The impact of urbanisation on UK bird assemblages:

a spatial and temporal evaluation

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Abstract

The urbanisation process has numerous and substantial impacts on ecosystems and biodiversity. Comprehending how different species react to environmental change through urbanisation is necessary if we are to better understand how to mitigate the negative impacts. Birds, which have relatively high mobility and many of which are sensitive to environmental change, are often used as indicators to determine how urbanisation affects biodiversity. However, most studies of the impacts of urbanisation on birds focus on a single city, or focus on multiple cities but use non-standardised data. Here, a standardised dataset of bird presence across the UK (BTO Atlas data) was used to compare urban and rural bird assemblages in terms of various spatial and temporal ecological patterns. The 100 most urban grid squares in the BTO dataset were selected, and compared with a random draw of 100 rural squares. The dataset comprised two time periods: 1970 and 2010. Temporal patterns of species richness and composition change were compared between rural and urban sites, as were differences in spatial variation in composition in 2010 (i.e. spatial beta-diversity). To compliment the community-level patterns, an analysis of individual winner and loser species (in terms of urbanisation) was undertaken. It was found that there were some large differences between urban and rural sites. While mean richness did not differ substantially, composition changed to a greater degree through time in urban areas, while in 2010 spatial variation in composition was lower in urban squares relative to rural squares. Together, these results indicate that urban areas are becoming more homogenous in terms of composition, which aligns with published studies that have argued biotic homogenisation of communities is a global environmental issue. The species doing well in urban areas (the winners) tend to be doing well nationwide, although the rate of increase in occupancy is generally greater in urban areas.

Acknowledgements

Contents

Chapter 1

Introduction

1.1 Background

Humans are having substantial impacts on all levels of biodiversity, from species through to ecosystems (Blowes et al. 2019). The rate at which anthropogenic drivers (loss of habitat, excessive fishing, pollution, climate change to name a few) have been extinguishing animal and plant species has accelerated in recent centuries (Ceballos et al., 2015). Because the typical urban region is highly populated, with energy supply and living space only two of the human population's many needs, urban regions are among the most clearly anthropogenic landscapes. The consequence of the urbanisation process is highly fragmented habitats and a disturbed local climate, both of which are known to be detrimental to biodiversity. Past research has shown that some native species are less abundant in urban areas relative to more natural, rural environments (Tratalos et al., 2007; Grimm et al., 2008). Coupled with the extirpation of specialist species in urban areas, this increases biotic homogeneization across cities (McKinney, 2006; Devictor et al., 2007). Indeed, big cities are considered to have the highest rates of local extinction of species of any pattern of land use (Chace & Walsh, 2006; Marzluff et al., 2001; McKinney, 2002).

When seeking to assess how urbanisation affects biodiversity, birds represent a useful study taxon on account of their rapid reaction to changes in habitat, the presence of many species in urban environments, and the availability of data on their presence and ecology in cities (Chace and Walsh, 2006; Pellissier et al., 2012). They are also, thanks to their diverse ecologies and life cycles, a useful taxon for studying how species' traits can change as a result of changes in the environment. Most ornithological studies along urban-rural gradients have found that avian communities' composition and diversity have been negatively affected by urbanisation (Chace & Walsh, 2006; Lepczyk

et al., 2017; McKinney, 2002, Fig. 1-1) which, as stated above, leads to bird composition becoming homogenised (Clergeau et al., 2006; La Sorte et al., 2014; Leveau et al., 2015). The differential impacts on migrants vs. resident birds can also lead to changes in seasonal diversity patterns.
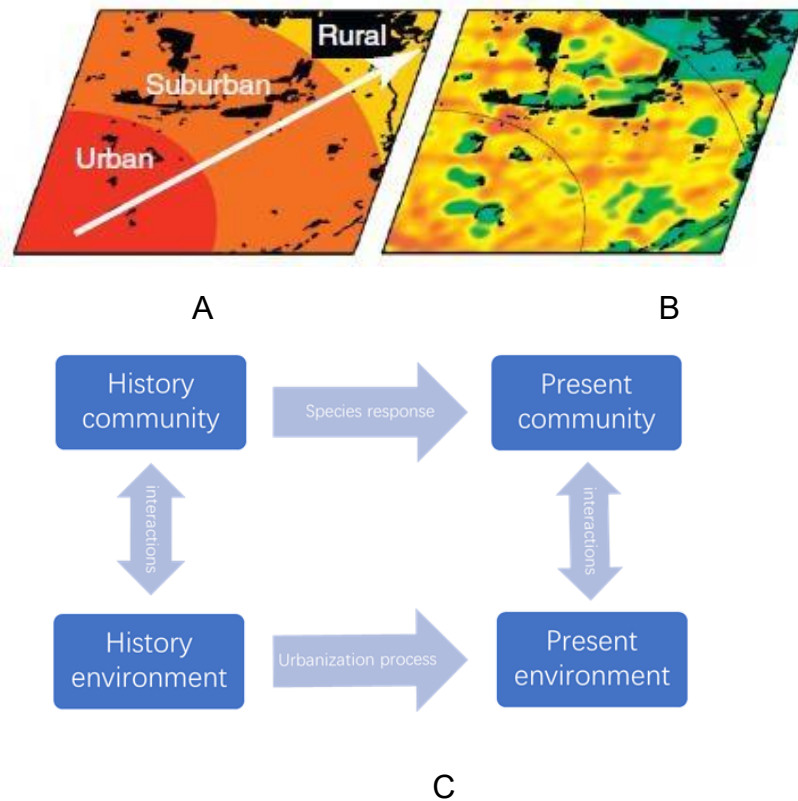
Fig 1-1 Studies using the urban-to-rural gradient approach to study biodiversity responses to environmental change tend to rely on one of two options: allocating sites to categories (i.e., urban or rural) or using the linear distance between the city centre and the rural matrix as shown in A. Alternatively, the two methods can be combined with measures of socioeconomic factors, land cover, land use, or built infrastructure metrics as shown in B to determine the degree to which remnant ecosystems have been urbanised (road density is depicted here). Data analysis often compares ecological responses across various urban classes or examines the individual effects of a condensed collection of explanatory variables, as in C (Ramalho et al., 2012).

1.2 Species responses

Understanding how species respond to urbanization is critical if we are to effectively manage and conserve biodiversity in cities. This is because the urbanization process is inevitable given the global rise in the human population size, coupled with the trend of increased rural to urban migration. The assembly of a biological community is guided by a limited set of drivers, their relative importance fluctuating over time and space. On a regional level, factors such as speciation, extirpation and dispersal are important. Local community assembly is a complex process, often resulting from a combination of factors that influence species interactions, cohabitation, and extirpation (Huston, 1999; Mittelbach et al., 2015). Human influence, and urbanisation in particular, plays a significant role at all scales, from the local (Fig 1-2) to the regional, ultimately affecting community assembly and the emergent diversity patterns in cities (e.g., beta-diversity; Fig 1-2).
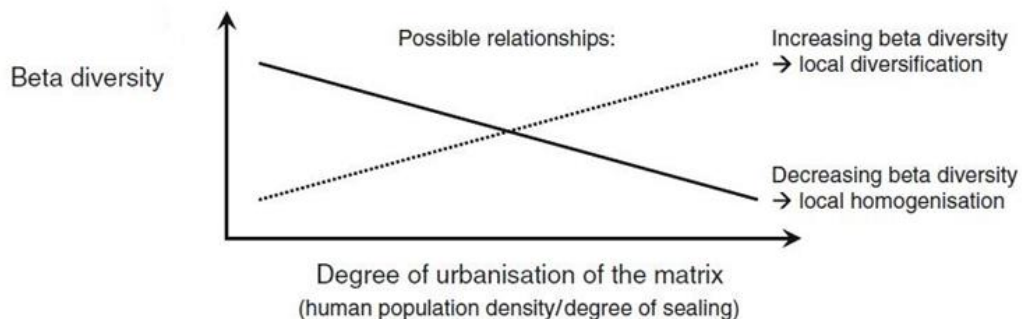
Fig.1-2 possible relationships between the degree of urbanisation within the urban matrix and beta diversity between similar habitat patches (Meffert and Dziock, 2013)

1.2.1 Spatial scale

Changes in the spatial scale of analysis can cause variations in a range of biodiversity patterns, including those involving species richness and

composition (Wiens et al., 1987; Rahbek, 2005). For example, according to Ferenc et al. (2019), although the proportion of natural vegetation and habitat heterogeneity play significant roles in determining urban communities richness of bird species at smaller spatial scales (Evans et al., 2009; Ferenc et al., 2014, 2016), these effects may not be discernible at large spatial scales (MacGregor-Fors et al., 2010). At the local scale, Beninde et al. (2015) found that abiotic and urban design variables were less influential than those concerned with local, biotic, and habitat characteristics. Other studies have demonstrated effects at the landscape level on birds in urban settings, typically concluding that urbanisation around patches of forest and riparian habitats affects the diversity and abundance of birds inside these areas (e.g., Munyenyembe et al. 1989, Smith and Schaefer 1992, Bolger et al. 1997, Germaine et al. 1998, Saab 1999), but these effects have not been consistently demonstrated over a number of studies (Berry and Bock 1998, Clergeau et al. 1998).

1.2.2 Temporal variation

1.2.2.1 Seasonal observation

Seasonal oscillations are in evidence for the majority of environmental phenomena, and especially of precipitation and temperature, but even regular oscillations can show variations that matter from a biological point of view. These disparities in distribution cause many ecosystems to encounter diverse seasonal circumstances that can favour completely different populations and food webs at specific times of the year (McMeans et al. 2015). The further the site is from the equator, the more significant seasonality tends to be. Numerous studies have proposed ways in which biodiversity patterns are altered by temporal fluctuations. For example, although scarce resources and interspecific competition can cause species to become extinct (Connell, 1978), seasonal fluctuations in environmental conditions might help similar species persist (Tilman & Pacala, 1993).

1.2.2.2 Long-term study

Besides seasonal oscillations, long-term observation and historical records show a connection between successions in the bird community and long-term environmental change from a decadal perspective. It has been reported that species richness increases and a trend develops towards less taxonomically equal assemblages, according to a continental study of 35 years of trends in the taxonomic composition of local bird assemblages in the United States (La Sorte and Boecklen 2005). These spatial patterns in historical trends point to the influences of regional habitat and climatic variations (La Sorte and Boecklen 2005; Stegen et al. 2013).

1.3 Beta-diversity

Species turnover, an essential element of spatial beta diversity, measures shifts in the composition of species across sites (Tuomisto, 2010a). Processes connected to geographical variations in efficient species turnover may be determined to be niche-based or 'neutral' on the basis of correlations with geographic and environmental distance (Soininen et al., 2007). This approach has recently been expanded to take into account temporal turnover, i.e., the turnover in species over time (Basset et al., 2015; Hatosy et al., 2013; Matsuoka et al., 2016) in order to quantify how community composition changes over time (Collins et al., 2000). Over time, communities may be stable, show directional change in composition, or stochastic variation. According to Magalhães et al. (2007), cases also occur where there are cyclic patterns in response to environmental perturbations, but the scarcity of research into temporal turnover means that there is insufficient information to differentiate between anthropogenic and natural change for most systems (Magurran, 2016; Mihoub et al., 2017).

1.3.1 Homogenization

Biotic homogenization is a significant factor in the current biodiversity crisis and is thought to significantly impact future trends in biodiversity (Olden & Poff, 2004; Olden, 2006). Urbanization is regarded as a powerful process in the production of biotic homogeneity and the loss of biodiversity (Blair, 2001; McKinney, 2006). While anthropogenic environmental disturbance has typically been seen as negatively affecting species, it has, in fact, been shown that some species may benefit from disturbance (Lewis et al., 2009; Williams et al., 2010; Jauni et al., 2015). Often the study of differential impacts of urbanisation on species focused on the specialist:generalist dichotomy, although this may be too simplistic (Kithahara et al. 2000). Most sensitive to loss or modification of habitat are proposed to be the habitat specialist species (Owens & Bennett 2000; Marvier et al. 2004; Julliard et al. 2006), whereas generalists are thought to be less affected, or even benefit from the process. This has led a number of authors to concentrate on processes leading to specialist species being replaced by fewer, generalist species, resulting in homogenisation across cities in a region.

Urban biotic homogenisation results in avian communities in urban areas being more similar to each other than expected (Clergeau et al. 2006, McKinney 2006, Olden et al. 2006). As outlined above, nesting location, food availability, and temperature are considered the primary factors of bird community assembly and all these characteristics are influenced by the urban environment, to the determinant of many species, but the benefit of a few. There may be a slight increase in local diversity as a result of suburban development (Marzluff, 2014), but diversity will be reduced when natural open space is converted in large amounts to a dense urban area because communities become dominated by the small number of species able to withstand and adapt to these conditions (Andersson 1994, Blair, 1996, Marzluff, 2005, McKinney, 2006, Sol et al., 2014). Avian trophic guilds are differentially affected, with those belonging to the

carnivore and scavenging guilds (Kettel et al. 2018) filtered out by the urbanisation process, for example (Evans et al. 2011).

1.3.2 Winners and losers

Species may be described as "winners" or "losers", in a urban ecological context, on the basis of how they fare in cities, i.e., whether they are affected negatively in some way. These effects can be measured in numerous ways. For example, changes in occupancy (local extinctions and colonization) and changes in abundance (population trends) are both crucial elements of biodiversity change and contribute in associated but distinct ways to biotic change (Dornelas. et al. 2019). Winners may be concentrated in select higher taxa and ecological groups, leading to even greater homogenisation at higher taxonomic levels.

It should be noted that, because the ways in which human-modified landscapes develop is complex, in many cases it may not be as simple as the replacement of "losers" by invading "winners" (Lôbo et al., 2011). As a result, biotic homogenisation patterns are often complex and noisy. One area of complexity is that climate change may potentially play a significant role in the determination of urban winners and losers, with species more adapted to colder conditions being particularly negatively affected by the combination of urbanisation and climate change (Tayleur et al., 2016).

1.3.3 Functional traits

Functional diversity refers to the importance and range of species traits that affect how the ecosystems function (Calow, 1987; Tilman, 2001). Functional traits are defined as those aspects of an organism that affect its fitness and function within the environment (Petchey and Gaston, 2006; Swenson, 2014; Hodgson et al. 2005; Gaucherand and Lavorel 2007). According to McKinney

et al., (2002), there are particular features and combinations of traits that allow species to better adapt to environmental changes resulting from urbanisation. This ability may vary depending on seasonality, location, and the city's design (Leveau, 2013), but these urban users are able to handle a wider range of climatic circumstances and seem to share certain types of traits (Hensley et al., 2019). For example, urban areas act as environmental filters that prevent the emergence of specialist species displaying traits including food specialisation, long-distance migration, and high sensitivity to human disturbance (Seress and Liker, 2015; Vaccaro, et al., 2022). A great deal of research has looked at the ways birds adapt to urban habitat from a functional trait perspective. Specific trait changes, including behavioural and communal traits and physiological changes, are summarised in Table 1-1 (Patankar et al., 2021).

Table 1-1. The number of research conducted on either single species (<4 species) or large communities (>4 species) for each of the bird attributes considered (Patrankar et al., 2021).

Traits	Number of studies (<4 species)	Number of studies (>4 species)	Total
Ecological (diversity, nesting, richness, diet, migration, composition, etc)	22	73	95
Life history (clutch size, breeding, activity time range, fitness, etc)	20	13	33
Physiological (body size, inflammatory response, endocrine traits, etc)	32	26	58
Behavioral (fear and stress, learning, song, aggression, etc)	74	25	99

Genetic (gene expression, genetic changes and divergence, etc)	4	2	6
Total	148	139	287

1.3.4 Cities' features that affect bird diversity

In urban areas, a variety of circumstances can affect the persistence of certain bird species. For instance, places with high population density are likely to keep fewer trees during the construction period, and to have less ground available in which the population can plant new trees (Barth et al., 2015). Additionally, such factors as human activity, the volume of traffic and the amount of noise and light in metropolitan areas may also impact bird species diversity (Lepczyk et al., 2008; Parris & Schneider, 2009; Summers et al., 2011). How birds use particular habitats can be influenced by additional factors including the presence / absence of interaction partners, including flowering plants and predators (Suri et al., 2017).

Although guidelines exist for conserving wildlife in urban areas (Soule, 1991; Shafer, 1997; Magle et al., 2012) which strongly emphasise the importance of both the pattern and quantity of natural habitat, recent studies have argued that quantity is more important than pattern, particularly for mobile species such as birds (Fahrig, 1997; Bunnell, 1999; Harrison and Bruna, 1999; Thomas et al., 2001; Lichstein et al., 2002; Alberti and Marzluff, 2004).

Although it is clear that many species avoid urban areas, a number of avian, small mammal and amphibian species have persevered in new or relict habitats within such areas (Blair, 1999; Blair & Launer, 1997; Riem et al., 2012), such as urban green spaces (Estevo et al., 2017; Schütz & Schulze, 2015; Threlfall et al., 2016; Tryjanowski et al., 2017). Urban green spaces also undertake a

number of additional ecosystem services, such as the filtering of polluted air, air cooling, and the buffering of noise pollution (Nowak et al., 2006; Ziter et al., 2019).

1.4 This study

1.4.1 Study areas and sites

The study area is the realm of UK covered by the British Trush of Ornithology (BTO) survey: the Atlas of Breeding Birds in Britain and Ireland (Sharrock, 2010; Gillings et al., 2019) (Fig. 1-3). To conduct a pairwise study of differences between urban and rural areas, 100 urban sites and 100 rural sites were selected using the base level sample unit adopted in the BTO census data of 10 km squares (Fig. 1-4). The classification of "urban" sites was defined as those with over 30% coverage of urban land use according to the Historic Land Dynamics Assessment (HILDA) dataset (1.4.2.2 Landcover data), and the "rural" sites in this study were defined as those with less than 10% coverage of urban land use. The threshold for "urban" sites was determined according to the urban percentage ranking list (i.e., all the squares ranked by % urbanization) to ensure these sites were most "urbanized" and dispersed geographically all over the UK. Within these constraints, each site was randomly selected and check through remote sensing data. Those sites located near very large water bodies were removed as this would causes issues in the percentage cover of terrestrial land use types within squares.

