Temporal and spatial dimensions of avian diversity: Patterns and drivers from the United Kingdom and beyond

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ABSTRACT

Quantifying change in diversity over time and space and identifying the drivers of that change is becoming critical due to increasing anthropogenic pressures such as climate and land use change. While much work has been done in this area, uncertainty remains around how and why diversity is changing due to the mixed directions and magnitudes of change found across scales, locations, measures, and taxa. Here, using datasets on avian presence from both the United Kingdom and biodiversity hotspots in the tropics, we explore how diversity has changed both spatially and temporally in response to human-induced changes and other abiotic factors. The thesis finds key roles for environmental gradients in driving dissimilarity across space within Britain while also finding that more speciose assemblages may be buffered from environmental change to a greater degree than less species-rich areas through time. We found evidence of widespread biotic homogenisation across Britain, largely driven by increases in generalist species. However, species benefitting from recent conservation action contributed to the patterns observed, highlighting that species identities are important to consider when assessing change in spatial beta-diversity through time. Alpha diversity across three dimensions (taxonomic, functional and phylogenetic) remained relatively stable through time across three sites located within biodiversity hotspot regions in the tropics, while no evidence of homogenisation was found. However, the overall stability masked changes in the underlying assemblage structure, calling attention to the dynamic properties of these areas and the need to consider multiple diversity metrics within assessments. Overall, this work provides a novel contribution, using new methodologies, to the study of biodiversity change across time and space.

Recommendations are made concerning future avenues of research, such as methodological recommendations to improve the analysis of homogenisation.

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“The fact is that no species has ever had such wholesale control over everything on Earth, living or dead, as we now have. That lays upon us, whether we like it or not, an awesome responsibility. In our hands now lies not only our own future, but that of all other living creatures with whom we share the Earth.” - David Attenborough

"Facts are meaningless. You could use facts to prove anything that’s even remotely true." – Homer Simpson

List of papers

This thesis incorporates the two following papers, which correspond to two of the four empirical chapters:

- **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*. (**Chapter 2**)
- **Wayman, J. P**., Sadler, J. P., Pugh, T. A., 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*(5), 925-939. (**Chapter 3**)

The following co-authors contributed to the work in the following ways:

Thomas J. Matthews[1,2]: Supervision, including contributing to the initial idea, methodology and analyses. Reviewed and edited the manuscript.

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1. Introduction

1.1 Research background

1.1.1 The Anthropocene

Biodiversity is currently facing a crisis as humans continue to modify and change the environment (Dirzo et al., 2014; Dornelas et al., 2019; McGill et al., 2015). Such is the impact of *Homo sapiens* on the natural world that many scientists agree that we are now in the 'Anthropocene', an epoch defined by the effect of people on the global environment (Lewis & Maslin, 2015). This period in time has been characterised by large-scale land use conversion, mainly to agricultural or urban land types (Seto et al., 2011), agricultural intensification (Zabel et al., 2019), a warming and changing climate (Bellard et al., 2012),increasing disturbance through increasing artificial light at night (Gaston et al., 2017), noise and air pollution (Saha & Padhy, 2011) and a growing populous mainly centred around large urban sprawls (Tratalos et al., 2007). However, while much work has been done to quantify and explore biodiversity changes during this recent period, uncertainty around how diversity change is measured, how it is changing over time and space, and what is driving that change, remains (Dornelas et al., 2023).

1.1.2 Measuring biodiversity

While it is generally agreed that we, as a collective, influence the planet to such a degree as to mark it as a new epoch, as evidenced by the rate of global extinctions (Barnosky et al., 2011; Ceballos et al., 2015), at more local scales how species assemblages are changing over time is less certain (Blowes et al., 2022; Dornelas et al., 2014, 2019, 2023). The uncertainty largely stems from the variability involved in measuring and quantifying biodiversity change. Species richness is one of the most employed metrics, a simple count of the number of species present within a given area at a certain time point (Cazalis, 2022; Chase et al., 2019; Currie, 1991; Hurlbert & Haskell, 2003; Lennon et al., 2004; McKinney, 2008). However, biodiversity change studies that focus exclusively on this measure are limited because they do not provide information on species identities, meaning that diversity changes driven by assemblage and species abundance changes are hidden (Hillebrand et al., 2018). For example, studies have identified areas where species richness has increased or remained stable over time while the underlying abundance distribution (Cazalis, 2022) or community composition (Dornelas et al., 2014) has significantly changed. Therefore, there is an urgent need for biodiversity change studies to include diversity measures that incorporate species identities that can identify change irrespective of species richness.

Beta-diversity is one such measure that has been used to examine community change in space and time (Baselga et al., 2015; Heino & Tolonen, 2017; Magurran et al., 2019; Nunes et al., 2020; Sinha et al., 2022). Several metrics have been proposed to measure beta-diversity, and these can be broadly divided into diversity partitioning approaches and variance-based approaches (Chao et al., 2012; Matthews et al., 2019). Regarding the former, the two primary partitioning approaches employed are multiplicative ($\beta = \gamma / \alpha$) and additive ($\beta = \gamma - \alpha$), where β = beta-diversity of a set of sites, γ = gamma diversity (i.e. the total richness of a set of sites), and α = mean richness of a set of sites (Whittaker, 1960, 1965; Tuomisto, 2010; Matthews et al., 2019). In this thesis, the multiplicative form is used referred to as 'Whittaker's beta-diversity (e.g., Whittaker, 1960). More recent measures of beta-diversity have focused on variance-based approaches, such as those in the BAS framework (Baselga, 2010, 2012), that measure the similarity or dissimilarity (e.g., by using Sørensen or Jaccard similarity) in species composition between two or more sites (see also; Tuomisto, 2010a, 2010b). In the BAS framework, total beta-diversity is then partitioned into two further measurements describing the degree to which species are replaced (turnover) and are part of the larger community (nestedness resultant dissimilarity) (Baselga, 2010).

While the composite total beta-diversity informs on the dissimilarity between assemblages across space or a single assemblage over time (see sections 1.1.4 and 1.1.5 below), the individual components are useful to understand what is driving that dissimilarity (Baselga, 2010). Turnover is particularly useful as it can be used to understand whether species are being replaced over time, which is obscured when using measures of alpha diversity. Seperating the components also gives the option to model the drivers of each, separately.

1.1.3 Taxonomic, functional and phylogenetic diversity

In the same way that studies that focus exclusively on species richness are limited due to a lack of individual species information and, therefore, potentially mask diversity change, studies that only use taxonomic metrics of diversity suffer from a similar drawback in that they assume all species interact with the environment in the same way (Sekercioglu, 2006). Using only taxonomic diversity, therefore, omits the vital role that functional and phylogenetic diversity play within assemblage dynamics (Devictor et al., 2010).

Functional traits, measurements of a species' morphological, physiological or phenological characteristics, provide a measure of how species interact with their environment and the ecological role they play within a larger community (Pigot et al., 2020). Including measures of function within studies is vital to understanding diversity change, as species undertake many roles within ecosystems (Pigot et al., 2020; Sekercioglu, 2006; Sekercioglu et al., 2016; Whelan et al., 2008). Therefore, species loss can reduce the occupied trait space, while species turnover can reduce or increase the space depending on the species identities and the assemblage composition (Devictor et al., 2010; tsianou et al., 2021).

While functional traits give a measure of how species interact with their environment and what ecosystem services they contribute to, phylogenetic diversity gives a measure of species age and evolutionary divergence between species within an assemblage (Faith, 1992). It can, therefore, contribute further information about conservation priorities, such as conserving evolutionary history (Funk & Burns, 2019; Redding et al., 2010) alongside further information on ecological or behavioural properties of species that may not be apparent within morphological trait databases (Mouquet et al., 2012).

As highlighted in section 1.1.1, gaps remain in our understanding of taxonomic diversity change and its drivers. Both functional and phylogenetic diversity changes are understood to an even lesser degree, primarily due to the complexities of measuring and compiling the data necessary to calculate such metrics. However, thanks to recent work undertaken to gather and publish the needed phylogenetic (Jetz et al., 2012) and functional (Tobias et al., 2022) data, these metrics can now be easily incorporated into studies, allowing for research examining change across all three dimensions of diversity.

1.1.4 Biodiversity in space

As human-mediated drivers of biodiversity change increase, understanding how assemblages are distributed in time and space, why they are structured in such a way, and what factors drive the dissimilarity between communities over space is fast becoming essential. If we can understand what drives compositional changes over space, then we can calculate to what degree dispersal limitation (Dambros et al., 2017; Lomolino et al., 2010; Nekola & White, 1999), niche filtering (Cornwell et al., 2006; Fowler et al., 2014; Weiher & Keddy, 1999) and the overlap between the two (Auffret & Thomas, 2019; Leibold & Chase, 2017) influence the assemblage structure. Understanding the role of abiotic filters can aid in assessing the degree to which future changes in the filters could impact assemblages and to what extent the communities are resilient against such changes (McCloy et al., 2022; Mellin et al., 2014). Looking at specific filters such as climate and land use, two environmental filters that influence the suitability of areas for species persistence and energy availability (i.e., the niche filtering hypothesis; Currie, 1991; Hurlbert & Haskell, 2003) can help predict how future change in those drivers could impact communities.

1.1.5 Biodiversity in time

While studying spatial beta-diversity (i.e., beta-diversity calculated across a set of sites) helps us understand the drivers of community assembly across space, it does little to inform us about how communities change and respond over time in the face of environmental perturbation. For such an assessment, studies commonly employ temporal beta-diversity (i.e., beta-diversity calculated for a single site over time), and there has been a recent increase in focus on temporal beta-diversity to accurately assess if and how communities are changing and why (Alba et al., 2022; Antão et al., 2020; Auffret & Thomas, 2019; Blowes et al., 2019, 2022; Dornelas et al., 2013, 2014, 2019; Pilotto et al., 2020).

At the local scale, mainly within temperate regions due to the biases in sampling and data availability (Culumber et al., 2019; Feeley et al., 2017; Stroud & Feeley, 2017; Titley et al., 2017), communities have predominantly been found to be relatively stable in terms of species richness, but dynamic across time in terms of community composition, driven by an increase in the turnover of species (i.e., the replacement of species through time; Antão et al., 2020; Blowes et al., 2019; Dornelas et al., 2014, 2019; Hillebrand et al., 2018; Nunes et al., 2020; Petchey et al., 2007; Tinoco et al., 2021; Tsianou et al., 2021). As local assemblages are part of a larger meta-community (Leibold et al., 2004), species loss can be compensated for by immigration from the wider regional species pool (Finderup Nielsen et al., 2019), enabling observed replacement.

While alterations in species assemblage composition have been attributed to various environmental drivers, such as climate (Davey et al., 2012; Pearce-Higgins et al., 2015), land use (Jungandreas et al., 2022; Newbold et al., 2015; Rurangwa et al., 2021), and pollution (Saha & Padhy, 2011), to name a few, stochastic change has also been highlighted within studies of temporal beta-diversity (Baselga et al., 2015; O'Sullivan et al., 2021; Stegen et al., 2013). Stochastic change is particularly evident in the tropics, where multiple studies have found changes in assemblage composition over time in areas outside of the immediate influence of people (Blake & Loiselle, 2015, 2016; Oliveira & dos Anjos, 2022; Stouffer et al., 2021). Therefore, stochastic variation is essential to consider within analyses of temporal beta-diversity to ensure that change is attributed correctly.

With impacts of human-mediated drivers predicted to increase and further impact assemblages (e.g., Bellard et al., 2012; Newbold, 2018; Pigot et al., 2023; Zabel et al., 2019), more evidence is therefore needed, especially within the tropics, to evaluate how assemblage diversity is changing over time at different scales to inform conservation policy further.

1.1.6 Biotic homogenisation

One major predicted impact of human-mediated disturbance on natural assemblages of species is a growing incidence of biotic homogenisation (McGill et al., 2015). For a set of sites in a given area, biotic homogenisation describes the decrease in community dissimilarity (i.e., spatial beta-diversity) over time, while heterogenisation describes the opposite (i.e., an increase in dissimilarity). Heterogenisation of a given area has been hypothesised to occur through increased niche space (i.e., increased habitat heterogeneity through time), the presence of newly introduced species, or the decline of widespread species within the area (Chase et al., 2019). Following the same logic, homogenisation occurs due to the opposite, i.e., the loss of niche space (i.e., decreased habitat heterogeneity), the loss of species confined to specific areas, or the increase of locally common species across a given area.

Usually, this process of homogenisation occurs because of increases in generalist species at the expense of specialist species that have a wider range of traits and, therefore, contribute to the trait space to a greater extent and, in some cases, uniquely. However, specialists are also usually less resilient to environmental changes (Clavel et al., 2011). Therefore, this replacement (i.e. the replacement of specialists by generalists) can lead to functional homogenisation as the occupied trait space within or between assemblages gets smaller. Indeed, Frishkoff et al. (2016) found that, within four regions of Costa Rica, habitat conversion and climate change favoured the same bird species, highlighting the degree to which generalist species are favoured by changes in the environment. Native generalist species can also become ‘losers’ instead of ‘winners’ during the biotic homogenisation process if they are displaced by invasive species. An example of such a process was documented in Israel by Colléony and Shwartz (2020) as native specialist and generalist bird species lost out to non-native invasive species. These community changes can have repercussions on ecosystem functioning as the occupied traits space shrinks and services such as pollination are lost (Wang et al., 2021).

Evidence of biotic homogenisation has been documented in the European (Le Viol et al., 2012; Sullivan et al., 2016) and North American (Cazalis, 2022) avifauna as well as in other taxa and locations (Britton et al., 2009; Carvalheiro et al., 2013; Clavel et al., 2011; Escobar-Ramírez et al., 2020; Fourcade et al., 2021; Knapp & Wittig, 2012; Mitchell et al., 2022;

Musters et al., 2019) with research finding the pattern at the global scale (Clavel et al., 2011; Davey et al., 2012; Hughes et al., 2022). However, while evidence of homogenisation is widespread, the method through which it is commonly assessed (i.e., declines in temporal spatial beta-diversity) has potential issues due to how it is calculated. If we take a hypothetical example, if one assemblage contains three species and another contains five, and over a set period of time, the first assemblage is colonised by the two species missing in the initial measurement, the two assemblages have homogenised. However, alpha diversity will have increased alongside functional and phylogenetic diversity. Therefore, more work is needed to understand the underlying changes that lead to decreases in temporal spatial beta-diversity to ensure that incidences of homogenisation are truly detrimental to biodiversity targets, such as species conservation ecosystem functioning and services.

1.1.7 Avian change through time and space

As mentioned in previous sections, birds play important roles within ecosystems, such as pollination, seed dispersal and carrion removal, while also providing important services for humans, such as pest control (Kross et al., 2016; Milligan et al., 2016). They are also important culturally, with millions of people worldwide participating in the past time of birdwatching, with nature interaction providing known human health benefits (Keniger et al., 2013). The importance of birds to many vital services, combined with their cultural importance, means that birds (class Aves) are one of the most well-inventoried and studied groups of taxa, making them an ideal study group. The International Union for the Conservation of Nature (IUCN) has assessed all of the currently extant bird diversity for the IUCN Red List (2022) and recent work has made morphological traits (Tobias et al., 2022) and phylogeny data (https://birdtree.org; Jetz et al., 2012) publicly available allowing studies to incorporate metrics making use of the three dimensions of diversity (e.g., Devictor et al., 2010; Rurangwa et al., 2021; Sinha et al., 2022). The relative conspicuousness of bird species, combined with standardised survey techniques to identify them by sight and sound, means that a relatively large body of data already exists, with citizen science programs such as eBird (https:/ebird.com) and BirdTrack within Britain (https://www.bto.org/our-science/projects/birdtrack/about) and further academic study contributing greater amounts each year.

Evidence on bird populations is pretty clear that in most regions, a large number of species are declining in abundance (Burns et al., 2021; Lees et al., 2022; Rosenberg et al., 2019). Within North America, it has been estimated that 3 billion birds have been lost since 1970 (Rosenberg et al., 2019), while in Europe, the number stands at 560 – 620 million between 1980 and 2017 (Burns et al., 2021). In both areas, long-distance migrants have been disproportionately affected, while other groups have suffered dramatic declines, such as farmland birds within Europe, which have decreased by 57% (Donald et al., 2001; Gregory et al., 2019; Rigal et al., 2023). However, woodland birds across Europe have been found to be more stable across the same time period, but populations within individual areas are in decline (Burns et al., 2021). Some groups even seem to be increasing, such as wetland birds within Europe and North America (Rosenberg et al., 2019; Tori et al., 2002). As previously stated in section 1.1.5, tropical locations are relatively understudied in comparison to temperate regions, a bias that extends to birds (Culumber et al., 2019; Lees et al., 2022). Although evidence of avian population change within the tropics is scarcer, individual studies have highlighted declines (Şekercioğlu et al., 2019).

Birds follow the same pattern of local-scale changes observed for other taxa in temporal studies of species richness, with syntheses finding local increases, decreases, and sites with no change all found (Dornelas et al., 2014; Jarzyna & Jetz, 2018; Schipper et al., 2016). However, other reviews have found that richness increase is the most common pattern (Leroy et al., 2023). As with patterns found across global studies, many local scale studies also show increases in turnover alongside consistent signs of homogenisation of communities (Hughes et al., 2022; Leroy et al., 2023; Liang et al., 2019; Sullivan et al., 2016). While some turnover is expected within systems not experiencing strong environmental change (Baselga et al., 2015; Diamond & May, 1977; Stegen et al., 2013), the direction and magnitude of changes in turnover point to changes above the expected background rate. Land use (Gaston et al., 2003; Liang et al., 2019; Rurangwa et al., 2021), climate change (Davey et al., 2012; Pearce-Higgins et al., 2015; Rushing et al., 2020), agriculture (Donald et al., 2001; Gregory et al., 2019; Jungandreas et al., 2022; Şekercioğlu et al., 2019), hunting and poaching (Brochet et al., 2016; Casas et al., 2009), invasive species (Colléony & Shwartz, 2020; Donald et al., 2010), pets or feral cats (Loss et al., 2015; Schlacher et al., 2013; Woods et al., 2003), pollution (Chilvers et al., 2021; Kühn & van Franeker, 2020), including artificial light at night (Van Doren et al., 2017), energy production (Bernardino et al., 2018; Thaxter et al., 2017) and general disturbance from human activities (Bernat-Ponce et al., 2021; Bowles, 1995; Schlacher et al., 2013; Shamoun-Baranes et al., 2011) all threaten bird species.

The IUCN Red List (2022) shows that currently, 1,481 extant avian species are threatened with extinction. This amounts to 13.5% of the extant species currently recognised, with the majority of these threatened species found in the tropics (Jenkins et al., 2013). Considering that up to 91% of birds have ranges that, during seasonal migration, extend into the tropics, while more than half are restricted completely to the tropics (Barlow et al., 2018), this makes the tropics a particularly important area of study over the coming decades.

With climate (Marzluff, 2017; Newbold, 2018; Şekercioğlu et al., 2012), land use change (Newbold, 2018) and agricultural intensification (Zabel et al., 2019) all predicted to increase, birds will come under increasing threat of extinction in the near future. One estimate predicts hundreds of extinctions within the tropics alone in response to climate change by 2100 (Şekercioğlu et al., 2012). Therefore, understanding how communities are changing in response to current environmental changes will provide a basis to further inform conservation practice in an increasingly uncertain future.

1.2 This study

1.2.1 Aims and scope

In light of previous ***research gaps*** identified in the introduction, this study sets out to (1) quantify whether avian communities are changing over time and space within Britain and select locations from the tropics, (2) evaluate how they are changing over time and space, (3) establish what is driving change across time and space, and (4) show whether current measures of biodiversity change (mainly those related to beta-diversity) are appropriate to identify homogenisation or heterogenisation. In light of these aims, the chapters look to address several research questions:

- What drives variation in avian community composition across space at the landscape scale? (Chapter 2).
- Are avian communities in Britain changing over time, and if so, what are the drivers of that change? (Chapter 3).
- Are changes in community composition in Britain driven by colonisation or extirpation? How do those changes relate to changes in spatial beta-diversity over time? (Chapter 4).

- Is temporal spatial beta-diversity appropriate to identify homogenisation and heterogenisation for conservation purposes? (Chapter 4).
- What patterns of change in spatial beta-diversity are observable within the tropics, and do these show evidence of homogenisation? (Chapter 5).

This thesis uses two separate datasets to answer the questions identified above. The first dataset describes avian species presence across the entirety of Britain within 10 km x 10 km grids (hectads). The second dataset consists of point count data collected across sampling routes in three sites located in two biodiversity hotspots located within the tropics (Mariarano, Madagascar; Cusuco National Park, Honduras; Calakmul, Mexico). The datasets are described in more detail within section 1.3 and the chapters in which they are used.

1.2.2 Overview of chapters

The chapters are presented as standalone papers, with references included for each. As chapters 2, 3, and 4 use the same dataset, and similar metrics are used across all chapters, some repetition of the methods and background is to be expected.

- Chapter 2 combines measures of ***taxonomic*** and ***functional pairwise beta-diversity*** with generalised dissimilarity modelling and abiotic variables to assess the drivers of dissimilarity across space in breeding bird assemblages within Great Britain. This work has been published in Frontiers in Ecology and Evolution (DOI: 10.3389/fevo.2021.620062).
- Chapter 3 uses the same British breeding bird dataset used in Chapter 2 (atlas data from 2010) alongside another period of sampling (from 1970) to look at temporal changes in breeding bird assemblages between the time points using measures of

taxonomic, ***functional*** and ***phylogenetic beta-diversity***. This work has been published in Global Ecology and Biogeography (DOI: 10.1111/geb.13468)

- Chapter 4 uses two atlas periods from the British Trust of Ornithology (BTO) data (1990 and 2010) to explore how effective ***temporal spatial beta-diversity*** is at quantifying assemblage ***homogenisation*** and ***heterogenisation*** using measures of extirpation and colonisation resultant homogenisation and heterogenisation.
- Chapter 5 examines temporal change in spatial beta-diversity and species occupancy at two ***biodiversity hotspots*** located within the tropics.
- Chapter 6 provides a synthesis of the results within the previous four chapters (2-5) to frame this thesis within the current state of biodiversity research while also discussing the future directions for such research within the wider field of macroecology.

1.3 Datasets and study locations

Two datasets are used within this work: avian breeding atlas data from the BTO and avian point count data from Operation Wallacea (OPWALL).

1.3.1 British trust of ornithology atlas

The BTO atlas data describes breeding bird presence within 10 km x 10 km grids (hectads) within the British Isles. The data were collected over three periods: BA1970 (1968 – 1972), BA1990 (1988 – 1991), and BA2010 (2008 – 2011). At least eight tetrads, smaller 2 km x 2km grids, were sampled each year within the larger hectads. Birds were recorded based on calls and visually. They were then ascribed a likelihood of breeding. The data are publicly available (Gillings et al., 2019), and the dataset is described in detail throughout the chapters and supplementary material.

1.3.2 Operation Wallacea

OPWALL is a scientific expeditions company that maintains biodiversity research conducted by experts at multiple locations worldwide, although most of the sites are concentrated within the tropics. The work is funded by student volunteers, who pay to attend expeditions. Here, we use a subset of the data with the longest temporal ranges. These sites are Cusuco National Park, Honduras (2007 – 2018) (Hoskins et al., 2020; Martin et al., 2021; Neate-Clegg et al., 2018), Calakmul Biosphere Reserve, Mexico (2014 – 2018) (Bohn et al., 2014; Pérez-Flores et al., 2021), and Mariarano, Madagascar (2011 – 2017) (Palfrey et al., 2019). All three of the sites are located within the tropics within areas considered to be biodiversity hotspots (Myers, 2003; Myers et al., 2000). The data are described in more detail within Chapter 5.

1.4 Summary and synthesis

Current research on biodiversity change over time and space has yielded mixed results about the direction and magnitude of change at various scales (Antão et al., 2020; Blowes et al., 2019; Chase et al., 2019; Dornelas et al., 2014, 2023). Even at the global scale, change is found to be largely non-directional (Dornelas et al., 2014, 2019). Where directional change has been found, various drivers ranging from climate change (Davey et al., 2012; Pearce-Higgins et al., 2015), land use/cover change (Jungandreas et al., 2022; Newbold et al., 2015, 2018; Rurangwa et al., 2021), invasive species interactions (Colléony & Shwartz, 2020) and various combinations of the three (Auffret & Thomas, 2019; Beissinger et al., 2023; Newbold et al., 2019; Sweeney & Jarzyna, 2022) have all been implicated to various degrees in differing ecosystems and at different scales. There is, therefore, a large ***knowledge gap*** regarding diversity change over time and space at different scales. Indeed, in a recent review, Dornelas et al. (2023, p.1) highlighted the variability across studies looking at diversity change across time and space and “how much remains unknown about the direction and magnitude of multiple biodiversity metrics at different scales”.

This thesis, taking data from both the tropics and Britain, aims to produce ***new knowledge*** on biodiversity change using multiple facets and metrics of diversity combined with ***novel*** methodological techniques to examine diversity change across time and space within the Anthropocene.

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2. Identifying the drivers of spatial taxonomic and functional beta-diversity of British breeding birds

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Abstract

Spatial variation in community composition may be driven by a variety of processes, including environmental filtering and dispersal limitation. While work has been conducted on the relative importance of these processes on various taxa and at varying resolutions, tests using high-resolution empirical data across large spatial extents are sparse. Here, we use a dataset on the presence/absence of breeding bird species collected at the 10 km x 10 km scale across the whole of Britain. Pairwise spatial taxonomic and functional beta-diversity and the constituent components of each (turnover and nestedness/richness loss or gain) were calculated alongside two other measures of functional change (mean nearest taxon distance and mean pairwise distance). Predictor variables included climate and land use measures, as well as a measure of elevation, human influence, and habitat diversity. Generalised dissimilarity modelling was used to analyse the contribution of each predictor variable to variation in the different beta-diversity metrics. Overall, we found that there was a moderate and unique proportion of the variance explained by geographical distance per se, which could highlight the role of dispersal limitation in community dissimilarity. Climate, land use, and human influence all also contributed to the observed patterns, but a large proportion of the explained variance in beta-diversity was shared between these variables and geographical distance. However, both taxonomic nestedness and functional nestedness were uniquely predicted by a combination of land use, human influence, elevation, and climate variables, indicating a key role for environmental filtering. These findings may have important conservation implications in the face of a warming climate and future land use change.

2.1 Introduction

Biodiversity is currently facing a multitude of global-scale threats from human activity (Dirzo et al., 2014; McGill et al., 2015). As the human footprint on the natural world grows, it is becoming increasingly important to understand how these factors are impacting ecological communities in order to inform conservation efforts and make predictions about impacts under future scenarios (Newbold, 2018; Soininen et al., 2018). Analysing spatial variation in species diversity is a powerful means of assessing the impact of different environmental factors on biodiversity as it provides us with information on what is currently limiting species ranges and occupation of sites. The analysis of spatial variation in biodiversity generally involves focusing on taxonomic changes between sites in the form of alpha (a) or, to a lesser extent, beta (β) diversity (Calderón-Patrón et al., 2016; Field et al., 2009; Soininen et al., 2018).

Comparing the alpha diversity of two communities separated in space provides a measure of the difference in the number of species between these sites but ignores species replacement/turnover (i.e., a species being extirpated from a site and another species colonising) and can, therefore, mask biodiversity change (Gonzalez et al., 2016). In contrast, beta-diversity provides a measure of community dissimilarity between sites (Koleff et al., 2003; Whittaker, 1960). Various metrics have been proposed to measure beta-diversity, which can be grouped into variance-based approaches (the focus of the present study) and diversity-partitioning approaches (Legendre and de Cáceres, 2013; Matthews et al., 2019). Recently, several variance-based metrics (e.g., the Sørensen index) have been partitioned into constituent components, such as species replacement/turnover (that is independent of richness differences) and species richness differences or 'nestedness' (Baselga, 2010). It has been argued that the study of these partitions provides insight into the drivers of compositional differences between sites (Baselga and Leprieur, 2015). Nestedness in this context is not ‘true’ nestedness (e.g., as measured by the nestedness metric based on the overlap and decreasing fill (NODF)), but rather a nestedness resultant dissimilarity that allows for the separation of dissimilarity due to turnover from that of nestedness (Baselga, 2012). For ease, we henceforth use the term ‘nestedness’ to describe nestedness resultant dissimilarity.

Standard beta-diversity metrics (herein termed ‘taxonomic beta-diversity’) assume all species are the same in terms of the role they play within an ecosystem (Sekercioglu, 2006), thereby ignoring the vital role that functional diversity plays in assemblage dynamics (Devictor et al., 2010; Eskildsen et al., 2015). Recently, several beta-diversity metrics have been expanded to incorporate functional information (Baselga and Leprieur, 2015; Cardoso et al., 2014) and can be used to shed light on the biotic/abiotic factors that cause variation in functional diversity between sites (Cardoso et al., 2014; Villéger et al., 2013). This evidence can be used to inform conservation activities such as protected area design and biological corridor selection (Socolar et al., 2016) and help protect ecosystem services (Cardinale et al., 2012; Galetti et al., 2013; Şekercioğlu et al., 2004). For example, bird communities play an important role in providing services such as pollination, pest control, and carrion removal (Wenny et al., 2011; Whelan et al., 2008), which are critical services for humans and other taxa. Therefore, using a beta-diversity measure that incorporates species traits and hence functionality is essential to gain a better understanding of biodiversity change and its consequences (Carvalho et al., 2020; Devictor et al., 2010; Jarzyna and Jetz, 2018; Tobias and Pigot, 2019).

Biological communities are predicted to vary spatially in the absence of anthropogenic influences (i.e. the natural pattern of distance decay in species similarity; Nekola and White, 1999) due to both dispersal limitation and niche filtering, among other factors (Lomolino et al., 2010). Dispersal limitation is hypothesised to impact the spatial variation in community composition by restricting the range of species through distance alone (Dambros et al., 2017), independent of environmental differences between the communities (Hubbel, 2001). Niche-filtering occurs when environmental gradients constrain communities to those species adapted and able to persist in local conditions (Cornwell et al., 2006; Weiher and Keddy, 1999). In addition, human-induced change (e.g., land-use change and climate change) are likely important drivers of both spatial taxonomic and functional beta-diversity (Barnagaud et al., 2017; Davey et al., 2012; Devictor et al., 2007).

The effect of dispersal on spatial beta-diversity can be assessed through the analysis of the geographic distance between sites, while the effect of environment can be tested by evaluating measures of habitat and land use types (hereafter 'land use') and climate (Fluck et al., 2020; Luck et al., 2013; Wieczynski et al., 2019). However, due to the spatial structuring of environmental gradients (i.e., a distance decay in environmental conditions), it is difficult to partition the unique effects of each (Leibold and Chase, 2017). Relating current land use and climate to spatial variation in community composition will also enable inferences to be made on how increases in the relative intensity of these drivers may impact spatial variation in the future (Barbet-Massin and Jetz, 2015).

The effect of land use on community composition is mostly a result of niche filtering, where species which are adapted to a specific land use type are unable to survive in contrasting land use types (Cornwell et al., 2006; Weiher and Keddy, 1999). Rapidly growing human populations (Tratalos et al., 2007) have facilitated considerable land use changes via increasing urbanisation in some areas of the world (Seto et al., 2012), and conversion of natural land to agriculture, as well as an overall intensification of agricultural practices (Zabel et al., 2019). There is strong evidence that these practices have disrupted communities, leading to pools of generalist species in heavily modified habitats via the exclusion, through filtering, of species with narrower environmental requirements (i.e., specialists) (Barnagaud et al., 2017; Clavel et al., 2011; Flohre et al., 2011; Hagen et al., 2017; McKinney, 2006; Vellend et al., 2007). Thus, in anthropogenic landscapes (such as those that occur across much of the UK), turnover is predicted to be low across large spatial scales, and communities are predicted to become more nested, with high redundancy in functional diversity (Liang et al., 2019; Weideman et al., 2020).

Climate is also an important environmental filter and can drive high spatial beta-diversity between regions due to differences in energy availability (energy richness hypothesis; Currie, 1991; Hurlbert and Haskell, 2003; Hutchinson, 1959), variation in species tolerance (physiological tolerance hypothesis; Root, 1988), and variation in speciation rates (the speciation rates hypothesis; Currie et al., 2004; Hua and Wiens, 2013). While there is mixed support for these hypotheses, substantial evidence exists showing that differences in species composition between sites are often correlated with climatic gradients (Currie et al., 2004). Additional filtering impacts may occur where land use change interacts with climate (Auffret and Thomas, 2019).

A better understanding of the role climate plays in driving spatial beta-diversity is essential in order to accurately predict the effects of future climate change on community composition. For example, species populations have been found to expand or contract their ranges in response to changing climatic conditions (Batt et al., 2017; Fox et al., 2014). As well as range shifts, shifting phenologies across the trophic web can lead to disruption of communities through cascade effects due to altered species interactions (Bell et al., 2019). Other impacts of a changing climate, such as more frequent severe weather events, are also increasingly recognised as significant drivers in spatial beta-diversity (Maxwell et al., 2019).

There are thus many potential drivers of spatial beta-diversity. However, few studies exist assessing the relative roles of these different drivers (e.g., land use, climate, human impacts) in terms of both taxonomic and functional beta-diversity, the aim of the present study. We use generalised dissimilarity models (GDMs) in combination with a dataset containing presence/absence data of British breeding birds collected at the 100 km2 scale over the entirety of the British Isles. We aim to (1) test the effect of geographic distance and a range of environmental variables (e.g., land use type, climate) on the spatial taxonomic and functional beta-diversity of British breeding bird communities and (2) evaluate the role of human influence on spatial beta-diversity patterns. While we do not set out to test the niche-filtering and dispersal-limitation hypotheses directly, we interpret increasing dissimilarity due to geographical distance as an indication that dispersal limitation may play a role in the structuring of communities. In contrast, increasing dissimilarity due to climate, land use, or human influence would point to a role for niche filtering.

2.2 Materials and Methods

2.2.1 Data collection

Species Composition Data

Data showing the summer (breeding) distributions of the British avifauna (Gillings et al., 2019) were collected during April – July over the period 2008 – 2011 (BA2010) by volunteers on behalf of the British Trust of Ornithology (BTO) and the Scottish Ornithologists' Club (SOC). Some fieldwork effort was permitted out of this field season, with specific instructions given on what evidence was permitted (see Gillings et al., 2019, for further information).

The dataset summarises the presence/absence of British bird species within 10 km x 10 km (100 km2) quadrats covering the British Isles on a continuous grid (Fig. 2.1.). Only species designated as being "confirmed" or "probable" breeders (Gillings et al., 2019) were retained here. Vagrant and pelagic species were excluded, but we retained introduced breeding species for the analysis (McInerny et al., 2018). While some introduced species' occupied ranges may reflect in part their initial introduction sites, many of these species are now established, so their presence exerts an influence on community structure, resource use, and competition (Lennon et al., 2000). Species under threat from human persecution (particularly hunting or egg-collecting) were also removed from the analyses as data for such species were provided at larger spatial grains (i.e. larger than 100 km^2) or their locations were omitted entirely (Gillings et al., 2019). All quadrats with less than 50% land and all island regions that were considered disconnected from the mainland were removed. A total of 2257 100 km^2 quadrats remained with a species pool containing 169 species (supplementary Table. S2.1.1).

Figure 2.1. Map displaying the study location (Great Britain) and its location within Europe. The lower proportion of the island is gridded with the quadrats used to sample the avifauna (while only a sample is shown here, the whole island was sampled).

Trait Data

Continuous morphometric variables were measured from museum specimens or extracted from literature and used to characterise the functional diversity of each community (defined as all the species present in each quadrat). We selected eight morphological traits to represent the functional role of birds: two estimates of beak length (culmen from tip-to-skull and tip-to-nares), beak width, beak depth, tarsus length, wing chord length, tail length, and body mass, with evidence showing all of these traits provide useful information about avian dietary niche, locomotion and ecological function (Pigot et al., 2020; Tobias and Pigot, 2019; Trisos et al., 2014). Further information on measurements, including sampling per species and methods, are published separately (Pigot et al., 2020).

A principal components analysis was performed using all eight traits, with the full eight axes extracted. All the axes were then standardised to a mean of 0 and a standard deviation of 1, producing a trait matrix (species x traits) with eight trait axes for each species. To test for the effect of raw trait variability, we also standardised the traits prior to another PCA. The results using both the raw traits and the standardised traits in the PCAs were comparable, so we report only the results using the raw traits within the PCA here. All eight axes were included as it has been shown that all the axes provide useful information, with even minor axes capturing significant variation in rare traits (Pigot et al., 2020).

Climate Data

Monthly temperature and precipitation data were downloaded from the UK Met Office, which provides climate data interpolated from local weather stations onto a 1 km x 1 km grid across the United Kingdom (Hollis et al., 2019). Data were downloaded from the period 2000 - 2011. For the breeding season (defined as the start of May to the end of July, as many arriving migrants in April will not yet be breeding), key climate variables were selected a priori, and averages were calculated. Precipitation (mm) was summed for each 100 km^2 quadrat over the breeding season for each year. The average temperature (°C) was calculated as the daily average temperature across the quadrat and the breeding season. The range in temperature was also calculated as the average mean maximum daily temperature over the breeding season minus the average mean minimum daily temperature. The mean of each of these climatic variables was then calculated over the 2000 - 2011 period to reduce the influence of yearly variation, leaving three measures of climate ($Tavg_{MEAN}$, $Prec_{MEAN}$, and $Range_{MEAN}$). Climate averages were also constructed over a more extended period (1960-2011) to test if birds were responding to longer-term climate variation. The majority of the GDMs fitted using the shorter period had a better fit, and thus, we only report the results using the 2000 – 2011 climate here.

Land Use Data

Data on land use were obtained from the EDINA environment digimap service for 2007 (Land Cover Map, 2007). These data provide land cover (23 land use classes) for the British Isles at a 25 m scale. From these data, the percentage cover for each land use within each 10 x 10 km quadrat was calculated. The woodland classes (coniferous woodland and broadleaved woodland) were grouped into one variable named ‘forest’, as were ‘grasslands’ (grouped from the improved grasslands and semi-natural grasslands categories) and ‘urban areas’ (grouped from the suburban and urban categories). Arable land was also included as a predictor variable. Shannon’s diversity index was calculated for each quadrat as a measure of land-use heterogeneity (hereafter called Shan).

Human Influence Index (HII)

The Human Influence Index (HII) was used to assess the contribution of human impact on the variation in community composition (WCS & CIESIN, 2005). The HII is derived from multiple data sources on population density, infrastructure (railroads, urban development, night-time lighting), and landcover ranging in date collected 1994 - 2005 (although in this version, about half of the measures were collected around 2000 instead of 1995, as was the case for the first version). The measures are each weighted differently in the methodology and then standardised, giving a measure of human impact ranging from zero (no human impact) to 100 (maximum human impact possible using the methodology). HII values were extracted from each of the 1 km^2 grid squares within each 100 km^2 quadrat. The average was taken over these values to obtain the mean HII within each quadrat. It is important to note here that there is some temporal disparity in the period the HII was developed over (see above) and the period the atlas was conducted (2008 - 2011). However, even with this small disparity, HII should provide a robust indication of the impact human influences other than land use have on spatial variation in taxonomic and functional composition.

Elevation Data

Elevation data were obtained from the shuttle radar topography mission (SRTM; Jarvis, Reuter, Nelson & Guevara, 2008). For each 100km^2 quadrat, data were extracted using 400 equally spaced points. The mean (Elevation) and the standard deviation (Elevation$_{SD}$) were then calculated from these data as measures of elevation and variability in the elevation across the area.

Testing for multicollinearity

Pearson's and Spearman's correlations were used to test for multicollinearity between the predictor variables. Elevation$_{SD}$ was removed due to the variable being strongly correlated with multiple other variables (Elevation, Tavg$_{MEAN}$, and Prec$_{MEAN}$). The climatic variables were found to be collinear with one another and with other variables (Supplementary Fig. S2.1.1a. and S2.1.1b.). Therefore, the climatic variables were combined using a principal components analysis (PCA). The PCA yielded three axes that explained all the variation of the original three climatic variables (hereafter, Climate 1 (81.90%), Climate 2 (13.54%), and Climate 3 (4.56%)). All the axes were retained in the models to capture all the variability that could be explained by climate. Scatter plots and correlations between the PCA axes and the raw climate variable showed that Climate 1 was positively correlated with average temperature and negatively correlated with average precipitation (Supplementary Fig.

S2.1.2.). Climate 2 and Climate 3 had less clear and more complex correlations with the original variables (Supplementary Fig. S2.1.2).

After substituting the climate variables with the PCA axes, all variables had correlations < 0.70, with two exceptions: Elevation and Climate 1, and urban land use and HII (Supplementary Fig. S2.1.1c. and S2.1.1d.). As a result, urban land use was removed from the analysis, and the human influence index, which is a composite measure including urban land use, was retained. Both Elevation and Climate 1 were retained because 1) both variables are known to be significant predictors of spatial variation in breeding avian communities, 2) the correlation was still below 0.8, and 3) GDM is known to be robust to multicollinearity to a certain degree (Glassman et al., 2017). A variance inflation factor test (VIF) was also performed, with all remaining variables <5 (Neter et al., 1983; Gareth et al., 2013).

2.2.2 Measuring spatial dissimilarity in community composition

Spatial Taxonomic and Functional Beta-Diversity

To enable assessment of taxonomic dissimilarity between the assemblages, pairwise taxonomic beta-diversity was calculated for each 100km² quadrat using the function *beta.pair* from the package ‘betapart’ (Baselga and Orme, 2012). This function computes the dissimilarity (here measured using Sørensen’s dissimilarity index, βsor; Baselga, 2010; Koleff et al., 2003) between an assemblage and every other assemblage present in the dataset to create a pairwise dissimilarity matrix.

Using Sørensen’s dissimilarity, total beta-diversity can then be partitioned into its two constituent components: dissimilarity due to turnover (BD_{TURN}) and nestedness resultant dissimilarity (BD_{NEST}), with $BD_{TOTAL} = BD_{TURN} + BD_{NEST}$. Turnover is the proportion of dissimilarity due to species replacement between two assemblages, whereas nestedness is the proportion of the dissimilarity due to one assemblage being a nested subset of another assemblage through either species loss or gain (Baselga, 2010). It is important to note that, unlike BD_{TURN}, BD_{TOTAL} and BD_{NEST} are not independent of species richness changes, as the measurements are dependent upon species richness gradients (Baselga and Leprieur, 2015).

A measure of functional beta-diversity was then calculated using Sørensen's dissimilarity index and Baselga's partitioning framework (Phylosor). For this approach, a global functional dendrogram was created containing all the UK breeding species, using an Euclidean trait distance matrix and the agglomerative hierarchical clustering method (UPGMA). This method produces a rooted tree with a constant weight assumption (i.e., where the distance between the root and all tips is equal), and this then describes the functional relationship between species (Petchey and Gaston, 2002). The *phylo.sor* function in the 'betapart' package (Baselga and Orme, 2012) was used to calculate functional dissimilarity based on the shared branch length of the functional dendrogram between each assemblage and every other assemblage (hereafter called FD_{TOTAL}). Although this method is usually used on phylogenies, here, it is used on a functional dendrogram to give a functional measure analogous to taxonomic beta-diversity, allowing for straightforward comparison. In addition, using a convex hull approach (the standard Baselga functional metric) was not possible here due to the size of the dataset and the computational demands of such an approach. FD_{TOTAL} was also partitioned into its constituent components of nestedness resultant dissimilarity (FD_{NEST}) and turnover (FD_{TURN}).

A Pearson's correlation was performed between the Euclidean distances (in the trait distance matrix) and the cophenetic distances (in the dendrogram) (Villéger et al., 2017).

The resultant correlation was high (Pearson's $r = 0.97$), indicating that the dendrogram provides an adequate measure of the functional distances between species.

MNTD (Mean Nearest Taxon Distance) and MPD (Mean Pairwise Distance)

As an alternative to Baselga's functional beta-diversity framework, mean nearest taxon distance (MNTD) and mean pairwise distance (MPD) were calculated. While MNTD is also sensitive to species richness differences, MPD is a measure that is mostly independent of species differences between sites (Miller et al., 2017). MNTD represents the mean distance (smallest non-diagonal value) between species in a community and is most sensitive to changes at the 'tips' of a dendrogram (Webb et al., 2002). MPD is a similar measure but is calculated as the mean between all non-diagonal elements between species within a community (Webb, 2000; Webb et al., 2008), so it is more sensitive to changes at the roots of the functional dendrogram. Here, the beta-diversity versions of MNTD and MPD, which calculate the same measures but between assemblages, are used. For ease, we refer to these as MNTD and MPD (Miller et al., 2017). MPD and MNTD were calculated using the *comdist* and *comdistnt* functions, respectively, in the R package 'picante' (Webb et al., 2008). MNTD and MPD were standardised by dividing each pairwise measure by the largest pairwise measure to produce dissimilarity bounded between 0 and 1. Standardising MPD and MNTD in this way allowed the measures to be modelled using GDMs.

Modelling variation in spatial beta-diversity

As a first step, multidimensional scaling (MDS) was applied to each of the pairwise measures. The first axes from the MDS were taken and plotted. These were then assessed visually for any pattern in the dissimilarity/similarity between assemblages.

Generalised dissimilarity modelling (GDM) was then used to model functional and taxonomic beta-diversity. GDM is a statistical technique (an extension of matrix regression) that can be used for assessing the relationship between environmental gradients and variation in community composition (Ferrier et al., 2007). The modelling accommodates non-linearity that is present in ecological datasets over large extents (Ferrier, 2002; Ferrier et al., 2007) and can also incorporate geographical distance. This is vital to include, as dispersal limitation modulated by distance is known to be an important driver of community composition (Keil et al., 2012). GDM can deal with higher multicollinearity among predictor variables than many commonly used regression models (Glassman et al., 2017) and uses monotonic I-splines that constrain the coefficients of the regressions to be positive for a non-decreasing fit and non-positive for a non-increasing fit. The I-splines allow the evaluation of predictor effects on the dissimilarity metrics through the height and slope. The maximum height represents the total deviance explained by the predictor while holding all the other predictors constant, while the slope displays the rate of compositional change across the predictor's range (Fitzpatrick et al., 2013; Fitzpatrick and Keller, 2015). We applied a modelling framework using GDM aimed at assessing the unique and shared roles of both geographic distance and environmental factors on our measures of beta-diversity (Supplementary Fig. S2.1.3).

A separate GDM was fitted with each of the taxonomic and functional beta-diversity metrics (i.e., BD_{TOTAL}, BD_{TURN}, BD_{NEST}, FD_{TOTAL}, FD_{TURN}, FD_{NEST}, MNTD and MPD) as response variables using the ‘gdm’ package in R (Fitzpatrick et al. 2020). As a first step, matrix permutation was used to assess the model significance and variable importance using the *gdm.varImp* function. Due to the large amount of memory and time required to model the full site-pair combinations (N = 2,545,896), only a subset of the data could be used for the matrix permutation and variable importance process (as recommended for datasets with a large number of sites when calculating variable importance; Fitzpatrick et al., 2020). First, 60% of the sites were randomly removed, leaving 407,253 site-pairs. Another 60% of the site-pair combinations were then removed from the remaining site-pairs, leaving a total of 162,901 site-pairs for analysis. The removal of the site-pairs, after the initial site removal, removes site-pairs randomly but does not remove all site-pair combinations (Fitzpatrick et al., 2020). The predictor variables were not scaled, which allows assessment of the impacts each of the predictors has along actual environmental gradients (e.g., Fitzpatrick et al., 2013; Heino et al., 2019).

For the matrix permutation process, a GDM was first run using all of the predictor variables. The rows of the environmental data were then permuted, and a GDM model was fitted to those data. Significance was then evaluated by comparing the deviance of the model with unpermuted data to the model using permuted data. Variable importance was assessed by permuting each of the variables in turn while holding the other variables constant (unpermuted). Variable importance was then assessed as the difference in deviance explained using the permuted and unpermuted variable, with more important variables explaining a larger proportion of the deviance when unpermuted. The process was then repeated after dropping the least important variable (backward elimination) with variable importance and significance recalculated. All variable importance scores reported in the text were calculated at this point. The first model where all variables were significant ($p < 0.05$) was identified, and this model was then fit using all the sites (i.e. the full dataset) (final model). One hundred permutations were used for model significance testing and variable importance scores (Ferrier et al., 2007; Heino et al., 2019). Uncertainty in the I-splines was then evaluated using a bootstrapping approach (Shryock et al., 2015). A total of 50% of the sites were first removed randomly from the dataset. From these data, a GDM model was fit, and the I-spline coefficients were extracted. For the bootstrapping, a further 80% of the sites were randomly removed, and a GDM model fit. The process was repeated 100 times. The I-splines were then plotted with error bands showing the standard deviation from the permutation process.

Variance shared between geographical distance and the environmental variables was calculated for each model, in turn, using the formula:

$$Vs = Vfull - (V\neg\neg full - Vg) - (V\neg\neg full - Ve),$$

Where Vs is the explained variance shared between the geographic predictor and the environmental variables, Vfull is the variance explained by the full model, Vg is the variance explained by the geographic distance-only model, and Ve is the variance explained by the model containing only the environmental variables (Ray-Mukherjee et al., 2013).

2.3 Results

Taxonomic and functional beta-diversity of the British avifauna

BD_{TOTAL} was higher on average (0.313 ± 0.142) than FD_{TOTAL} (0.285 ± 0.126). In both cases, overall beta-diversity was determined mostly by the turnover component (0.225 ± 0.121 (71.88% of the total) and 0.195 ± 0.108 (68.42% of the total), for BD_{TURN} and FD_{TURN}, respectively). Nestedness was responsible for a smaller proportion on average for both measures (Fig. 2.2.). Average MPD (0.799 ± 0.045) was higher than MNTD (0.255 ± 0.125) (Fig. 2.2.), as is to be expected.

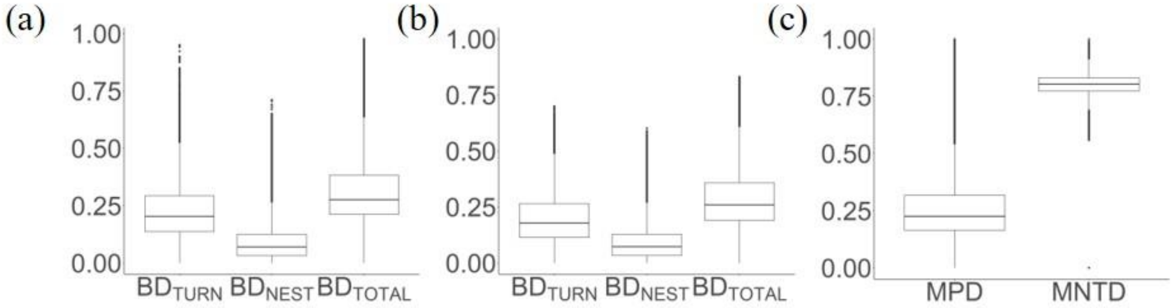

Figure 2.2.Boxplots of pair-wise dissimilarity measures of community composition for British breeding birds. Row (a) displays taxonomic spatial dissimilarity (turnover, nestedness resultant dissimilarity, and total), row (b) is functional pairwise dissimilarity (turnover, nestedness resultant dissimilarity, and total), and row (c) shows mean pairwise distance (MPD) and mean nearest taxon distance (MNTD). The horizontal line within the box represents the median, the box indicates the inter-quartile range (IQR), and the whiskers show data 1.5 times the IQR. Points highlight outliers.

Spatial variation in taxonomic and functional beta-diversity

Heat maps of the community metrics showed clear spatial patterns in the different beta-diversity metrics. A north-south divide was present for BD_{TOTAL} (Fig. 2.3a) and FD_{TOTAL} (Fig. 2.3e) and for the turnover component of each (Fig. 2.3b and Fig. 2.3f, respectively). Alternatively, this could also be interpreted as a divide along the classic ‘Tees-exe line’ that roughly divides the uplands and lowlands of Britain (Prakash and Rumsey, 2018). The west of Wales was more similar to the north of England and parts of Scotland than the south of England for total beta-diversity and turnover for both metrics, representing elevation changes between upland and lowland regions (Fig. 2.3a,b,e,f). The eastern coastal regions in Scotland were more congruent with southern regions than with inland and west coast Scottish assemblages (Fig. 2.3a,b,e,f). Nestedness patterns generally mirror the other metrics, but the patterns were patchier (i.e. the divides between regions (north/south and Tees-exe line) were less delineated). The south-west of England and the west coast of Wales were a closer match with most of Scotland than they were with the majority of southern

England (Fig. 2.3c and 2.3g), again closely matching the ‘Tees-exe line’ (Prakash and Rumsey, 2018).

