







RESEARCH ARTICLE

Unravelling the complexities of biotic homogenization and heterogenization in the British avifauna

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Abstract

1. Biotic homogenization is a process whereby species assemblages become more similar through time. The standard way of identifying the process of biotic homogenization is to look for decreases in spatial beta-diversity. However, using a single assemblage-level metric to assess homogenization can mask important changes in the occupancy patterns of individual species.
2. Here, we analysed changes in the spatial beta-diversity patterns (i.e. biotic heterogenization or homogenization) of British bird assemblages within 30km × 30km regions between two periods (1988–1991 and 2008–2011). We partitioned the change in spatial beta-diversity into extirpation and colonization-resultant change (i.e. change in spatial beta-diversity within each region resulting from both extirpation and colonization). We used measures of abiotic change in combination with Bayesian modelling to disentangle the drivers of biotic heterogenization and homogenization.
3. We detected both heterogenization and homogenization across the two time periods and three measures of diversity (taxonomic, phylogenetic, and functional). In addition, both extirpation and colonization contributed to the observed changes, with heterogenization mainly driven by extirpation and homogenization by colonization. These assemblage-level changes were primarily due to shifting occupancy patterns of generalist species.
4. Compared to habitat generalists, habitat specialists had significantly (i) higher average contributions to colonization-resultant change (indicating heterogenization within a region due to colonization) and (ii) lower average contributions to extirpation-resultant change (indicating homogenization from extirpation). Generalists showed the opposite pattern.

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5. Increased extirpation-resultant homogenization within regions was associated with increased urban land cover and decreased habitat diversity, precipitation, and temperature. Changes in extirpation-resultant heterogenization and colonization-resultant heterogenization were associated with differences in elevation between regions and changes in temperature and land cover.
6. Many of the 'winners' (i.e. species that increased in occupancy) were species that had benefitted from conservation action (e.g. buzzard (*Buteo buteo*)). The 'losers' (i.e. those that decreased in occupancy) consisted primarily of previously common species, such as cuckoo (*Cuculus canorus*).
7. Our results show that focusing purely on changes in spatial beta-diversity over time may obscure important information about how changes in the occupancy patterns of individual species contribute to homogenization and heterogenization.

KEYWORDS

beta-diversity, colonization, dissimilarity, extirpation, generalists, specialists

1 | INTRODUCTION

Biotic homogenization (Olden, 2006; Olden & Rooney, 2006) is defined as a process whereby species communities or assemblages become taxonomically, functionally, and/or phylogenetically more similar to one another across space and time due to extirpation and colonization dynamics (Hughes et al., 2022). Homogenization is usually identified through decreases in assemblage composition dissimilarity (herein, 'dissimilarity') over time (temporal-spatial β -diversity) and can have impacts on ecosystem functions and services (Wang et al., 2021) due to alterations in the assemblage composition of key groups, such as pollinators (Carvalho et al., 2013). One such process that can lead to homogenization across a sampled region is the extirpation of specialist species from individual assemblages and the colonization of generalists already present in other assemblages in the sampled region (Clavel et al., 2011). It is generally agreed that anthropogenically generated disturbances such as land-use change and climate change largely favour the expansion of generalist species due to their flexible habitat, dietary and climatic requirements, alongside typically greater adaptability than more specialized species (Callaghan et al., 2019; Davey et al., 2012; Frishkoff et al., 2016; Ibáñez-Álamo et al., 2017; Le Viol et al., 2012; Mitchell et al., 2022). However, the literature on local diversity change across time and space remains contradictory due to the difficulties of disentangling the nuances of what drives change (Jarzyna & Jetz, 2017). Indeed, across ecological time-series datasets, patterns of change in alpha diversity were centred around zero, but with increases, decreases, and stability observed across the utilized datasets (Dornelas et al., 2014). Regarding beta-diversity, Dornelas et al. (2014) found an overall decrease in temporal beta-diversity, potentially resulting from increased biotic homogenization. In terms of extirpation and colonization changes that may lead to increased biotic homogenization, across time-series data spanning 10 or more years, rates are

increasing at similar rates over time, but with differences at the local scale (some accelerating, some decelerating) (Dornelas et al., 2019). Across the literature, various outcomes at different scales have been reported concerning biotic homogenization, including increases in spatial β -diversity over time (i.e. heterogenization; Marchetti et al., 2006; Socolar et al., 2016). However, what is general to most studies looking at change in dissimilarity over time and space is the focus on the overall metric of change, which overlooks how individual species are changing in occupancy and what changes contribute to the observed patterns of homogenization and heterogenization. Therefore, the relationship between the increase (heterogenization) or decrease (homogenization) in dissimilarity over time (temporal-spatial β -diversity) and the underlying extirpations and colonizations leading to that change is often overlooked.

Temporally, increases in spatial β -diversity (i.e. heterogenization) across a region can be attributed to an increased variation in the number and composition of habitats (temporal habitat heterogeneity, increasing the niche space available), the presence of newly introduced species that stay confined to specific areas (i.e. they do not propagate across the region), and the decline of widespread species or species shared among different locations (Chase et al., 2019). Conversely, decreases in spatial β -diversity (i.e. homogenization) can occur due to the opposite, that is the loss of habitat diversity through time, loss of species confined to specific areas, and the increase of locally common species across the measured region. Homogenization does not always equate to a decrease in either gamma (γ) or alpha (α) diversity (Rooney et al., 2007). Indeed, depending upon the initial community configurations within a set region, both extirpation and colonization can increase differentiation (i.e. heterogenization) if the colonizing or extirpated species was present in >50% or <50% of the sites within the studied region, respectively. An example is provided in Marchetti et al. (2006), where biotic heterogenization occurred over time within Californian (US) fish assemblages, but as a result of

high colonization at some sites, including invasive species, and low corresponding extirpation in other sites. Therefore, how assemblage dissimilarity is assessed likely influences the outcomes, something not often considered in biotic homogenization studies, which typically only incorporate broad-scale measures of dissimilarity.

One way to improve upon the assessment of assemblage composition change is through the incorporation of extirpation and colonization-resultant change. As species losses and gains can both increase (heterogenization) or decrease (homogenization) spatial β -diversity within a given region depending upon the initial local species occupancy, examining the contribution of extirpation and colonization to changing dissimilarity can provide a more fine-scale assessment of changes in local assemblage composition (Figure 1). Therefore, determining whether colonization or extirpation is driving patterns in homogenization, and assessing the relative contributions of each measure, is vital to understand any observed

homogenization processes. Such understanding is also necessary to define whether a homogenization process is potentially detrimental, as may be the case if specialists are extirpated at the expense of widespread generalists (Clavel et al., 2011; Davey et al., 2012; Devictor et al., 2008) or if it is due to stochastic variation in common species dynamics. The latter could be due to, for example, increases in the occupancy of locally common species across the regional sites without the subsequent loss of specialist species, and thus no decreases in specialist alpha diversity (Sullivan et al., 2016; Figure 1).

Here, using atlas data of British breeding birds within 10×10 km (hectad) grid squares across two time periods (1988–1991 and 2008–2011; Gillings et al., 2019), we investigate whether regional bird assemblages (a focal hectad and its immediate neighbours, hereafter referred to as a $[30 \text{ km} \times 30 \text{ km}]$ 'region') within Britain are undergoing homogenization or heterogenization by comparing spatial β -diversity in regions between the time points (Baselga, 2010; Baselga



$$\begin{aligned} \alpha \text{ diversity (focal hectad (green))} &= 3 \\ \gamma \text{ diversity (whole region (orange))} &= 4 \\ \beta W (\gamma/\alpha) \text{ diversity} &= 1.71 \\ \Delta\beta_{\text{TOTAL}} &= \beta'W - \beta W \end{aligned}$$

Definitions

α diversity: Alpha diversity, the number of species within a single area.

$\bar{\alpha}$: The mean α diversity across multiple areas.

γ diversity: Gamma diversity, the number of species across multiple areas.

βW : Whittaker's beta-diversity.

$\Delta\beta_{\text{TOTAL}}$: The measure of change in βW over time, calculated as $\beta'W$. (Whittaker's beta in the later time period) minus βW (Whittaker's beta in the first time period).

$\Delta\beta_E$: Total extirpation resultant change. Made up of $\Delta\beta_{E-}$ (extirpation resultant homogenisation) and $\Delta\beta_{E+}$ (extirpation resultant heterogenisation). Positive values indicate higher extirpation resultant heterogenization than extirpation resultant homogenisation, while negative values indicate the opposite.

$\Delta\beta_C$: Total colonisation resultant change. Made up of $\Delta\beta_{C-}$ (colonisation resultant homogenisation) and $\Delta\beta_{C+}$ (colonisation resultant heterogenisation). Positive values indicate higher colonisation resultant heterogenization than colonisation resultant homogenisation, while negative values indicate the opposite.

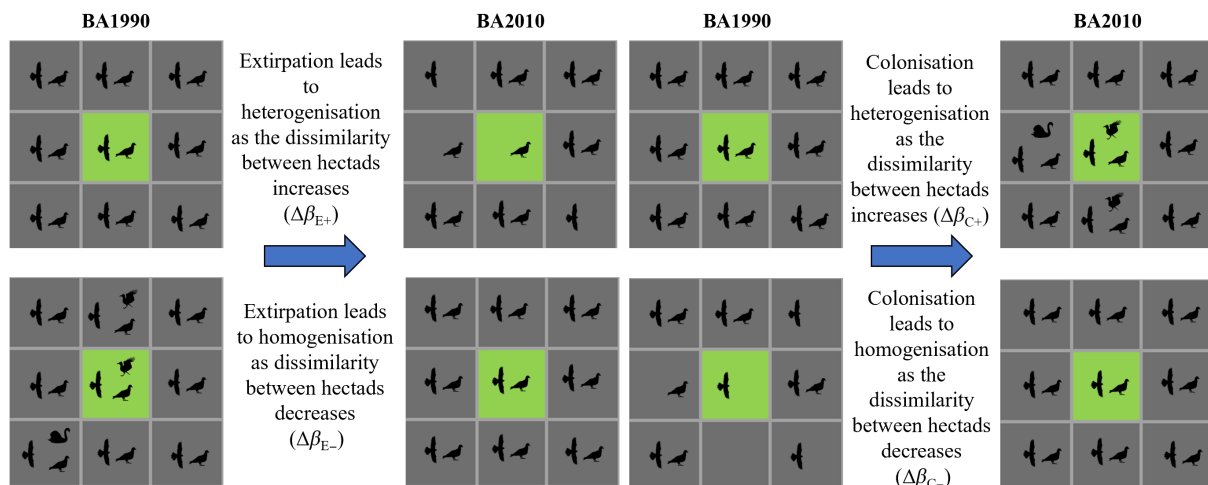


FIGURE 1 Conceptual diagram showing how species colonization and extirpation from local regions (where the green square is the focal hectad and the eight grey squares are the neighbouring hectads included in the region) can lead to either increased or decreased dissimilarity (spatial β -diversity) over time. Shown at the top of the figure are definitions of the components used to calculate colonization and extirpation-resultant change.