Fig.1-3. A map indicating the location of the study (Great Britain) within Europe. The British Trust of Ornithology employed grids across the island to display the 10km × 10km hectads used to sample the British avifauna over two different atlas periods: BA1970 (1968-1972) and BA2010 (2008-2011).
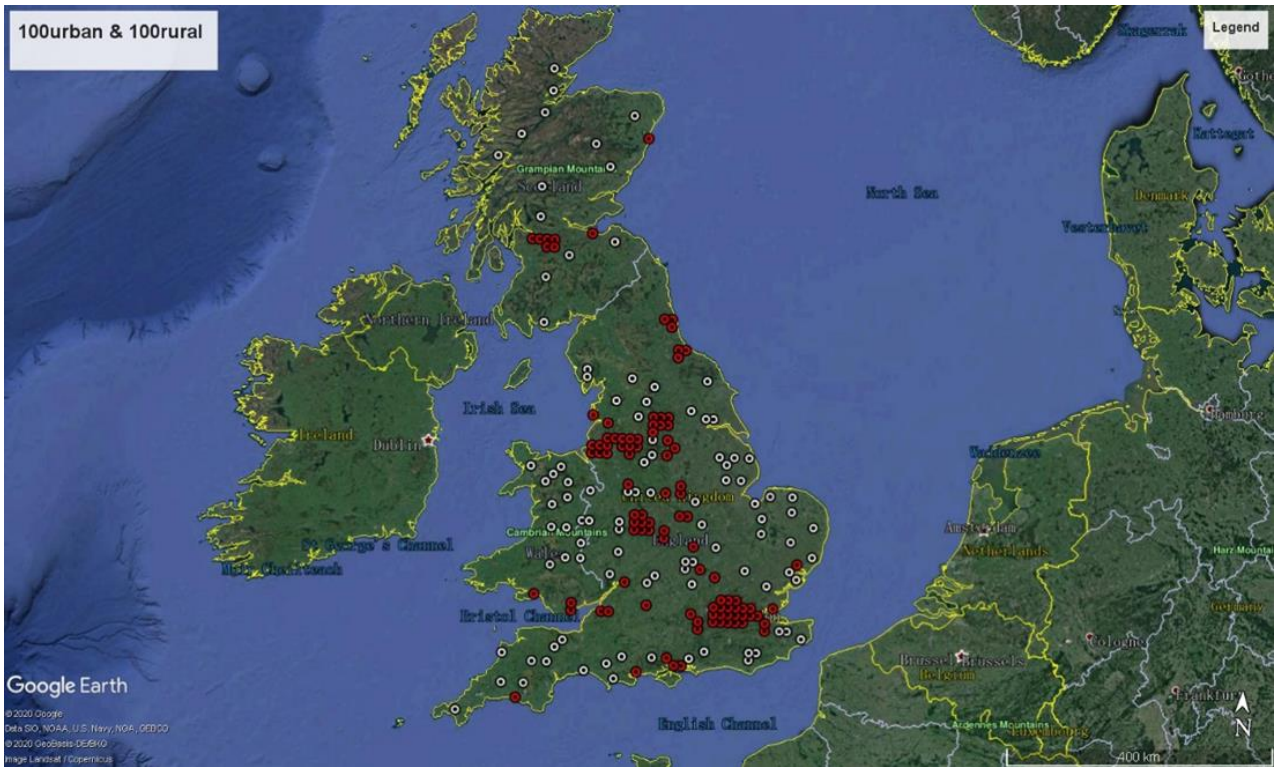
Fig **1-4.** The site map of this study with urban sites shaded as red and rural sites as white (based on geographical location on Google Earth).

1.4.2   Bird data and environment data

1.4.2.1   BTO data (Atlas Open Data)

The bird species data are from the BTO atlases of bird distribution (all species), under the atlas project of the Atlas of Breeding Birds in Britain and Ireland, including two periods of records: 1968-1972 (referred to as 1970 data) and 2007-2011 (referred to as 2010 data).

The BTO atlas of bird distribution data are records of breeding birds assembled through the systematic sampling of citizen experts. The atlas data record breeding and wintering bird species' presence in the 10km by 10km grid squares. At least eight out of 25 tetrads (2 x 2 km squares) in each 10-km square were sampled for a fixed 1 or 2 hours.

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The dataset comprises 1,410,938 records of 465 bird species in 3,880 grid cells in the different census periods. Thus, the dataset can be used to describe stability, colonization and extinction of individual bird species within grids across a 40 year period. Observation records were available for the breeding status of each detected species in all grid cells (Gillings, et al. 2019). Comprehensive methodological information pertaining to survey methodologies may be found within each atlas publication (Balmer et al., 2013; Gibbons et al., 1993; Lack, 1986; Sharrock, 1976). Small differences in sampling method between the two periods are as follows:

1970 Data: The survey was conducted by either individuals or teams of surveyors who visited 10 km squares. During their visits, they focused on the primary habitats inside each square in order to identify breeding species. The square was accessible for unlimited visits and durations.

2010 Data: The surveyors conducted fixed-time inspections to tetrads and also made supplemental records. The recording technique in the 2010 survey was improved by implementing submission of raw data for every hour, as opposed to summarising the data across visits. (Gillings et al., 2019).

1.4.2.2   Landcover data

The land use data came from the Historic Land Dynamics Assessment (HILDA) data set (version 2.0). HILDA is a reconstruction model combining multiple harmonized and consistent data streams, including aerial photographs, national inventories, historic land cover products, land cover statistics and historic land cover maps (Fuchs et al., 2013, 2015). HILDA data resolution is in 1 km squares and cover the region of EU-27 plus Switzerland, with a ten year time interval for the period 1900 to 2010. This historical land cover dataset is classified into 6 thematic resolutions, including urban (settlements), cropland, forest, grassland,

water and others (bare soil or beaches. etc).

1.4.2.3   Human Influence data

The human influence data are derived from the Global Human Influence Index Dataset (HII) from the Last of the Wild Project, Version 2, 2005 (LWP-2). The Human Influence Index (HI) is an index converted from a global dataset with spatial resolution of 1km grid cells, and was created from a package of layers related to human activities, including population density, built-up areas, night time lights, land use, coastlines, roads, and rivers. In this way, it provides an overall picture of pressures from human population, infrastructure and how humans use and access the land. It thus provides an integrated measure of direct human influence on terrestrial ecosystems as recorded by the Wildlife Conservation Society (WCS) and the Columbia University Centre for International Earth Science Information Network (CIESIN).

1.4.2.4   Climate data

Climate data were collected from WorldClim (WorldClim - Historical climate data, https://worldclim.org/data/worldclim21.html, 2020-2022,).

The annual average precipitation data and mean temperature data were collected from the bioclimatic variables of WorldClim 2. The WorldClim 2 dataset provides climate data for global terrestrial areas at a resolution of about 1 km squares. This climate dataset is subject to monthly interpolation of temperature (minimum, maximum and average), wind speed, vapour pressure, precipitation and solar radiation (Fick et al., 2017). The bioclimatic variables are derived from monthly temperature and rainfall values to generate biologically meaningful variables. The 1970 data and 2010 data were selected from the dataset for each respective BTO data study period.

1.4.2.5 Temporal change

Temporal change in richness and composition were calculated based on the 1968-72 and 2007-10 atlas data. The temporal beta-diversity partitioning will be specified in the next section (Methods).

1.4.2.6 The dataset for this study

The dataset is compiled from the above data to produce one specific dataset for this study covering all the aspects from species data to environmental data. The dataset contains the information detailed in Table 1-2.

Table 1-2 A typical example for columns in the dataset for this study.

Cha = change in a particular land-use type across the two time periods. Acronyms are described in the text.

Sites	Urban features		Climate data		Land use data	Bird diversity		Other predictors
grid	city	population	Precipitation (Prec, cha_prec)	Temperature (tmax, tmin, tavg, cha_tavg)	Landcover (%) (Forest, crop, grass, urban, cha_forest, cha_crop, cha_grass, cha_urban)	Species richness, richness change	Temporal and spatial beta-diversity indices (sne, sor, sim)	HI (%); Classification [urban or rural]; Latitude; Longitude

The climate means are for the average for that climate variable across the breeding season (defined as May – July) for a 30-year period. For precipitation, this is the average across the breeding season for summed precipitation (I.e., total rainfall within the 10km² cell). All the "cha" climate variables are the slopes of an OLS regression through the climate data over the period 1961-2011. For example, cha_tavg is the slope for average temperature over the breeding season (May – July). Figure1-5 provides an illustration of how climatic variables have changed in the UK across the study time period.
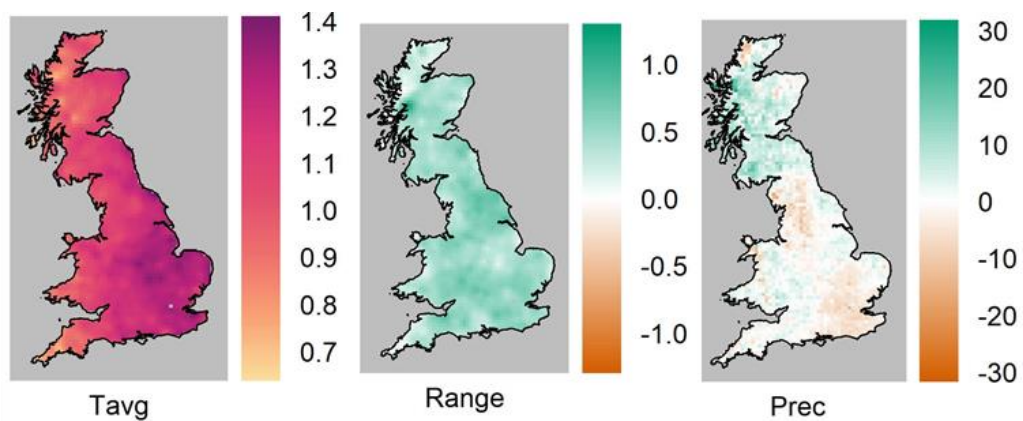
Fig. 1-5. Heat maps of the temporal change of measures of climate in Britain during the avian breeding season (March to the end of July) between 1970 and 2010. Tavg: average temperature; Range: the average maximum temperature minus the minimum for each month; Prec: total precipitation in the breeding season.

The land use data include the percentage of each type of landcover (forest, cropland, urban, grassland) within a grid square. Cha_landcover (forest, crop, grass, urban) is the 1970 land use percentage minus the 2010 land use percentage. Figure 1-6 illustrates how a selection of the land use change variables vary across the study system.
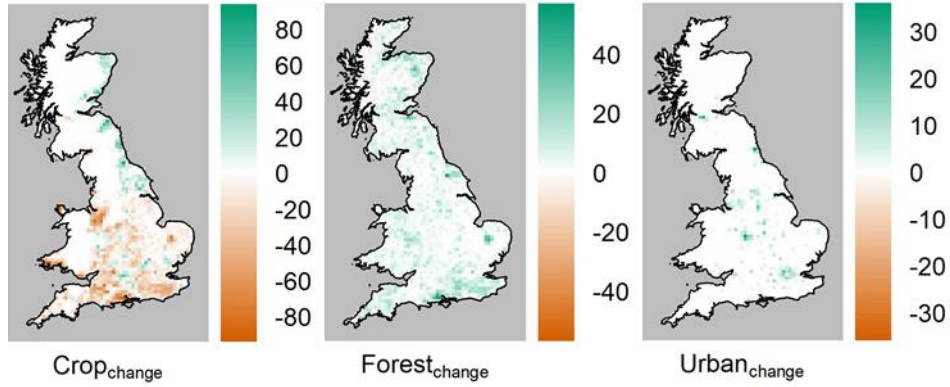
Fig. 1-6. Heat maps of the temporal change observed for various types of land cover and land use (LULC) between 1970 and 2010. The values represent the change within each hectad between the 1970 and 2010 periods.

1.5 Methods

Analyses of paired species and environmental datasets that are both spatial and temporally sampled is necessarily complex. Several complementary statistical approaches are used here and each are briefly described. The methods statements in the relevant chapters provide further description and justification of the approaches.

1.5.1 Temporal beta-diversity

The Sorensen index was used to calculate temporal beta-diversity. Baselga (2010, 2012) developed a strategy for splitting total dissimilarity into separate components according to whether the dissimilarity was the result of nestedness or turnover. The two Sorensen index partitions for a single pair of cells are displayed below (Equation 1-1).

$$\beta_{sor} = \beta_{sim} + \beta_{sne} \equiv \frac{b+c}{2a+b+c} = \frac{b}{b+a} + \left(\frac{c-b}{2a+b+c}\right)\left(\frac{a}{b+a}\right)$$

Equation 1-1

where, a is the number of shared species between two cells, b the number of species unique to the poorest site and c the number of species unique to the richest site.

β_{sor} is Sørensen dissimilarity,

β_{sim} is Simpson dissimilarity (= turnover component of Sørensen dissimilarity),

β_{sne} is the nestedness component of Sørensen dissimilarity (A Baselga et al., 2012).

1.5.2 Paired t-test

In pairwise tests of variables, a paired t test was used to compare the amount of change within two groups for the same subjects (Semenick, 1990; Kim, 2015). The null hypothesis is that the expectation is zero (Hsu & Lachenbruch, 2014).

1.5.3 Generalized linear models (GLMs)

The purpose of generalized linear models (GLMs) as used here is to evaluate relationships between environmental factors and species richness and beta-diversity. GLMs use link functions and different families (e.g., normal, Poisson) to handle non-normal data (Bolker et al., 2009). While the change in richness can be considered a count variable, the possibility that it could be negative (i.e., a decrease in richness through time) made the use of a Poisson GLM impossible, so the Gaussian GLM was determined to represent the best choice. To select the best regression model, all models were ranked using Akaike's Information Criterion (AIC; Akaike, 1973), a popular way to assess the suitability of a number of potentially non-nested models. However, due to the presence of mutli-model uncertainty, all models with a delta AIC value < 2 are also presented. The explained variance (pseudo R^2) was used as a relevant summary statistic for GLMs (Nakagawa et al, 2013).

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1.5.4   NMDS

Non-metric multidimensional scaling (NMDS) techniques were developed by Kruskal (1964) and Shepard (1972) to the number of dimensions used for plotting multidimensional data (Matthews, 1978). NMDS strategies make it possible to visualise relationships between dissimilarities in the composition matrix and Euclidean distances between species, and were used here to visualise variation in species composition between urban and rural sites.

1.5.5   PERMANOVA

Permutational multivariate analysis of variance (PERMANOVA) assesses the simultaneous response of one or more variables to one or more factors in an ANOVA experimental design through the use of permutation (Anderson, 2014). It was used in this study to test for significant differences in species composition between urban and rural squares.

1.5.6   RDA

Redundancy analysis (RDA) was used to examine variations between the sites in species composition as well as which variables drove this variation. RDA extends multiple regressions to multivariate response data (Rao, 1964; Legendre & Legendre, 2012). The examined data are separated into a response matrix containing the variables to be explained (here, species richness or turnover within each site) and an explanatory matrix (e.g., environmental variables within each site). RDA is discussed in detail in Legendre and Legendre (2012).

1.5.7   Indicator species analysis

Rather than sample the whole population, a useful approach for monitoring purposes of ecological management and conservation is the selection of a group of indicator species' presence or abundance. The suitability of a species

as an indicator depends on its ability to: i) represent the environment's biotic or abiotic condition; (ii) provide evidence of the effects of environmental change; or (iii) forecast the variety of other species, taxa, or communities in a given area (Carignan et al., 2002; De Caceres et al., 2010). Indicator species analysis was carried out by means of the "multipatt" function from the R package "indispecies" (De Caceres et al., 2016), which calculates species-groups association patterns of species significantly related with the urban or rural group.

1.6 Research gaps and novelty

Although many studies analyse empirical data concerning the influence of urbanization on ecosystem (Marzluff et al., 2001), macroecological analyses are lacking. Some previous studies have focused on the environmental factors driving variation in species richness and community composition in urban areas. However, these analyses are undertaken mostly in static time periods over one to two breeding seasons (Fidino et al., 2017), and typically in individual cities. Some studies have studied temporal change in multiple bird species, but in relation to seasonal change (Caula et al., 2008; Leveau et al., 2015; Tzortzakaki et al., 2018), or simply focused on single species (Paradis et al., 2000; Bonnet-Lebrun et al., 2020). Similarly, many previous urban-rural gradient studies focus on only a single gradient (from one city) (Tiwary et al., 2016; Echeverria-Caro et al., 2022). This study differs from these previous works in that it focuses on a standardised dataset encompassing multiple urban areas across the UK with full records of all detected bird species sampled in two time periods across 40 years.

1.7 Aims and scope

This study aims to provide an assessment of how bird assemblages in urban and rural areas in the UK differ, both spatially and temporally, in terms of a range of ecological and biogeographic patterns. The following study questions were

asked:

i) How have the species richness and community compositions of urban bird assemblages changed under the pressures of the urbanization process, as well as broader land use change and climate change, over a period 40 years? And how does this change compare to that witnessed in rural sites over the same time period?

ii) What are the roles of different abiotic factors in driving changes in the richness and composition of bird assemblages in the UK across space and time, for both urban and rural sites?

iii) Do urban areas have lower spatial beta-diversity than rural areas, and thus are more homogenous in terms of composition?

iv) What bird species represent the winners and losers as a result of urbanization in the UK? Linked to this, do any species represent potential indicators of urbanization impacts?

1.8 Summary of the chapters

Chapter 2 provides an outline of the bird distribution status in multiple UK cities. The species richness trends and changes between 1970 and 2010 for birds are examined to understand the urban-rural difference through time.

Chapter 3 studies species richness and beta diversity of birds over time, and assesses how changes differ between urban and rural areas. A simple examination of species richness trends and changes between 1970 and 2010 for birds is provided to understand the urban-rural difference through time. The species richness and beta-diversity indices are taken as response variables which are influenced by other factors, and explore the possible drivers of the change and the variation across urban and rural areas.

Chapter 4 examines the spatial variation in bird community composition across the UK, and tests whether patterns of spatial variation differ between

urban and rural sites. The results show that there is greater variation in community composition between rural than between urban sites, and the human influence index is shown to be and important driver of compositional differences.

Chapter 5 identifies the winner and loser bird species in regards to urbanisation in the UK, as well as identifying species that can be used as indicators of urban and rural land-uses. Finally, Chapter 6 provides a general discussion of the thesis' findings, drawing together the results and providing ideas for future research.

Chapter 2

General temporal trends in UK urban bird assemblages

2.1 Introduction

Ecosystems and biodiversity patterns are being completely transformed by humans (Blowes et al., 2019). Over the past few centuries, the rate of animal species extinction driven by anthropogenic pressures—such as habitat loss, overfishing, pollution, and climate change—has been extraordinarily rapid (Ceballos et al., 2015). Urban regions typically have a relatively high human population with a great number of human needs, such as living space and energy supply, making them one of the most anthropogenically transformed landscapes globally. As a result, habitats are severely fragmented and the local climate is disturbed, both of which have a detrimental effect on biodiversity. Studies have shown that many native species are either not present in cities or are less abundant in urban areas than they were in the original rural environments (Tratalos et al., 2007; Grimm et al., 2008), which leads to higher biotic homogeneity and additional loss of biodiversity (McKinney, 2006; Devictor et al., 2007). Of all land use types, it has been shown that many big cities have the highest local species extirpation rates (Chace & Walsh, 2006; Marzluff et al., 2001; McKinney, 2002).

Researchers in the UK have started to look closely at the variables influencing the distribution and abundance of birds in urban areas (Chamberlain et al. 2004; Tratalos et al. 2007, Fuller et al. 2008, Evans et al. 2009), as well as temporal trends in bird feeding in residential gardens in towns and cities (Plummer et al. 2019). Since the 1960s, the UK populations of several birds have decreased, to the point where many are now considered rare or endangered (Barnes et al., 2021). The status of British bird populations is continuing to worsen, according to the fifth review of Birds of Conservation Concern (BoCC5), which evaluated 245 species and updated their allocation to Red, Amber, and Green lists of conservation concern. The number of species

on the Red List has increased from 36 at the time of the initial 1996 evaluation to 70 (or 29% of those reviewed) (Stanbury et al., 2021).