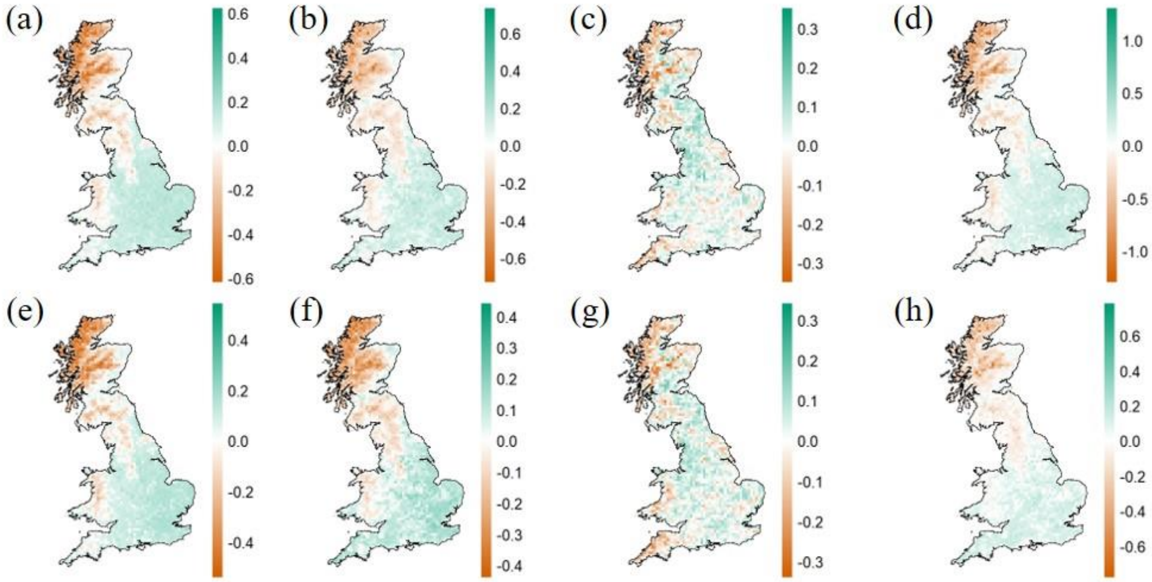

Figure 2.3. Heat maps of community dissimilarity in British breeding birds based on the first axis from a principal component analysis (PCoA) for taxonomic and functional beta-diversity, turnover, and nestedness resultant dissimilarity. Colours represent the ordering scores obtained from the PCoA, with areas displaying similar colours more similar and areas with differing colours less similar in terms of community composition. The first three maps on the first row (a-c) are for taxonomic beta-diversity (BD_{TOTAL}, BD_{TURN}, and BD_{NEST}, respectively), and the first three maps on the second row (e-g) are for functional beta-diversity (FD_{TOTAL}, FD_{TURN}, and FD_{NEST}, respectively). Mean nearest taxon distance (d) and mean pairwise distance (h) are the last maps on each row, respectively.

The pattern for MNTD was largely the same as that found for total taxonomic and functional beta-diversity and turnover for both metrics (Fig. 2.3d). MPD showed a pattern similar to that of nestedness for both taxonomic and functional beta-diversity (Fig. 2.3h).

Modelling the drivers of spatial beta-diversity

Overall, the variance explained by all the final models (bar those for MPD, FD_{NEST}, and BD_{NEST}) was high, with between 55.61% and 68.45% variance explained (Table. 2.1.). The variance explained by the final GDM models for MPD, FD_{NEST}, and BD_{NEST} was lower (between 9.60% and 12.09%) (Table. 2.1.). The deviance explained for the functional metrics was lower than for the taxonomic metrics (Table. 2.1.).

For all final models, the deviance explained by GDM models using only geographical distance as a predictor of dissimilarity was lower than the deviance explained by the models run using only the significant environmental variables (Table. 2.1.). However, there was overlap in the deviance explained by geographical distance and the environmental variables. Between 19.31% and 23.42% of the variance explained was shared within the MNTD, taxonomic, and functional beta-diversity models, excluding the FD_{NEST} and BD_{NEST} models (Table. 2.1.). For the nestedness components, the geographical distance between sites explained a low percentage of deviance (Table. 2.1.). Geographic distance was non-significant in the MPD model.

Table 2.1. (Next page) Results of generalised dissimilarity models (GDMs) analysing the spatial taxonomic and functional beta-diversity of British breeding birds as a function of environmental variables and geographical distance. Also included are the results from models analysing mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) between sites. Variable importance scores were calculated using a subset of the data through permutation of each one of the predictors in turn while holding all other predictors constant. The variable importance is then the mean difference in variation described by the model, including the non-permuted variable and the permuted variable. Therefore, the higher the importance score, the more important that variable is to explaining variation in the community dissimilarity metric. For individual variable descriptions, see the main text.

	Taxonomic			Functional				
	Total	Turn	Nest	Total	Turn	Nest	MPD	MNTD
GDM Deviance	74977	80731	143637	68867	85707	143167	25588	74664
Null Deviance	237649	213424	163388	196464	193057	159253	28306	202198
Variance Explained (%)	68.45	62.17	12.09	64.95	55.61	10.10	9.60	62.97
Intercept	0.13	0.06	0.06	0.12	0.05	0.06	1.53	0.10
Geographic Only (%)	28.04	29.72	1.43	27.95	28.17	1.22	0.00	26.30
Environment Only (%)	61.33	55.87	12.00	56.68	49.08	10.05	9.60	55.98
Shared (%)	20.92	23.42	1.34	19.68	21.64	1.17	0.00	19.31
Variable Importance								
Geographic	10.83	9.95	0.04	9.16	11.42	1.87	0.00	9.68
Climate 1	6.57	3.71	25.05	5.56	3.48	31.64	7.01	10.72
Climate 2	0.00	0.35	0.00	0.27	0.45	0.00	0.00	0.00
Climate 3	0.00	0.00	0.00	0.38	0.13	4.39	0.00	0.26
Arable	1.55	2.88	0.00	0.95	2.83	0.00	0.00	1.00
Forest	1.46	1.82	6.92	0.58	0.74	6.40	0.00	1.09
Grass	0.95	0.52	0.00	0.82	0.46	0.00	0.00	0.90
Shan	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Elevation	5.64	2.14	2.43	1.38	1.07	0.00	37.81	1.34
HII	1.61	1.19	4.51	2.60	1.48	5.12	15.22	3.48

Drivers of taxonomic beta-diversity

The following results (and those in the ‘Drivers of functional beta-diversity’ section) relate to the final models (i.e., the models that have been simplified using the permutation approach described in the methods).

BD_{TOTAL} was most impacted by geographical distance, Climate 1, Elevation, and HII (in order of decreasing importance, Table. 2.1.). BD_{TOTAL} rose gradually with geographical distance and Elevation, with a sharper rise observed for Climate 1 initially, followed by a levelling out (Fig. 2.4a). HII had an initial effect on total beta-diversity, with a small but sharp increase observed over initial environmental dissimilarity, but then levelled off and remained relatively constant (Supplementary Fig. S2.1.4). Arable, forest, and grass cover were also in the final BD_{TOTAL} model (Supplementary Fig. S2.1.4.).

Geographical distance, Climate 1, and arable land cover (in order of decreasing importance) had similar impacts on BD_{TURN} as they did on BD_{TOTAL} (Fig. 2.4b). Elevation and forest cover were the two other most important variables in regard to these response variables, with turnover increasing sharply with forest cover initially before levelling off and a near-linear increase with elevation (Supplementary Fig. S2.1.5.). HII, grass cover, and Climate 2 were also included in the final BD_{TURN} model (Supplementary Fig. S2.1.5.).

Geographical distance was relatively unimportant for predicting BD_{NEST}, although it was included in the final model. The best predictor (the predictors with the highest variable importance values; Table. 2.1.) for BD_{NEST} was Climate 1, and its relationship was similar to that found for BD_{TOTAL} (Fig. 2.4c). Forest cover, HII, and elevation were also in the final model (Supplementary Fig. S2.1.6.).

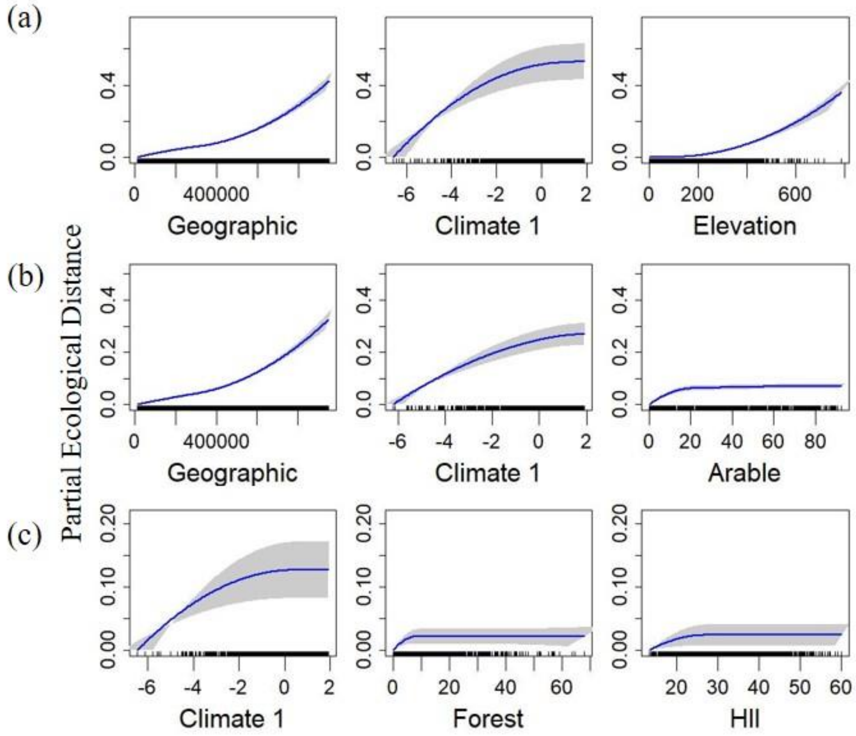

Figure 2.4. Plotted I-splines of the three most important variables (determined from the variable importance score) from generalised dissimilarity models analysing the relationship between environmental and geographic gradients and spatial community composition in British breeding birds. Plots on row (a) are for total Sorensen's beta-diversity (BD_{TOTAL}), (b) are for the turnover component (BD_{TURN}), and (c) are for the nestedness resultant dissimilarity (BD_{NEST}). Climate 1 is the first axis from a principal component analysis calculated from the average temperature, range of temperature, and precipitation over the months of May to July across the 2000 – 2011 period. Elevation is the average elevation across each 100km^2 quadrat. Forest and Arable are the percentage of each land use within each quadrat. The human influence index (HII) is the average human influence across each quadrat. Geographic is the geographic distance between sites. Curves show the relationship between the gradients and community dissimilarity obtained using I-splines. The most important variables are on the left, with decreasing variable importance to the right. Blue lines show the I-Spline correlations, with standard deviation (grey shaded area) calculated through bootstrapping (100 permutations) on a portion of the dataset. A rug plot on the x-axis shows the spread of the data. Note the varying y-axis for each measure.

Drivers of functional beta-diversity

FD_{TOTAL} had a similar relationship with geographic distance, Climate 1 and HII as was observed with BD_{TOTAL}, and they were also the three most important predictors (Fig. 2.5a). Elevation had an almost linear relationship with FD_{TOTAL} (Supplementary Fig. S2.1.7.). Arable, grass, and forest cover, along with the other two climate axes (Climate 2 and Climate 3), were also included in the final FD_{TOTAL} model (Supplementary Fig. S2.1.7.).

The main difference between the FD_{TURN} and BD_{TURN} final models was the inclusion of Climate 3 for FD_{TURN} and a slight difference in the ordering of the variable importance (Table. 2.1. and Supplementary Fig. S2.1.8.). FD_{NEST}, as with BD_{NEST}, was also unaffected by geographical distance, and this time, was not included in the final model (Table. 2.1.). FD_{NEST} was impacted by Climate 1, forest cover, HII, climate 3, and geographical distance (Fig. 2.5c and Supplementary Fig. S2.1.9.).

MNTD was mainly impacted by Climate 1, geographical distance, HII, Elevation, and forest cover (Fig. 2.6a and Supplementary Fig. S2.1.10.). Overall, the final MNTD model contained the same significant predictors as in the final models for BD_{TOTAL} and FD_{TOTAL}, and similar relationships were found with all the predictors, although the order was slightly different (Supplementary Fig. S2.1.10.). MPD was the only measure not predicted by geographical distance (Table. 2.1.). MPD was found to increase sharply with Elevation before levelling off around 100m (Fig. 2.6b). HII was the next best predictor of MPD, and its relationship was different to that found with the other measures, with a curvilinear increase observed midway through the gradient (Fig. 2.6b). The relationship between Climate 1 and MPD was also different to that found between the predictor and the other response variables, with a threshold effect found near the tail end of the gradient (Fig. 2.6b).

It should be noted that a large majority of the predictors were close in their variable importance scores across the models (Table. 2.1.). The geographical distance between sites was the exception across the models, as it was the most important predictor by a large proportion in all but the two nestedness, and MPD/MNTD models. It is also important to note that although multicollinearity was assessed, the geographic structuring of certain predictors may mean that the permutation of the variables may not have resulted in large importance values if geographic distance was retained in the model.

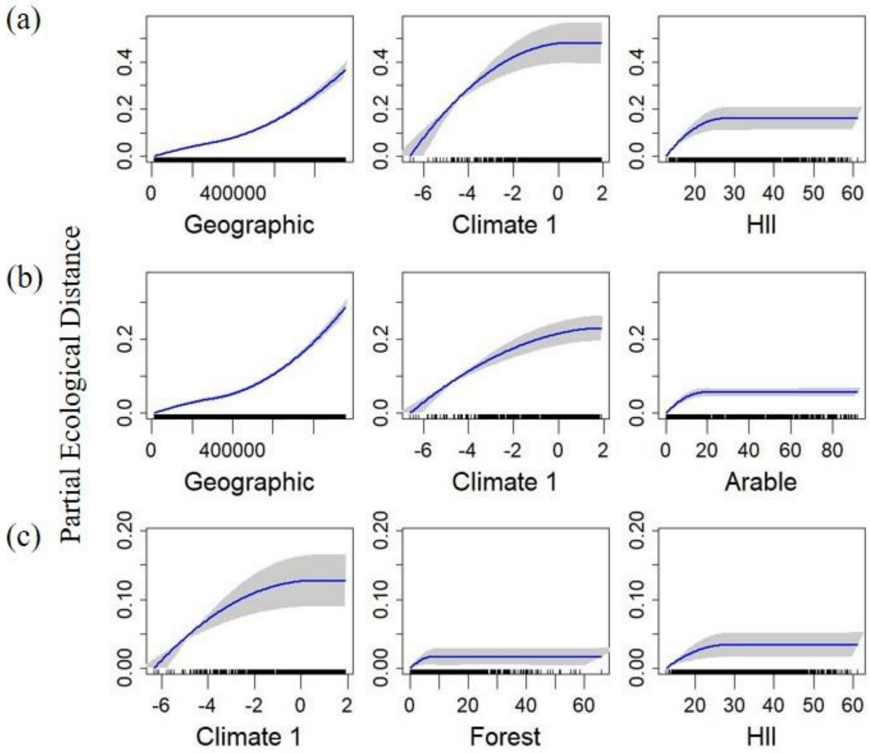

Figure 2.5. Plotted I-splines of the three most important variables (determined from the variable importance score) from generalised dissimilarity models analysing the relationship between environmental and geographic gradients and spatial community composition in British breeding birds. Plots on row (a) are for total functional beta-diversity (FD_{TOTAL}), (b) are for the turnover component (FD_{TURN}), and (c) are for the nestedness resultant dissimilarity (FD_{NEST}). Climate 1 is the first axis from a principal component analysis calculated from the average temperature, range of temperature, and precipitation over the months of May to July across the 2000 – 2011 period. Forest and Arable are the percentage of each land use within each quadrat. The human influence index (HII) is the average human influence across each quadrat. Geographic is the geographical distance between sites. Curves show the relationship between the gradients and community dissimilarity obtained using I-splines. The most important variables are on the left, with decreasing variable importance to the right. Blue lines show the I-Spline correlations, with standard deviation (grey shaded area) calculated through bootstrapping (100 permutations) on a portion of the dataset. A rug plot on the x-axis shows the spread of the data. Note the varying y-axis for each measure.

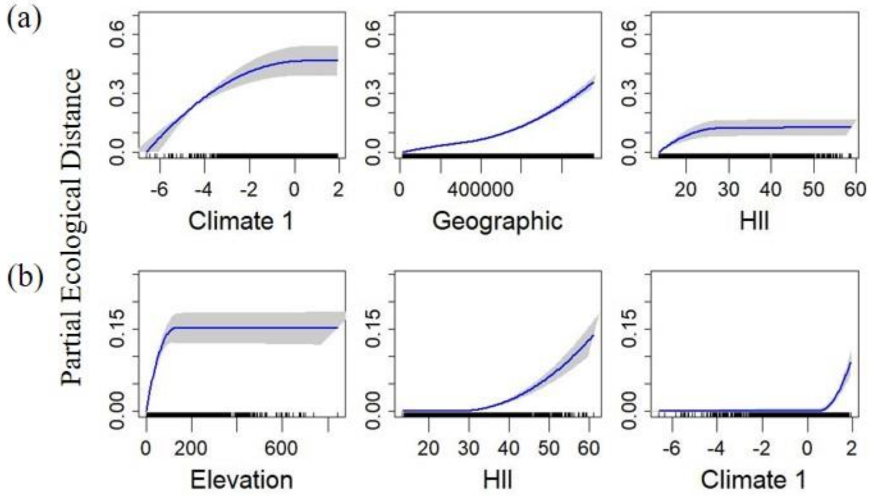

Figure 2.6. Plotted I-splines of the three most important variables (determined from the variable importance score) from generalised dissimilarity models analysing the relationship between environmental and geographic gradients and spatial community composition in British breeding birds. Plots on row (a) are for mean nearest taxon distance (MNTD), and (b) are for mean pairwise distance (MPD). Climate 1 is the first axis from a principal component analysis calculated from the average temperature, range of temperature, and precipitation over the months of May to July across the 2000 – 2011 period. Elevation is the average elevation across each 100km2 quadrat. The human influence index (HII) is the average human influence across each quadrat. Geographic is the geographical distance between sites. Curves show the relationship between the gradients and community dissimilarity obtained using I-splines. The most important variables are on the left, with decreasing variable importance to the right. Blue lines show the I-Spline correlations, with standard deviation (grey shaded area) calculated through bootstrapping (100 permutations) on a portion of the dataset. A rug plot on the x-axis shows the spread of the data. Note the varying y-axis for each measure.

2.4 Discussion

We found that variation in overall spatial functional and taxonomic beta-diversity (and their turnover components) of British breeding avian assemblages is driven by a combination of geographical distance per se and environmental gradients. The environment-only models explained more deviance than the geographic distance-only models, but there was also a relatively large, shared variance explained component. Previous studies have suggested that this shared component be considered as an indirect effect of climate (climate distance, Mazel et al., 2017; Qian et al., 2021). This may suggest that geographic distance plays a comparatively small role in predicting compositional differences between assemblages in contrast to the environment. This aligns with previous studies that have shown that spatial variation in community composition for a wide range of taxa can be attributed to a combination of deterministic (including contemporary and historical) and stochastic factors (Baselga et al., 2015; Carvalho et al., 2020; Dobrovolski et al., 2012; Glassman et al., 2017; Melo et al., 2009; Steinitz et al., 2006; Vicente et al., 2013). However, we also found that the differences in species loss/gain between sites (as measured by nestedness resultant dissimilarity) were explained mostly by differences in climate and, to a lesser extent, land use. Overall variation explained by the nestedness models was, however, much lower than for the total beta-diversity and turnover models. The lower explanatory power of the nestedness models implies that other drivers not included here may be impacting dissimilarity between sites due to species loss and gains.

Geographical Distance

Both BD_{TOTAL} and FD_{TOTAL} were driven mostly by the turnover component, highlighting that compositional differences between communities in Britain are mainly a result of different species being replaced. This is consistent with other beta-diversity studies across multiple taxa (see Soininen et al., 2018). A slow initial increase followed by a steeper rise in the slope of the I-splines of geographical distance with respect to turnover highlights a north-south divide, or a divide between the ‘Tees-exe’ line, in community dissimilarity. The observed impact of distance could be due to dispersal limitation, geographical barriers, or historical factors (Barnagaud et al., 2017; Dobrovolski et al., 2012; Nekola and White, 1999; Soininen et al., 2007). Here, we expect it to be a combination of all these factors, as well as an intertwining of distance with climate and land use.

FD_{TURN} was lower than BD_{TURN}, indicating that the species that are being turned over across communities share some functional traits. Petchey et al. (2007) found that many co-occurring species in British breeding birds were functionally similar, indicating low functional diversity across Britain as a whole and within individual communities. The low functional alpha diversity observed by Petchey et al. (2007) may explain the lower functional turnover compared to the taxonomic turnover observed here.

Nestedness made up a lower proportion of the total beta-diversity for both the taxonomic and functional metrics. Functional nestedness was mostly on par with taxonomic nestedness (Fig. 2.2.), highlighting that species lost/gained between assemblages were not functionally redundant (Petchey et al., 2007). The functional distinction of species lost/gained spatially between communities highlights that there is a significant difference between northern/southern communities. The observed pattern is partially congruent with elevational peaks in Britain (the Tees-exe line; Prakash and Rumsey, 2018). The pattern is also supported by MPD, a measure independent of species richness (Fig. 2.3h). It is interesting to note that of the variables that were significant in the MPD model, elevation was the most important and had a threshold effect, with any communities over ~100m being dissimilar to those at lower elevations (Fig. 2.6b). The results found here align with previous evidence that indicates the importance of elevational gradients as environmental filters (Sanders and Rahbek, 2012; Pigot et al., 2016).

Climate

Climate1 was included in the top three most important variables for all the final models (Table. 2.1.). The impact of climate was similar across all final models (except for the MPD model), with an almost linear relationship observed with dissimilarity before a levelling off.

As the correlations with the original climate variables showed a positive correlation with average temperature and a negative correlation with precipitation, this relates to a divide between warmer, drier, and wetter, cooler regions. The near linear relationship between partial ecological distance and Climate 1 for many of the metrics, therefore, shows a divide in terms of assemblage composition between these two types of regions. Climate was also the best predictor of nestedness by a large margin. This may point to the climatic filtering of certain species, with a divide between north and south Britain. However, the overall pattern for both measures was patchy (Fig. 2.2c and 2.2g). With global warming predicted to change the seasonality and severity of rainfall within Britain in the coming decades (Watts et al., 2015), these results indicate that drier and hotter summers in the future could lead to shifts in community composition.

Land Use and the Human Influence Index

While the overall impact of the different land-use types differed, the form of the relationship between the various land-use predictors and all the measures of beta-diversity were similar. After an initial sharp increase in community dissimilarity over the first small portion of the range of the environmental gradient, the dissimilarity levelled out. This impact over the initial environmental dissimilarity highlights the difference in community composition between areas with none of that land cover and those with just a small percentage.

HII impacted spatial variation in communities in much the same way as the land-use predictors. After an initial increase in dissimilarity between communities with increasing HII, there was a levelling off. There are several reasons why this could be the case. For example, Tratalos et al. (2007) found that the richness of all species increased initially faster with household densities (one of the measures included in the HII) than urban adapted species, but these then declined significantly after peaking at a very low density. For urban areas captured within HII, this could highlight the initial homogenisation impact of urbanisation, with urban areas similar after this initial disturbance driven by an increase in generalists and loss of specialists (Davey et al., 2012). However, as HII is a composite measure, this cannot be conclusively confirmed from these results alone. The human influence captured in this measure may also be masked at this scale as it is likely that a remnant of suitable habitat with lower human disturbance exists within a hectad or near a hectad (Fattorini et al., 2016). As this study is also only considering presence/absence, it also makes no inferences about abundance, which is likely more sensitive to human influence and which could be very different between quadrats (Tratalos et al., 2007).

Future climate and land-use change

The importance of both climate and land-use variables points towards potential future disruption of community composition if these drivers increase in intensity as is expected (Seto et al., 2012; Watts et al., 2015). The latitudinal divide between northern and southern (or highland and lowland) community composition also indicates that future warming could see species extirpations/extinctions from the colder, northern regions of the UK (Tayleur et al., 2016). This would also likely see an increased similarity of the northern communities with southern communities as species extend their ranges in the north (Hickling et al., 2006). However, species extending their ranges from Europe could obscure this impact, so studies approaching this question should focus on species identities. Indeed, this has already been observed in the study of bird abundance within England, with resident and short-distance migrants increasing in abundance through time, potentially at the expense of long-distance migrants, habitat specialists and cold-associated species (Pearce-Higgins et al., 2015). With many rare species also dispersal limited, future changes in land use and climate could potentially extirpate some of the few rare bird species Britain has (Baur, 2014).

Limitations

While we consider a range of predictors, we have not included measures of biotic interactions. Competitive interactions and predator presence/abundance can all have an impact on spatial beta-diversity (Korňan and Svitok, 2018; Wittwer et al., 2015). Abundance differences between sites were also not directly considered due to a lack of appropriate data. Given that a species' abundance can be an important determinant of that species' influence on ecosystem functioning (Gaston et al., 2018; Winfree et al., 2015), future studies aiming to analyse spatial variation in community and functional composition should attempt to analyse measures of population size.

2.5 Conclusions

Spatial variation in both the taxonomic and functional composition of UK breeding birds is driven mainly by species turnover, which can be explained through a combination of geographical distance per se and environmental gradients. The unique variance explained by distance alone could reflect an important role for dispersal limitation in driving these patterns, but more work is needed, as this variance component could also be due to a process not considered here. In contrast, species loss/gain, observed through nestedness between sites, was driven mainly by environmental factors. Future climate warming and land-use change could lead to an increase in the loss of species, particularly cold-adapted or rare and dispersal-limited, from communities, particularly in the north and in the uplands.

With turnover driving these patterns, broad-ranging conservation efforts would be preferable to conservation focused on target areas (Si et al., 2016).

Future work should look for potential synergies between climate and land use in order to assess if future increases in both could potentially have larger than expected impacts on biodiversity based on the individual effects of each in isolation (Brook et al., 2008; de Chazal and Rounsevell, 2009; Frishkoff et al., 2016; Mantyka-pringle et al., 2012). Future comparison between the results presented here and results of similar tests from areas in different climate regions or in less disturbed regions than the UK would also be informative. For example, in tropical systems, it would be expected that, as the UK is a post-perturbation system and rates of habitat loss will be higher in the tropics, land use will play a larger role in driving community composition dissimilarity between sites than found here (Hansen et al., 2013). Another potential future research direction could be to assess whether other taxonomic groups within the British Isles have similar patterns of functional or taxonomic beta-diversity or whether the patterns observed here are bird-specific.

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

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Abstract

Anthropogenic effects on the natural world continue to be at the forefront of biodiversity research as climate change, urbanisation and agricultural intensification all increase. Recently, an increased focus has been placed on attributing changes in these anthropogenic effects to changes in biodiversity.

Using morphological trait measurements and a dataset of presence-absence data for British breeding birds surveyed in 10 x 10km hectads across two time periods, we calculated temporal taxonomic and functional beta-diversity for each hectad alongside species richness change, 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. 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.

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

These results add to the growing body of evidence on temporal biodiversity change and allow for comparisons and synthesis. They also help inform those at the forefront of British

bird conservation about what areas may need priority, such as those at higher elevations and less speciose communities.

3.1. Introduction

Recently, there has been an increasing focus in ecology on analysing biodiversity change through time and identifying the drivers of that change (Dornelas et al. 2014; Antão et al. 2020; Blowes et al. 2019; 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 (Newbold, 2018; Thomas et al., 2004; Urban, 2015; Wieczynski et al., 2019). Of the two drivers, land use change is generally acknowledged as the largest current driver of biodiversity loss (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Seto, Güneralp, & Hutyra, 2012; Sohl, 2014; Tratalos et al., 2007; Zabel et al., 2019). However, warming temperatures are impacting species through range alterations/niche tracking (Batt, Morley, Selden, Tingley, & Pinsky, 2017; Fox et al., 2014; Tayleur et al., 2015) and shifting phenologies (Bell et al., 2019). These impacts will likely intensify, and climate change is expected to match or exceed land-use change as the leading biodiversity change driver this century (Newbold, 2018).

While 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, Bonthoux & Balent, 2015; Stegen et al., 2013). Indeed, many biodiversity models (e.g., the equilibrium theory of island biogeography and neutral models; Hubbell, 2001; MacArthur & Wilson, 1967) predict the temporal turnover of species in a community as a theoretically stochastic process.

Two main factors hinder many biodiversity change studies. First, appropriate time-series data covering species composition from sites at two or more time points are required

(Antão et al., 2020; Dornelas et al., 2018). However, due to the resources required to collect time-series data, most studies analysing assemblage diversity change use a space-for-time substitution, analysing dissimilarity between sites within the same study system and time period (e.g. Swenson, Anglada-Cordero, & Barone, 2011). Whilst space-for-time analyses assume that communities are at equilibrium, temporal analyses do not (Damgaard, 2019).

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

An effective and widely used tool for analysing change in composition is temporal beta-diversity (Baselga et al., 2015; Shimadzu, Dornelas, & Magurran, 2015; Matthews, Sadler, Carvalho, Nunes, & Borges, 2019). 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, Isabelle, Frédéric, & Vincent, 2009; Jarzyna & Jetz, 2017; Schipper et al., 2016), decreases (Konvicka, Fric, & Benes, 2006; Tingley & Beissinger, 2013; Wilson, Gutiérrez, Gutiérrez & Monserrat, 2007), or no systematic change (Dornelas et al., 2014; Petchey, Evans, Fishburn, & Gaston, 2007) in diversity. 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 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, Chamberlain, Newson, Noble & Johnston, 2012; Lennon, Greenwood, & Turner, 2000), and we expected turnover to be the main component of both functional and taxonomic 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 (Jung, Scharlemann & Rowhani, 2020).

3.2. Materials and Methods

3.2.1 Data Collection

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 during 1968 – 1972 (BA1970) and 2008 – 2011 (BA2010) by volunteers on behalf of the British Trust of 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 10km x 10km (100km^2) hectads covering the British Isles on a continuous grid (Supplementary Fig. S3.1.1). 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 less than 50% land or comprised offshore islands (see Appendix S3.1 in the Supporting Information for more details).

Trait data

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

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

Climate Data

We downloaded monthly temperature and precipitation data for 1960 to 2011 (ten 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 1km x 1km grid across the UK (Hollis, McCarthy, Kendon, Legg, & Simpson, 2019). For each hectad, we calculated 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 the average temperature (°C) as the mean monthly temperature across the breeding months for each year (1960 – 2011). We selected this variable because it impacts species' metabolic loads, and temperature increases are thought to reduce this load and allow more energy for reproduction (Lennon et al., 2000). Temperature has been found to be a predictor of avian occurrence and abundance in the breeding season (Jarzyna, Zuckerberg, Porter, Finley, & Maurer, 2015; Jiguet et al., 2010; McDonald, McClure, Rolek & Hill, 2012). We summed precipitation (mm) 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, Hubert & Struyf, 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 standard deviation 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 the average temperature of the coldest month (Cold), and change in the average temperature of the warmest month (Warm). We repeated this for the standard deviation to measure how variation around the mean changed across time ($Tavg_{SD}$, $Range_{SD}$, $Prec_{SD}$, $Cold_{SD}$, and $Warm_{SD}$).

Land Use Data

We obtained data for land-use change from the Historic Land Dynamics Assessment (HILDA, Version 2.0) model (Fuchs, Herold, Verburg, & Clevers, 2012). The HILDA model uses multiple data streams of land cover to reconstruct historic LULC change, including where transitions have occurred (e.g. from forest to settlement). We obtained land cover data on the basis of dominant, gross LULC changes for 1970 and 2010 (Fuchs et al., 2012; Fuchs, Herold, Verburg, Clevers, & Eberle, 2015). From these data, we calculated the number of $1km^2$ 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 % change) within the hectads over the 1970-2010 period (Urbanchange, Cropchange, and Forestchange). HILDA also provides the number of times a 1km x 1km 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 ($Total_{change}$). 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 latter to give a measure of difference (Shan).

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 standard deviation from these data (Elevation and $Elevation_{SD}$, respectively).

We used Pearson's correlations to test for multicollinearity between the predictor variables. Elevation and Elevation$_{SD}$ had an absolute correlation above 0.70 (-0.78), as did Tavg and Warm (0.84). Therefore, we removed Elevation$_{SD}$ and Warm.

3.2.2. Measuring compositional change through time

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, Gaston, & Lennon, 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 due to species replacement between the two time periods, whereas nestedness (hereafter, BD$_{NEST}$) is the proportion of the dissimilarity due to the earlier or later assemblage being a nested subset of the other through either species loss or gain (Baselga, 2010). We also calculated a simple measure of taxonomic change (2010 species richness – 1970 species richness) (SP$_{change}$).

We then calculated functional beta-diversity using Sørensen's dissimilarity index and 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 where 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 called 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 due 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 actual distances between the species. The correlation was high (Pearson's $r = 0.80$), showing that the dendrogram provided a good measure of the functional distances between species.

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

As an alternative to Baselga's temporal functional beta-diversity framework, we calculated the beta-diversity versions of mean nearest taxon distance (MNTD) and mean pairwise distance (MPD) (see Appendix S3.3 for more details regarding these metrics).

We calculated MPD¬ and MNTD with the *comdist* and *comdistnt* functions, respectively, in the R package 'picante' (Kembel et al., 2010; Webb, Ackerly & Kembel, 2008). We plotted values of all metrics to identify any spatial clustering of areas of high or low change.

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 between the dissimilarity between sites in the earlier period and the dissimilarity between sites in the later period (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 1000 multiple site functional and taxonomic beta-diversity values for both time periods from a random sample of 1/5 of the 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, Giraud & Loomis, 2005; Poe, Welsh & Champ, 1997), 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}).

3.2.3. Modelling variation in temporal beta-diversity

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 (see Appendix S3.3 for further details) with the function *rf_tuning* in the package 'spatialRF' (Benito, 2021). We selected the combination that best fit the data (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, Nussbaum, Wright, Heuvelink & Griller, 2018). We then assessed the 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 utilised to run the models in the package 'spatialRF' (Benito, 2021; Wright & Ziegler 2017).

Because random forest is a stochastic algorithm, we ran twenty 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. Because variation in climate and other predictors may be spatially structured, we repeated the above with the spatial coordinates omitted from the model.

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

3.3. Results

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 (Supplementary Fig. S3.4.1). However, precipitation and range in temperature decreased in some areas over the period (977 [43.6%] and 12 [0.5%] of the hectads, respectively) (Supplementary Fig. S3.4.1). The standard deviations of precipitation, range in temperature, and temperature in the warmest month increased in most areas, whereas the standard deviation of average temperature decreased, and the standard deviation of the average temperature in the coldest month increased in some areas and decreased in others. Average Cold_{FAT} (1.62 ± 0.15) and Warm_{FAT} (1.57 ± 0.16) were similar.

Land-use change

The area of forest and urban land cover both increased on average, but variation was high (4.4% ± 6% and 0.6% ± 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 (Supplementary Fig. S3.4.2). Cropland decreased on average but with large variation (- 4.9% ± 16.7%) (Supplementary Fig. S3.4.2). All but 69 hectads had some form of

LULC change over the 40 years between the atlases, and the average number of transitions between LULC types was 19.8 ± 19.1. Shannon's index increased in 1654 grid cells and decreased in 447 (average change 0.1 ± 0.2) (Supplementary Fig. S3.4.2).

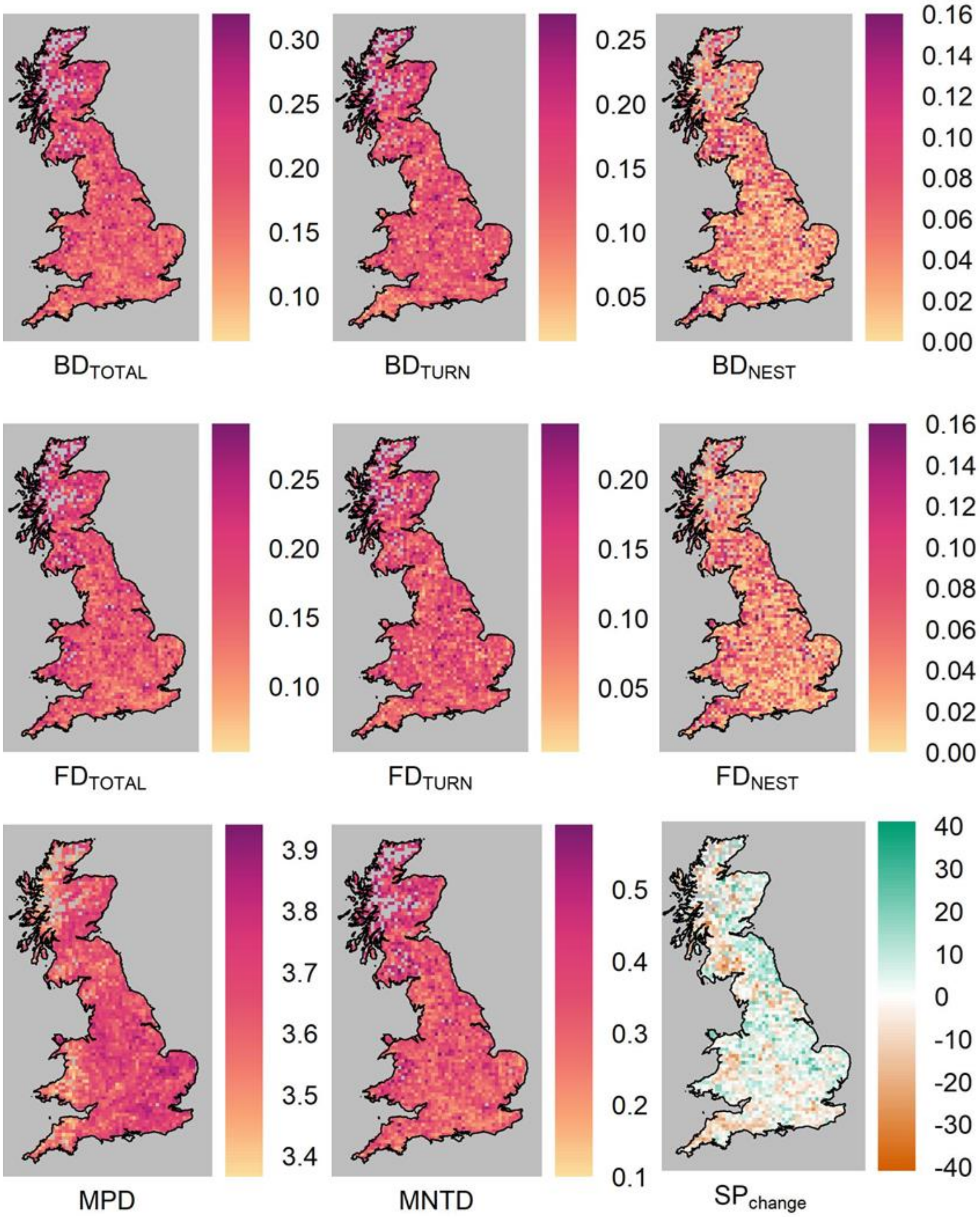

Figure 3.1. Temporal change observed in breeding bird communities in Britain between 1970 and 2010 within 10km x 10km hectads for different taxonomic and functional metrics: the temporal taxonomic beta-diversity (BD_{TOTAL}), taxonomic turnover (BD_{TURN}), taxonomic nestedness resultant dissimilarity (BD_{NEST}), temporal functional beta-diversity (FD_{TOTAL}),

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

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}; Fig. 3.1). There appeared to be clustering of areas with increases or decreases in species richness, although there was no strong latitudinal or longitudinal divide (Fig. 3.1). Mean SP_{change} was slightly negative on average 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 (1095 and 1054 assemblages, respectively).

For taxonomic beta-diversity, the mean total taxonomic beta-diversity (BD_{TOTAL}) was 0.20 ± 0.06 (range = 0.08 – 0.54). BD_{TOTAL} was mainly driven by turnover (BD_{TURN}, 0.15 ± 0.06, range = 0 – 0.46, mean % of BD_{TOTAL} = 75%) with nestedness responsible for a lower portion on average (BD_{NEST}, 0.05 ± 0.05, range = 0 – 0.29, mean % of BD_{TOTAL} = 25%). There was no strong signal of species loss or gain at the hectad level over the period (Fig. 3.1).

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}, 0.13 ± 0.05 (mean % of FD_{TOTAL} = 72%) and 0.05 ± 0.04 (mean % of FD_{TOTAL} = 28%), respectively), highlighting no systematic loss of functional diversity. However, the mean total functional beta-diversity (FD_{TOTAL}) was 0.18 ± 0.05 (range = 0.08 – 0.42), lower than the mean BD_{TOTAL} (Fig. 3.1). In addition, the change in FD_{TOTAL} was greater in upland areas than in the lowlands (Fig. 3.1).

By contrast, mean pairwise distance (MPD) was higher in lowland areas (mainly the south-east) than in uplands (Fig. 1.). Average MPD across the hectads was 3.64 ± 0.11 (range = 3.15 – 3.94), and average mean nearest neighbour distance (MNTD) was 0.36 ± 0.11 (range = 0.15 – 1.10) (Fig. 3.1).

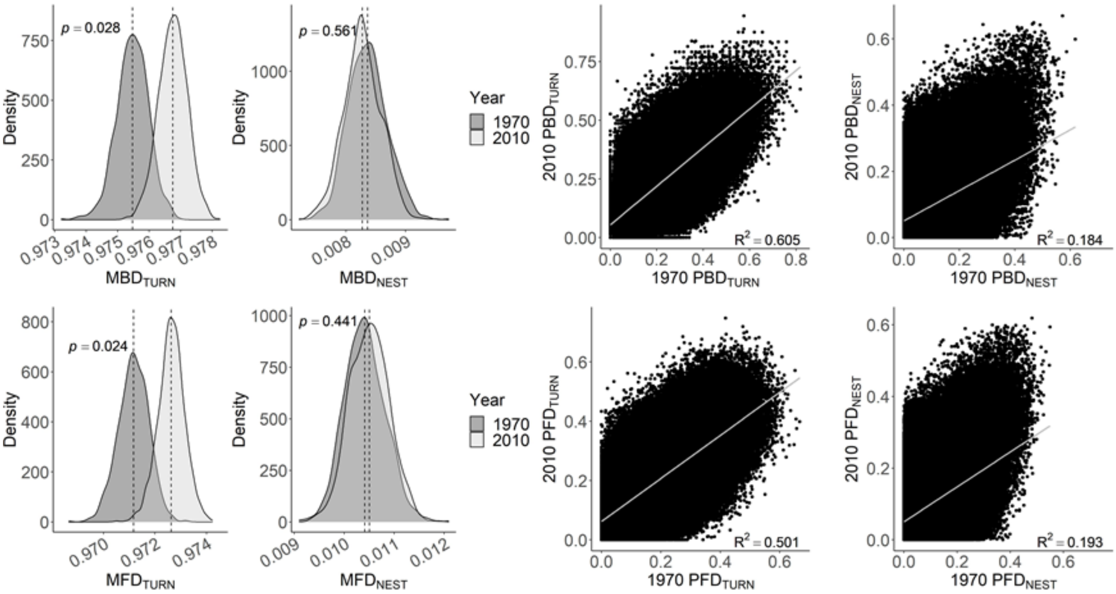

Figure 3.2. Spatial change in taxonomic and functional beta-diversity of British bird breeding assemblages between 1970 and 2010. The density plots on the left show the turnover and nestedness components for both taxonomic (MBD_{TURN} and MBD_{NEST}) and functional (MFD_{TURN} and MFD_{NEST}) beta-diversity. 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 to 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 solid grey lines show the relationship between the metrics using OLS linear regression. Fit (R^2) from the regression is shown in the bottom right-hand corner.

Spatial taxonomic and functional beta-diversity change

The spatial structure of dissimilarities changed between 1970 and 2010, as shown by the low correlations between pairwise taxonomic nestedness (PBD_{NEST}; $R^2 = 0.18$, Mantel $p<0.001$) and pairwise functional nestedness (PFD_{NEST}; $R^2 = 0.19$, Mantel $p<0.001$), in the two time periods. Therefore, overall, pairs of sites became less nested (Fig. 3.2). There was no low-level correlation observed for either pairwise taxonomic turnover or pairwise functional turnover (Fig. 3.2). 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 to 1970 (both $p <0.05$) (Fig. 3.2). The sampled values of multiple taxonomic nestedness (MBD_{NEST}) and multiple functional nestedness (MFD_{NEST}) in 1970 and 2010 overlapped considerably (Fig. 3.2).

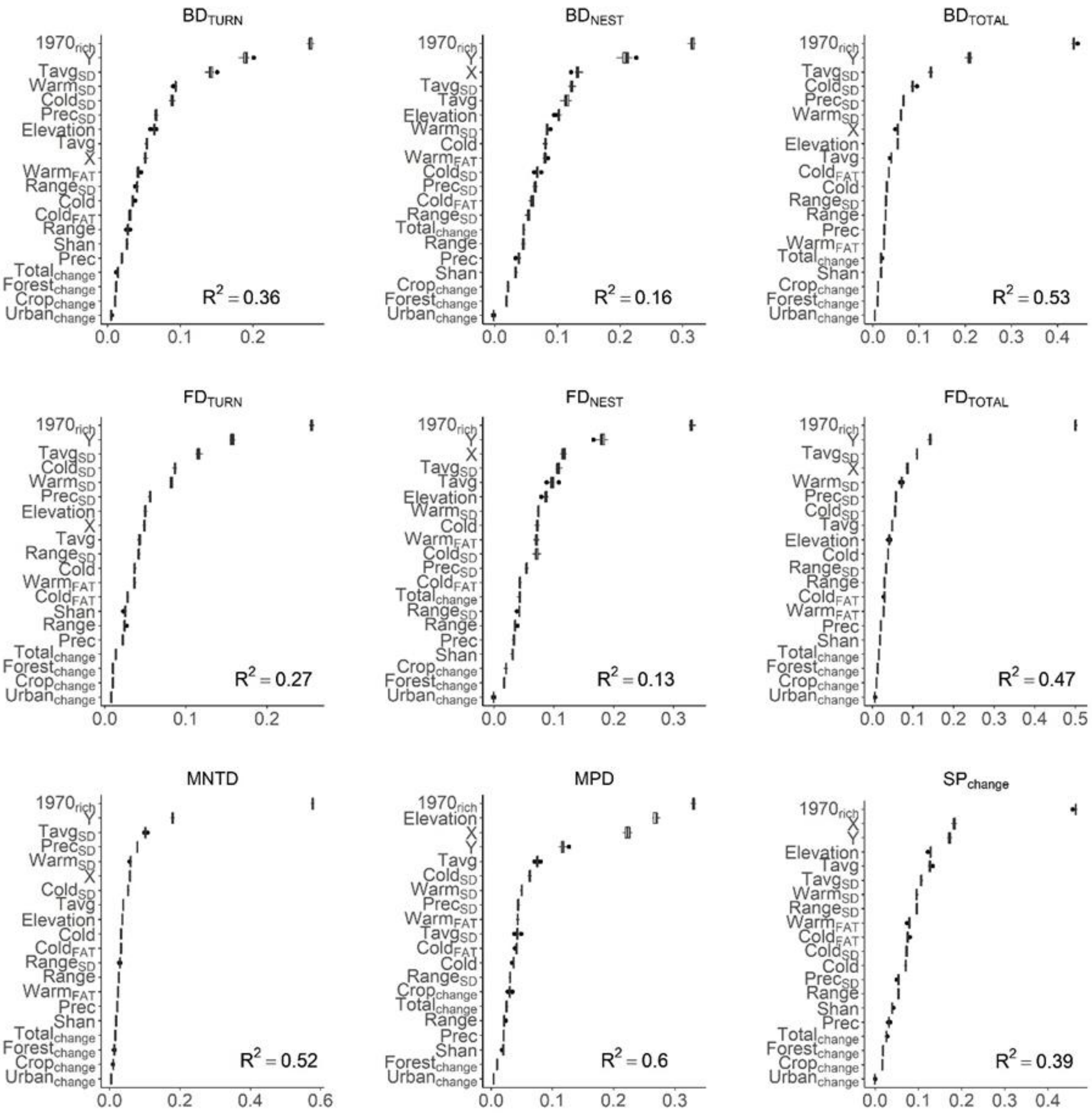

Figure 3.3. Variable importance scores from spatial random forest models for different measures of temporal change in assemblages (100km^2 hectads) of British birds from 1970 to 2010. The mean model explanatory power (R^2) is in the lower right of each plot. The metrics of assemblage composition change are; 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}), and 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.

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) (Fig. 3.3). Models trained on 75% of the data explained, on average, between 4% ± 3% (BD_{NEST}) and 50% ± 16% (MPD) of variation across the 20 training sets containing 25% of the data (Tables. S5.1 & S5.2, respectively).

Across all the models, the order of variable importance was similar. For all metrics except MPD, species richness in 1970 was the most important variable by a relatively large margin (Fig. 3.3). The variable importance for species richness and elevation in the MPD models was similar. Coordinates were also ranked highly across the models, with latitude more important than longitude for all metrics except for SP_{change} (Fig. 3.3). Changes in the standard deviation of the climatic variables were consistently ranked higher than the mean equivalent in all models except nestedness, MPD and SP_{change} (Fig. 3.3). LULC predictors were consistently poor predictors across the response metrics, although the difference in importance between these and most other variables was low (Fig. 3.3). Partial plots for the three most important variables (calculated using variable importance scores; see Appendix S3.6 for plots displaying all the variables) showed that all taxonomic and functional beta-diversity measures decreased with increasing species richness in 1970 and increased slightly with change in the standard deviation of average temperature ($Tavg_{SD}$; although the lines were largely stable, with functional nestedness and taxonomic nestedness flat) (Figs. 3.4 – 3.5). SP_{change} also decreased with increasing species richness in 1970 and elevation but increased slightly with increasing change in average temperature (Tavg; Fig. 3.4).

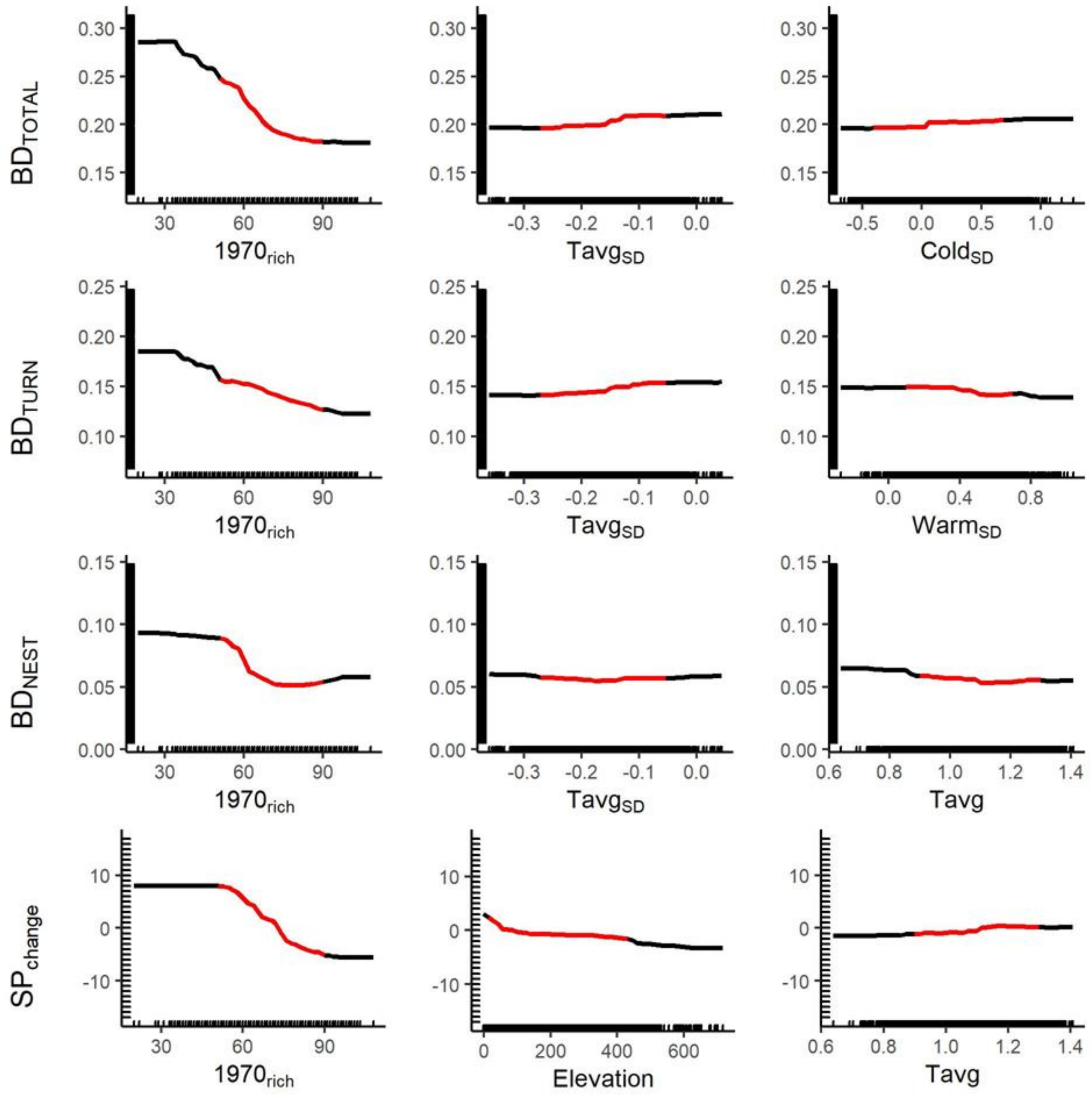

Figure 3.4. Partial plots of the marginal effect of each of the top three most important predictor variables (calculated from median random forest importance scores) on the temporal taxonomic beta-diversity (BD$_{TOTAL}$) of British breeding bird communities from 1970 – 2010, and its component parts, turnover (BD$_{TURN}$) and nestedness resultant dissimilarity (BD$_{NEST}$). Also shown are the partial plots for species richness change (SP$_{change}$). Each partial plot shows the mean marginal effect of the predictor variable across 20 random forest models for each metric. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). Variables are ordered according to median importance across the models (left to right).