& Orme, 2012). Given that anthropogenic land-use change as a process has been happening in Britain since at least the Neolithic, with periods of further intensification (such as the Industrial Revolution) (Bibby, 2009; Rackham, 1986; Robinson, 2014), one could argue that Britain represents a system disturbed to such an extent (Willis & Birks, 2006) that the biotic homogenization of assemblages has already occurred. However, evidence suggests that assemblage composition in Britain has continued to shift (Wayman et al., 2022). For example, Sullivan et al. (2016; see also White, Montgomery, Storchová, et al., 2018, for a similar example) found that breeding bird communities became more homogenous over time (1994–2012) across Britain, mainly driven by decreases in moderately generalist species populations and increases in the most generalist. However, the extirpation and colonization dynamics that underpin these observed patterns remain unknown.

Utilizing three dimensions of diversity (taxonomic, functional and phylogenetic), we assess whether changes in total spatial β -diversity and turnover within regions using the three diversity dimensions are congruent across space. We then test whether changes are driven by accompanying changes in land cover, climate, and habitat heterogeneity between the periods or if elevation impacts the direction of change. Finally, we assess the contribution of species extirpations and colonizations to changes in taxonomic spatial β -diversity (i.e. patterns of biotic heterogenization and homogenization) within regions through time. We partitioned this extirpation and colonization-resultant change ($\Delta\beta_E$ and $\Delta\beta_C$, respectively) into its different components. These components relate to changes in the occupancy patterns of locally common (colonization-resultant homogenization ($\Delta\beta_{C-}$) and extirpation-resultant heterogenization ($\Delta\beta_{E+}$)) and locally rare species (colonization-resultant heterogenization ($\Delta\beta_{C+}$) and extirpation-resultant homogenization ($\Delta\beta_{E-}$)) (Tatsumi et al., 2021). We illustrate these different facets and how they relate to changes in spatial β -diversity in Figure 1. Using these metrics, we test whether the contribution level to the different facets of extirpation and colonization-resultant change statistically differ across bird guilds (habitat specialization, trophic niche, and migration type).

Based on the above, we test four primary hypotheses. First, we expect regional assemblages to have mainly homogenized (i.e. reductions in spatial β -diversity) between the periods based on earlier studies within the same system and period (Sullivan et al., 2016; White, Montgomery, Storchová, et al., 2018). Second, we expect $\Delta\beta_{E+}$ and $\Delta\beta_{C-}$ to be the main contributors to changes in spatial beta-diversity across Britain (as they relate to locally common species occupancy changes). Third, we hypothesize that habitat generalists will be the primary driver of $\Delta\beta_{C-}$ and $\Delta\beta_{E+}$, and habitat specialists, which tend to be locally rare depending on the local land use and cover, will be the primary driver of $\Delta\beta_{E-}$ and $\Delta\beta_{C+}$. Finally, we hypothesize that species with initially larger range sizes (within Britain) in the earlier period should mainly contribute to $\Delta\beta_{E+}$ and $\Delta\beta_{C-}$, as the more extensive initial range means they are likely to be more common locally (Howard et al., 2023; Xu et al., 2023). This, therefore, increases the probability that decreases in local occupancy (extirpations) will lead to extirpation-resultant heterogenization ($\Delta\beta_{E+}$) and

that increases in occupancy (colonizations) will cause colonization-resultant homogenization ($\Delta\beta_{C-}$) as they colonize remaining areas (White, Montgomery, & Lennon, 2018). The opposite should be true for species with smaller initial ranges (i.e. they are more likely to be locally rare).

2 | MATERIALS AND METHODS

2.1 | Species' occurrence data

Breeding presence/absence data for British birds were collected by the British Trust of Ornithology (BTO) and the Scottish Ornithologists Club (SOC) during two 4-year periods: the 1988–1991 (BA1990) and 2008–2011 (BA2010) atlases. In both periods, surveyors visited a minimum of eight tetrads (2×2km squares) within each hectad (10×10km squares) across the British Isles. Surveys were similarly timed for both atlases, with at least 16h spent surveying per hectad (see Gillings et al., 2019 for further details). We excluded pelagic, vagrant, and non-native species, as well as species of conservation concern whose ranges in the atlases were presented at coarse spatial grains, leaving 159 species (see Appendix S1 for the species list). Following the recommendation by Gillings et al. (2019), we used data for birds classified as 'breeding' in BA1990 and 'probable' or 'confirmed' breeders in BA2010 (as each atlas used its own classifications). We then removed hectads with less than 50% landmass and those disconnected from the mainland. Finally, we excluded hectads with fewer than two immediate neighbours, leaving a sample size of 2291 hectads.

2.2 | Trait data

We derived nine continuous avian trait measurements from the AVONET database (Tobias et al., 2022) to assess functional changes. These traits—secondary length, tarsus length, wing chord length, tail length, two beak length estimates (culmen from tip to skull and tip to nares), beak width, beak depth, and body mass—reflect species' locomotion, foraging behaviour, dietary niche, and ecological function (Pigot et al., 2020; Tobias & Pigot, 2019; Trisos et al., 2014). See Tobias et al. (2022) and Pigot et al. (2020) for trait measurement and collation details and discussion on how the traits relate to avian ecological functions.

To calculate functional diversity, we first log₁₀-transformed and standardized all traits. A principal components analysis was performed using the 159 species and the transformed traits. We retained all axes (see Pigot et al., 2020) and employed an agglomerative hierarchical clustering method (unweighted pair group method with arithmetic mean) to create a functional dendrogram for all species, generating a rooted tree (Petchev & Gaston, 2007). We tested if the functional distances between species in the dendrogram were accurate using the *tree.quality* function from the 'BAT' R package (Cardoso et al., 2024). The quality was 0.86, showing that the tree

provided a good representation of the true distances between species within the functional space (Matthews et al., 2023).

We also extracted data from AVONET on migration type (sedentary, partial migrant, or migratory) and trophic niche (aquatic predator, granivore, aquatic herbivore, terrestrial herbivore, invertivore, omnivore, or vertivore) for each species to test for differences in the amount of extirpation and colonization-resultant change that could be attributed to different species guilds (see Section 2.7). Using Sullivan et al. (2016), we extracted a species habitat specialization index and quartile. The index was calculated based on population density across the habitats within which the species was present. Therefore, a low score indicates a generalist species, with little difference in the density of that species across the habitat types it was found in. Quartiles were also obtained (Q1 to Q4, indicating generalist, moderately generalist, moderately specialist and specialist species) for all species in the dataset. The quartiles were obtained to compare groups of equal size when assessing the colonization and extirpation differences between them.

2.3 | Phylogenetic data

We used the Ericson backbone phylogenetic trees from Jetz et al. (2012) to compute phylogenetic diversity measures. Where necessary, we updated species names to match the Jetz et al. (2012) taxonomy (see Appendix S1 for the entire species list). We selected 3000 full trees from the posterior distribution of Jetz et al. (2012). Using these trees, we created a maximum clade credibility tree with TreeAnnotator (v1.10.4, Drummond & Rambaut, 2007), setting node heights to median heights without burn-in. We dealt with negative branch lengths using the *tree.zero* function in the 'BAT' package

(Cardoso et al., 2024). We pruned the consensus tree to retain only species in the British breeding bird dataset.

2.4 | Climate and land cover data

We obtained the UK Met Office's monthly precipitation and average temperature data for 1981–2011 (Hollis et al., 2019). We calculated the average temperature (°C) and total precipitation for each year from April to July (the breeding season) for each region using the moving-window approach (focal hectad and its immediate neighbours). To account for potential lag effects of climate, we then averaged yearly values across 1981–1991 and 2001–2011 for each region and atlas period. The change in temperature (Δ Temperature) was calculated as the later average minus the earlier average for each region. We repeated the process with the standard deviation in temperature across each period (using the yearly means) for change in temperature variability (Δ Temperature_{SD}), precipitation (Δ Precipitation) and its variability (Δ Precipitation_{SD}).

We obtained land cover change data from the Land Cover Change 1990–2015 dataset (Rowland et al., 2020) and used a moving window approach (Figure 2) to calculate the land cover change between 1990 and 2015 for each hectad and its surrounding neighbours (i.e. region). We calculated the percentage of land cover change for Urban, Woodland, Freshwater, Grassland, and Other (including inland rock, saltwater, supra-littoral rock and littoral rock) land classes, using each as an individual predictor. We also calculated Shannon's evenness of land cover for each region in each period and computed the change as the latter value minus the earlier value.

Additionally, we calculated the elevation of each region using data from the shuttle radar topography mission by extracting data



FIGURE 2 (a) Map of the study area (Britain) with all of the 10km × 10km grids (hectads) used displayed ($N=2291$). The plot on the right (b) shows the moving window calculation, with the smaller filled squares highlighting the focal hectads and the larger coloured squares showing the windows for spatial beta-diversity calculation. For each focal hectad, multiple site β -diversity and other variables were calculated using the focal hectad and the surrounding eight neighbours (i.e. the eight unfilled smaller squares surrounding the focal hectad).

from 1600 equally separated points within each region and taking the average.

2.5 | Change in multiple site β -diversity

For each hectad, we assessed assemblage changes between the two periods to determine the extent of homogenization or heterogenization in breeding bird communities across Britain. We employed multiple site β -diversity measures that calculate dissimilarity across a region (Baselga et al., 2015; Baselga & Orme, 2012). These measures are optimal for detecting homogenization and heterogenization as they account for multi-site co-occurrence patterns, consider spatial heterogeneity among multiple sampled sites, and avoid the statistical dependence arising from averaging pairwise dissimilarities (Baselga et al., 2015; Baselga & Orme, 2012). We applied two approaches to calculate multiple site β -diversity: Whittaker's β -diversity (Jost, 2007; Whittaker, 1960) and the BAS framework (Baselga, 2010).

