





RESEARCH ARTICLE

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

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Abstract

Aim: The aim was to identify the primary drivers of compositional change in breeding bird assemblages over a 40-year period.

Location: Britain.

Time period: From 1970 to 2010.

Major taxa studied: Birds.

Methods: Using morphological trait measurements and a dataset of presence-absence data for British breeding birds surveyed in 10 km × 10 km hectads during two time periods, we calculated temporal taxonomic and functional beta diversity for each hectad alongside the change in species richness, mean nearest taxon distance (MNTD) and mean pairwise distance (MPD). We also estimated potential drivers of beta diversity, including climatic and land-use and land-cover (LULC) change variables, elevation and assemblage species richness in 1970 (1970_{rich}). We used 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.

Results: Initial (1970) species richness was the most important predictor (highest importance score) across all models, with areas characterized by higher initial richness experiencing less assemblage change overall. The 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.

Main conclusions: The composition of British breeding bird assemblages changed substantially between 1970 and 2010. Spatial heterogeneity increased, both taxonomically and functionally. 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 explained only small to moderate amounts of variation, suggesting that stochastic assembly change or finer-scale drivers might be drivers of temporal changes in assemblage composition.

KEYWORDS

beta diversity, British birds, climate change, community ecology, land cover, land use, macroecology

1 | INTRODUCTION

Recently, there has been an increasing focus in ecology on analysing biodiversity change through time and identifying the drivers of that change (Antão et al., 2020; Blowes et al., 2019; Dornelas et al., 2014; Pilotto et al., 2020). Climate and land-use and land-cover (LULC) change have both been identified as predictors of biodiversity change globally and linked, either directly or indirectly, to increased extinction risk in many taxa in the coming decades (Lindisfarne & Rayner, 2015; Newbold, 2018; Thomas et al., 2004; Wicczynski et al., 2019). Of the two, LULC change is generally acknowledged as the largest current driver of biodiversity loss (Bellard et al., 2012; Seto et al., 2012; Sohl, 2014; Tratalos et al., 2007; Zabel et al., 2019). However, warming temperatures are impacting species through range alterations/niche tracking (Batt et al., 2017; Fox et al., 2014; Tayleur et al., 2015) and shifting phenologies (Bell et al., 2019). These impacts will probably intensify, and climate change is expected to match or exceed LULC change as the leading biodiversity change driver this century (Newbold, 2018).

Although deterministic processes (e.g., LULC and climate change) can drive assemblage change, non-deterministic processes (e.g., stochastic change) have also been identified as drivers (Baselga et al., 2015; Stegen et al., 2013). Many biodiversity models (e.g., the equilibrium theory of island biogeography and neutral models; Hubbell, 2001; Mac Arthur & Wilson, 1967) predict the temporal turnover of species in a community as a theoretically stochastic process.

Two main factors hinder many studies of biodiversity change. 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, owing to the resources required to collect time-series data, most studies analysing temporal assemblage change use a space-for-time substitution, analysing dissimilarity between sites within the same study system and time period (e.g. Swenson et al., 2011). Space-for-time analyses assume that communities are at equilibrium, whereas 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 the roles of individual species in their community (Şekercioğlu, 2006).

An effective and widely used framework for analysing change in composition is temporal beta diversity (Baselga et al., 2015; Matthews et al., 2019; Shimadzu et al., 2015). Temporal beta-diversity metrics capture changes in the 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 (Christian et al., 2009; Jarzyna & Jetz, 2017; Schipper et al., 2016), decreases (Konvicka et al., 2006; Tingley & Beissinger, 2013; Wilson et al., 2007) or no systematic change (Dornelas et al., 2014; Petchey et al., 2007) in diversity through time. Further evidence of temporal biodiversity change and any drivers of that change is thus needed.

Here, we use measures of temporal taxonomic and functional beta diversity to analyse patterns of assemblage change in British breeding bird assemblages. To assess how assemblage diversity changed spatially, we used two complementary analyses to identify changes in the spatial dissimilarity structure and overall heterogeneity. Based on previous work on temporal diversity change, we expected i) average temperature change to be selected as an important variable (defined by the importance score in the random forest modelling) in driving diversity patterns (Davey et al., 2012; Lennon et al., 2000), and ii) turnover to be the main component of both taxonomic and functional compositional change, with no overall pattern of consistent species 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 (e.g., Jung et al., 2020).

2 | MATERIALS AND METHODS

2.1 | Data collection

2.1.1 | Species composition data

Data on the summer (breeding) distributions of the British avifauna recorded over two 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 for Ornithology (BTO) and the Scottish Ornithologists' Club (SOC). Each atlas (the data collected over each sampling period) consists of data on the presence or absence of British bird species within 10 km × 10 km (100 km²) hectads covering the British Isles on a continuous grid (Supporting Information Figure S1.1). We 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 difference in the proportion of benchmark species found in each hectad in each sampling period) or had < 50% land or comprised offshore islands (for more details, see Supporting Information Appendix S1 and S2).

2.1.2 | Trait data

We selected nine continuous traits (eight morphometric traits and body mass) measured from museum specimens or extracted from the literature to characterize 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 et al., 2014).

We \log_{10} -transformed measures of all traits, then standardized them to a mean of zero and an *SD* of one. We then entered measures of all traits into a principal components analysis (PCA) and extracted all axes, because all axes, including the minor axes, have been shown to provide useful information with regard to these trait data (Pigot et al., 2020).