Knowing how bird species and communities react to urbanization is essential if successful urban plans and biodiversity conservation strategies are to be designed and implemented (Croci et al., 2008; Jokimäki et al., 2018). Many studies discussing the impact of urbanization explain species change over time by focusing mainly on local scales and a specific city or a few local areas (Blair, 1996). Some studies focus on larger scales when comparing rural and urban avifauna (Arison, et al., 2014). For example, Tryjanowski et al. (2015) analysed winter bird richness in 26 urban areas across Poland and suggested that the main driver affecting bird communities is food resources. However, these analyses were undertaken only in static (i.e., single) time periods and there is a need for larger scale studies covering more representative cities and samples from multiple time periods in order to find the general patterns of bird diversity change under the pressure of urbanization (Tryjanowski et al., 2015).

The purpose of this chapter is to provide an outline of bird distribution patterns in multiple UK cities. Study sites were selected along an urban-rural gradient to enable comparisons to be conducted between urban and rural areas. Each site is combined with meta data associated with human influences, including land use composition, climate data, geographical position and human population. A simple examination of species richness trends and changes for birds between 1970 and 2010 is provided to understand the urban-rural difference over time. Species richness and beta-diversity indices are used as response variables and the possible drivers of changes in these variables, and the variation across urban and rural areas, is explored. The aim of this chapter is to provide a general overview of the bird assemblages of the thesis study sites, providing the necessary context to develop the subsequent three

empirical chapters.

2.2 Materials and methods

To avoid unnecessary repetition across chapters, all the detailed information regarding the data and calculation of the response variables are provided in the previous chapter (Introduction, Materials and Methods). As such, this section just provides a brief overview of the data and analytical strategy.

2.2.1 Study areas and data selection

This study covers the area of Britain including England, Scotland and Wales. The bird data used are from the British Trust for Ornithology (BTO) breeding bird survey, and two time periods were analysed: 1968-1972 (referred to as 1970) and 2007-2011 (2010). The BTO Bird Atlas data are records of breeding and wintering bird species detected in 3,880 grid squares (10 km grid cell size) and the dataset contains 1,410,938 records detailing detections of 465 bird species (Gillings et al., 2019). 100 urban squares were selected as well as 100 rural squares. Species richness of each square in each of the two time periods was used as a response variable, as was change in richness between the two time periods, and compositional change measured using Sorensen's (temporal) beta-diversity index. The climate data were collected from WordClim (version 2020-2022), containing monthly temperature, precipitation, solar radiation, vapour pressure and wind speed (Fick et al., 2017). For each grid square, land-use data were sourced from Historic Land Dynamics Assessment (HILDA) data sets (version 2.0), Human Influence data were taken from the Last of the Wild Project, Version 2, 2005 (LWP-2). The sampled squares were 10x10 km areas as shown in Fig 2-1 below, containing 1 km square land use pixels according to the HILDA data resolution. Each 10km square thus contains 100 1km pixels of land use type.

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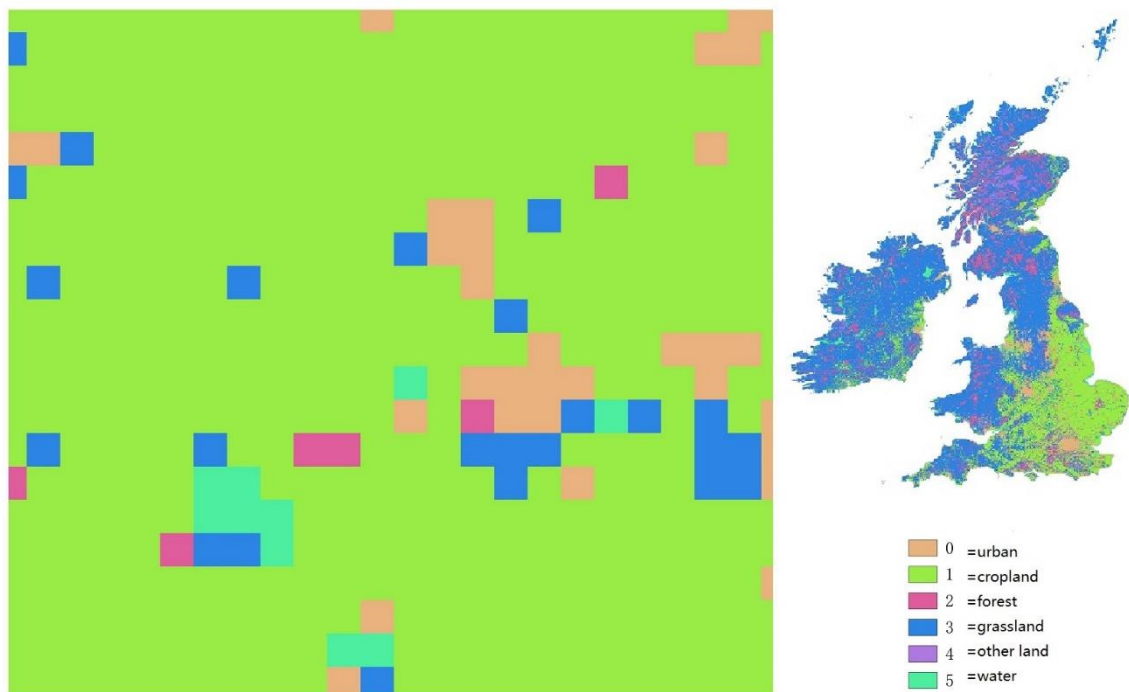
Fig 2-1 The left hand plot shows the land cover status of a randomly sampled grid square, while the right hand plots shows the general land cover status of the UK. The classification of land cover types in the legends are those defined by HILDA. In the left plot, each pixel represents 1 km square resolution, and therefore the percentage of a certain type of land cover is easily calculated as the number of selected pixels over 100.

2.2.2 Analysis

A paired t test was used to compare the mean richness, mean richness change and mean temporal beta-diversity (Sorensen index) between the two time periods (1970 and 2010), between urban and rural grid squares. In all cases, the null hypothesis was that there was no significant difference between urban and rural squares. OLS linear regression models were used to test for linear relationships between the human influence index and 2010 richness, richness change (between 1970 and 2010), and temporal beta-diversity, for urban and

rural squares separately. ANCOVA was used to test for significant differences in slope between urban and rural sites, for each relationship. Finally, to assess how patterns changed across the UK, the models and ANCOVA were re-run using latitude as a predictor.

2.3 Results

Over the 40 years from 1970 to 2010, British birds have experienced long term climate and environmental changes likely to affect species richness and diversity. By comparing the total species richness in 1970 and 2010, it is found that in 1970, the average richness of rural birds (i.e., birds in the rural grid squares) were 75 species, slightly larger than that of urban birds (i.e., species in the urban squares) at 74. However, the 2010 result is opposite; the urban squares have a larger average species richness (76), while the average species richness for rural birds remained at 75. However, the differences are clearly small and the mean value of species richness between urban areas and between rural areas was not significantly different between 1970 and 2010 (paired t-test $P > 0.05$; see Table 2-1).

2.3.1 Species richness

Table 2-1. Comparison of urban and rural communities between 1970 and 2010 with pairwise t-tests comparing richness change and beta-diversity between urban and rural squares

Class	Species richness		Richness	Beta-diversity	P-value
	1970	2010	change	(beta.sor)	(t-test)
Urban	74.08	76.01	1.93	0.2047	0.1585 (richness change)
Rural	75.20	75.01	-0.19	0.1852	0.0025(beta.sor)

Similar to the mean values of species richness, the distributions of richness values were similar in urban and rural squares, for both 1970 and 2010 (Figure 2-2). However, the amount of richness changes and compositional change differed between urban and rural squares. The boxplot in Figure 2-2 shows that the median value of temporal change of species richness (measured using Sorensen's beta-diversity) over 40 years was higher in urban areas than in rural areas. The results of paired 2 sample t-tests showed that there is significant deviation in beta-diversity between rural and urban areas (p-value (beta.sor) = 0.0025), but not in terms of richness change (Table 2-1).

In general, the number of bird species in urban areas was not significantly different from the number in rural areas in the same time period, but the situation changes when comparing the 2010 data with the 1970 data in regard to species composition. To understand how the rural and urban bird communities shifted over the 40-year period, it is necessary to establish the drivers of this change.
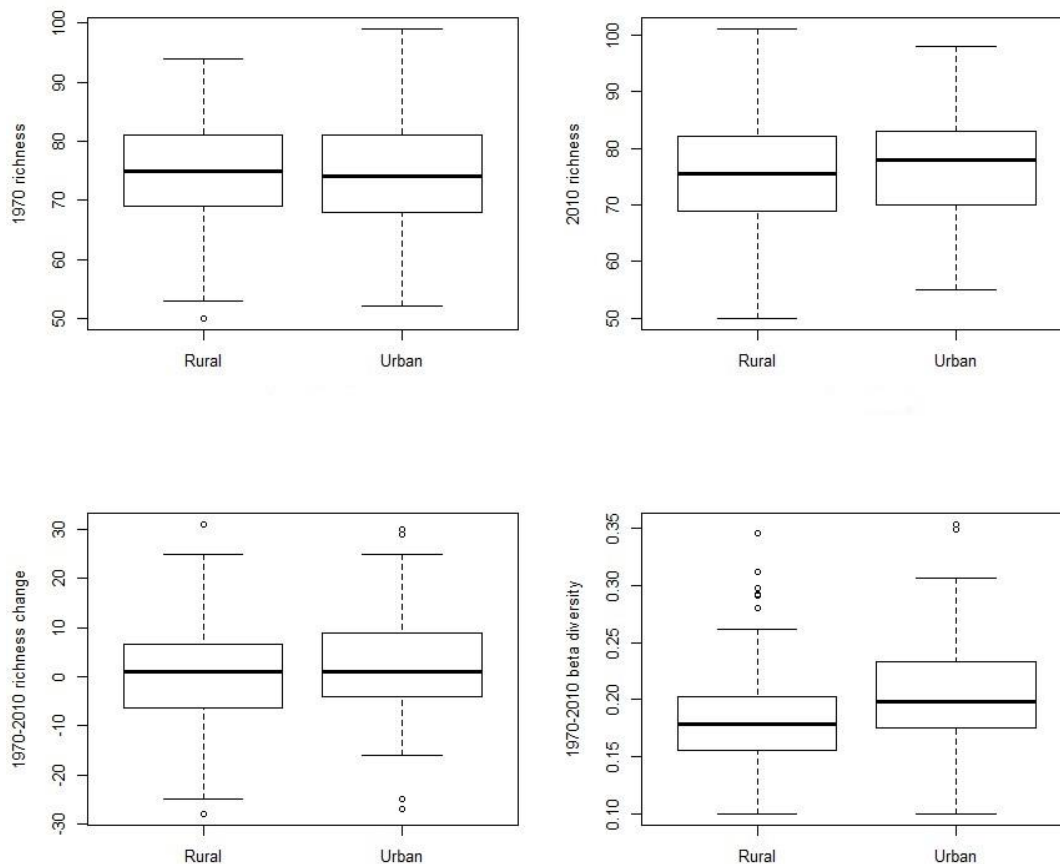
Figure. 2-2 Boxplots comparing distributions of species richness (in 1970 and 2010) (top row), richness change between the time periods (bottom left), and compositional change (bottom right), measured using the Sorensen beta-diversity index, between rural and urban squares.

2.2.1 Human influence

As outlined in the previous section, there are significant differences between rural and urban areas in terms of temporal beta-diversity. As the two groups of sites are selected according to the percentage of urban landcover, the impact of human activities in urban areas may be important in explaining the rural-urban difference. The Human Influence Index (HI) was used as a composite index of human activities covering human population pressure, human land use and infrastructure, and human access. In order to evaluate the impacts of

human activities on species change, the Human Influence Index was related to species richness and the temporal beta diversity index using linear regression (Fig 2-2 and Fig 2-3). The HI value for the rural areas ranged from 15 to 40, while in urban areas it was, as expected, higher, between 40 and 65.
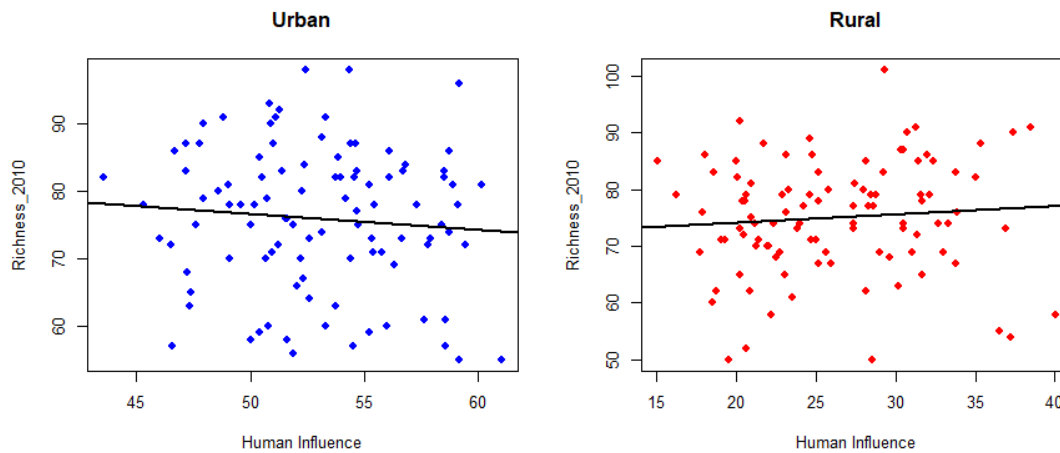
Figure 2-3. Relationship between the human influence index and species richness in 2010, for urban and rural grid squares. The black line is the fit of a linear regression model. Note, not all fits are significant (P-values presented in the text).

Fig. 2-3 shows the result of comparing species richness in 2010 with the human influence indices. There was a slight negative but non-significant (slope = -0.24, P = 0.38) slope in urban areas and a slight positive but non-significant trend in rural areas (slope = 0.15, P = 0.41), indicating that human influence generally reduced species richness in urban areas, but had the opposite effect in rural areas, but the effects were relatively small and non-significant.
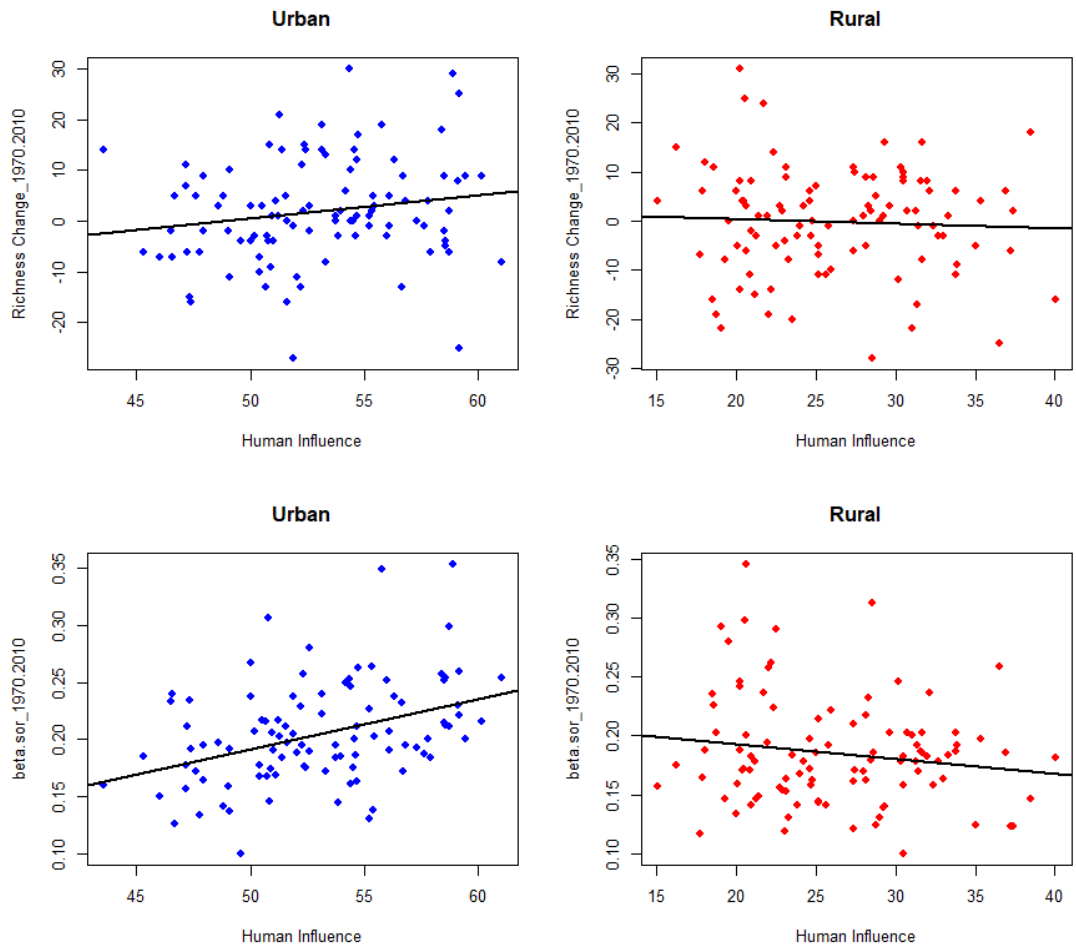
Figure 2-4. Relationships between human influence and richness change & beta diversity (between 1970 and 2010), for urban and rural squares. Black lines are least square regression fits. Note, not all fits are significant (P-values presented in the text).

Fig. 2-3 illustrates the effect of HI on changes in species richness and beta diversity between the two time periods. In the urban areas, both species richness change (slope = 0.46, P = 0.08) and temporal beta diversity (slope = 0.0044, P = <0.001) increased with increasing human influence, while the opposite trends were observed for rural areas (slopes = -0.096, P = 0.62 for richness change; slopes = -0.0012, P = 0.13 for temporal beta diversity), although the latter were non-significant. To examine the difference between rural and urban regression lines, for each response metric, an analysis of co-

variance (ANCOVA) was undertaken.

Table 2-2 Analysis of Covariance Table for richness change. HI = human influence index; Type = urban or rural. + additive predictor effects; * interactive effects.

Model	F	P
Model 1: Richness change ~ HI + Type		
Model 2: Richness change ~ HI * Type	2.85	0.09

Table 2-3 Analysis of Covariance Table for temporal beta-diversity. HI = human influence index; Type = urban or rural. + additive predictor effects; * interactive effects.

Model	F	P
Model 3: Beta.sor ~ HI + Type		
Model 4: Beta.sor ~ HI * Type	17.49	<0.001

Table 2-3 presents the ANCOVA (analysis of covariance) results for both richness change and temporal beta-diversity. For the pair of models 1 and 2 in Table 2-3, ANCOVA indicates there is no significant difference in the slope of the richness change–HI relationship between urban and rural sites. In contrast, there is a significant difference in the slopes between urban and rural sites for temporal beta-diversity (Models 3 and 4; Table 2-4).

2.3.2 Latitudinal variation

It is important to consider that results may vary across the UK for reasons other than HI. As such, the analyses were re-run using latitude as a predictor rather than HI. The results (Fig 2-5) indicate that there is a positive relationship between latitude and beta-diversity (beta-diversity increases in sites toward the north of the UK), but not for species richness change other.