We employed Whittaker's multiple site beta (β) diversity metric (γ /average α ; Matthews et al., 2019) (also known as taxonomic β -diversity, hereafter referred to as βW) and a recent method by Tatsumi et al. (2021) to calculate the proportions of homogenization and heterogenization due to colonization and extirpation changes. We computed βW for each hectad in each period using a moving-window approach (βW calculated for each hectad and its immediate neighbours [i.e. region], following White, Montgomery, Storchová, et al., 2018; Figure 2). We calculated the change in βW between periods as the difference between βW in BA2010 and βW in BA1990, referred to as $\Delta\beta_{\text{TOTAL}}$, following Tatsumi et al. (2021).

We partitioned the change in βW for each region into total extirpation and colonization-related changes ($\Delta\beta_{\text{E}}$ and $\Delta\beta_{\text{C}}$, respectively) and the proportion attributable to homogenization and heterogenization for both (see Figure 1). $\Delta\beta_{\text{E-}}$ = extirpation-resultant homogenization, the proportion of homogenization resulting from extirpation, $\Delta\beta_{\text{E+}}$ = extirpation-resultant heterogenization, the proportion of heterogenization resulting from extirpation, $\Delta\beta_{\text{C-}}$ = colonization-resultant homogenization, the proportion of homogenization resulting from colonization, and $\Delta\beta_{\text{C+}}$ = colonization-resultant heterogenization, the proportion of heterogenization resulting from colonization. As $\Delta\beta_{\text{E}}$ and $\Delta\beta_{\text{C}}$ are the sum of the homogenization and heterogenization-resultant components ($\Delta\beta_{\text{E-}}$ and $\Delta\beta_{\text{E+}}$, and $\Delta\beta_{\text{C-}}$ and $\Delta\beta_{\text{C+}}$, respectively), negative values for each highlight overall homogenization. In contrast, positive values show the opposite (i.e. heterogenization).

This partitioning framework allows investigation of the underlying causes of homogenization or heterogenization, determining whether the observed $\Delta\beta_{\text{TOTAL}}$ change results from species extirpation or colonization in the region (Figure 1). We also calculated the species-specific contributions to colonization and extirpation processes ($\Delta\beta_{\text{CSP}}$ and $\Delta\beta_{\text{ESP}}$, respectively), revealing how much each species contributed to extirpation and colonization-resultant change in each region. As $\Delta\beta_{\text{CSP}}$ and $\Delta\beta_{\text{ESP}}$ can be either negative or positive,

each measure also shows whether a species mainly contributes to homogenization or heterogenization-resultant change through colonization or extirpation. Summing the two measures then yields the total species contribution ($\Delta\beta_{\text{SP}}$), with a positive value indicating changes in the species' occupancy overall contributed to heterogenization in the region and a negative value indicating the opposite (i.e. homogenization). Due to how the measures are calculated, they either reflect locally common ($\Delta\beta_{\text{E+}}$ and $\Delta\beta_{\text{C-}}$) or locally rare ($\Delta\beta_{\text{E-}}$ and $\Delta\beta_{\text{C+}}$) species dynamics. See Tatsumi et al. (2021) for more details on the partitioning framework. We employed Wilcoxon one-sample tests to determine if each metric (i.e. $\Delta\beta_{\text{TOTAL}}$, $\Delta\beta_{\text{C-}}$, $\Delta\beta_{\text{C+}}$, $\Delta\beta_{\text{E-}}$, and $\Delta\beta_{\text{E+}}$) significantly differed from zero.

For comparison with $\Delta\beta_{\text{TOTAL}}$, we also calculated regional change in spatial β -diversity using the BAS framework (Baselga, 2010). The framework computes multiple site β -diversity of a region using Sorensen's dissimilarity, decomposing it into turnover (replacement between assemblages) and nestedness-resultant dissimilarity (dissimilarity due to assemblages being nested subsets of one another). We calculated this measure to test the congruence between $\Delta\beta_{\text{TOTAL}}$ and the Sorensen equivalent.

Using the *beta.multi* function from the 'betapart' R package (Baselga & Orme, 2012), we calculated multiple site β -diversity and turnover for each hectad and its immediate neighbours in each period. We then subtracted the BA2010 values for total β -diversity and turnover from the BA1990 values for each hectad, yielding change measures between the two periods ($\text{MBD}_{\text{TOTAL}}$ and MBD_{TURN} for multiple site total β -diversity change and multiple site turnover change, respectively).

We repeated the process for phylogenetic diversity using the *phylo.beta.multi* function from the 'betapart' package and the phylogenetic tree described in section 2.3, calculating phylogenetic multiple site β -diversity and turnover ($\text{MPD}_{\text{TOTAL}}$ and MPD_{TURN} , respectively). We repeated the phylogenetic β -diversity process using the functional dendrogram to produce multiple site functional measures for total β -diversity and turnover ($\text{MFD}_{\text{TOTAL}}$ and MFD_{TURN} , respectively).

2.6 | Modelling change

To model change in each of the calculated metrics, we used intrinsic conditional autoregressive modelling. We retained all explanatory variables, including the average alpha diversity in the first sampling period across all hectads within a region (AlphaT1), within each model for each metric. This approach accounts for autocorrelation within the error term and has previously been used successfully on BTO atlas data in combination with the same moving window approach (White, Montgomery, Storchová, et al., 2018). This was performed under Bayesian inference using the Integrated Nested Laplace Approximation (INLA) with a normally distributed and uninformative prior for all covariates (precision of 0.001). Spatial errors were given log-gamma priors (precision of 0.005). All previously calculated explanatory variables were included in the model

for each of the calculated metrics. All explanatory variables were centred and scaled to aid convergence and enable interpretation. We also included the latitude and longitude of the region centroid (i.e. the focal hectad centroid) in each model to relax the assumption of the model that spatial errors are stationary (Beale et al., 2014) and improve the accuracy of the credible interval estimation (Beale et al., 2010, 2014). All models were fitted using the package R-INLA (Rue et al., 2009).

2.7 | Group differences

To assess if species habitat specialization impacts total contribution to $\Delta\beta_C$ or $\Delta\beta_E$, we compared average colonization and average extirpation across the specialization quartiles using a Kruskal–Wallis test, and a Dunn test was then used to check which groups were statistically different from one another. We also regressed, using standard OLS models, average $\Delta\beta_C$ and $\Delta\beta_E$ against the species specialization index values. We repeated the Kruskal–Wallis and Dunn tests for both migration type and trophic niche.

All analysis was undertaken in R (v4.2.1; R Core Team, 2022). The data and scripts needed to run the analyses are openly available (<https://doi.org/10.6084/m9.figshare.24131949>).

3 | RESULTS

3.1 | Regional homogenization and heterogenization

Spatial patterns and averages of Whittaker's multiple site β -diversity metric (mean $\Delta\beta_{TOTAL} = -0.12 \pm 0.18$), multiple site β -diversity (MBD_{TOTAL} = -0.06 ± 0.08), multiple site functional diversity (MFD_{TOTAL} = -0.06 ± 0.07), and multiple site phylogenetic diversity (MPD_{TOTAL} = -0.06 ± 0.08) were generally consistent, revealing regional homogenization across much of Britain and heterogenization in specific regions such as the Scottish Highlands, Lake District, North-central England, South Wales, and South-east England (Figure 3g; Figure S2.1). Turnover decreased on average for MBD_{TURN} (-0.017 ± 0.074), MPD_{TURN} (-0.019 ± 0.073), and MFD_{TURN} (-0.016 ± 0.071), and the patterns were congruent with total change (MBD_{TOTAL}, MPD_{TOTAL} and MFD_{TOTAL}; Figures S2.2–S2.4). However, not all regions were consistent in terms of the direction of change (homogenization or heterogenization) across the metrics of dissimilarity. For example, of 554 regions with positive change between the periods for MBD_{TOTAL}, 76 and 49 of those same regions were negative for MPD_{TOTAL} and MFD_{TOTAL}, respectively, highlighting that functional and phylogenetic change did not always follow taxonomic change.

On average, a given region (i.e. a focal hectad and its immediate neighbours) experienced 12.3 ± 4.6 regional colonizations (i.e. species new to the region as a whole) and 150 ± 52 hectad-level colonizations in total (i.e. species new to individual hectads). In

comparison, average extirpations across a region were 6.3 ± 3.3 with an average of 78 ± 30 hectad-level extirpations. Together, both results show high temporal–spatial turnover. Colonization-resultant change ($\Delta\beta_C$) and extirpation-resultant change ($\Delta\beta_E$) spatial patterns corresponded well with $\Delta\beta_{TOTAL}$ patterns, with positive $\Delta\beta_E$ change aligning with positive $\Delta\beta_{TOTAL}$ and negative $\Delta\beta_C$ change aligning with negative $\Delta\beta_{TOTAL}$ (Figure 3c,d,g). As positive values for all the metrics indicate heterogenization and negative values show homogenization, this highlights that areas that primarily underwent homogenization (negative $\Delta\beta_{TOTAL}$) were driven mainly by colonization, while areas that heterogenised were driven by extirpation. The average values of $\Delta\beta_{E-}$ and $\Delta\beta_{E+}$ were -0.11 ± 0.05 and 0.15 ± 0.09 , respectively (Figure 3a,b), indicating the presence of both extirpation-resultant heterogenization and extirpation-resultant homogenization, respectively. However, extirpations mainly caused heterogenization, with an average $\Delta\beta_E$ of 0.05 ± 0.08 . There were 677 regions with negative $\Delta\beta_E$ and 1614 with positive $\Delta\beta_E$ (Figure 3c). Average $\Delta\beta_{C-}$ and $\Delta\beta_{C+}$ values were -0.31 ± 0.17 and 0.14 ± 0.05 , respectively (Figure 3d,e), indicating the presence of both colonization-resultant homogenization and colonization-resultant heterogenization, respectively. However, colonizations predominantly led to homogenization, with an average $\Delta\beta_C$ of -0.16 ± 0.17 across Britain. $\Delta\beta_C$ was negative in 1981 regions and positive in 308 (Figure 3f). Using a Wilcoxon one-sample test, metrics $\Delta\beta_E$, $\Delta\beta_{E+}$, and $\Delta\beta_{C+}$ were found to be significantly higher than zero ($p < 0.001$), while $\Delta\beta_{TOTAL}$, $\Delta\beta_{E-}$, $\Delta\beta_C$, and $\Delta\beta_{C-}$ were significantly lower ($p < 0.001$).