2.1.3 | Climate data

We downloaded monthly temperature and precipitation data for 1960–2011 (10 years before the first Atlas period to capture lag effects) from the UK Met Office, which provides climate data interpolated from local weather stations onto a 1 km \times 1 km grid across the UK (Hollis et al., 2019). For each hectad, we calculated the change in several climate variables for the breeding season (defined as the start of March to the end of July), selected a priori. We calculated average temperature (in degrees Celsius) as the mean monthly temperature across the breeding months for each year (1960–2011). We selected this variable because it impacts the metabolic load of species, and increases in temperature are thought to reduce this load and allow more energy for reproduction (Lennon et al., 2000); also, temperature has been found to be a predictor of avian occurrence and abundance in the breeding season (Jarzyna et al., 2015; Jiguet et al., 2010; McDonald et al., 2012). We summed precipitation (in millimetres) for each hectad over the breeding season for each year. We calculated the range in temperature as the mean 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 each year. To assess the effect of unusually cold or warm periods, we calculated the “fat tail” for the coldest and warmest months across the 40-year period (Cold_{FAT} and Warm_{FAT}). The fat tail is the duration of the period in the tails of the distribution relative to that in the central mass, calculated as $(Q\ 0.975 - Q\ 0.025)/(Q\ 0.875 - Q\ 0.125)$, where Q is the quantile function (Brys et al., 2006).

To calculate climatic change, we averaged each of the climate variables over two periods to match each atlas (1960–1970 and 2001–2011) and also calculated the *SD* for each. We then subtracted the earlier mean from the later one to give the change in average

temperature (Tavg), change in the range of temperature (Range), change in precipitation (Prec), change in average temperature of the coldest month (Cold) and change in the average temperature of the warmest month (Warm). We repeated this for the *SD* to measure how variation around the mean changed across time (Tavg_{SD} , Range_{SD} , Prec_{SD} , Cold_{SD} and Warm_{SD}).

2.1.4 | Land-use data

We obtained data for land-use change from the Historic Land Dynamics Assessment (HILDA, v.2.0) model (Fuchs et al., 2012). The HILDA model uses multiple data streams of land cover to reconstruct historical LULC change, including where transitions have occurred (e.g., from forest to settlement). We obtained land-cover data relating to dominant, gross LULC changes for 1970 and 2010 (Fuchs et al., 2012, 2015). From these data, we calculated the number of 1 km² grid cells within each hectad classed as settlements (hereafter, urban land use), cropland and forest in 1970. We repeated this process with the 2010 data and subtracted the number of grid cells present in each land-use class in 1970 from the number of grid cells present in the same class in 2010. This provided a measure of the land-use change (converted to percentage change) within the hectads over the 1970–2010 period ($\text{Urban}_{\text{change}}$, $\text{Crop}_{\text{change}}$ and $\text{Forest}_{\text{change}}$). HILDA also provides the number of times a 1 km \times 1 km grid cell transitioned (changed primarily from one LULC class to another) between 1970 and 2010. We summed all transitions within each hectad to give a measure of total LULC change ($\text{Total}_{\text{change}}$). We calculated Shannon's diversity index for each hectad to capture the amount and variability in land-cover types, then subtracted the earlier measure from the later to give a measure of difference (Shan).

2.1.5 | Elevation data

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 *SD* from these data (Elevation and SD_{elev} , respectively).

We used Pearson's correlations to test for multicollinearity between the predictor variables. The $\text{Mean}_{\text{elev}}$ and SD_{elev} had an absolute correlation $> .70$ ($-.78$), as did Tavg and Warm (.84). Therefore, we removed SD_{elev} and Warm .

2.2 | Measuring compositional change through time

2.2.1 | Temporal taxonomic and functional beta diversity

We calculated taxonomic dissimilarity between 1970 and 2010 for each hectad with the function *beta.temp* from the R package

"betapart" (Baselga & Orme, 2012). This function 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 et al., 2003).

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 dissimilarity attributable to species replacement between the two time periods, whereas nestedness (hereafter, BD_{NEST}) is the proportion of the dissimilarity attributable to the earlier or later assemblage being a nested subset of the other through either loss or gain of species (Baselga, 2010). We also calculated a simple measure of taxonomic change (2010 species richness minus 1970 species richness = SP_{change}).

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

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 real distances between the species. The correlation was relatively high (Pearson's $r = 0.80$), showing that the dendrogram provided a reasonable measure of the functional distances between species.

2.2.2 | Mean nearest neighbour distance and 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 distance (MPD) (for more details regarding these metrics, see Supporting Information Appendix S3).

We calculated MPD and MNTD with the *comdist* and *comdistnt* functions, respectively, in the R package "picante" (Kembel

et al., 2010; Webb et al., 2008). We plotted values of all metrics to identify any spatial clustering of areas of high or low change.

2.2.3 | Change in spatial taxonomic and functional beta diversity

We performed two complementary analyses to test whether different aspects of spatial beta diversity changed. Changes in the spatial dissimilarity structure (i.e., similar sites becoming dissimilar and vice versa) can be detected as low-level correlations (i.e., weak correlations) between the dissimilarity between sites in the earlier period and the dissimilarity between sites in the later period, and where the relationship between the two is not 1:1 (Baselga et al., 2015). We calculated pairwise dissimilarities between each hectad and every other hectad during both time periods. We then used Mantel tests (Mantel, 1967) to assess the significance of the correlation of the turnover (PBD_{TURN} ; i.e., pairwise beta-diversity turnover) and nestedness (PBD_{NEST}) dissimilarities between sites across the two time periods. We repeated this process for functional turnover (PFD_{TURN}) and nestedness (PFD_{NEST}).

In contrast to pairwise dissimilarities, multiple site beta diversity provides information about the overall spatial heterogeneity of assemblages (Baselga et al., 2015; Baselga & Orme, 2012). Multiple site beta diversity (here referred to as MBD_{TOTAL} ; i.e., total multiple site 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 *beta.sample* function in the package "betapart" to generate 1,000 multiple site taxonomic and functional beta-diversity values for both time periods from a random sample of one-fifth of all sites (Baselga et al., 2015; Baselga & Orme, 2012). We compared the distributions for both the turnover and nestedness resultant dissimilarity portions for each period with the function *mded* (in the package "mded"; Aizaki, 2014; Poe et al., 1997, 2005), which quantifies the difference between two non-independent empirical distributions. We repeated this process for multiple site functional beta diversity (MFD_{TOTAL}) and its constituent components (nestedness, MFD_{NEST} ; and turnover, MFD_{TURN}).

