the data by removing some species (e.g. marine species and vagrants), and removing  
109 hectads that were calculated to have potentially low sample completeness (defined as the  
110 difference in the proportion of benchmark species found in each hectad in each sampling  
111 period) or had less than 50% land or comprised offshore islands (see Appendix S1 in the  
112 Supporting Information for more details).

#### 113 *Trait data*

114 We selected nine continuous traits (eight morphometric traits and body mass) measured from  
115 museum specimens or extracted from the literature to characterise the functional diversity of  
116 each assemblage (all species present in a hectad) (Pigot et al., 2020). All traits selected (two

117 estimates of beak length (culmen from tip-to-skull and tip-to-nares), beak width, beak depth,  
118 secondary length, tarsus length, wing chord length, tail length, and body mass) provide  
119 information about dietary niche, locomotion, and ecological function (Pigot et al., 2020;  
120 Tobias & Pigot, 2019; Trisos, Petchey, & Tobias, 2014).

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

#### 125 *Climate Data*

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

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 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 ( $T_{avg}$ ), change in the range of temperature ( $Range$ ), change in precipitation  
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 ( $T_{avgSD}$ ,  $Range_{SD}$ ,  $Prec_{SD}$ ,  
153  $Cold_{SD}$ , and  $Warm_{SD}$ ).

#### 154 *Land Use Data*

155 We obtained data for land-use change from the Historic Land Dynamics Assessment  
156 (HILDA, Version 2.0) model (Fuchs, Herold, Verburg, & Clevers, 2012). The HILDA model  
157 uses multiple data streams of land cover to reconstruct historic LULC change, including  
158 where transitions have occurred (e.g. from forest to settlement). We obtained land cover data  
159 on the basis of dominant, gross LULC changes for 1970 and 2010 (Fuchs et al., 2012; Fuchs,  
160 Herold, Verburg, Clevers, & Eberle, 2015). From these data, we calculated the number of  
161  $1\text{km}^2$  grid cells within each hectad classed as settlements (hereafter urban land-use), cropland,  
162 and forest in 1970. We repeated this process with the 2010 data and subtracted the number of  
163 grid cells present in each land-use class in 1970 from the number of grid cells present in the  
164 same class in 2010. This provided a measure of the land-use change (converted to % change)  
165 within the hectads over the 1970-2010 period ( $Urban_{change}$ ,  $Crop_{change}$ , and  $Forest_{change}$ ).



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  
170 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  
174 hectad, we used 400 equally spaced points to extract data. We then calculated the average and  
175 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 **Measuring compositional change through time**

#### 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  
184 assemblage and the later assemblage within the same hectad. We used Sørensen's  
185 dissimilarity index ( $BD_{TOTAL}$ ; Baselga, 2010; Koleff, Gaston, & Lennon, 2003).

186 We partitioned total beta-diversity ( $BD_{TOTAL}$ ) into its two constituent components, turnover  
187 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

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

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

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

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

212 As an alternative to Baselga's temporal functional beta-diversity framework, we calculated  
213 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  
216 the R package 'picante' (Kembel et al., 2010; Webb, Ackerly & Kembel, 2008). We plotted  
217 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*

219 We performed two complementary analyses to test whether different aspects of spatial beta-  
220 diversity changed. Changes in the spatial dissimilarity structure (i.e., similar sites becoming  
221 dissimilar and vice-versa) can be detected as low-level correlations between the dissimilarity  
222 between sites in the earlier period and the dissimilarity between sites in the later period  
223 (Baselga et al., 2015). We calculated pairwise dissimilarities between each hectad and every  
224 other hectad during both time periods. We then used Mantel tests (Mantel, 1967) to assess the  
225 significance of the correlation of the turnover ( $PBD_{\text{TURN}}$ , i.e., pairwise beta-diversity  
226 turnover) and nestedness ( $PBD_{\text{NEST}}$ ) dissimilarities between sites across the two time periods.  
227 We repeated this process for functional turnover ( $PFD_{\text{TURN}}$ ) and nestedness ( $PFD_{\text{NEST}}$ ).