3.2 | Drivers of regional change

In this section and those following, we only describe the effects of predictors with credible intervals that do not span zero. In our INLA models, total β -diversity change measures ($\Delta\beta_{TOTAL}$, MBD_{TOTAL}, MPD_{TOTAL}, MFD_{TOTAL}) exhibited congruent patterns in regard to the effects of predictor variables (Figure S2.3). Positive effects included Elevation, Δ Precipitation_{SD}, Latitude, Woodland (the change in the proportion of a region covered by woodland), and Other (change in other land cover classes), while negative effects were observed for Shannon Evenness (habitat heterogeneity), Δ Temperature, and Grassland. Urban and Longitude were also negative for $\Delta\beta_{TOTAL}$, and Δ Temperature_{SD} was negative for MBD_{TOTAL} and MFD_{TOTAL}. The variable with the largest effect size was Longitude for $\Delta\beta_{TOTAL}$ [median = 0.039, CI = (0.020, 0.058)], MBD_{TOTAL} [median = 0.023, CI = (0.015, 0.032)], and MFD_{TOTAL} [median = 0.023, CI = (0.015, 0.031)], and Temperature for MPD_{TOTAL} [median = -0.026 , CI = (-0.035 , -0.017)] (Figure S2.2).

For turnover measures (MBD_{TURN}, MPD_{TURN}, MFD_{TURN}), Δ Precipitation, Latitude, and Other had positive effects (Figure S2.2). Grassland and Δ Temperature_{SD} both had negative effects for all the measures (Figure S2.2). Elevation had a positive effect on both MBD_{TURN} and MPD_{TURN}, and Urban and Freshwater were also positive for MBD_{TURN} (Figure S2.2). Latitude had the largest absolute effect size for all of the turnover measures (Figure S2.2).

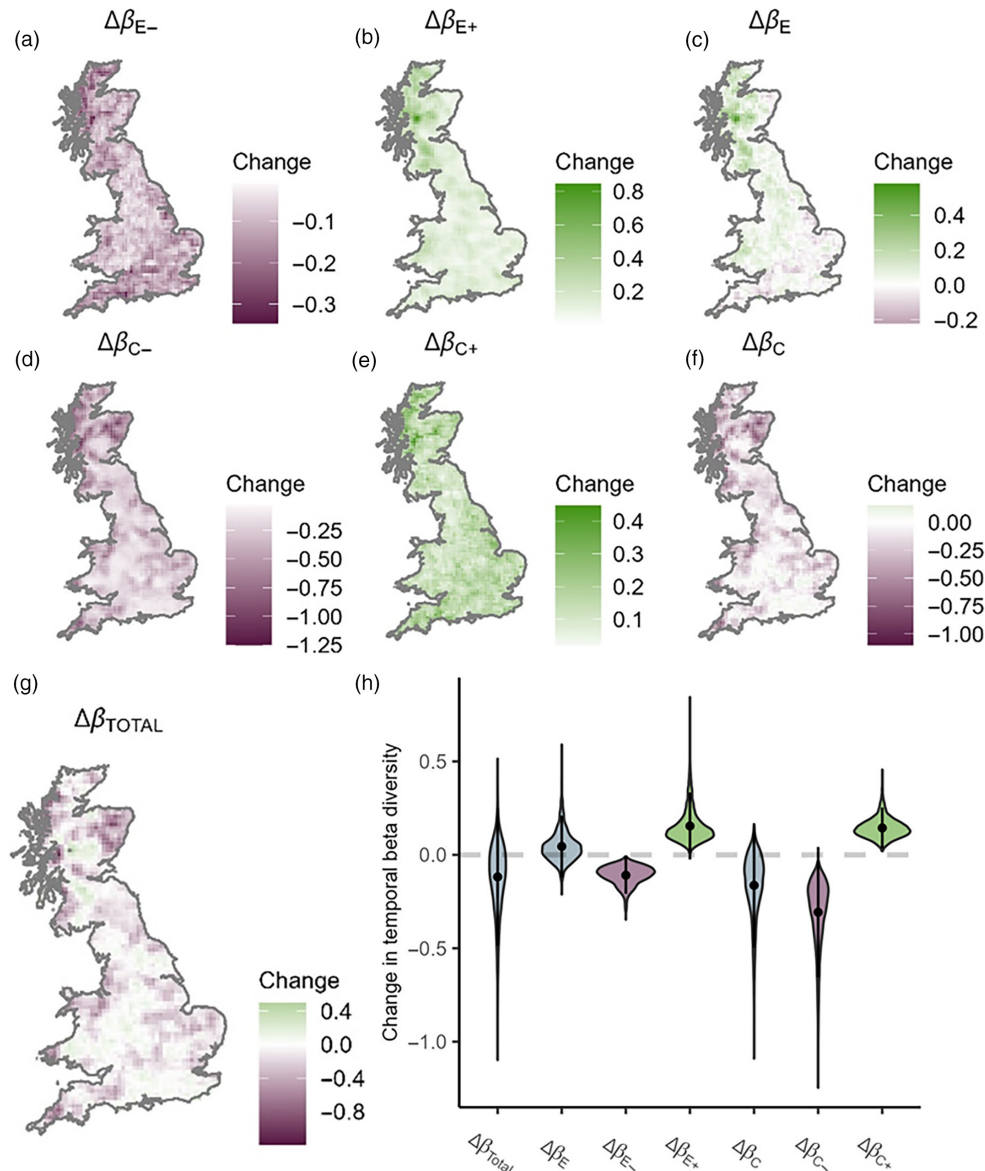


FIGURE 3 Maps of change between two sampling periods (BA1990 and BA2010) for breeding bird communities across Britain for measures of (a) extirpation-resultant homogenization ($\Delta\beta_{E-}$) (b) heterogenization ($\Delta\beta_{E+}$) (c) total extirpation-resultant change ($\Delta\beta_E$), (d) colonization-resultant homogenization ($\Delta\beta_{C-}$), (e) colonization-resultant heterogenization ($\Delta\beta_{C+}$), (f) total colonization-resultant change ($\Delta\beta_C$), and (g) change in Whittaker's β -diversity. For all metrics, negative values indicate homogenization and positive values indicate heterogenization. All values were calculated using moving windows (30 km \times 30 km) around focal hectads ($N=2291$). The violin plot (h) shows the median (dot) of each measure across all British hectads, alongside the 1.5 interquartile range (whiskers).

For $\Delta\beta_C$, negative effects were observed for $\Delta\text{Temperature}_{SD}$, Woodland, Grassland and Freshwater, while positive effects were found for Shannon Evenness, $\Delta\text{Precipitation}_{SD}$, $\Delta\text{Temperature}$, and Latitude (Figure 4a). Woodland, Grassland, Urban, and $\Delta\text{Temperature}_{SD}$ were negative for $\Delta\beta_{C+}$. Shannon Evenness, Elevation, $\Delta\text{Precipitation}_{SD}$, $\Delta\text{Precipitation}$, $\Delta\text{Temperature}$, Longitude, and Latitude were all positive for $\Delta\beta_{C+}$ (Figure 4a). Shannon Evenness, $\Delta\text{Precipitation}_{SD}$, $\Delta\text{Temperature}$, and Latitude were positive for $\Delta\beta_{C-}$ (Figure 4a). $\Delta\text{Temperature}_{SD}$, $\Delta\text{Precipitation}$, Longitude, Woodland, Grassland and Freshwater all had a negative effect (Figure 4a). The largest absolute effect sizes were

$\Delta\text{Temperature}_{SD}$ for $\Delta\beta_C$ and Longitude for both $\Delta\beta_{C-}$ and $\Delta\beta_{C+}$ (Figure 4a).

For $\Delta\beta_E$, Elevation, $\Delta\text{Precipitation}$, $\Delta\text{Temperature}$, Latitude, Woodland and Freshwater were all positive (Figure 4b). Negative effects were found for $\Delta\text{Temperature}_{SD}$ and Longitude (Figure 4b). For $\Delta\beta_{E+}$, Elevation, $\Delta\text{Precipitation}$, $\Delta\text{Temperature}$, Latitude, and Other were all positive (Figure 4b). $\Delta\text{Temperature}_{SD}$, Longitude, Grassland and Urban were all negative (Figure 4b). Woodland, Grassland, Urban, and $\Delta\text{Temperature}_{SD}$ all had a positive effect for $\Delta\beta_{E-}$ (Figure 4b). Shannon Evenness, $\Delta\text{Precipitation}$, $\Delta\text{Temperature}$, and Latitude were all found to be negative (Figure 4b). Latitude had

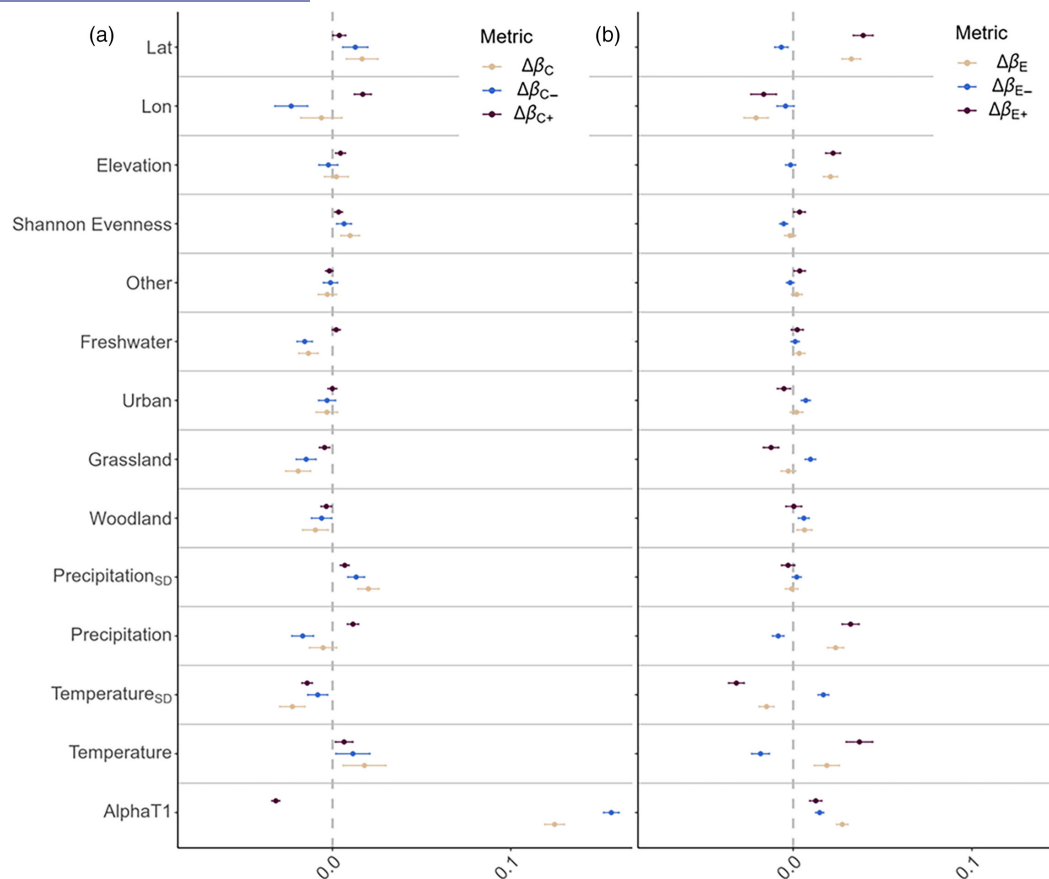


FIGURE 4 Effect sizes and confidence intervals from the Integrated Nested Laplace Approximation models for (a) total colonization-resultant change ($\Delta\beta_C$) and its two components (colonization-resultant homogenization [$\Delta\beta_{C-}$] and heterogenization [$\Delta\beta_{C+}$]); and (b) total extirpation-resultant change ($\Delta\beta_E$) and its two components (extirpation-resultant homogenization [$\Delta\beta_{E-}$] and heterogenization [$\Delta\beta_{E+}$]). All models were run using data calculated from moving windows (30 km \times 30 km) around focal hectads ($N = 2291$).

the largest effect size for $\Delta\beta_E$ and $\Delta\beta_{E+}$, while $\Delta\text{Temperature}$ was the largest for $\Delta\beta_{E-}$.