2.3 | Modelling variation in temporal beta diversity

2.3.1 | Random forest regression

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 hyperparameters (for further details, see Supporting Information Appendix S3) with the function *rf_tuning* in the package "spatialRF" (Benito, 2021). We selected the combination that fitted the data best [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 (X) (Georganos et al., 2021; Hengl et al., 2018)]. We then assessed spatial autocorrelation of the residuals from the random forest models with Moran's 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 used to run the models in the package "spatialRF" (Benito, 2021; Wright & Ziegler, 2017).

Given that random forest is a stochastic algorithm, we ran 20 replicates for each of the 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) with permutations within each forest (Breiman, 2001). We recorded the median and SD of 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. Given that variation in climate and other predictors might be structured spatially, 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 SD.

3 | RESULTS

3.1 | Climate change between 1960 and 2010

Precipitation and range in temperature increased across most of Britain, and all changes in average temperature and mean temperature in the coldest month were positive (Supporting Information Figure S4.1). However, precipitation and range in temperature decreased in some areas over the period [977 (43.6%) and 12 (0.5%) of the hectads, respectively; Supporting Information Figure S4.1]. The SDs of precipitation, range in temperature, and temperature in the warmest month increased in most areas, whereas the SD of average temperature decreased, and the SD 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 similar.

3.2 | 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 (Supporting Information Figure S4.2). Cropland decreased on average, but with large variation ($-4.9 \pm 16.7\%$; Supporting Information Figure 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 1,654 grid cells and decreased in 447 (average change 0.1 ± 0.2 ; Supporting Information Figure S4.2).

3.3 | Changes in taxonomic assemblage composition through time

Change in all taxonomic measures was relatively uniform across Britain, but with a clear spatial pattern found in species richness change (SP_{change} ; Figure 1). There appeared to be clustering of areas with increases or decreases in species richness, although there was no strong latitudinal or longitudinal divide (Figure 1). Mean SP_{change} was slightly negative across the hectads, but with large variation (-0.21 ± 10.95 , range = -39 to 41) and a median of zero. Slightly more assemblages had a net loss of species than a net gain (1,095 and 1,054 assemblages, respectively).

For taxonomic beta diversity, mean total taxonomic beta diversity (BD_{TOTAL}) was $.20 \pm .06$ (range = $.08$ – $.54$). The BD_{TOTAL} was mainly driven by turnover (BD_{TURN} : $.15 \pm .06$, range = 0 – $.46$, mean percentage of BD_{TOTAL} = 75%) with nestedness responsible for a lower portion on average (BD_{NEST} : $.05 \pm .05$, range = 0 – $.29$, mean percentage of BD_{TOTAL} = 25%). There was no strong signal of species loss or gain at the hectad level over the period (Figure 1).

3.4 | Changes in functional assemblage composition through time

The pattern of temporal functional beta diversity across the assemblages was similar to taxonomic beta diversity, with higher average turnover than nestedness [FD_{TURN} : $.13 \pm .05$ (mean percentage of FD_{TOTAL} = 72%) and FD_{NEST} : $.05 \pm .04$ (mean percentage of FD_{TOTAL} = 28%), respectively], highlighting no systematic loss of functional diversity. However, mean total functional beta diversity (FD_{TOTAL}) was $.18 \pm .05$ (range = $.08$ – $.42$), and thus lower than mean BD_{TOTAL} (Figure 1). In addition, the change in FD_{TOTAL} was greater in upland areas than in the lowlands (Figure 1).

In contrast, mean pairwise distance (MPD) was higher in lowland areas (mainly the south-east) than in uplands (Figure 1). Average MPD across the hectads was 3.64 ± 0.11 (range = 3.15 – 3.94), and average mean nearest neighbour distance (MNTD) was 0.36 ± 0.11 (range = 0.15 – 1.10) (Figure 1).