MPD and MNTD had opposite relationships with 1970$_{rich}$ (MPD increasing, MNTD decreasing) (Fig. 3.5). In addition, MPD decreased with elevation and increased slightly with

Tavg (Fig. 3.5), whereas MNTD increased slightly with Tavg_{SD} and decreased slightly with a change in the standard deviation of precipitation (Prec_{SD}). Other variables had a limited effect (Fig. 3.5).

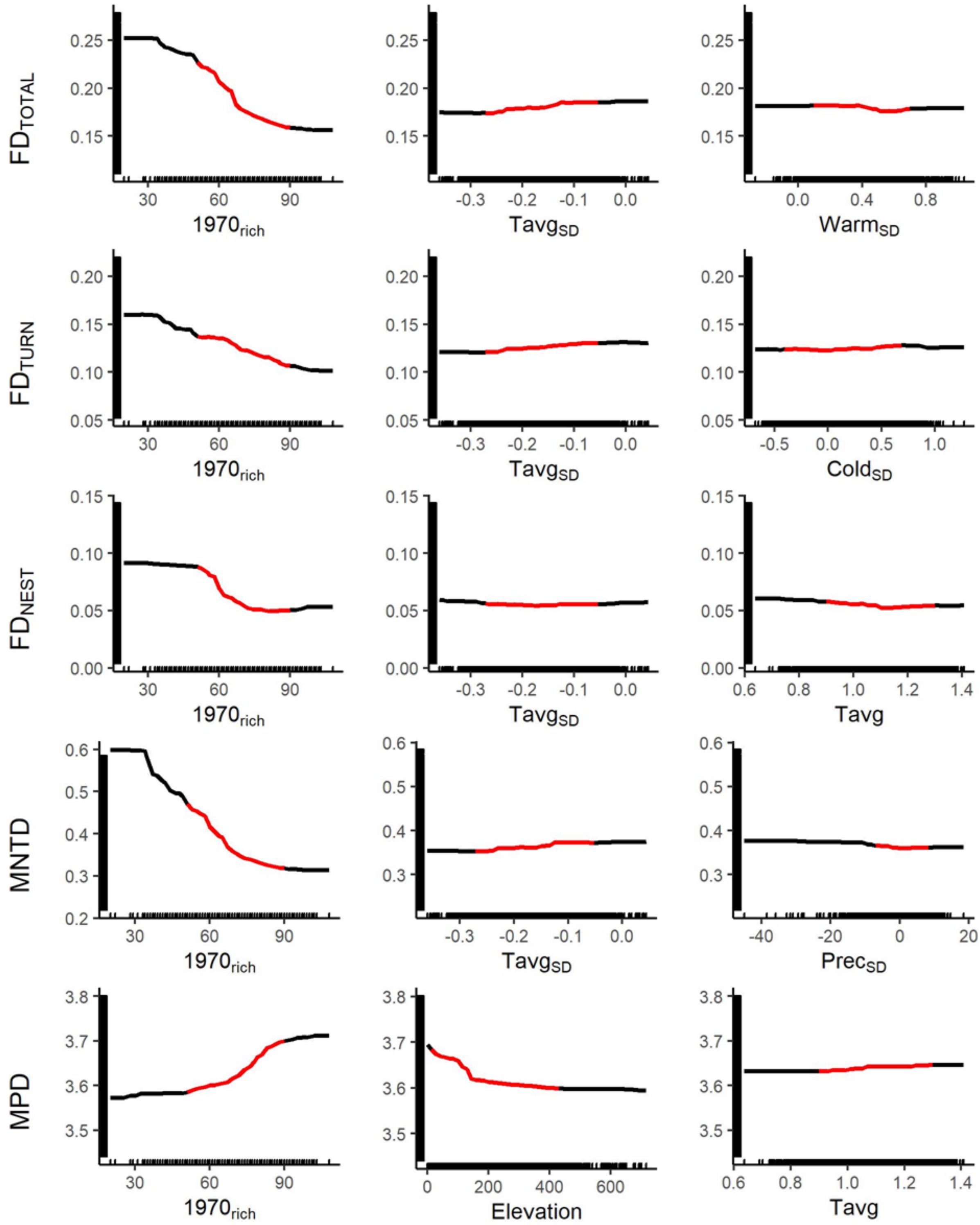

Figure 3.5. (Previous page) Partial plots of the marginal effect of each of the top three most important predictor variables (calculated from median random forest importance scores) had on the temporal functional beta-diversity (FD_{TOTAL}) of British breeding bird communities from 1970 – 2010, and its component parts turnover (FD_{TURN}), nestedness resultant dissimilarity (FD_{NEST}), and 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 predictor variables value (the red section of the lines). Variables are ordered according to median importance across the models (left to right).

All relationships between the composition change metrics and the predictors strengthened in the absence of spatial coordinates, but none of the relationships changed to any great extent (see Appendix S3.7).

3.4. Discussion

3.4.1. 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; Dornelas et al. 2018; Nunes et al. 2020; Petchey et al. 2007; Tinoco et al. 2021; Tsianou, Touloumis & Kallimanis 2021). Functional change was slightly lower on average 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).

Observed composition changes were mainly influenced by the number of species present in the assemblage in the earlier period, with larger assemblages changing relatively less than smaller ones. Because 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 may mean that more diverse assemblages may be protected to an extent against temporal disturbance, perhaps because they have a wider array of traits (and therefore functions), leading to a better functioning system and, therefore, more resilience (Jarzyna & Jetz, 2017; Weeks, Naeem, Lasky, & Tobias, 2020 PREPRINT). 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 species richer sites could be due to facilitation between species, with negative relationships between turnover and diversity expected when communities are characterised by strong interspecific facilitative interactions (Shurin, 2007; Pandit & Kolasa, 2012).

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

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 period) through time for both taxonomic and functional turnover. Pairs of sites also became less functionally and taxonomically nested. Given that the number of sites that gained or lost species was roughly even, and the functional pattern matched the taxonomic, the decrease in nestedness may 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 2130 hectads (226% increase), and the range of the cuckoo (*Cuculus canorus*) decreased from 2107 to 1258 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 to the results presented here, Baselga et al. (2015) found no change in the 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. Because 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 may be stochastic (Baselga et al., 2015; O'Sullivan, Terry & Rossberg, 2021; Stegen et al. 2013; Terry & Rossberg, 2021), or perhaps inappropriate or missing covariates. For example, the increases in the distribution of buzzard likely are due to enhanced protection. Declines in the distribution of the cuckoo have been attributed to grassland degradation, phenological changes in hosts, and conditions along migratory routes (Hewson, Thorup, Pearce-Higgins, & Atkinson, 2016). Such factors, and likely those affecting other species, were not considered in our modelling.

3.4.2. 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 may 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 up-slope) 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 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 standard deviation of average temperature were the most important. These findings generally are consistent with work that used data from earlier periods and highlighted that change in average temperature drove compositional change of British birds, although we found a weaker effect of climate than these studies in general (Davey et al., 2012; Davey, Devictor, Jonzén, Lindström, & Smith, 2013; White, et. al. , 2018). The importance scores of climate relative to both spatial coordinates and species richness in 1970 was generally low. This may be due to the resolution at which the assemblages were sampled. Climatic conditions were more relevant to avian temporal assemblage dissimilarity at finer (5 km x 5 km) compared to coarser resolutions (up to 80km x 80km) in New York

State, although this resolution dependence was not as strong for temporal turnover in the same study (Jarzyna et al., 2015).

When considering the impact, or lack thereof, of LULC variables within the models, there are several potential factors. As can be seen from the 90% central range lines in the partial plots (red lines; Supplementary Figs. S3.6.1 – S3.6.9), $\text{Urban}_{\text{change}}$ was heavily zero-inflated. Low recorded land-use change may be due to the measure of land change. The base LULC data used here was the dominant LULC type on a 1 km^2 grid. Therefore, for urban land to be classified as increasing or decreasing in a 1 km^2 grid cell within the larger 100 km^2 hectad, that 1km^2 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 urbanised 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 km^2, and agricultural intensification, all of which potentially drive assemblage change (Boulinier et al., 1998; Hendershot et al., 2020).

3.4.3. 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, O’Hara, Caplat, Hickler, & Smith, 2015). Hunting along the migratory route and abiotic and biotic variables within wintering grounds can impact populations, potentially causing fewer migrants to reach Britain and, therefore, not utilising the maximum available areas (Lormée et al., 2019; Vickery et al., 2014).

Sampling effects can have impacts on analyses of assemblage composition (Neate-Clegg et al., 2020). While 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, Adler, & Şekercioğlu, 2018; Mccaffrey, 2005). We accounted for potential sampling bias by removing the grid cells in which the number of benchmark species detected considerably changed (Gillings et al., 2019; Appendix S3.1). In addition, the atlases censuses are conducted over four years, so they should provide a more accurate picture of species colonisations 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, as the data were not available to explore that here.

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

3.5. Conclusions

Although British breeding bird assemblages changed in both time and space between 1970 and 2010, that change does not appear to be 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 more species-rich assemblages at lower elevations, and indeed, larger assemblages appeared somewhat buffered to change. Although no consistent signal of species loss or gains was found, these presence-absence data do not incorporate abundance. Indeed, across a similar time period (1970 – 2017), the estimated drop 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 may 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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4. Unravelling the complexities of temporal biotic homogenisation and heterogenisation: avian assemblage dynamics in Britain

Abstract

The replacement of ecological specialists by generalists leads to species assemblages becoming more taxonomically, phylogenetically, and functionally similar, with implications for ecosystem functions and services. The standard way of identifying this process of temporal biotic homogenisation is to look for decreases in assemblage dissimilarity (spatial beta-diversity) over time. However, using a single metric to assess homogenisation without looking at the underlying occupancy changes can mask positive changes, an example of which would be increases in species benefiting from conservation action. In this study, we use measures of taxonomic beta-diversity to partition the effects of extirpation and colonisation in British breeding bird communities into biotic homogenisation and heterogenisation. Using Bayesian spatial regression models, we explore the influence of climate, land cover, and species specialization on the changes observed between survey periods separated by two decades (1988–1991 and 2008–2011). We show that the change in regional assemblages was mainly in the direction of homogenisation, characterised by decreased spatial beta-diversity and turnover between sampling periods. Homogenisation was evident across all measures of dissimilarity, including phylogenetic and functional metrics. In areas where increased turnover was observed, this was largely due to local extirpations of species, whereas decreased turnover was largely driven by local colonisations. The dominant dynamic across Britain was a mosaic of heterogenisation-by-extirpation interspersed with homogenisation-by-colonisation of common habitat generalists. Our results show that patterns of dissimilarity change inferred from temporal spatial beta-diversity do not necessarily equate to increased or decreased alpha or gamma diversity or loss of specialisation, arising instead from complex histories of colonisation and

extirpation. Such temporal patterns should only be interpreted with caution and in the light of species identities, particularly in the context of conservation planning.

4.1. Introduction

Biotic homogenisation (Olden, 2006; Olden & Poff, 2004; Olden & Rooney, 2006) is typically defined as a process where specialist species are replaced by generalists over time and space to create communities that are taxonomically, functionally, and often phylogenetically (Hughes et al., 2022) more similar to one another. The similarity, or dissimilarity, betweeen groups of assemblages is usually measured through spatial beta-diversity, a metric that calculates the degree to which different communities are differentiated from one another or nested subsets. Homogenisation is usually identified through decreases in community dissimilarity over time (temporal spatial beta-diversity). True biotic homogenisation, i.e., the replacement of specialists by generalists, can have impacts on ecosystem functions and services (Wang et al., 2021), causing decreases in the diversity and alterations in the community composition of key groups, such as pollinators (Carvalheiro et al., 2013). However, while it is generally agreed that anthropogenically generated disturbance such as a land-use change (Frishkoff et al., 2014; Ibáñez-Álamo et al., 2017; Karp et al., 2018; Mitchell et al., 2022) and climate change (Britton et al., 2009; Davey et al., 2012) are largely favouring the expansion of generalist species (Davey et al., 2012), the literature on local diversity change across time and space remains contradictory due to the intricacies in disentangling the nuances of what is driving change (Jarzyna & Jetz, 2017; Tingley & Beissinger, 2013). Indeed, even at the global level, patterns of change seem largely non-directional (Dornelas et al., 2019), with various outcomes at different scales reported with respect to biotic homogenisation, including increases in spatial beta-diversity (β-diversity) over time (Marchetti et al., 2006; Socolar et al., 2016). However, what is general to most of the studies looking at the change in dissimilarity over time and space is the omittance of species identities due to the focus on the overall metric of change. Therefore, the relationship between the increase (heterogenisation) or decrease (homogenisation) in dissimilarity over time (spatial temporal beta-diversity) and the underlying extirpations and colonisations leading to that change is often overlooked.

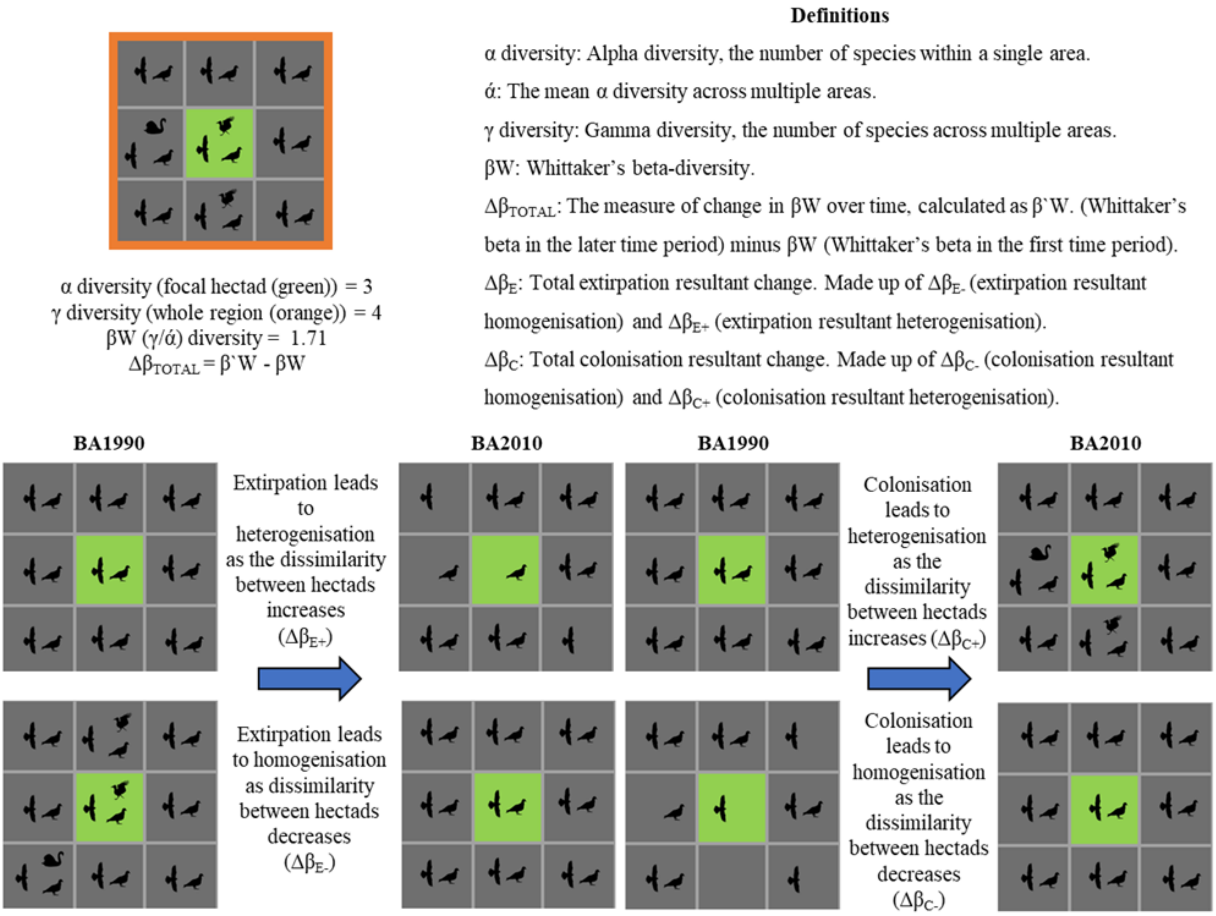
Temporally, increases in β-diversity (i.e., heterogenisation) across a region can be attributed to greater variation in habitats over time (temporal habitat heterogeneity, increasing the niche space available), the presence of newly introduced species that stay confined to specific areas (i.e., they do not propagate across the region), and/or the decline of widespread or jointly occurring species among different locations (Chase et al., 2019). Conversely, decreases in β-diversity (i.e., homogenisation) can occur due to the opposite, i.e., the loss of habitat diversity, species confined to specific areas, and/or the increase of locally common species across the measured region. Homogenisation does not always mean that the region experiences 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 colonisation can increase differentiation (i.e., heterogenisation) if the colonising 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 heterogenisation occurred over time within Californian (US) fish assemblages but as a result of high colonisation at some sites, including invasive species, and low corresponding extirpation in other sites. To take another example, Rooney et al. (2004) found that although the average dissimilarity in upland forest stands in Wisconsin (US) decreased (homogenised) across the sampled region over time, certain individual pairs became more dissimilar, highlighting the increase in distinctiveness within individual sites. Therefore, how assemblage dissimilarity is assessed likely influences the outcomes, something not often considered in biotic homogenisation 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 colonisation-resultant change. As species losses and gains can both increase (heterogenisation) or decrease (homogenisation) β-diversity within a given region depending upon the initial local prevalence of the species involved, examining the contribution of extirpation and colonisation to changing dissimilarity can provide a more fine-scale assessment of changes in local assemblage compositions (Fig.4.1). Therefore, understanding whether colonisation or extirpation is driving patterns in homogenisation, and assessing the relative contributions of each measure, is vital to comprehending whether any observed homogenisation is ‘true biotic homogenisation’ (i.e., the replacement of specialists by generalists) (Clavel et al., 2011; Davey et al., 2012; Devictor et al., 2007, 2008; Liang et al., 2019) or if it is due to stochastic variation in common species dynamics driving a ‘perceived homogenisation’. 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 functional alpha diversity (Sullivan et al., 2016; Fig.4.1).

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) (Rackham, 1986; Robinson, 2014), continuing into the 21st century (Bibby, 2009). One could thus argue Britain represents a system that has been disturbed to such an extent that there are no “true” wildlife refuges left (Willis & Birks, 2006). This means that avian communities are largely structured spatially post-disturbance, but evidence suggests the assemblage composition of areas is still shifting. For example, Sullivan et al. (2016) found that breeding bird communities became more homogenous over time (1994–2012) across Britain, driven largely by decreases in moderately generalist species populations and increases in the most generalist. A similar pattern of biotic homogenisation was found using atlas (presence/absence) level data, largely driven by changes in climatic variables (White et al., 2018b). However, the extirpation and colonisation dynamics driving those patterns are not known.

Here, using atlas data of British breeding birds within 10 x 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 grid and its immediate neighbours) within Britain are undergoing homogenisation or heterogenisation by comparing β-diversity in regions between the time points (Baselga, 2010; Baselga & Orme, 2012). Utilising three dimensions of diversity (taxonomic, functional and phylogenetic), we assess whether changes in total β-diversity and turnover using the three metrics 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 test whether changes in taxonomic β-diversity within regions are driven by colonisations or extirpations of species and if the level of contribution to the different facets of extirpation and colonisation-resultant change statistically differ across bird guilds (habitat specialisation, trophic niche, and migration type).

Overall, we expect regional assemblages to have mainly homogenised (i.e. reductions in β-diversity) between the periods based on earlier studies within the same locale and time period (Sullivan et al., 2016; White et al., 2018a). Different facets of extirpation and colonisation-resultant change ($\Delta\beta_E$ and $\Delta\beta_C$, respectively) relate to locally common (colonisation-resultant homogenisation ($\Delta\beta_{C-}$) and extirpation-resultant heterogenisation ($\Delta\beta_{E+}$)) and locally rare species (colonisation-resultant heterogenisation ($\Delta\beta_{C+}$) and extirpation-resultant homogenisation ($\Delta\beta_{E-}$)) (Tatsumi et al., 2021). Figure 1 provides an illustration of these different facets and how they relate to changes in β-diversity. Therefore, we expect $\Delta\beta_{E+}$ and $\Delta\beta_{C-}$ to be the main dynamics across Britain, habitat generalists to be the main 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, to be the main driver of $\Delta\beta_{E-}$ and $\Delta\beta_{C+}$. Species with initially larger range sizes (within Britain) in the earlier time period should mainly contribute to extirpation-resultant heterogenisation and colonisation-resultant homogenisation, as the larger 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 heterogenisation ($\Delta\beta_{E+}$) if these species retain occupancy in at least one area within the region and that increases in occupancy (colonisations) will cause colonisation-resultant homogenisation ($\Delta\beta_{C-}$) as they colonise remaining areas (White et al. 2018a). The opposite should then be true for species with smaller initial ranges (i.e., they are more likely to be locally rare).



Definitions

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

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

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

βW: Whittaker's beta-diversity.

$\Delta\beta_{TOTAL}$: 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).

$\Delta\beta_C$: Total colonisation resultant change. Made up of $\Delta\beta_{C-}$ (colonisation resultant homogenisation) and $\Delta\beta_{C+}$ (colonisation resultant heterogenisation).

α diversity (focal hectad (green)) = 3
γ diversity (whole region (orange)) = 4
βW ($\gamma/\acute{\alpha}$) diversity = 1.71
$\Delta\beta_{TOTAL} = \beta`W - \beta W$

Extirpation leads to heterogenisation as the dissimilarity between hectads increases ($\Delta\beta_{E+}$)

Extirpation leads to homogenisation as dissimilarity between hectads decreases ($\Delta\beta_{E-}$)

Colonisation leads to heterogenisation as the dissimilarity between hectads increases ($\Delta\beta_{C+}$)

Colonisation leads to homogenisation as the dissimilarity between hectads decreases ($\Delta\beta_{C-}$)

Figure 4.1. Conceptual diagram showing how species colonisation and extirpations 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 beta-diversity) over time. Shown at the top of the figure are definitions of the components used to calculate colonisation and extirpation resultant change.

4.2. Materials and Methods

4.2.1. 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 four-year periods: 1988 – 1991 (BA1990) and 2008 – 2011 (BA2010) atlases. In both periods, surveyors visited a minimum of eight tetrads (2 km x 2 km squares) within each hectad (10 km x 10 km squares) across the British Isles. Surveys were similarly timed for both atlases, with at least 16 hours spent per hectad (see Gillings et al., 2019 for further details). We excluded pelagic, vagrant, and non-native species, as well as species whose ranges in the atlases were presented at coarse spatial grains due to persecution and egg-collecting concerns, resulting in 159 species for analysis (see Appendix S1 for the full species list). Following Gillings et al. (2019), we used data for birds classified as "breeding" in BA1990 and "probable" or "confirmed" breeders in BA2010. 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 2,291 hectads.

4.2.2. 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, dietary niche, and ecological function (Pigot et al., 2020; Tobias & Pigot, 2019; Trisos et al., 2014). See Tobias et al. (2022) for trait measurement and collation details.

For the calculation of functional diversity, we first log10-transformed and standardised all traits to remove the right skew present in the trait data and to bring the traits onto comparable scales, respectively. Using all UK species, a principal components analysis (PCA) was performed on the transformed traits to produce uncorrelated axes, retaining all axes as even those explaining minimal variation have been shown to be informative (Pigot et al., 2020). We employed the agglomerative hierarchical clustering method (UPGMA) to create a functional dendrogram using the PCA axes from section 2.2 for all species, generating a rooted tree (Petchey & Gaston, 2007). We tested if the functional distances in the dendrogram represented true distances using the *tree.quality* function from the “BAT” package (Cardoso et al. 2022). The quality was 0.86, showing that the tree was a good representation of the true distances of the species within the functional space (Matthews et al., 2023). We opted for using a dendrogram due to the high number of sites, as calculating functional β diversity using convex hulls or hypervolumes (e.g., Mammola & Cardoso, 2020) would require impractically extensive computing resources.

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 colonisation resultant change that could be attributed to different species guilds (see section 2.7). Using Sullivan et al. (2016), we extracted a species habitat specialisation index and quartile (Q1 to Q4, indicating generalist, moderately generalist, moderately specialist and specialist species) for all species in the dataset. As Sullivan et al. (2016) collected data between 1994 and 2012 across Britain and included species abundance, their specialisation indices are more accurate than those we could calculate using presence-absence data for the same period.

4.2.3. Phylogenetic data

We used the Ericson backbone phylogenetic trees from Jetz et al. (2012), which includes 9,993 species, to compute phylogenetic diversity measures. We updated species names to match the phylogeny where taxonomic nomenclature had changed or species were grouped (e.g., common/Scottish crossbill; see supporting S1 for the entire species list). We selected 3,000 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 (as Jetz et al.'s trees are post-burn-in). The resulting consensus tree had a few negative branch lengths, which is not uncommon with maximum clade credibility trees. We addressed this by converting negative branches to zero and shortening the two branches below by the same absolute value, maintaining ultrametric trees without polytomies. Finally, we pruned the consensus tree to retain only the tips of species in the British breeding bird dataset.

4.2.4. Climate and land cover data

We obtained monthly precipitation and average temperature data for 1981–2011 from the UK Met Office (Hollis et al., 2019) and calculated the average temperature (°C) and total precipitation for each year from April to July (the breeding season) for each region (focal hectad and its immediate neighbours). We then averaged yearly values across 1981–1991 and 2001–2011 to create mean values per region for each atlas period. The change in temperature (ΔTemperature) 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 ($\Delta\text{Temperature}_{SD}$) and for precipitation (ΔPrecipitation) and its variability ($\Delta\text{Precipitation}_{SD}$).

We obtained land cover change data from the Land Cover Change 1990–2015 dataset (Rowland et al. 2020) and used a moving window approach (Fig.4.2) 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.

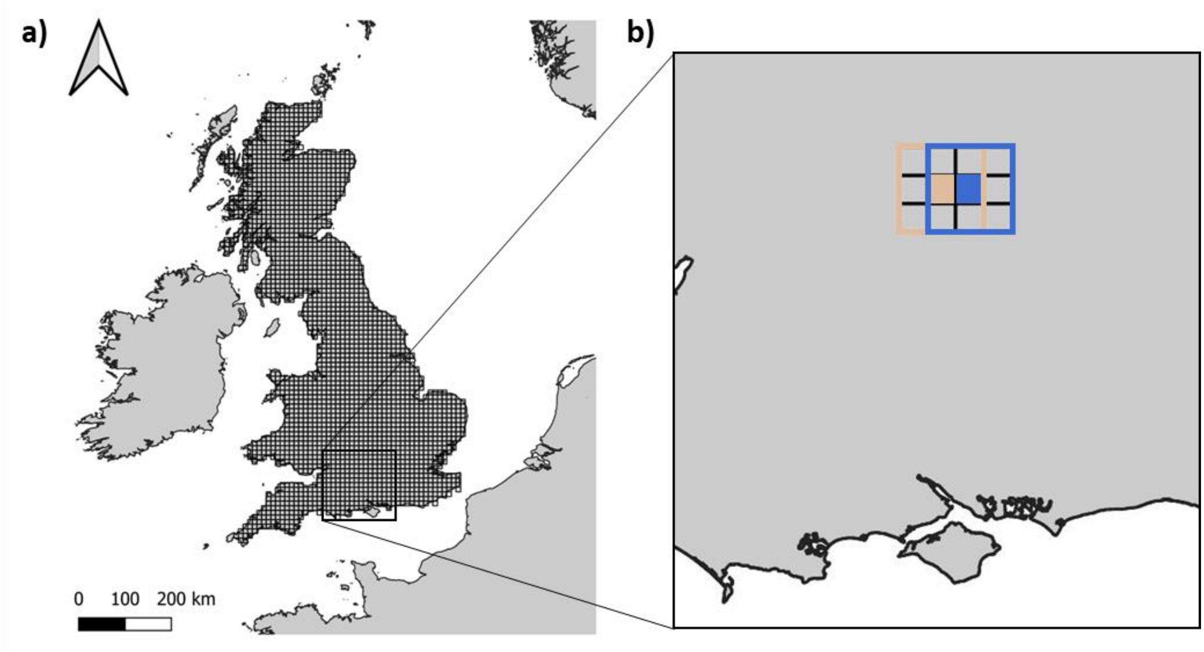


Figure 4.2. a) Map of the study area (Britain) with all of the 10km x 10km grids (hectad) used displayed. The plot on the right (b) shows the moving window calculation, with the smaller filled squares highlighting the focal hectad and the larger squares showing the window for spatial beta-diversity calculation. For each hectad, multiple β-diversity and other variables were calculated using the focal hectad and the surrounding eight neighbours.

Additionally, we calculated the elevation of each region using data from the shuttle radar topography mission (SRTM) by extracting data from 1600 equally separated points within each region. We then took the average across the extracted data points within a region.

4.2.5. Change in multiple β-diversity

For each hectad, we assessed assemblage changes between the two periods to determine the extent of homogenisation or heterogenisation in breeding bird communities across Britain. We employed multiple β-diversity measures that calculate dissimilarity across a region (Baselga et al., 2015; Baselga & Orme, 2012). These measures are optimal for detecting homogenisation and heterogenisation 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). Using species presence-absence data along with the functional and phylogenetic data calculated earlier, we applied two approaches to calculate multiple β-diversity: Whittaker's β-diversity (Jost, 2007; Whittaker, 1960) and the BAS framework (Baselga, 2010).

4.2.5.1. *Whittaker's β-diversity and colonisation/extirpation resultant change*

We employed Whittaker's multiple beta (β) diversity metric (γ / average α) (also known as taxonomic beta-diversity, hereafter referred to as βW; Matthews et al., 2019) and a recent method by Tatsumi et al. (2021) to calculate homogenisation and heterogenisation proportions 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 eight neighbours (hereafter defined as a region), following Barnagaud et al., 2017; McKnight et al., 2007; White et al., 2018a; Fig.4.2). Hectads with less than eight neighbours were included if they had at least two neighbouring hectads. We calculated the change in βW between time periods as the difference between βW in BA2010 and βW in BA1990, referred to as $\Delta\beta_{TOTAL}$, following Tatsumi et al. (2021). Positive values indicate heterogenisation, while negative values signify homogenisation (Fig.4.1).

We partitioned the change in βW for each region into total extirpation and colonization-related changes ($\Delta\beta_E$ and $\Delta\beta_C$, respectively) and the proportion attributable to homogenisation and heterogenisation for both ($\Delta\beta_{E-}$ and $\Delta\beta_{E+}$, and $\Delta\beta_{C-}$ and $\Delta\beta_{C+}$, for extirpation and colonization, respectively). This partitioning framework allows investigation of the underlying causes of homogenisation or heterogenisation, determining whether the observed $\Delta\beta_{TOTAL}$ change results from species extirpation or colonization in the region (Fig.4.1). It can also identify species-specific contributions, revealing which species drive the dominant pattern through extirpation or colonization. Due to how the measures are calculated, they either reflect locally common ($\Delta\beta_{E+}$ and $\Delta\beta_{C-}$) or locally rare ($\Delta\beta_{E-}$ and $\Delta\beta_{C+}$) species dynamics. See Tatsumi et al. (2021) for more details on the partitioning framework.

Finally, we employed Wilcoxon one-sample tests to determine if each metric (i.e., $\Delta\beta_{TOTAL,}$ $\Delta\beta_{C-}$, $\Delta\beta_{C+}$, $\Delta\beta_{E-}$, and $\Delta\beta_{C+}$) significantly differed from zero.

4.2.5.2. *BAS framework*

For comparison with $\Delta\beta_{TOTAL}$, we also calculated regional change in β-diversity using the BAS framework (Baselga, 2010). This framework is one commonly used within studies of beta-diversity. The framework computes multiple 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 $\Delta\beta_{TOTAL}$ and the Sorensen equivalent.

Using the *beta.multi* function from the "betapart" R package (Baselga & Orme, 2012), we calculated multiple β-diversity and turnover for each hectad and its immediate neighbours in each time period. We then subtracted the BA2010 value for total β-diversity and turnover from the BA1990 value for each hectad, yielding change measures between the two periods (MBD_{TOTAL} and MBD_{TURN} for multiple total β-diversity change and multiple turnover changes, 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 4.2.3, calculating phylogenetic multiple β-diversity and turnover (MPD_{TOTAL} and MPD_{TURN}, respectively). We repeated the phylogenetic β-diversity process using the functional dendrogram to produce multiple functional measures for total β-diversity and turnover (MFD_{TOTAL} and MFD_{TURN}, respectively).

4.2.6. Modelling change

To model change in each of the calculated metrics, we used intrinsic conditional autoregressive modelling. We retained all explanatory variables within each model for each metric. This approach accounts for autocorrelation within the error term and has been used successfully on BTO atlas data previously with the same moving window approach (White et al., 2018b). This was performed under Bayesian inference using the Integrated Nested Laplace Approximation (INLA) using 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).

4.2.7. Group differences

To assess if habitat specialisation of species impacts total contribution to $\Delta\beta_C$ or $\Delta\beta_E$, we compared average colonisation and average extirpations of the specialisation quartiles using a Kruskal-Wallis test and a Dunn test 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 specialisation 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 (DOI 10.5061/dryad.hx3ffbgm6).

4.3. Results

4.3.1. Regional homogenisation and heterogenisation

Spatial patterns and averages of Whittaker's multiple β-diversity metric (mean $\Delta\beta_{TOTAL}$ = -0.12 ± 0.18), multiple β-diversity (MBD_{TOTAL} = -0.06 ± 0.08), multiple functional diversity (MFD_{TOTAL} = -0.06 ± 0.07), and multiple phylogenetic diversity (MPD_{TOTAL} = -0.06 ± 0.08) were generally consistent, revealing regional homogenisation across much of Britain and heterogenisation in specific regions such as the Scottish Highlands, Lake District, North-central England, South Wales, and South-east England (Fig.4.3g & Supplementary Fig. S4.2.1). 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}; Supplementary Fig. S4.2.1). However, not all regions were consistent in terms of the direction of change (homogenisation or heterogenisation) 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 (White et al., 2018b).

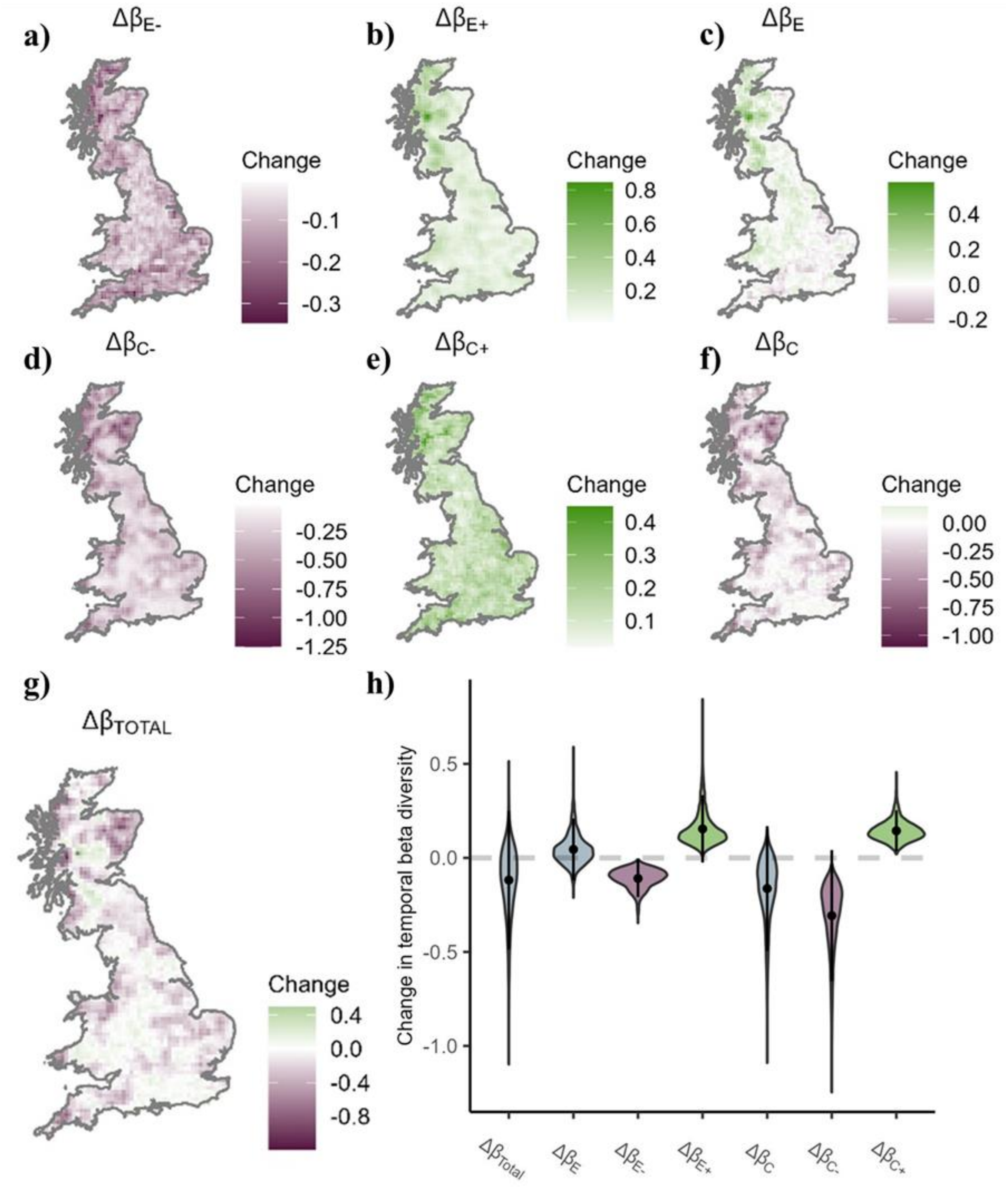


Figure 4.3. Maps of change between two sampling periods (BA1990 and BA2010) for breeding bird communities across Britain for measures of **(a)** extirpation resultant homogenisation ($\Delta\beta_{E-}$) **(b)** heterogenisation ($\Delta\beta_{E+}$) **(c)** total extirpation resultant change ($\Delta\beta_{E}$), **(d)** colonisation resultant homogenisation ($\Delta\beta_{C-}$), **(e)** colonisation resultant heterogenisation ($\Delta\beta_{C+}$), **(f)** total colonisation resultant change ($\Delta\beta_{C}$), and **(g)** change in Whittaker's β-diversity. For all metrics, negative values indicate homogenisation and positive values indicate heterogenisation. All values were calculated using moving windows around focal hectads. The violin plot **(h)** shows the median (dot) of each measure across all British hectads, alongside the 1.5 interquartile range (whiskers).

On average, a given region (i.e., a focal hectad and its immediate neighbours) experienced 12.3 ± 4.6 regional colonisations (i.e., species new to the region as a whole) and 150 ± 52 hectad level colonisations 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. Both results together show high temporal spatial turnover. Colonisation 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 $\Delta\beta_{TOTAL}$ (Fig.4.3c,d,g). The average values of $\Delta\beta_{E-}$ and $\Delta\beta_{E+}$ were -0.11 ± 0.05 and 0.15 ± 0.09, respectively (Fig.4.3a,b), indicating the presence of both extirpation resultant heterogenisation and extirpation resultant homogenisation, respectively. Extirpations mainly caused heterogenisation, with an average $\Delta\beta_E$ of 0.05 ± 0.08. There were 677 regions with negative $\Delta\beta_E$ and 1614 with positive $\Delta\beta_E$ (Fig.4.3c). Average $\Delta\beta_{C-}$ and $\Delta\beta_{C+}$ values were -0.31 ± 0.17 and 0.14 ± 0.05, respectively (Fig.4.3d,e), indicating the presence of both colonisation resultant homogenisation and colonisation resultant heterogenisation, respectively. Colonisations predominantly led to homogenisation, 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 (Fig.4.3f). 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 ($p < 0.001$).

4.3.2. Drivers of regional change

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 with credible intervals that do not span zero (Fig. S4.2.2). Positive effects included Elevation, $Precipitation_{SD}$, Longitude, 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), ΔTemperature, and Grassland. Credible intervals spanning zero were found for Freshwater, ΔPrecipitation, Urban (except for $\Delta\beta_{TOTAL}$), and $\Delta\text{Temperature}_{SD}$ (except for MBD_{TOTAL} and MFD_{TOTAL}). Latitude was positive for all measures except $\Delta\beta_{TOTAL}$. 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)] (Fig. S4.2.2).

In this section and those following, we only describe the effects of predictors with credible intervals that do not span zero. For turnover measures (MBD_{TURN}, MPD_{TURN}, MFD_{TURN}), ΔPrecipitation, Latitude, and Other had positive effects (Fig. S4.2.2). Grassland and $\Delta\text{Temperature}_{SD}$ both had negative effects for all the measures (Fig. S4.2.2). Elevation had a positive effect on both MBD_{TURN} and $MPD_{TURN,}$ and Urban and Freshwater were also positive for MBD_{TURN} (Fig. S4.2.2). Latitude had the largest absolute effect size for all of the turnover measures (Fig. S4.2.2).

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, $\Delta\text{Precipitation}_{SD}$, ΔTemperature, and Latitude (Fig.4.4a). Woodland, Grassland, Urban, and $\Delta\text{Temperature}_{SD}$ were negative for $\Delta\beta_{C+}$. Shannon Evenness, Elevation, $\Delta\text{Precipitation}_{SD}$, ΔPrecipitation, ΔTemperature, Longitude, and Latitude were all positive for $\Delta\beta_{C+}$ (Fig.4a). Shannon Evenness, $\Delta\text{Precipitation}_{SD}$, ΔTemperature, and Latitude were positive for $\Delta\beta_{C-}$ (Fig.4.4a). $\Delta\text{Temperature}_{SD}$, ΔPrecipitation, Longitude, Woodland, Grassland and Freshwater all had a negative effect (Fig.4.4a). The largest absolute effect sizes were ΔTemperature$_{SD}$ for Δβ$_C$ and Longitude for both Δβ$_{C-}$ and Δβ$_{C+}$ (Fig.4.4a).

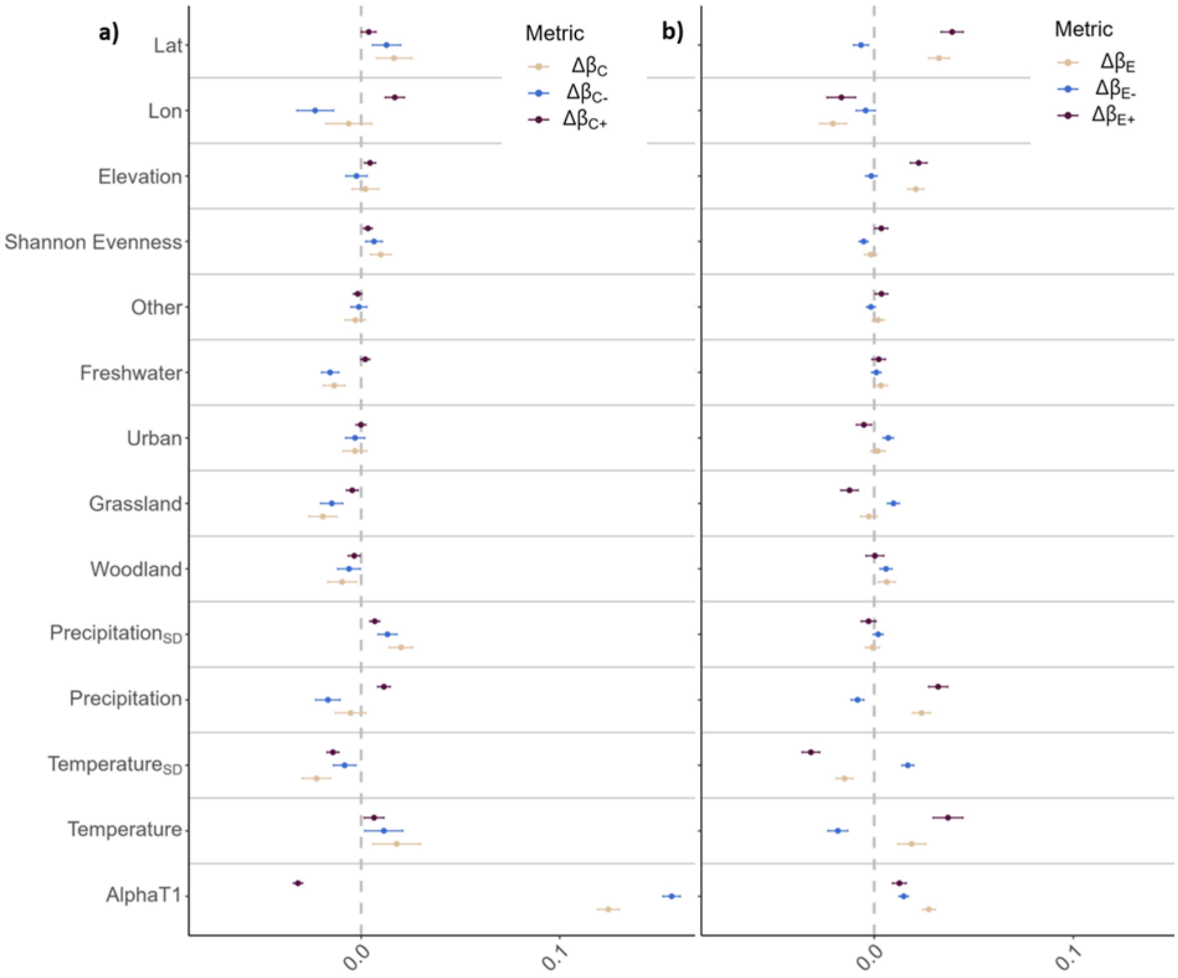


Figure 4.4. Effect sizes and confidence intervals from the Integrated Nested Laplace Approximation (INLA) models for **a)** total colonisation resultant change (Δβ$_C$) and its two components, colonisation resultant homogenisation (Δβ$_{C-}$) and heterogenisation (Δβ$_{C+}$) and **b)** total extirpation resultant change (Δβ$_E$) and its two components; extirpation resultant homogenisation (Δβ$_{E-}$) and heterogenisation (Δβ$_{E+}$).

For Δβ$_E$, Elevation, ΔPrecipitation, ΔTemperature, Latitude, Woodland, and Freshwater were all positive (Fig.4.4b). Negative effects were found for ΔTemperature$_{SD}$ and Longitude (Fig.4.4b). For Δβ$_{E+}$, Elevation, ΔPrecipitation, ΔTemperature, Latitude, and Other were all positive (Fig.4.4b). ΔTempature$_{SD}$, Longitude, Grassland and Urban were all negative (Fig.4.4b). Woodland, Grassland, Urban, and ΔTemperature$_{SD}$ all had a positive effect for

$\Delta\beta_{E-}$ (Fig.4.4b). Shannon Evenness, ΔPrecipitation, ΔTemperature, and Latitude were all found to be negative (Fig.4.4b). Latitude had the largest effect size for $\Delta\beta_{E}$ and $\Delta\beta_{E+}$, while ΔTemperature was the largest for $\Delta\beta_{E-}$.

4.3.3. Guild differences

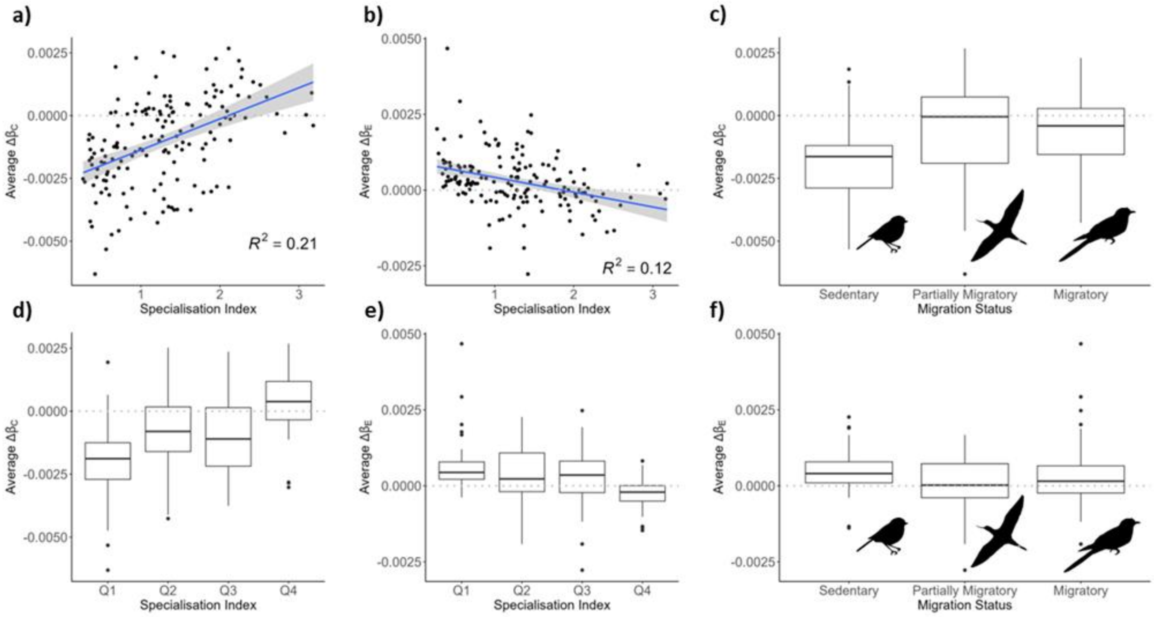


Figure 4.5. Observed changes in average colonisation ($\Delta\beta_{C}$) and extirpation ($\Delta\beta_{E}$) in relation to the habitat specialisation index (where increased values indicate increased specialisation; **a** and **b**), quartiles of habitat specialisation (where Q1 is generalist and Q4 is specialist; **d** and **e**), and migratory status (**c** and **f**). For **a** and **b**, the fitted line is from a linear ordinary least squares model, with grey shading showing the 95% confidence interval.

Habitat specialists were found to have significantly higher average $\Delta\beta_{C}$ (0.0002 ± 0.0013) than those found for generalists (-0.002 ± 0.0015, $p < 0.001$) and moderately specialist species (-0.001 ± 0.0015, $p < 0.01$; Fig.4.5a,d), according to a Dunn test. Generalists also had significantly lower $\Delta\beta_{C}$ than moderately generalist species (-0.0009 ± 0.0017, $p < 0.01$; 4.5a,d). Specialists (Q4) had significantly lower average $\Delta\beta_{E}$ (-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, $p < 0.01$; 4.5b,e). While these patterns of positive $\Delta\beta_{C}$ and negative $\Delta\beta_{E}$ for specialists and negative $\Delta\beta_{C}$ and positive $\Delta\beta_{E}$ for generalists were found to be the general pattern at the regional assemblage level, some species within each quartile exhibited contrasting colonisation and extirpation resultant change (Fig.6a). Species with an initially larger range size (number of hectads in BA1990) were found to generally have larger $\Delta\beta_E$ and lower $\Delta\beta_C$ (Fig.4.6b,c).

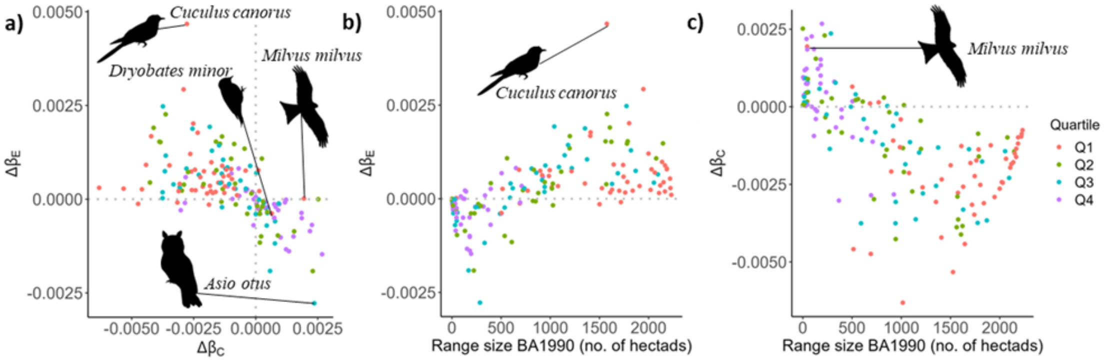


Figure 4.6. Relationship between the measures of colonisation ($\Delta\beta_C$) and extirpation ($\Delta\beta_E$) with habitat specialism (**b**) and habitat specialism alongside range size (**b** and **c**). The quartiles range from the most generalist (Q1) to the most specialist (Q4).

For migration type, both migratory (-0.001 ± 0.001) and partially migratory species (-0.001 ± 0.002) had significantly higher average $\Delta\beta_C$ than sedentary species (-0.002 ± 0.002, $p < 0.001$ and $p < 0.01$ for migratory and partially migratory species, respectively; Fig.4.5c). No significant differences were found for average $\Delta\beta_E$ (Fig.4.5f). Regarding trophic niche, the only significant difference was found between aquatic predators and omnivores ($p < 0.05$) for $\Delta\beta_C$.