228 In contrast to pairwise dissimilarities, multiple site beta-diversity provides information about  
229 the overall spatial heterogeneity of assemblages (Baselga et al., 2015; Baselga & Orme,  
230 2012). Multiple site beta-diversity (here referred to as  $MBD_{\text{TOTAL}}$ , i.e., total multiple site  
231 beta-diversity) can also be partitioned into its constituent components, nestedness ( $MBD_{\text{NEST}}$ )  
232 and turnover ( $MBD_{\text{TURN}}$ ). To test for increases or decreases in heterogeneity, we used the  
233 *beta.sample* function in the package 'betapart' to generate 1000 multiple site functional and  
234 taxonomic beta-diversity values for both time periods from a random sample of 1/5 of the  
235 sites (Baselga et al., 2015; Baselga & Orme, 2012). We compared the distributions for both

236 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  
244 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).

248 We included coordinates of hectad centres as predictor variables (latitude [Y] and longitude  
249 [X] (Georganos et al., 2021; Hengl, Nussbaum, Wright, Heuvelink & Gräler, 2018)). We then  
250 assessed spatial autocorrelation of the residuals from the random forest models with Moran’s  
251 I index (Anselin 2010; Moran 1948). We used a Euclidean distance matrix between all sites  
252 with model residuals in Moran’s I tests, implemented as standard in the functions utilised to  
253 run the models in the package ‘*spatialRF*’ (Benito, 2021; Wright & Ziegler 2017).

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  
256 (defined as the increase in mean square error with a random variable instead of the original)  
257 with permutations within each forest (Breiman, 2001). We recorded the median and SD of  
258 variable importance across the 20 models.

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

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

### 269 **3 Results**

#### 270 *Climate change between 1960 and 2010*

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

#### 280 *Land-use change*

281 The area of forest and urban land cover both increased on average but variation was high  
282 ( $4.4\% \pm 6\%$  and  $0.6\% \pm 2.5\%$ , respectively) and cover of these classes decreased in some

283 areas (167 and 54 grid cells, respectively). Forest increases were scattered throughout Britain  
284 in clusters, whereas increases in urban land were largely congruent with already built-up  
285 areas (Fig. S4.2). Cropland decreased on average but with large variation ( $-4.9\% \pm 16.7\%$ )  
286 (Fig. S4.2). All but 69 hectads had some form of LULC change over the 40 years between the  
287 atlases, and the average number of transitions between LULC types was  $19.8 \pm 19.1$ .  
288 Shannon's index increased in 1654 grid cells and decreased in 447 (average change  $0.1 \pm 0.2$ )  
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  
292 spatial pattern found in species richness change ( $SP_{\text{change}}$ ; Fig. 1). There appeared to be  
293 clustering of areas with increases or decreases in species richness, although there was no  
294 strong latitudinal or longitudinal divide (Fig. 1). Mean  $SP_{\text{change}}$  was slightly negative across  
295 the hectads but with large variation ( $-0.21 \pm 10.95$ , range = -39 to 41) and a median of zero.  
296 Slightly more assemblages had a net loss of species than a net gain (1095 and 1054  
297 assemblages, respectively).

298 For taxonomic beta diversity, mean total taxonomic beta-diversity ( $BD_{\text{TOTAL}}$ ) was  $0.20 \pm 0.06$   
299 (range = 0.08 – 0.54).  $BD_{\text{TOTAL}}$  was mainly driven by turnover ( $BD_{\text{TURN}}$ ,  $0.15 \pm 0.06$ , range =  
300 0 – 0.46, mean % of  $BD_{\text{TOTAL}} = 75\%$ ) with nestedness responsible for a lower portion on  
301 average ( $BD_{\text{NEST}}$ ,  $0.05 \pm 0.05$ , range = 0 – 0.29, mean % of  $BD_{\text{TOTAL}} = 25\%$ ). There was no  
302 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  
305 taxonomic beta-diversity, with higher average turnover than nestedness ( $FD_{\text{TURN}}$ ,  $0.13 \pm 0.05$   
306 (mean % of  $FD_{\text{TOTAL}} = 72\%$ ) and  $0.05 \pm 0.04$  (mean % of  $FD_{\text{TOTAL}} = 28\%$ ), respectively),