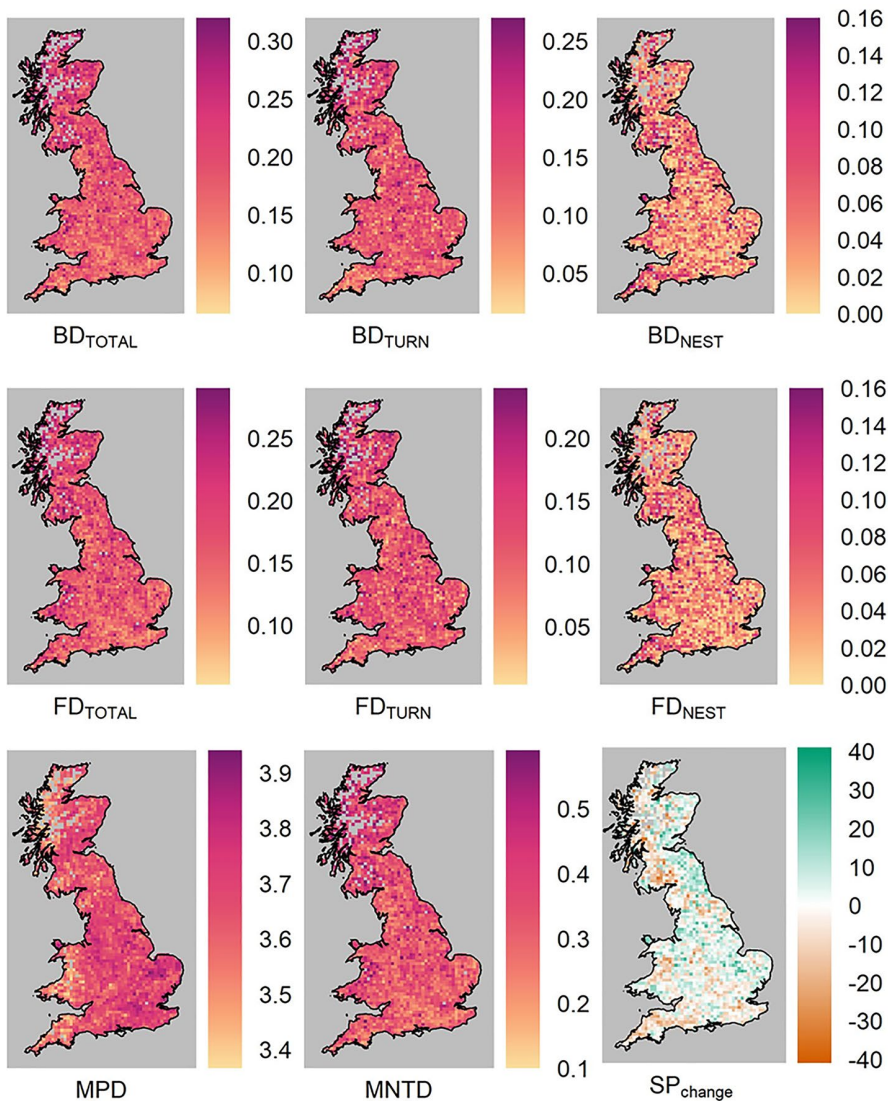


FIGURE 1 Temporal change observed in breeding bird communities in Britain between 1970 and 2010 within 10 km × 10 km hectads for the following taxonomic and functional metrics: the temporal taxonomic beta diversity (BD_{TOTAL}), taxonomic turnover (BD_{TURN}), taxonomic nestedness resultant dissimilarity (BD_{NEST}), temporal functional beta diversity (FD_{TOTAL}), functional turnover (FD_{TURN}), functional nestedness resultant dissimilarity (FD_{NEST}) and 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 for Ornithology (BTO). Grey areas indicate where grids were removed owing 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). Given that the scale varies among measures, they are not directly comparable with one another

3.5 | Spatial taxonomic and functional beta-diversity change

The spatial structure of dissimilarities changed between 1970 and 2010, as shown by the low correlations/weaker relationships between pairwise taxonomic nestedness (PBD_{NEST} ; $R^2 = 0.18$, Mantel $p < .001$) and pairwise functional nestedness (PFD_{NEST} ; $R^2 = 0.19$, Mantel $p < .001$) in the two time periods, and the clear deviation of the slope of the relationships from one (Figure 2). Overall, pairs of sites became less nested (Figure 2). The correlations/relationships between the two time periods for pairwise taxonomic turnover (PBD_{TURN} ; $R^2 = 0.61$, Mantel $p < .05$) and pairwise functional turnover (PFD_{TURN} ; $R^2 = 0.50$, Mantel $p < .05$) were lower/weaker (although still significant) and the slopes were much closer to one (Figure 2). Heterogeneity across the region changed significantly, as evidenced by significantly higher turnover in the sampled multiple taxonomic turnover (MBD_{TURN}) and multiple functional turnover (MFD_{TURN}) values for 2010 compared with 1970 (both $p < .05$; Figure 2). The sampled values of multiple taxonomic nestedness (MBD_{NEST}) and

multiple functional nestedness (MFD_{NEST}) in 1970 and 2010 overlapped considerably (Figure 2).

3.6 | Random forest models

The random forest models explained between 13% (FD_{NEST}) and 60% (MPD) of the variation in the temporal beta-diversity metrics based on average OOB R^2 values (across 20 random forest models; Figure 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 25% of the data (Supporting Information Tables S5.1 and S5.2, respectively).

Across all the models, the order of variable importance was similar. For all metrics, species richness in 1970 was the most important variable by a relatively large margin (Figure 3). Coordinates were also ranked highly across the models, with latitude being more important than longitude for all metrics except for SP_{change} (Figure 3). Changes in the SD of the climatic variables