4.4. Discussion

Across Britain, regional assemblage changes between BA1990 and BA2010 were driven mainly by the colonisation 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 homogenisation, patterns of regional avian homogenisation/heterogenisation in the UK are largely driven by the changing fortunes of generalists across the period. Expansions and contractions of local generalist populations are causing local colonisations 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 (Gaston & Fuller, 2007; Lennon et al., 2004). We also found sedentary species had significantly lower average $\Delta\beta_C$ (-0.002 ± 0.001) than migrants and partial migrants (0.001 ± 0.001 and 0.001 ± 0.002, respectively), highlighting that between the periods, sedentary species were the main proponents of regional colonisation homogenisation, i.e., range increases leading to a negative $\Delta\beta_C$ (Pearce-Higgins et al., 2015). However, individual species' contributions to the assemblage-level metrics $\Delta\beta_E$ and $\Delta\beta_C$ were complex and highlight 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, and hence an apparent biotic homogenisation, this homogenisation was, in fact, largely driven by generalist species colonisations across a given region. The main proponents of such colonisation change, i.e., the “winners”, were largely species that have benefited from increased conservation action due to past persecution. For example, goshawk (*Accipiter gentilis*), buzzard (*Buteo buteo*) (Table.4.1), hobby (*Falco subbuteo*), red kite (*Milvus milvus*), and peregrine (*Falco peregrinus*) all increased their ranges and contributed to increased regional homogenisation because of actions taken to increase their populations between the surveyed time periods (e.g. Banks et al., 2010; Harris et al., 2021). However, while these changes decreased dissimilarity within regions and therefore contributed to apparent homogenisation, they did not lead to a decrease in α diversity or impoverishment of an area, as is commonly assumed with ‘true biotic homogenisation’.

Table 4.1. The three species with the highest total species-level impact on Whittaker's β–diversity (ΔβSP) for both homogenisation resultant change (negative) and heterogenisation resultant change (positive) and what contributions came from colonisation or extirpation change. Species occurrence refers to recorded presence within individual hectads (10 x 10 km). T1 displays the species occurrences in BA1990, and T2 the occupancy in BA2010.

		Number of occurrences (max *N* = 2291)			**Species-level impact on β–diversity ($\Delta\beta_{SP}$)**		
	Species	**T1**	**T2**	**Net Change**	**$\Delta\beta_E$**	**$\Delta\beta_C$**	**Total**
Negative $\Delta\beta_C$ shows a species-level contribution to colonisation homogenisation (i.e., a species colonising new areas within a region where it is already common (>50% occupancy) or a locally rare species increasing occupancy above 50%)							
Top three negative **$\Delta\beta_C$**	Buzzard (*Buteo buteo*)	1015	2160	1145	0.69	-14.46	-13.77
	Greater Spotted Woodpecker (*Dendrocopos major*)	1525	2048	523	0.64	-12.20	-11.56
	Barn Owl (*Tyto alba*)	690	1563	873	-0.28	-10.86	-11.14
Positive $\Delta\beta_C$ shows a species-level contribution to colonisation heterogenisation (i.e., locally rare or absent species that are colonising new areas in the region)							
Top three positive **$\Delta\beta_C$**	Water Rail (*Rallus aquaticus*)	194	376	182	-3.36	6.12	2.76
	Little Egret (*Egretta garzetta*)	0	163	163	0	5.76	5.76
	Long-eared Owl (*Asio otus*)	285	319	34	-6.35	5.40	-0.95
Negative $\Delta\beta_E$ shows a species-level contribution to extirpation homogenisation (i.e., locally rare species being extirpated from areas or a locally common species decreasing to below 50% occupancy)							
Top three negative **$\Delta\beta_E$**	Long-eared Owl (*Asio otus*)	285	319	34	-6.35	5.40	-0.95
	Quail (*Coturnix coturnix*)	222	297	75	-4.39	5.26	0.87
	Hawfinch (*Coccothraustes coccothraustes*)	169	61	-108	-4.38	1.32	-3.06
Positive $\Delta\beta_E$ shows a species-level contribution to extirpation heterogenisation (i.e., locally common species being extirpated from areas within a region)							
Top three positive **$\Delta\beta_E$**	Cuckoo (*Cuculus canorus*)	1575	1281	-294	10.70	-6.35	4.35

Spotted Flycatcher (*Muscicapa striata*)	1947	1873	-74	6.70	-6.66	0.04
Goldcrest (*Regulus regulus*)	1775	1932	157	5.67	-8.57	-2.90

Regions that experienced increases in dissimilarity (heterogenisation) 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 (Fig. 4.5e), 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 heterogenisation and homogenisation that do not reflect the general dramatic decrease. Also included were tree sparrow (*Passer montanus*), turtle dove (*Streptopelia turtur*), willow tit (*Poecile montanus*) and lesser spotted woodpecker (*Dendrocopos minor*), all included as habitat generalists and 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. These patterns show that species that were once considered common can quickly become threatened (i.e., generalist species are not always the "winners" (Julliard et al., 2004; Sweeney & Jarzyna, 2022)). Furthermore, as common species are the most abundant and widespread, subsequent declines can have large ramifications on ecosystem services (Carlo & Morales, 2016; Gaston & Fuller, 2007; Palacio et al., 2016). In contrast, recent colonisers to areas can also contribute to increased heterogenisation of a region as long as their overall occupancy stays below 50%. For example, little egrets (*Egretta garzetta*) are one of Britain's most recent colonisers with a large contribution to regional heterogenisation between the two atlas periods (Table.4.1).

Whilst Sullivan et al. (2016), in their analysis of the abundance patterns of UK birds, concluded that homogenisation 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 homogenisation also corresponded with overall homogenisation, and this is likely to be an area of interest to conservationists, given it involves the loss of species that were already locally rare and did not colonise 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*). Therefore, 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 prioritisation (Perez Rocha et al., 2023; Xia et al., 2022).

Implications of the results for conservation and management

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 being significant for both $\Delta\beta_{E+}$ and $\Delta\beta_{C+}$. As $\Delta\beta_{E+}$ is linked to locally common species loss and $\Delta\beta_{C+}$ to increases in a locally uncommon species, this could indicate that species have shifted their distributions upslope in response to increased temperatures as they track their climatic niche, along with a general loss of more upland species (Alba et al., 2022; Davey et al., 2012; Gillings et al., 2015). Alternatively, the observed changes in $\Delta\beta_{E+}$ and $\Delta\beta_{C+}$ in upland areas could be in response to the land cover change in lowland areas as species look to find suitable habitat (Jungandreas et al., 2022; Sharps et al., 2023).

Several variables were highlighted as driving increases and decreases in $\Delta\beta_{E-}$ through time. This measure shows whether specialist species – those which are likely to be range-restricted and locally uncommon – are going extinct within regions. Increased land cover of woodland and grassland both decreased the amount of $\Delta\beta_{E-}$ within an area, meaning less locally rare species extirpations. This could be due to increased habitat cover or appropriate maintenance of current habitat cover, something that is important to habitat specialists (Barnes et al., 2023; Kumpula et al., 2023) with evidence of increasing woodland specialists within the UK in response to recent woodland expansion (Burton et al., 2018). Although $\Delta\beta_{E-}$ also increased with increased urban cover, this can likely be put down to existing urban areas mainly increasing between the periods, i.e., increases were largely congruent with areas already heavily urbanised (S4.2.3). Therefore, specialist species inhabiting areas around urban centres were unlikely to be disturbed by expansions to an already urbanised area (i.e., their habitat was outside of this area). 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 et al., 2018b). Indeed, all measures increased with land diversity, temperature, and precipitation (apart from $\Delta\beta_{C-}$ for temperature and land diversity), highlighting the role that instability has on assemblages (White et al., 2018b). This could have implications as both land use and climate change increase in the future, creating further instability within systems that could contribute to increased diversity change (Newbold, 2018).

Limitations of the study and future research directions.

While the data used here are suitable for looking at broad-scale patterns in extirpation and colonisation, underlying changes in abundance structure, masked by the use of only presence-absence data, may reveal early shifts and patterns of population change with respect to homogenisation and heterogenisation before species are fully extirpated from an area (Dornelas et al., 2019; Magurran et al., 2019; Sullivan et al., 2016). Also, while we account for broad-scale changes in land cover, we do not include specific information on land-use changes and the intensification or fragmentation of land cover, which may explain some of the colonisation and extirpation dynamics observed. Indeed, the loss of many farmland birds from the south-east of England has largely been attributed to intensification and fragmentation (Donald et al., 2001; Newton, 2004; Rigal et al., 2023). In some cases, the occupancy of migratory species in the UK may also be influenced by factors affecting their wintering grounds and migration routes (Vickery et al., 2014), which is also not accounted for here.

4.5. Conclusions

Temporal homogenisation is commonly seen as an indicator of impoverishment in terms of the biological diversity of communities. In cases where homogenisation is caused by the combined loss of unique species (either distributionally rare or functionally unique) and the spread of generalist or introduced species, this is indeed the case. Here, however, we show that such patterns must be interpreted with caution, as homogenisation driven by the expansion of species through local colonisation leads not only to increases in diversity but also to increased homogenisation of a region. These species may be habitat or dietary generalists, but their increase, if they are a naturally occurring species, does not necessarily lead to an impoverishment of local alpha diversity. Also, the loss of species locally can lead to increased heterogenisation of a region, but this does not mean an increase in local alpha diversity. Overall, in work looking at biotic homogenisation, steps should be made to account for species identities and their contribution to patterns of temporal spatial β-diversity to ensure that the interpretation of homogenisation and heterogenisation is valid and that conservation measures are developed appropriate to the species dynamics underpinning the observed changes.

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5. Temporal spatial beta-diversity patterns of avian diversity in three tropical biodiversity hotspot sites

Abstract

Measuring and quantifying diversity over time and space is vital to understanding how communities and regions are changing during the Anthropocene. However, this is often hard to achieve in tropical regions where long-term monitoring data are generally lacking. This is important because tropical ecosystems represent particular conservation priorities due to the high numbers of threatened and endemic species they support. Using three sites located in poorly studied, endemic-rich tropical forest types (Yucatan karstic lowland seasonal forest (Calakmul, Mexico), Mesoamerican tropical montane cloud forest (Cusuco, Honduras) and Malagasy dry forest (Mariarano, Madagascar)), all within biodiversity hotspots, we quantified changes in avian assemblages over time. We looked for changes in multiple beta-diversity (overall site dissimilarity) and pairwise beta-diversity (dissimilarity between pairs of sites) to determine whether individual assemblages within the regions were becoming more similar or dissimilar to one another over time. Using measures of species occupancy alongside colonisation and extirpation partitioning, we also assessed which individual species were driving any observed changes. The three regions remained relatively stable across time, with no evidence in either Cusuco or Mariarano of heterogenisation or homogenisation. The overall site heterogenisation changed within Calakmul, with significantly higher turnover found between the first and last year of sampling ($p < 0.05$). All sites experienced significant changes in the pairwise dissimilarity structure (i.e., the dissimilarity between individual pairs of sites), as evidenced by low correlations between pairwise dissimilarity values in the first year of sampling compared to the last. Species that decreased in occupancy were found to be listed as least concern on the IUCN red list. While the sites were found to be relatively stable over time, the underlying changes in spatial dissimilarity point to complex dynamics that require further

study. These results conform to the findings from local scales across the globe, mainly that species richness remains stable, but communities are dynamic in space and time. The findings also highlight the need to continue long-term monitoring programs to understand and quantify change over the coming decades, where human influence from drivers such as land use and climate change is predicted to increase within the tropics.

5.1 Introduction

Assessing how biodiversity is changing over time and space is recognised as an increasingly important priority due to the impact of human disturbance (i.e., the Anthropocene; Lewis & Maslin, 2015), a period in which extinction rates are predicted to rise sharply (Barnosky et al., 2011). As such, researchers are increasingly attempting to understand and quantify how species and communities are responding to anthropogenically-driven changes in climate and land use (Antão et al., 2020; Beissinger et al., 2023; Newbold et al., 2019; Rurangwa et al., 2021). Whilst temperate regions are all well studied due to the increased availability of long-term ecological data, tropical areas have received much less attention (Culumber et al., 2019; Feeley et al., 2017; Stroud & Feeley, 2017; Titley et al., 2017). This is in spite of the fact that the tropics are currently experiencing habitat loss, in particular, forests, at a much faster rate than any other region on Earth (Hansen et al., 2013). Biodiversity is also at its greatest within the tropics (Gaston, 2000), and extinctions are predicted to occur disproportionately within this region (Dirzo et al., 2014; Pimm et al., 2014). The tropics also include the majority of biodiversity hotspots, areas with exceptional concentrations of endemic species (Myers, 2003; Myers et al., 2000), making them important conservation priorities and valuable areas of study. Particularly, hotspots are areas that would likely benefit from long-term monitoring data that is vital to conservation and policy (Hughes et al., 2017; Laurance et al., 2012). Unfortunately, temporal ecological datasets within the tropics are generally lacking (Avolio et al., 2015; Dornelas et al., 2013), hindering our ability to assess change over time.

Most of the long-term ecological studies that have taken place within the tropics have generally corroborated patterns found elsewhere across the globe (Blowes et al., 2019). At the local scale, they show increases, decreases or no change in species richness but decreasing spatial dissimilarity (spatial beta-diversity) and an increase in temporal turnover (temporal beta-diversity) (Blowes et al., 2019; Dornelas et al., 2014; Hillebrand et al., 2018). The increase in species turnover (i.e., species replacement) over time is driven by meta-community processes (Leibold et al., 2004), with species loss compensated for by immigration from the wider region (Finderup Nielsen et al., 2019). For example, Tinoco et al. (2021) found no change in avian richness from 2006 to 2016 within the Andes of Ecuador and instead found a re-ordering of communities as species compositions and abundances changed. However, species replacement is not necessarily equal, and widespread losses of specialist species, coupled with increases of generalists, can lead to 'biotic homogenisation' across a set of sites within a region (Finderup Nielsen et al., 2019; McKinney & Lockwood, 1999; Olden et al., 2016; Olden & Rooney, 2006). This aspect of change is predicted to increase over time due to the growing influence of humans on the biosphere (McGill et al., 2015).

Biotic homogenisation is frequently measured through an assessment of the spatial beta-diversity (the dissimilarity between assemblages) of a given area over time, with increases in the measure (i.e., temporal spatial beta-diversity) seen as evidence of heterogenisation and decreases as evidence of homogenisation (see Chapter 4). While most studies examining temporal spatial beta-diversity focus only on taxonomic diversity (i.e., how species identities change between assemblages over time), it is important to also consider both functional and phylogenetic diversity to fully understand how communities are changing through time (Devictor et al., 2007; Heino & Tolonen, 2017; Olden et al., 2018). Taxonomic homogenisation (i.e., the reduction in taxonomic spatial beta-diversity through time) describes the loss or replacement of native, specialist, and rare species with invasive, generalist and common species (Olden & Poff, 2004). Functional diversity is measured as the diversity of species traits within an assemblage or area, which in turn gives a measure of functioning, as traits influence how a species interacts with the environment and the role they play within an assemblage. Functional homogenisation occurs when the functional dissimilarity between assemblages reduces over time, indicating that communities are becoming functionally more similar to one another (Clavel et al., 2011; Olden & Poff, 2004). This reduction in similarity can be due to the loss of specialist species that usually have unique roles within communities and, therefore, a broader range of traits, or the replacement of specialist species with generalists that usually have a narrower range of traits. Therefore, it is important to assess changes as reductions in functional dissimilarity between assemblages over time can potentially indicate reduced functioning and subsequent declines in ecosystem services and overall health (Wang et al., 2021). Phylogenetic homogenisation results from decreased phylogenetic dissimilarity between assemblages over time (Winter et al., 2009). As phylogenetic diversity is a measure of the age and the relatedness of species, decreases in the dissimilarity between assemblages result from the loss or replacement of endemic or rare species that are often evolutionary distinct from other species in the community, which subsequently reduces the total genetic diversity within a given area (Winter et al., 2009). Decreases in phylogenetic dissimilarity between areas can also impact ecosystem services, as species that are evolutionary unique are also likely to be specialist species (Wang et al., 2021). As each type of diversity measure relates to a different type of homogenisation or heterogenisation, including all three in studies of diversity change is vital, given changes in the metrics can be uncoupled through time (Hillebrand et al., 2018; Li et al., 2020; Robroek et al., 2017).

Here, using three avian point-count datasets collected within tropical biodiversity hotspots between 2008 and 2018, we assess if the avian communities within each location are a) declining in taxonomic, functional or phylogenetic diversity, b) show directional change in temporal spatial beta-diversity consistent with either homogenisation or heterogenisation in any or all of the three diversity metrics, c) whether observed changes are driven by extirpation or colonisation resultant changes (Tatsumi et al., 2021; Chapter 4) and d) whether changes in diversity are mirrored with changes in occupancy for indicator species at each of the three sites. As local patterns of richness and diversity have been found to increase, decrease and remain centred around zero, we do not make predictions on these aspects of change (Blowes et al., 2019; Dornelas et al., 2014). We do, however, expect decreases in spatial beta-diversity across all three measures of diversity (i.e., taxonomic, functional and phylogenetic) over time, consistent with global comparisons of findings at the local scale (Blowes et al., 2019; McGill et al., 2015)

5.2 Materials and Methods

5.2.1 Locations

Figure 5.1. Global map showing the locations of the three sites within the two biodiversity hotspots used in the study.

To assess how spatial beta-diversity and the associated colonisation and extirpation dynamics change over time, we used three biodiversity datasets collected by Operation Wallacea (hereafter, Opwall) over differing time periods. Opwall is a scientific expedition organisation that is funded by student volunteers to enable scientists and researchers to conduct monitoring at sites worldwide, with a large focus on the tropics. We selected three sites which lie within tropical biodiversity hotspots: Mesoamerican cloud forest (Cusuco National Park, Honduras); Malagasy dry forest (Mariarano and Matsedroy forests (collectively referred to as Mariarano forest), Madagascar); and lowland karstic seasonal forest (Calakmul biosphere reserve, Mexico) (Fig.5.1).

Cusuco, *Honduras*

Cusuco National Park, Cortes, NW Honduras (15°290–15°320 N, 88°130–88°260 W) is located within the Mesoamerican biodiversity hotspot (Myers, 2003; Myers et al., 2000) and is internationally recognised due to its high levels of avian taxonomic richness (Martin et al., 2021) and both regional-level and micro-level endemism (49 species described to date are only found within the park; Martin et al., 2021). The park consists of a core protected area of 7,325 ha surrounded by a buffer zone 16,870 ha in size (Hoskins et al., 2020). The park has a steep elevational gradient, with a peak elevation of 2243 m asl. This gradient, alongside other factors, means that the vegetation varies across the landscape. Habitats such as semi-arid pine forest, moist pine forest, and moist broadleaf forest are all found within the park, with many species in the genera *Quercus* (Fagaceae), *Liquidambar* (Altingiaceae), and *Pinus* (Pinacceae). At the highest elevations, elfin forest (*bosque enano*) can be found along the exposed mountain ridges. The buffer zone of the park allows for human encroachment and settlement and, therefore, suffers from anthropogenic disturbance. Anthropogenic land use can be found within the park, including pasture for cattle, coffee plantations, and villages. The human population in the park is ~40,000 people within 38 communities (Neate-Clegg et al., 2018). In terms of the avifauna, the park has been comprehensively inventoried using point counts, mist-netting, and opportunistic observations. The total species richness of the park stands at 263 species, with more detected and likely present but not yet fully confirmed (Martin et al., 2021).

Calakmul, Mexico

Calakmul biosphere reserve (18°36’20.99” N, 89°56’39.98” W) is an extensive expanse of lowland seasonal karstic tropical forest that, together with the adjoining Mayan biosphere reserve in the Peten province in Northern Guatemala, constitutes the largest tract of continuous forest remaining in Mesoamerica. A UNESCO World Heritage Site of Culture and Nature, it covers an area of 723,000 ha and connects two state reserves (Balam-kim and Balam-ku), with the total area of all three reserves comprising 1,200,000 ha. Unlike other forests within the Yucatan region, forests within the Calakmul region were never historically used for timber production. As the area also has little to no agriculture, its ecosystems remain largely intact. Northern parts of Calakmul are comprised primarily of deciduous tropical forests, with a canopy of between 8-20 m. These trees lose their leaves during the dry season (December to May). A large majority of the reserve is covered by medium-deciduous trees, with an average canopy of between 15-40 m (Beletsky, 1999). The dominant species within these forests are ramon (*Brosimium alicastrum*), chicozapote (*Manilkara zapota*), ceiba (*Ceiba pentandra*), zapotillo (*Calocarpum viride*), chechem (*Metopium browneii*), chaca rojo (*Bursera sumaruba*), copalio (*Protium copal*), tzalan (*Lysiloma latisiliquum*) and caoba (*Swietenia macrophylla*) (Bohn et al., 2014). With no permanent lakes or rivers, biodiversity relies on temporary lakes, named aguadas, that form during the rainy season and can last until the dry season for water resources. More than 350 resident or migratory bird species have been recorded within the reserve. Humans are present within the Calakmul eco-region, with more than 20,000 people occupying the area. They live within traditional villages with the main source of income related to agriculture involving the burning of forest and the felling of trees.

Mariarano, Madagascar

Mariarano, here defined as the Mariarano classified forest (15°29′S, 46°41′E) and the immediately adjacent Matsedroy forest fragment (15°29′S, 46°38′E) (hereafter referred to collectively as the Mariarano forest) represent one of the last few patches of unprotected dry deciduous forest larger than 8 km2 remaining in Western Madagascar (Moat & Smith, 2007; Nicoll, 2003). Forests within the area receive no formal protection and are threatened by fires, charcoal production and agricultural expansion (Long et al., 2012). The study area sits within the Mahamavo watershed, approximately 80 km northeast of Mahajanga City. The site encompasses approximately 65 km2 and comprises a matrix of low-lying, dry deciduous forest interspersed with areas of wetlands, scrub habitats, agricultural land, and lightly wooded grassland (Evans et al., 2013; Moat & Smith, 2007). The study site is situated within a low-lying area and reaches a peak elevation of 80 m asl (Evans et al., 2013; Moat & Smith, 2007). The area experiences a tropical savannah climate (Peel et al., 2007) with consistent temperatures but a highly variable monthly rainfall (1 mm – 360 mm). A distinct wet season peaks between December and February, followed by a pronounced dry season between July and September. Despite a lack of formal protection, the study site supports high numbers of regionally endemic birds (63 species, 66.3% of all species recorded at the site over a nine-year period) (Palfrey et al., 2019).

5.2.2 Sampling and species data

The length of each dataset for each site differed due to the year each site was set up, alongside other factors. Long-term monitoring in Cusuco has run from 2007 to 2018, but no data are available for 2009 due to a military coup within Honduras restricting access. This also impacted the expertise of the observer pool, and, therefore, it was removed from the subsequent analysis. Calakmul was sampled annually from 2014 to 2018. Mariarano was sampled annually from 2011 to 2017. However, we removed 2013 as the sampling in Matsedroy in this year was reduced compared to previous and subsequent years. All sampling across the sites was conducted over eight-week research seasons each year, running between June and August.

Bird surveys at each site were carried out using permanent point count sites (Bibby et al., 2002) located along transects ranging in length from 1 km to 4 km. Points were separated by at least 200 m, with some up to 400 m apart. The number of points differed between transects and between sites, with Cusuco having between two and eight, Mexico having consistently ten points per transect, and Madagascar having between eight and ten. Unlimited radius circular point counts were performed on each point for 10 minutes, with each bird heard or seen recorded along with their distance from the observer. Observers were skilled ornithologists trained on local bird identifications before the onset of the season (if necessary). The observers were also randomised between the transects across the season to reduce the impact of skill and observer bias. Point counts were not conducted in heavy rain or other adverse weather conditions and typically started at dawn (between 05:30 and 06:00, depending on the site) and lasted for a maximum of three hours, depending on the transect length. Species flying above the forest canopy were not recorded. See Martin et al. (2017) for more details on how point count surveys were conducted.

Sampling each year aimed to capture at least three repetitions on each point, with at least one sample performed in reverse to account for potential diel bias (i.e., bias in the species recorded due to the time of day; Neate-Clegg et al., 2018). However, occasionally, various logistical and circumstantial reasons meant that this was not always possible. As we were interested in looking at patterns of temporal spatial beta-diversity, sampling had to be consistent for each transect across years to ensure that each yearly calculation was comparable to the next. Therefore, for this analysis, for each of the three sites, we used a subset of transects that had been fully surveyed every year. Individual points on transects were not surveyed every year for a variety of logistical reasons. We, therefore, corrected the data by either removing points that had not been sampled across all years (transect shortening) or removed individual transect replicates that were not complete. We chose whichever option minimised data loss in each instance. This reduction meant that we used 18 transects consisting of a total of 87 individual points for Cusuco, eight transects consisting of a total of 66 individual points for Mariarano, and 14 transects consisting of 136 individual points for Calakmul.

5.2.3 Analysis

We first aggregated data to the transect level for each sampling replicate and converted all counts to presence-absence data. As the number of samples differed between transects, we then used a sub-sampling approach on the aggregated transect data. At each site, we assessed as our baseline the minimum number of replicates (complete transect sampling occasions) completed across the transects, which was two samples for each site. We then randomly selected two sampling occasions on each transect with more than two samples 100 times, generating 100 presence-absence matrices for each transect for each year.

Trait and phylogenetic data

Using the AVONET database (Tobias et al., 2022), we extracted nine continuous 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) for all of the species present within each of the sites across the studied periods. The selected traits reflect avian species and their interactions with the environment (locomotion, dietary niche, and ecological function) (Pigot et al., 2020; Tobias & Pigot, 2019; Trisos et al., 2014).

We log-transformed (base 10) all of the traits (to remove the right skew present) and standardised them all to have a mean of zero and SD of one (to bring them onto comparable scales). A principal components analysis was then undertaken using the transformed traits to yield uncorrelated axes. We then retained all nine produced axes, as even axes that contain relatively little explained variation have been shown to be informative for datasets like ours (Pigot et al., 2020). These axes were then used to create a functional dendrogram for each site using all the species found in the sites between the first and last years of sampling. We created the dendrogram using the agglomerative hierarchical clustering method (UPGMA). This method produces a rooted tree (Petchey & Gaston, 2007). We used the function *tree.quality* within the package "BAT" (Cardoso et al. 2022) to test that the functional trees were representative of the true functional distances between the species within each site. All trees had values of above 0.82, which highlights a good representation of the functional space (0.82, 0.90 and 0.95 for Cusuco, Mariarano and Calakmul, respectively; Matthews et al., 2023).

We then extracted data from AVONET on the trophic niche, trophic level and habitat specialism for each species within each site (Tobias et al., 2022). We extracted these data to test for differences in the occupancy changes (see “Richness and occupancy” section below) for each guild within each site.

To compute phylogenetic measures of beta-diversity, we first obtained the Ericson backbone phylogenetic trees from Jetz et al. (2012). These trees contain 9,993 avian species. Binomial names of species were updated from the initial collection in the field to match those used in the phylogenies. In total, 3,000 trees from the full posterior distribution of Jetz et al. (2012) were selected and used to create a maximum clade credibility tree with TreeAnnotator (v1.10.4, Drummond & Rambaut, 2007). Node heights were set to median without burn-in as the Jetz trees are post-burn-in. The consensus tree produced had a few negative branch lengths, not uncommon with maximum credibility trees, which were converted to zero. We then shortened the two immediate branches below those converted to zero by the same absolute value, therefore maintaining an ultrametric tree without polytomies. Finally, we produced one tree for each site by retaining only the tips present at the respective site.

Richness and occupancy

We calculated total species richness for each transect within each site and across all transects (i.e., the site as a whole). We repeated the process for functional diversity using the *treedive* function within the package “vegan” (Oksanen et al., 2022) and for phylogenetic diversity using the *pd* function in the package “picante” (Kembel et al., 2010). For each species, we calculated the proportion occupancy, the number of transects occupied / the total number of transects for each year. We then calculated the percentage of detections for each species, measured as the number of transect detections across the whole dataset divided by the overall total number of species detections. Using the guild data obtained from AVONET, we assessed how the average occupancy of each group changed over time using Kruskal Wallis and Dunn tests. Finally, we took the twenty species with the highest percentage of detections for each site and plotted the proportion of occupancy across the years.

Spatial beta-diversity calculation

For each year for each of the three sites, we used the BAS framework (Baselga, 2010) to calculate measures of community dissimilarity. This framework is commonly used within ecological community studies and measures the amount of dissimilarity between pairs of sites (pairwise) or a region as a whole (multiple) and then partitions the total dissimilarity (total beta-diversity) into dissimilarity caused by species turnover (replacement between assemblages) and nestedness-resultant dissimilarity (the degree to which assemblages are nested subsets of one another) (Baselga, 2010).

Using the *beta.multi* function from the “betapart” R package (Baselga & Orme, 2012), we calculated multiple beta-diversity and its constituent components for each year and site in turn. This was repeated 100 times using the sub-sampled transect data. We then used the *beta.pair* function from the same package to calculate pairwise beta-diversity between each transect and every other transect in each site for each year. This was again repeated 100 times, and the average and standard deviation were taken.

We then repeated the process of calculating multiple and average pairwise beta-diversity for both functional and phylogenetic data. For both functional and phylogenetic data, we used the *phylo.beta.multi* and the *phylo.beta.pair* functions contained within the “betapart” package with either the functional dendrograms or the phylogenetic trees described in ‘Trait and phylogenetic data’ (Baselga & Orme, 2012). As with taxonomic beta-diversity, these calculations were repeated 100 times using the sub-sampled data, with averages and standard deviations taken for the pairwise measurements.

To assess shifts in spatial beta-diversity between the first and last year of sampling for each site, we also looked for changes in the spatial dissimilarity structure and the overall site heterogeneity. Low-level correlations between the turnover or nestedness pairwise dissimilarity values of sites between two time periods are indicative of changes in the spatial dissimilarity structure (i.e., similar sites becoming more dissimilar and vice-versa; Baselga et al., 2015). To assess if sites did change, we computed pairwise dissimilarities between all pairs of individual point counts after sub-sampling them down to the same levels (two repeats on each point). We then used Mantel tests to assess the significance of the correlation between the turnover and nestedness components for each of the diversity measures (taxonomic, functional and phylogenetic). This was repeated for each of the sites in turn.

In contrast to pairwise measures, multiple beta-diversity is a measure of overall site heterogeneity (Baselga et al., 2015; Baselga & Orme, 2012). We repeatedly sampled 20% of the points for each country site 1000 times and calculated multiple beta-diversity and its constituent components each time for each of the diversity measures (taxonomic, functional and phylogenetic) to create a distribution of values (Baselga et al., 2015; Baselga & Orme, 2012). We then compared the generated turnover and nestedness distributions statistically between the first and last years of sampling using the *mded* function, which calculates the difference between two non-independent empirical distributions within the R package “mded” (Aizaki, 2014; Poe, Giraud & Loomis, 2005; Poe, Welsh & Champ, 1997).

Temporal spatial variation partitioning: colonisation and extirpation resultant change

To assess changes in the extirpation and colonisation of species over the measured time periods for each site, we used Whittaker's beta-diversity (measured as gamma diversity / average alpha diversity, hereafter βW; Matthews et al., 2019) and the partitioning framework introduced by Tatsumi et al. (2021). The partitioning framework divides up the contributions of extirpation ($\Delta\beta_E$) and colonisation ($\Delta\beta_C$) across an area to overall homogenisation (decreases in βW across a region) and heterogenisation (increases in βW). These metrics then relate to these individual components - namely, extirpation resultant homogenisation ($\Delta\beta_{E-}$), extirpation resultant heterogenisation ($\Delta\beta_{E+}$), colonisation resultant homogenisation ($\Delta\beta_{C-}$) and colonisation resultant heterogenisation ($\Delta\beta_{C+}$). Due to the method of calculation, $\Delta\beta_{E-}$ and $\Delta\beta_{C+}$ relate to rare species (below 50% occupancy) dynamics and $\Delta\beta_{E+}$ and $\Delta\beta_{C-}$ relate to common species dynamics (above 50% occupancy) (Tatsumi et al., 2021). See Tatsumi et al. (2021) and Chapter 4 (Fig.4.1) for more details on the partitioning framework.

5.3 Results

5.3.1 Species richness, functional diversity and phylogenetic diversity changes

Overall species richness across the entire sampling periods stood at 168, 177 and 59 for Cusuco, Calakmul and Mariarano, respectively. Subsampling from the available samples created variation in richness across the transects and sites, indicating that sampling variation existed between the periods and observers (Fig.5.2). At the country level, the species richness pattern for Cusuco was largely multimodal, with both Calakmul and Mariarano being fairly stable (Supporting Table S5.1.1). At the transect level, there was more variation between transects within years and for individual transects across years (Fig.5.2). However, the patterns were broadly like those seen at the country level. Both functional and phylogenetic diversity mainly followed the patterns observed for species richness, with exceptions for some transects (Fig.5.2).

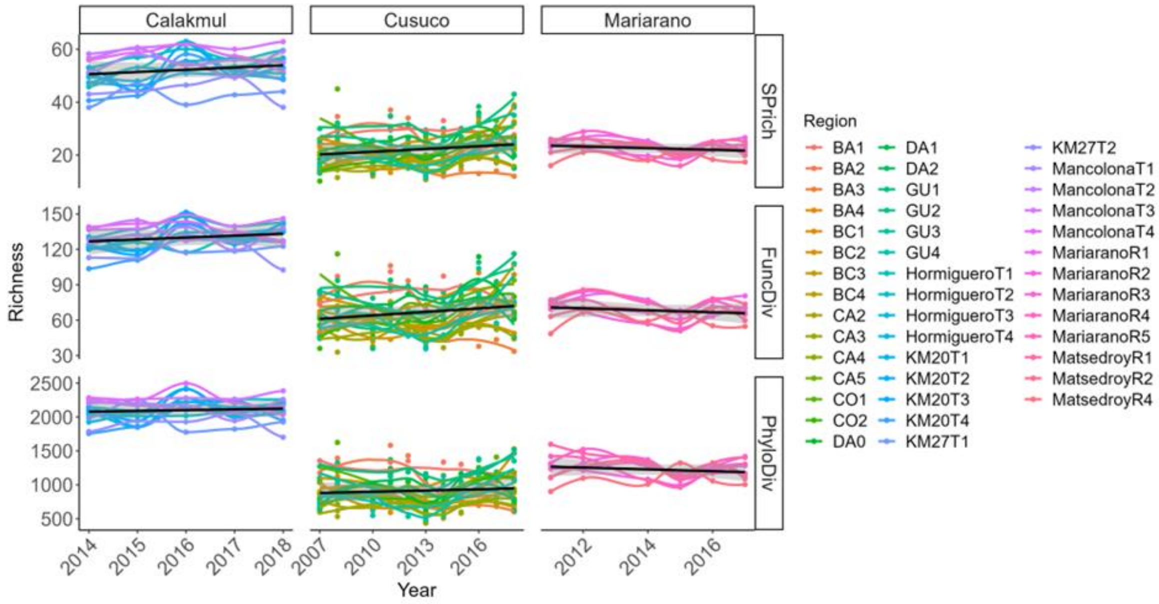
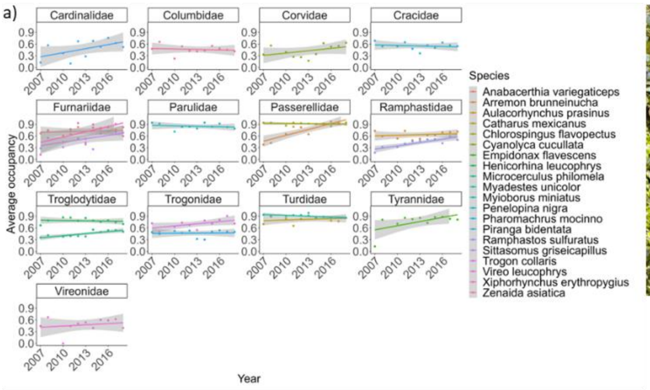


Figure 5.2. Species richness (SPrich), functional diversity (FuncDiv) and phylogenetic diversity (PhyloDiv) in each transect over the surveyed period. Each value was obtained by sub-sampling the data for each transect down to the minimum sampling effort (two samples per transect). This was repeated 100 times for each transect within each year. Solid black lines show a simple linear model fit for average values across all of the sites.

5.3.2 Occupancy changes

Occupancy of the species found with the highest percentage of detections across the dataset mainly increased or remained relatively stable, with some exceptions (Figs.5.3-5.5). For example, Malagasy brush warbler (*Nesillas typica*), Coquerel's coua (*Coua coquereli*), and hook-billed vanga (*Vanga curvirostris*) all decreased in occupancy in the Mariarano site (Fig.5.3), while white-fronted parrot (*Amazona albifrons*) and red-crowned ant tanager (*Habia rubiuca*) were found to decrease overall in terms of occupancy in Calakmul (Fig.5.5).



Resplendent quetzal (*Pharomachrus mocinno*).
Xavier Sentier (https://www.flickr.com/)

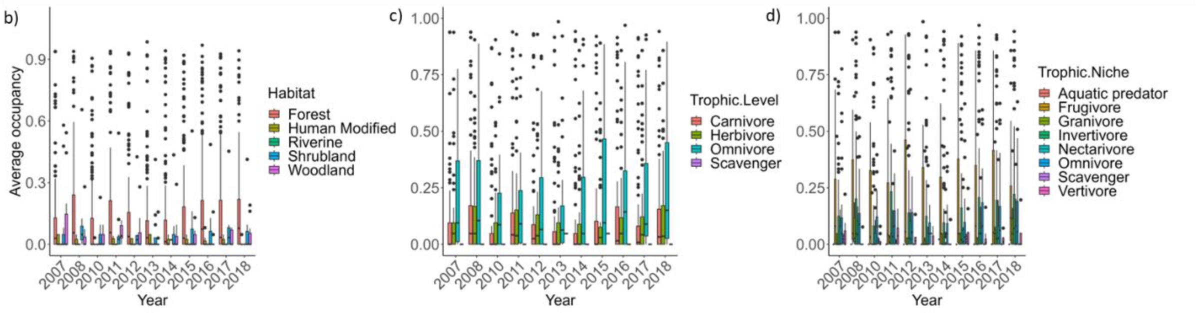
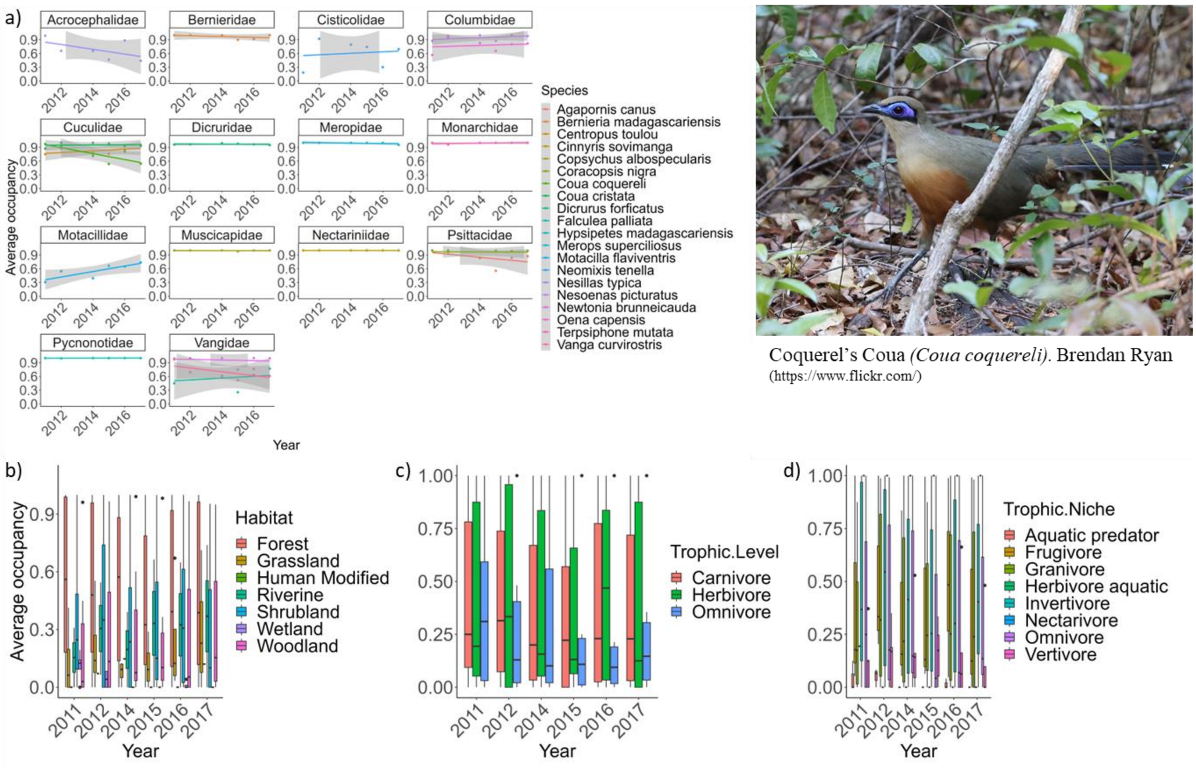


Figure 5.3. Occupancy patterns for species and guilds within Cusuco National Park, Honduras. Occupancy was calculated as the proportion of transects occupied within each year. This was averaged across 100 sub-samples of the transect data (two samples selected each time). **a)** displays the average occupancy across the sampled years for the twenty species with the highest percentage of detections across the transects. Boxplots show the average occupancy across all the species within each guild for **b)** habitat, **c)** tropic level and **d)** trophic niche.

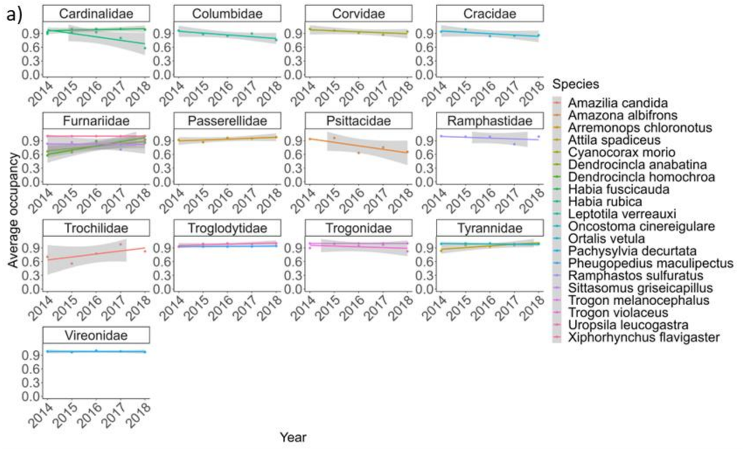
Average occupancy did not significantly change between years according to habitat affiliation, trophic level, or trophic niche for most groups across the three locations, with a few exceptions. Wetland birds in Calakmul decreased in average occupancy (9.43, $p < 0.1$), with significant changes identified between the first and last sampling years (2.64, $p < 0.1$) and between 2014-2015 (2.64, $p < 0.1$). However, it should be noted that only a small number (N=3) of species were classed as wetland affiliated, and average occupancy was low across the groups across the time series. Birds affiliated with human-modified habitat increased in average occupancy (9.73, $p < 0.05$) within Calakmul, with the change between 2015 – 2016 significant (-2.70, $p < 0.05$), although average occupancy across the time series was low (nine species; average occupancy 0.033 ± 0.56). Within Cusuco, forest birds fluctuated somewhat in occupancy across the time series (28.90, p < 0.01), with the main change identified between 2008 – 2010 (3.20, p < 0.1). Within Mariarano, average occupancy was significantly different across the time series for wetland species (11.68, p < 0.05), but no two individual years were found to be significantly different.



Coquerel's Coua *(Coua coquereli).* Brendan Ryan (https://www.flickr.com/)

Figure 5.4. Occupancy patterns for species and guilds within Mariarano, Madagascar. Occupancy was calculated as the proportion of transects occupied within each year. This was averaged across 100 sub-samples of the transect data (two samples selected each time). **a)** displays the average occupancy across the sampled years for the twenty species with the highest percentage of detections across the transects. Boxplots show the average occupancy across all the species within each guild for **b)** habitat, **c)** tropic level and **d)** trophic niche.

When looking at trophic level and trophic niche, only Cusuco carnivores (20.94, p < 0.05) and invertivores (20.26, p < 0.05) significantly changed in average occupancy levels across the time series, whilst within Calakmul, aquatic predators were the only group to experience significant change (10.59, p < 0.05) with the average occupancy levels between 2014 and 2018 found to be significantly changed (2.82, p < 0.05).



Red crowned ant tanager *(Habia rubica)*.
Brian Gratwicke (https://www.flickr.com/)

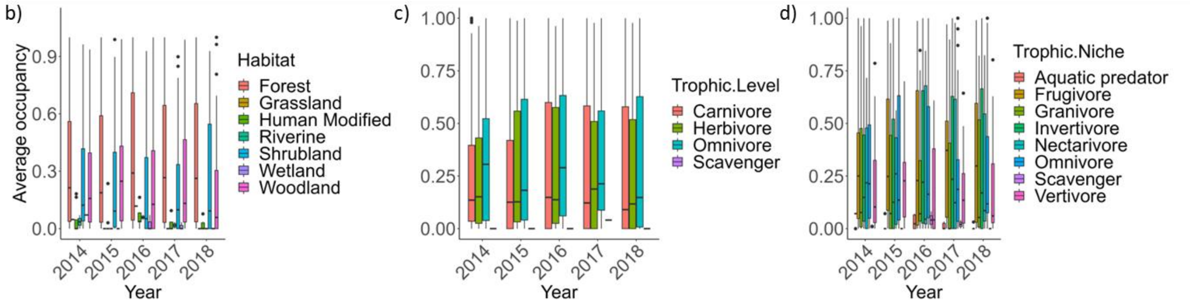


Figure 5.5. Occupancy patterns for species and guilds within Calakmul biosphere reserve, Mexico. Occupancy was calculated as the proportion of transects occupied within each year. This was averaged across 100 sub-samples of the transect data (two samples selected each time). **a)** displays the average occupancy across the sampled years for the twenty species with the highest percentage of detections across the transects. Boxplots show the average occupancy across all the species within each guild for **b)** habitat, **c)** tropic level and **d)** trophic niche.

5.3.3 Temporal spatial beta-diversity

Taxonomic, functional, and phylogenetic pairwise beta-diversity were all higher than the multiple beta-diversity equivalent for all sites, highlighting the increased heterogeneity observed between pairs of sites compared to the regions as wholes (Fig. 5.6). Pairwise measurements for all three diversity metrics broadly followed the same patterns as multiple measures (Fig. 5.6). Across all country sites, spatial beta-diversity in all years was primarily driven by the turnover component (Fig. 5.6). Across the measured temporal duration, Cusuco saw a slight decrease in total spatial beta-diversity, although the last year of sampling (total spatial beta-diversity = 0.54 ± 0.01, 2018) was higher than the first (0.53 ± 0.01, 2007) and the range was small across years (0.45 ± 0.01 – 0.54 ± 0.01; Fig. 5.6).

Turnover followed a similar pattern to total beta-diversity (range 0.36 ± 0.01 – 0.047 ± 0.01), while nestedness increased overall but saw increases and decreases across the measured period (range 0.07 ± 0 – 0.13 ± 0.01; Fig. 5.6). However, when comparing the first and last years of sampling across the measurements there was no observable change, highlighting changing spatial dynamics within the time-series with no loss of overall dissimilarity (Fig. 5.6). Mariarano peaked in total spatial beta-diversity at the mid-point of the temporal sampling (0.31 ± 0.01), but otherwise the total beta-diversity remained relatively stable (range 0.23 ± 0.02 – 0.31 ± 0.01; Fig. 5.6). Turnover and nestedness followed a similar pattern, with no substantial increase or decrease in either measure across the years (Fig. 5.6). Calakmul decreased in beta-diversity across the sampled years, although the difference across the sampled years was again small (range 0.34 ± 0.01 – 0.40 ± 0.01; Fig. 5.6).

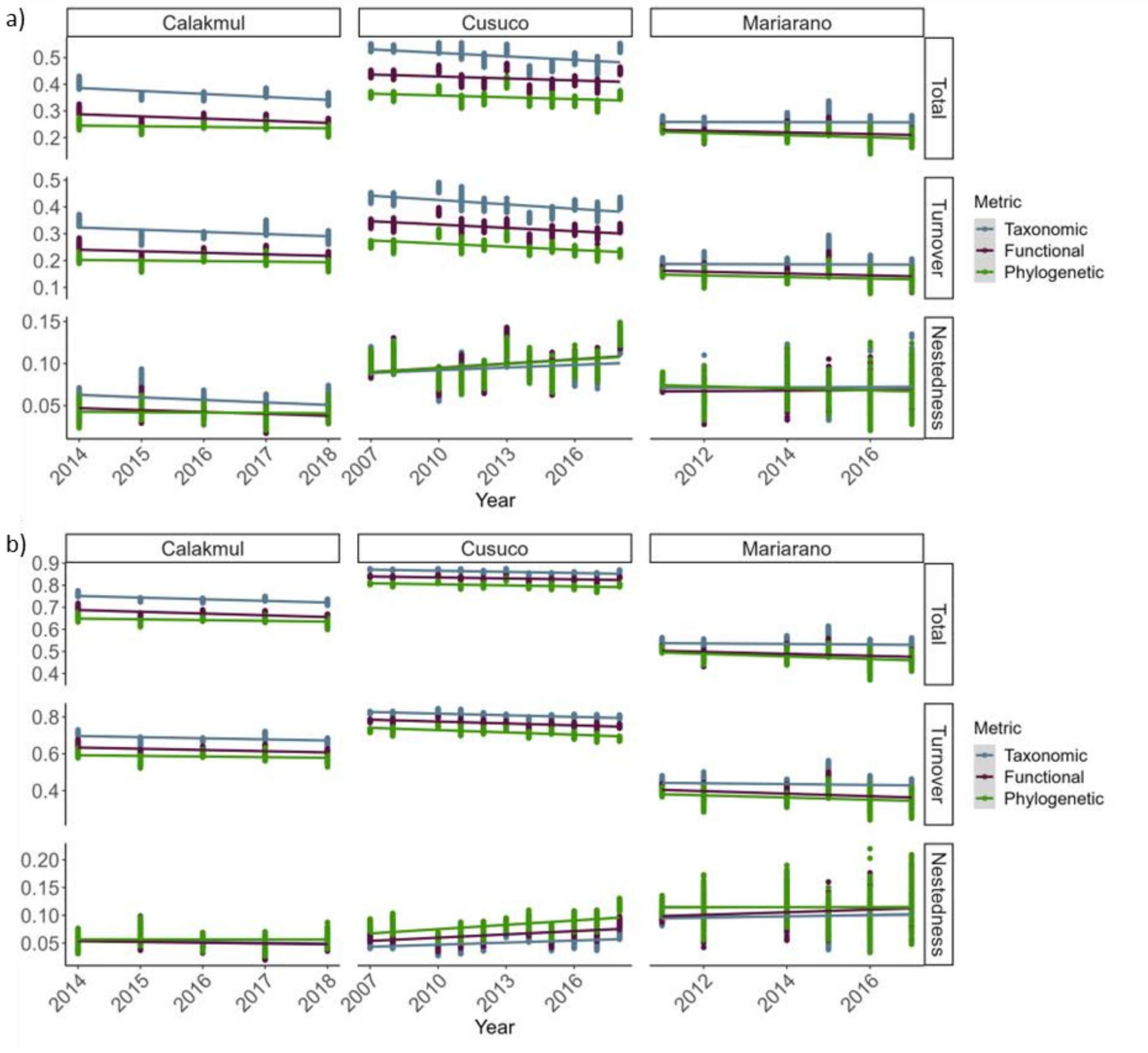


Figure 5.6. Multiple (**a**) and pairwise (**b**) taxonomic, functional and phylogenetic spatial beta-diversity (beta-diversity measured using Sorensen's beta-diversity; 'Total') and the constituent components ('Turnover' and 'Nestedness') across the measured time period for the three sites within the two biodiversity hotspots (Calakmul biosphere reserve, Mexico; Cusuco national park, Honduras; Mariarano, Madagascar).

When comparing the distributions of sampled multiple beta-diversity values for each site, the overall heterogeneity across all of the locations did not change significantly between the first and last years of sampling (Supplementary Figs S5.3 – S5.5), with the exception of multiple functional turnover in Calakmul which was significantly higher in the last year compared to the first ($p < 0.05$, Supplementary Fig. S5.5). In comparison to the lack of significant change in heterogeneity, the spatial dissimilarity structure of all sites, measured through correlations between pairwise values in the first year compared to the last, except for Mariarano, shifted significantly between the first and last year of sampling. This is shown by the low correlations observed between the dissimilarity matrices for both turnover and nestedness across the sites (Supplementary Figs S5.4 – S5.5). Turnover shifted significantly between the first and last sampling year for Mariarano for both taxonomic ($r^2 = 0.018$, Mantel $p < 0.01$; $r^2 = 0.004$) and phylogenetic (Mantel $p < 0.05$; $r^2 = 0.006$) pairwise dissimilarity (Fig S5.3) but functional turnover (Mantel $p = 0.089$; $r^2 = 0.004$) and nestedness showed no significant change across all of the measures ($r^2 = 0.001$, Mantel $p = 0.62$; $r^2 = 0.001$, Mantel $p = 0.49$; and $r^2 = 0.001$, Mantel $p = 0.80$ for taxonomic, functional and phylogenetic pairwise nestedness, respectively; Supplementary Fig S5.3). All the results taken together imply that, although the spatial heterogeneity across all the sites within each country did not change significantly, apart from functional heterogeneity in Calakmul, the spatial dissimilarity structure did significantly change as pairs of sites became more or less similar between the start and end of sampling.