307 highlighting no systematic loss of functional diversity. However, mean total functional beta-  
308 diversity ( $FD_{TOTAL}$ ) was  $0.18 \pm 0.05$  (range = 0.08 – 0.42), lower than mean  $BD_{TOTAL}$  (Fig.  
309 1). In addition, change in  $FD_{TOTAL}$  was greater in upland areas than in the lowlands (Fig. 1).  
310 By contrast, mean pairwise distance (MPD) was higher in lowland areas (mainly the south-  
311 east) than in uplands (Fig. 1). Average MPD across the hectads was  $3.64 \pm 0.11$  (range =  
312 3.15 – 3.94) and average mean nearest neighbour distance (MNTD) was  $0.36 \pm 0.11$  (range =  
313 0.15 – 1.10) (Fig. 1).

#### 314 *Spatial taxonomic and functional beta-diversity change*

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

#### 325 *Random forest models*

326 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  
329  $4\% \pm 3\%$  ( $BD_{NEST}$ ) 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  $SP_{\text{change}}$  (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  $SP_{\text{change}}$  (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 ( $T_{\text{avgSD}}$ ; although the lines were largely stable,  
344 with functional nestedness and taxonomic nestedness flat) (Figs. 4 - 5).  $SP_{\text{change}}$  also  
345 decreased with increasing species richness in 1970 and elevation, but increased slightly with  
346 increasing change in average temperature ( $T_{\text{avg}}$ ; Fig. 4).

347 MPD and MNTD had opposite relationships with  $1970_{\text{rich}}$  (MPD increasing, MNTD  
348 decreasing) (Fig. 5). In addition, MPD decreased with elevation and increased slightly with  
349  $T_{\text{avg}}$  (Fig. 5), whereas MNTD increased slightly with  $T_{\text{avgSD}}$  and decreased slightly with  
350 change in standard deviation of precipitation ( $\text{Prec}_{\text{SD}}$ ). Other variables had a limited effect  
351 (Fig. 5).

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

#### 355 **4 Discussion**



356 **Assemblage change**

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

369 Observed composition changes were mainly influenced by the number of species present in  
370 the assemblage in the earlier period, with larger assemblages changing relatively less than  
371 smaller ones. Because taxonomic nestedness, and therefore total taxonomic beta-diversity,  
372 are not independent of species richness gradients, we cannot make assumptions on the basis  
373 of these results. Taxonomic turnover, however, did not depend on these gradients.

374 Comparatively lower turnover in sites with greater species richness may mean that more  
375 diverse assemblages may be protected to an extent against temporal disturbance, perhaps  
376 because they have a wider array of traits (and therefore functions) leading to a better  
377 functioning system and therefore more resilience (Jarzyna & Jetz, 2017; Weeks, Naeem,  
378 Lasky, & Tobias, 2020 PREPRINT). The hectads with higher initial species richness could  
379 also have been located in areas that were less disturbed (for example, in conservation  
380 reserves), although we found little evidence for less disturbance using coarse-resolution

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

385 Although species richness changes were centred around zero, the variation around the  
386 average indicates that many assemblages did change, in some cases quite substantially. Large  
387 losses from some areas were nearly equally balanced by large gains in others, similar to  
388 results found for changes in plant communities at local scales globally (Vellend et al., 2013).  
389 This could relate to species ranges increasing or decreasing, or alternatively to factors such as  
390 conservation and biodiversity-focused land management efforts (Rittenhouse et al. 2012; Reif  
391 2013; Inger et al. 2015).

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

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

#### 416 **Elevation, climate change, and LULC change**

417 Assemblage composition changed more in upland areas in Britain than in lowland regions.  
418 Species richness increased slightly in the lowlands and decreased in the uplands, which may  
419 indicate that upland species (such as those in the Scottish Highlands) are more at risk of local  
420 extirpation. These losses could result from either increased competition (as species' ranges  
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  
423 that more species-rich communities changed less than less species-rich communities, and  
424 species richness is known to often decrease with elevation (Guo et al., 2013).