The lower 2 plots in Fig 2-5 show the significant positive trend between beta-diversity and latitude, with a slope of 0.0073 for urban (P = 0.0177) and 0.1170 for rural (P < 0.001) sites.
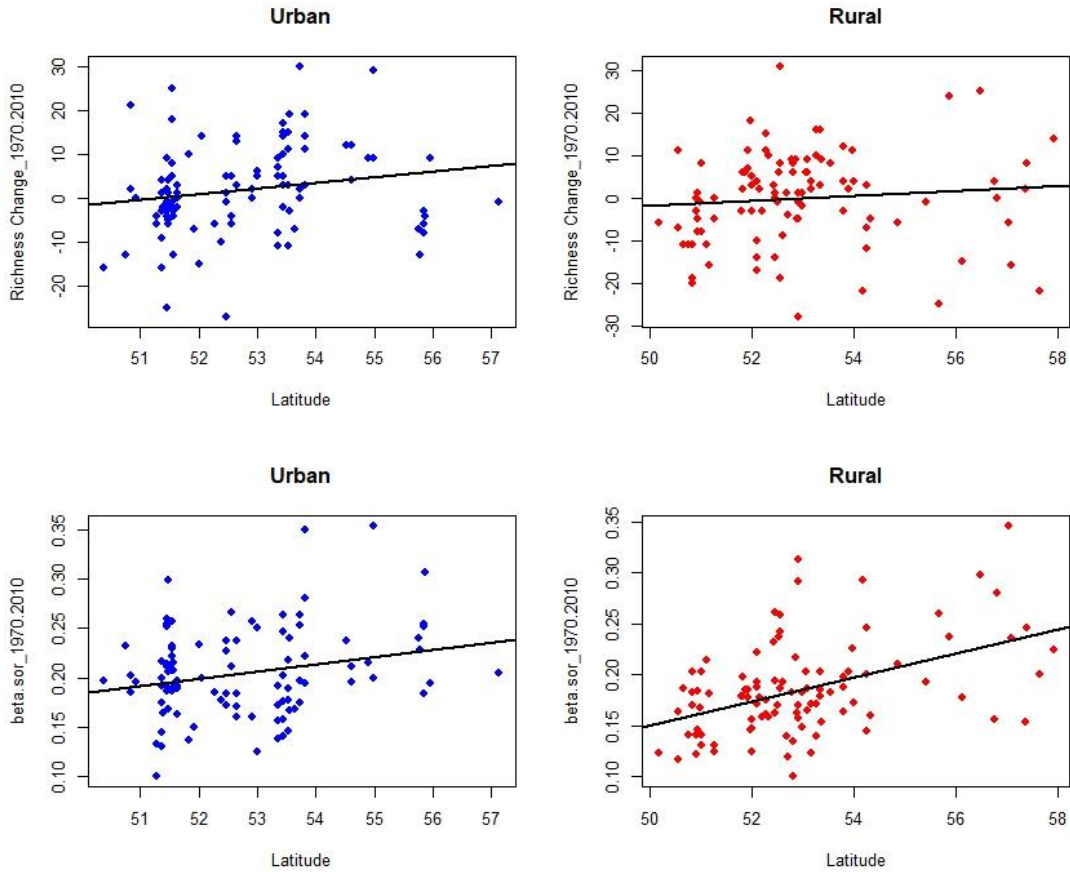
Fig 2-5. The relationship between latitude and species richness change (1970-2010) / beta-diversity. The least square regression fits are presented in the plots.

Table 2-4 Analysis of Covariance Table for richness change and latitude. Type = urban or rural. + additive predictor effects; * interactive effects.

Model	F	P
Model 5: Richness change ~ latitude+Type		
Model 6: Richness change ~ latitude*Type	0.603	0.4384

Table 2-5 Analysis of Covariance Table for temporal beta-diversity and latitude. Type = urban or rural. + additive predictor effects; * interactive effects.

Model	F	P
Model 7: Beta.sor ~ latitude + Type		
Model 8: Beta.sor ~ latitude * Type	1.40	0.23813

Tables 2-4 and 2-5 present the ANCOVA results for both richness change and temporal beta-diversity, with latitude as the continuous predictor. The results indicate that there is no significant difference in the slope of the richness change – latitude relationship between urban and rural sites. It is thus inferred that there is regional variation in the relationship between latitude and beta-diversity, but this is the same for urban and rural sites. In conclusion, avian temporal beta-diversity differs from south to north, and this regional variation is not affected by the urban-rural classification.

Besides HI and latitude, the effects of other environmental factors on species richness and beta-diversity were also examined, including land cover types, temperature and precipitation. However, no significant relationships were observed. More details are included in the appendix (Figure A2-1 to A2-4).

2.3 Discussion

Primary analysis was conducted in this chapter to explore patterns of change in species richness and temporal beta-diversity between 1970 and 2010, separately for urban and rural squares. The results show that the urban bird communities were not significantly different from the rural bird communities in terms of mean species richness. For the temporal analyses, although the total species richness did not fluctuate drastically, it was found that species composition change through time did differ, with greater change observed in urban communities. Additionally, there was an observed rise in temporal beta-

diversity as one moved from the south of the UK to the north. The observed regional variation was shown to be unaffected by other environmental parameters, including the urban:rural classifier. The land cover map shown in Figure 2-1(b) presents a general observation that the northern regions (higher latitudes) exhibit a larger prevalence of wooded areas, while the southern regions (lower latitudes) show a greater extent of arable and urbanised land. However, it is important to note that this research did not find a statistically significant association between latitude and land cover type.

In this analysis, it was interesting to find that the bird species richness and beta-diversity in urban areas was very close to that in rural areas in 1970, and the total number of species detected in urban sites even exceeded those in rural areas in 2010. In previous studies, rural habitat with less urbanization pressure has been found to contain more species and higher diversity than urban habitats (e.g., Chamberlain et al., 2018; Dadam et al., 2019). Several studies indicate that some features in urban habitats may have positive effects on some particular species, such as urban-dwelling birds (Chapter 5; Chace & Walsh 2006; Evans et al., 2009; MacGregor-Fors et al., 2009). For example, MacGregor-Fors' study (2011) provided evidence that the features and prosperity of vegetation cover in cities are positively related to urban bird generalist species richness and abundances (Lim & Sodhi 2004; Melles 2005; MacGregor-Fors 2008). However, this result does not support the hypothesis that the urban environment is more attractive than the rural environment for birds. Bird community structure is not simply a function of species richness but also species abundance and composition (Clergeau et al., 1998). In this study, the analysis was based on BTO Atlas data, which is a collection of binomial data representing species presence and absence for each sampling grid square. For further analysis, species abundance and density data are needed in order to better evaluate bird community differences between urban

and rural areas.

Considering the effects of human influence on bird communities, it was found that human influence played an important role in the urban-rural disparity, particularity in regard to composition change (i.e., temporal beta-diversity), where the HI–beta-diversity relationship significantly differed between urban and rural areas. The HI had a negative relationship with species richness and beta-diversity in rural areas. Many ornithological studies have demonstrated that the species richness and beta-diversity of bird species declines with increasing artificial disturbance (e.g., Batten 1972; Hohtola 1978; Bessinger & Osborne 1982; Bezzel 1985, Jokimäki 1992). However, for urban areas with higher levels of human disturbance, the effect of HI was positive for urban bird communities, which means that birds living in the urban environment tend to concentrate in more "urbanized" areas. The idea that certain species do well in highly disturbed environments (i.e., the winners of urbanisation) is examined more closely in Chapter 5 of this thesis. Previous studies have shown that urbanized areas provide extra heat and food supplies, which possibly attracts generalist species, and human-related food resources for birds can have massive ecological impacts on birds' abundance, distribution and behaviour, especially during winter (Tryjanowski et al, 2015). While such processes are also likely to occur in rural areas to some extent, it is likely that they occur at much higher rates in urban areas due to the greater density of humans.

Human influence (HI) may be assumed to have a strong linear association with biodiversity change metrics. However, the effect of HI on temporal beta-diversity differed between the urban and rural sites. This is likely partly because the categorization techniques used to identify "urban" regions here can result in the inclusion of other land covers, such as agricultural areas and artificial green spaces inside cities. In addition, as the HI is a compiled index

including multiple aspects of human activities (e.g., land use condition, infrastructure, population density and human access efficiency), further study is needed to identify the detailed mechanisms by which each type of artificial factor reshapes the habitat, with subsequent influence on bird species' richness and diversity. Further discussion about additional possible drivers of human influence will be conducted in the following chapters. For example, climate change and land use change will be discussed and their contribution to the observed richness change and temporal beta-diversity will be evaluated.

It should also be noted that the classification as urban or rural in this study is derived solely from the percentage of land use types within a grid square. The shape, distance, location and nestedness of different land cover types are not discussed in this study. However, these topological conditions are likely important drivers of changes in bird distributions and beta-diversity (e.g., Clergeau et al., 2001; Fischer et al., 2011; Redlich et al., 2018) in the sampling areas, where habitat is often highly fragmented and disturbed due to human activities. In more fragmented landscapes like highly urbanized areas, the rates of extinction and turnover are higher at local scales, while bird communities can sometimes be seen to be functioning as meta populations at a regional scale (Boulinier et al., 2001). Therefore, in interpreting the results presented in this chapter, it is important to bear in mind that they relate to regional scale patterns and should not be used to make inferences regarding very local scale population change. Overall, the results here have illustrated that there are some notable differences in changes in avian community structure across time in the UK as a function of urbanisation, but that such change is partly obscured when one focuses only on species richness differences. This finding sets up the subsequent three chapters, providing general context of the study system and an overview of the main differences between urban and rural bird communities in the UK.

Chapter 3

Temporal variation in the composition of UK bird

communities: a comparison of urban and rural

assemblages

3.1 Introduction

The process of urbanization involves many aspects of environmental change and has had profound effects on biodiversity (Aronson et al., 2014). Many bird species are sensitive to the environmental change caused by urbanization, which can have important environmental consequences given that birds play a vital role in both the structure and function of ecosystems (Tanalgo et al., 2015). Research has shown that bird species might respond differently to urbanization in different biogeographical areas (González-Oreja, 2011; Leveau et al., 2017; Ortega-Álvarez and MacGregor-Fors, 2009). Learning about the mechanisms of avian community response to urbanisation will help us better predict the degradation of ecosystems under the pressure of urbanization (Simmonds et al., 2019). Most studies of urbanisation impacts on biodiversity use a space-for-time substitution process, e.g., urban-rural gradient studies (Clergeau et al., 1998; Garaffa et al., 2009; Mao et al., 2019; Pithon et al., 2021). However, to truly understand the impacts of urbanisation, it is necessary to look at changes in community properties across time, and to see how such changes manifest in both urban and rural control areas. In addition, as was made clear in Chapter 2, it is important to look not only at changes in species richness, which most previous studies have done (e.g., McKinney, 2008; Choate et al., 2018), but also to changes in composition, which may be quite severe even in the face of minimal richness change.

Climate is one of the most important determinants of the distribution of many bird species (Root, 1988; Mehlman, 1997; Venier et al., 1999). Considerable evidence suggests that global warming is strongly affecting terrestrial ecosystems, including the earlier occurrence of such spring events as leafing, bird migration and egg-laying, and poleward altitudinal shifts of avian species. Moreover, a combination of climate change and other disturbances is likely to

exceed the resilience of many ecosystems and lead to biotic degradation (Şekercioğlu et al., 2012). The change in climate change has been proven to affect the geographical distribution of avian communities in Europe (Hughes, 2000; McCarty, 2001). European bird monitoring data show that bird species distributions have changed as predicted in the 21st century due to climate change (Huntley et al., 2008; Gregory et al., 2009), and the record of long-term bird monitoring projects in North America matches the European experience (Stephens et al., 2016).

Land use changes are important drivers of geographical distribution shifts and changes in richness in birds. Under the pressure of global urbanization, the natural land cover is being replaced as human activities modify land use. In recent decades, anthropological modified land use change has caused a widespread loss of habitat and decline in biodiversity and is recognized as a major driver of the current biodiversity crisis, receiving a great deal of attention from researchers (Myers et al., 2000; Brooks et al., 2002; Tasser et al. 2008; Zimmermann et al. 2010). As birds are known to be sensitive to vegetation structure, the change of vegetation composition is a deterministic factor affecting bird species' diversity (Cody, 1985). Native bird species, which usually rely on original natural habitat, mostly have reduced fitness in modified habitats marked by drastic change in the original habitat's structure (Gascon et al., 1999). In addition, current studies suggest that the effects of land use change on biodiversity might be seriously underestimated as biota need time to respond to environmental change and lags exist between the loss and degradation of habitat degradation and the extirpation of species (Dullinger et al., 2013; Rüdisser et al., 2015).

Apart from drivers such as climate and land use, additional anthropogenic variables in cities also influence urban bird communities, including population

density, traffics and roads, lighting conditions, etc. For example, a study based in Sheffield linked avian population dynamics with the size of the surrounding human population (Fuller et al. 2009), and Gagné's 2016 study found that human population size has a negative effect on species richness, with impervious surface cover and air pollution also drivers of species reduction. A study by Melles (2005) also found connections between urban bird diversity and neighbourhood socio-economic characteristics.

There is increasing appreciation that the focus on species richness does not explain the whole story of changes in biotic communities through time in response to different drivers. Indeed, there is a growing recognition that such a focus does not accurately reflect the functional features of biodiversity (Gagic et al., 2015; Bregman et al., 2016). To better understand how bird communities respond to environment changes from a functional perspective, the analysis of functional guilds and functional traits is required; this provides deeper insights into the relationship between environmental factors and avian community dynamics (Barnagaud et. al. 2017)

The aim of this chapter is to study the patterns of bird species richness change and temporal beta diversity under urbanization processes, across a forty-year time period (1970-2010). All the study sites are selected along an urban-rural gradient to enable comparisons to be carried out between different habitat types. Each site has sourced meta data associated with human influences, land use composition, climate data, geographical position and human population. Species richness change and beta-diversity indices are used as response variables, and a range of predictors are used explore the possible drivers of the change and the variation across urban and rural areas. As outlined above, most studies of urbanisation impact on birds use a spatial framework. While studies have discussed avian temporal change in cities,

these are mostly concerned with seasonal change (e.g., Leveau et al. 2015). This chapter takes a different approach, focusing on large-scale temporal change in avian assemblage richness and composition, and how such changes vary across an urbanisation gradient. Furthermore, an examination of certain avian functional groups and their relationships with the different environmental variables was undertaken to provide a complementary perspective to the taxonomic diversity-focused research.

3.2 Materials and methods

To avoid unnecessary repetition across chapters, all the detailed information regarding the data and calculation of the response variables are provided in Chapter 1. As such, this section just provides a brief overview of the data and analytical strategy.

3.2.1 Study areas and data selection

This study covers the area of Britain islands including England, Scotland and Wales. The bird data used are from the British Trust for Ornithology (BTO) breeding bird survey, and two time periods were analysed: 1968-1972 (referred to as 1970) and 2007-2011 (2010). The dataset used in this chapter includes landcover data from Historic Land Dynamics Assessment (HILDA) data sets (version 2.0), climate data from WorldClim (http://worldclim.org/version2), and Human Influence data from the Last of the Wild Project, Version 2, 2005 (LWP-2). Richness change and temporal beta-diversity were used as response variables.

In chapter 2, only overall temporal beta-diversity (Sorensen index; Beta.sor) was analysed. Here, I further partitioned Sorensen's index into turnover (Beta.sim) and nestedness (Beta.sne) components, and analysed patterns in these in addition to Sorensen's index. The approaches for calculating and

partitioning beta-diversity indices were proposed by Baselga (2010, 2012).

3.2.2 Data analysis

3.2.2.1 GLMs

Gaussian generalized linear models (GLMs) were used for evaluating the relationship between environmental factors and species richness change and temporal beta-diversity (Table 3-1). While richness change can be considered a count variable, as it could be negative (i.e., a site lost richness), it was not possible to use a Poisson GLM. All the models were first built using all predictors, including climatic factors, different types of land use change, including "forest", "grassland", "arable" and "urban", "tavg" (which stands for the slope of average temperature change), and "prec_cha" (the slope of precipitation change over the breeding season). A site's urban:rural classification was also included as a categorical predictor. In order to select the best model in each case, a full set of models considering all possible combinations of predictors were fitted using the MuMIn R package (Barton et al., 2015) and ranked using the Akaike Information Criteria (AIC). The model with the smallest AIC was selected as the best. However, given there may be multimodel uncertainty, all models with ΔAIC < 2 are also presented (Burnham & Anderson, 2002). A pseudo R^2 was calculated as a measure of the explained variance (R^2) as 1- (deviance of the best model/ deviance of the original hypothetical model) (Nakagawa et al, 2013). Variable importance values were calculated as the sum of AIC weights across all models in which a predictor was included. To deal with potential spatial autocorrelation, a spatial autocovariate was constructed using the co-ordinates of the grid squares (radius of 50km around each site) and the spdep R package (Bivand et al., 2015). This autocovariate was used as a normal predictor variable in the model selection. All continuous predictor variables were scaled (mean = 0, SD = 1) to enable

easier comparison of model coefficients. Variance inflation factors were used to check for multicollinearity between predictors (all VIFs were < 10).

Table 3-1. The response and predictor variables used in the GLMs

Response variables	predictors
Species richness change 1970-2010	Change in forest areas amount
	Change in arable area amount
Beta.sor	Change in grassland area amount
(total temporal beta-diversty)	Change in urban area amount
Beta.sne	Slope of temperature change
(temporal nestedness)	Slope of precipitation change
Beta.sim	Classification of sites (urban:rural)
(temporal turnover)	HI
	Latitude

3.2.2.2 RDA

Redundancy analysis (RDA) seeks to project the variation between urban and rural bird communities and how this variation is related to different environment explanatory variables (McArdle & Anderson, 2001). RDA was used to examine which variables were important for driving compositional differences between urban and rural sites. The CCA (Canonical Correspondence study) approach, as described by Ter Braak (1986), serves a similar function. In addition, the DCA (Detrended Correspondence Analysis) procedure, introduced by Hill and Gauch Jr (1980), can be used to enhance the study of many variables in the RDA. In the present investigation, using DCA it was observed that the lengths of the gradient of the species data were found to be less than 3 (Table A2 in the appendix). This indicates that the distributional shape of the data is more linear rather than unimodal (Borcard et al., 2011). Consequently, RDA is preferable to

CCA and was thus used here.

This analysis contains 8 selected different abiotic factors which have been found to be influential in previous chapters, including human influence (HI), average temperature in 2010 (tavg_10), change in average temperature across 1970-2019 (slope_tav), precipitation in 2010 (prec_10), change in precipitation (slope_prec), forest percentage in 2010 (forest_10), cropland percentage in 2010 (crop_10) and mean elevation (mean_elev). Human influence and urban_10 (urban percentage in 2010) were highly correlated (r = 0.89) and thus urban_10 was taken out of the analysis. An RDA model was fitted using all predictors and the rda function in the vegan R package. A backward selection process was employed to simplify the model, following the procedure outlined in Borcard et al (2011). The full RDA model was plotted using two triplots (both using scaling type 3), one plotting the sites (distinguishing between urban and rural sites) and one plotting functional groups.

3.2.3 Functional groups

To assess how composition patterns changed across different functional groups of birds, all species were classified based on their trophic niche (carnivore, herbivore and omnivore) and residency status (migrant vs. resident), using information in the AVONET database (Tobias et al., 2022). Both of these traits have been shown to be important in the ecology of birds and their response to disturbance (Tobias et al., 2022). For example, migrants have been shown to be particularly susceptible to human impacts, as they may experience change in both their breeding and wintering grounds. Across all the rural and urban sites, the frequency of these different categories of bird were then counted. As such, this is not a species-level analysis per se, but accounts for the frequency of species across sites (e.g., if a blackbird is present in 50 urban and rural sites, it is counted 50 times). The proportions of the different groups across the two

sampling periods (1970 and 2010), and across urban and rural sites separately, were then assessed. An RDA analysis was then undertaken, using the functional grouping composition within sites as the objects of focus rather than species composition.