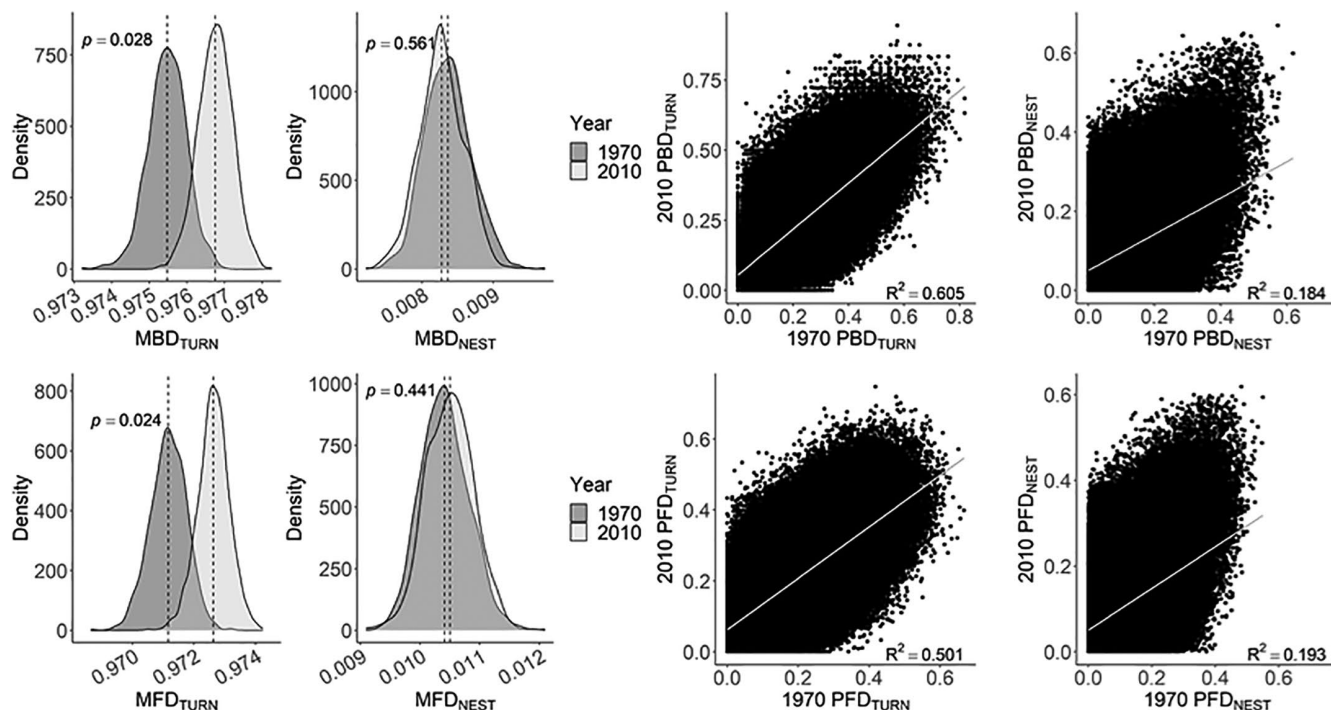


FIGURE 2 Spatial change in taxonomic and functional beta diversity of British bird breeding assemblages between 1970 and 2010. The density plots on the left show the turnover and nestedness components for both taxonomic (MBD_{TURN} and MBD_{NEST}) and functional (MFD_{TURN} and MFD_{NEST}) beta diversity. 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 corner. The plots on the right show the correlations between pairwise dissimilarities calculated in 1970 and 2010 for both taxonomic (PBD_{TURN} and PBD_{NEST}) and functional (PFD_{TURN} and PFD_{NEST}) beta diversity. The continuous grey lines show the relationship between the metrics using ordinary least squares linear regression (the slopes clockwise from top-left are 0.92, 0.46, 0.49 and 0.73). The fit (R^2) from the regression is shown in the bottom right-hand corner

were consistently ranked higher than the mean equivalent in all models except nestedness, MPD and SP_{change} (Figure 3). The LULC predictors were consistently poor predictors across the response metrics, although the difference in importance between these and most other variables was low (Figure 3).

Partial plots for the three most important variables (calculated using variable importance scores; for plots displaying all the variables, see Supporting Information Appendix S6) showed that all taxonomic and functional Baselga beta-diversity measures decreased with increasing species richness in 1970 and increased slightly with change in the SD of average temperature ($Tavg_{SD}$); although the lines were largely stable, with functional nestedness and taxonomic nestedness being flat; Figures 4 and 5). SP_{change} also decreased with increasing species richness in 1970 and elevation, but increased slightly with increasing change in average temperature ($Tavg$; Figure 4).

Mean pairwise distance and MNTD had opposite relationships with 1970_{rich} (MPD increasing and MNTD decreasing; Figure 5). In addition, MPD decreased with elevation and increased slightly with $Tavg$ (Figure 5), whereas MNTD increased slightly with $Tavg_{SD}$ and decreased slightly with change in SD of precipitation ($Prec_{SD}$). Other variables had a limited effect (Figure 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 Supporting Information Appendix S7).

4 | DISCUSSION

4.1 | Temporal assemblage change

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 assemblages were replaced rather than lost systematically, consistent with previous work on temporal patterns of community change (Antão et al., 2020; Blowes et al., 2019; Dornelas et al., 2014, 2018; Nunes et al., 2020; Petchey et al., 2007; Tinoco et al., 2021; Tsianou et al., 2021). Functional change was slightly lower on average than taxonomic change across the assemblages, highlighting that the assemblages were less functionally disturbed despite the taxonomic change (see also Tsianou et al., 2021). However, 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 distinct traits, as shown by nearly proportional changes in both taxonomic and functional nestedness (Petchey et al., 2007).