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 deviation 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),  $Urban_{change}$  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<sup>2</sup> grid. Therefore, for urban land to be classified as increasing  
443 or decreasing in a 1km<sup>2</sup> grid cell within the larger 100km<sup>2</sup> hectad, that 1km<sup>2</sup> 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<sup>2</sup>, 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 Aytakin, & 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.

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

486 Although British breeding bird assemblages changed in both time and space between 1970  
487 and 2010, that change does not appear to be driven by coarse-resolution LULC change.  
488 Climate change played a relatively larger role, although its impact was still limited in general.  
489 This could indicate that stochastic processes, or perhaps finer-resolution factors not included  
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  
492 elevations, and indeed, larger assemblages appeared somewhat buffered to change. Although  
493 no consistent signal of species loss or gains was found, these presence-absence data do not  
494 incorporate abundance. Indeed, across a similar time period (1970 – 2017), the estimated  
495 drop in the abundance of North American birds was 2.9 billion (Rosenberg et al. 2019). Work  
496 incorporating abundance, or looking at how individual species or functional groups may have  
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  
499 other post perturbation systems are required to confirm the generality of these findings.

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786 019-10775-z

787 **vi. Conflict of interest**

788 The authors declare no conflict of interest.

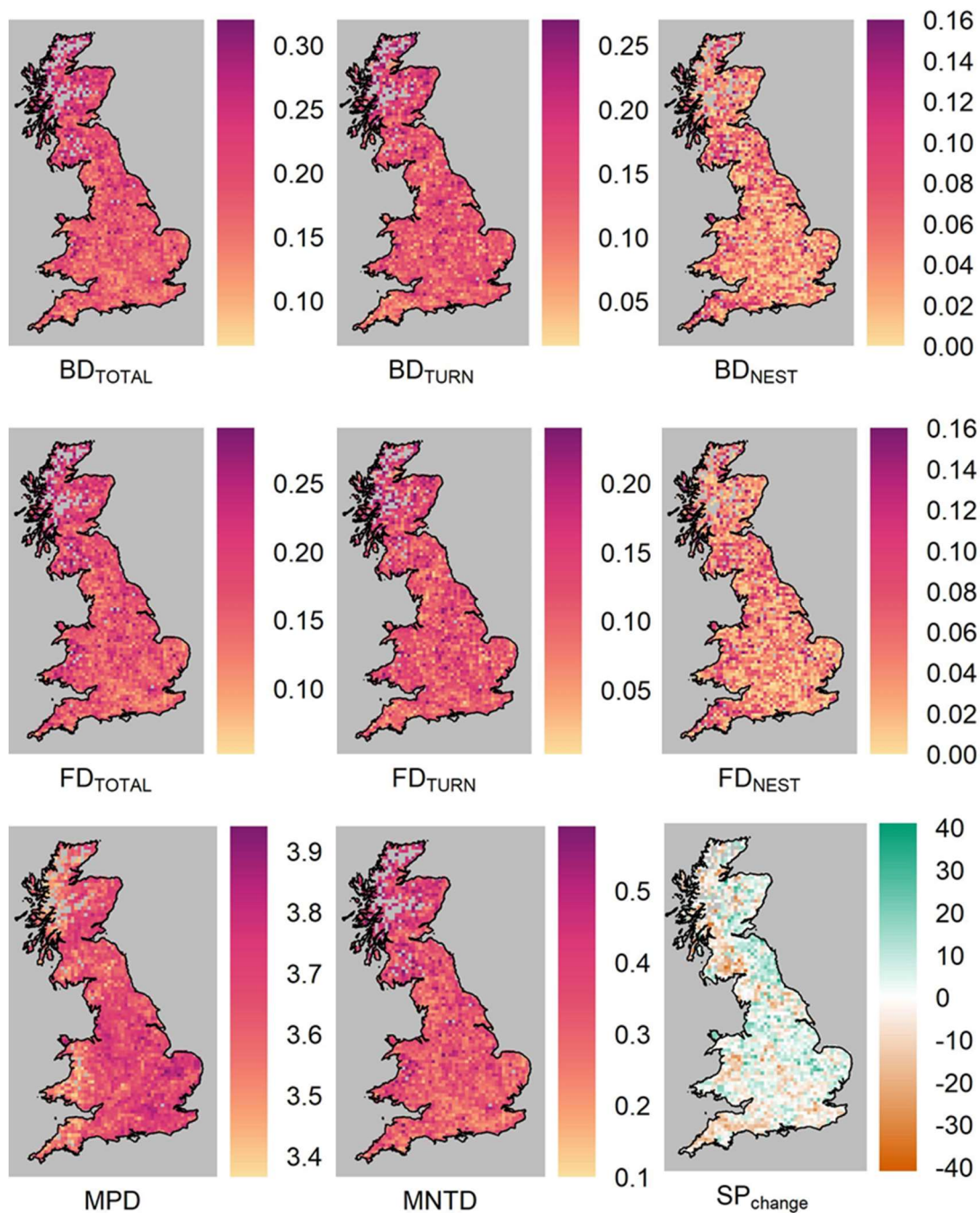
789 **vii. Data availability statement**