5.3.4 Ecopart

Mariarano was fairly stable in terms of extirpation from transects across time with both $\Delta\beta_{E+}$ and $\Delta\beta_{E-}$ largely cancelling each other out (Fig. 5.7). However, as $\Delta\beta_{E-}$ did not decrease over time, this also meant a steady stream of extirpation resultant homogenisation, i.e., species with less than 50% occupancy being extirpated from sites (Fig. 5.7). $\Delta\beta_C$ was more variable, with an increase in $\Delta\beta_{C+}$ in 2015 followed by an increase in $\Delta\beta_{C-}$ the following year. Calakmul had an increasing $\Delta\beta_E$ across the sampled period, mainly driven by a reduction in $\Delta\beta_{E-}$. $\Delta\beta_C$ was fairly stable, with both $\Delta\beta_{C+}$ and $\Delta\beta_{C-}$ moving toward zero.

Cusuco was much more variable than either Mariarano or Calakmul. Overall ΔβE decreased between the first year and the last of the sampling, with both $\Delta\beta_{E+}$ and $\Delta\beta_{E-}$ high in all years but with an overall tendency back toward zero. $\Delta\beta_{C}$ exhibited the opposite trend, with the colonisation between the first and second years of sampling leading mainly to homogenisation, but an overall increase led to a positive $\Delta\beta_{C}$ between the penultimate and last year. As with the measures of extirpation, both $\Delta\beta_{C+}$ and $\Delta\beta_{C-}$ showed a tendency toward zero. Overall, the high fluctuations show species composition changes above and beyond that observed within the other two sites (Fig. 5.7).

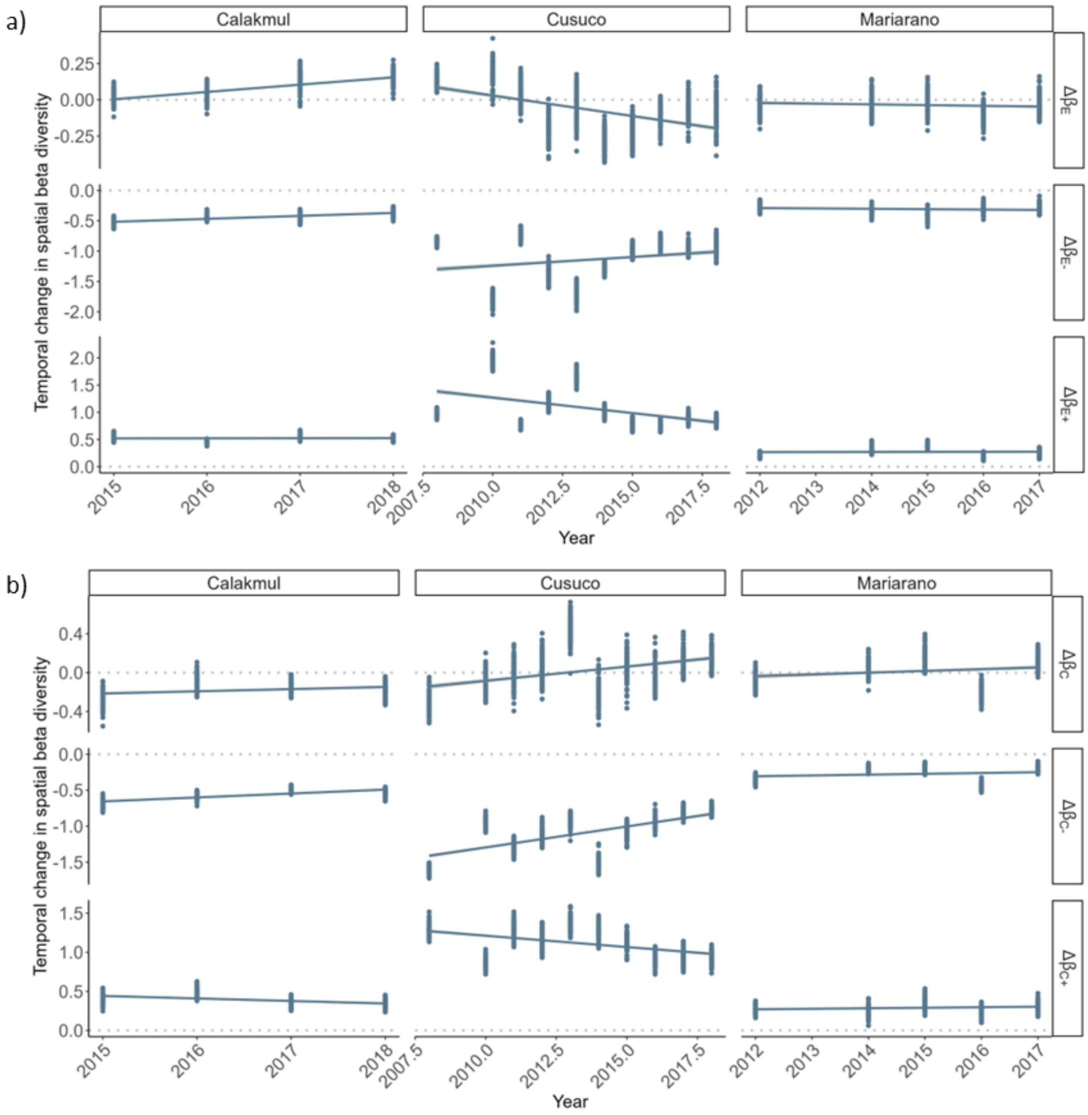


Figure 5.7. (Previous page) Change in spatial beta-diversity, measured here using Whittaker's beta partitioned into **a**) total extirpation resultant change ($\Delta\beta_E$) and its two components, extirpation resultant homogenisation ($\Delta\beta_{E-}$) and heterogenisation ($\Delta\beta_{E+}$) and **b**) total colonisation resultant change ($\Delta\beta_C$) and its two components; colonisation resultant homogenisation ($\Delta\beta_{C-}$) and heterogenisation ($\Delta\beta_{C+}$) for each of the three sites. Yearly values represent change between that year and the previous sampling year.

5.4 Discussion

While it has been predicted that, due to increasing anthropogenic drivers such as land use change, spatial beta-diversity, i.e., the dissimilarity between communities, should decrease within a given region over time (McGill et al., 2015), here we show that three sites within tropical biodiversity hotspots had relatively stable richness and diversity over the time periods measured with no evidence of homogenisation (Lindholm et al., 2020; Olden & Poff, 2004; Olden & Rooney, 2006). However, while there was no evidence of homogenisation or systematic species loss, the underlying pairwise dissimilarity structure changed significantly for all sites, and the overall site heterogeneity changed for Calakmul. These results together indicate that the sites did not lose functionality or richness at the site level, as shown by the overall stable taxonomic, functional and phylogenetic richness over the periods. However, examination of the distributions of sampled multiple beta-diversity values and the pairwise dissimilarity structure using the individual points highlighted that the individual assemblages did experience alterations across time (Blowes et al., 2019; Dornelas et al., 2014; Tinoco et al., 2021). These findings shed light on the avian dynamics within the two biodiversity hotspots and contribute to the growing literature on diversity change over time within the tropics.

Changes in the overall alpha diversity of the sites were fairly uniform over time across all three sites, agreeing with previous studies on the stability of local species richness (Blowes et al., 2019; Dornelas et al., 2014; Hillebrand et al., 2018). However, while individual transects within Mariarano were relatively stable, in both Cusuco and Calakmul, individual transects showed a range of increases, decreases and stable alpha diversity patterns. This increased variability at the transect scale not only highlights the impact of scale on alpha diversity changes and potentially spatial beta-diversity (Dumbrell et al., 2008; Keil et al., 2011; Whittaker et al., 2001; Zhang et al., 2015) but it is also slightly surprising, given that both Calakmul and Cusuco receive at least nominal protection whilst Mariarano receives none. This contrast in species richness and diversity change over time could be due to several factors. While Mariarano is biodiverse and rich in endemics, the wider region in which it sits has been disturbed greatly over time. Therefore, species inhabiting this area are likely contained to a degree, with less scope to disperse to other areas. Mariarano also has a smaller species pool than the other two regions used here (Palfrey et al., 2019), so it could be expected that species richness would fluctuate relatively less compared to the more species-rich sites, based on the available species pool alone. In terms of potential drivers, Calakmul and Cusuco have a more variable climate and greater elevational gradients compared to those found in Mariarano, which could have contributed to higher rates of spatial beta-diversity change. For example, Calakmul has experienced an increasing frequency of droughts in recent years (Pérez-Flores et al., 2021), while there is evidence that climate change has caused shifts in species elevations within Cusuco (Neate-Clegg et al., 2018) both of which could have led to increased community change.

Transects within Cusuco showed a range of changes across the sampled period. While a slight decrease in multiple turnover was observed, this was in tandem with an increase in multiple nestedness alongside individual increases and decreases in the various measures of richness used across the transects. These observed results could be due to the particularly heterogeneous landscape of Cusuco, with sites situated along a strong elevational gradient as well as being subject to fluctuations in poaching activity, temperature and precipitation (including extreme weather events) (Martin et al., 2021). The changes in beta-diversity are also evidenced by the colonisation and extirpation dynamics, with large fluctuations found across the sampled period. Alternatively, the changes could be due to longer-term climatic change altering the elevations at which species are found (Neate-Clegg et al., 2018) or due to increased or fluctuating human encroachment or land cover change (Rurangwa et al., 2021).

Changes in both functional and phylogenetic spatial beta-diversity followed taxonomic beta-diversity closely, highlighting low functional redundancy in the communities (i.e., species colonisations and extirpations added and removed from the functional space, respectively) and no evidence of homogenisation in either of those metrics (Clavel et al., 2011; Winter et al., 2009). However, changes in the pairwise dissimilarity structure point towards changes between individual assemblages over time but not to an extent to influence the overall community heterogeneity (Baselga et al., 2015; Rooney et al., 2004). The exception was found in Calakmul, where turnover increased across the sampled area. As $\Delta\beta_C$ was negative overall and $\Delta\beta_E$ was positive across the measured time within Calakmul, this points toward extirpation resultant heterogenisation, i.e., increased turnover due to species loss from sites. To drive this change, species above 50% site occupancy need to be lost, therefore increasing dissimilarity across the sampled area (Chapter 4). These observed changes could be due to stochastic processes, whereby species colonised and were extirpated from individual sites in a random-like manner (Baselga et al., 2015; Stegen et al., 2013). Alternatively, the changes could be driven by environmental disturbance or perturbations (Britton et al., 2009; Davey et al., 2012; Frishkoff et al., 2014; Ibáñez-Álamo et al., 2017; Karp et al., 2012; Mitchell et al., 2022; Rurangwa et al., 2021), species interactions (Korňan

& Svitok, 2018; Martorell & Freckleton, 2014; Wittwer et al., 2015), or issues related to the utilized point-count methodology (Sliwinski et al., 2016; Whitman et al., 1997). Indeed, changes in community composition over time have been found in areas of the tropics that are considered “untouched”, highlighting that bird communities within such areas are often naturally dynamic (Blake & Loiselle, 2015, 2016; Oliveira & dos Anjos, 2022; Stouffer et al., 2021).

Limitations

While we show that there is no noticeable homogenisation or heterogenisation using presence-absence (i.e., binary) data, assemblage-level analysis may mask underlying trends in abundance or local extinction of individual species (Dornelas et al., 2019). Therefore, the coarser results obtained are expected when using only binary presence/absence data (Legendre, 2014) and may not be reflective of the underlying changes in species abundance distributions (Sullivan et al., 2016). Change in the abundance distributions would not necessarily be present within presence/absence analyses but would influence the structure of communities as species became more or less dominant over time (Blowes et al., 2022; Tinoco et al., 2021).

5.5 Conclusions

These findings add to the ongoing discourse on the complexities involved with understanding patterns of temporal spatial beta-diversity whilst also highlighting the need for more long-term monitoring programs within the tropics. While no evidence for directional homogenisation or heterogenisation was found, a significant change was observed over the relatively short time periods sampled despite species richness remaining relatively constant across the sampling periods. We emphasize the importance of continuing long-term ecological monitoring in tropical sites, as even areas that are nominally well protected, such as Calakmul and Cusuco, can show diversity changes and community alterations over time that warrant further study (Beaudrot et al., 2016; Stouffer et al., 2021; Tinoco et al., 2021). Our study also highlights the complexities of studying spatial beta-diversity patterns over time and adds to the growing evidence base surrounding spatial beta-diversity change within biodiversity hotspots within the tropics (Antão et al., 2020; Blowes et al., 2019; Dornelas et al., 2014; Newbold et al., 2019)

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6. Synthesis and future perspectives

6.1 Research summary

This thesis aimed to add to and increase our understanding of diversity and community change within avian communities. Two datasets were utilised, one located within a temperate region (Britain) and one comprising various locations within the tropics. Using these datasets, this thesis probes the drivers of diversity and community change within space (Chapter 2), across time (Chapter 3) and across both time and space within biodiversity hotspots (Chapter 5). Drivers of both spatial diversity and temporal diversity change were assessed for Britain, with the key findings showing that diversity may stabilise communities over time within British bird communities (i.e., more species-rich sites exhibited lower turnover) and that both environmental gradients and distance *per se* contribute uniquely to diversity differences across space, but with a large amount of variance shared between the two. A clear distinction between assemblage composition in both space and time within Britain was found between the island's lowlands and uplands along the "Tees-exe" line (Prakash & Rumsey, 2018). With climate change expected to further raise average temperatures, these patterns may be altered in the future as species shift upslope or are lost entirely (Alba et al., 2022; Davey et al., 2012; Gillings et al., 2015; Neate-Clegg et al., 2018).

While communities are expected to become more homogenous over time in response to increasing anthropogenic pressures and human-mediated environmental change (Clavel et al., 2011; McGill et al., 2015), we show in Chapter 4 that measuring biotic homogenisation is not necessarily straightforward. Specifically, analysing change in spatial beta-diversity over time – a commonly used approach (e.g., Marchetti et al., 2006; Socolar et al., 2016) – may not adequately capture biotic homogenisation on its own, especially within already largely disturbed landscapes such as Britain (Bibby, 2009; Robinson, 2014; Willis & Birks, 2006). For UK Birds, it was found that changes in both decreases and increases in spatial beta-diversity across the measured period were mainly driven by generalist species being extirpated and colonising specific areas. However, the species with the highest contributions to homogenisation were those that have benefited from conservation action within Britain, such as buzzard (*Buteo buteo*), while heterogenisation was driven by once common species that are being lost from large areas of their range (e.g., cuckoo (*Cuculus canorus*)). Accounting for species-specific occupancy changes alongside measures of extirpation and colonisation and the relative contribution of each to patterns of homogenisation and heterogenisation can aid a more comprehensive understanding of community change over time (Tatsumi et al., 2021). These findings have important implications for conservation studies, highlighting the need to consider multiple metrics of diversity when assessing change.

Overall, while adding to the evidence and discourse surrounding diversity change in the Anthropocene, this thesis also highlights the fact that change is complex and continued research is both warranted and needed to gain a clearer understanding of biodiversity change and ensure the appropriate conservation measures are implemented.

6.2 Synthesis

6.2.1 Drivers of biodiversity in space

While analysing spatial biodiversity patterns is an interesting research endeavour in its own right, biodiversity change over space is often used as an alternative to temporal studies, i.e. a “space for time substitution” (Calderón-Patrón et al., 2016; Field et al., 2009; Heino et al., 2019; Xia et al., 2022). There are criticisms of this approach (Damgaard, 2019; Lovell et al., 2023), mainly due to the limitations involving the transferability of findings alongside the causality that can appropriately be apportioned to the relationships found (Lovell et al., 2023). However, in the absence of long-term monitoring efforts (e.g. due to the resources required to maintain monitoring through time), it remains one of the only ways that drivers of community change can be examined, albeit with reference to the known limitations (Damgaard, 2019; Lovell et al., 2023). This thesis does not seek to extrapolate from the findings; instead, it aims to explore what drives composition over space, exploring the relative contributions of niche filtering and dispersal limitation.

Generalised dissimilarity models (GDMs) have been utilised fairly widely in the study of spatial beta-diversity since the method was first proposed (Ferrier, 2002; Ferrier et al., 2002; Mokany et al., 2022). Since that point, GDMs have been used to examine patterns and drivers of community composition within aquatic beetles (Heino et al., 2019), riverine birds (Sinha et al., 2022), and ants (Fitzpatrick et al., 2011), to name a few examples. The main advantage of GDMs is the ability to explore patterns of species diversity and assemblage dissimilarity over large scales (Ferrier et al., 2007). Within the thesis, GDMs were used to explore the relative contributions of abiotic drivers to the assemblage dissimilarity of breeding birds across Britain (Chapter 2).

As with other studies examining spatial beta-diversity, turnover (i.e., the replacement of species between assemblages) was found to be the dominant component of total beta-diversity (Carvalho et al., 2020; Sinha et al., 2022). Nestedness (i.e., the degree to which assemblages are nested subsets of more speciose assemblages) contributed to total beta-diversity to a lesser degree than turnover, but the variance in nestedness patterns was explained primarily by environmental gradients, highlighting the degree to which species may be dependent upon climatic and land use gradients within Britain, as shown by species loss and gains between sites along the gradient. The main proportion of variance explained by distance and environmental drivers for total beta-diversity and turnover was shared between the two, although both explained unique variation in the patterns of diversity change. As the shared variance may relate to the indirect effects of climate within Britain, as the climate varies along geographical structuring at the landscape scale (i.e., climatic distance; Mazel et al., 2017; Qian et al., 2021), geographic distance alone may play a relatively small role in the turnover of species between assemblages. Therefore, this highlights the potentially large role that niche filtering may have on assemblage dissimilarity (Baselga et al., 2015; Carvalho et al., 2020; Dobrovolski et al., 2012; Melo et al., 2009; Steinitz et al., 2006). Alternatively, other factors wrapped up in distance, such as land use and human influence, could play a larger role than climate distance. There was, however, a unique proportion of variance explained by distance alone for turnover. This likely shows the impact of dispersal limitation acting on assemblage dissimilarity, geographical barriers (such as the observed Tees-exe line; Prakash & Rumsey, 2018), or historical factors (Barnagaud et al., 2017; Dobrovolski et al., 2012; Nekola & White, 1999; Soininen et al., 2007).

6.2.2 Temporal biodiversity change

Within Britain, between 1970 and 2010, the assemblage-level (i.e., hectad) composition of breeding birds changed significantly, dominated by the turnover of species (Chapter 3). This finding is consistent with studies of local and regional temporal biodiversity change across multiple taxa (Baselga et al., 2015; Blowes et al., 2019; Dornelas et al., 2014; Pilotto et al., 2020; Stegen et al., 2013) and highlights that bird assemblages did not undergo systematic species loss, as would be evidenced by high temporal nestedness. In comparison to spatial beta-diversity, temporal beta-diversity was not driven to any great extent by changes in abiotic variables. Instead, change seemed largely predicted by the initial species richness of assemblages, pointing to resilience in more speciose areas (Jarzyna & Jetz, 2017; Weeks et al., 2022), potentially due to strong interspecific facilitative interactions (Pandit & Kolasa, 2012; Shurin, 2007). The functional change was lower than taxonomic change, indicating that there was functional redundancy in the species involved in the turnover process (Tsianou et al., 2021). However, changes in taxonomic nestedness were proportional to their functional equivalent, highlighting that the species lost and gained from assemblages contributed uniquely to the available trait space (Petchey & Gaston, 2007).

In comparison, sites located within biodiversity hotspots outside of the UK, which were sampled at smaller spatial scales than the UK bird data, also did not experience systematic loss of diversity, with turnover also the dominant component of change (Chapter 5). While the overall site compositional heterogeneity, measured as a shift in the sampled distribution of multiple spatial beta-diversity over time, changed significantly in Britain, only Calakmul increased in spatial turnover over time out of the three sites within the tropics. However, the pairwise dissimilarity structure, i.e., the degree to which sites are similar or dissimilar to one another, did significantly change at all three hotspot sites. This is not unexpected, as other sites “untouched” within the tropics experienced changes in structure but not alpha diversity across time (Blake & Loiselle, 2015, 2016; Oliveira & dos Anjos, 2022; Stouffer et al., 2021).

6.2.3 Biotic homogenisation

Biotic homogenisation has predominantly been associated with declines in spatial beta-diversity over time, a method that ignores the underlying species extirpations and colonisations that contribute to the overall increase or decrease in dissimilarity (Olden &

Rooney, 2006; Tatsumi et al., 2021). This oversight has potential implications in already disturbed systems that are undergoing conservation efforts to restore species, as these colonisations, once above a certain regional occupancy level, would contribute to apparent homogenisation (a process which is often viewed negatively in the ecological literature). As incidences of biotic homogenisation are predicted to increase alongside the ever-growing human footprint (Beger, 2021; Clavel et al., 2011; McGill et al., 2015), understanding the limitations of current approaches is vital to accurately assessing and attributing change in diversity.

To examine the underlying changes of homogenisation and heterogenisation, within the thesis, a recently developed method by Tatsumi et al. (2021) that partitions the relative contributions of extirpation and colonisation to homogenisation or heterogenisation resultant assemblage change was used (Fig.4.1). It was found that while areas within Britain mainly homogenised between 1990 and 2010, this was largely due to colonisation by generalist species, as evidence by colonisation resultant homogenisation ($\Delta\beta_{C-}$) being the widespread driver. However, a large signal of specialist species loss was not discovered, which would be evident in large values of extirpation resultant homogenisation ($\Delta\beta_{E-}$). Indeed, areas where heterogenisation was observed were characterised by high values of extirpation resultant heterogenisation ($\Delta\beta_{E+}$), highlighting the extirpation of locally common species. Specialist species appeared to be balanced in $\Delta\beta_{C+}$ and $\Delta\beta_{E-}$, showing no sign of systematic loss (Fig.4.5). Therefore, overall, patterns were congruent with evidence that the spread of generalists is contributing to increased homogenisation of assemblages, as found in other locations and taxa (Britton et al., 2009; Cazalis, 2022; Fourcade et al., 2021; Le Viol et al., 2012; Mitchell et al., 2022; Musters et al., 2019; Sullivan et al., 2016), but without the subsequent loss of specialist species. However, while the broad scale metrics agreed with patterns observed in previous studies, the underlying changes in species contributions to extirpation and colonisation change highlighted the potential issues with the measure on its own.

As outlined above, the ‘winners’ between the two periods were largely species that have benefited from conservation measures in the recent past, including many birds of prey that were subjected to high levels of persecution within Britain (Banks et al., 2010; Burnside et al., 2021; Harris et al., 2021). The ‘losers’, i.e., species that contributed highly to $\Delta\beta_E$, were species once common within Britain but have since declined precipitously, such as the cuckoo (*Cuculus canorus*) (Table 4.1). Therefore, the patterns of homogenisation within Britain include contributions from species whose increases are cause for optimism, while the patterns of heterogenisation are primarily driven by decreases in once common species that could be cause for concern.

While there is a large evidence base for biotic homogenisation, there are also studies that have found the opposite (i.e., heterogenisation, Marchetti et al., 2006; McLean et al., 2019). Indeed, a recent meta-analysis shows that evidence from local assemblages shows mixed results between homogenisation and heterogenisation (Blowes et al., 2022). Therefore, further research, including measures of species contributions to observed patterns, is required to understand whether homogenisation is a ubiquitous phenomenon that decreases the diversity and functioning of natural systems.

6.3 Limitations

As with most research, there are limitations involving the data and methods used within this work. Sampling effects can lead to incorrect conclusions and driver attributions in studies of biodiversity change. Throughout the thesis, attempts are made to control for the potential impact of sampling errors and effects, such as sub-sampling (Chapter 5) and removal of data that are potentially erroneous (Chapter 3); there remain some potential issues within the datasets. The British Trust of Ornithology atlas data (Gillings et al., 2019) is fairly robust due to data being collected over four years and supplied at the presence/absence level (i.e., species are less likely to be missed). However, both within the BTO data and the sites used from the tropics, observer bias (Cunningham et al., 1999; Farmer et al., 2012) and sampling locations (2 km x 2km smaller sampling units within the overall 10 km x 10 km hectads for the BTO data; Mentges et al., 2021) could have contributed to sampling effects on the results obtained (Chapters 2 – 4). However, the effects of observers should be uniform across the BTO data due to the number of years used in each atlas. Within the tropics data, Opwall randomly assigns observers to different routes throughout the season and provides training to all ornithologists employed.

Other predictors may also play a role in driving the changes in biodiversity that were found in space and time, such as competitive interactions, predator/prey abundance (Korňan and Svitok, 2018; Wittwer et al., 2015), migration route hazards (such as hunting) or conditions within wintering grounds (Lormée et al., 2019; Vickery et al., 2014). We consider binary (presence/absence) data alone, but changes can occur in the underlying abundance structure with no effect found at the binary scale (Magurran et al., 2019; Tinoco et al., 2021). As a species' local abundance can have a large impact on the influence it has on ecosystem functioning (Gaston et al., 2018; Winfree et al., 2015), this lack of data across the chapters, but in particular Chapter 5, could mean that patterns of change were overlooked.

6.4 Conservation and management implications

Biotic homogenisation is not always a negative process, especially in disturbed ecosystems or those that are benefiting from conservation efforts. Adopting a species-specific approach, coupled with measures of landscape-scale changes, will enable more accurate assessments of assemblage change, with the ability to identify specific areas that are characterised by high incidences of extirpation resultant homogenisation. The ability to assess species-specific contributions toward extirpation and colonisation resultant change also enables the identification of rare species that are being lost locally, characterised by negative $\Delta\beta_E$ (e.g., Hawfinch (*Coccothraustes coccothraustes*); Table 4.1).

As climate and land use change are both predicted to increase globally in future (Newbold, 2018; Soininen et al., 2018; Zabel et al., 2019), understanding how species respond to these abiotic drivers in time and space can help inform conservation policy and management plans. For instance, understanding that more speciose assemblages may be more resilient to environmental perturbations than those that are less species-rich (Chapter 3) points to the need to increase focus on those areas with naturally or anthropogenically lower taxonomic diversity, while a key divide between the lowlands and uplands of Britain in terms of species composition and diversity change shows that conservation and management priorities may need to be specifically tailored to each area (Chapter 2).

While diversity within Britain is well-studied, it is also at a crisis point. In the most recent state of nature report, almost 1,500 species are now threatened with extinction from the isle, 16% of the current extant biodiversity (Burns et al., 2023). The average abundance of 753 terrestrial species has declined by 19%, the distributions of flowering plants have declined by 54%, and the abundance of 13 species of seabird has fallen by an average of 24% (Burns et al., 2023). Changes in the abundance indicator for breeding birds have declined by 14% since 1970, with farmland birds showing a precipitous 58% decline (Burns et al., 2023). What the report shows is that continued monitoring and research on species change and drivers, such as that presented within this thesis, alongside targeted conservation action, needs to proceed unabated to ensure that interventions promote recovery and the current trend of biodiversity decline is halted and reversed.

6.5 Future directions

Potential future directions for research on biodiversity change within the Anthropocene have been discussed throughout the chapters and the synthesis. Here, we provide more detail on those future directions:

- Collecting and utilising robust abundance data across longer time scales will yield the insights needed to understand biodiversity change. This is especially important in assessments of homogenisation as the underlying abundance structure can change without observable community change at the binary data level (Dornelas et al., 2019; Magurran et al., 2019; Sullivan et al., 2016; Tinoco et al., 2021). Coupling this with increased data at the appropriate scales and baselines will enable us to truly understand the impact that humans have had during the brief period we have inhabited the earth.
- The inclusion of functional diversity in the analyses used within the thesis further highlights the importance of considering multiple dimensions of diversity when undertaking studies of assemblage change. However, while it is important to understand change using broad-scale measures such as those used here, future work should look to link changes in functional diversity to observable ecosystem roles and functioning as a whole (Pigot et al., 2020).

- Spatial beta-diversity – specifically the analysis of changes in spatial beta-diversity through time – may not be appropriate to identify biotic homogenisation within Britain and likely other similar systems. However, further work needs to be conducted across a broad variety of locations and taxa to examine the relative contributions of colonisation and extirpation to observed patterns of temporal spatial beta-diversity to assess whether observed homogenisation patterns are truly “biotic homogenisation” as defined in Chapter 4 (Olden & Poff, 2004). Alongside this work, the ability to measure functional and phylogenetic extirpation and colonisation using a similar framework to that provided by Tatsumi et al. (2021) would enable a deeper insight into the impacts of homogenisation on ecosystem functioning and services.
- Whilst this thesis approached spatial and temporal change at the scales the data were obtained, research has shown that changes in biodiversity are scale-dependent (Chase et al., 2018, 2019; Gregory et al., 2023; Whittaker et al., 2001; Zhang et al., 2015). While scale dependency has been given a larger focus within biodiversity change studies, more work needs to be conducted to understand the role that scale plays in homogenisation patterns to inform the scales at which conservation efforts should be targeted (Blowes et al., 2022).

6.6 Closing remarks

Diversity change over time and space is complicated and nuanced, with taxa, location, and both the temporal and spatial scale impacting the findings and the conclusions that can be made. Therefore, our ability to predict future patterns of biodiversity change in response to growing environmental perturbations relies on continued research and evidence about how biodiversity is currently changing and what drives that change. The research presented adds to the growing body of evidence surrounding diversity change, both spatial and temporal, with recommendations made about future steps that can give a clearer picture of biodiversity change during the Anthropocene.

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Appendices

Chapter 2

Appendix S2.1: Supplementary figures and tables

Supplementary Table 2.1.1. All the species included within the study.

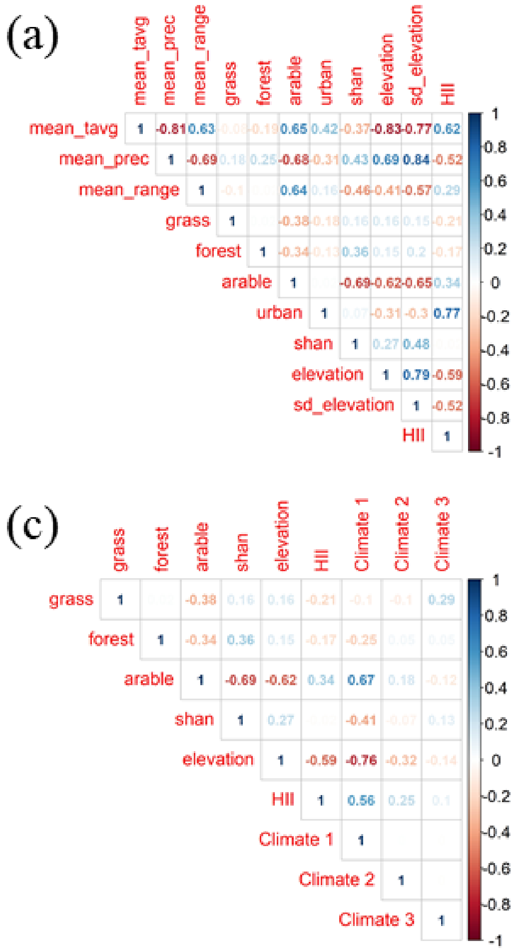
Common Name	Scientific Name
Red-throated Diver	*Gavia stellata*
Black-necked Grebe	*Podiceps nigricollis*
Marsh Harrier	*Circus aeruginosus*
Hen Harrier	*Circus cyaneus*
Goshawk	*Accipiter gentilis*
Sparrowhawk	*Accipiter nisus*
Buzzard	*Buteo buteo*
Golden Eagle	*Aquila chrysaetos*
Osprey	*Pandion haliaetus*
Kestrel	*Falco tinnunculus*
Merlin	*Falco columbarius*
Hobby	*Falco subbuteo*
Peregrine	*Falco peregrinus*
Red Grouse	*Lagopus lagopus*
Ptarmigan	*Lagopus muta*
Black Grouse	*Lyrurus tetrix*
Capercaillie	*Tetrao urogallus*
Red-legged Partridge	*Alectoris rufa*
Grey Partridge	*Perdix perdix*
Quail	*Coturnix coturnix*
Pheasant	*Phasianus colchicus*
Golden Pheasant	*Chrysolophus pictus*
Lady Amherst's Pheasant	*Chrysolophus amherstiae*
Water Rail	*Rallus aquaticus*
Spotted Crake	*Porzana porzana*
Corncrake	*Crex crex*
Moorhen	*Gallinula chloropus*
Coot	*Fulica atra*
Oystercatcher	*Haematopus ostralegus*
Common/Scottish Crossbill*	*Loxia curvirostra/scotica*
Avocet	*Recurvirostra avosetta*
Stone-curlew	*Burhinus oedicnemus*
Rock/Water Pipit*	*Anthus petrosus/spinoletta*
Little Ringed Plover	*Charadrius dubius*
Ringed Plover	*Charadrius hiaticula*
Dotterel	*Charadrius morinellus*
Golden Plover	*Pluvialis apricaria*
Lapwing	*Vanellus vanellus*
Snipe	*Gallinago gallinago*
Woodcock	*Scolopax rusticola*
Black-tailed Godwit	*Limosa limosa*
Black-throated Diver	*Gavia arctica*

Whimbrel	*Numenius phaeopus*
Curlew	*Numenius arquata*
Redshank	*Tringa totanus*
Greenshank	*Tringa nebularia*
Common Sandpiper	Actitis hypoleucos
Rock Dove	*Columba livia*
Stock Dove	*Columba oenas*
Woodpigeon	*Columba palumbus*
Collared Dove	*Streptopelia decaocto*
Turtle Dove	*Streptopelia turtur*
Ring-necked Parakeet	*Psittacula krameri*
Cuckoo	*Cuculus canorus*
Barn Owl	*Tyto alba*
Little Owl	*Athene noctua*
Tawny Owl	*Strix aluco*
Long-eared Owl	*Asio otus*
Short-eared Owl	*Asio flammeus*
Nightjar	*Caprimulgus europaeus*
Swift	*Apus apus*
Bittern	*Botaurus stellaris*
Kingfisher	*Alcedo atthis*
Green Woodpecker	*Picus viridis*
Great Spotted Woodpecker	*Dendrocopos major*
Lesser Spotted Woodpecker	*Dryobates minor*
Woodlark	*Lullula arborea*
Skylark	*Alauda arvensis*
Sand Martin	*Riparia riparia*
Swallow	*Hirundo rustica*
House Martin	*Delichon urbicum*
Tree Pipit	*Anthus trivialis*
Meadow Pipit	*Anthus pratensis*
Yellow Wagtail	*Motacilla flava*
Grey Wagtail	*Motacilla cinerea*
Pied/White Wagtail	*Motacilla alba*
Dipper	*Cinclus cinclus*
Wren	*Troglodytes troglodytes*
Dunnock	*Prunella modularis*
Robin	*Erithacus rubecula*
Nightingale	*Luscinia megarhynchos*
Black Redstart	*Phoenicurus ochruros*
Redstart	*Phoenicurus phoenicurus*
Whinchat	*Saxicola rubetra*
Stonechat	*Saxicola rubicola*
Wheatear	*Oenanthe oenanthe*
Little Egret	*Egretta garzetta*
Ring Ouzel	*Turdus torquatus*
Blackbird	*Turdus merula*
Song Thrush	*Turdus philomelos*

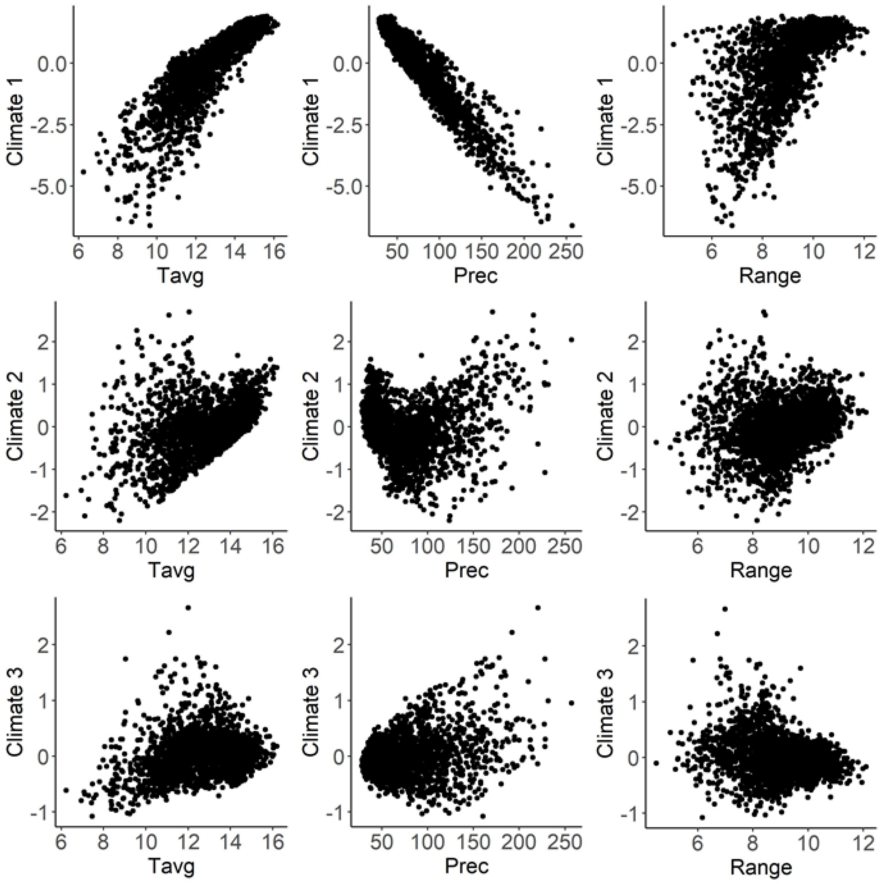
Redwing	*Turdus iliacus*
Mistle Thrush	*Turdus viscivorus*
Cetti's Warbler	*Cettia cetti*
Grasshopper Warbler	*Locustella naevia*
Sedge Warbler	*Acrocephalus schoenobaenus*
Grey Heron	*Ardea cinerea*
Reed Warbler	*Acrocephalus scirpaceus*
Dartford Warbler	*Sylvia undata*
Lesser Whitethroat	*Sylvia curruca*
Whitethroat	*Sylvia communis*
Garden Warbler	*Sylvia borin*
Blackcap	*Sylvia atricapilla*
Wood Warbler	*Phylloscopus sibilatrix*
Chiffchaff	*Phylloscopus collybita*
Willow Warbler	*Phylloscopus trochilus*
Goldcrest	*Regulus regulus*
Firecrest	*Regulus ignicapilla*
Spotted Flycatcher	*Muscicapa striata*
Pied Flycatcher	*Ficedula hypoleuca*
Bearded Tit	*Panurus biarmicus*
Long-tailed Tit	*Aegithalos caudatus*
Marsh Tit	*Poecile palustris*
Willow Tit	*Poecile montanus*
Crested Tit	*Lophophanes cristatus*
Coal Tit	*Periparus ater*
Blue Tit	*Cyanistes caeruleus*
Great Tit	*Parus major*
Nuthatch	*Sitta europaea*
Treecreeper	*Certhia familiaris*
Jay	*Garrulus glandarius*
Magpie	*Pica pica*
Chough	*Pyrrhocorax pyrrhocorax*
Jackdaw	*Coloeus monedula*
Rook	*Corvus frugilegus*
Carrion Crow	*Corvus corone*
Raven	*Corvus corax*
Starling	*Sturnus vulgaris*
House Sparrow	*Passer domesticus*
Mute Swan	*Cygnus olor*
Tree Sparrow	*Passer montanus*
Chaffinch	*Fringilla coelebs*
Greenfinch	*Chloris chloris*
Goldfinch	*Carduelis carduelis*
Siskin	*Spinus spinus*
Linnet	*Linaria cannabina*
Twite	*Linaria flavirostris*
Common/Lesser Redpoll*	*Acanthis flammea/cabaret*
Bullfinch	*Pyrrhula pyrrhula*

Hawfinch	*Coccothraustes coccothraustes*
Snow Bunting	*Plectrophenax nivalis*
Yellowhammer	*Emberiza citrinella*
Cirl Bunting	*Emberiza cirlus*
Reed Bunting	*Emberiza schoeniclus*
Corn Bunting	*Emberiza calandra*
Greylag Goose	*Anser anser*
Canada Goose	*Branta canadensis*
Egyptian Goose	*Alopochen aegyptiaca*
Little Grebe	*Tachybaptus ruficollis*
Shelduck	*Tadorna tadorna*
Mandarin Duck	*Aix galericulata*
Wigeon	*Mareca penelope*
Gadwall	*Mareca strepera*
Teal	*Anas crecca*
Mallard	*Anas platyrhynchos*
Great Crested Grebe	*Podiceps cristatus*
Pintail	*Anas acuta*
Garganey	*Spatula querquedula*
Shoveler	*Spatula clypeata*
Red-crested Pochard	*Netta rufina*
Pochard	*Aythya ferina*
Tufted Duck	*Aythya fuligula*
Eider	*Somateria mollissima*
Common Scoter	*Melanitta nigra*
Goldeneye	*Bucephala clangula*
Hooded Crow	*Corvus cornix*
Red-breasted Merganser	*Mergus serrator*
Goosander	*Mergus merganser*
Ruddy Duck	*Oxyura jamaicensis*
Red Kite	*Milvus milvus*

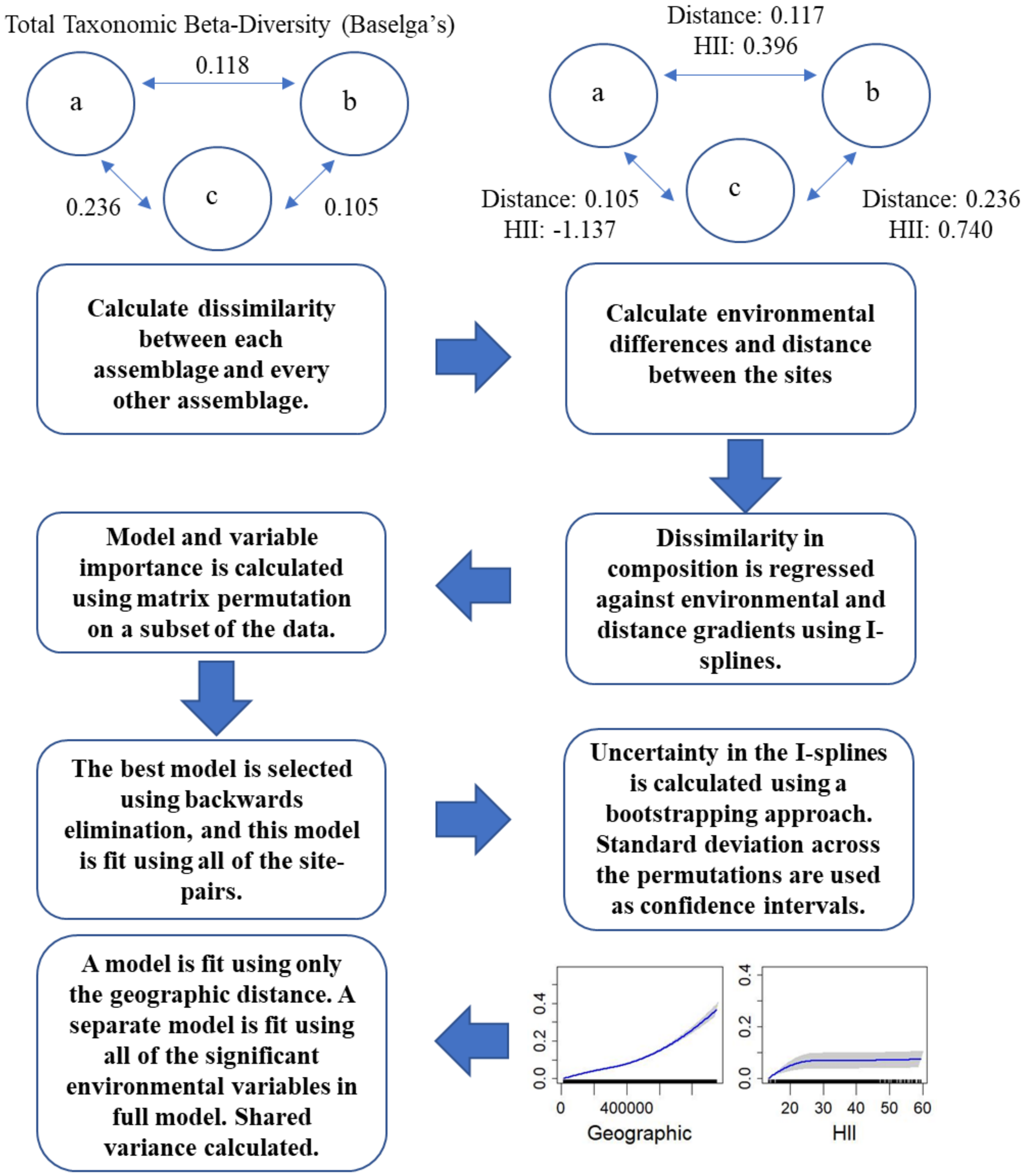
*These species/subspecies were aggregated to species level



Supplementary Figure. 2.1.1. Correlation plots of the variables considered for inclusion in the models. Plots a and b show the Pearson’s and Spearman’s correlations, respectively, between all variables considered. Plots c and d show the Pearson’s and Spearman’s correlations, respectively, between the variables selected for the final models.



Supplementary Figure. 2.1.2. Scatter plots showing the correlation between the original climate variables (average temperature (Tavg), average total precipitation (Prec), and average range in temperature (Range)) and the resultant axes from a principal component analysis.



Calculate dissimilarity between each assemblage and every other assemblage.

Calculate environmental differences and distance between the sites

Dissimilarity in composition is regressed against environmental and distance gradients using I-splines.

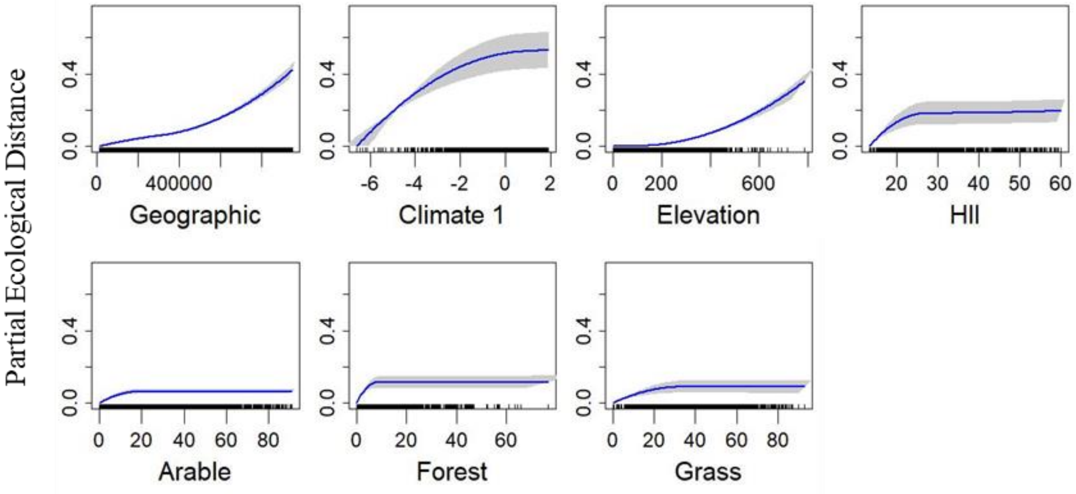
Model and variable importance is calculated using matrix permutation on a subset of the data.

The best model is selected using backwards elimination, and this model is fit using all of the site-pairs.

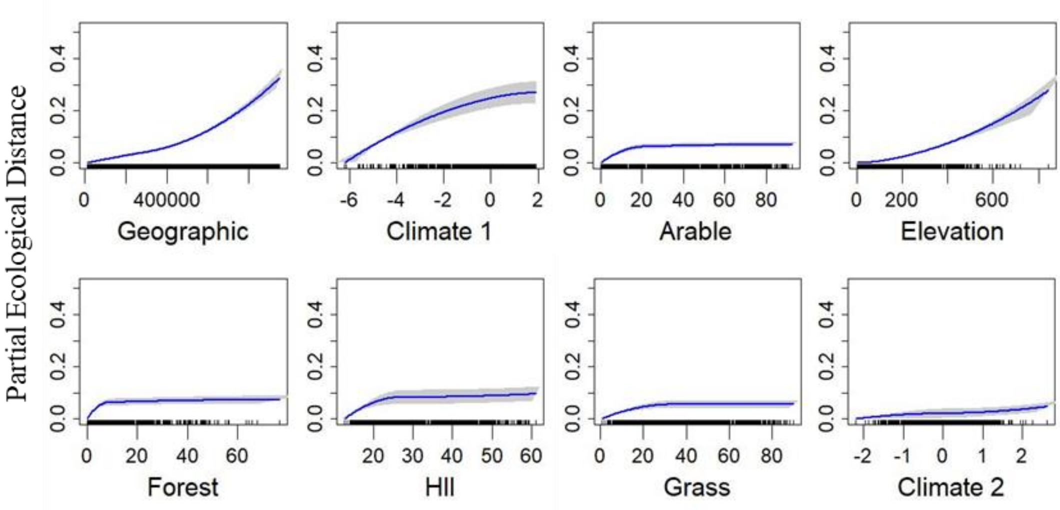
Uncertainty in the I-splines is calculated using a bootstrapping approach. Standard deviation across the permutations are used as confidence intervals.

A model is fit using only the geographic distance. A separate model is fit using all of the significant environmental variables in full model. Shared variance calculated.

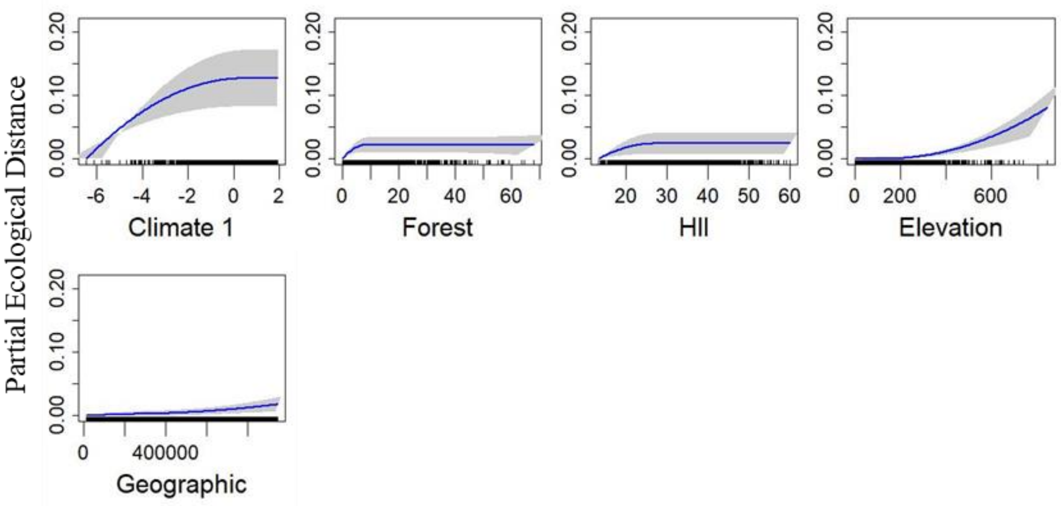
Supplementary Figure. 2.1.3. Flow chart displaying the process of fitting generalized dissimilarity models utilized in this study. In the top row, a, b, and c are different sites.



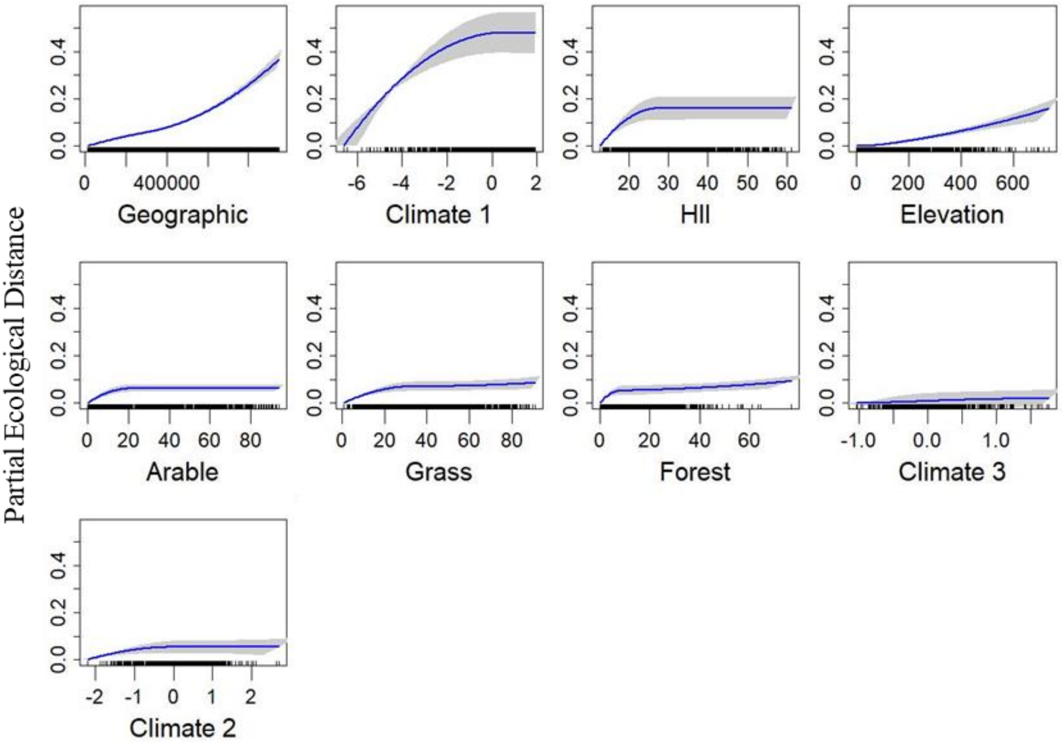
Supplementary Figure. 2.1.4. Plotted I-splines of the significant, important variables (determined from variable importance scores) from a generalised dissimilarity model analysing the relationship between environmental gradients and geographic distance (Geographic), and spatial variation in community the composition (total Sorenson's beta-diversity) of British breeding birds. Climate 1 is the first axis from a principal component analysis using three measures of average climate (temperature, range, and precipitation). All the land use predictors (Forest, Grass, and Arable) are percentage cover. HII is the human influence index, calculated as the average within each quadrat. Curves show the relationship between the gradients and community dissimilarity obtained using I-splines. The most important variables are on the left with decreasing variable importance to the right (top to bottom). Blue lines show the I-Spline correlations, with standard deviation (grey shaded area) calculated through bootstrapping (100 permutations) on a portion of the dataset. A rug plot on the x axis shows the spread of the data. Note the varying y-axis for each measure.