3.3 Results

In order to study the drivers of temporal change in species richness and composition (temporal beta-diversity) of birds across 40 years from 1970 to 2010, changes in land use amounts and climatic change were used as predictor variables in a set of generalized linear models, with species richness change and beta-diversity indices as response variables. Due to its potential importance, 1970 species richness (initial richness) was also included in the models to account for species richness effects, as was a spatial autocovariate to deal with spatial autocorrelation. The final best models were selected based on AIC values, combined with the relative importance weight ranking list of each predictor variable. It should be noted that the "best model" only means the model with the lowest AIC value, and this is not necessarily the "true" model. For each analysis, for ease only the best model is presented in the text, while all models with ΔAIC < 2, as well as the variable importance values for all predictors, are presented in the Appendix (Tables A4-1 to A4-8). It is worth stressing that for all model analyses there was some degree of model uncertainty, i.e. multiple models with ΔAIC < 2. However, the best model always contained the variables with the largest variable importance scores, and thus discussion of the best model is roughly equivalent to discussing the variables with the highest importance scores.
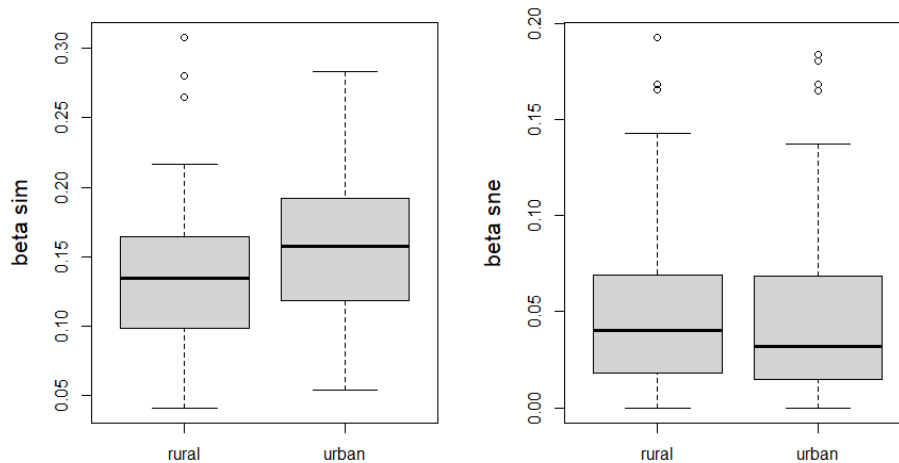
Figure 3-1. Boxplots of the turnover (sim) and nestedness (sne) components of overall temporal beta diversity, across urban and rural squares.

The plots in Figures 3-1 above and boxplot in Chapter 2 show the general patterns of species richness change and beta-diversity between urban and rural areas. As outlined in Chapter 2, species richness change in rural areas is not significantly different from that in rural areas. However, the results of beta-diversity indices show that the Sørensen dissimilarity (beta.sor) in urban areas was generally higher than in rural areas. Figure 3-1 indicates that this pattern of greater temporal beta-diversity in urban areas was driven by greater turnover rather than nestedness.

3.3.1 Species richness models

Table 3-2 GLM results using richness changes as the response variable. Model summary corresponds to the best model identified using AIC based model selection

Predictors	Importance	Estimate	P	Significance

	(descending)			35
Spatial auto covariate (A3)	1.00	1.8852	0.000313	***
X1970_pred (1970 richness)	1.00	-5.3276	3.44×10^{-14}	***
Slope_tmin (slope of minimum temperature)	1.811	1.53	0.01428	*
Latitude	0.59	1.3851	0.06774	.
Slope_precipitaion	0.44	-1.0876	0.1116	
Best: A3 + slope_tmin + X1970_pred + lat + Slope_precipitation	AIC = 1448.713		pseudoR^2 = 0.32	

(Significance codes: 0 '***'; 0.001 '**'; 0.01 '*'; 0.05 '.')

Table 3-2 shows the 5 predictor variables in the best model for richness change as the response variable: the spatial auto covariate, 1970 species richness, the slope of change of minimum temperature (during the 1970 breeding season), latitude and the change of precipitation.

According to the best model, species richness change is positively related to the change of minimum temperature, but has a negative relationship with the 1970 richness. Thus, the results imply that rising minimum temperatures are promoting bird species richness, and that sites with higher 1970 richness tend to experience less change.

None of the land-use change variables were selected in the best model, and the variable importance values for these were low. In addition, the urban:rural site classification variable was also not included in the best model. Overall, it appears that, for the change in species richness, the bird community's initial diversity matters most, which matches with the findings in Chapter 2.
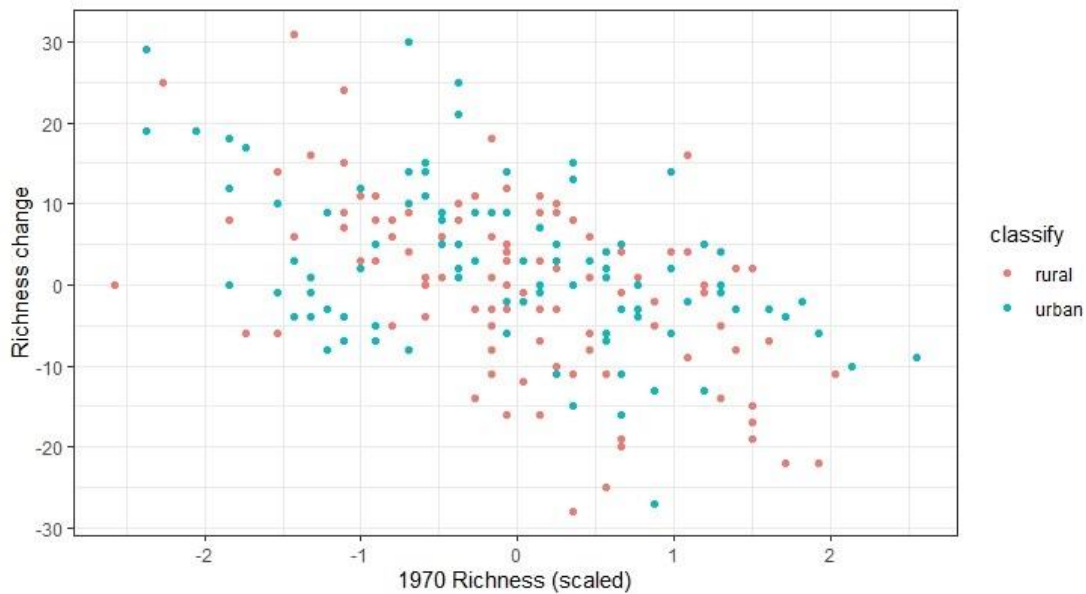
Figure 3-2 Relationship between initial site richness and richness change (from 1970 to 2010). Points are coloured based on a site's urban:rural classification. All predictor variables were scaled to ensure a mean value of 0 and standard deviation of 1.

Figure 3-2 displays the relationship between initial richness and richness change, with rural and urban sites presented in different colours. The plot illustrates well that there is a clear declining trend between richness change and 1970 richness, i.e., the richness change is higher in the sampling sites which initially have lower richness in 1970. Thus, it is clear that this is a strong pattern in UK bird communities at this scale, which may have substantial

implications regarding community resilience (i.e., higher diversity = higher community resilience).

3.3.2 Beta diversity models

In this subsection, the temporal beta-diversity indices were used as response variables: beta.sor, beta.sne and beta.sim (as presented in Table 3-1).

Table 3-3 GLM model summary using beta.sor (the Sørensen dissimilarity index) as the response variable. Results are presented for the best model found using AIC model selection.

Predictors	Importance (descending)	Estimate	P	Significance
X1970_pred (1970 richness)	1.00	-0.01325	$9.95 * 10^{-6}$	***
Latitude	1.00	0.01362	$6.08 * 10^{-6}$	***
HI	0.79	0.01069	0.000238	**
Best : HI + lat + X1970_pred			AIC = -714.8	pseudoR^2 = 0.26

(Significance codes: 0 '***' ; 0.001 '**' ; 0.01 '*' ; 0.05 '.')

Table 3-3 shows the predictors (1970 richness, latitude and HI) included in the accepted best model for the Sørensen dissimilarity index (beta.sor). The best model result indicates that 1970 richness is negatively associated with beta.sor, while the HI index has a positive relationship with beta.sor. The results also show that the spatial covariate was not in the best model. As such, the results indicate that initial site richness is still important in terms of temporal beta-diversity. Again, land use change variables did not feature in the best model, and all had low importance scores.

Table 3-4 GLM model summary using beta.sim (the Simpson dissimilarity index) as the response variable. Results are presented for the best model found using AIC model selection.

Predictors	Importance (descending)	Estimate	P	Significance
Latitude	0.99	0.3009	0.000237	***
X1970_pred (1970 richness)	0.65	-0.006835	0.04691	*
Change of average temperature	0.65	0.008077	0.05577	.
HI	0.54	0.009841	0.005191	**
Change of crop	0.51	-0.005553	0.1170	
Best : HI + lat + slope_tav + X1970_pred +cha_crop			AIC = -652.531	pseudoR^2 =0.15

(Significance codes: 0 '***' ; 0.001 '**' ; 0.01 '*' ; 0.05 '.')

Table 3-4 shows the predictors (1970 richness, latitude, HI, change of average temperature and change of crop land) in the best model for the temporal Simpson dissimilarity index. The best model indicates that the beta.sim decreases in those sites where the 1970 richness and change of crop cover percentage is higher. In addition, the HI shows a positive trend with beta.sim, which means that the more artificially disturbed areas sustain higher temporal turnover than the less disturbed areas. In contrast to the beta.sor model, here land-use change (specifically change in crop amount) was included in the best model, but the negative coefficient is counter-intuitive as it indicates greater land-use change equates to lower temporal compositional turnover. Figure 3-3 presents the relationship between 1970 richness and turnover (Simpson's dissimilarity index). There is still a negative relationship between the two, although the trend is less clear than for richness change.
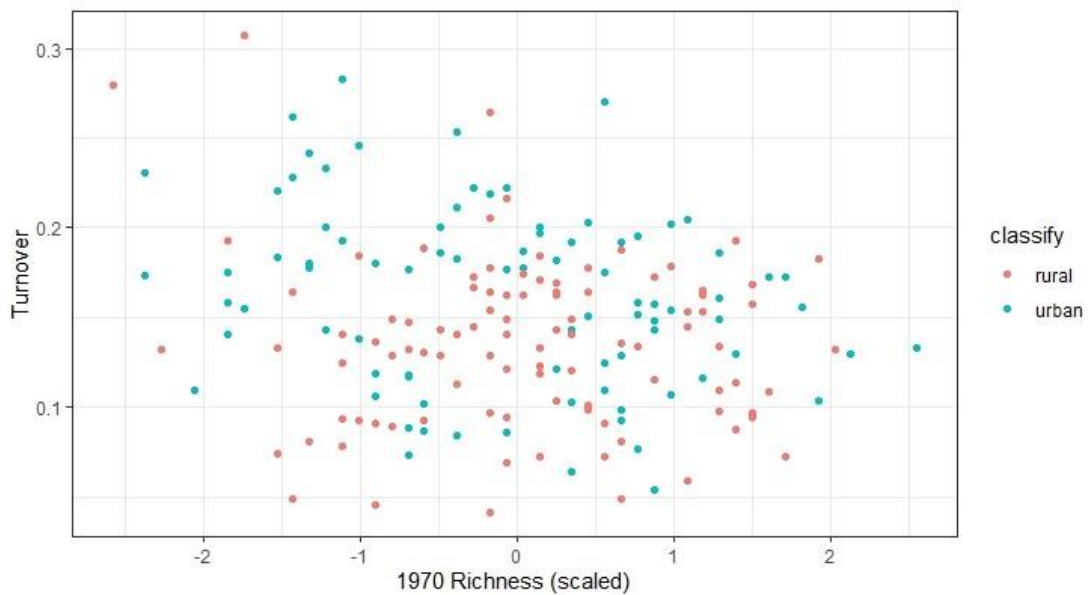
Figure 3-3 The relationship between initial site richness and temporal turnover, with points coloured based on their urban:rural classification.

Table 3-5 GLM model summary using beta.sne (the dissimilarity due to nestedness) as the response variable. Results are presented for the best model found using AIC model selection.

predictors	Importance (descending)	Estimate	P	Significance
X1970_pred (1970 richness)	0.82	-0.006534	0.0295	*
Spatial auto covariate (A5)	0.72	-2.2068	0.0475	*
Slope_tav (slope of average temperature)	0.57	-0.006766	0.0242	*
Best : A5 + slope_tav + X1970_pred		AIC = - 699.504	pseudoR^2 =0.078	

(Significance codes: 0 '***' ; 0.001 '**' ; 0.01 '*' ; 0.05 '.')

Table 3-5 shows the best model for beta.sne, with 1970 richness, the spatial covariate and change in temperature (slope of average temperature in breeding season) included as predictors. The best model shows that all the predictors are negatively related to beta.sne, which means that the beta.sne is lower in the sites with higher initial richness and higher average temperature. No land-use change variables featured in the best model. The R^2 of the best model was the lowest (0.078) across all best models.

3.3.3 Functional groups

Figure 3-4 presents the overall summary of the functional groupings of species in the dataset in the years 1970 and 2010, for all species together and then split by species found in urban and rural sites separately. The predominant trophic niche of the focal avifauna is carnivore (which includes both insectivores and vertivores), indicating a higher prevalence of carnivorous birds compared to herbivorous and omnivorous eating styles. The proportion of avian dietary niches exhibited little variation over a span of four decades, with a marginal decline seen in the omnivorous category (from 32% to 30%) and a corresponding rise in herbivorous consumption (from 24% to 26%). Meanwhile, the carnivorous component remained constant at 44%. Moreover, it is noteworthy that the frequency of migratory species exceeded that of resident species in both 1970 and 2010. Results were relatively consistent across urban and rural species, but note that there is an overlap in species here (i.e., many species found in urban areas are also found in rural areas) (Fig 3-4).
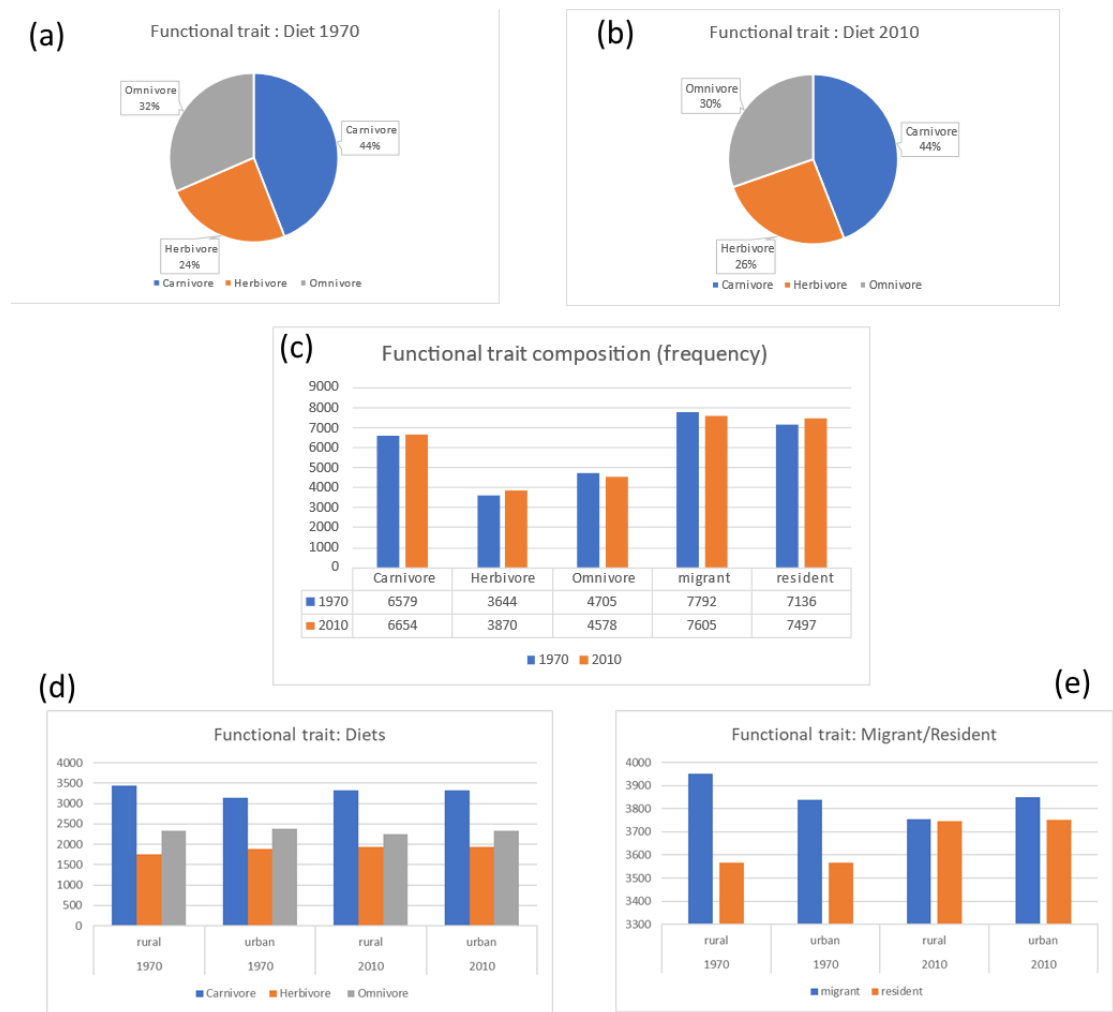
Fig 3-4 (a) The composition of species diets in percentages in 1970 and (b) shows that in 2010, and (c) compares the various functional groups between 1970 and 2010. (d) and (e) show the same as (c) but separately for the species found in urban sites and those found in rural sites. The y-axis in (c-e) is frequency. Note that in (e) the y-axis starts at 3300.