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.

792 **vii. Tables embedded in the text (each table complete with title and footnotes)**

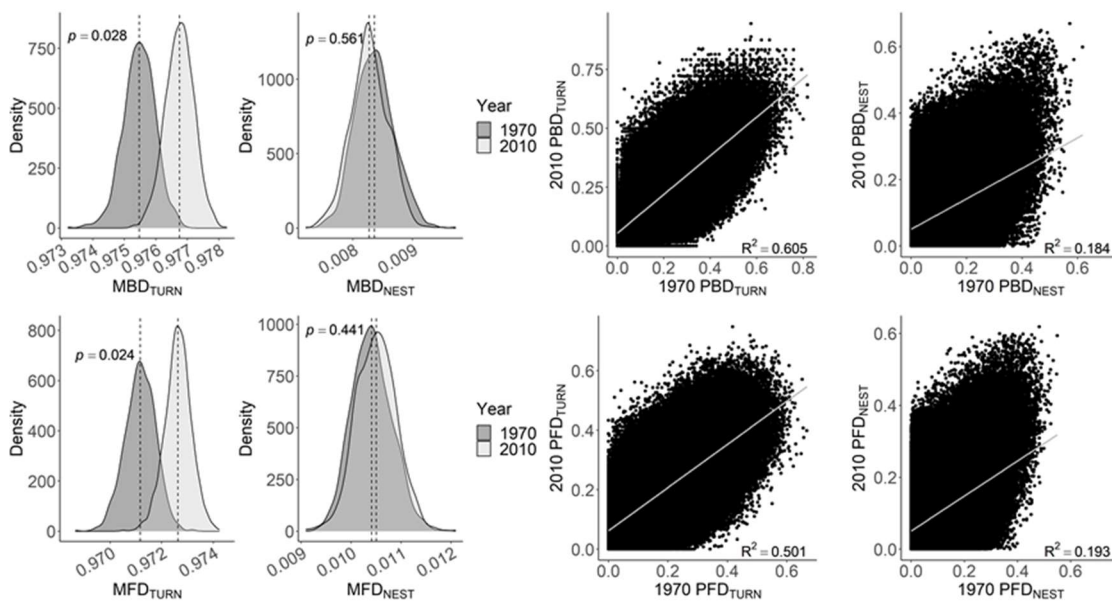
793 **viii. Figures embedded in the text (each with a figure legend)**