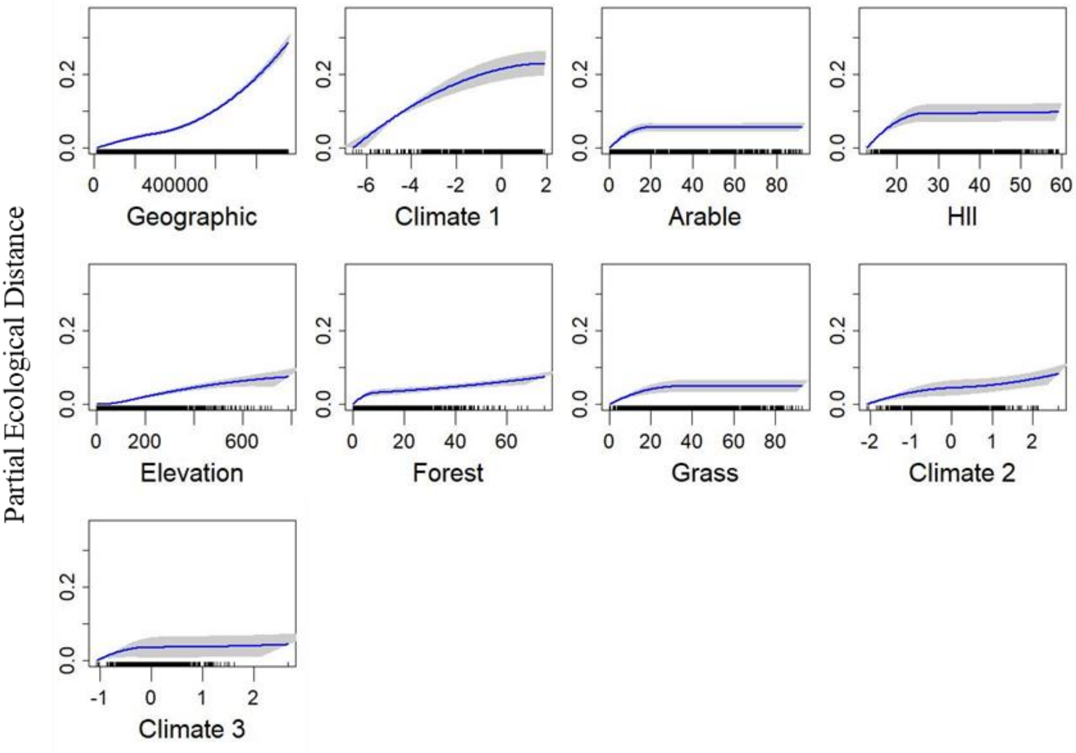
Supplementary Figure. 2.1.5. Plotted I-splines of the significant, important variables (determined from variable importance scores) from a generalised dissimilarity model analysing the relationship between environmental gradients and geographic distance (Geographic), and spatial variation in community the composition (turnover component of Sorenson's beta-diversity) of British breeding birds. Climate 1 and Climate 2 are the first and second axes, respectively, from a principal component analysis using three measures of average climate (temperature, range, and precipitation). All the land use predictors (Forest, Grass, and Arable) are percentage cover. HII is the human influence index, calculated as the average within each quadrat. Curves show the relationship between the gradients and community dissimilarity obtained using I-splines. The most important variables are on the left with decreasing variable importance to the right (top to bottom). Blue lines show the I-Spline correlations, with standard deviation (grey shaded area) calculated through bootstrapping (100 permutations) on a portion of the dataset. A rug plot on the x axis shows the spread of the data. Note the varying y-axis for each measure.



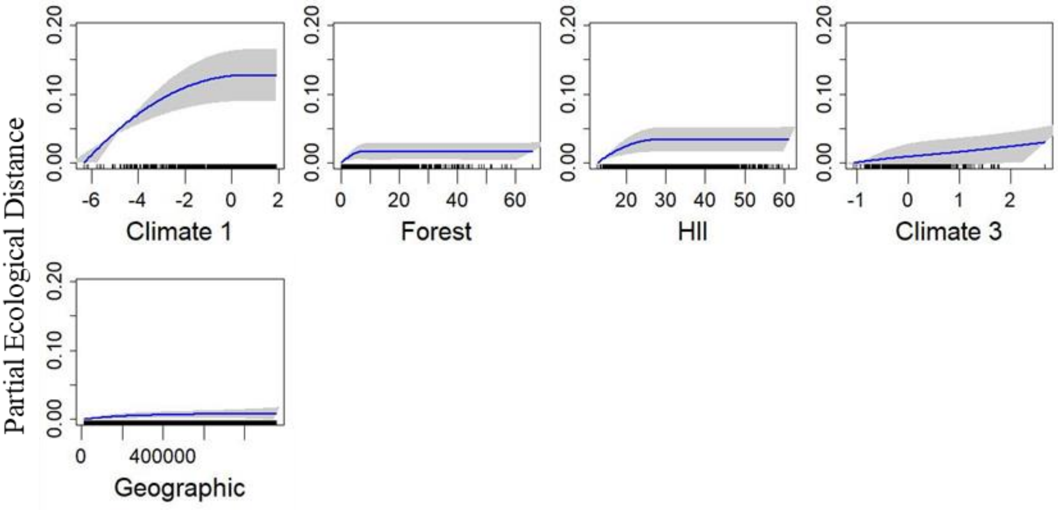
Supplementary Figure. 2.1.6. Plotted I-splines of the significant, important variables (determined from variable importance scores) from a generalised dissimilarity model analysing the relationship between environmental gradients and geographic distance (Geographic), and spatial variation in community the composition (nestedness resultant dissimilarity component of Sorenson's beta-diversity) of British breeding birds. Climate 1 is the first axis from a principal component analysis using three measures of average climate (temperature, range, and precipitation). All the land use predictors (Forest) are percentage cover. HII is the human influence index, calculated as the average within each quadrat. Curves show the relationship between the gradients and community dissimilarity obtained using I-splines. The most important variables are on the left with decreasing variable importance to the right (top to bottom). Blue lines show the I-Spline correlations, with standard deviation (grey shaded area) calculated through bootstrapping (100 permutations) on a portion of the dataset. A rug plot on the x axis shows the spread of the data. Note the varying y-axis for each measure.



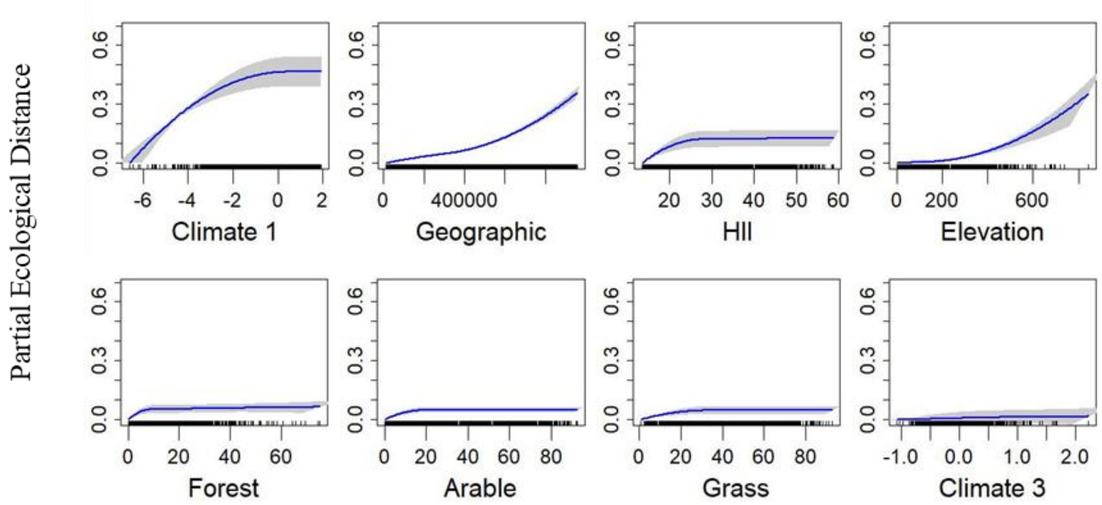
Supplementary Figure. 2.1.7. Plotted I-splines of the significant, important variables (determined from variable importance scores) from a generalised dissimilarity model analysing the relationship between environmental gradients and geographic distance (Geographic), and spatial variation in community the composition (total functional Sorenson's beta-diversity) of British breeding birds. Climate 1, Climate 2, and Climate 3 are the first, second, and third axes, respectively, from a principal component analysis using three measures of average climate (temperature, range, and precipitation). All the land use predictors (Forest, Grass, and Arable) are percentage cover. HII is the human influence index, calculated as the average within each quadrat. Curves show the relationship between the gradients and community dissimilarity obtained using I-splines. The most important variables are on the left with decreasing variable importance to the right (top to bottom). Blue lines show the I-Spline correlations, with standard deviation (grey shaded area) calculated through bootstrapping (100 permutations) on a portion of the dataset. A rug plot on the x axis shows the spread of the data. Note the varying y-axis for each measure.



Supplementary Figure. 2.1.8. Plotted I-splines of the significant, important variables (determined from variable importance scores) from a generalised dissimilarity model analysing the relationship between environmental gradients and geographic distance (Geographic), and spatial variation in community the composition (turnover component of functional Sorenson's beta-diversity) of British breeding birds. Climate 1, Climate 2, and Climate 3 are the first, second, and third axes, respectively, from a principal component analysis using three measures of average climate (temperature, range, and precipitation). All the land use predictors (Forest, Grass, and Arable) are percentage cover. HII is the human influence index, calculated as the average within each quadrat. Curves show the relationship between the gradients and community dissimilarity obtained using I-splines. The most important variables are on the left with decreasing variable importance to the right (top to bottom). Blue lines show the I-Spline correlations, with standard deviation (grey shaded area) calculated through bootstrapping (100 permutations) on a portion of the dataset. A rug plot on the x axis shows the spread of the data. Note the varying y-axis for each measure.



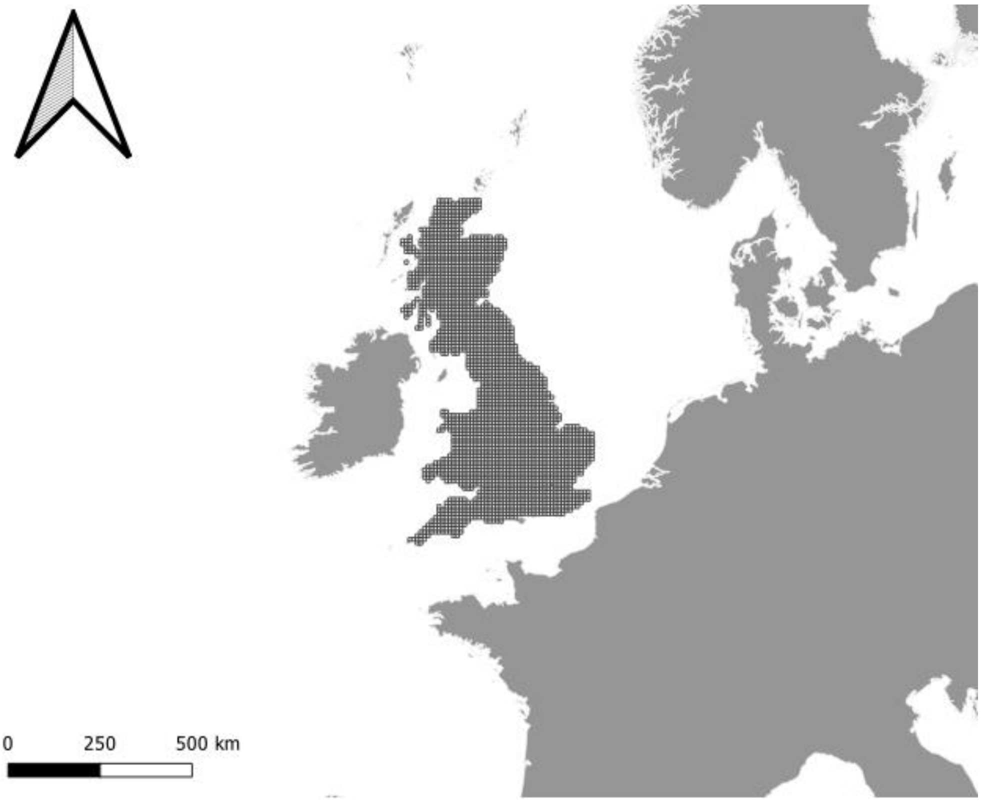
Supplementary Figure. 2.1.9. Plotted I-splines of the significant, important variables (determined from variable importance scores) from a generalised dissimilarity model analysing the relationship between environmental gradients and geographic distance (Geographic), and spatial variation in community the composition (nestedness resultant dissimilarity component of functional Sorenson's beta-diversity) of British breeding birds. Climate 1 and Climate 3 are the first and third axes, respectively, from a principal component analysis using three measures of average climate (temperature, range, and precipitation). All the land use predictors (Forest) are percentage cover. HII is the human influence index, calculated as the average within each quadrat. Curves show the relationship between the gradients and community dissimilarity obtained using I-splines. The most important variables are on the left with decreasing variable importance to the right (top to bottom). Blue lines show the I-Spline correlations, with standard deviation (grey shaded area) calculated through bootstrapping (100 permutations) on a portion of the dataset. A rug plot on the x axis shows the spread of the data. Note the varying y-axis for each measure.



Supplementary Figure. 2.1.10. Plotted I-splines of the significant, important variables (determined from variable importance scores) from a generalised dissimilarity model analysing the relationship between environmental gradients and geographic distance (Geographic), and spatial variation in community the composition (mean nearest taxon distance (MNTD)) of British breeding birds. . Climate 1 and Climate 3 are the first and third axes, respectively, from a principal component analysis using three measures of average climate (temperature, range, and precipitation). All the land use predictors (Forest, Grass, and Arable) are percentage cover. HII is the human influence index, calculated as the average within each quadrat. Curves show the relationship between the gradients and community dissimilarity obtained using I-splines. The most important variables are on the left with decreasing variable importance to the right (top to bottom). Blue lines show the I-Spline correlations, with standard deviation (grey shaded area) calculated through bootstrapping (100 permutations) on a portion of the dataset. A rug plot on the x axis shows the spread of the data. Note the varying y-axis for each measure.

Chapter 3

Appendix S3.1: Study location, data preparation, and British Trust of Ornithology sampling methodology for two Atlas periods (1968 – 1972 and 2007 – 2011)



Supplementary Figure. 3.1.1. A map showing the study location (Great Britain) within Europe. Grids across the island show the 10km x 10km hectads used to sample British avifauna by the British Trust of Ornithology over two separate atlas periods: BA1970 (1968-1972) and BA2010 (2008-2011).

Data preparation

Atlas data were collected by the British trust of Ornithology from April to July over the periods 1988-1991 and 2007 – 2011. Some fieldwork effort was permitted out of the April-July field season during both atlases but was only promoted to observers during the 2008-2011 season. Specific instructions on what observations constituted breeding behaviour were given to volunteers, with these breeding behaviours then grouped into different categories of likelihood that that species was indeed breeding within the 10km x 10km area (‘possible’, ‘probable’, and ‘confirmed’) (Gillings et al., 2019). Data were also collected for an atlas covering 1988-1991 (BA1990), but this was excluded from the present analysis. This atlas was excluded because it utilised a method that may have resulted in less effort being expended to locate rare or elusive species, as well as having poorer coverage than both BA1970 and BA2010, which both had similar coverage (Gillings et al., 2019).

We removed pelagic species, vagrant species, and those species supplied at a larger spatial grain (due to fears of human persecution), and only retained species designated as 'probable' or 'confirmed' breeders, leaving 169 species (see Wayman et al., 2021 for further details). Several species (Water Pipit, Rock Pipit, Common Redpoll, Lesser Redpoll, Crossbill, and Scottish Crossbill) that were recorded as sub-species in the separate atlases were grouped to species level (Rock Pipit, Common Redpoll, and Crossbill) (see Table S2.1). All hectadss with less than 50% land (following Petchey et al. (2007) and White et al. (2018)) and all-island regions that we considered primarily disconnected from the mainland were removed. Gillings et al. (2019) used Frescalo (FREquency SCAling Local; Hill 2012) to assess survey completeness, calculating the number of "benchmark" species (locally common and widespread species) found in each cell. We removed all hectads that showed an absolute deviation more than two times the standard deviation (SD) in the percentage of benchmark species found between BA1970 and BA2010 (N = 87) to control for sampling intensity differences between the two atlases (Gillings et al., 2019), leaving 2238 hectads.

Sampling Methodology

For the 2007-2011 Bird Atlas, the regional organiser aimed to accumulate survey coverage of at least eight tetrads (2km x 2km squares) per hectad in the breeding season, accounting for 32% of the entire 10km x 10km hectad. The tetrads were selected to capture all major land use groups within the larger hectad. Each of these tetrads was visited at least twice in both winter and during the breeding season. These visits were timed (either one hour or two hours long), and raw data were submitted each hour rather than summarised across visits. Greater emphasis was also placed on casual records to counteract perceived under-recording of scarce species in BA1990. Survey effort was >= 16 hours per 10km square but would have been greater where more than eight tetrads were surveyed, where visits were two hours in duration, and where more supplementary recording effort was undertaken (called "roving records", allowing for casual observations to be recorded). Data were queried through a "validation module" on the BTO website. This allowed Atlas Regional Validators to view all the records and make decisions on unusual data points. They could flag these unusual observations for the original observer, and the observer could then decide to delete the observation, edit the observation if they agreed that an error had been made (for example, if the grid location had been input incorrectly), or email the validator with a clarification that the record was indeed correct.

For the 1968 – 1972 Atlas, individuals or teams of surveyors visited the 10km x 10km hectads, and they could visit it as many times as they wished, for as long as they wished. This meant that multiple independent surveyors probably visited the same 10km x 10km hectad over the breeding season. At the end of the season, each surveyor submitted a single recording card for each 10km square they visited, with evidence about whether each species they had recorded were breeding. Rare and elusive (such as nocturnal) species were less likely to be detected in squares that were visited for less time (for example, those in more remote areas). No effort data were produced.

See Sharrock (1976), Balmer et al. (2013), and Gillings et al. (2019) for more information.

Sharrock, J. T. R. (1976). *The Atlas of Breeding Birds in Britain and Ireland*. T. & A.D. Poyser, Berkhamsted.

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Petchey, O. L., Evans, K. L., Fishburn, I. S., & Gaston, K. J. (2007). Low functional diversity and no redundancy in British avian assemblages. Journal of Animal Ecology, 76(5), 977–985. https://doi.org/10.1111/j.1365-2656.2007.01271.x

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White, H. J., Montgomery, W. I., Storchová, L., Hořák, D., & Lennon, J. J. (2018). Does functional homogenisation accompany taxonomic homogenisation 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

Appendix S3.2: Species included in the study.

Table 3.2.1. All the species included within the study.

Common Name	Scientific Name
Canada Goose	*Branta canadensis*
Greylag Goose	*Anser anser*
Mute Swan	*Cygnus olor*
Egyptian Goose	*Alopochen aegyptiaca*
Shelduck	*Tadorna tadorna*
Mandarin Duck	*Aix galericulata*
Garganey	*Spatula querquedula*
Shoveler	*Spatula clypeata*
Gadwall	*Mareca strepera*
Wigeon	*Mareca penelope*
Mallard	*Anas platyrhynchos*
Pintail	*Anas acuta*
Teal	*Anas crecca*
Red-crested Pochard	*Netta rufina*
Pochard	*Aythya ferina*
Tufted Duck	*Aythya fuligula*
Eider	*Somateria mollissima*
Common Scoter	*Melanitta nigra*
Goldeneye	*Bucephala clangula*
Goosander	*Mergus merganser*
Red-breasted Merganser	*Mergus serrator*
Ruddy Duck	*Oxyura jamaicensis*
Red Grouse	*Lagopus lagopus*
Ptarmigan	*Lagopus muta*
Capercaillie	*Tetrao urogallus*
Black Grouse	*Lyrurus tetrix*
Grey Partridge	*Perdix perdix*
Golden Pheasant	*Chrysolophus pictus*
Lady Amherst's Pheasant	*Chrysolophus amherstiae*
Pheasant	*Phasianus colchicus*
Quail	*Coturnix coturnix*
Red-legged Partridge	*Alectoris rufa*
Nightjar	*Caprimulgus europaeus*
Swift	*Apus apus*
Cuckoo	*Cuculus canorus*
Rock Dove	*Columba livia*
Stock Dove	*Columba oenas*
Woodpigeon	*Columba palumbus*
Turtle Dove	*Streptopelia turtur*
Collared Dove	*Streptopelia decaocto*
Water Rail	*Rallus aquaticus*
Corncrake	*Crex crex*

Spotted Crake	*Porzana porzana*
Moorhen	*Gallinula chloropus*
Coot	*Fulica atra*
Little Grebe	*Tachybaptus ruficollis*
Great Crested Grebe	*Podiceps cristatus*
Black-necked Grebe	*Podiceps nigricollis*
Stone-curlew	*Burhinus oedicnemus*
Oystercatcher	*Haematopus ostralegus*
Avocet	*Recurvirostra avosetta*
Lapwing	*Vanellus vanellus*
Golden Plover	*Pluvialis apricaria*
Ringed Plover	*Charadrius hiaticula*
Little Ringed Plover	*Charadrius dubius*
Dotterel	*Charadrius morinellus*
Whimbrel	*Numenius phaeopus*
Curlew	*Numenius arquata*
Black-tailed Godwit	*Limosa limosa*
Woodcock	*Scolopax rusticola*
Snipe	*Gallinago gallinago*
Common Sandpiper	*Actitis hypoleucos*
Redshank	*Tringa totanus*
Greenshank	*Tringa nebularia*
Red-throated Diver	*Gavia stellata*
Black-throated Diver	*Gavia arctica*
Bittern	*Botaurus stellaris*
Grey Heron	*Ardea cinerea*
Little Egret	*Egretta garzetta*
Osprey	*Pandion haliaetus*
Golden Eagle	*Aquila chrysaetos*
Sparrowhawk	*Accipiter nisus*
Goshawk	*Accipiter gentilis*
Marsh Harrier	*Circus aeruginosus*
Hen Harrier	*Circus cyaneus*
Red Kite	*Milvus milvus*
Buzzard	*Buteo buteo*
Barn Owl	*Tyto alba*
Little Owl	*Athene noctua*
Long-eared Owl	*Asio otus*
Short-eared Owl	*Asio flammeus*
Tawny Owl	*Strix aluco*
Kingfisher	*Alcedo atthis*
Lesser Spotted Woodpecker	*Dryobates minor*
Great Spotted Woodpecker	*Dendrocopos major*
Green Woodpecker	*Picus viridis*
Kestrel	*Falco tinnunculus*
Merlin	*Falco columbarius*

Hobby	*Falco subbuteo*
Peregrine	*Falco peregrinus*
Ring-necked Parakeet	*Psittacula krameri*
Jay	*Garrulus glandarius*
Magpie	*Pica pica*
Chough	*Pyrrhocorax pyrrhocorax*
Jackdaw	*Coloeus monedula*
Rook	*Corvus frugilegus*
Carrion Crow	*Corvus corone*
Hooded Crow	*Corvus cornix*
Raven	*Corvus corax*
Coal Tit	*Periparus ater*
Crested Tit	*Lophophanes cristatus*
Marsh Tit	*Poecile palustris*
Willow Tit	*Poecile montanus*
Blue Tit	*Cyanistes caeruleus*
Great Tit	*Parus major*
Bearded Tit	*Panurus biarmicus*
Woodlark	*Lullula arborea*
Skylark	*Alauda arvensis*
Sand Martin	*Riparia riparia*
Swallow	*Hirundo rustica*
House Martin	*Delichon urbicum*
Cetti's Warbler	*Cettia cetti*
Long-tailed Tit	*Aegithalos caudatus*
Wood Warbler	*Phylloscopus sibilatrix*
Willow Warbler	*Phylloscopus trochilus*
Chiffchaff	*Phylloscopus collybita*
Sedge Warbler	*Acrocephalus schoenobaenus*
Reed Warbler	*Acrocephalus scirpaceus*
Grasshopper Warbler	*Locustella naevia*
Blackcap	*Sylvia atricapilla*
Garden Warbler	*Sylvia borin*
Lesser Whitethroat	*Sylvia curruca*
Whitethroat	*Sylvia communis*
Dartford Warbler	*Sylvia undata*
Firecrest	*Regulus ignicapilla*
Goldcrest	*Regulus regulus*
Wren	*Troglodytes troglodytes*
Nuthatch	*Sitta europaea*
Treecreeper	*Certhia familiaris*
Starling	*Sturnus vulgaris*
Song Thrush	*Turdus philomelos*
Mistle Thrush	*Turdus viscivorus*
Redwing	*Turdus iliacus*
Blackbird	*Turdus merula*

Ring Ouzel	*Turdus torquatus*
Spotted Flycatcher	*Muscicapa striata*
Robin	*Erithacus rubecula*
Nightingale	*Luscinia megarhynchos*
Pied Flycatcher	*Ficedula hypoleuca*
Black Redstart	*Phoenicurus ochruros*
Redstart	*Phoenicurus phoenicurus*
Whinchat	*Saxicola rubetra*
Stonechat	*Saxicola rubicola*
Wheatear	*Oenanthe oenanthe*
Dipper	*Cinclus cinclus*
Tree Sparrow	*Passer montanus*
House Sparrow	*Passer domesticus*
Dunnock	*Prunella modularis*
Yellow Wagtail	*Motacilla flava*
Grey Wagtail	*Motacilla cinerea*
Pied/White Wagtail	*Motacilla alba*
Meadow Pipit	*Anthus pratensis*
Tree Pipit	*Anthus trivialis*
Rock/Water Pipit*	*Anthus petrosus/spinoletta*
Chaffinch	*Fringilla coelebs*
Hawfinch	*Coccothraustes coccothraustes*
Bullfinch	*Pyrrhula pyrrhula*
Greenfinch	*Chloris chloris*
Twite	*Linaria flavirostris*
Linnet	*Linaria cannabina*
Common/Lesser Redpoll*	*Acanthis flammea/cabaret*
Common/Scottish Crossbill*	*Loxia curvirostra/scotica*
Goldfinch	*Carduelis carduelis*
Siskin	*Spinus spinus*
Snow Bunting	*Plectrophenax nivalis*
Corn Bunting	*Emberiza calandra*
Yellowhammer	*Emberiza citrinella*
Cirl Bunting	*Emberiza cirlus*
Reed Bunting	*Emberiza schoeniclus*

*These species/subspecies were aggregated to species level

Appendix S3.3: MNTD, MPD, and random forest methodology

Mean nearest taxon distance (MNTD) and mean pairwise distance (MPD)

MNTD represents the mean distance (smallest non-diagonal value) between species in an assemblage and is most sensitive to changes at the 'tips' of a dendrogram (Webb, Ackerly, McPeek, & Donoghue, 2002). Here we calculate the beta-diversity version of MNTD (also known as betaNTI and betaMNTD) that calculates the same measure, but between assemblages, or in this case, between the same assemblage in 1970 and 2010 (Miller, Farine, & Trisos, 2017; Matthews et al., 2020). So, for MNTD, this calculated the mean distance between a species in 1970 and its nearest functional equivalent in 2010. An average is then taken across the assemblage. MPD is a similar measure but is calculated as the mean between all non-diagonal elements in the pairwise distance matrix (Webb, 2000; Webb, Ackerly, & Kembel, 2008), so it is more sensitive to changes at the roots of the functional dendrogram. Again, we calculated the beta-diversity version of MPD (also known as betaNRI and betaMPD) that calculates the distance between each species in 1970 and every species in the 2010 assemblage. A mean is then taken across the species.

Random forests

Random forests are an ensemble learning method that are robust to over-fitting and non-linearity through the implementation of bootstrapped-based regression that builds individual trees with subsets of the predictor variables and data in parallel and then averages over the trees to make predictions at unsampled sites contained within the data not subset ("out-of-the-bag" data (OOB)) for building the trees (Breiman, 2001; Cutler et al., 2007; Prasad, Iverson, & Liaw, 2006).

Random forest regression requires that three main hyperparameters be chosen; the number of trees, the number of predictors used to build each component tree, and the minimum node size (Prasad et al., 2006). Firstly, a random forest was fitted to each of the response variables. The forests were then tuned using combinations of the three hyperparameters mentioned above using the function *rf_tuning* in the package 'spatialRF' (Bentio, 2021). Five values were used for each parameter (500, 1000, 1500, 2000, and 2500 for number of trees (*ntree*); 2, 3, 5, 7 and 9 for number of variables (*mtry*); and 5, 10, 15, 20, and 25 for minimum node size (*minN*)) yielding 125 combinations. The combination that achieved the best fit to the data (evaluated using the R^2 of the fit to the OOB data) was selected.

Spatial cross-validation was used to assess predictive performance. Spatial cross-validation splits the data into spatially distinct training and testing blocks (75% training, and 25% retained for testing). This was performed utilising the function *rf_evaluate* in the package ‘spatialRF’ (Benito, 2021).

The out of the bag (OOB) R^2 was calculated within the *ranger* function in the package ‘ranger’ (Wright & Ziegler, 2017).

References

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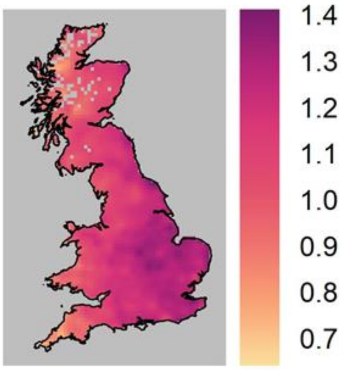
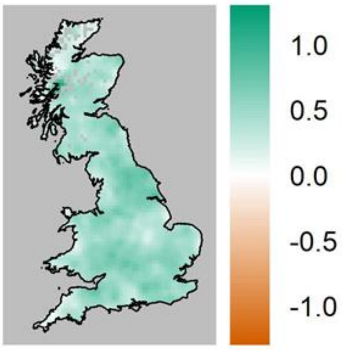
Wright, M. N., & Ziegler, A. (2017). ranger: A Fast Implementation of Random Forests for High Dimensional Data in C++ and R. *Journal of Statistical Software*, *77*(1), 1-17. doi:10.18637/jss.v077.i01

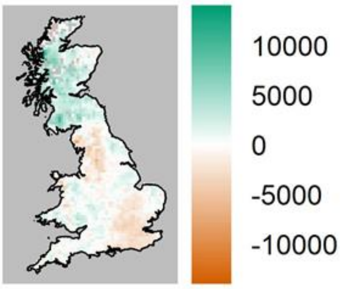
Appendix S3.4: Heat maps of climate and land-use change



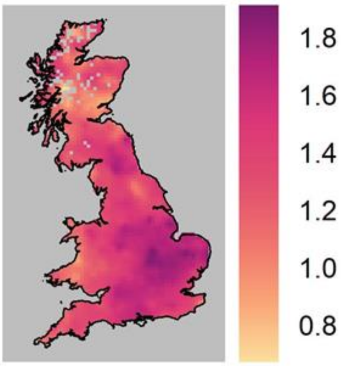
Tavg



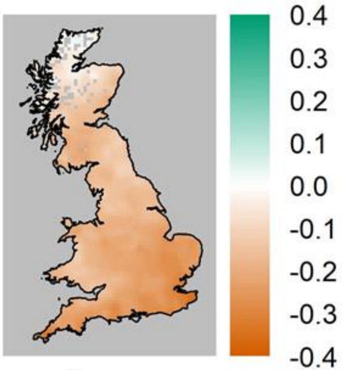
Range



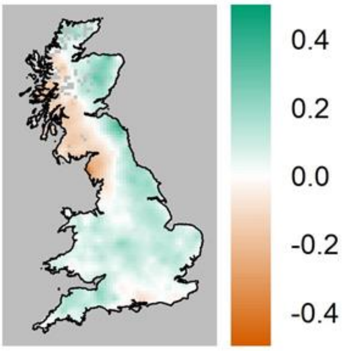
Prec



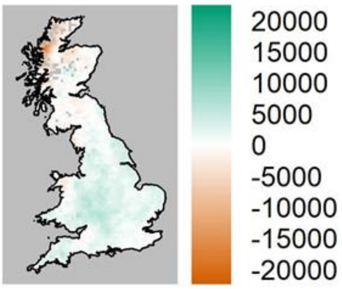
Cold



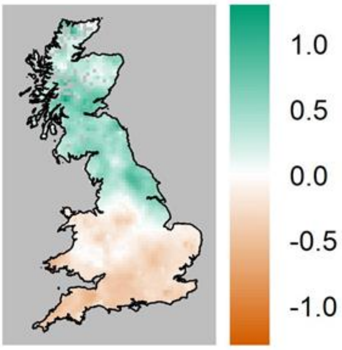
Tavg$_{SD}$



Range$_{SD}$



Prec$_{SD}$



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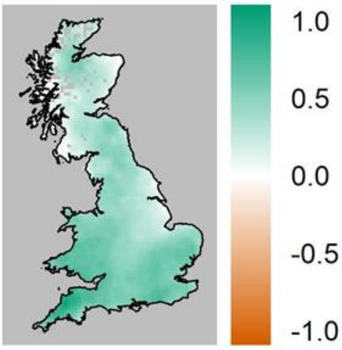
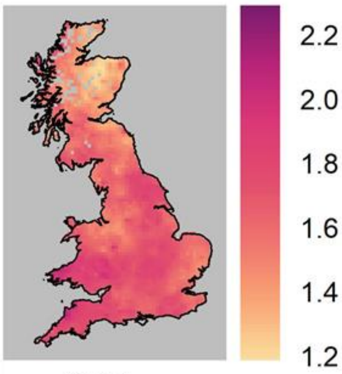
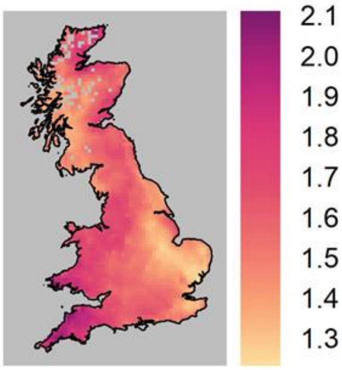


Warm$_{SD}$



Cold$_{FAT}$



Warm$_{FAT}$

Fig. S3.4.1. Heat maps of the temporal change of measures of climate in Britain during the avian breeding season (March to the end of July) between 1970 and 2010. We used five measures; average temperature (Tavg), range in temperature (the average maximum temperature for each month, minus the minimum (Range)), total precipitation (summed across the breeding season (Prec)), average temperature in the coldest month (Cold), and average temperature in the warmest month (Warm; not shown here as it was removed due to collinearity with other variables). Climatic change was calculated as the difference between a 10-year average for 1970 (1960 – 1970) and 2010 (2001 – 2011) that corresponded to Atlas data collected by the British Trust of Ornithology during those periods. This was also repeated for the standard deviation for each climatic variable (standard deviation of the later period minus the standard deviation of the earlier). We also calculated the fat tails (the relative proportion of time spent in the tails of the distribution compared to that spent in the central mass) for the warmest and coldest months over a 50-year period (1960 – 2010) to account for extreme weather events.

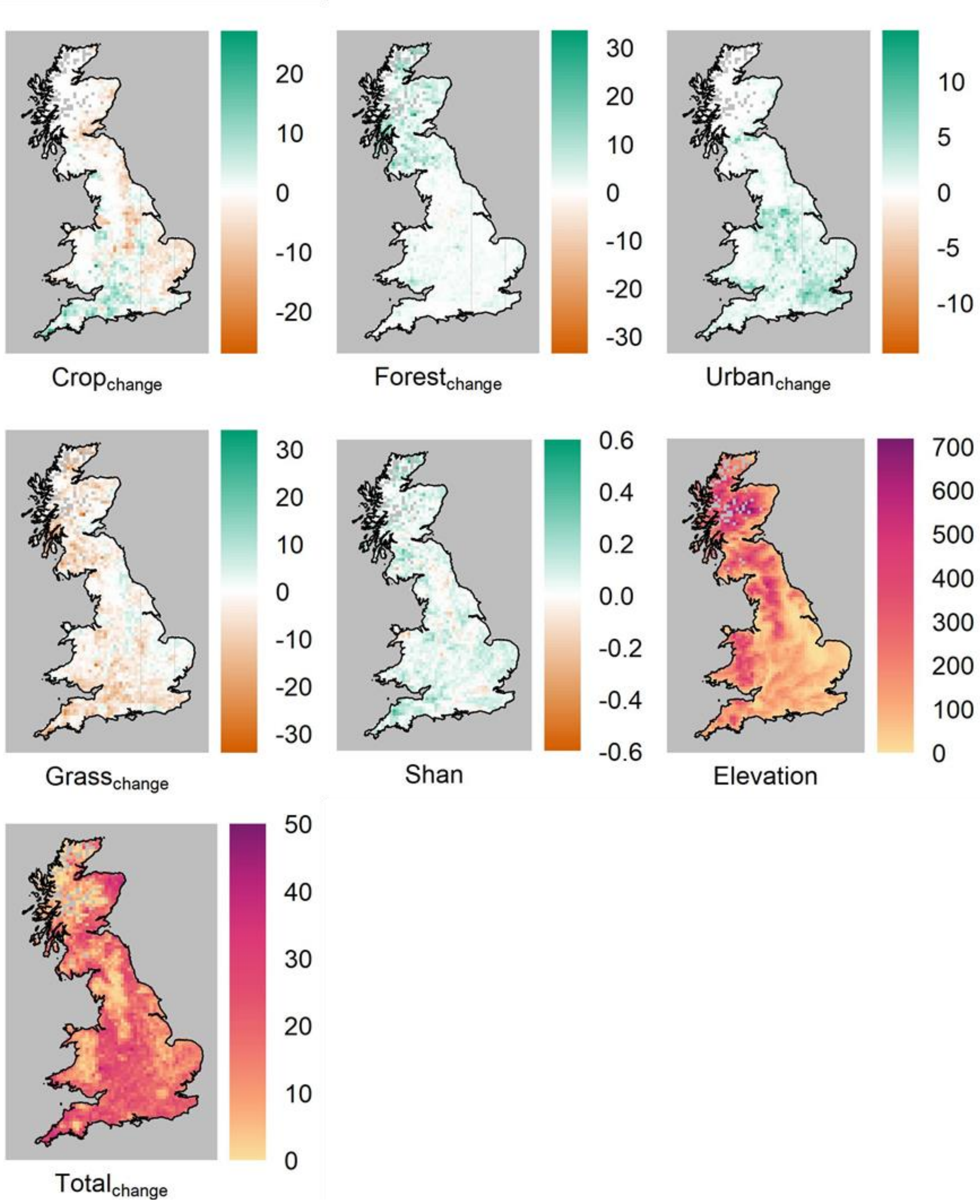


Fig. S3.4.2. Heat maps of the temporal change observed for different classes of land cover and land use (LULC), Shannon's diversity index (Shan), total hectad transitions ($\text{Total}_{\text{change}}$), and of mean elevation, in Britain between 1970 and 2010. The values represent the change within each hectad between the 1970 and 2010 periods, except for the mean elevation (Elevation) map, calculated as the average over 400 evenly spaced points across each 10km x 10km hectad.

Appendix S3.5: Random forest evaluation

Table S3.5.1. Performance for random forest models evaluating the importance of climatic change, land use and land cover (LULC) change, Shannon's index change, elevation, latitude, longitude, and initial species richness on various metrics of biodiversity change in British breeding bird assemblages. Full model results are for a random forest run using all the data and then tested on the same data. Out-of the bag (OOB) R^2 is computed by constructing the component decision trees in the model on a bootstrap sampled set of the data and tested on the remaining data. The fit is then averaged across decision trees to yield the final OOB R^2. The root mean squared error (RMSE) is the average difference between the observed outcomes and the values predicted by the model. Twenty spatially independent training and testing datasets were constructed from the data, with 75% of the data in the training sets and 25% in the testing sets. Random forests were run on each of the training sets and then tested on the corresponding training set yielding 20 performance measures for each metric. The mean of these performance measures and the standard deviation was then calculated and provided below. All models were run including coordinates (denoted with "XY") and without coordinates.

	Taxonomic			Functional		
	BD_{TOTAL}	BD_{TURN}	BD_{NEST}	FD_{TOTAL}	FD_{TURN}	FD_{NEST}
Full Model XY						
OOB R^2	0.52	0.36	0.16	0.47	0.27	0.13
RMSE	0.02	0.02	0.02	0.02	0.02	0.02
Testing XY						
R^2	0.3 ± 0.2	0.2 ± 0.17	0.04 ± 0.03	0.29 ± 0.14	0.14 ± 0.13	0.05 ± 0.04
Full Model						
OOB R^2	0.53	0.36	0.16	0.46	0.27	0.11
RMSE	0.02	0.02	0.02	0.02	0.02	0.02
Testing						
R^2	0.31 ± 0.21	0.2 ± 0.17	0.04 ± 0.03	0.31 ± 0.14	0.14 ± 0.13	0.05 ± 0.04
RMSE	0.05	0.05	0.05	0.04	0.05	0.05

Table S3.5.2. Performance for random forest models evaluating the importance of various climatic change, land use and land cover (LULC) change, Shannon's index change, elevation, latitude, longitude, and initial species richness on various metrics of biodiversity change in British breeding bird assemblages. Full model results are for a random forest run using all of the data and then tested on the same data. Out-of the bag (OOB) R^2 is computed by constructing the component decision trees in the model on a bootstrap sampled set of the data and tested on the remaining data. The fit is then averaged across decision trees to yield the final OOB R^2. The root mean squared error (RMSE) is the average difference between the observed outcomes and the values predicted by the model. Twenty spatially independent training and testing datasets were constructed from the data, with 75% of the data in the training sets and 25% in the testing sets. Random forests were run on each of the training sets and then tested on the corresponding training set yielding 20 performance measures for each metric. The mean of these performance measures and the standard deviation was then calculated and provided below. All models were run including coordinates (denoted with “XY”) and without coordinates.

	Taxonomic	Functional	
	SP_{Change}	MPD	MNTD
Full Model XY			
OOB R^2	0.39	0.60	0.52
RMSE	3.58	0.03	0.03
Testing XY			
R^2	0.17 ± 0.04	0.5 ± 0.16	0.31 ± 0.18
Full Model			
OOB R^2	0.39	0.60	0.48
RMSE	3.56	0.03	0.03
Testing			
R^2	0.17 ± 0.04	0.5 ± 0.15	0.32 ± 0.18
RMSE	10.07 ± 0.99	0.08 ± 0.02	0.09 ± 0.02

Appendix S3.6: Partial plots with spatial coordinates

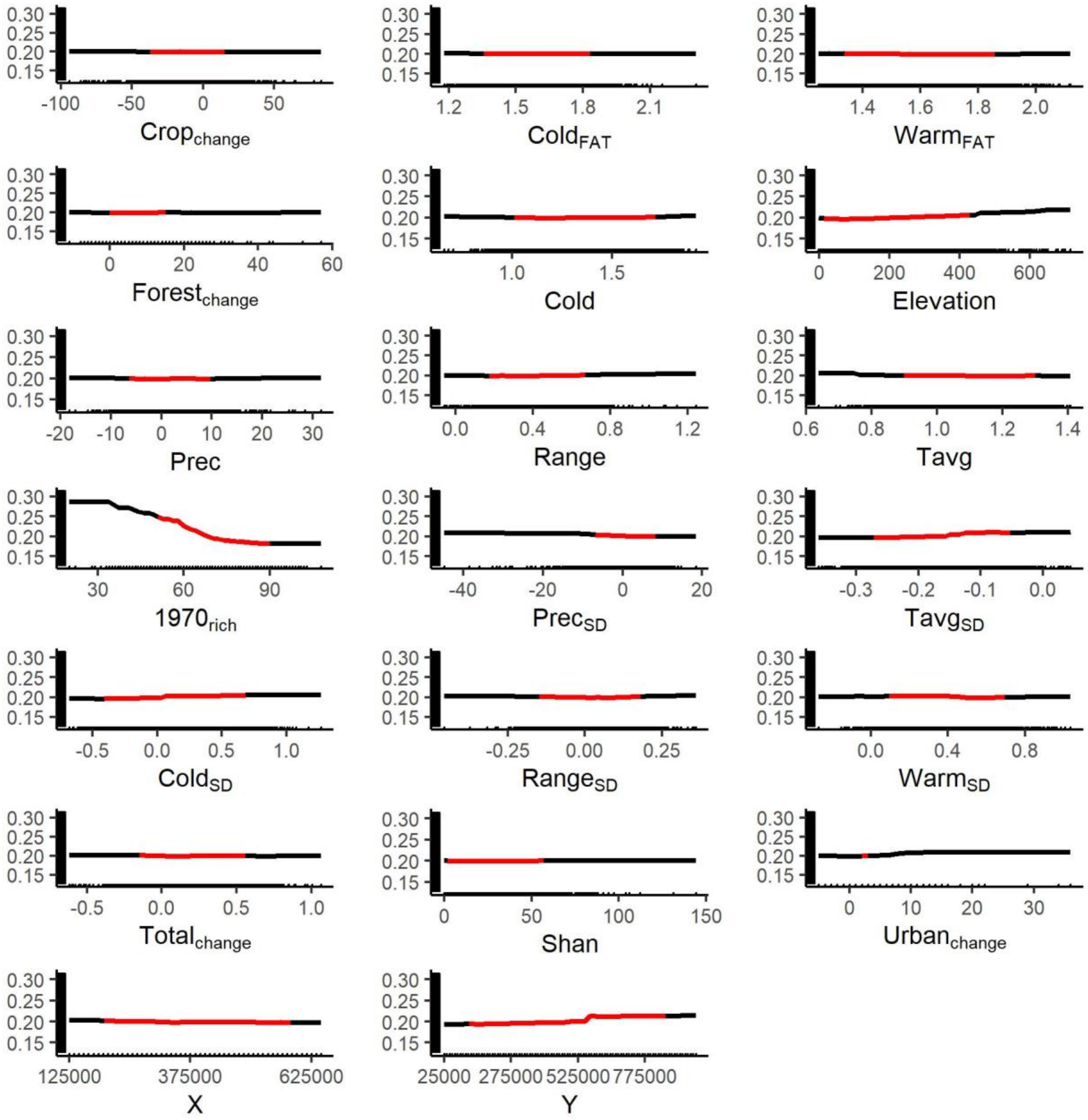


Figure. S3.6.1. Partial plots of the marginal effect each of the explanatory variables had on the total temporal taxonomic beta-diversity (BD_{TOTAL}) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

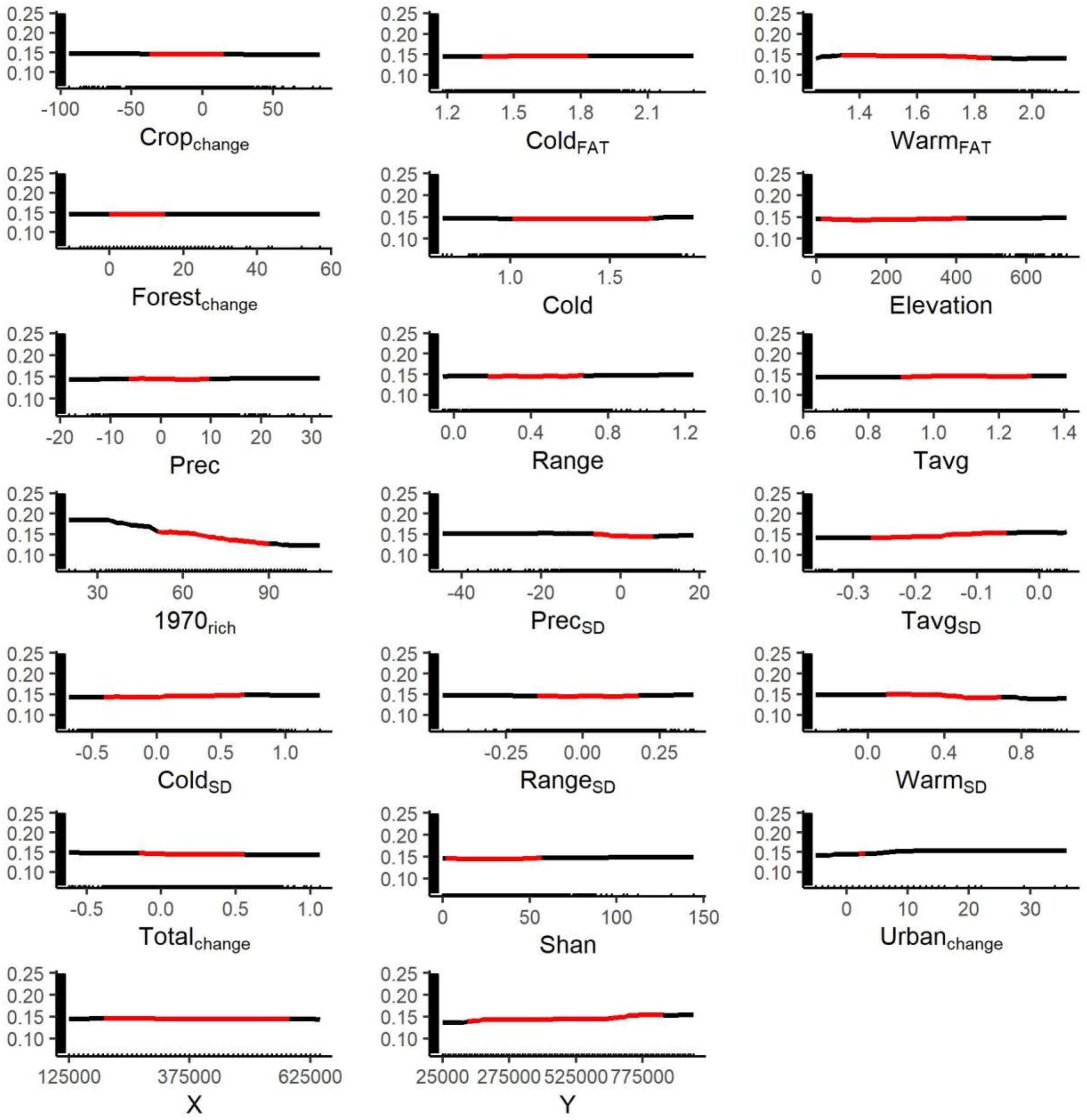


Figure. S3.6.2. Partial plots of the marginal effect each of the explanatory variables had on the turnover component of the temporal taxonomic beta-diversity (BD_{TURN}) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