3.3 | Guild differences

Habitat specialists were found to have a significantly higher average species-specific contribution to colonization ($\Delta\beta_{CSP}$) (0.0002 ± 0.0013) than generalists (-0.002 ± 0.0015 , $p < 0.001$) and moderately specialist species (-0.001 ± 0.0015 , $p < 0.01$; **Figure 5a,d**), according to a Dunn test. Generalists also had significantly lower $\Delta\beta_C$ than moderately generalist species (-0.0009 ± 0.0017 , $p < 0.01$; **Figure 5a,d**). Specialists (Q4) had a significantly lower average species-specific contribution to extirpation ($\Delta\beta_{ESP}$) (-0.0002 ± 0.0005) than generalists (Q1, 0.0006 ± 0.0008 , $p < 0.001$), moderately generalist species (Q2; 0.0003 ± 0.0009 , $p < 0.01$) and moderately specialist species (Q3; 0.0002 ± 0.0009 , $p < 0.01$; **Figure 5b,e**). While these patterns of positive $\Delta\beta_{CSP}$ and negative $\Delta\beta_{ESP}$ for specialists and negative $\Delta\beta_{CSP}$ and positive $\Delta\beta_{ESP}$ for generalists were found to be the general pattern at the regional assemblage level, some species within each quartile exhibited contrasting colonization and extirpation-resultant change (**Figure 6a**). Species with an initially larger range size (number

of hectads in BA1990) were found to generally have larger average $\Delta\beta_{ESP}$ and lower average $\Delta\beta_{CSP}$ (**Figure 6b,c**).

For migration type, both migratory (-0.001 ± 0.001) and partially migratory species (-0.001 ± 0.002) had significantly higher average $\Delta\beta_{CSP}$ than sedentary species (-0.002 ± 0.002 , $p < 0.001$ and $p < 0.01$ for migratory and partially migratory species, respectively; **Figure 5c**). No significant differences were found for average $\Delta\beta_{ESP}$ (**Figure 5f**). Regarding trophic niche, the only significant difference was aquatic predators having a higher average $\Delta\beta_{CSP}$ compared to omnivores ($p < 0.05$).

4 | DISCUSSION

Across Britain, regional assemblage changes between the first atlas in 1988–1991 and the second in 2008–2011 were driven mainly by the colonization and extirpation of common habitat generalists (see also Sullivan et al., 2016). Therefore, and in contrast to the view that changes in the distributions of specialist species are contracting and driving homogenization, assemblage-level patterns of regional avian homogenization/heterogenization in the UK are primarily driven by the changing fortunes of generalists

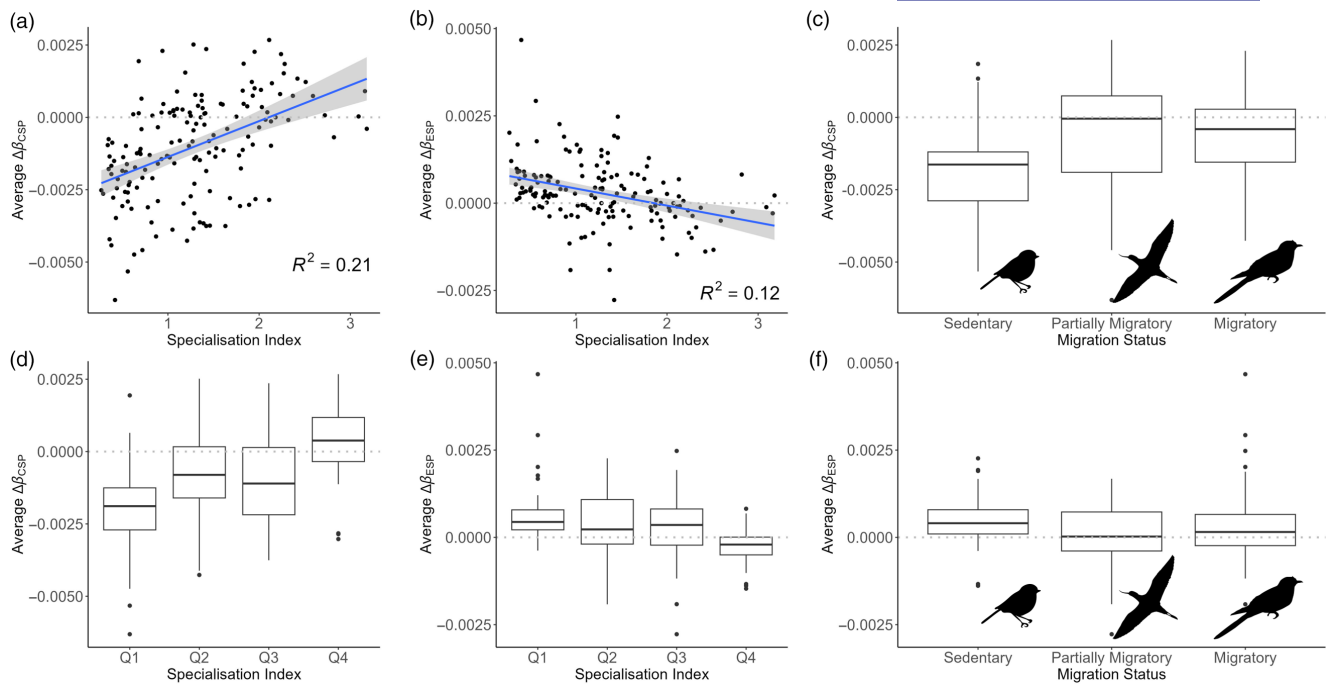


FIGURE 5 Observed changes in average species-specific colonization ($\Delta\beta_{CSP}$) and extirpation ($\Delta\beta_{ESP}$) in relation to the habitat specialization index (where increased values indicate increased specialization; a, b), quartiles of habitat specialization (where Q1 is generalist and Q4 is specialist; d, e), and migratory status (c, f) ($N = 2291$). For (a, b), the fitted line is from a linear ordinary least squares model, with grey shading showing the 95% confidence interval ($N = 2291$).

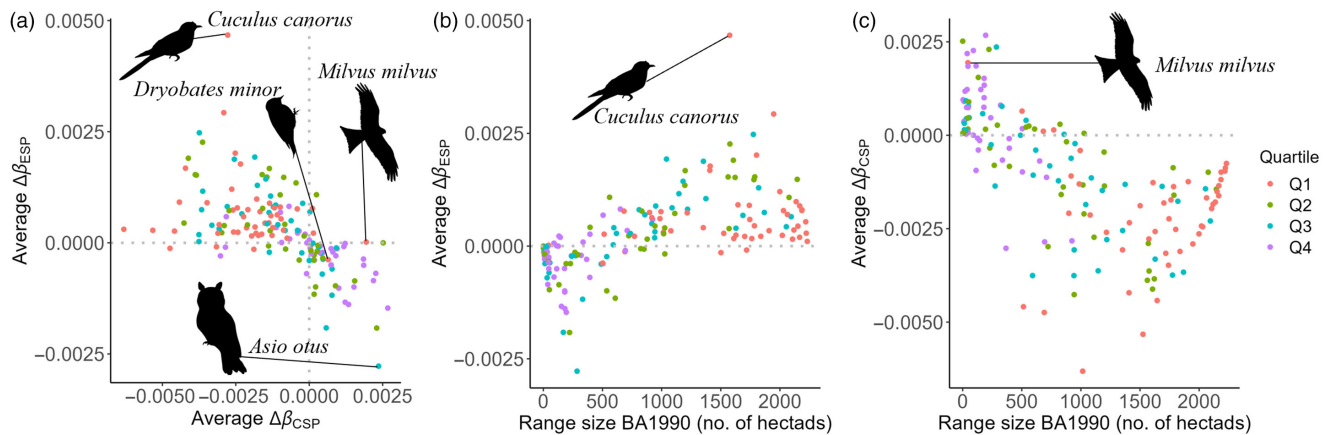


FIGURE 6 Relationship between the measures of average species-specific colonization ($\Delta\beta_{CSP}$) and extirpation ($\Delta\beta_{ESP}$) with habitat specialism (a), and habitat specialism alongside range size (b, c) ($N = 2291$). The quartiles range from the most generalist (Q1) to the most specialist (Q4).

across the period. While this does not mean that specialist populations are increasing or even remaining stable, it does mean that expansions and contractions of local generalist populations are causing local colonizations and extirpations, leading to decreases and increases in local dissimilarity, respectively. This highlights the importance of locally common and generalist species in driving regional patterns of diversity (Lennon et al., 2004). We also found sedentary species had significantly lower average species-specific contribution to colonization ($\Delta\beta_{CSP}$) (-0.002 ± 0.001) than migrants and partial migrants (0.001 ± 0.001 and 0.001 ± 0.002 , respectively), showing that between the periods sedentary

species were the main proponents of regional colonization homogenization, that is range increases leading to a negative $\Delta\beta_{CSP}$ (Pearce-Higgins et al., 2015). However, overall, individual species contributions to the assemblage-level metrics $\Delta\beta_E$ and $\Delta\beta_C$ were complex, highlighting the need to account for species identities when conducting research looking at temporal assemblage change (Rooney et al., 2007).