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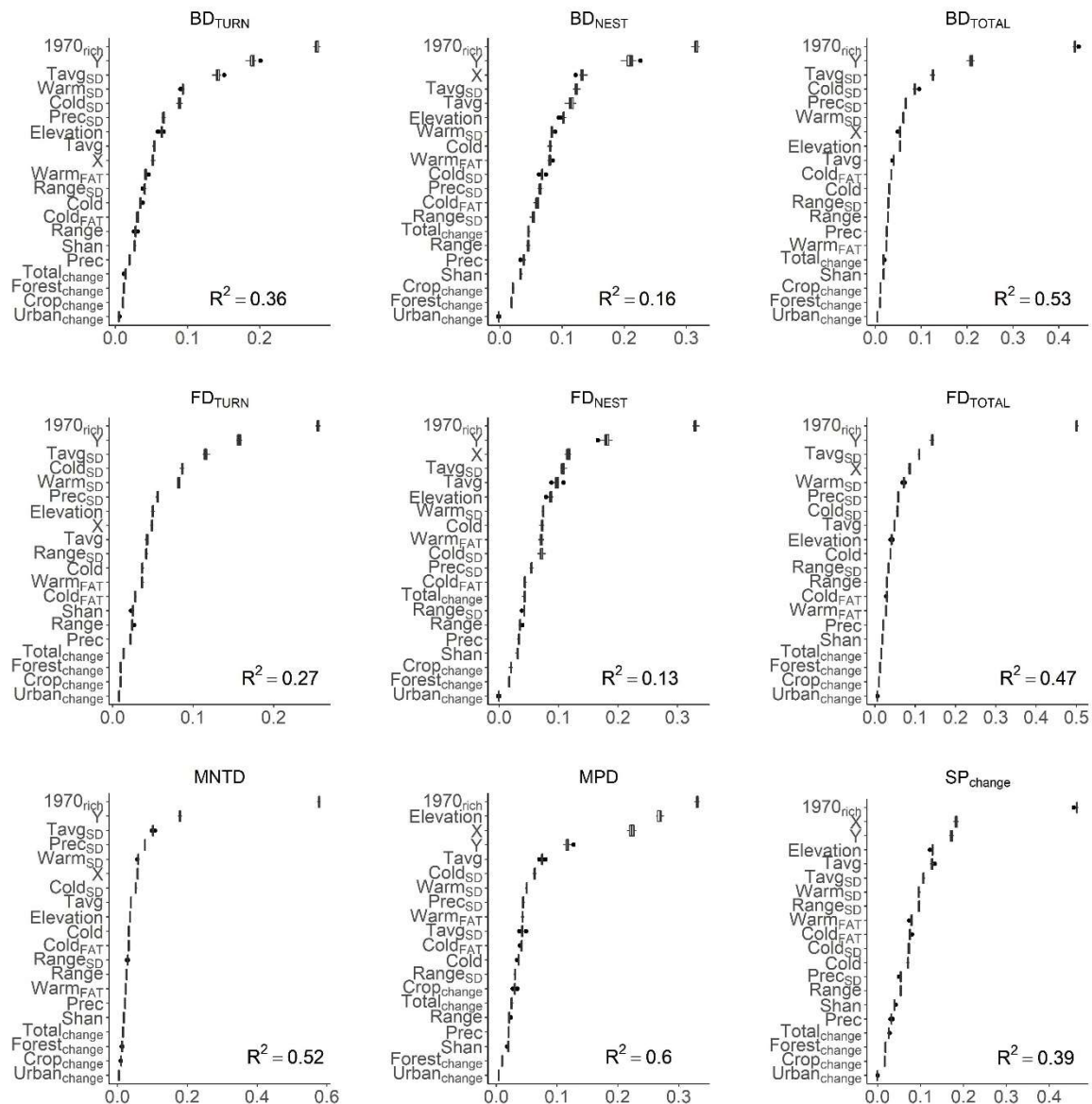
795 Fig. 1. Temporal change observed in breeding bird communities in Britain between 1970 and  
 796 2010 within 10km x 10km hectads for different taxonomic and functional metrics: the temporal  
 797 taxonomic beta diversity ( $BD_{TOTAL}$ ), taxonomic turnover ( $BD_{TURN}$ ), taxonomic nestedness  
 798 resultant dissimilarity ( $BD_{NEST}$ ), temporal functional beta diversity ( $FD_{TOTAL}$ ), functional  
 799 turnover ( $FD_{TURN}$ ), functional nestedness resultant dissimilarity ( $FD_{NEST}$ ), species richness  
 800 change ( $SP_{change}$ ), and two additional measures of functional change: mean pairwise distance