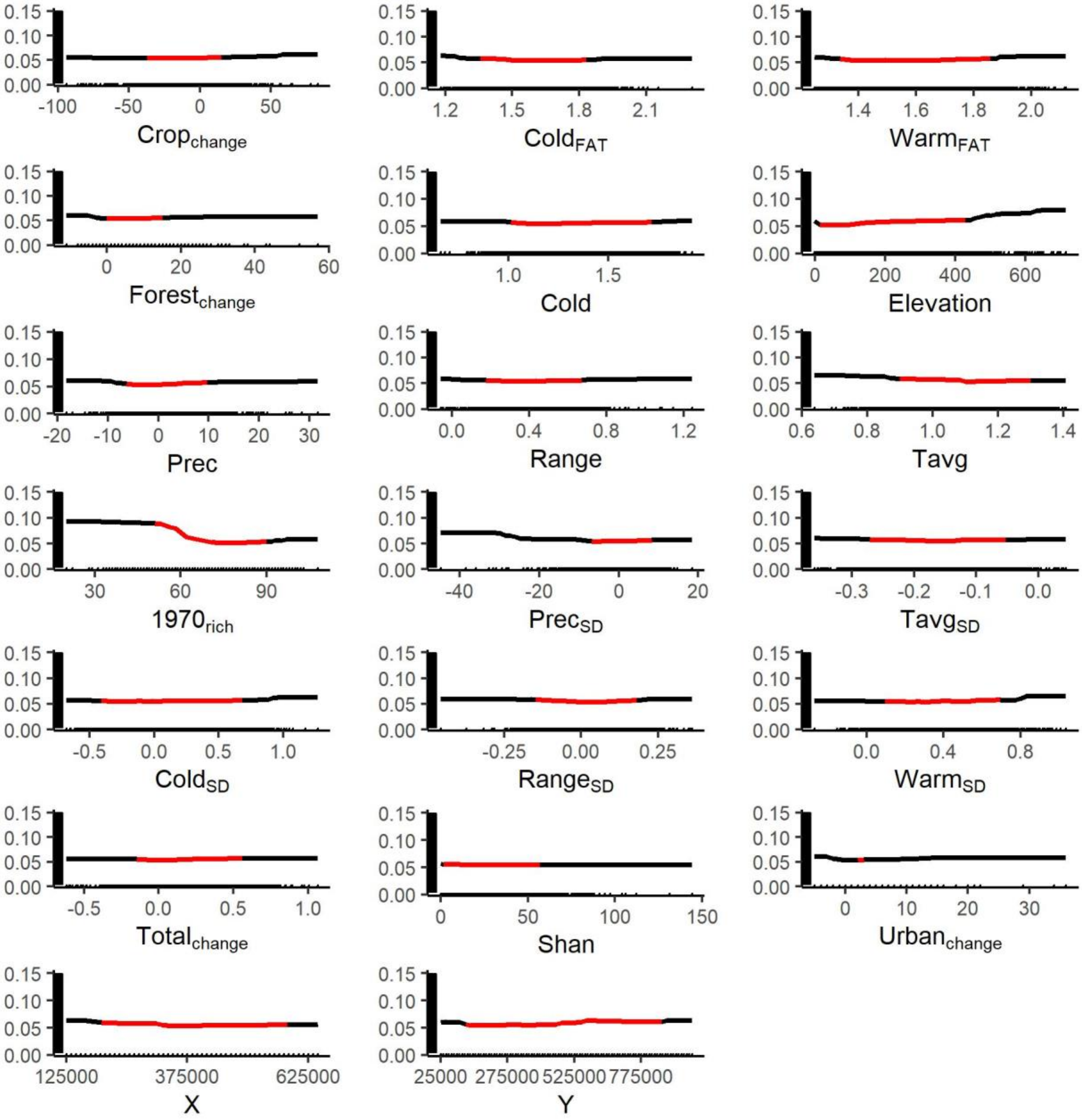


Figure. S3.6.3. Partial plots of the marginal effect each of the explanatory variables had on the nestedness component of the temporal taxonomic beta-diversity (BD_{NEST}) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

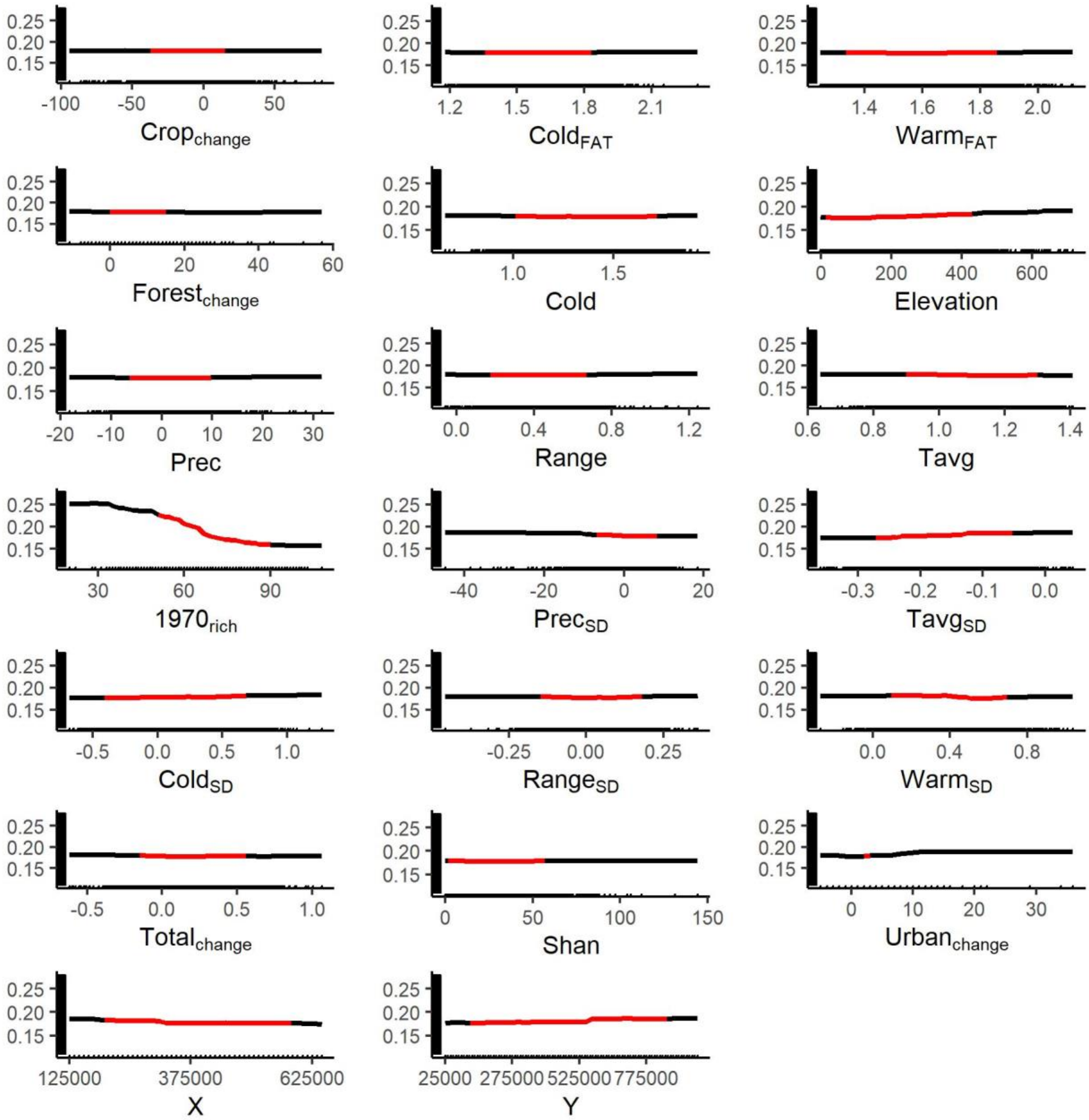


Figure. S3.6.4. Partial plots of the marginal effect each of the explanatory variables had on the total temporal functional beta-diversity (FD_{TOTAL}) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

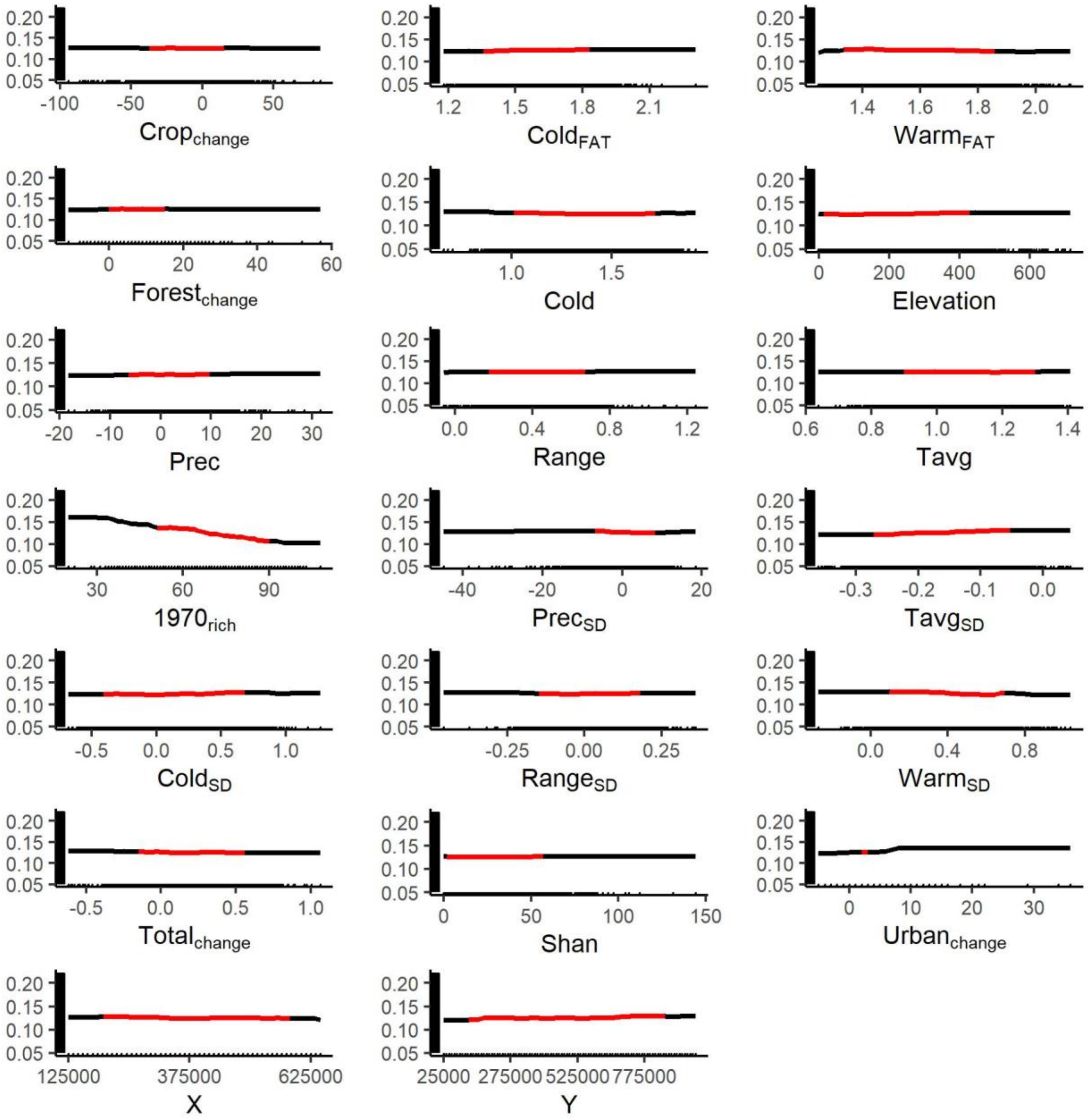


Figure. S3.6.5. Partial plots of the marginal effect each of the explanatory variables had on the turnover component of the temporal functional beta-diversity (FD_{TURN}) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

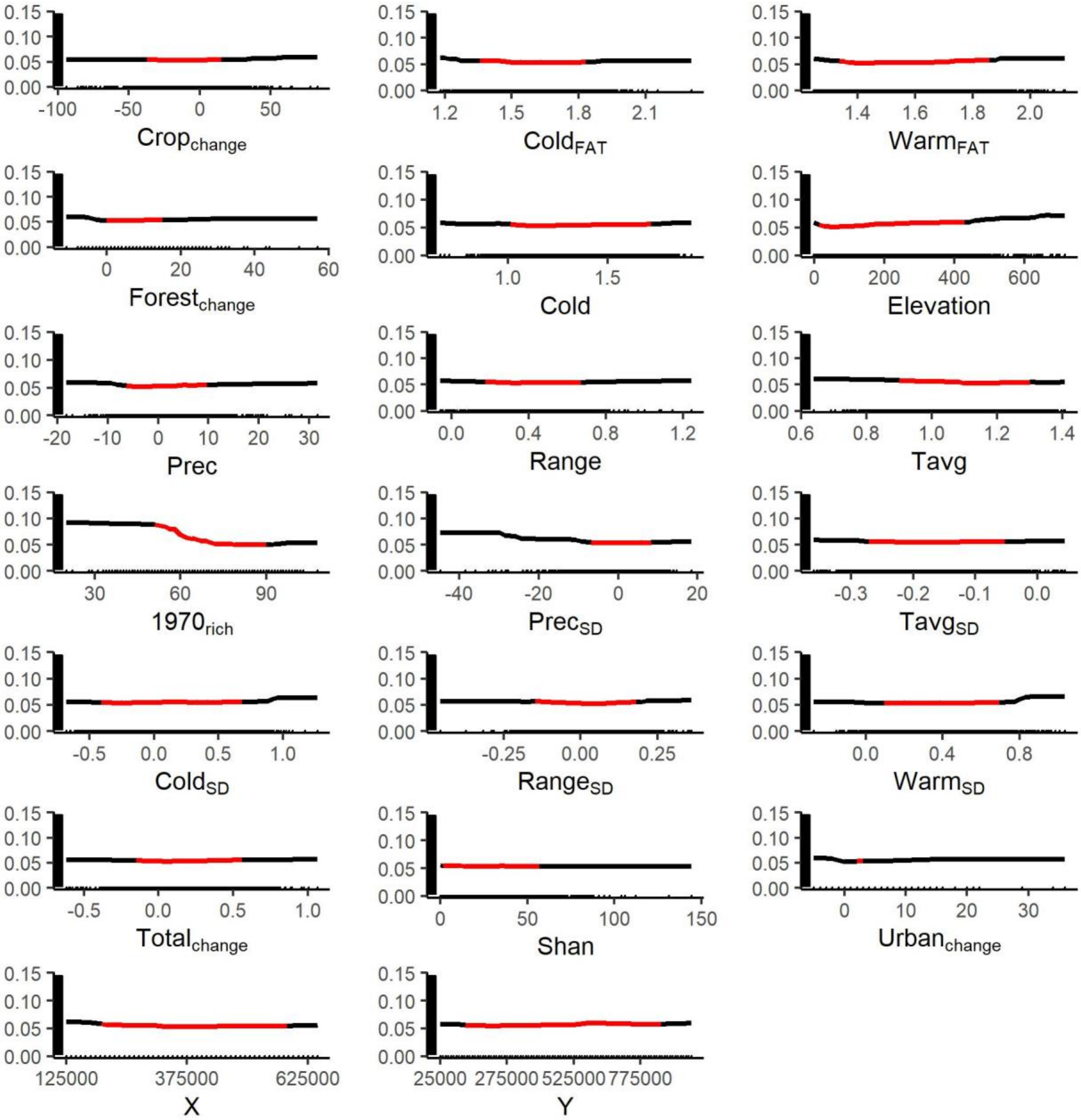


Figure. S3.6.6. Partial plots of the marginal effect each of the explanatory variables had on the nestedness resultant dissimilarity component of the temporal functional beta-diversity (FD$_{NEST}$) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

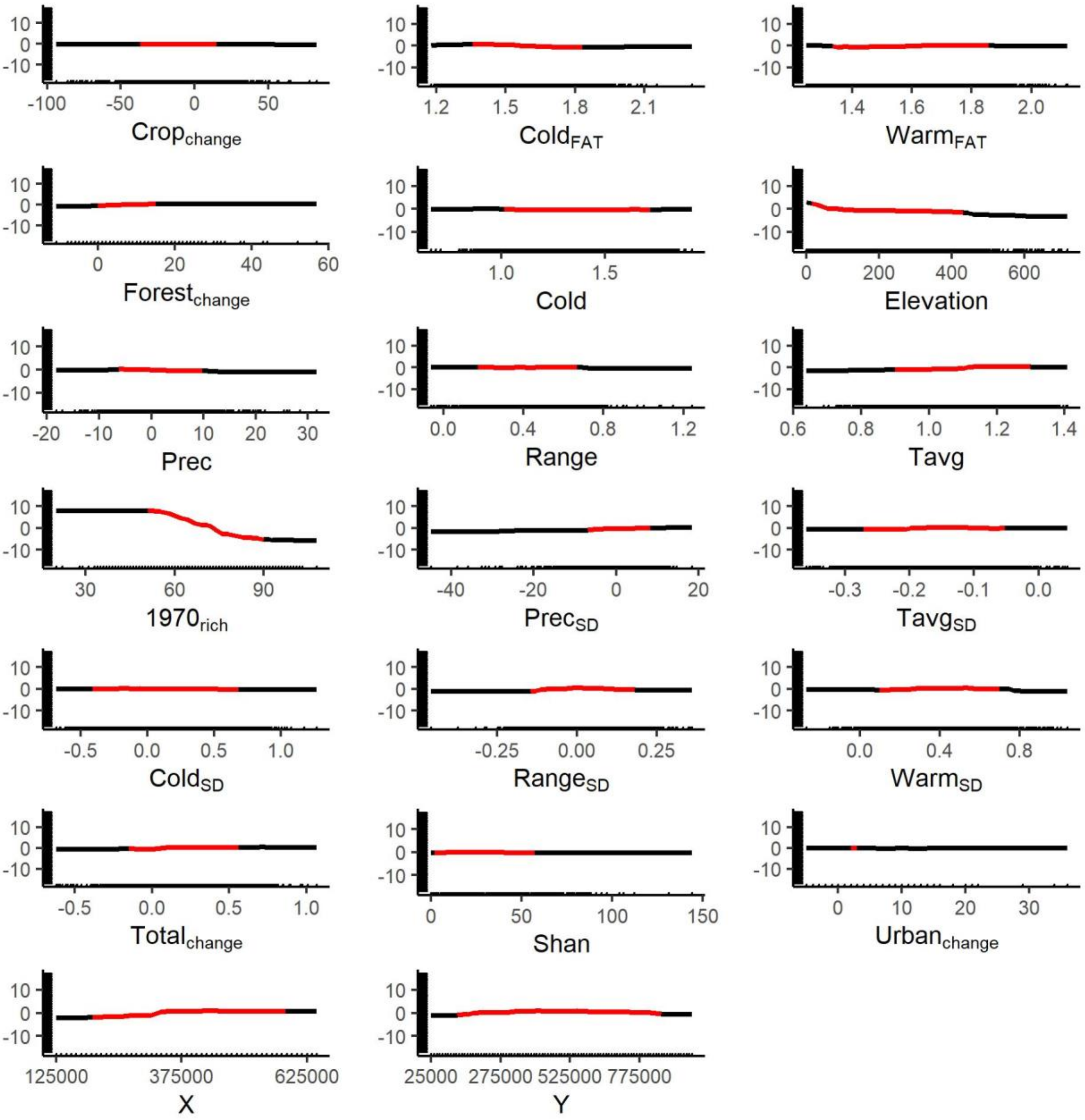


Figure. S3.6.7. Partial plots of the marginal effect each of the explanatory variables had on the species richness change (SP_{change}) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

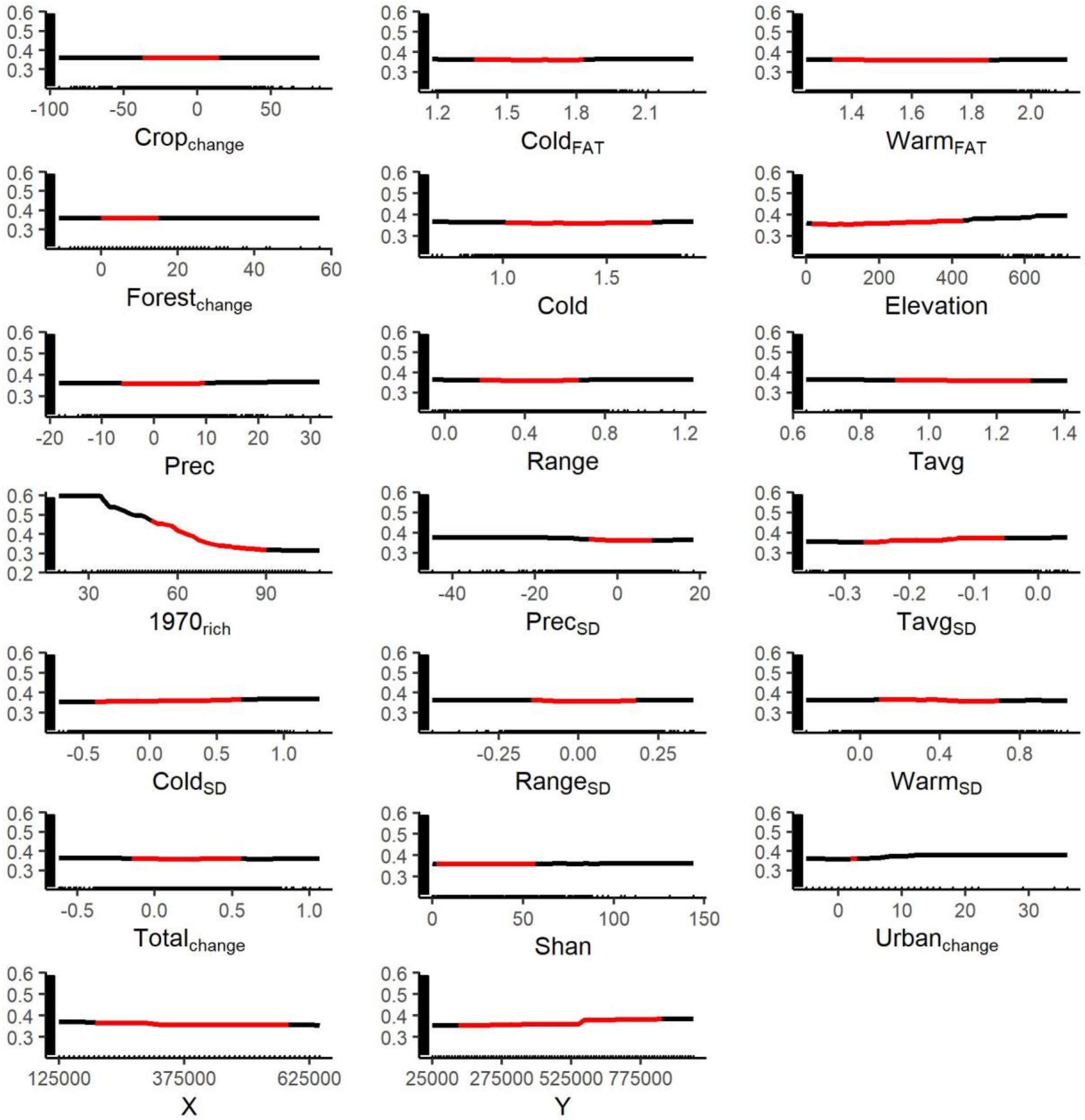


Figure. S3.6.8. Partial plots of the marginal effect each of the explanatory variables had on the mean nearest taxon distance (MNTD) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

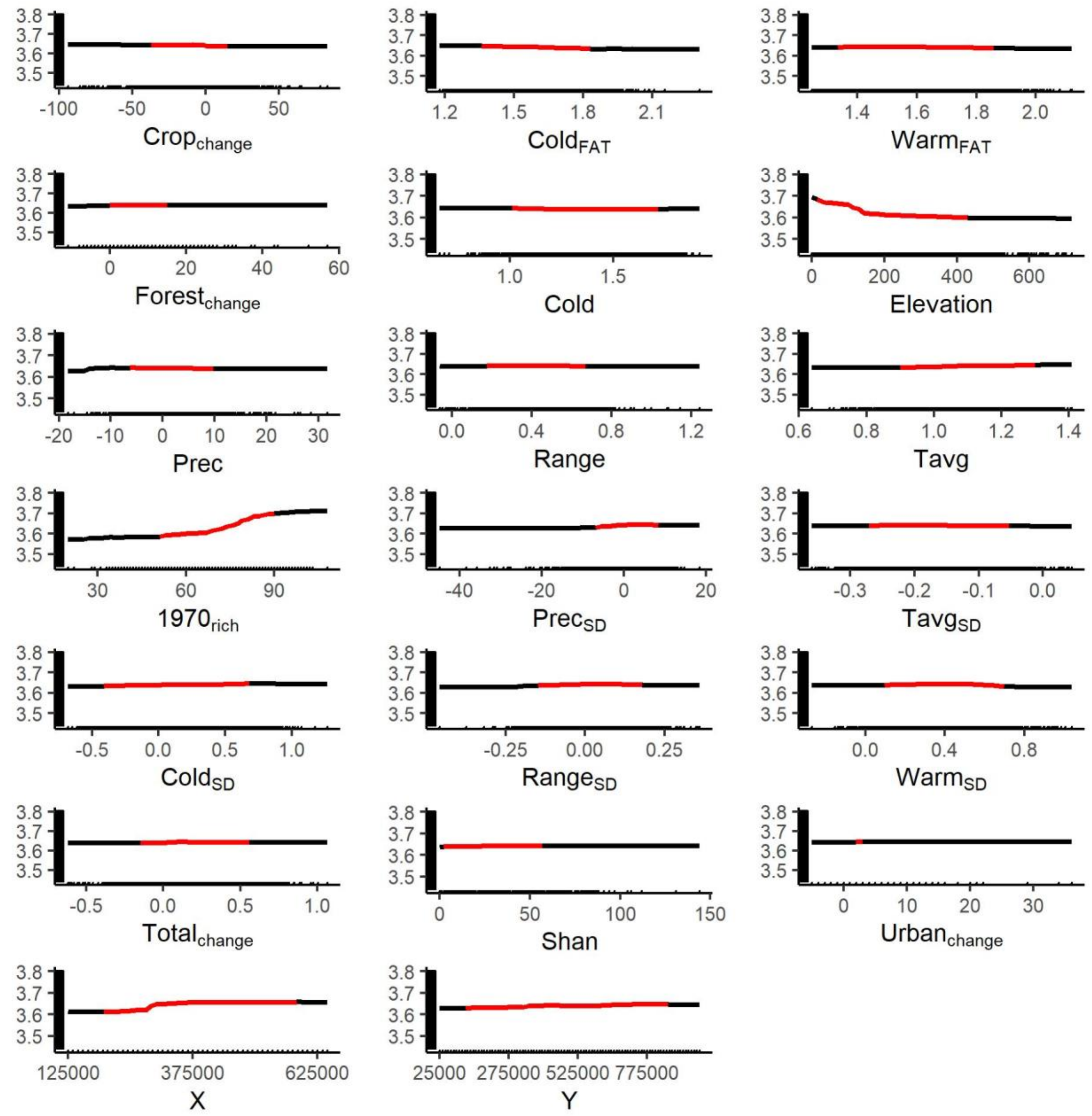


Figure. S3.6.9. Partial plots of the marginal effect each of the explanatory variables had on the mean pairwise distance (MPD) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

Appendix S3.7: Partial plots without spatial coordinates

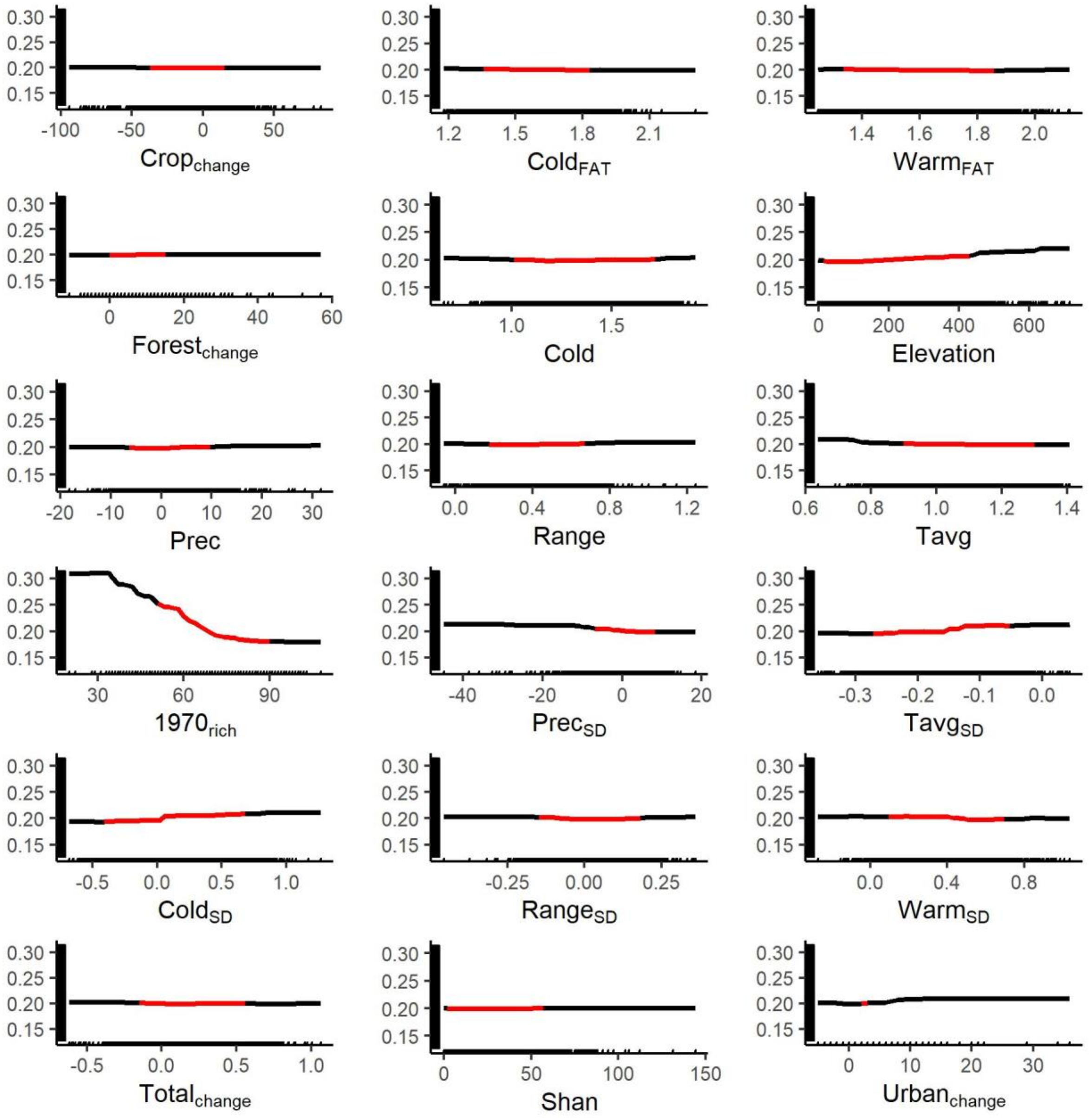


Figure. S3.7.1. Partial plots of the marginal effect each of the explanatory variables had on the total temporal taxonomic beta-diversity (BD_{TOTAL}) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

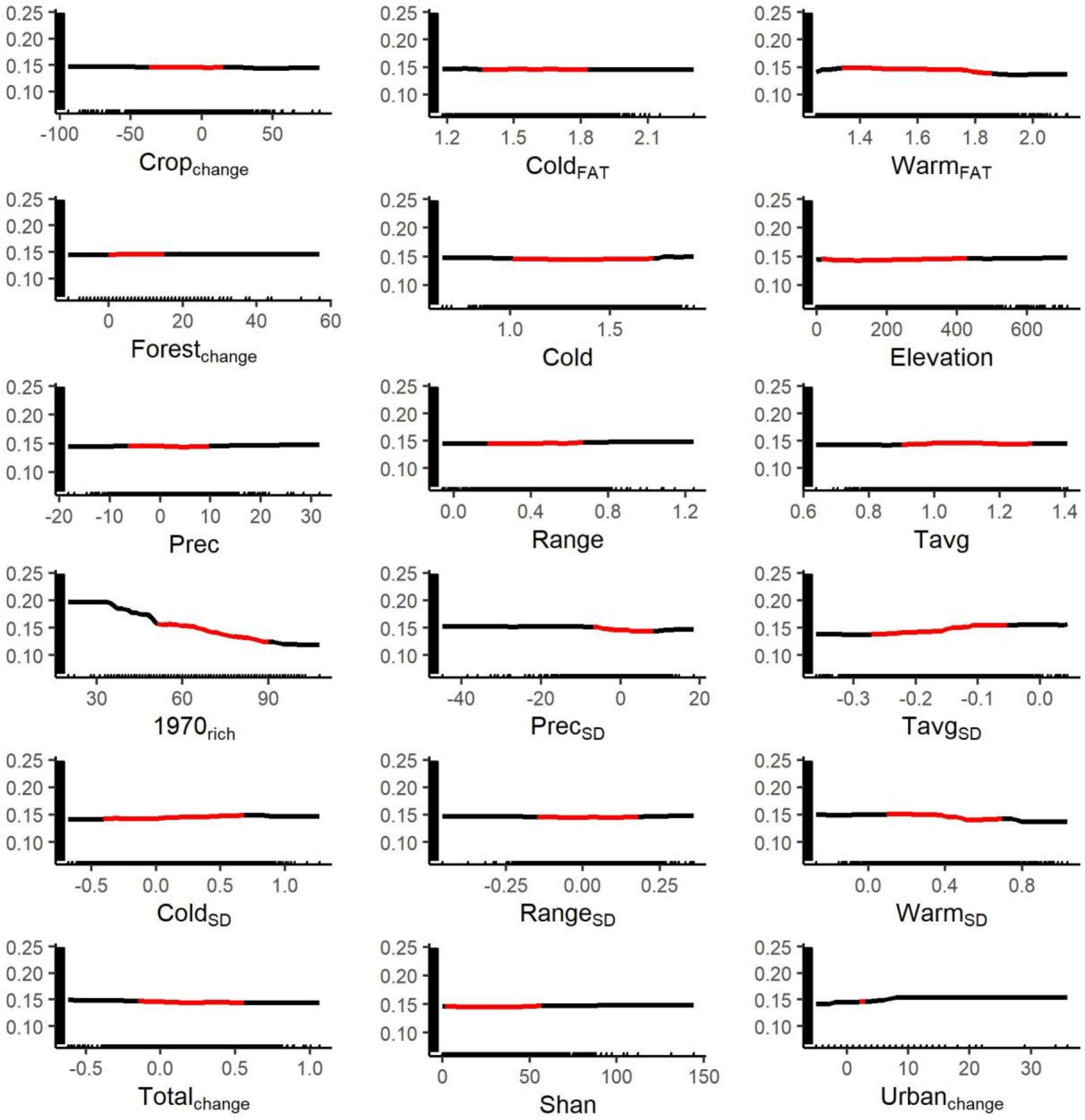


Figure. S3.7.2. Partial plots of the marginal effect each of the explanatory variables had on the turnover component of the temporal taxonomic beta-diversity (BD$_{TURN}$) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

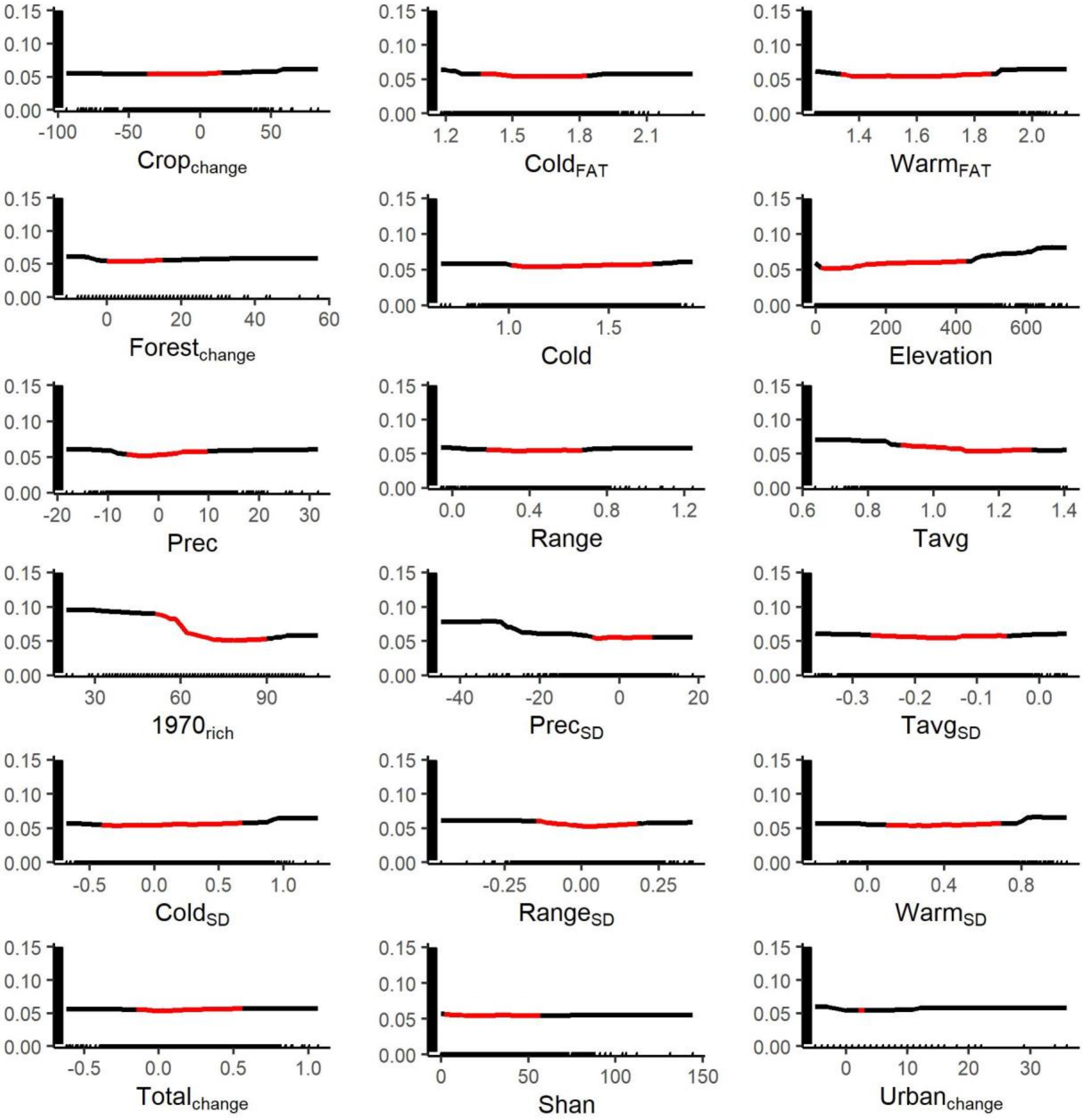


Figure. S3.7.3. Partial plots of the marginal effect each of the explanatory variables had on the nestedness component of the temporal taxonomic beta-diversity (BD_{NEST}) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

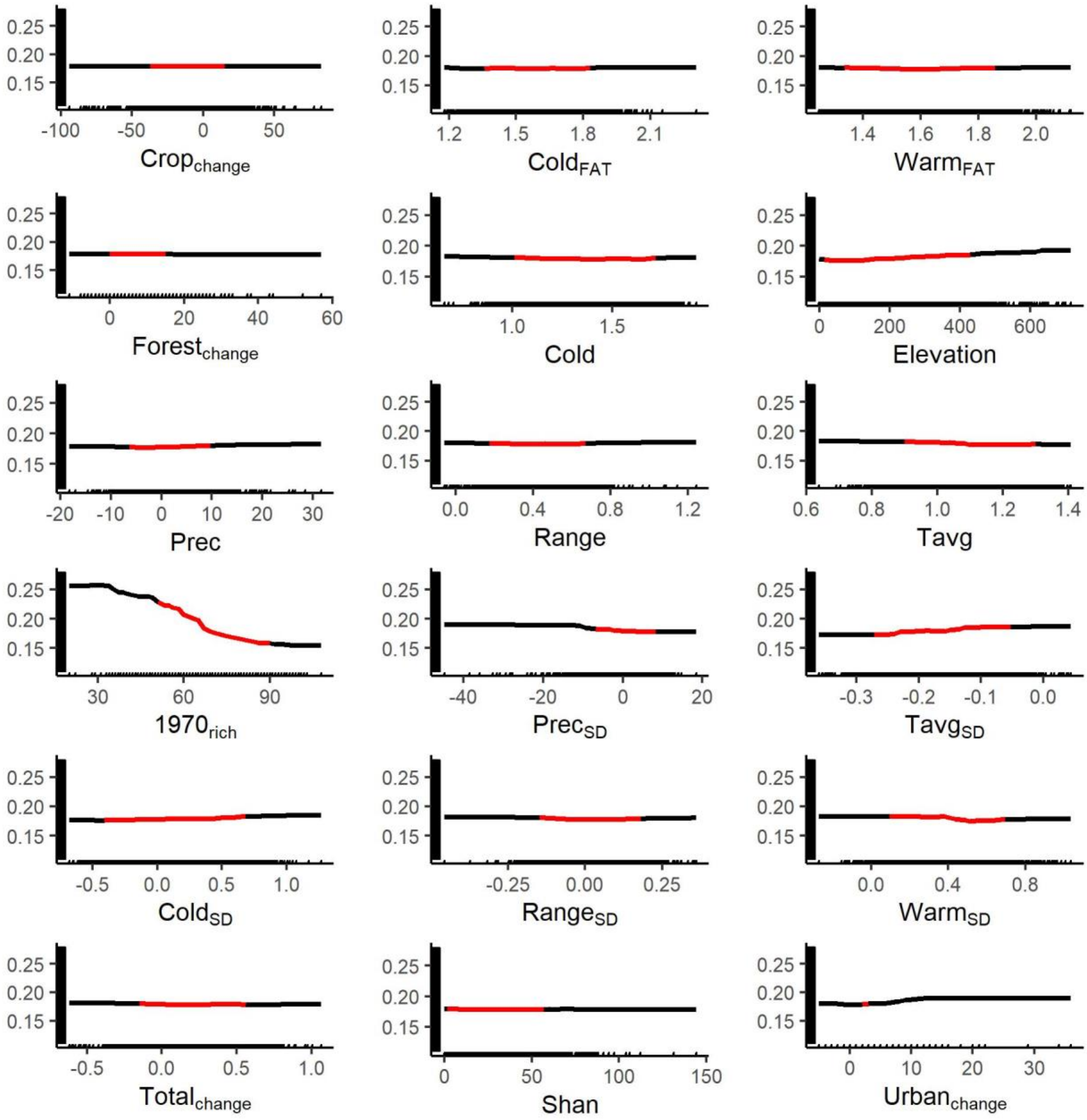


Figure. S3.7.4. Partial plots of the marginal effect each of the explanatory variables had on the total temporal functional beta-diversity (FD_{TOTAL}) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

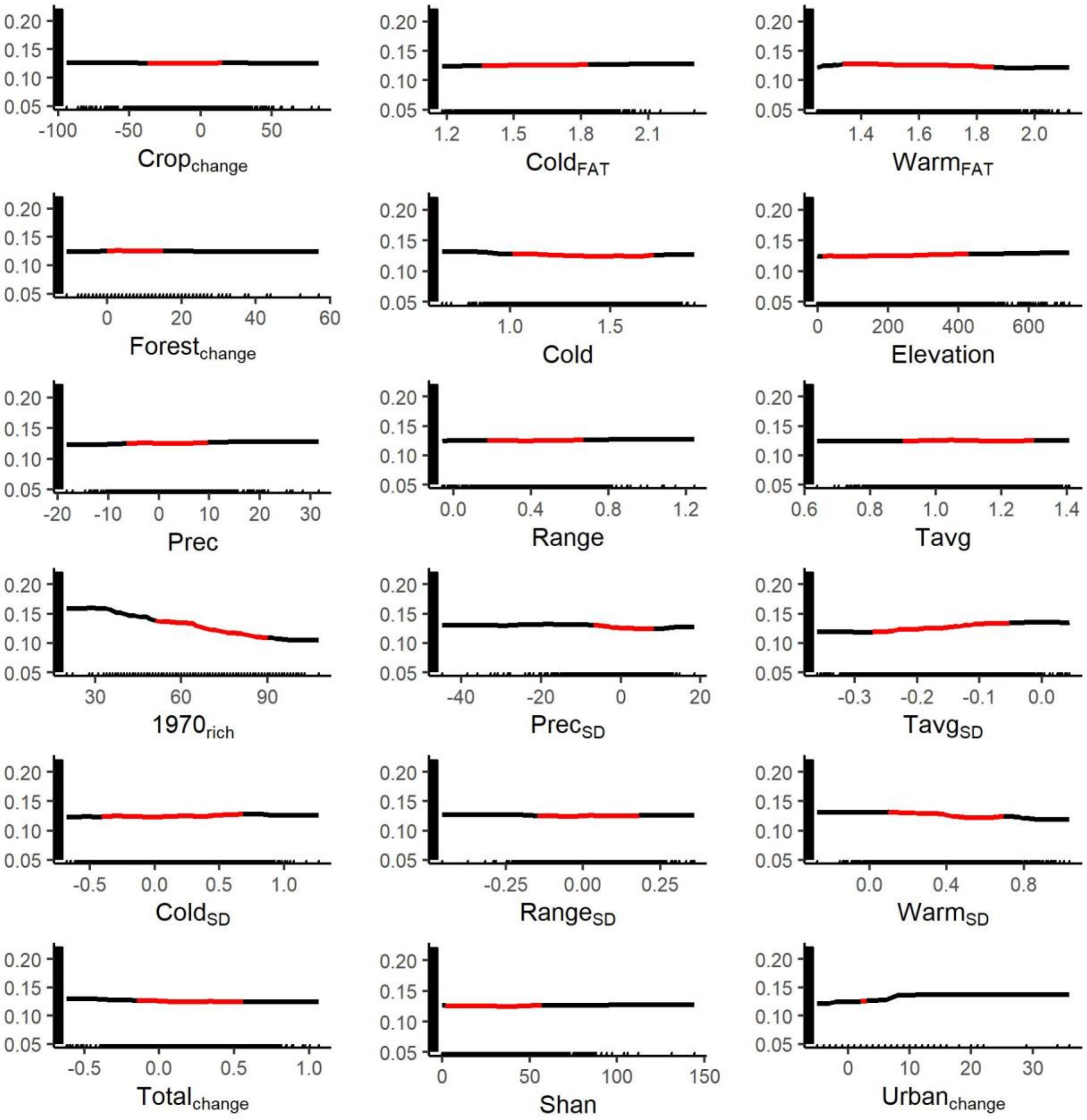


Figure. S3.7.5. Partial plots of the marginal effect each of the explanatory variables had on the turnover component of the temporal functional beta-diversity (FD$_{TURN}$) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

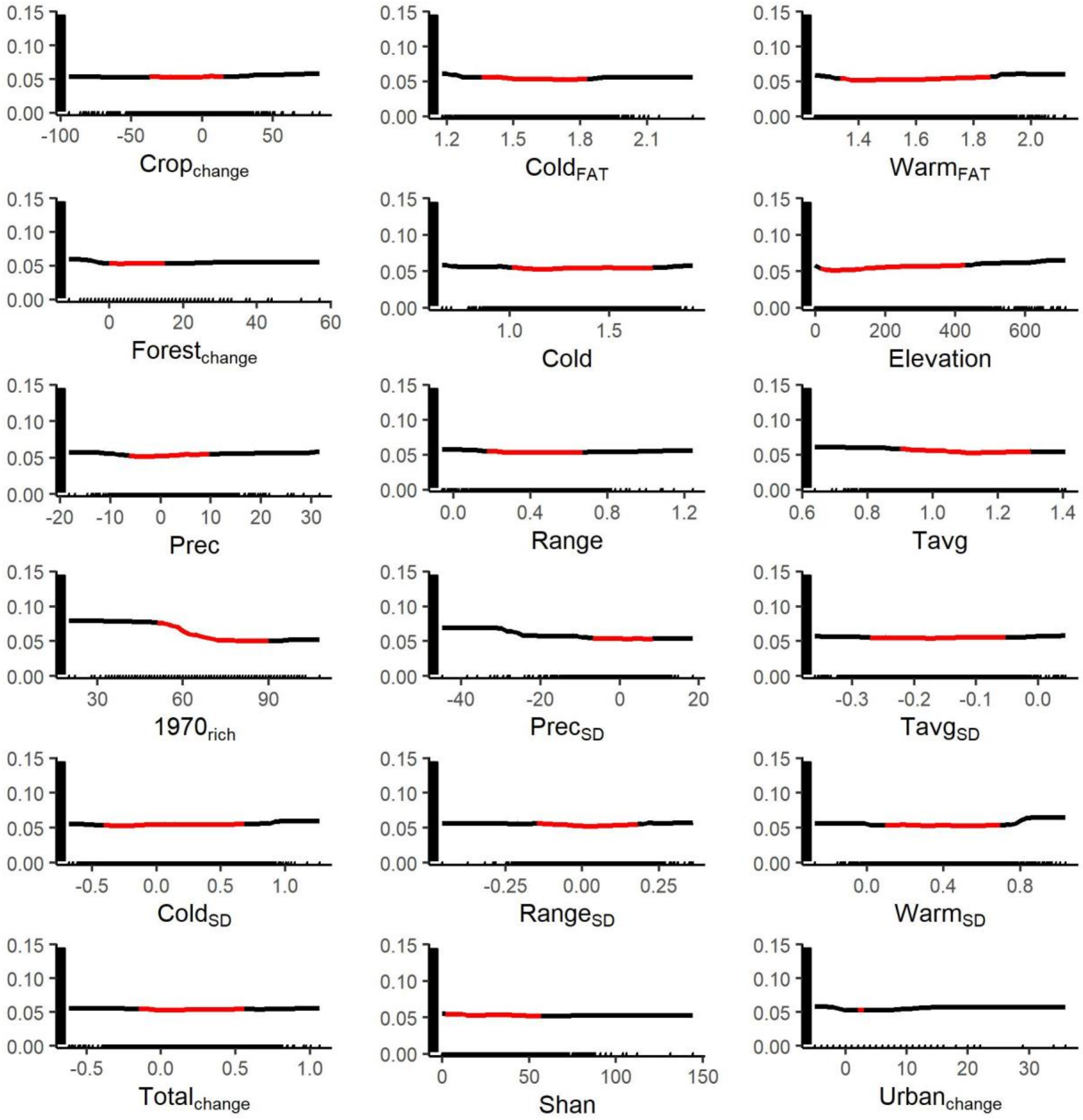


Figure. S3.7.6. Partial plots of the marginal effect each of the explanatory variables had on the nestedness resultant dissimilarity component of the temporal functional beta-diversity (FD_{NEST}) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

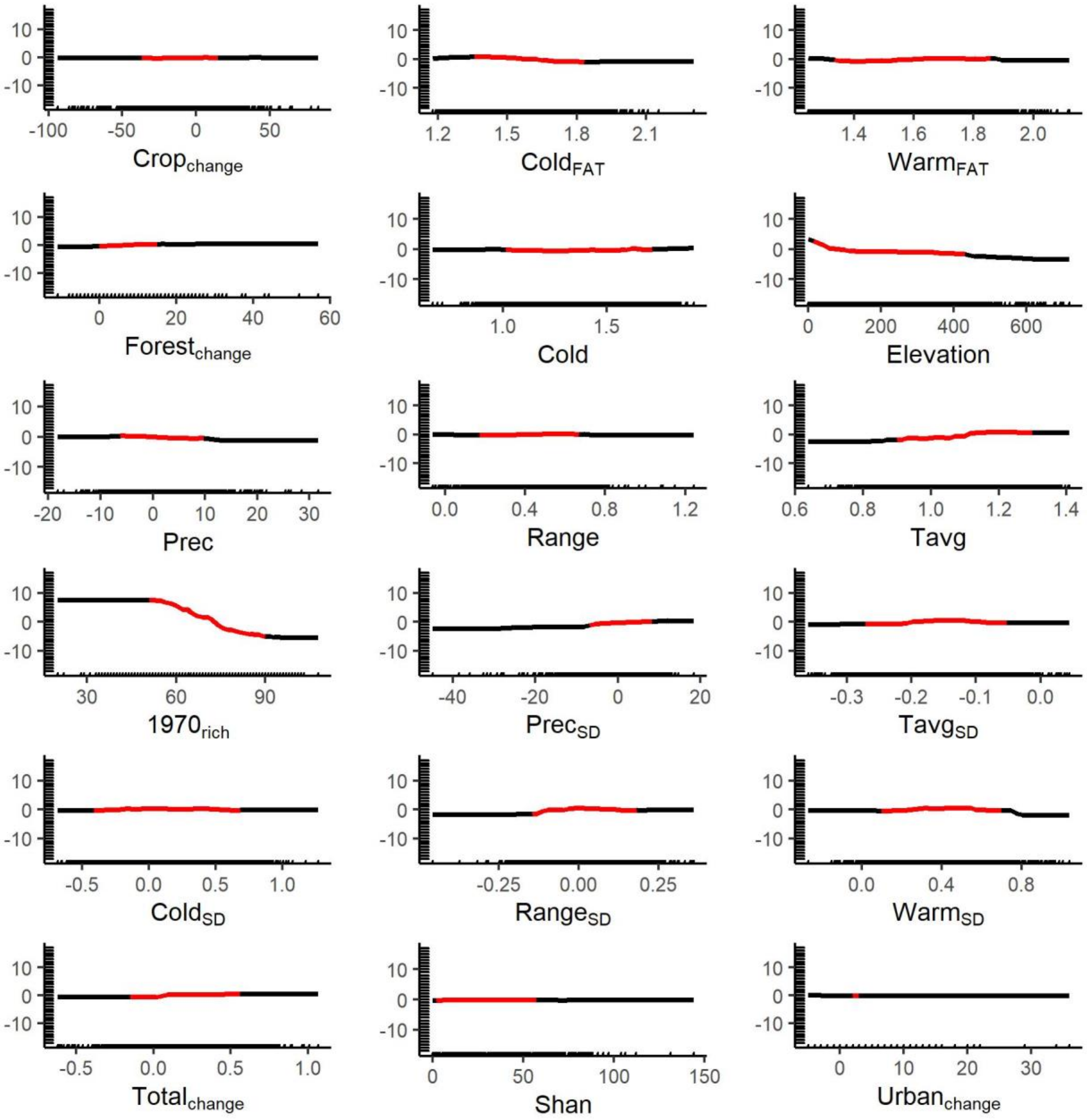


Figure. S3.7.7. Partial plots of the marginal effect each of the explanatory variables had on the species richness change (SP_{change}) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

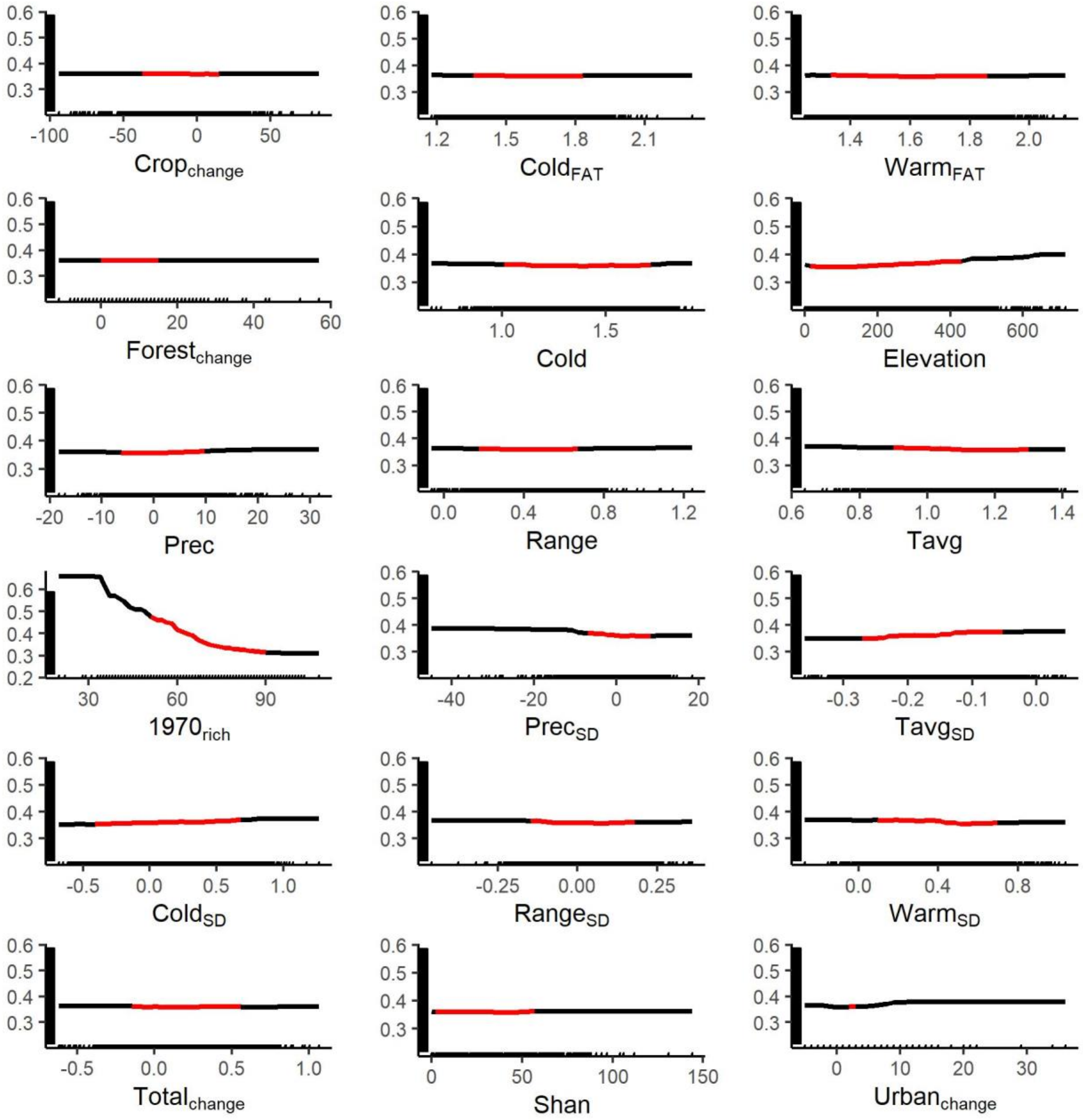


Figure. S3.7.8. Partial plots of the marginal effect each of the explanatory variables had on the mean nearest taxon distance (MNTD) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

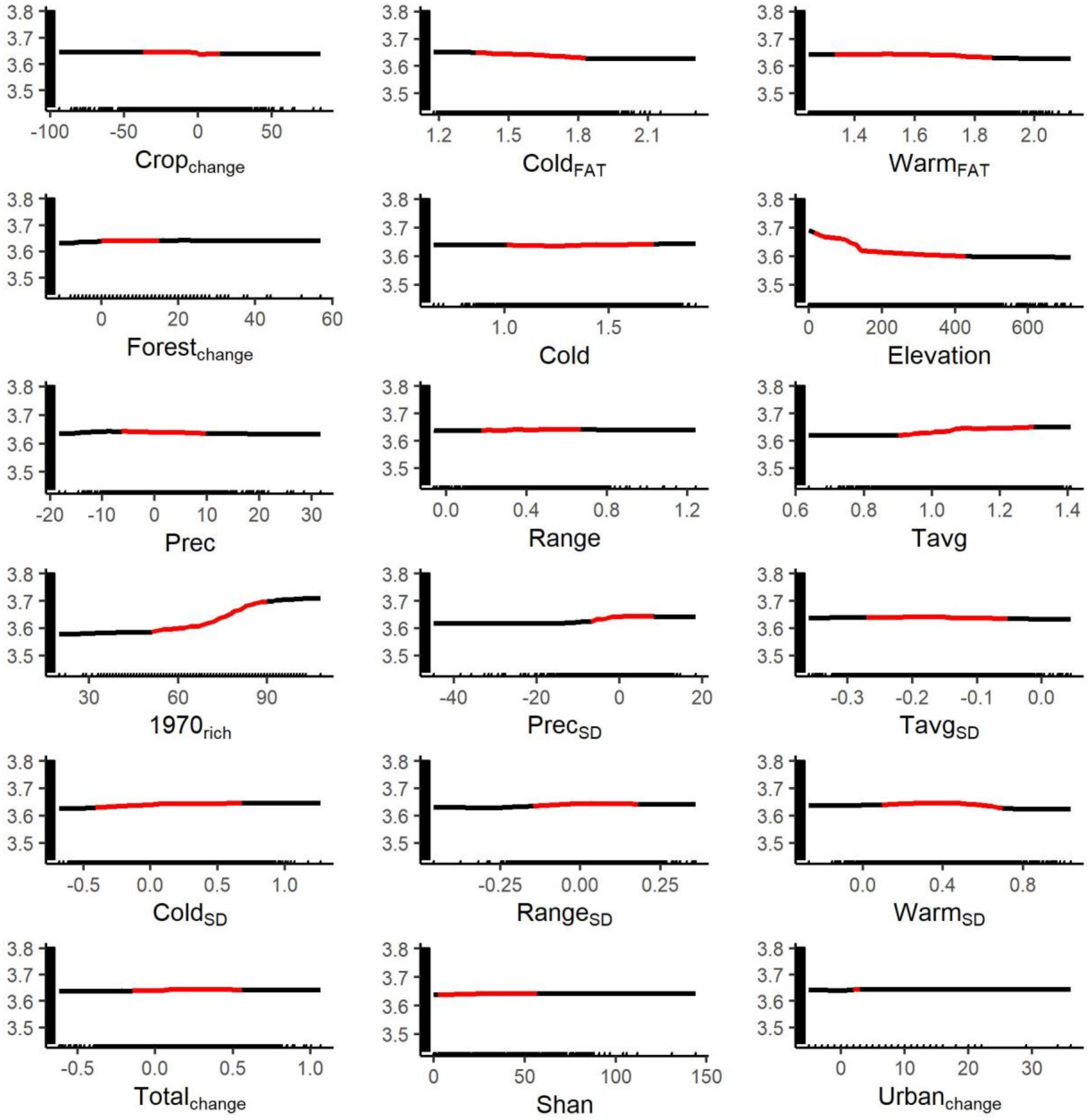


Figure. S3.7.9. Partial plots of the marginal effect each of the explanatory variables had on the mean pairwise distance (MPD) of British breeding bird communities between the periods 1970 – 2010. Each partial plot shows the mean marginal effect of the predictor variable across 50 random forest models. Effects of the predictor variables were assessed across the central 90% of the predictor variables value (the red section of the lines). This ensured that extreme values of change did not skew our analyses and lead to spurious conclusions.