While the overall change in the fortunes of generalist species led to an overall decrease in β -diversity across all calculated metrics, supporting our original hypothesis, and indicating an apparent biotic homogenization, this homogenization was primarily driven by

Species	Number of occurrences (max N = 2291)			Species-level impact on β -diversity		
	BA1990	BA2010	Net change	$\Delta\beta_{ESP}$	$\Delta\beta_{CSP}$	Total ($\Delta\beta_{SP}$)
Negative $\Delta\beta_{CSP}$ shows a species-level contribution to colonization homogenization (i.e. a species colonizing new areas within a region where it is already common (>50% occupancy), or a locally rare species increasing occupancy above 50%)						
Top three negative $\Delta\beta_{CSP}$						
<i>Buteo buteo</i>	1015	2160	1145	0.69	-14.46	-13.77
<i>Dendrocopos major</i>	1525	2048	523	0.64	-12.20	-11.56
<i>Tyto alba</i>	690	1563	873	-0.28	-10.86	-11.14
Positive $\Delta\beta_{CSP}$ shows a species-level contribution to colonization heterogenization (i.e. locally rare, or absent species that are colonizing new areas in the region)						
Top three positive $\Delta\beta_{CSP}$						
<i>Rallus aquaticus</i>	194	376	182	-3.36	6.12	2.76
<i>Egretta garzetta</i>	0	163	163	0	5.76	5.76
<i>Asio otus</i>	285	319	34	-6.35	5.40	-0.95
Negative $\Delta\beta_{ESP}$ shows a species-level contribution to extirpation homogenization (i.e. locally rare species being extirpated from areas, or a locally common species decreasing to below 50% occupancy)						
Top three negative $\Delta\beta_{ESP}$						
<i>Asio otus</i>	285	319	34	-6.35	5.40	-0.95
<i>Coturnix coturnix</i>	222	297	75	-4.39	5.26	0.87
<i>Coccothraustes coccothraustes</i>	169	61	-108	-4.38	1.32	-3.06
Positive $\Delta\beta_{ESP}$ shows a species-level contribution to extirpation heterogenization (i.e. locally common species being extirpated from areas within a region)						
Top three positive $\Delta\beta_{ESP}$						
<i>Cuculus canorus</i>	1575	1281	-294	10.70	-6.35	4.35
<i>Muscicapa striata</i>	1947	1873	-74	6.70	-6.66	0.04
<i>Regulus regulus</i>	1775	1932	157	5.67	-8.57	-2.90

generalist species colonizations across a given region. The main proponents of such colonization change, that is the 'winners', were predominantly species that have benefited from increased conservation action due to past persecution. For example, goshawk (*Accipiter gentilis*), buzzard (*Buteo buteo*) (Table 1), hobby (*Falco subbuteo*), red kite (*Milvus milvus*), and peregrine (*Falco peregrinus*) all increased their ranges and contributed to increased regional homogenization because of actions taken to increase their populations between the surveyed time periods (Stanbury et al., 2021). As others have also shown (e.g. Wilson et al., 2018), these results encouragingly demonstrate that effective conservation interventions can yield dramatic effects on the recovery of British bird species. However, while these changes decreased dissimilarity within regions, contributing to apparent homogenization, they did not lead to a decrease in α diversity or an impoverishment of an area.

Regions that experienced increases in dissimilarity (heterogenization) and, therefore, turnover and β -diversity, were mainly driven by the loss of locally common species from several areas within a region. Although these species were mainly generalists (Figure 5e), they included cuckoo (*Cuculus canorus*), whose

extirpation across much of its previous range in Britain, combined with an increase in areas where it was locally common, led to patterns of heterogenization and homogenization that do not reflect the general dramatic decrease of the cuckoo's British range. Also included were tree sparrow (*Passer montanus*), turtle dove (*Streptopelia turtur*), and lesser spotted woodpecker (*Dendrocopos minor*), all classified as habitat generalists by Sullivan et al. (2016), all of which were once common across the whole or sections of Britain in the 1990 atlas, meaning the loss of these species from some, but not all, hectads in an area increased dissimilarity within the region. Our results provide further evidence that these species, all of which are red-listed in the UK (Stanbury et al., 2021), represent essential national conservation priorities. More generally, these patterns show that species once considered common can quickly experience range declines and potentially become threatened in part or all of their range (i.e. generalist species are not always the 'winners'; Sweeney & Jarzyna, 2022—an important lesson for conservationists). In contrast, recent colonizers to areas can also contribute to increased heterogenization of a region as long as their overall occupancy stays below 50%. For example,

TABLE 1 The three species with the highest total species-level impact on Whittaker's β -diversity ($\Delta\beta_{SP}$) for both homogenization-resultant change (negative) and heterogenization-resultant change (positive) and what contributions came from colonization ($\Delta\beta_{CSP}$) or extirpation change ($\Delta\beta_{ESP}$). All measures were calculated for each moving window (30 km \times 30 km) for each of the focal hectads (N = 2291) and then summed across all moving windows for each species. Species occurrence refers to recorded presence within individual hectads (10 \times 10 km).

little egrets (*Egretta garzetta*) are one of Britain's most recent colonizers with a large contribution to regional heterogenization between the two atlas periods (Table 1).

While Sullivan et al. (2016), in their analysis of the abundance patterns of UK birds, concluded that homogenization in UK communities was driven by the changing distributional and abundance patterns of generalists, we have found that there is still a signal of locally rare species loss as identified by $\Delta\beta_{E-}$. This is prominent mainly in the south-east of England, as shown by $\Delta\beta_{E-}$ being the dominant component of total $\Delta\beta_E$. This area of extirpation-related homogenization also corresponded with overall homogenization, and this is likely to be of interest to conservationists, given it involves the loss of species that were locally rare and did not colonize new areas within the locale to offset extirpations. This loss was driven partly by those species listed above, but also redpoll (*Carduelis flammea*), hawfinch (*Coccothraustes coccothraustes*), nightingale (*Luscinia megarhynchos*), and corn bunting (*Emberiza calandra*). Overall, focusing only on general assemblage-level patterns and metrics obscures species-level trends that may be of more importance for the conservation and maintenance of diverse assemblages, as well as for detecting which species may need prioritization (Perez Rocha et al., 2023; Xia et al., 2022).

4.1 | Drivers of spatial diversity change

The patterns in $\Delta\beta_E$ were roughly divided along the Tees-exe line, which separates the uplands from the lowlands within Britain (Prakash & Rumsey, 2018; Wayman et al., 2021). This is reinforced by elevation and temperature being significant predictors of both $\Delta\beta_{E+}$ and $\Delta\beta_{C+}$, as well as an increase in all multiple site beta-diversity measures with increasing latitude. As $\Delta\beta_{E+}$ is linked to locally common species loss and $\Delta\beta_{C+}$ to increases in locally uncommon species, this could indicate that species have shifted up-slope in response to increased temperatures as they track their climatic niche, along with a general loss of more upland species (Gillings et al., 2015). All total measures of beta-diversity change also increased with elevation, along with MBD_{TURN} and MPD_{TURN} , further highlighting the increased change along elevational gradients. Alternatively, the observed changes in $\Delta\beta_{E+}$ and $\Delta\beta_{C+}$ in upland areas could be in response to land cover change in lowlands forcing species to seek suitable habitat elsewhere (Jungandreas et al., 2022).

Several variables were highlighted as driving increases and decreases in $\Delta\beta_{E-}$ through time. This measure shows whether locally uncommon species—likely range-restricted and specialists—are going extinct within regions. Increased land cover of woodland and grassland decreased the amount of $\Delta\beta_{E-}$ within an area, meaning fewer locally rare species extirpations. This could be due to increased habitat cover or appropriate maintenance of current habitat cover, which is essential to habitat specialists (Barnes et al., 2023), with evidence of increasing woodland specialists within the UK in response to recent woodland expansion (Burton et al., 2018). Although

$\Delta\beta_{E-}$ increased with increased urban cover, this is likely due to existing urban areas mainly increasing between the periods, that is increases were largely congruent with areas already heavily urbanized (Figure S2.5). Therefore, locally rare species inhabiting areas around urban centres were unlikely to be disturbed by expansions to an already urbanized area (i.e. that species already persisted in a hectad with a certain amount of urban cover, so a slight increase had little impact compared to other areas). In contrast, $\Delta\beta_{E-}$ increased with Shannon evenness (habitat diversity), precipitation and temperature, highlighting that unstable areas (larger changes in these abiotic variables over time) may cause locally rare species extirpations (White, Montgomery, Storchová, et al., 2018). Indeed, all measures of colonization- and extirpation-resultant change increased with land diversity, temperature, and precipitation (apart from $\Delta\beta_{C-}$ for temperature and land diversity), highlighting the effect of abiotic instability on assemblages (White, Montgomery, Storchová, et al., 2018). This may have implications as future land use and climate change create further instability within systems that could contribute to increased diversity change (Newbold, 2018).

4.2 | Study limitations and future research directions

While the data used here are suitable for looking at broad-scale patterns in extirpation and colonization, underlying changes in abundance structure, masked by the use of only presence-absence data, may reveal early shifts and patterns of population change. Such changes may include responses to negative interactions between colonizers and species already present in an area before species are entirely extirpated from an area and contribute to patterns of homogenization and heterogenization (Dornelas et al., 2019; Magurran et al., 2019; Sullivan et al., 2016). We do not include fine-scale land-use changes or account for intensification or fragmentation, which may explain some of the colonization and extirpation dynamics observed. Indeed, the loss of many farmland birds from the south-east of England has largely been attributed to agricultural intensification and fragmentation (Newton, 2004; Rigal et al., 2023). The occupation of migratory species in the UK may also be influenced by factors affecting their wintering grounds and migration routes, which are not considered in this study (Vickery et al., 2014).

5 | CONCLUSIONS

Biotic homogenization is commonly seen as an indicator of impoverishment in terms of the biological diversity of communities. This is indeed the case in cases where homogenization is caused by the combined loss of unique species (either distributionally rare or functionally unique) and the spread of generalist or introduced species. Here, however, we show that such patterns must be interpreted with caution, as homogenization driven primarily by the expansion of species through local colonization leads to increases

in alpha diversity. These species may be habitat or dietary generalists, but their increase, if they are naturally occurring, does not necessarily lead to an impoverishment of local taxonomic or functional alpha diversity. Also, the loss of species locally can lead to increased heterogenization of a region, but this does not mean an increase in local taxonomic, phylogenetic, or functional alpha diversity. Overall, in work looking at biotic homogenization, steps should be made to account for species identities and their contribution to patterns of temporal-spatial β -diversity. This will ensure that any interpretation of homogenization and heterogenization patterns is valid and that any resultant development of conservation measures is grounded in the species dynamics underpinning the observed changes.