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



807

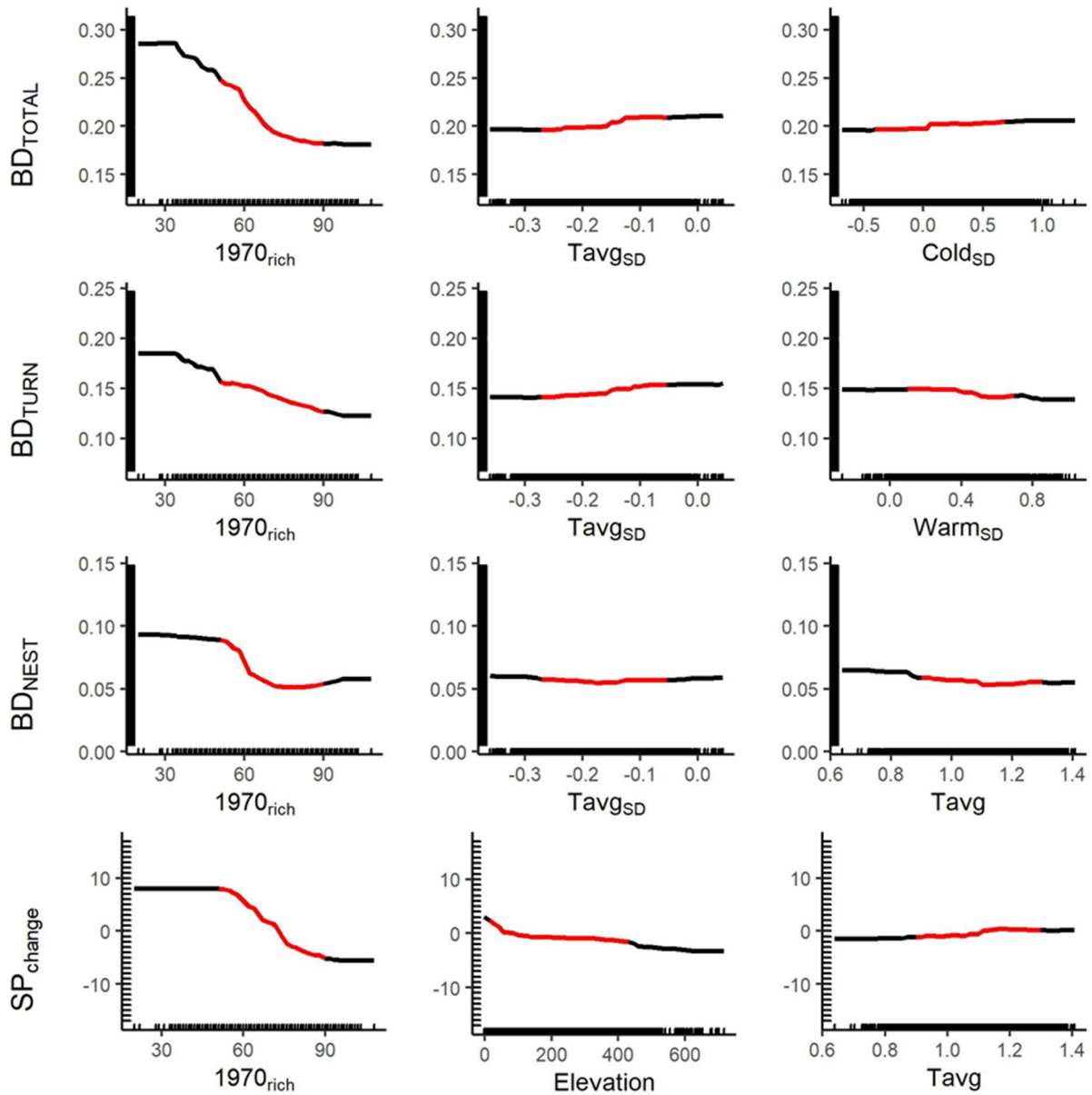
808 Fig. 2. Spatial change in taxonomic and functional beta-diversity of British bird breeding  
 809 assemblages between 1970 and 2010. The density plots on the left show the turnover and  
 810 nestedness components for both taxonomic (MBD<sub>TURN</sub> and MBD<sub>NEST</sub>) and functional  
 811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



817

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

826 (most important first), with the values on the x-axis showing the variable importance of each  
 827 predictor. For each variable in each plot, the vertical line is the median importance across the  
 828 20 models, and the box indicates the inter-quartile range (IQR). Points highlight outliers, and  
 829 the whiskers show data 1.5 times the IQR.