Next, an ordination analysis was undertaken to get a deeper knowledge of how the different functional groupings vary across urban and rural sites, and respond to environmental variables. Species were categorised as herbivores, carnivores, or omnivores, as well as based on their migratory behaviour, distinguishing between migrants and residents. The environmental predictors included in the analysis were the human influence index (HI), land cover variables, temperature, and precipitation. The results suggest that the

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functional groupings seen in urban areas were not substantially different from those in rural sites (refer to Figure 3-5). The application of the backwards selection procedure yielded a final set of three predictors, namely average temperature, cropland coverage, and precipitation change. Notably, the best model did not include variables such as temperature change and forest. The model was found to be significant (P = 0.001). Additionally, the model accounted for 8.08% of the variance (inertia), suggesting that it is a meaningful, but somewhat limited, predictor of the outcome.
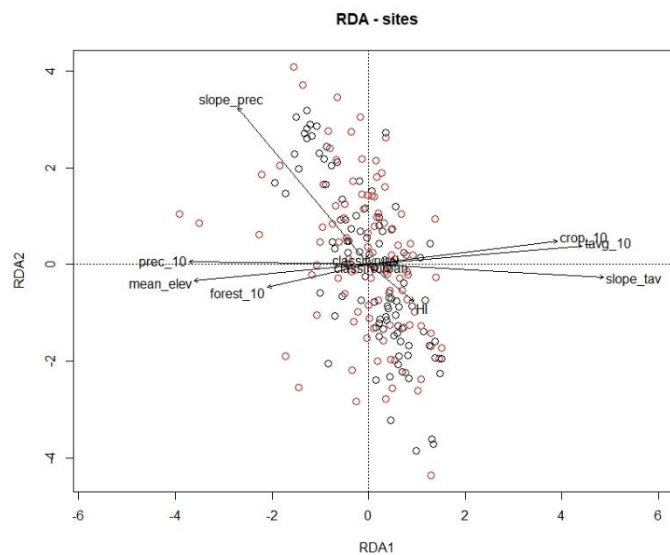
Figure 3-5 An RDA plot showing differences in composition (in terms of the functional groupings) between urban (black circles) and rural (red circle) sites, with the effects of variables shown as arrows. HI = human influence; slope_prec = change in precipitation; slope_tav = change in temperature; tavg_10 = average temperature; crop_10 = amount of grid square that is cropland; forest_10 = percentage of forest grid square.
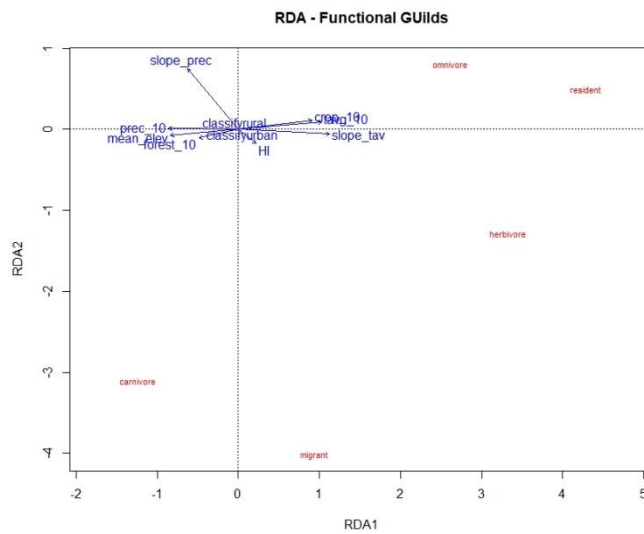
Figure 3-6 An RDA plot showing the functional groups (diet and migration/resident) with the effects of variables shown as arrows. All the arrows / variables were the same as in Figure 3-5.

Figure 3-6 provides an alternative plotting method of the RDA, focusing on functional groups. It can be inferred that the functional groups are associated with environmental variables to different degrees. The HI was positively related with migrant species but change of precipitation had a negative relationship with migratory birds. For herbivore, omnivore and resident birds, they were associated more with croplands and warmer and drier regions. The patterns for individual species will be evaluated in more detail in Chapters 4 and Chapter 5.

3.4 Discussion

In this chapter, several sets of generalized linear model were built to study the patterns of species richness change and temporal beta-diversity between 1970 and 2010. In general, the overall species richness increased slightly when the 2010 data are compared with that for 1970. According to the results of the GLMs,

the most important predictors are species richness in 1970 and, in some models, the spatial auto covariate, with the former defining the initial status of the bird community. For the remaining predictors, the change of temperature (slope of minimum/average temperature in breeding season), latitude and the index of human influence were typically more important than types of land use, etc. Interestingly, the urban–rural classification variable was less important than HI in the temporal beta-diversity model comparisons, indicating perhaps that the effect of urbanisation on temporal composition change is multifaceted and better captured by HI than a simple urban–rural dichotomy.

Generally, in this study, where temporal beta-diversity is analysed at the scale of 10 km squares (Bird Atlas grain size), initial species richness, and geographical distance and location (i.e., latitude) are the most important factors in the models, while climate ranks second, followed by land use. This result agrees with Keil et al. (2012), who found that climate and land use effects are grain-dependent; while climate is more important with coarse grains, land-cover effects performed better at finer grains. More generally, the results align, at least partly with previous studies that showed that the deterministic process driven by environmental change can result in the temporal variation in species assemblages (Baselga et al. 2015), although these processes seem to be modulated by initial site richness (Wayman et al., 2022). In particular, it seems that sites with higher initial richness underwent less richness change and are thus potentially more buffered and resilient to environmental change (Wayman et al., 2022). The concept of resilience can be characterised as the ability of a community to effectively absorb and subsequently recuperate from various forms of disruption, while simultaneously preserving the overall functionality and stability of both the community and the larger ecosystem (Ives and Carpenter, 2007; Côté and Darling, 2010). Based on the results presented here, it seems that a greater level of initial richness might result in an increased level of community

resilience (see also Wayman et al., 2022). This observation also provides evidence for the argument that the resilience of bird communities to climate change and land use change is influenced by both the intrinsic properties of the community itself (e.g., richness, range of traits) and the combined and interactive impacts of climate change and fragmentation (Jetz et al., 2007; Kampichler et al., 2012; Yalcin and Leroux, 2018).

3.4.1 Temperature

Discounting the spatial autocovariate, after the bird community's initial richness, and latitude in certain models, the change in temperature (during the breeding season) was often the next most important predictor. Temperature affects species migration efficiency (Holmes & Sherry 2001; Sanderson et al. 2006; Yamaura et al. 2009), and breeding quality and location, and thus overall fitness, may also be affected by increased temperature (Ockendon et al. 2012; Morrison et al. 2013). However, different measures of temperature and change behave diversely in the richness change models and beta-diversity models, according to my results. The "average temperature" was important for beta-diversity (particularly turnover) while "minimum temperature" was more important for richness change. This result may indicate that the "minimum temperature" may have positive effects on breeding birds' surviving rate, and thus increases richness, while changes in "average temperature" are the most important drivers of change in composition.

Previous studies have revealed that many bird species, particularly in Europe, are tracking climate warming (Devictor et al., 2008). During the breeding season, bird species need high enough incubation temperatures to guarantee their developmental period and decrease the incidence of embryo mortality (Nord et al, 2011). Therefore, the "minimum temperature" could be

regarded as a control trigger for the successful incubation of breeding birds. It should also be noted that the temperature effect usually positively correlates with latitude and elevation, with the former also being an important variable in many of the best models. This correlation may cause difficulty in segregating the effects of temperature and latitude (Lennon et al., 2000). For further understanding of how temperature drives UK bird species dynamics in the long term, more information is needed including larger sample sizes, and data on species abundances and the behaviour and climatic niches of individual species.

3.4.2 Land use

Land use intensification under urbanization pressure is considered to negatively affect biodiversity and ecosystem functioning at regional scales, as the natural land cover is replaced by artificial land use of altered structure (Davis & Glick, 1978, Krummel et al. 1987). Several studies have shown that the similarity of human-dominated land cover provides a strong filter for birds (Harrison et al., 1992, Dormann et al., 2007), promoting homogenization of avian assemblages across cities (Olden and Poff, 2003).

However, the results from the GLMs (both richness change and beta-diversity models) show that land use change variables were not that important, with the exception of change in cropland in the temporal turnover best model. They also imply that the HI is typically more important than change in individual land-use cover types (forest, crop, grass and urban). This result indicates that each type of land use contributes differently to bird species composition, and it is not the change in one land-use type that is important. Rather, it is the cumulative effect of land use change and other anthropogenic impacts, which are captured by metrics such as HI, which is

most important. It is worth noting that, in other studies, researchers often paid more attention to finer scale vegetation and habitat features (e.g., green spaces in cities; Azman et al., 2011; Tscharntke et al., 2008). Here, we focused on coarse scale grid squares that comprise multiple habitat types. A such, it is possible that the scale of analysis is too coarse to accurately determine land-use change effects. One additional possible explanation is that the relationship between urbanization percentage and temporal beta-diversity is not linear, but has a threshold (Andren, 1994; Fahrig, 2003; Watson et al., 2005; Matthews & Rigal, 2021), and is thus not well captured by linear regression models. For further study on this topic, the location and nestedness of land cover at finer scales should be analysed.

3.4.3 Functional traits

This study found that the beta-diversity of birds was impacted by different variables such as HI and changed species composition changed through time. However, the coarse functional groupings analysed exhibited little change. This finding is consistent with other research which suggests that changes in taxonomic diversity may not mirror changes in functional components (Monnet et al., 2014; Gagic et. al., 2015; Bregman et al., 2016). The observation of a negative link between changes in precipitation and migratory bird dynamics is intriguing. Numerous prior investigations have shown a tendency among migratory species to have a preference for climates characterised by higher levels of precipitation (Ramenofsky, 2012; Pearce−Higgins et al., 2015), and it may be that migratory species are particularly sensitive to changes in precipitation regimes. There are two caveats to the functional analyses presented here. First, a 40-year gap may obscure variations in the change of functional diversity. Second, this analysis is based on coarse scale functional groupings rather than fine-scale analysis of quantitative trait data, which were

lacking for many of the focal species when the thesis was submitted. However, the recent publication of avian trait databases (e.g., Tobias et al., 2022) means future research can more easily assess these questions. In particular, it would be advantageous to use functional diversity indices and further categorise functional features into more comprehensive groupings, hence facilitating a more detailed analysis.

3.4.4 Stochasticity

The results of the GLMs for species richness change and beta-diversity might be influenced by stochastic process, due to random colonisation–extinction dynamics (Baselga et al., 2015). This stochasticity, which may also be driven by differences in sampling processes between squares, will also result in the turnover of bird communities (Stegen et al., 2013).

The R^2 for all models was relatively low, indicating that important predictors were missing, and / or that stochastic processes dominate. Finer scale sampling (grid cells below 10 km squares), as well as larger number of samples, may provide better results. As would the inclusion of finer scale predictor variables (e.g., finer-scale habitat features). Finally, all the models were based on two individual years with a 40 years gap, which is restricted by the availability of bird atlas data in the UK. With more sampling points through time, more comparisons could be made to build more detailed temporal models, which would likely have greater explanatory power.

This chapter only presents a broad overview of the temporal changes seen in the avian assemblages studied. However, the following chapters will provide more comprehensive analyses and discussion pertaining to individual bird species.

Chapter 4

Spatial variation in UK bird composition: a comparison

between urban and rural areas

4.1 Introduction

Spatial beta diversity is driven by numerous intrinsic and extrinsic factors at different scales, both spatial and temporal, including land cover and climatic environmental conditions (Fleishman et al., 2003; Soininen et al., 2007; Socolar et al., 2017; Zellweger et al., 2017). Patterns of beta diversity provide insight into natural variation in species composition, in addition to how human activities are causing increased homogenisation or differentiation (Yen et al., 2017). Knowledge of spatial beta diversity is used to design and interpret the results of field sampling, estimate ecological reference conditions and measure responses of communities to environmental change (Nally et al., 2004).

Variation in species composition across space may reflect turnover and/or nestedness (Baselga, 2010; Soininen et al., 2018; Ulrich et al., 2017). Turnover refers to changes in the identities of species independent of changes in species richness. Nested assemblage refers to a situation in which species-poor communities are proper subsets of those in species-rich locations (Patterson & Atmar, 1986). Spatial nestedness is a common pattern among biotas worldwide (Wright et al., 1998), and indicates that spatial differences in composition may often be due to richness differences. It is important to distinguish between turnover and nestedness when interpreting spatial beta diversity patterns (Baselga, 2010).

The pattern of spatial variation in community composition has generated considerable interest in the field of community ecology, likely because combining geographic patterns of species turnover with data on abiotic factors can increase our understanding of how species respond to changing environmental conditions. Many empirical studies have linked geographic patterns of beta-diversity to environmental conditions (e.g., Gaston et al., 2007;

Soininen et al., 2007 Baselga, 2008; Dobrovolski et al., 2012; Wayman et al., 2021). Independent of environmental factors, communities separated in space are expected to differ in composition to some degree as a result of the distance decay in community similarity (Underwood & Chapman 1996; Wayman et al., 2021; Graco-Roza et al., 2022). This decay of compositional similarity with increasing geographic distance is driven by multiple factors, such as dispersal limitation and historical legacies (Soininen et al., 2007). Some studies have found that beta diversity is driven by environmental heterogeneity (habitat and climate dissimilarity) (e.g. Veech et al., 2007; Keller et al., 2009; Winter et al., 2010; Chocron et al., 2015), whereas others have concluded that geographic distance is the more important driver (Tuomisto et al., 2003; Qian et al., 2005).

Spatial variation in the composition of urban communities is less understood, but it is expected that it will be reduced by increased biotic homogenisation in urban areas (discussed in Chapter 3). The growing human population in cities (Cincotta et al., 2000) is leading to increased urbanization which is altering natural ecosystems in multiple ways. Such alterations often lead to changes in species composition, particularly the replacement of habitat specialists with habitat generalists and non-native species (Clergeau et al., 2006, McKinney, 2006, Kark et al., 2007), a process that consequently results in biotic homogenization. The process of homogenization occurs in many regions across the globe (e.g., Clergeau et al., 2006, McKinney, 2006) and is known to reduce the resilience of ecosystems to environmental change. Many studies have been conducted to evaluate urbanization's impact in potentially homogenizing ecological communities (e.g., Clergeau et al., 2006; McKinney, 2006; La Sorte et al., 2008; Sorace & Gustin, 2008; Magura et al., 2010), but few have compared multiple urban areas at the same spatial resolution as is done here.

In this chapter, I examine the spatial variation in bird community composition

across the UK, and test whether patterns of spatial variation differ between urban and rural sites. A selection of analytical tools to assess spatial community composition differences are employed, including PERMANOVA, spatial beta-diversity and redundancy analysis (RDA). Due to the previously reported increased biotic homogenisation in urban areas following human introductions and extirpations, it is reasonable to posit the hypothesis that there will be greater variation in community composition between rural sites than between urban sites, and the human influence index is predicted to be an important driver of spatial beta diversity in UK birds.

4.2 Materials and methods

4.2.1 Study areas and data selection

This study covers the area of Britain islands including England, Scotland and Wales. The data used are from the British Trust for Ornithology (BTO) breeding bird survey, and two time periods were analysed: 1968-1972 (referred to as 1970) and 2007-2011 (2010).

For each grid square, land-use and climate data were sourced from Historic Land Dynamics Assessment (HILDA) data sets (version 2.0) and WorldClim, and Human Influence data were taken from the Last of the Wild Project, Version 2, 2005 (LWP-2).

4.2.2 Data analysis

4.2.2.1   Non-metric multidimensional scaling (NMDS)

Non-metric multidimensional scaling (NMDS) is a method for visualizing the dissimilarity between sites in terms of species composition. In this study, NMDS was used with Bray-Curtis similarity to examine the spatial variation in composition and visualise differences in composition between urban and rural

bird communities. The metaMDS function in the vegan R package (Dixon, 2003; Oksanen et al., 2013) was used. This function tries to find a stable solution using several random starts, with standardized scaling of results.

4.2.2.2   PERMANOVA

PERMANOVA provides a way of statistically testing for differences in composition between urban and rural sites. The test is equivalent to an ANOVA but in the case of multivariate data (Anderson, 2001). In this study, the PERMANOVA framework was used to test for differences between urban and rural groups. One assumption is that within-group dispersion is similar between groups. This was tested using the betadisper and TukeyHSD.betadisper functions to check whether the within group dispersion varies across urban and rural groups. This method is based on the Studentized range statistic and Tukey's 'Honest Significant Difference' method (Abdi & Williams, 2010).

4.2.2.3   Beta-diversity distance dissimilarity

Pairwise spatial beta-diversity was calculated between all urban and rural sites separately. Total beta-diversity (Beta.sor) and the turnover component (Beta.sim) were calculated (see Chapter 1). These values were regressed against the geographic distance between sites using OLS linear regression. As the data points are not independent, the P-values of the OLS slopes cannot be interpreted. As such, Mantel's correlation tests were instead used in each case. The distance between sites was calculated from the geographic locations (latitude and longitude).

4.2.2.4   RDA

Redundancy analysis (RDA) was used to examine the dissimilarity of bird groups in urban and rural areas, and to investigate the relationship between this dissimilarity and other environmental explanatory factors. The DCA

(Detrended Correspondence Analysis) procedure, introduced by Hill and Gauch Jr (1980), was used to enhance the study of many variables in the RDA (more details was described in Chapter 3 RDA method), and it was observed that the lengths of the gradient of the species data were found to be less than 3 (Table A5 in the appendix). This indicates that the distributional shape of the data is more linear rather than unimodal (Borcard et al., 2011). Consequently, RDA is preferable to CCA and was thus used here.

This study analysed the effects of eight abiotic variables which have been previously shown to have significant influence on community composition, as discussed in Chapter 3. The RDA model was constructed by using all predictors and employing the rda function included in the vegan R package. Next, a reverse selection methodology was used to streamline the model, according to the protocol described in Borcard et al. (2011). Two triplots were used to plot the whole RDA model. Both triplots used scaling type 3 (see Borcard et al., 2011). One triplot was used to plot the sites, discriminating between urban and rural sites, while the other triplot was used to plot the species.

More detailed information about these data and the methods employed are specified in Chapter 1 and Chapter 3.

4.3 Results

In general, the results show that the composition of rural bird communities significantly differs from urban bird communities, but that urban communities are nested within rural communities in the ordination space (i.e. most species in urban sites are also found in rural sites, but rural sites contain species not found in urban areas). As a result, the spatial beta-diversity of rural bird communities is higher than that of urban bird communities.
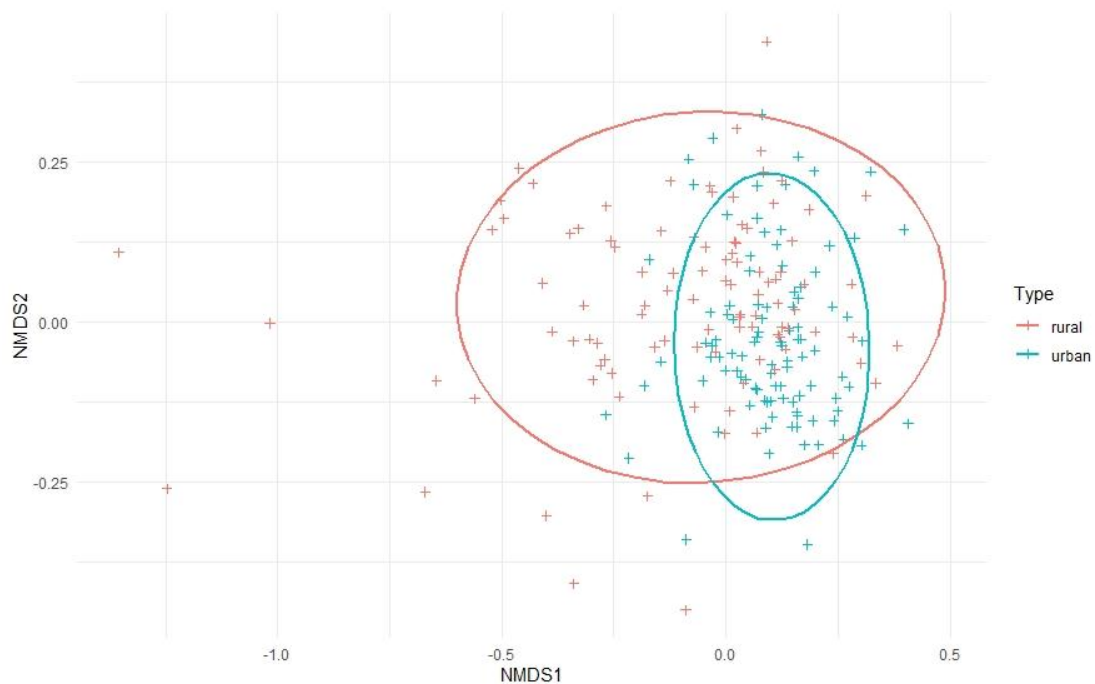
Figure 4-1 NMDS plot illustrating differences in composition between urban (blue +) and rural (red +) sites. The ellipses represent the 95% confidence intervals around the points in each group.