AUTHOR CONTRIBUTIONS

Joseph P. Wayman, Jonathan P. Sadler, and Thomas J. Matthews conceived the ideas. Joseph P. Wayman designed the methodology with input from all authors. Joseph P. Wayman prepared and analysed the data. Joseph P. Wayman led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and script required to run the analyses are openly available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.hx3ffbgm6> (Wayman et al., 2024).

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REFERENCES

- Barnes, A. E., Davies, J. G., Martay, B., Boersch-Supan, P. H., Harris, S. J., Noble, D. G., Pearce-Higgins, J. W., & Robinson, R. A. (2023). Rare and declining bird species benefit most from designating protected areas for conservation in the UK. *Nature Ecology & Evolution*, 7(1), 92–101. <https://doi.org/10.1038/s41559-022-01927-4>
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1), 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga, A., Bonthoux, S., & Balent, G. (2015). Temporal beta diversity of bird assemblages in agricultural landscapes: Land cover change vs. stochastic processes. *PLoS One*, 10(5), e0127913. <https://doi.org/10.1371/journal.pone.0127913>
- Baselga, A., & Orme, C. D. L. (2012). betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3(5), 808–812.
- Beale, C. M., Brewer, M. J., & Lennon, J. J. (2014). A new statistical framework for the quantification of covariate associations with species distributions. *Methods in Ecology and Evolution*, 5(5), 421–432. <https://doi.org/10.1111/2041-210X.12174>
- Beale, C. M., Lennon, J. J., Yearsley, J. M., Brewer, M. J., & Elston, D. A. (2010). Regression analysis of spatial data. *Ecology Letters*, 13(2), 246–264. <https://doi.org/10.1111/j.1461-0248.2009.01422.x>
- Bibby, P. (2009). Land use change in Britain. *Land Use Policy*, 26, S2–S13.
- Burton, V., Moseley, D., Brown, C., Metzger, M. J., & Bellamy, P. (2018). Reviewing the evidence base for the effects of woodland expansion on biodiversity and ecosystem services in the United Kingdom. *Forest Ecology and Management*, 430, 366–379. <https://doi.org/10.1016/j.foreco.2018.08.003>
- Callaghan, C. T., Major, R. E., Wilshire, J. H., Martin, J. M., Kingsford, R. T., & Cornwell, W. K. (2019). Generalists are the most urban-tolerant of birds: A phylogenetically controlled analysis of ecological and life history traits using a novel continuous measure of bird responses to urbanization. *Oikos*, 128(6), 845–858.
- Cardoso, P., Mammola, S., Rigal, F., & Carvalho, J. (2024). BAT: Biodiversity assessment tools. R package version 2.9.6. <https://CRAN.R-project.org/package=BAT>
- Carvalho, L. G., Kunin, W. E., Keil, P., Aguirre-Gutiérrez, J., Ellis, W. N., Fox, R., Groom, Q., Hennekens, S., Van Landuyt, W., Maes, D., Van de Meutter, F., Michez, D., Rasmont, P., Ode, B., Potts, S. G., Reemer, M., Roberts, S. P. M., Schaminée, J., WallisDeVries, M. F., & Biesmeijer, J. C. (2013). Species richness declines and biotic homogenization have slowed down for NW-European pollinators and plants. *Ecology Letters*, 16(7), 870–878. <https://doi.org/10.1111/ele.12121>
- Chase, J. M., McGill, B. J., Thompson, P. L., Antão, L. H., Bates, A. E., Blowes, S. A., Dornelas, M., Gonzalez, A., Magurran, A. E., Supp, S. R., Winter, M., Bjorkman, A. D., Brulheide, H., Byrnes, J. E. K., Cabral, J. S., Elahi, R., Gomez, C., Guzman, H. M., Isbell, F., ... O'Connor, M. (2019). Species richness change across spatial scales. *Oikos*, 128(8), 1079–1091. <https://doi.org/10.1111/oik.05968>
- Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: Toward a global functional homogenization? *Frontiers in Ecology and the Environment*, 9(4), 222–228. <https://doi.org/10.1890/080216>
- Davey, C. M., Chamberlain, D. E., Newson, S. E., Noble, D. G., & Johnston, A. (2012). Rise of the generalists: Evidence for climate driven homogenization in avian communities. *Global Ecology and Biogeography*, 21(5), 568–578. <https://doi.org/10.1111/j.1466-8238.2011.00693.x>
- Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A., & Couvet, D. (2008). Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography*, 17(2), 252–261. <https://doi.org/10.1111/j.1466-8238.2007.00364.x>
- Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., & Magurran, A. E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science*, 344(6181), 296–299.
- Dornelas, M., Gotelli, N. J., Shimadzu, H., Moyes, F., Magurran, A. E., & McGill, B. J. (2019). A balance of winners and losers in the Anthropocene. *Ecology Letters*, 22(5), 847–854. <https://doi.org/10.1111/ele.13242>
- Drummond, A. J., & Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, 7(1), 214. <https://doi.org/10.1186/1471-2148-7-214>
- Frishkoff, L. O., Karp, D. S., Flanders, J. R., Zook, J., Hadly, E. A., Daily, G. C., & M'Gonigle, L. K. (2016). Climate change and habitat conversion favour the same species. *Ecology Letters*, 19(9), 1081–1090. <https://doi.org/10.1111/ele.12645>
- Gillings, S., Balmer, D. E., Caffrey, B. J., Downie, I. S., Gibbons, D. W., Lack, P. C., Reid, J. B., Sharrock, J. T. R., Swann, R. L., & Fuller, R. J. (2019). Breeding and wintering bird distributions in Britain and Ireland from citizen science bird atlases. *Global Ecology and Biogeography*, 28(7), 866–874. <https://doi.org/10.1111/geb.12906>

- Gillings, S., Balmer, D. E., & Fuller, R. J. (2015). Directionality of recent bird distribution shifts and climate change in Great Britain. *Global Change Biology*, 21(6), 2155–2168. <https://doi.org/10.1111/gcb.12823>
- Hollis, D., McCarthy, M., Kendon, M., Legg, T., & Simpson, I. (2019). HadUK grid—A new UK dataset of gridded climate observations. *Geoscience Data Journal*, 6, 151–159. <https://doi.org/10.1002/gdj3.78>
- Howard, C., Marjakangas, E.-L., Morán-Ordóñez, A., Milanesi, P., Abuladze, A., Aghababayan, K., Ajder, V., Arkumarev, V., Balmer, D. E., Bauer, H.-G., Beale, C. M., Bino, T., Boyla, K. A., Burfield, I. J., Burke, B., Caffrey, B., Chodkiewicz, T., Del Moral, J. C., Mazal, V. D., ... Willis, S. G. (2023). Local colonisations and extinctions of European birds are poorly explained by changes in climate suitability. *Nature Communications*, 14(1), 4304. <https://doi.org/10.1038/s41467-023-39093-1>
- Hughes, E. C., Edwards, D. P., & Thomas, G. H. (2022). The homogenization of avian morphological and phylogenetic diversity under the global extinction crisis. *Current Biology*, 32(17), 3830–3837. e3. <https://doi.org/10.1016/j.cub.2022.06.018>
- Ibáñez-Álamo, J. D., Rubio, E., Benedetti, Y., & Morelli, F. (2017). Global loss of avian evolutionary uniqueness in urban areas. *Global Change Biology*, 23(8), 2990–2998. <https://doi.org/10.1111/gcb.13567>
- Jarzyna, M. A., & Jetz, W. (2017). A near half-century of temporal change in different facets of avian diversity. *Global Change Biology*, 23(8), 2999–3011. <https://doi.org/10.1111/gcb.13571>
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, 491(7424), 444–448. <https://doi.org/10.1038/nature11631>
- Jost, L. (2007). Partitioning diversity into independent alpha and Beta components. *Ecology*, 88(10), 2427–2439. <https://doi.org/10.1890/06-1736.1>
- Jungandreas, A., Roilo, S., Strauch, M., Václavík, T., Volk, M., & Cord, A. F. (2022). Response of endangered bird species to land-use changes in an agricultural landscape in Germany. *Regional Environmental Change*, 22(1), 19. <https://doi.org/10.1007/s10113-022-01878-3>
- Le Viol, I., Jiguet, F., Brotons, L., Herrando, S., Lindström, Å., Pearce-Higgins, J. W., Reif, J., Van Turnhout, C., & Devictor, V. (2012). More and more generalists: Two decades of changes in the European avifauna. *Biology Letters*, 8(5), 780–782.
- Lennon, J. J., Koleff, P., Greenwood, J. J. D., & Gaston, K. J. (2004). Contribution of rarity and commonness to patterns of species richness. *Ecology Letters*, 7(2), 81–87. <https://doi.org/10.1046/j.1461-0248.2004.00548.x>
- Magurran, A. E., Dornelas, M., Moyes, F., & Henderson, P. A. (2019). Temporal β diversity—A macroecological perspective. *Global Ecology and Biogeography*, 28(12), 1949–1960. <https://doi.org/10.1111/geb.13026>
- Marchetti, M. P., Lockwood, J. L., & Light, T. (2006). Effects of urbanization on California's fish diversity: Differentiation, homogenization and the influence of spatial scale. *Biological Conservation*, 127(3), 310–318. <https://doi.org/10.1016/j.biocon.2005.04.025>
- Matthews, T. J., Aspin, T. W. H., Ulrich, W., Baselga, A., Kubota, Y., Proios, K., Triantis, K. A., Whittaker, R. J., & Strona, G. (2019). Can additive beta diversity be reliably partitioned into nestedness and turnover components? *Global Ecology and Biogeography*, 28(8), 1146–1154. <https://doi.org/10.1111/geb.12921>
- Matthews, T. J., Wayman, J. P., Whittaker, R. J., Cardoso, P., Hume, J. P., Sayol, F., Proios, K., Martin, T. E., Baiser, B., Borges, P. A. V., Kubota, Y., dos Anjos, L., Tobias, J. A., Soares, F. C., Si, X., Ding, P., Mendenhall, C. D., Sin, Y. C. K., Rheindt, F. E., ... Rigal, F. (2023). A global analysis of avian island diversity–area relationships in the Anthropocene. *Ecology Letters*, 26(6), 965–982. <https://doi.org/10.1111/ele.14203>
- Mitchell, S. L., Edwards, D. P., Martin, R. W., Deere, N. J., Voigt, M., Kastanya, A., Karja, A., Akbar, P. G., Jordan, K., Tasirin, J., Zakaria, Z., Martin, T., Supriatna, J., Winarni, N., Davies, Z. G., & Struebig, M. J. (2022). Severity of deforestation mediates biotic homogenization in an island archipelago. *Ecography*, 2022(7), 1–14. <https://doi.org/10.1111/ecog.05990>
- Newbold, T. (2018). Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. *Proceedings of the Royal Society B: Biological Sciences*, 285(1881), 20180792. <https://doi.org/10.1098/rspb.2018.0792>
- Newton, I. (2004). The recent declines of farmland bird populations in Britain: An appraisal of causal factors and conservation actions. *Ibis*, 146(4), 579–600. <https://doi.org/10.1111/j.1474-919X.2004.00375.x>
- Olden, J. D. (2006). Biotic homogenization: A new research agenda for conservation biogeography. *Journal of Biogeography*, 33(12), 2027–2039. <https://doi.org/10.1111/j.1365-2699.2006.01572.x>
- Olden, J. D., & Rooney, T. P. (2006). On defining and quantifying biotic homogenization. *Global Ecology and Biogeography*, 15(2), 113–120. <https://doi.org/10.1111/j.1466-822X.2006.00214.x>
- Pearce-Higgins, J. W., Eglinton, S. M., Martay, B., & Chamberlain, D. E. (2015). Drivers of climate change impacts on bird communities. *Journal of Animal Ecology*, 84(4), 943–954. <https://doi.org/10.1111/1365-2656.12364>
- Perez Rocha, M., Morris, T. J., Cottenie, K., & Schwalb, A. N. (2023). Limitations of beta diversity in conservation site selection. *Ecological Indicators*, 154, 110732. <https://doi.org/10.1016/j.ecoli.2023.110732>
- Petchey, O. L., & Gaston, K. J. (2007). Dendrograms and measuring functional diversity. *Oikos*, 116(8), 1422–1426. <https://doi.org/10.1111/j.0030-1299.2007.15894.x>
- Pigot, A. L., Sheard, C., Miller, E. T., Bregman, T. P., Freeman, B. G., Roll, U., Seddon, N., Trisos, C. H., Weeks, B. C., & Tobias, J. A. (2020). Macroevolutionary convergence connects morphological form to ecological function in birds. *Nature Ecology & Evolution*, 4(2), 230–239. <https://doi.org/10.1038/s41559-019-1070-4>
- Prakash, R. O., & Rumsey, F. (2018). Biodiversity in the United Kingdom. In *Global biodiversity* (pp. 443–468). Apple Academic Press.
- R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Rackham, O. (1986). *The history of the countryside: The classic history of Britain's landscape. Flora, and Fauna*. JM Dent.
- Rigal, S., Dakos, V., Alonso, H., Auniņš, A., Benkó, Z., Brotons, L., Chodkiewicz, T., Chylarecki, P., de Carli, E., del Moral, J. C., Domşa, C., Escandell, V., Fontaine, B., Foppen, R., Gregory, R., Harris, S., Herrando, S., Husby, M., Ieronymidou, C., ... Devictor, V. (2023). Farmland practices are driving bird population decline across Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 120(21), e2216573120. <https://doi.org/10.1073/pnas.2216573120>
- Robinson, M. (2014). The ecodynamics of clearance in the British Neolithic. *Environmental Archaeology*, 19(3), 291–297. <https://doi.org/10.1179/1749631414Y.0000000028>
- Rooney, T. P., Olden, J. D., Leach, M. K., & Rogers, D. A. (2007). Biotic homogenization and conservation prioritization. *Biological Conservation*, 134(3), 447–450. <https://doi.org/10.1016/j.biocon.2006.07.008>
- Rowland, C. S., Marston, C. G., Morton, R. D., & O'Neil, A. W. (2020). Land cover map 1990 (25m raster, GB) v2. NERC Environmental Information Data Centre. <https://doi.org/10.5285/1be1912a-916e-42c0-98cc-16460fac00e8>
- Rue, H., Martino, S., & Chopin, N. (2009). Approximate Bayesian inference for latent gaussian models by using Integrated Nested Laplace Approximations. *Journal of the Royal Statistical Society, Series B: Statistical Methodology*, 71(2), 319–392. <https://doi.org/10.1111/j.1467-9868.2008.00700.x>
- Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How should beta-diversity inform biodiversity conservation? *Trends in*