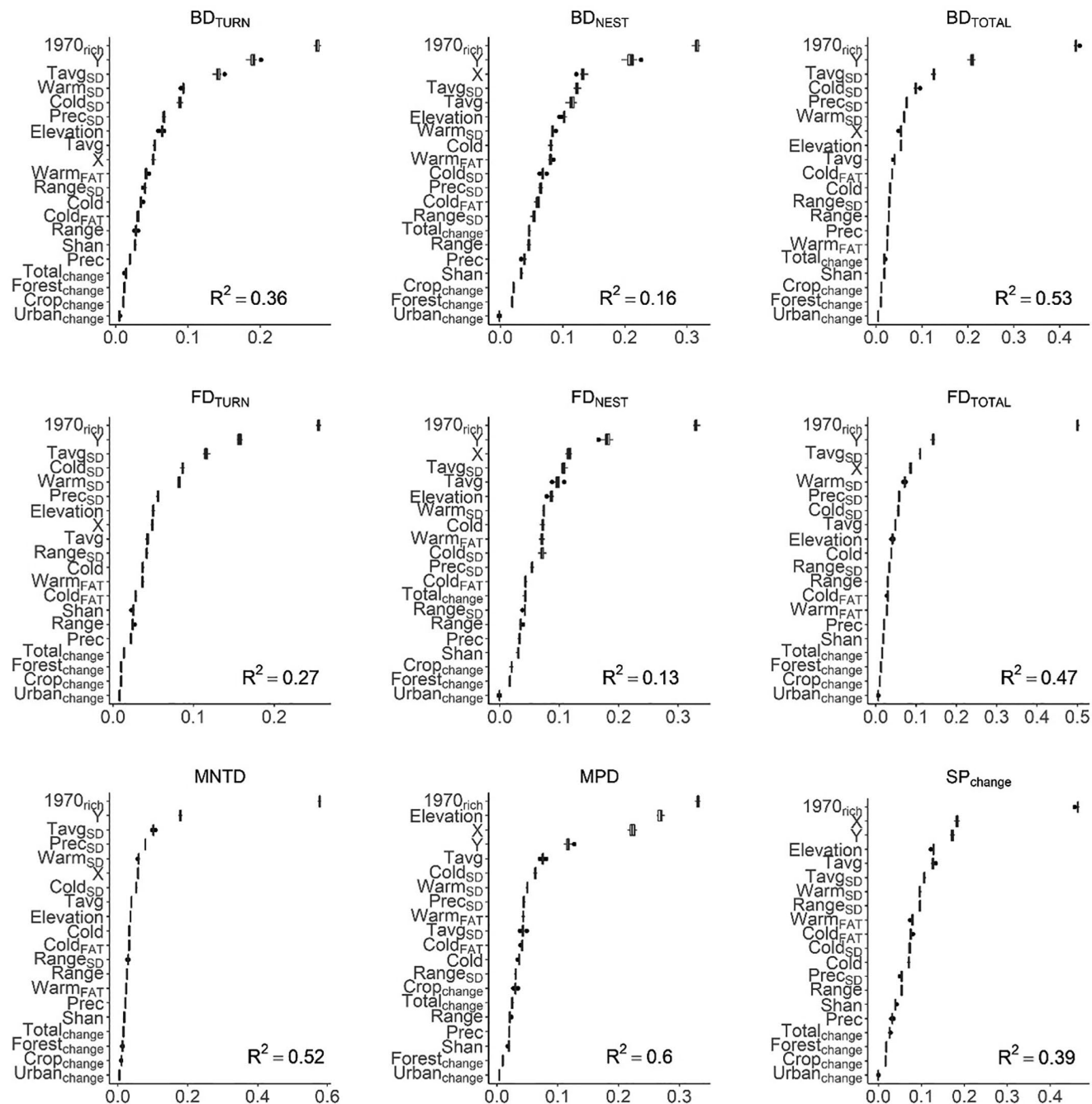


FIGURE 3 Variable importance scores from spatial random forest models for different measures of temporal change in assemblages (100 km² hectads) of British birds from 1970 to 2010. The mean model explanatory power (R^2) is in the lower right of each plot. The metrics of assemblage composition change are as follows: 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}), mean pairwise distance (MPD) and mean nearest taxon distance (MNTD). Variables are ranked in descending order of importance (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 interquartile range (IQR). Points highlight outliers, and the whiskers show data 1.5 times the IQR

Observed changes in composition were influenced mainly by the number of species present in the assemblage in the earlier period, with larger assemblages changing relatively less than smaller ones. Given that taxonomic nestedness, and therefore total taxonomic beta diversity, are not independent of species richness gradients, we cannot make

assumptions on the basis of these results. Taxonomic turnover, however, did not depend on these gradients. Comparatively lower turnover in sites with greater species richness could mean that more diverse assemblages might be protected to an extent against temporal disturbance, perhaps because they have a wider array of traits (and therefore functions),

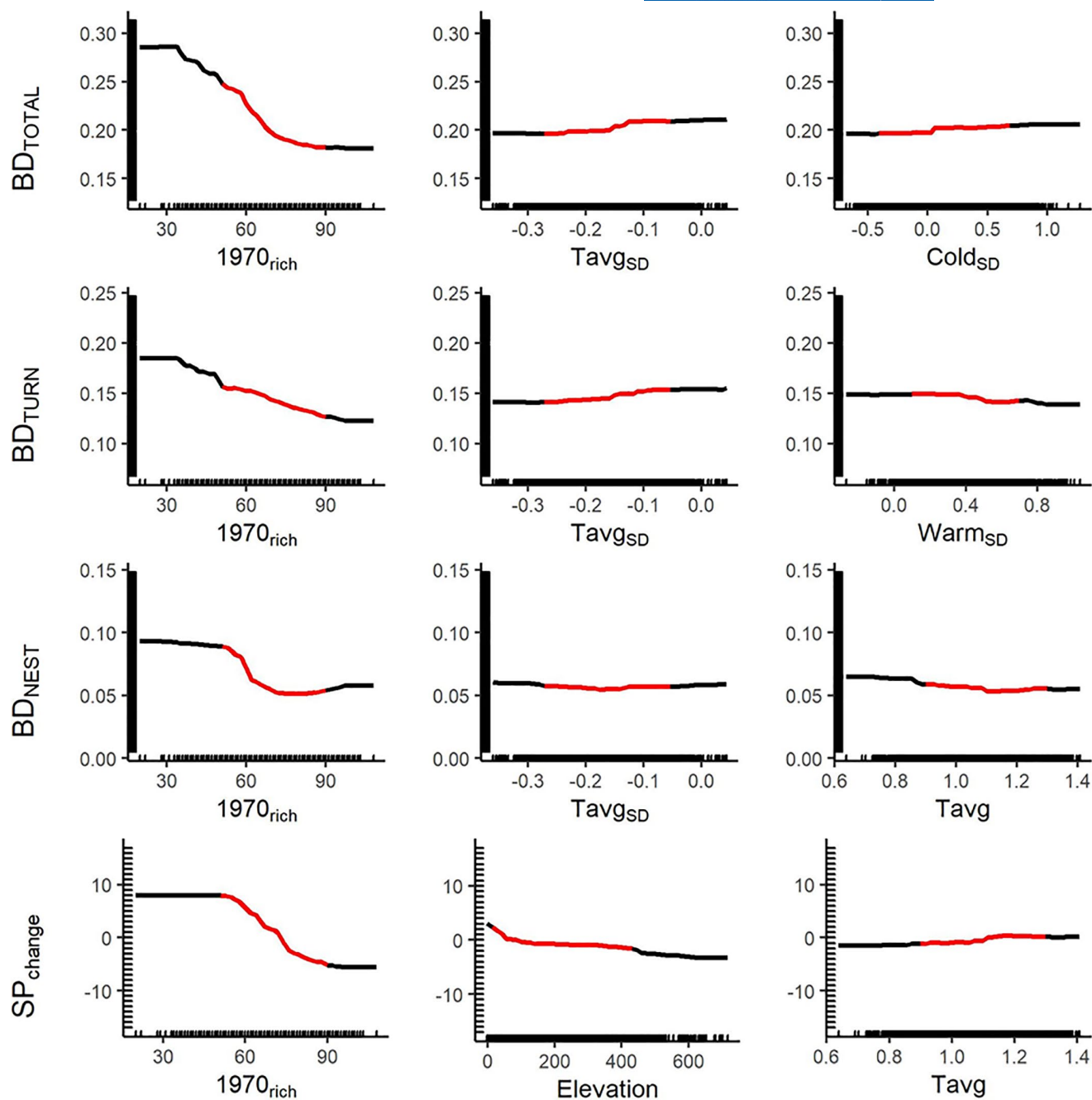
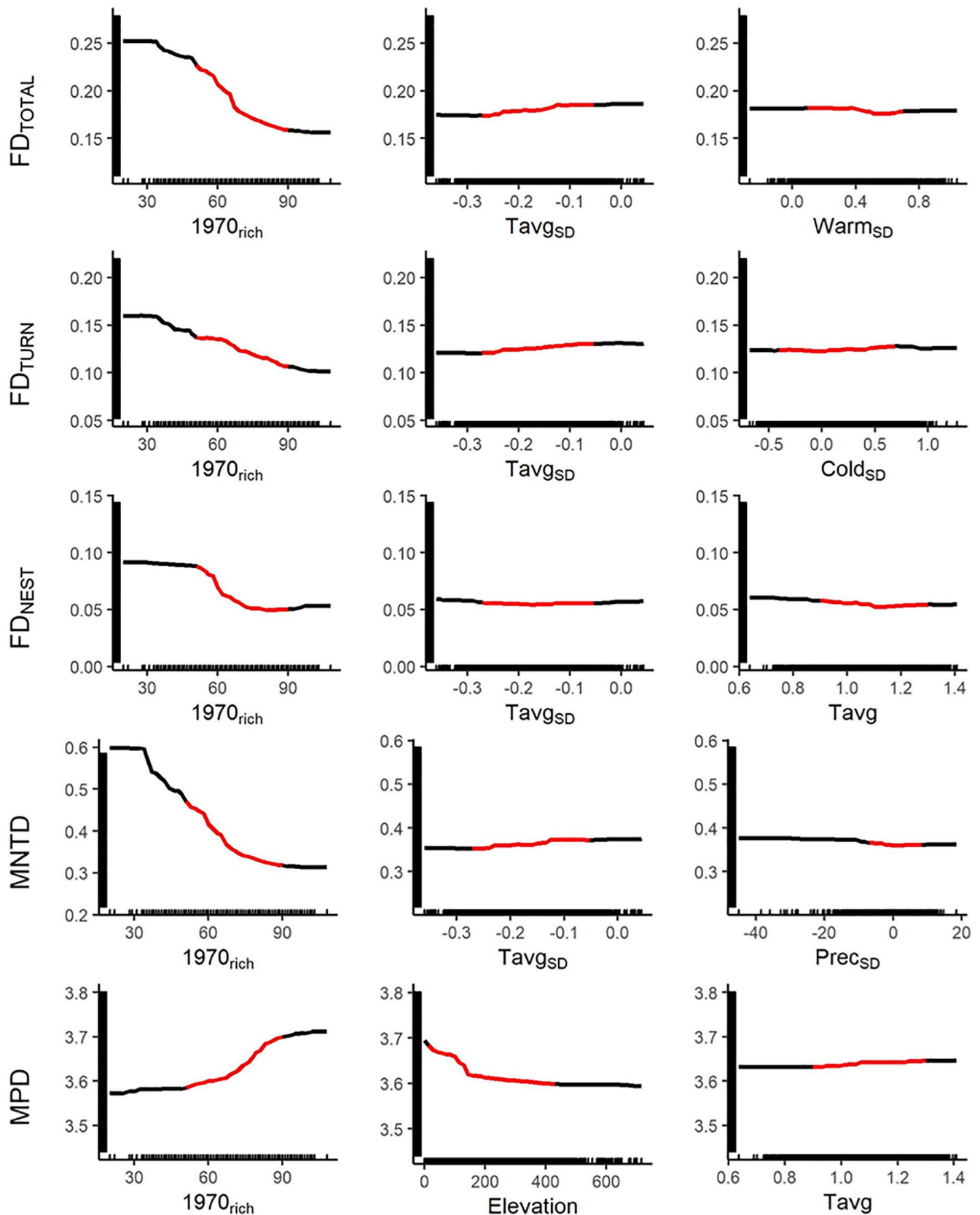