4.3.1 NMDS results

The NMDS plot (Figure 4-1) shows the different patterns of bird species composition for urban and rural bird communities. From the plot (Figure 4-1), it is inferred that rural bird communities have larger variation in composition than those in urban sites. The plot provides a visual display showing that rural sites have more diverse bird communities while urban bird communities tend to be more homogeneous. It also shows the nested relationship of urban bird communities within rural sites; the urban bird species can largely be regarded as a subset of rural species.

4.3.2 PERMANOVA results

PERMANOVA was used to statistically test for differences in composition

between rural and urban sites: a significant difference was observed (P=0.001; Table 4-1), meaning that the composition of species in urban areas are significantly different from those in rural areas. This result matches with the NMDS result. In addition, the within-group dispersion test was also significant (P=0.01), indicating that the spread of sites in terms of composition differed between the two groups (Table 4-2). This again matches the NMDS results, highlighting the wider spread of rural sites in the ordination space.

Table 4-1 Results of the PERMANOVA comparing the composition of urban and rural sites

	df	Sum of sgs	R2	F	Pr	significant
type	1	1.40	0.093	20.20	0.001	***
residual	198	13.76	0.91			
total	199	15.17	1.00			

Table 4-2 Results of the dispersion test comparing the composition of urban and rural sites

type	Df	Sum Sq	Mean Sq	F	N	Pr(>F)	significant
Groups	1	0.12	0.12	27.82	99	0.01	**
Residuals	198	0.86	0.0043				

4.3.3 Beta-diversity

Figure 4-2 shows the relationship between distance and turnover and total beta-diversity, for both rural and urban sites. In general, there are positive distance effects on beta-diversity in both urban and rural sites, indicating that the further apart sites are the higher the spatial beta-diversity. The rural sites exhibited a

stronger positive relationship between distance and turnover/total beta-diversity than urban sites. Table 4-3 provides the Mantel correlation results for urban and rural sites. These are in agreement with Figure 4-2, with the Mantel correlations of beta-diversity and turnover (against distance) for the urban communities (0.47 and 0.38) being lower than those for the rural communities (0.60 and 0.55), indicating that distance decay in compositional similarity is reduced for urban sites, and thus spatial beta-diversity of urban areas is lower than that of rural areas.
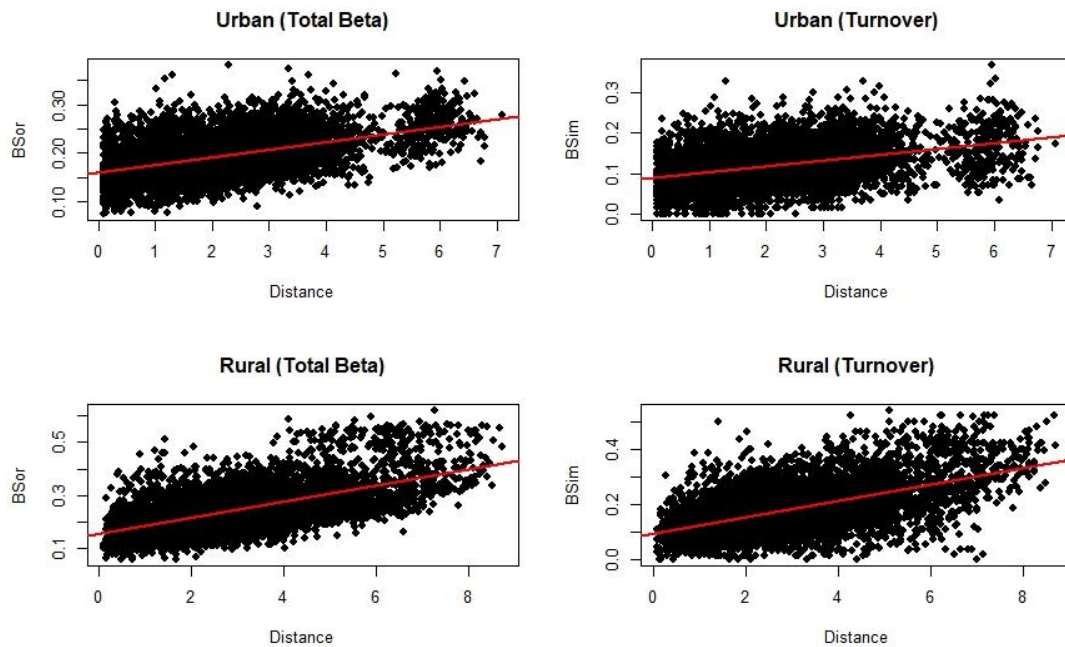
Figure 4-2. The relationship between overall spatial beta-diversity (Sorensen index) and the turnover component, and spatial distance (auto-distance/similarity matrix based on latitude and longitude), for urban and rural sites. The red lines are the fits of OLS linear regression models.

Table 4-3. Mantel correlation test results for the correlation between the two beta-diversity metrics and distance, for urban and rural sites separately

Mantel correlation	Urban	Rural
Beta.sim (turnover)	0.38	0.55
Beta.sor (total beta diversity)	0.47	0.60

4.3.4 RDA

The human influence index was the main variable separating sites along RDA axis 2, and resulted in almost a perfect split between urban and rural sites (Figure 4-3). The percentage of cropland and temperature change were important variables driving composition in rural sites. Average temperature, precipitation and mean elevation were important variables along RDA axis 1, with urban sites being warmer, lower elevation and experiencing less precipitation. The backwards selection process did not result in any predictors being dropped (i.e., all predictors were included in the best model). This model was significant ($P = 0.001$) and explained 25.84% of the variance (intertia).
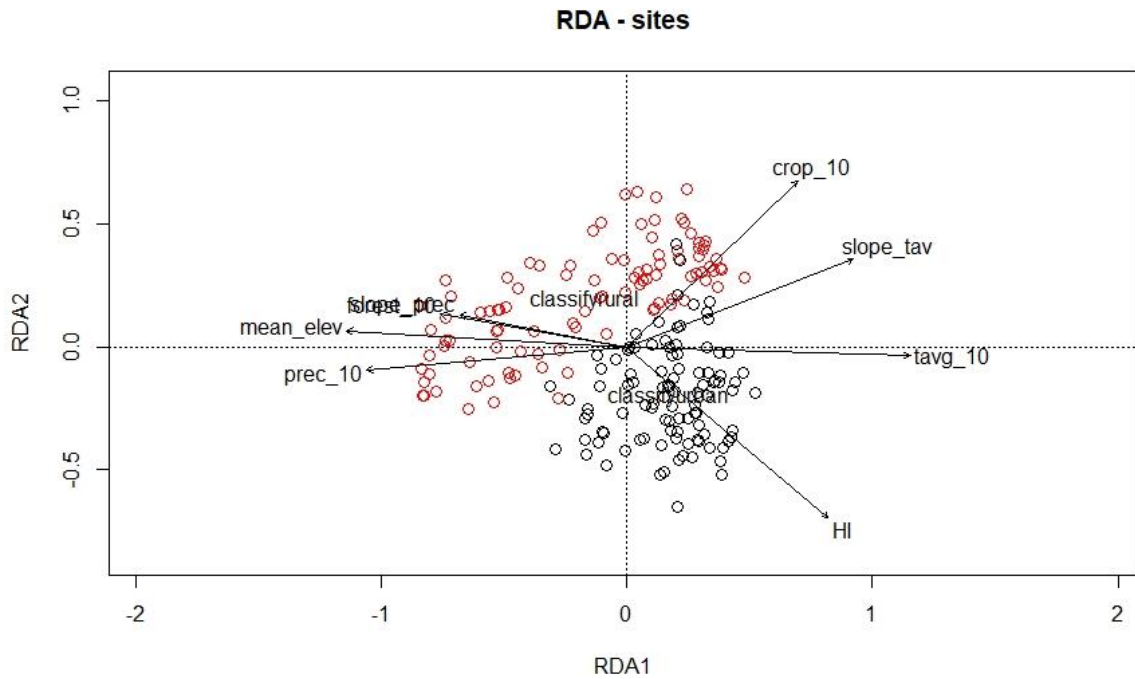
Figure 4-3 An RDA plot showing differences in composition between urban (black circles) and rural (red circle) sites, with the effects of variables shown as arrows. HI = human influence; slope_tav = change in temperature; crop_10 = amount of grid square that is cropland.
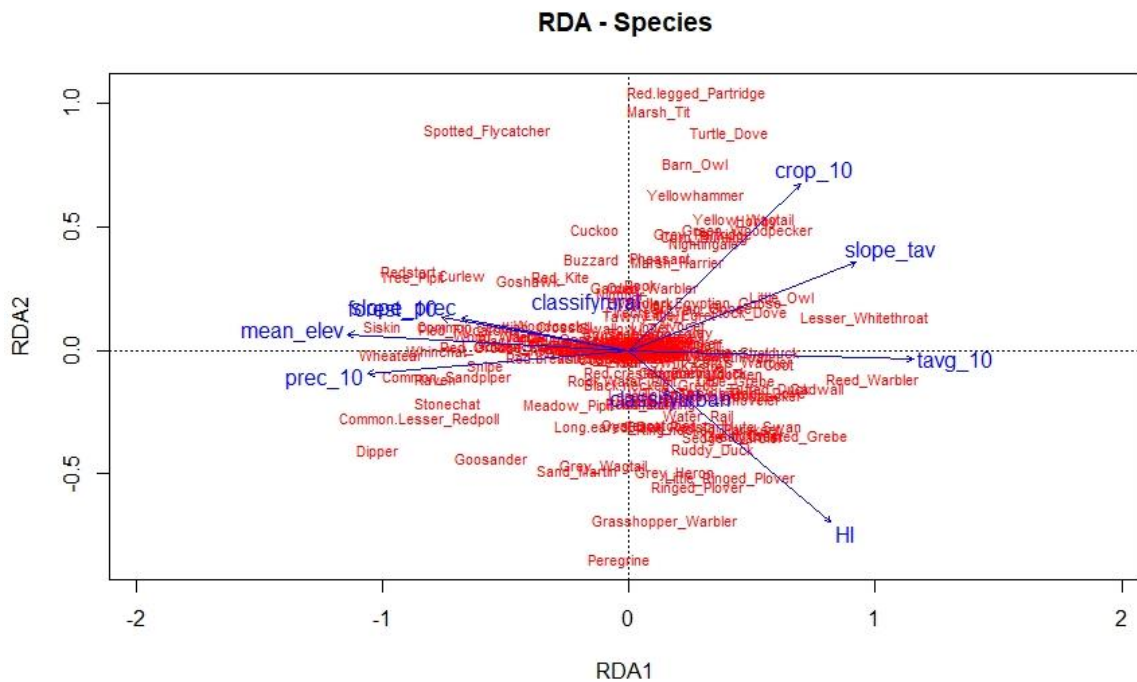
Figure 4-4 An RDA plot illustrating species rather than sites, with the effects of variables shown as arrows. HI = human influence; slope_tav = change in temperature; crop_10 = amount of grid square that is cropland; tavg_10 = temperature in 2010.

Figure 4-4 provides an alternative plotting method of the RDA, focused on species. It can be inferred that different bird species are associated to different degrees with the eight predictor variables. For example, grasshopper warbler *(Locustella certhiola)*, grey heron *(Adrea cinerea)*, ruddy duck *(Oxyura jamaicensis)* and peregrine falcon *(Falco peregrinus)* were examples of species associated with large amounts of HI (i.e., species characteristic of urban sites), whereas cuckoo *(Cuculus canorus)* and spotted flycatcher *(Muscicapa striata)* showed the opposite trend. Barn owl *(Tyto alba)*, turtle dove *(Streptopelia turtur)* and red legged partridge *(Alectoris rufa)* were more associated with greater cropland percentage, while siskin and redstart were more associated with forest percentage.

These individual species patterns are discussed in greater depth in Chapter 5.

4.4 Discussion

In this chapter, it was found that rural bird communities significantly differ from urban bird communities in terms of species composition. Specifically, urban sites have more similar composition than rural sites, which agrees with the hypothesis that urbanization is reducing spatial beta-diversity and increasing homogenization (White et al., 2018; García-Navas et al., 2020).

The NMDS result indicates that rural sites were characterised by a broader range of species composition than urban sites, and that urban sites were nested within rural sites (i.e. the composition of urban squares comprised a subset of the species found in rural squares). Thus, the bird community composition of urban areas can be considered as a subset of the rural bird community. The PERMANOVA test also confirms significant differences between rural and urban areas in terms of species composition. The wide range in composition of rural sites makes sense given that rural squares could contain a broad range of land use types (forest, grassland, cropland etc), whereas urban squares were likely to be more homogenous. Ecologically speaking, urbanization provides highly modified and fragmented habitats, which will cause sensitive bird species to avoid the urban areas and mean only those species that are able to survive the harsh conditions can persist (Kowarik, 2011; Lepczyk et al., 2017). The biotic homogenisation caused by urbanization usually occurs through the replacement of non-urban specialist species by urban adapted, typically generalist species (Shochat et al. 2006; Lososová et al. 2012; Sol et al. 2014). However, the results indicate that these species that occur in urban areas are almost all also found in rural squares. This could be due to the fact that the UK is a post-perturbation system, and even the rural squares are generally highly

disturbed from a wilderness point of view (Wayman et al., 2022). The similarity in richness between urban and rural sites (result from Chapter 2) does not contradict with the result presented here that biotic homogenization (relative to rural sites) is a characteristic of urban sites. This is because species richness and composition are different measures: sites can be similar in richness but differ strongly in composition. To take a simple example, two rural sites can contain three species each (ABC in site 1 and CDE in site 2) and two urban sites can contain three specie each also (ABC in site 1 and ABC in site 2): richness is the same for both rural and urban, but homogenisation is much larger in the urban sites. What the results are telling us is that urban and rural sites contain similar numbers of species, but that there is larger variation in the composition of rural sites compared to urban. This is likely because urban bird communities contain many generalists and fewer rare species (Buhk et al., 2017).

According to a fundamental biogeographic principle, there is a negative relationship between ecological communities' similarity and geographic distance (Fattorini, 2010; Qian et al., 2020; Graco-Roza et al., 2022). Thus, as expected, from the diversity-distance plots (Figure 4-2), there is a clear trend that the beta-diversity of both urban and rural sites is positively related to distance. In other words, the further sites are apart, the greater the degree of spatial beta diversity. The "distance-decay effect" is a result of complex ecological phenomena, including dispersal limitation and historical legacies (e.g. glaciation impacts) and the strength of the relationship is modulated by spatial extent, latitude location, organism traits and types of ecosystems (Soininen et al., 2007; Graco-Roza et al., 2022). For example, a study by Fluck (2020) found that geographical distance and climate have combined effects on the spatial distribution of the avifauna in Amazonia. Gaston (2007) also found that turnover is related not only to average environmental conditions but also to the spatial

variations in those conditions. This is an important point, as in reality it is difficult to separate pure distance effects from spatial variation in environmental conditions (Wayman et al., 2021). The sampling sites in this study were distributed over quite a broad spatial scale and, as these sites are not evenly distributed in the sampling grid, it is particularly difficult to partial out the effects of environmental variation and pure distance effects.

An important result in the present chapter is that the distance-turnover regression line for rural sites had a steeper slope than that of urban sites. The comparison of beta-diversity between urban and rural sites also shows that the rural bird communities had higher beta-diversity than the urban areas. This result provides additional evidence that urban bird communities are becoming taxonomically homogenized. The study of Luck & Smallbone (2011) found that similarity–distance relationships are substantially influenced by the processes involved in urbanization, which is in agreement with my finding that urbanization promotes similarity within bird communities.

The RDA results show the relationship between species composition and abiotic factors. As expected, there is a near perfect division of urban and rural sites in the RDA space. Across sites, human influence stands out as an important determinant of species composition, which makes sense and illustrates that human activities significantly restrict bird composition in urban areas. This aligns with the findings of previous studies that have shown various factors in urban areas, including building density and the presence of cats, act to reduce species diversity (Kauhala et al., 2015; Santiago-Alarcon et al., 2017). For rural sites, the percentage of arable land and change in average temperature were important variables. This illustrates perhaps that agricultural areas support relatively distinct bird communities; several UK bird species are associated with croplands, such as yellowhammer and corn

bunting. It also indicates that climate change may have large impacts on UK bird composition going forward (Eglington & Pearce-Higgins, 2012; Howard et al., 2020; Lehikoinen et al., 2021).

The RDA only provides the general picture of the interaction between selected factors and bird composition. To fully understand the relationship between these factors and the distributions of individual species, further study based on species-specific distribution and occupancy models is needed. Going forward, it will also be interesting to assess how specific characteristics of different urban areas (e.g. building density, population size, amount of green space) at finer scales act to drive variation in species composition.

Chapter 5

Identifying the avian winners and losers from urbanisation

in the UK

5.1 Introduction

Biotic homogenization is a concept frequently used to describe the current biodiversity crisis, but its use often raises more questions than answers. Homogenization generally refers to increased similarity over time, or across space, in terms of community composition (Rahel, 2000). According to McKinney and Lockwood (1999), biotic homogenization occurs when the modified environment drives some species extinct from an area ("losers") and the geographic expansion of others ("winners"). In particular, it is theorised to result from the replacement of specialist native species by generalists and widespread introduced species (McKinney et al., 1999). Thus, the predictable consequence of biotic homogenization is the generation of similar communities, often dominated by a few winners and high vulnerability (Tabarelli et al., 2012; Ibarra & Martin, 2015; Finderup et al., 2019), although species richness may not always decline to any substantial degree.

As a complex synthesis of human activities, urbanization has been proved to greatly modify the natural environment and be a major threat to biodiversity (McKinney, 2006; Fenoglio, 2020; Escobar-Ibáñez, 2020). Urbanization has many significant effects on biodiversity, including disruption of ecosystem processes, fragmentation of natural habitats, the creation of heat islands, and pollution (McKinney, 2002; Voogt, 2003; Fischer et al., 2012; Ferenc et al. 2013). Previous studies have shown that breeding bird abundance may be higher in urban than in rural areas, but species richness is often lower than in rural habitats (Cam et al., 2000; Palomino & Carrascal, 2003; Puga-Caballero et al., 2014). However, the results presented in Chapter 2 of this thesis illustrate that the richness of urban and rural bird assemblages in the UK, at least when viewed at regional spatial scales, can be relatively similar. It has also been shown that urban avian communities usually have higher similarity

to each other when compared to communities in less anthropogenically disturbed habitats (Clergeau et al. 2006, McKinney 2006).