- Ecology & Evolution*, 31(1), 67–80. <https://doi.org/10.1016/j.tree.2015.11.005>
- Stanbury, A. J., Eaton, M. A., Aebischer, N. J., Balmer, D. E., Brown, A. F., Douse, A., Lindley, P., McCulloch, N., Noble, D. G., & Win, I. (2021). The status of our bird populations: The 5th Birds of Conservation Concern in the United Kingdom, Channel Islands and Isle of Man and 2nd IUCN Red List assessment of extinction risk for Great Britain. *British Birds*, 114, 723–747.
- Sullivan, M. J. P., Newson, S. E., & Pearce-Higgins, J. W. (2016). Changing densities of generalist species underlie apparent homogenization of UK bird communities. *Ibis*, 158(3), 645–655. <https://doi.org/10.1111/ibi.12370>
- Sweeney, C. P., & Jarzyna, M. A. (2022). Assessing the synergistic effects of land use and climate change on terrestrial biodiversity: Are generalists always the winners? *Current Landscape Ecology Reports*, 7(4), 41–48. <https://doi.org/10.1007/s40823-022-00073-8>
- Tatsumi, S., Iritani, R., & Cadotte, M. W. (2021). Temporal changes in spatial variation: Partitioning the extinction and colonisation components of beta diversity. *Ecology Letters*, 24(5), 1063–1072. <https://doi.org/10.1111/ele.13720>
- Tobias, J. A., & Pigot, A. L. (2019). Integrating behaviour and ecology into global biodiversity conservation strategies. *Philosophical Transactions of the Royal Society B*, 374(1781), 20190012.
- Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J. M., Yang, J., Sayol, F., Neate-Clegg, M. H. C., Alioravainen, N., Weeks, T. L., Barber, R. A., Walkden, P. A., MacGregor, H. E. A., Jones, S. E. I., Vincent, C., Phillips, A. G., Marples, N. M., Montañó-Centellas, F. A., Leandro-Silva, V., Claramunt, S., ... Schleuning, M. (2022). AVONET: Morphological, ecological and geographical data for all birds. *Ecology Letters*, 25(3), 581–597. <https://doi.org/10.1111/ele.13898>
- Trisos, C. H., Petchey, O. L., & Tobias, J. A. (2014). Unraveling the interplay of community assembly processes acting on multiple niche axes across spatial scales. *The American Naturalist*, 184(5), 593–608. <https://doi.org/10.1086/678233>
- Vickery, J. A., Ewing, S. R., Smith, K. W., Pain, D. J., Bairlein, F., Škorpilová, J., & Gregory, R. D. (2014). The decline of Afro-Palaearctic migrants and an assessment of potential causes. *Ibis*, 156(1), 1–22. <https://doi.org/10.1111/ibi.12118>
- Wang, S., Loreau, M., de Mazancourt, C., Isbell, F., Beierkuhnlein, C., Connolly, J., Deutschman, D. H., Doležal, J., Eisenhauer, N., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Lepš, J., Polley, H. W., Reich, P. B., van Ruijven, J., Schmid, B., Tilman, D., ... Craven, D. (2021). Biotic homogenization destabilizes ecosystem functioning by decreasing spatial asynchrony. *Ecology*, 102(6), e03332. <https://doi.org/10.1002/ecy.3332>
- Wayman, J. P., Sadler, J. P., Pugh, T. A., Martin, T. E., Graham, L., White, H. J., Tobias, J. A., & Matthews, T. J. (2024). Data from: Unravelling the complexities of biotic homogenisation and heterogenization. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.hx3ffbgm6>
- Wayman, J. P., Sadler, J. P., Pugh, T. A., Martin, T. E., Tobias, J. A., & Matthews, T. J. (2021). Identifying the drivers of spatial taxonomic and functional beta-diversity of British breeding birds. *Frontiers in Ecology and Evolution*, 9, 620062.
- Wayman, J. P., Sadler, J. P., Pugh, T. A. M., Martin, T. E., Tobias, J. A., & Matthews, T. J. (2022). Assessing taxonomic and functional change in British breeding bird assemblages over time. *Global Ecology and Biogeography*, 31, 925–939. <https://doi.org/10.1111/geb.13468>
- White, H. J., Montgomery, I. W., & Lennon, J. J. (2018). Contribution of local rarity and climatic suitability to local extinction and colonization varies with species traits. *Journal of Animal Ecology*, 87(6), 1560–1572. <https://doi.org/10.1111/1365-2656.12881>
- White, H. J., Montgomery, W. I., Storchová, L., Hořák, D., & Lennon, J. J. (2018). Does functional homogenization accompany taxonomic homogenization of British birds and how do biotic factors and climate affect these processes? *Ecology and Evolution*, 8(15), 7365–7377. <https://doi.org/10.1002/ece3.4267>
- Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 30(3), 279–338. <https://doi.org/10.2307/1943563>
- Willis, K. J., & Birks, H. J. B. (2006). What is natural? The need for a long-term perspective in biodiversity conservation. *Science*, 314(5803), 1261–1265. <https://doi.org/10.1126/science.1122667>
- Wilson, M. W., Balmer, D. E., Jones, K., King, V. A., Raw, D., Rollie, C. J., Rooney, E., Ruddock, M., Smith, G. D., Stevenson, A., Stirling-Aird, P. K., Wernham, C. V., Weston, J. M., & Noble, D. G. (2018). The breeding population of peregrine falcon *Falco peregrinus* in the United Kingdom, Isle of Man and Channel Islands in 2014. *Bird Study*, 65(1), 1–19.
- Xia, Z., Heino, J., Yu, F., He, Y., Liu, F., & Wang, J. (2022). Spatial patterns of site and species contributions to β diversity in riverine fish assemblages. *Ecological Indicators*, 145, 109728. <https://doi.org/10.1016/j.ecolind.2022.109728>
- Xu, W.-B., Blowes, S. A., Brambilla, V., Chow, C. F. Y., Fontrodona-Eslava, A., Martins, I. S., McGlenn, D., Moyes, F., Sagouis, A., Shimadzu, H., van Klink, R., Magurran, A. E., Gotelli, N. J., McGill, B. J., Dornelas, M., & Chase, J. M. (2023). Regional occupancy increases for widespread species but decreases for narrowly distributed species in metacommunity time series. *Nature Communications*, 14(1), 1463. <https://doi.org/10.1038/s41467-023-37127-2>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Species used in the study.

Appendix S2. Supporting figures.

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