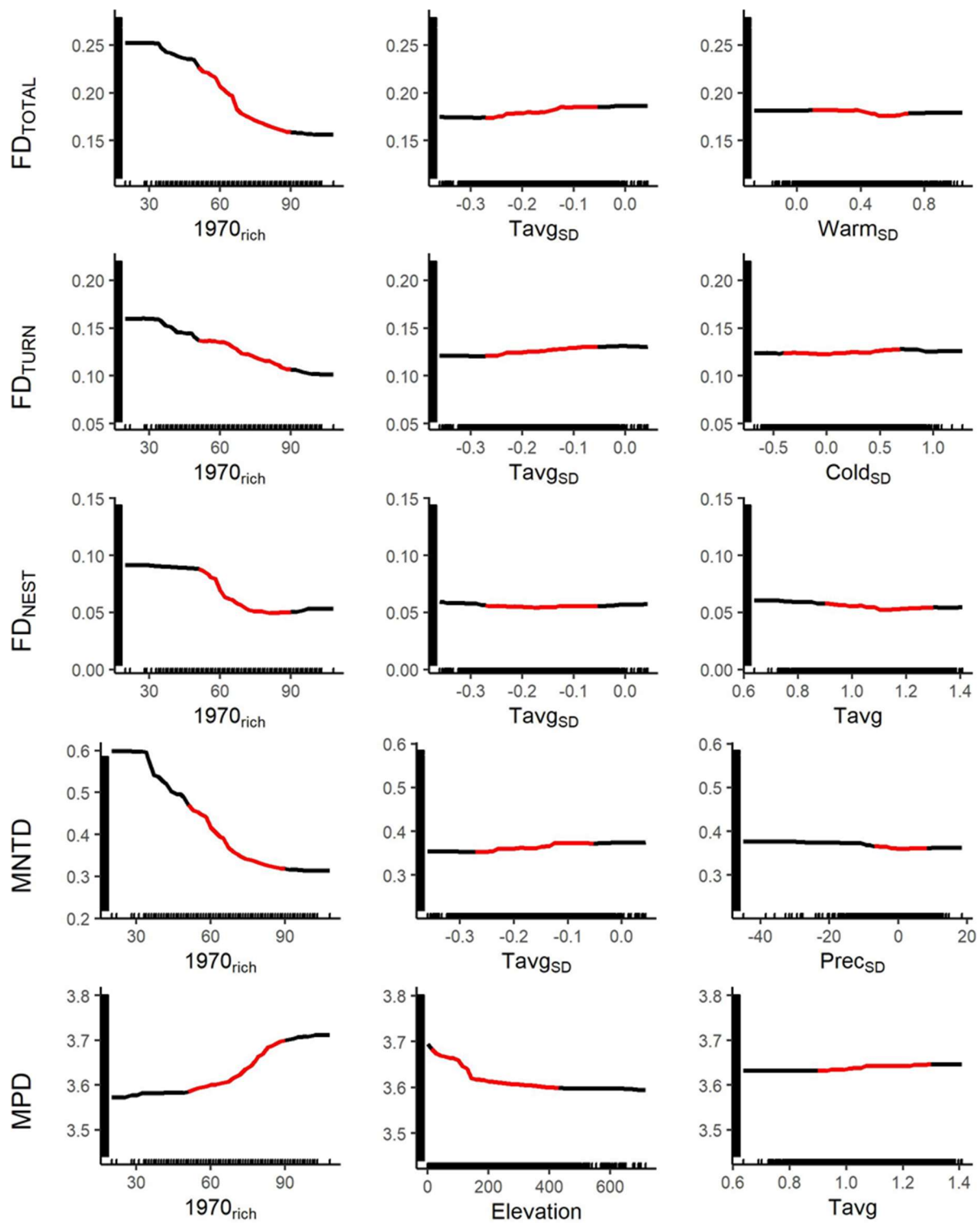


830

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

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





840

841 Fig. 5. Partial plots of the marginal effect of each of the top three most important predictor  
 842 variables (calculated from median random forest importance scores) had on the temporal  
 843 functional beta-diversity ( $FD_{TOTAL}$ ) of British breeding bird communities from 1970 – 2010,  
 844 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  
846 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).