FIGURE 4 Partial plots of the marginal effect of each of the top three most important predictor variables (calculated from median random forest importance scores) on the temporal taxonomic beta diversity (BD_{TOTAL}) of British breeding bird communities from 1970 to 2010 and its component parts, turnover (BD_{TURN}) and nestedness resultant dissimilarity (BD_{NEST}). Also 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 values of the predictor variables (the red section of the lines). Variables are ordered according to median importance across the models (left to right). 1970_{rich} is the hectad species richness in 1970. $Tavg_{SD}$ is the change in the standard deviation of mean temperature across the period. $Cold_{SD}$ is the change in the standard deviation of mean temperature in the coldest month across the period. $Tavg$ is the change in the average temperature across the period. $Warm_{SD}$ is the change in the standard deviation of mean temperature in the warmest month across the period

leading to a better-functioning system and therefore more resilience (Jarzyna & Jetz, 2017; Weeks, Naeem, et al., 2020). The hectads with higher initial species richness could 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 LULC

and climate change variables. Alternatively, the lower observed change in sites with higher species richness could be attributable to facilitation between species, with negative relationships between turnover and diversity expected when communities are characterized by strong inter-specific facilitative interactions (Pandit & Kolasa, 2012; Shurin, 2007).



Although changes in species richness were centred around zero, the variation around the average indicates that many assemblages did change, in some cases substantially. Large losses from some

areas were almost 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

FIGURE 5 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 functional beta diversity (FD_{TOTAL}) of British breeding bird communities from 1970 to 2010 and its component parts, turnover (FD_{TURN}), nestedness resultant dissimilarity (FD_{NEST}), 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 each metric. Effects of the predictor variables were assessed across the central 90% of the values of the predictor variables (the red section of the lines). Variables are ordered according to median importance across the models (left to right). 1970_{rich} is the hectad species richness in 1970. $Tavg_{SD}$ is the change in the standard deviation of mean temperature across the period. $Cold_{SD}$ is the change in the standard deviation of mean temperature in the coldest month across the period. $Tavg$ is the change in the average temperature across the period. $Warm_{SD}$ is the change in the standard deviation of mean temperature in the warmest month across the period. $Prec_{SD}$ is the change in the standard deviation of mean total precipitation across the period

increasing or decreasing or, alternatively, to factors such as conservation- and biodiversity-focused land-management efforts (Inger et al., 2015; Reif, 2013; Rittenhouse et al., 2012).