Chapter 4

Appendix S4.1: Species used in the study

Common name	Binomial name	Order	Family	Family (common name)
Avocet	Recurvirostra avosetta	Charadriiformes	Recurvirostridae	Stilts and Avocets
Barn Owl	Tyto alba	Strigiformes	Tytonidae	Barn-Owls
Bearded Tit	Panurus biarmicus	Passeriformes	Panuridae	Bearded Reedling
Black Grouse	Lyrurus tetrix	Galliformes	Phasianidae	Pheasants, Grouse, and Allies
Black Redstart	Phoenicurus ochruros	Passeriformes	Muscicapidae	Old World Flycatchers
Blackbird	Turdus merula	Passeriformes	Turdidae	Thrushes and Allies
Blackcap	Sylvia atricapilla	Passeriformes	Sylviidae	Sylviid Warblers
Black-necked Grebe	Podiceps nigricollis	Podicipediformes	Podicipedidae	Grebes
Black-tailed Godwit	Limosa limosa	Charadriiformes	Scolopacidae	Sandpipers and Allies
Black-throated Diver	Gavia arctica	Gaviiformes	Gaviidae	Loons
Blue Tit	Cyanistes caeruleus	Passeriformes	Paridae	Tits, Chickadees, and Titmice
Bullfinch	Pyrrhula pyrrhula	Passeriformes	Fringillidae	Finches, Euphonias, and Allies
Buzzard	Buteo buteo	Accipitriformes	Accipitridae	Hawks, Eagles, and Kites
Canada Goose	Branta canadensis	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Carrion Crow	Corvus corone	Passeriformes	Corvidae	Crows, Jays, and Magpies
Cetti's Warbler	Cettia cetti	Passeriformes	Scotocercidae	Bush Warblers and Allies
Chaffinch	Fringilla coelebs	Passeriformes	Fringillidae	Finches, Euphonias, and Allies
Chiffchaff	Phylloscopus collybita	Passeriformes	Phylloscopidae	Leaf Warblers
Chough	Pyrrhocorax pyrrhocorax	Passeriformes	Corvidae	Crows, Jays, and Magpies
Cirl Bunting	Emberiza cirlus	Passeriformes	Emberizidae	Old World Buntings
Coal Tit	Periparus ater	Passeriformes	Paridae	Tits, Chickadees, and Titmice
Collared Dove	Streptopelia decaocto	Columbiformes	Columbidae	Pigeons and Doves
Common Sandpiper	Actitis hypoleucos	Charadriiformes	Scolopacidae	Sandpipers and Allies
Common/Lesser Redpoll	Acanthis flammea/cabaret	Passeriformes	Fringillidae	Finches, Euphonias, and Allies
Common/Scottish Crossbill	Loxia curvirostra/scotica	Passeriformes	Fringillidae	Finches, Euphonias, and Allies
Coot	Fulica atra	Gruiformes	Rallidae	Rails, Gallinules, and Coots
Corn Bunting	Emberiza calandra	Passeriformes	Emberizidae	Old World Buntings
Corncrake	Crex crex	Gruiformes	Rallidae	Rails, Gallinules, and Coots
Crested Tit	Lophophanes cristatus	Passeriformes	Paridae	Tits, Chickadees, and Titmice

Cuckoo	Cuculus canorus	Cuculiformes	Cuculidae	Cuckoos
Curlew	Numenius arquata	Charadriiformes	Scolopacidae	Sandpipers and Allies
Dartford Warbler	Sylvia undata	Passeriformes	Sylviidae	Sylviid Warblers
Dipper	Cinclus cinclus	Passeriformes	Cinclidae	Dippers
Dotterel	Charadrius morinellus	Charadriiformes	Charadriidae	Plovers and Lapwings
Dunnock	Prunella modularis	Passeriformes	Prunellidae	Accentors
Eider	Somateria mollissima	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Firecrest	Regulus ignicapilla	Passeriformes	Regulidae	Kinglets
Gadwall	Mareca strepera	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Garden Warbler	Sylvia borin	Passeriformes	Sylviidae	Sylviid Warblers
Garganey	Spatula querquedula	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Goldcrest	Regulus regulus	Passeriformes	Regulidae	Kinglets
Golden Pheasant	Chrysolophus pictus	Galliformes	Phasianidae	Pheasants, Grouse, and Allies
Golden Plover	Pluvialis apricaria	Charadriiformes	Charadriidae	Plovers and Lapwings
Goldeneye	Bucephala clangula	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Goldfinch	Carduelis carduelis	Passeriformes	Fringillidae	Finches, Euphonias, and Allies
Goosander	Mergus merganser	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Goshawk	Accipiter gentilis	Accipitriformes	Accipitridae	Hawks, Eagles, and Kites
Grasshopper Warbler	Locustella naevia	Passeriformes	Locustellidae	Grassbirds and Allies
Great Crested Grebe	Podiceps cristatus	Podicipediformes	Podicipedidae	Grebes
Great Spotted Woodpecker	Dendrocopos major	Piciformes	Picidae	Woodpeckers
Great Tit	Parus major	Passeriformes	Paridae	Tits, Chickadees, and Titmice
Green Woodpecker	Picus viridis	Piciformes	Picidae	Woodpeckers
Greenfinch	Chloris chloris	Passeriformes	Fringillidae	Finches, Euphonias, and Allies
Greenshank	Tringa nebularia	Charadriiformes	Scolopacidae	Sandpipers and Allies
Grey Heron	Ardea cinerea	Pelecaniformes	Ardeidae	Herons, Egrets, and Bitterns
Grey Partridge	Perdix perdix	Galliformes	Phasianidae	Pheasants, Grouse, and Allies
Grey Wagtail	Motacilla cinerea	Passeriformes	Motacillidae	Wagtails and Pipits
Greylag Goose	Anser anser	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Hawfinch	Coccothraustes coccothraustes	Passeriformes	Fringillidae	Finches, Euphonias, and Allies
Hen Harrier	Circus cyaneus	Accipitriformes	Accipitridae	Hawks, Eagles, and Kites
Hobby	Falco subbuteo	Falconiformes	Falconidae	Falcons and Caracaras

Hooded Crow	Corvus cornix	Passeriformes	Corvidae	Crows, Jays, and Magpies
House Martin	Delichon urbicum	Passeriformes	Hirundinidae	Swallows
House Sparrow	Passer domesticus	Passeriformes	Passeridae	Old World Sparrows
Jackdaw	Coloeus monedula	Passeriformes	Corvidae	Crows, Jays, and Magpies
Jay	Garrulus glandarius	Passeriformes	Corvidae	Crows, Jays, and Magpies
Kestrel	Falco tinnunculus	Falconiformes	Falconidae	Falcons and Caracaras
Kingfisher	Alcedo atthis	Coraciiformes	Alcedinidae	Kingfishers
Lapwing	Vanellus vanellus	Charadriiformes	Charadriidae	Plovers and Lapwings
Lesser Spotted Woodpecker	Dryobates minor	Piciformes	Picidae	Woodpeckers
Lesser Whitethroat	Sylvia curruca	Passeriformes	Sylviidae	Sylviid Warblers
Linnet	Linaria cannabina	Passeriformes	Fringillidae	Finches, Euphonias, and Allies
Little Egret	Egretta garzetta	Pelecaniformes	Ardeidae	Herons, Egrets, and Bitterns
Little Grebe	Tachybaptus ruficollis	Podicipediformes	Podicipedidae	Grebes
Little Owl	Athene noctua	Strigiformes	Strigidae	Owls
Little Ringed Plover	Charadrius dubius	Charadriiformes	Charadriidae	Plovers and Lapwings
Long-eared Owl	Asio otus	Strigiformes	Strigidae	Owls
Long-tailed Tit	Aegithalos caudatus	Passeriformes	Aegithalidae	Long-tailed Tits
Magpie	Pica pica	Passeriformes	Corvidae	Crows, Jays, and Magpies
Mallard	Anas platyrhynchos	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Mandarin Duck	Aix galericulata	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Marsh Harrier	Circus aeruginosus	Accipitriformes	Accipitridae	Hawks, Eagles, and Kites
Marsh Tit	Poecile palustris	Passeriformes	Paridae	Tits, Chickadees, and Titmice
Meadow Pipit	Anthus pratensis	Passeriformes	Motacillidae	Wagtails and Pipits
Merlin	Falco columbarius	Falconiformes	Falconidae	Falcons and Caracaras
Mistle Thrush	Turdus viscivorus	Passeriformes	Turdidae	Thrushes and Allies
Moorhen	Gallinula chloropus	Gruiformes	Rallidae	Rails, Gallinules, and Coots
Mute Swan	Cygnus olor	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Nightingale	Luscinia megarhynchos	Passeriformes	Muscicapidae	Old World Flycatchers
Nightjar	Caprimulgus europaeus	Caprimulgiformes	Caprimulgidae	Nightjars and Allies
Nuthatch	Sitta europaea	Passeriformes	Sittidae	Nuthatches
Osprey	Pandion haliaetus	Accipitriformes	Pandionidae	Osprey
Oystercatcher	Haematopus ostralegus	Charadriiformes	Haematopodidae	Oystercatchers
Peregrine	Falco peregrinus	Falconiformes	Falconidae	Falcons and Caracaras
Pheasant	Phasianus colchicus	Galliformes	Phasianidae	Pheasants, Grouse, and Allies
Pied Flycatcher	Ficedula hypoleuca	Passeriformes	Muscicapidae	Old World Flycatchers

Pied/White Wagtail	Motacilla alba	Passeriformes	Motacillidae	Wagtails and Pipits
Pochard	Aythya ferina	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Ptarmigan	Lagopus muta	Galliformes	Phasianidae	Pheasants, Grouse, and Allies
Quail	Coturnix coturnix	Galliformes	Phasianidae	Pheasants, Grouse, and Allies
Raven	Corvus corax	Passeriformes	Corvidae	Crows, Jays, and Magpies
Red Grouse	Lagopus lagopus	Galliformes	Phasianidae	Pheasants, Grouse, and Allies
Red Kite	Milvus milvus	Accipitriformes	Accipitridae	Hawks, Eagles, and Kites
Red-breasted Merganser	Mergus serrator	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Red-crested Pochard	Netta rufina	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Red-legged Partridge	Alectoris rufa	Galliformes	Phasianidae	Pheasants, Grouse, and Allies
Redshank	Tringa totanus	Charadriiformes	Scolopacidae	Sandpipers and Allies
Redstart	Phoenicurus phoenicurus	Passeriformes	Muscicapidae	Old World Flycatchers
Red-throated Diver	Gavia stellata	Gaviiformes	Gaviidae	Loons
Redwing	Turdus iliacus	Passeriformes	Turdidae	Thrushes and Allies
Reed Bunting	Emberiza schoeniclus	Passeriformes	Emberizidae	Old World Buntings
Reed Warbler	Acrocephalus scirpaceus	Passeriformes	Acrocephalidae	Reed Warblers and Allies
Ring Ouzel	Turdus torquatus	Passeriformes	Turdidae	Thrushes and Allies
Ringed Plover	Charadrius hiaticula	Charadriiformes	Charadriidae	Plovers and Lapwings
Ring-necked Parakeet	Psittacula krameri	Psittaciformes	Psittaculidae	Old World Parrots
Robin	Erithacus rubecula	Passeriformes	Muscicapidae	Old World Flycatchers
Rock Dove	Columba livia	Columbiformes	Columbidae	Pigeons and Doves
Rock/Water Pipit	Anthus petrosus/spinoletta	Passeriformes	Motacillidae	
Rook	Corvus frugilegus	Passeriformes	Corvidae	Crows, Jays, and Magpies
Ruddy Duck	Oxyura jamaicensis	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Sand Martin	Riparia riparia	Passeriformes	Hirundinidae	Swallows
Sedge Warbler	Acrocephalus schoenobaenus	Passeriformes	Acrocephalidae	Reed Warblers and Allies
Shelduck	Tadorna tadorna	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Short-eared Owl	Asio flammeus	Strigiformes	Strigidae	Owls
Shoveler	Spatula clypeata	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Siskin	Spinus spinus	Passeriformes	Fringillidae	Finches, Euphonias, and Allies
Skylark	Alauda arvensis	Passeriformes	Alaudidae	Larks

Snipe	Gallinago gallinago	Charadriiformes	Scolopacidae	Sandpipers and Allies
Song Thrush	Turdus philomelos	Passeriformes	Turdidae	Thrushes and Allies
Sparrowhawk	Accipiter nisus	Accipitriformes	Accipitridae	Hawks, Eagles, and Kites
Spotted Flycatcher	Muscicapa striata	Passeriformes	Muscicapidae	Old World Flycatchers
Starling	Sturnus vulgaris	Passeriformes	Sturnidae	Starlings
Stock Dove	Columba oenas	Columbiformes	Columbidae	Pigeons and Doves
Stonechat	Saxicola rubicola	Passeriformes	Muscicapidae	Old World Flycatchers
Stone-curlew	Burhinus oedicnemus	Charadriiformes	Burhinidae	Thick-knees
Swallow	Hirundo rustica	Passeriformes	Hirundinidae	Swallows
Swift	Apus apus	Caprimulgiformes	Apodidae	Swifts
Tawny Owl	Strix aluco	Strigiformes	Strigidae	Owls
Teal	Anas crecca	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Tree Pipit	Anthus trivialis	Passeriformes	Motacillidae	Wagtails and Pipits
Tree Sparrow	Passer montanus	Passeriformes	Passeridae	Old World Sparrows
Treecreeper	Certhia familiaris	Passeriformes	Certhiidae	Treecreepers
Tufted Duck	Aythya fuligula	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Turtle Dove	Streptopelia turtur	Columbiformes	Columbidae	Pigeons and Doves
Twite	Linaria flavirostris	Passeriformes	Fringillidae	Finches, Euphonias, and Allies
Water Rail	Rallus aquaticus	Gruiformes	Rallidae	Rails, Gallinules, and Coots
Wheatear	Oenanthe oenanthe	Passeriformes	Muscicapidae	Old World Flycatchers
Whimbrel	Numenius phaeopus	Charadriiformes	Scolopacidae	Sandpipers and Allies
Whinchat	Saxicola rubetra	Passeriformes	Muscicapidae	Old World Flycatchers
Whitethroat	Sylvia communis	Passeriformes	Sylviidae	Sylviid Warblers
Wigeon	Mareca penelope	Anseriformes	Anatidae	Ducks, Geese, and Waterfowl
Willow Tit	Poecile montanus	Passeriformes	Paridae	Tits, Chickadees, and Titmice
Willow Warbler	Phylloscopus trochilus	Passeriformes	Phylloscopidae	Leaf Warblers
Wood Warbler	Phylloscopus sibilatrix	Passeriformes	Phylloscopidae	Leaf Warblers
Woodcock	Scolopax rusticola	Charadriiformes	Scolopacidae	Sandpipers and Allies
Woodlark	Lullula arborea	Passeriformes	Alaudidae	Larks
Woodpigeon	Columba palumbus	Columbiformes	Columbidae	Pigeons and Doves
Wren	Troglodytes troglodytes	Passeriformes	Troglodytidae	Wrens
Yellow Wagtail	Motacilla flava	Passeriformes	Motacillidae	Wagtails and Pipits
Yellowhammer	Emberiza citrinella	Passeriformes	Emberizidae	Old World Buntings

Appendix S4.2 Supplementry figures

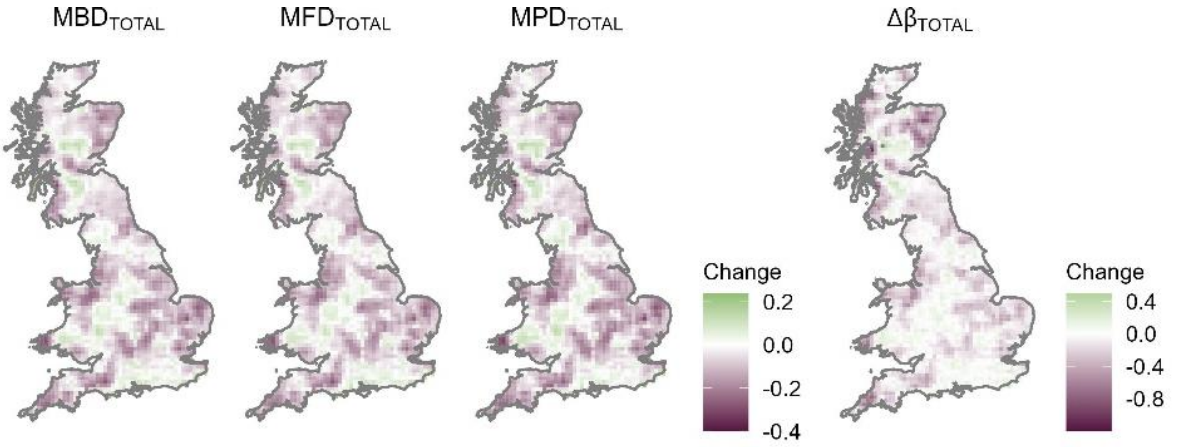


Figure S4.2.1: Maps of change between two sampling periods (1990 and 2010) for breeding bird communities across Britain for measures of (left to right) Sorensen's taxonomic multiple beta-diversity, Sorensen's functional multiple beta-diversity, Sorensen's Phylogenetic beta-diversity and change in Whittaker's β diversity. For all metrics, negative values indicate homogenisation and positive values indicate heterogenisation. All values were calculated using moving windows around focal hectads.

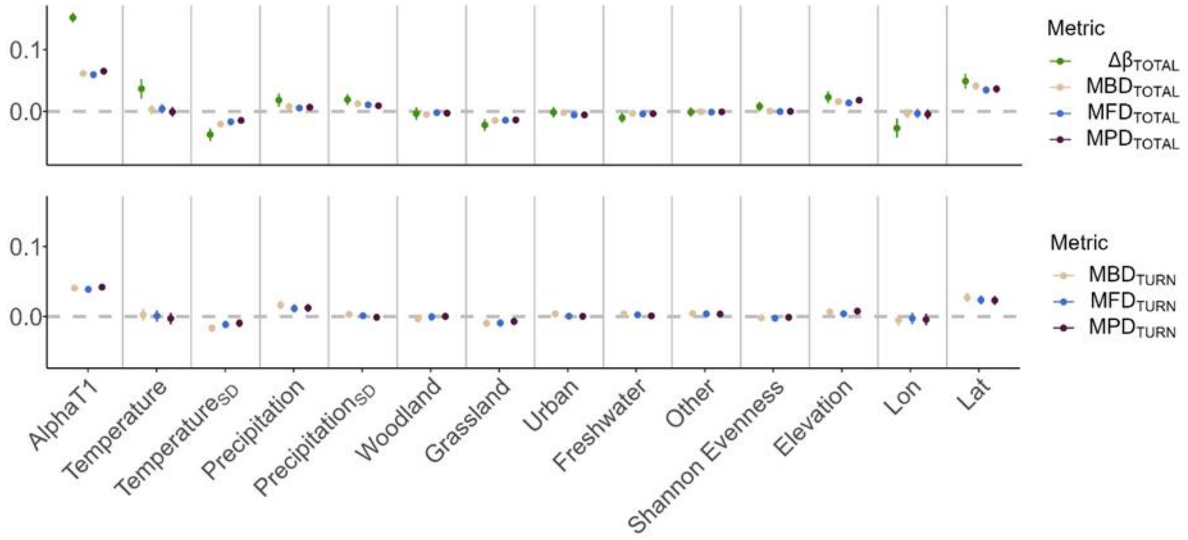


Figure S4.2.2: Inla model results. Results from the INLA models for measures of Sorensen's taxonomic multiple beta-diversity (MBD_{TOTAL}), Sorensen's functional multiple beta-diversity (MFD_{TOTAL}), Sorensen's Phylogenetic beta-diversity (MPD_{TOTAL}) and change in Whittaker's β diversity ($\Delta\beta_{TOTAL}$).

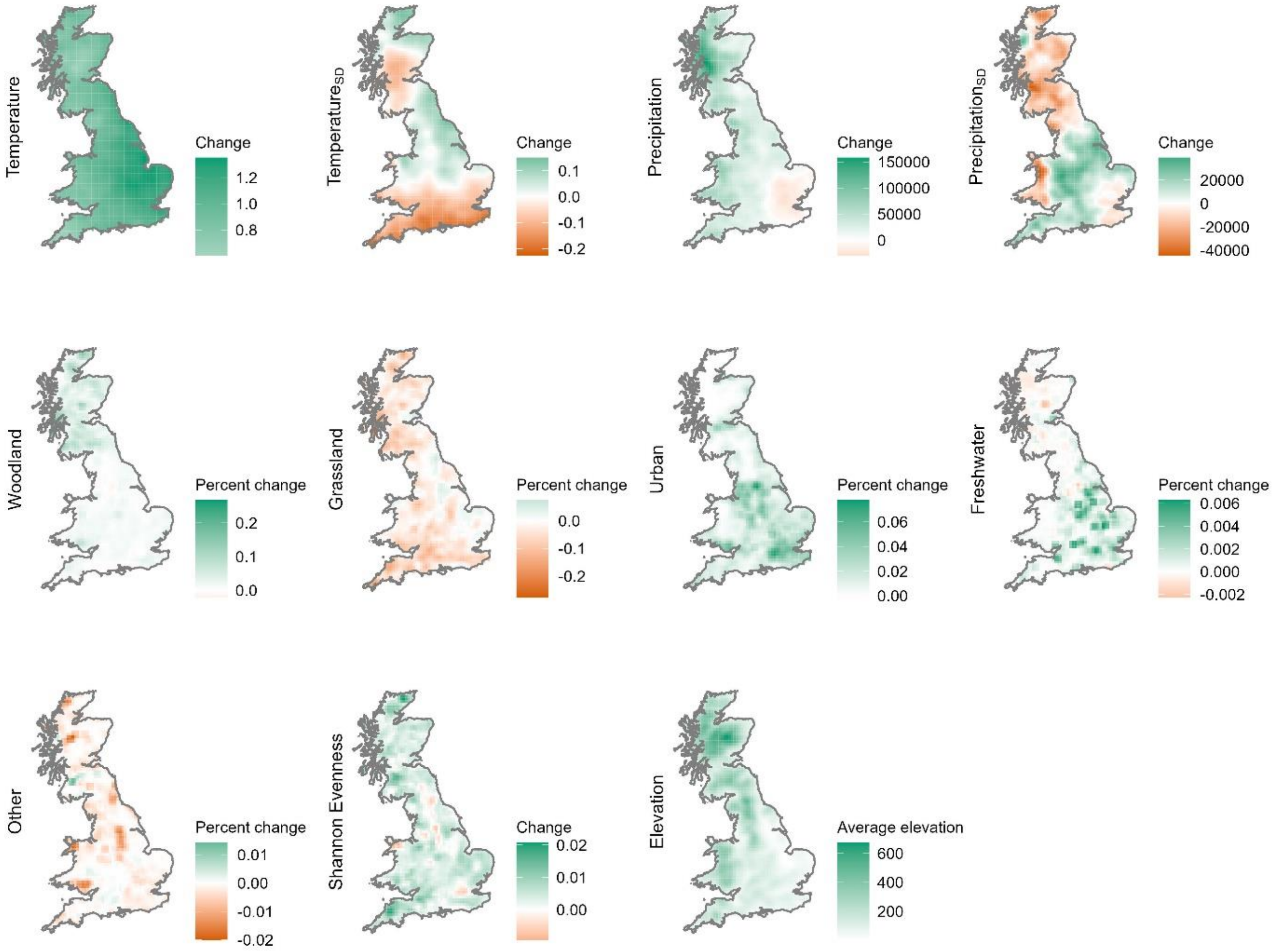


Figure S4.2.3: Maps showing change in the explanatory variables between two-time periods, 1981-1991 and 2001-2011 for the climatic variables (Temperature, Temperature$_{SD}$, Precipitation, and Precipitation$_{SD}$) and 1990 and 2015 for all land cover variables (Woodland, Urban, Grassland, Freshwater, Other and Shannon Evenness).

Chapter 5

Table S5.1. Multiple beta-diversity across all of the sampled transects for each country location. Each measure was calculated using 100 samples from the overall sample pool, each time sampled down to the minimum number samples found for one transect across the time series (two samples for each country).

			Multiple								
			Taxonomic			Functional			Phylogenetic		
Country	Year	Species Richness	Total	Turn	Nest	Total	Turn	Nest	Total	Turn	Nest
Honduras	2007	19.43 ± 0.22	0.53 ± 0.01	0.44 ± 0.01	0.1 ± 0.01	0.44 ± 0.01	0.34 ± 0.01	0.1 ± 0.01	0.36 ± 0.01	0.26 ± 0.01	0.1 ± 0.01
	2008	25.67 ± 0.51	0.53 ± 0.01	0.43 ± 0.01	0.1 ± 0.01	0.44 ± 0.01	0.33 ± 0.01	0.11 ± 0.01	0.35 ± 0.01	0.25 ± 0.01	0.11 ± 0.01
	2010	17.41 ± 0.17	0.54 ± 0.01	0.47 ± 0.01	0.07 ± 0	0.45 ± 0.01	0.38 ± 0.01	0.07 ± 0	0.38 ± 0.01	0.3 ± 0.01	0.08 ± 0.01
	2011	23.95 ± 0.42	0.52 ± 0.01	0.43 ± 0.02	0.09 ± 0.01	0.41 ± 0.01	0.33 ± 0.02	0.09 ± 0.01	0.33 ± 0.01	0.25 ± 0.01	0.08 ± 0.01
	2012	22.14 ± 0.34	0.49 ± 0.01	0.41 ± 0.01	0.08 ± 0.01	0.4 ± 0.01	0.32 ± 0.01	0.08 ± 0.01	0.34 ± 0.01	0.26 ± 0.01	0.09 ± 0.01
	2013	17.8 ± 0.23	0.53 ± 0.01	0.4 ± 0.01	0.13 ± 0.01	0.47 ± 0.01	0.34 ± 0.01	0.13 ± 0.01	0.4 ± 0.01	0.29 ± 0.01	0.12 ± 0.01
	2014	19.74 ± 0.29	0.45 ± 0.01	0.36 ± 0.01	0.09 ± 0.01	0.38 ± 0.01	0.28 ± 0.01	0.1 ± 0.01	0.33 ± 0.01	0.23 ± 0.01	0.1 ± 0.01
	2015	22.53 ± 0.47	0.47 ± 0.01	0.38 ± 0.01	0.08 ± 0.01	0.4 ± 0.01	0.31 ± 0.01	0.09 ± 0.01	0.34 ± 0.01	0.25 ± 0.01	0.09 ± 0.01
	2016	26 ± 0.41	0.5 ± 0.01	0.41 ± 0.01	0.09 ± 0.01	0.41 ± 0.01	0.31 ± 0.01	0.1 ± 0.01	0.34 ± 0.01	0.24 ± 0.01	0.1 ± 0.01
	2017	24.26 ± 0.41	0.47 ± 0.01	0.38 ± 0.01	0.09 ± 0.01	0.39 ± 0.01	0.29 ± 0.01	0.1 ± 0.01	0.32 ± 0.01	0.22 ± 0.01	0.1 ± 0.01
	2018	25.53 ± 0.42	0.54 ± 0.01	0.41 ± 0.01	0.12 ± 0.01	0.45 ± 0.01	0.32 ± 0.01	0.13 ± 0.01	0.36 ± 0.01	0.23 ± 0.01	0.13 ± 0.01
Madagascar	2011	23.2 ± 0.31	0.26 ± 0.01	0.18 ± 0.01	0.08 ± 0.01	0.23 ± 0.01	0.16 ± 0.01	0.07 ± 0	0.23 ± 0	0.15 ± 0.01	0.08 ± 0
	2012	24.66 ± 0.74	0.24 ± 0.01	0.18 ± 0.02	0.07 ± 0.02	0.2 ± 0.01	0.14 ± 0.01	0.06 ± 0.01	0.2 ± 0.01	0.13 ± 0.02	0.06 ± 0.02
	2014	22.24 ± 0.68	0.25 ± 0.02	0.17 ± 0.02	0.08 ± 0.02	0.22 ± 0.01	0.15 ± 0.01	0.07 ± 0.02	0.21 ± 0.01	0.13 ± 0.01	0.08 ± 0.02
	2015	19.84 ± 0.54	0.31 ± 0.01	0.25 ± 0.02	0.06 ± 0.01	0.26 ± 0.01	0.19 ± 0.02	0.07 ± 0.01	0.23 ± 0.01	0.17 ± 0.01	0.07 ± 0.01
	2016	22.91 ± 0.61	0.23 ± 0.02	0.17 ± 0.02	0.06 ± 0.02	0.19 ± 0.02	0.13 ± 0.02	0.06 ± 0.02	0.19 ± 0.02	0.13 ± 0.02	0.06 ± 0.02
	2017	22.59 ± 0.77	0.25 ± 0.02	0.16 ± 0.02	0.09 ± 0.02	0.2 ± 0.01	0.13 ± 0.02	0.07 ± 0.02	0.19 ± 0.01	0.12 ± 0.02	0.07 ± 0.02
Mexico	2014	49.32 ± 0.99	0.4 ± 0.01	0.35 ± 0.01	0.06 ± 0.01	0.3 ± 0.01	0.26 ± 0.01	0.04 ± 0.01	0.25 ± 0.01	0.21 ± 0.01	0.04 ± 0.01
	2015	51.16 ± 1.42	0.36 ± 0.01	0.28 ± 0.01	0.07 ± 0.01	0.26 ± 0.01	0.21 ± 0.01	0.05 ± 0.01	0.22 ± 0.01	0.18 ± 0.01	0.04 ± 0.01
	2016	55.3 ± 0.81	0.35 ± 0.01	0.29 ± 0.01	0.06 ± 0.01	0.27 ± 0.01	0.23 ± 0.01	0.04 ± 0.01	0.25 ± 0.01	0.21 ± 0.01	0.04 ± 0
	2017	52.6 ± 0.89	0.37 ± 0.01	0.33 ± 0.01	0.04 ± 0.01	0.27 ± 0.01	0.24 ± 0.01	0.03 ± 0.01	0.25 ± 0.01	0.21 ± 0.01	0.04 ± 0.01
	2018	52.84 ± 0.93	0.34 ± 0.01	0.28 ± 0.01	0.06 ± 0.01	0.25 ± 0.01	0.21 ± 0.01	0.04 ± 0.01	0.23 ± 0.01	0.18 ± 0.01	0.05 ± 0.01

Table S5.2. Pairwise beta-diversity across all of the sampled transects for each country location. Each measure was calculated using 100 samples from the overall sample pool, each time sampled down to the minimum number samples found for one transect across the time series (two samples for each country).

			Pairwise								
			Taxonomic			Functional			Phylogenetic		
Country	Year	Species Richness	Total	Turn	Nest	Total	Turn	Nest	Total	Turn	Nest
Honduras	2007	19.43 ± 0.22	0.87 ± 0	0.82 ± 0	0.05 ± 0	0.84 ± 0	0.78 ± 0	0.06 ± 0	0.81 ± 0	0.73 ± 0.01	0.08 ± 0.01
	2008	25.67 ± 0.51	0.87 ± 0	0.82 ± 0.01	0.05 ± 0	0.84 ± 0	0.77 ± 0.01	0.06 ± 0.01	0.8 ± 0	0.72 ± 0.01	0.08 ± 0.01
	2010	17.41 ± 0.17	0.87 ± 0	0.84 ± 0	0.03 ± 0	0.84 ± 0	0.8 ± 0	0.04 ± 0	0.81 ± 0	0.75 ± 0	0.06 ± 0
	2011	23.95 ± 0.42	0.87 ± 0	0.82 ± 0.01	0.04 ± 0.01	0.83 ± 0	0.77 ± 0.01	0.06 ± 0.01	0.79 ± 0	0.72 ± 0.01	0.07 ± 0.01
	2012	22.14 ± 0.34	0.86 ± 0	0.81 ± 0	0.04 ± 0	0.83 ± 0	0.77 ± 0.01	0.06 ± 0.01	0.8 ± 0	0.73 ± 0.01	0.07 ± 0.01
	2013	17.8 ± 0.23	0.87 ± 0	0.8 ± 0	0.07 ± 0	0.85 ± 0	0.77 ± 0	0.08 ± 0	0.83 ± 0	0.74 ± 0.01	0.08 ± 0.01
	2014	19.74 ± 0.29	0.85 ± 0	0.79 ± 0	0.06 ± 0	0.82 ± 0	0.74 ± 0.01	0.08 ± 0.01	0.79 ± 0	0.7 ± 0.01	0.09 ± 0.01
	2015	22.53 ± 0.47	0.85 ± 0	0.8 ± 0.01	0.05 ± 0.01	0.82 ± 0	0.76 ± 0.01	0.06 ± 0.01	0.79 ± 0.01	0.72 ± 0.01	0.07 ± 0.01
	2016	26 ± 0.41	0.85 ± 0	0.81 ± 0	0.05 ± 0	0.83 ± 0	0.76 ± 0.01	0.07 ± 0.01	0.79 ± 0	0.7 ± 0.01	0.09 ± 0.01
	2017	24.26 ± 0.41	0.85 ± 0	0.8 ± 0.01	0.05 ± 0	0.82 ± 0	0.75 ± 0.01	0.07 ± 0.01	0.78 ± 0.01	0.69 ± 0.01	0.09 ± 0.01
	2018	25.53 ± 0.42	0.86 ± 0	0.8 ± 0	0.06 ± 0	0.84 ± 0	0.75 ± 0	0.09 ± 0	0.8 ± 0	0.68 ± 0.01	0.12 ± 0.01
Madagascar	2011	23.2 ± 0.31	0.54 ± 0.01	0.45 ± 0.01	0.09 ± 0.01	0.51 ± 0.01	0.41 ± 0.01	0.1 ± 0.01	0.51 ± 0.01	0.39 ± 0.01	0.12 ± 0.01
	2012	24.66 ± 0.74	0.52 ± 0.01	0.42 ± 0.03	0.1 ± 0.03	0.47 ± 0.01	0.37 ± 0.03	0.1 ± 0.02	0.46 ± 0.01	0.35 ± 0.03	0.11 ± 0.03
	2014	22.24 ± 0.68	0.53 ± 0.02	0.41 ± 0.03	0.12 ± 0.02	0.49 ± 0.02	0.38 ± 0.02	0.11 ± 0.03	0.48 ± 0.02	0.35 ± 0.02	0.13 ± 0.02
	2015	19.84 ± 0.54	0.59 ± 0.01	0.52 ± 0.02	0.07 ± 0.02	0.53 ± 0.01	0.44 ± 0.02	0.09 ± 0.02	0.51 ± 0.01	0.41 ± 0.02	0.1 ± 0.02
	2016	22.91 ± 0.61	0.5 ± 0.02	0.42 ± 0.03	0.08 ± 0.03	0.45 ± 0.02	0.35 ± 0.03	0.11 ± 0.03	0.45 ± 0.03	0.35 ± 0.04	0.1 ± 0.03
	2017	22.59 ± 0.77	0.53 ± 0.02	0.4 ± 0.03	0.13 ± 0.03	0.47 ± 0.02	0.34 ± 0.03	0.12 ± 0.03	0.45 ± 0.02	0.32 ± 0.03	0.13 ± 0.03
Mexico	2014	49.32 ± 0.99	0.76 ± 0	0.71 ± 0.01	0.05 ± 0.01	0.7 ± 0.01	0.65 ± 0.01	0.05 ± 0.01	0.66 ± 0.01	0.6 ± 0.01	0.05 ± 0.01
	2015	51.16 ± 1.42	0.73 ± 0	0.67 ± 0.01	0.07 ± 0.01	0.66 ± 0.01	0.6 ± 0.01	0.07 ± 0.01	0.62 ± 0.01	0.56 ± 0.01	0.07 ± 0.01
	2016	55.3 ± 0.81	0.73 ± 0	0.67 ± 0.01	0.05 ± 0	0.67 ± 0.01	0.62 ± 0.01	0.05 ± 0.01	0.65 ± 0.01	0.6 ± 0.01	0.05 ± 0.01
	2017	52.6 ± 0.89	0.74 ± 0	0.7 ± 0.01	0.04 ± 0.01	0.67 ± 0.01	0.63 ± 0.01	0.04 ± 0.01	0.65 ± 0.01	0.6 ± 0.01	0.05 ± 0.01
	2018	52.84 ± 0.93	0.72 ± 0.01	0.67 ± 0.01	0.06 ± 0.01	0.66 ± 0.01	0.6 ± 0.01	0.05 ± 0.01	0.63 ± 0.01	0.57 ± 0.01	0.06 ± 0.01

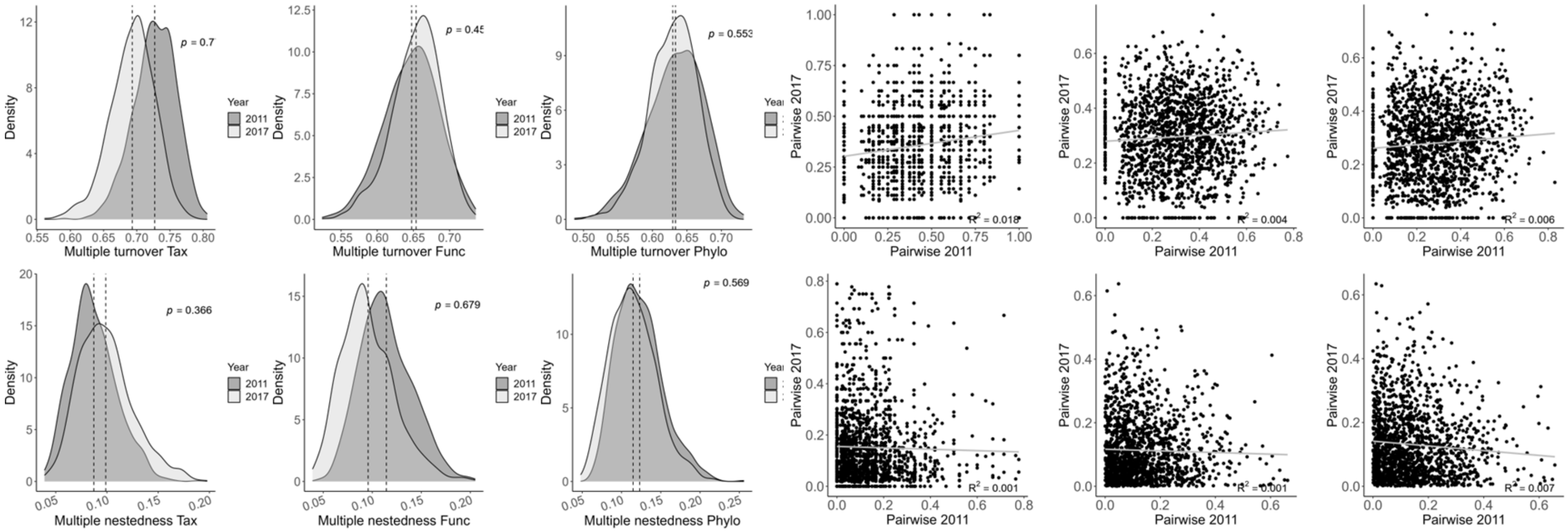


Figure S5.3. Spatial change between the first and last year of sampling within Mariarano, Madagascar. Density plots (**L**) display the turnover (**top row**) and nestedness (**bottom row**) components for taxonomic, functional and phylogenetic beta-diversity. Dashed grey lines show the mean value of the metric across the sampled distribution. P-values from empirical tests comparing the distributions are displayed in the top right corner. Relationships between the pairwise distributions (**R**) for taxonomic, functional and phylogenetic beta-diversity. The solid grey line shows the fit from an OLS linear regression. Fit (R^2) from the regression is displayed in the bottom right corner.

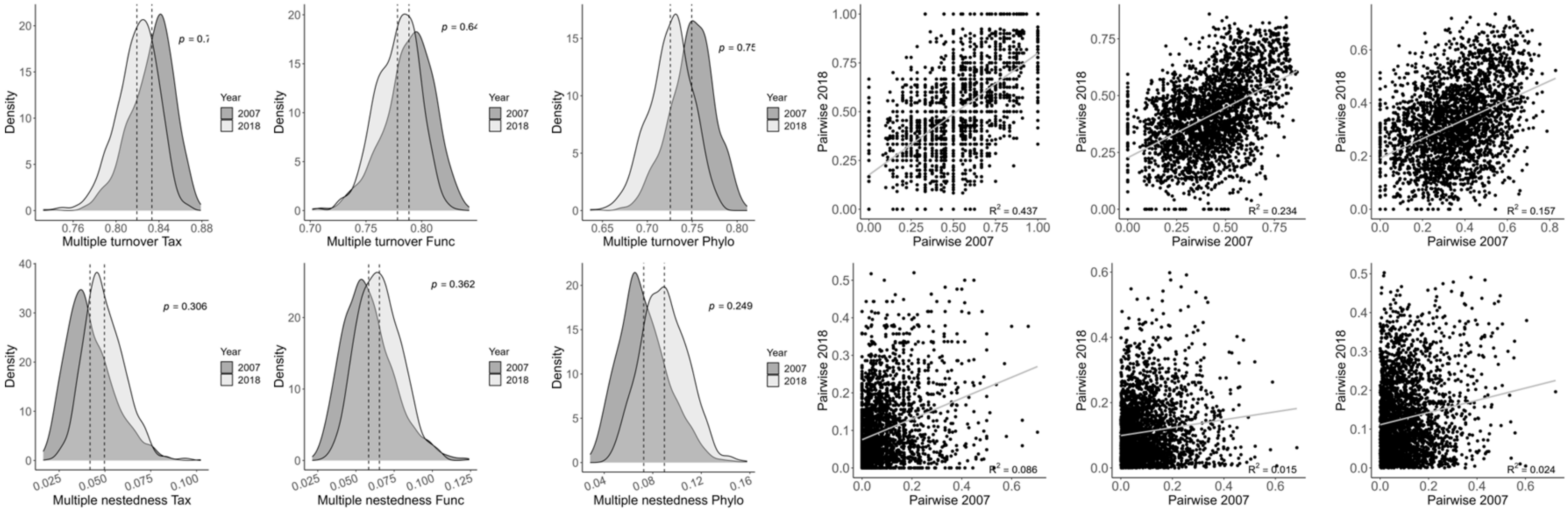


Figure S5.4. Spatial change between the first and last year of sampling within Cusuco, Honduras. Density plots (**L**) display the turnover (**top row**) and nestedness (**bottom row**) components for taxonomic, functional and phylogenetic beta-diversity. Dashed grey lines show the mean value of the metric across the sampled distribution. P-values from empirical tests comparing the distributions are displayed in the top right corner. Relationships between the pairwise distributions (**R**) for taxonomic, functional and phylogenetic beta-diversity. The solid grey line shows the fit from an OLS linear regression. Fit (R^2) from the regression is displayed in the bottom right corner.

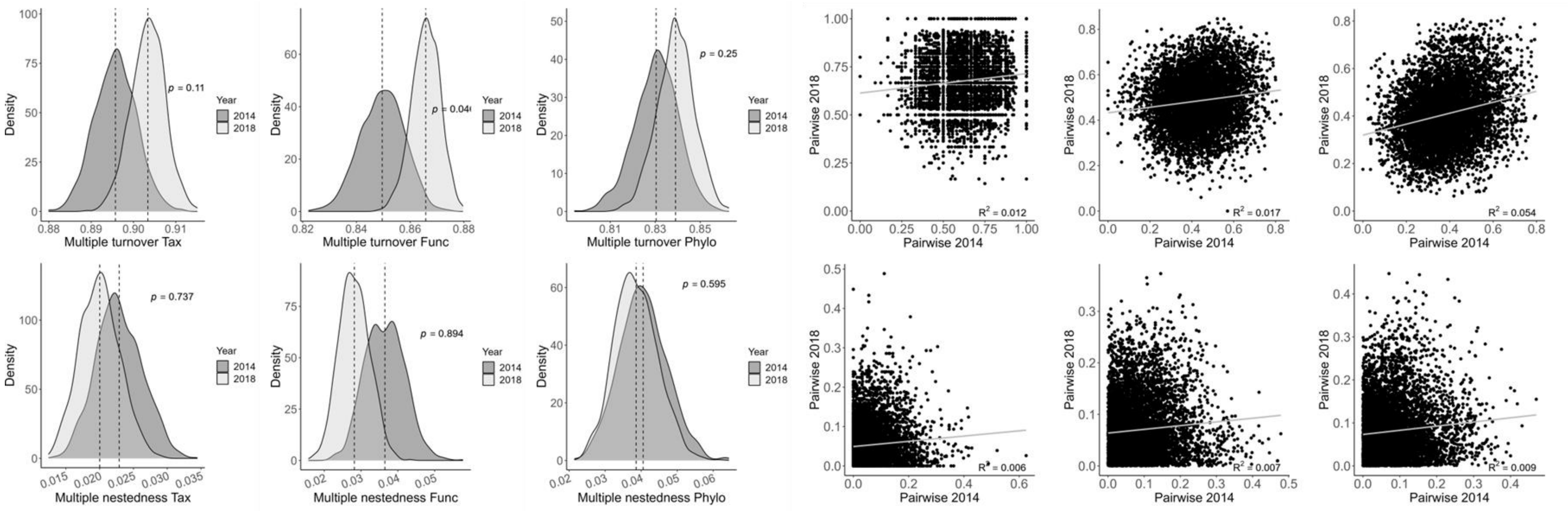


Figure S5.5. Spatial change between the first and last year of sampling within Calakmul, Mexico. Density plots (**L**) display the turnover (**top row**) and nestedness (**bottom row**) components for taxonomic, functional and phylogenetic beta-diversity. Dashed grey lines show the mean value of the metric across the sampled distribution. P-values from empirical tests comparing the distributions are displayed in the top right corner. Relationships between the pairwise distributions (**R**) for taxonomic, functional and phylogenetic beta-diversity. The solid grey line shows the fit from an OLS linear regression. Fit (R^2) from the regression is displayed in the bottom right corner.