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 beta diversity in each time period) through time for both taxonomic and functional turnover. Pairs of sites also became less taxonomically and functionally nested. Given that the numbers of sites that gained or lost species were roughly even, and the functional pattern matched the taxonomic pattern, the decrease in nestedness might be driven by the loss or gain of functionally unique or rare species. For example, the range of the common buzzard (*Buteo buteo*) increased from 940 to 2,130 hectads (226% increase), and the range of the cuckoo (*Cuculus canorus*) decreased from 2,107 to 1,258 hectads (60% decrease). All things being equal, these changes in distribution would decrease nestedness between areas in which buzzards were absent and those in which buzzards were present or, in the case of the cuckoo, between areas in which cuckoos were present and those in which cuckoos were absent.

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

4.2 | Elevation, climate change and LULC change

Assemblage composition changed more in upland areas in Britain than in lowland regions. Species richness increased slightly in the

lowlands and decreased in the uplands, which might indicate that upland species (such as those in the Scottish Highlands) are more at risk of local extirpation. These losses could result from either increased competition (as species ranges shift upslope) or environmental filtering in upland areas through time. Alternatively, the 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 species richness is known often to decrease with elevation (Guo et al., 2013).

Climate change variables had higher importance scores in the models than LULC change variables, but less so than species richness in 1970 and elevation; change in average temperature and change in the SD of average temperature were the most important. These findings are generally consistent with previous work that used data from earlier periods and found that change in average temperature drove compositional change of British birds (Davey et al., 2012, 2013; White et al., 2018), although we found a weaker effect of climate. We found that the importance scores of climate variables relative to both spatial coordinates and species richness in 1970 were generally low. This might be attributable to the resolution at which the assemblages were sampled. For example, previous work has shown that climatic conditions are more relevant to overall avian temporal assemblage dissimilarity at finer (5 km × 5 km) compared with coarser resolutions (up to 80 km × 80 km) in New York State, although this resolution dependence is not as strong for temporal turnover (Jarzyna et al., 2015).

In regard to the impact, or lack thereof, of LULC variables within the models, there are several potential factors to consider. As can be seen from the 90% central range lines in the partial plots (red lines; Supporting Information Figures S6.1–S6.9), $Urban_{change}$ was heavily zero-inflated. Low recorded land-use change might be attributable to the measure of land change. The base LULC data used here were the dominant LULC type on a 1 km² grid. Therefore, for urban land to be classified as increasing or decreasing in a 1 km² grid cell within the larger 100 km² hectad, that 1 km² grid cell must have changed from mainly urban to another land use or from another land use to mainly urban. Such change is uncommon in an extensively urbanized country, such as the UK. The UK can be described as a post-perturbation system where considerable LULC change has already occurred, and the pace, range and intensity of LULC change has slowed in recent decades. Different results are expected for other countries, particularly many tropical

countries, where LULC change is more prominent (e.g., Rurangwa et al., 2021). Our LULC data also do not account for fragmentation, small changes in LULC within each 1 km² and agricultural intensification, all of which can potentially drive assemblage change (Boulinier et al., 1998; Hendershot et al., 2020).

4.3 | Limitations and considerations

A potentially confounding factor is the impact of wintering grounds or hazards during the passage to Britain for the migratory species included in this study. British migratory species have different responses to differences in temperature, with long-distance migrants preferring colder springs and resident species preferring warmer springs (Wittwer et al., 2015). Hunting along the migratory route and abiotic and biotic variables within wintering grounds can also impact populations, potentially causing fewer migrants to reach Britain and therefore reducing the likelihood that such species will occupy the maximum available suitable areas (Lormée et al., 2019; Vickery et al., 2014).

Sampling effects can have impacts on analyses of assemblage composition (Neate-Clegg et al., 2020). Although the use of citizen scientists has some drawbacks, including the over- or under-sampling of some areas (Neate-Clegg et al., 2020), citizen scientists can collect good-quality data that are valuable for detecting trends in assemblages and populations (Horns et al., 2018; McCaffrey, 2005). We accounted for potential sampling bias by removing the grid cells that changed considerably in the number of benchmark species detected (Gillings et al., 2019; Supporting Information Appendix S1). In addition, the censuses in the atlases are conducted over 4 years and should therefore provide a more accurate picture of species colonizations and extirpations than a singular year of sampling. Notwithstanding, sampling effects are possible, particularly in regions that are difficult to sample. Another potential factor is the selection of tetrads for surveying. Although this information is not available in the published data (Gillings et al., 2019), if the selection of tetrads was biased towards public lands (where development is often restricted) in one or both of the atlases, then results could be misleading (Mentges et al., 2021). A potential avenue could be to incorporate the percentage of public and private land into future work. Future work could also investigate the differences between sampling years within the atlases, because the data were not available to explore that here.

Species traits are not stationary in time and space and are likely to 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 change in composition within or between assemblages. However, the extent of this variation appears to be negligible in relationship to interspecific variation for birds generally (see Tobias, et al., in press), suggesting that both our use of species trait averages and our assumption that trait values are constant across the region were justified.

Although British breeding bird assemblages changed in both time and space between 1970 and 2010, that change does not appear to have been driven by coarse-resolution LULC change. Climate change played a relatively larger role, although its impact was still limited in general. This could indicate that stochastic processes, or perhaps finer-resolution factors not included here, are driving temporal dissimilarity. The observed change was relatively greater for less species-rich assemblages at higher elevations than for more species-rich assemblages at lower elevations, and larger assemblages appeared somewhat buffered to change. Although no consistent signal of species loss or gain was found, these presence-absence data do not incorporate abundance. Indeed, across a similar time period (1970–2017), the estimated reduction in the abundance of North American birds was 2.9 billion (Rosenberg et al., 2019). Work incorporating abundance, or looking at how individual species or functional groups might have been impacted by LULC or climate change, should therefore be a priority to assess further 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.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data table with variables has been made available as supplementary material along with scripts to run the analyses. See Gillings et al. (2019) for how to access original atlas data.

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BIOSKETCH

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SUPPORTING INFORMATION

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