One important aspect of the process of biotic homogenisation is differences in the abilities of species to resist anthropic disturbance and exploit urban spaces. According to this ability, species have been categorized into 2 main types: (1) "urban avoiders" (McKinney 2002) and/or "urban-sensitive" (Garden et al. 2007) species that are more sensitive to habitat change, and (2) "urban exploiters" (McKinney 2002) and/or "synanthropic" (Marzluff et al. 2001) species which are well adapted and able to exploit urbanized areas. Although environmental disturbances are regarded as factors having a negative impact on species, cities still provide favourable conditions and available resources and serve as refuges for some species. Furthermore, the urban ecosystem acts as a filter, filtering species with particular tolerance levels and specific traits (Croci et al., 2008; Liere et al., 2019; Sol et al., 2020).

Building on the results of previous chapters, which focused on community level patterns, this chapter focuses on individual species' different responses to urbanisation over a forty-year period. Most of the previous studies that discuss this issue were concerned with the response of one selected species to urbanisation, or focused on multiple species but only in a single city. This study is based on 2 groups of sites (urban and rural) across the UK and the analysis of multiple bird species, and seeks to describe the patterns of change for individual species at a regional scale. Put another way, the chapter aims to determine the winners and losers, in regard to birds in urban areas in the UK. Two main analyses were undertaken: an indicator analysis and an analysis of temporal change in the occupancy of urban squares. Preliminary analysis revealed that aquatic species were overrepresented in urban squares. Thus,

the indicator analysis was based purely on terrestrial species, while including aquatic species in the occupancy analysis to enable a comparison.

5.2 Materials and methods

5.2.1 Study areas and data selection

This study covers the area of Britain islands including England, Scotland and Wales. The data used are from the British Trust for Ornithology (BTO) breeding bird survey, and two time periods were analysed: 1968-1972 (referred to as 1970) and 2007-2011 (2010).

5.2.2 Methods

5.2.2.1 Terrestrial indicator species

Indicator species analysis was conducted by using the "multipatt" function from the R package "indicspecies" (De Caeres et al., 2016); this analysis used association patterns of species with urban or rural squares to identify species that are indicators of either. The association function used was "IndVal.g". An association threshold of 0.40 was used to classify species as indicators. The focus of this analysis was to identify terrestrial indicator species and thus to begin, all waterbird species were identified and removed.

5.2.2.2 Winners and Losers

To analyse which species were winning or losing during the 40 years, the number of urban squares occupied by each species was calculated (i.e. the occupancy of the 100 urban squares). As the number of squares occupied in 1970 varied considerably across species, percentage change was calculated and used to rank species and identify winners and losers. In addition, the

general occupancy trend for each species was calculated using all BTO squares to provide a nationwide baseline. More detailed information for these data and methods are provided in Chapter 1.

5.3 Results

5.3.1 Terrestrial indicator species

Table 5-1 presents the result of species classified as indicator species for each of the rural and urban categories among all the species covering the 200 selected sites, of which 100 are classified as rural and 100 as urban sites. The association values for all species were statistically significant. These two lists of species have no overlap species, indicating that the indicator species for urban areas differ completely from those for rural areas. Looking at the long-term population trends (using data provided by BTO Woodward et al., 2020) for the species selected as rural indicators reveals that all are declining nationally. However, the population trend for "urban indicators" is more complicated. The grasshopper warbler and lesser spotted woodpecker have declining trends while the ring-necked parakeet (*Psittacula krameri*) and Cetti's warbler (*Cettia cetti*) have experienced increased abundances.

Table 5-1. Results of the indicator species analysis, with the list of species classified as indicators of both rural and urban habitats. The association of Pearson's coefficient (higher values = more associated with that land use group) for each species is provided.

Group rural	association	Group urban	association
Spotted flycatcher	0.807	Grasshopper warbler	0.632
Siskin	0.648	Lesser spotted	0.532
Redstart	0.638	woodpecker	
Tree pipit	0.628	Ring necked	0.500
Wheatear	0.575	parakeet	
Whinchat	0.522	Cetti's warbler	0.470
Pied flycatcher	0.507	Black redstart	0.436

5.3.2 Identifying urban winners and losers

Table 5-2 and Figure 5-1 present the urban winner species, based on percentage change in the number of urban squares occupied. Together with the baseline trend, which is calculated from the overall data from more than 2000 squares around the UK, the general trend is that the winning species are increasing in the number of sites across the UK. However, the rate of increase is generally higher (sometimes much higher) in urban areas than across the country as a whole.

Table 5-2 The list of urban winners, ranked by percentage increase in the number of urban squares occupied in 1970 and 2010. Inf represents cases where zero squares were occupied in 1970. Values in the baseline column are the percentage increase in number of squares occupied by the species nationwide.

Species	1970	2010	Difference	Percentage	Baseline
Peregrine	0	67	67	Inf	240.95
Ruddy duck	0	31	31	Inf	1076.92
Cetti's warbler	0	29	29	Inf	12650.00
Greylag goose	4	62	58	1450.00	1050.00
Gadwall	4	57	53	1325.00	502.17
Buzzard	7	80	73	1042.86	115.13
Raven	4	35	31	775.00	78.83
Mandarin duck	6	38	32	533.33	1668.18
Hobby	7	42	35	500	382.44
Oystercatcher	11	59	48	436.36	32.92
Grey heron	16	71	55	343.75	46.39
Sparrowhawk	32	93	61	190.62	39.71
Shelduck	18	48	30	166.67	57.70
Canada goose	46	95	49	106.52	215.03
Grey wagtail	51	91	40	78.43	18.40
Nuthatch	57	86	29	50.88	34.43
Tufted duck	66	94	28	42.42	56.97
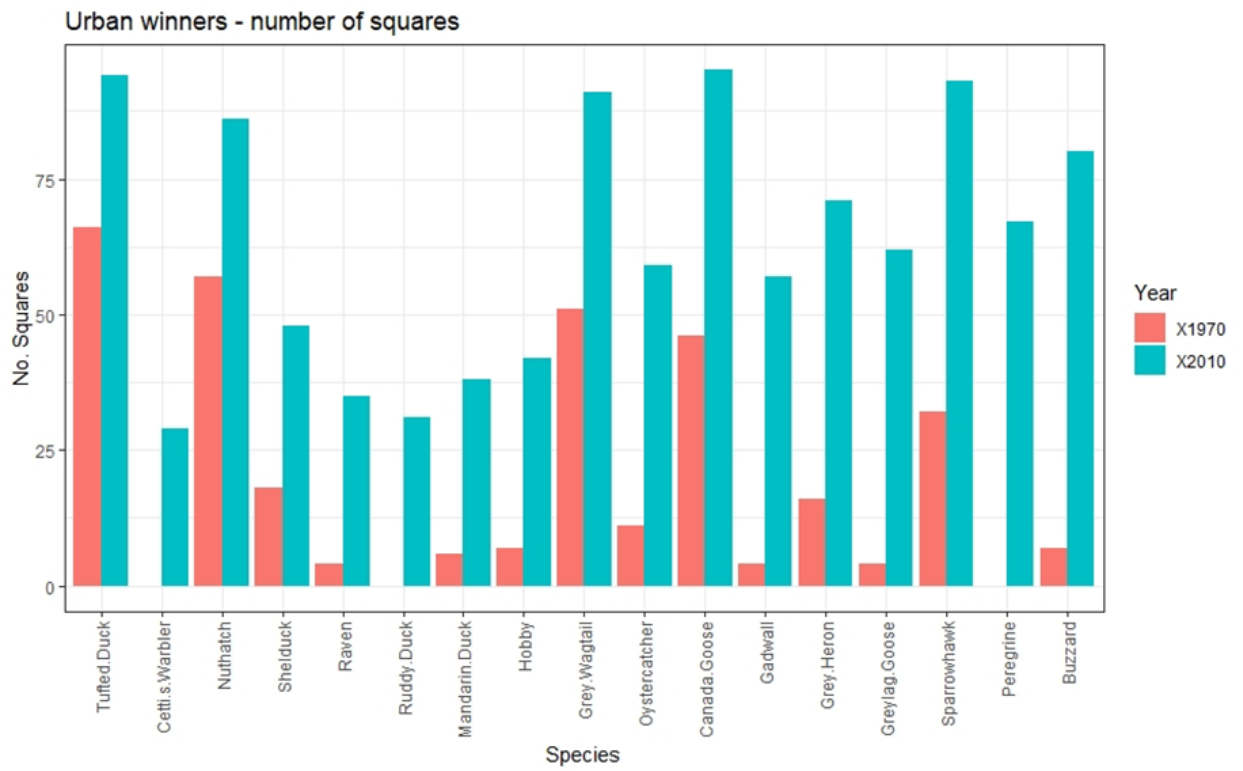
Figure 5-1. The number of squares occupied by urban winners in 1970 and 2010.

Table 5-3 and Figure 5-2 present the urban loser species. All the loser species were also decreasing according to the baseline trend data, but again the rate of decrease was generally higher in the urban squares.

Table 5-3 The list of urban losers, ranked by percentage decrease in the number of urban squares occupied in 1970 and 2010. Values in the baseline column are the percentage decrease in number of squares occupied by the species nationwide.

Species	1970	2010	Difference	Percentage	Baseline
Whinchat	44	3	-41	-93.18	-53.05
Wood warbler	41	4	-37	-90.24	-62.37
Turtle dove	63	7	-56	-88.89	-61.38
Tree pipit	67	9	-58	-86.57	-41.25
Redstart	42	6	-36	-85.71	-40.63
Corn bunting	67	13	-54	-80.60	-64.73
Snipe	56	12	-44	-78.57	-42.96
Common redpoll	80	19	-61	-76.25	-34.06
Yellow wagtail	82	27	-55	-67.07	-33.54
Woodcock	42	14	-28	-66.67	-55.98
Spotted flycatcher	97	36	-61	-62.89	-13.12
Willow tit	77	30	-47	-61.04	-63.67
Tree sparrow	93	39	-54	-58.06	-40.34
Marsh tit	54	23	-31	-57.41	-27.24
Grey partridge	90	39	-51	-56.67	-43.97
Cuckoo	94	41	-53	-56.38	-41.89
Yellow hammer	97	66	-31	-31.96	-26.66
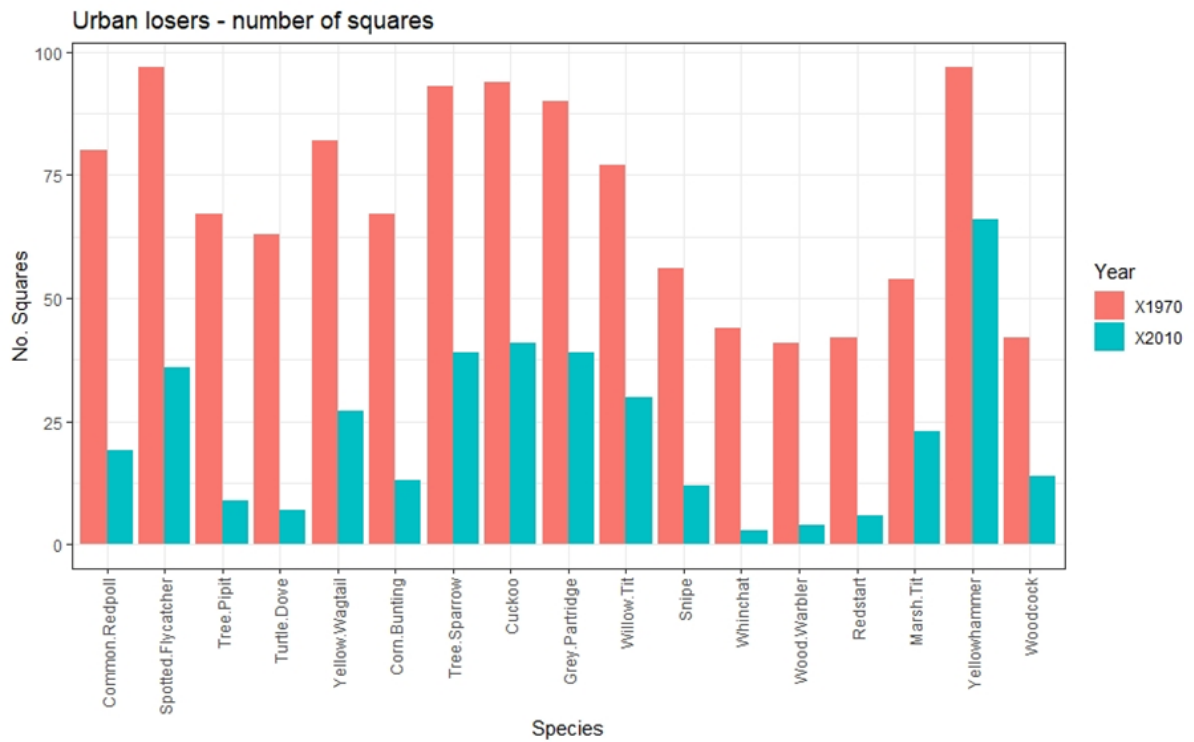
Figure 5-2. The number of squares occupied by urban losers in 1970 and 2010.

5.4 Discussion

5.4.1 The indicator species

Analysing the indicator species within 200 selected urban and rural sites allowed the most representative bird species associated with rural and urban land use classifications. Identified indicator species are expected to be closely associated with either the urban or rural land-use, but it should be noted that the latter incorporates a large range of habitat types (e.g., forest, grassland, cropland) and thus indicator species for rural sites should be interpreted with a degree of a caution. That being said, one notable observation was that the general population trends of rural indicator species were mostly declining (Fig

5-3). Figure 5-3 show the declining species population trends of 5 rural indicators: spotted flycatcher (*Muscicpa striata*), wheatear (*Oenanthe oenanthe*), whinchat (*Saxicola rubetra*) and tree pipit (*Anthus trivials*). (Woodward et al., 2020). Ideally, the rural indicators should represent the bird species which prefer rural areas with less disturbance by humans. The decline of rural indicators would then relate to the severe situation that sensitive rural species were threatened and in need of conservation. The rural indicators in this chapter could also be described as "urban avoiders" (Tryjanowski et al., 2020).
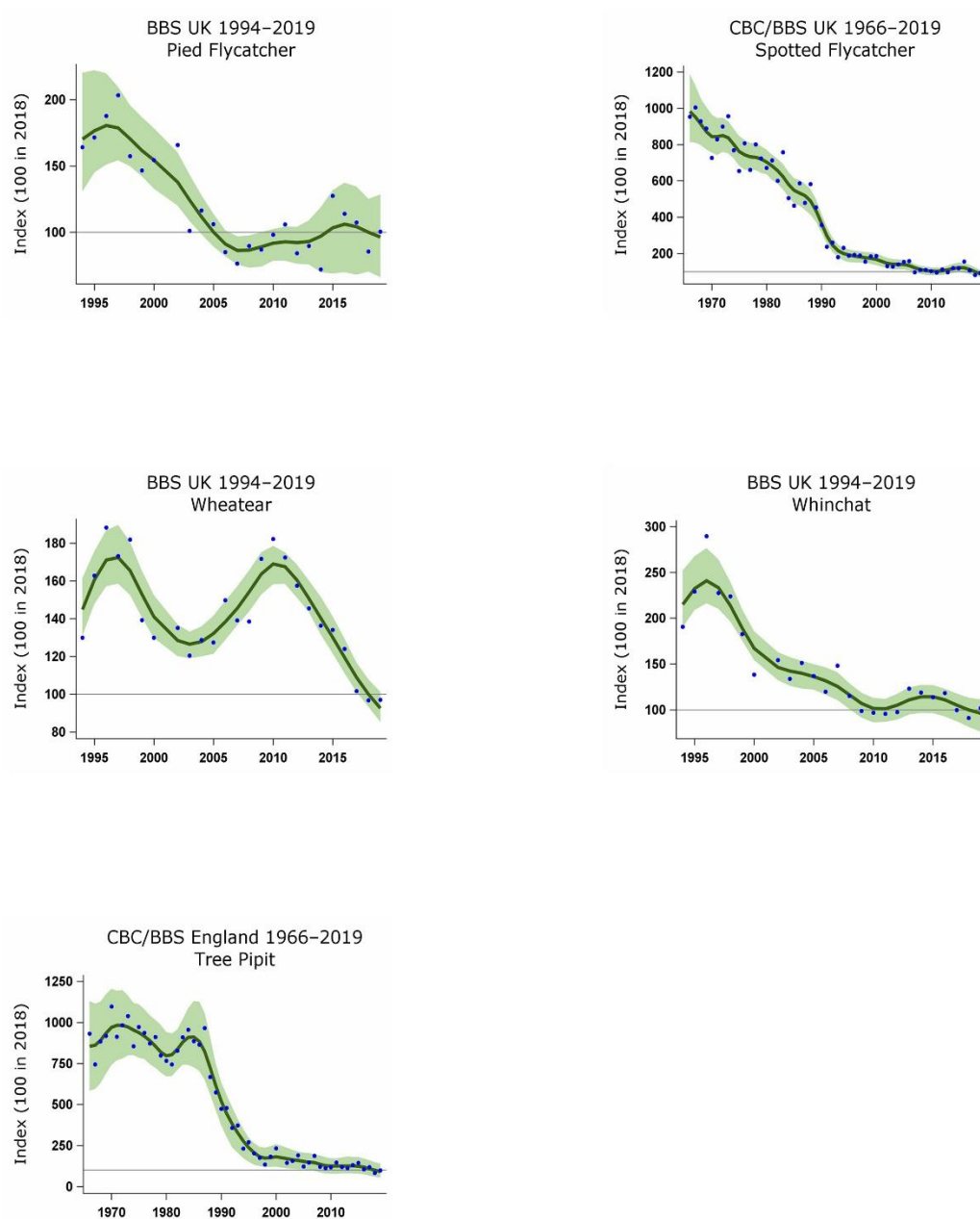
Figure 5-3. Temporal population trends for five UK bird species (Rural Indicators) (Figure sourced from BTO, Woodward et al., 2020). The y-axis (Index) represents estimate of annual total count for species population (Thomas, 1993). Species data are from CBC/BBS (CBC refers to Common Birds Census; Marchant, 1990). BBS refers to Breeding Bird Survey. The monitoring function of CBC was replaced by BBS after 2001.

Things were different for the urban indicators, which were more widely spread and with mostly positive population trends. That is in accord with the fact that human modified areas were expanding, enhancing the habitat and feeding opportunities for urban-adapted species. These "urban exploiters" share multiple dietary traits and occupy boarder species niches than "urban avoiders". (Palacio, 2020). However, the analyses showed that some of the "urban indicators" were also declining. For example, the grasshopper warbler (*Locustella certhiola*), which is a widely spread species across the British Isles. The BTO records (BBS UK 1994-2019) showed that the species' population was generally declining through time (Fig. 5-4 upper left), albeit with fluctuations, in the UK due to the decrease in the amount of suitable breeding habitat (Gilbert, 2012). A similar pattern was observed for another species identified as an urban indicator, the lesser spotted woodpecker, which was also experiencing reductions from 1982 to 2000 (Fig. 5-4 lower left). It should be noted that neither of these species (grasshopper warbler and lesser spotted woodpecker [*Dryobates minor*]) are typically viewed as urban species, and thus it is interesting that they were designated as urban indicators through the indicator analysis. It is unlikely that either species is a true urban specialist. Rather, it is likely that they were mainly present in habitats in the peripheries and edges of urban areas (e.g. woodlands and marshland), possibly in nature reserves that are often located around the edges of cities or in riparian habitats in the cities. This could point to an issue with undertaking analyses of urbanisation at regional scales, particularly in the UK where most urban areas are relatively small. This issue is further discussed in Chapter 6.
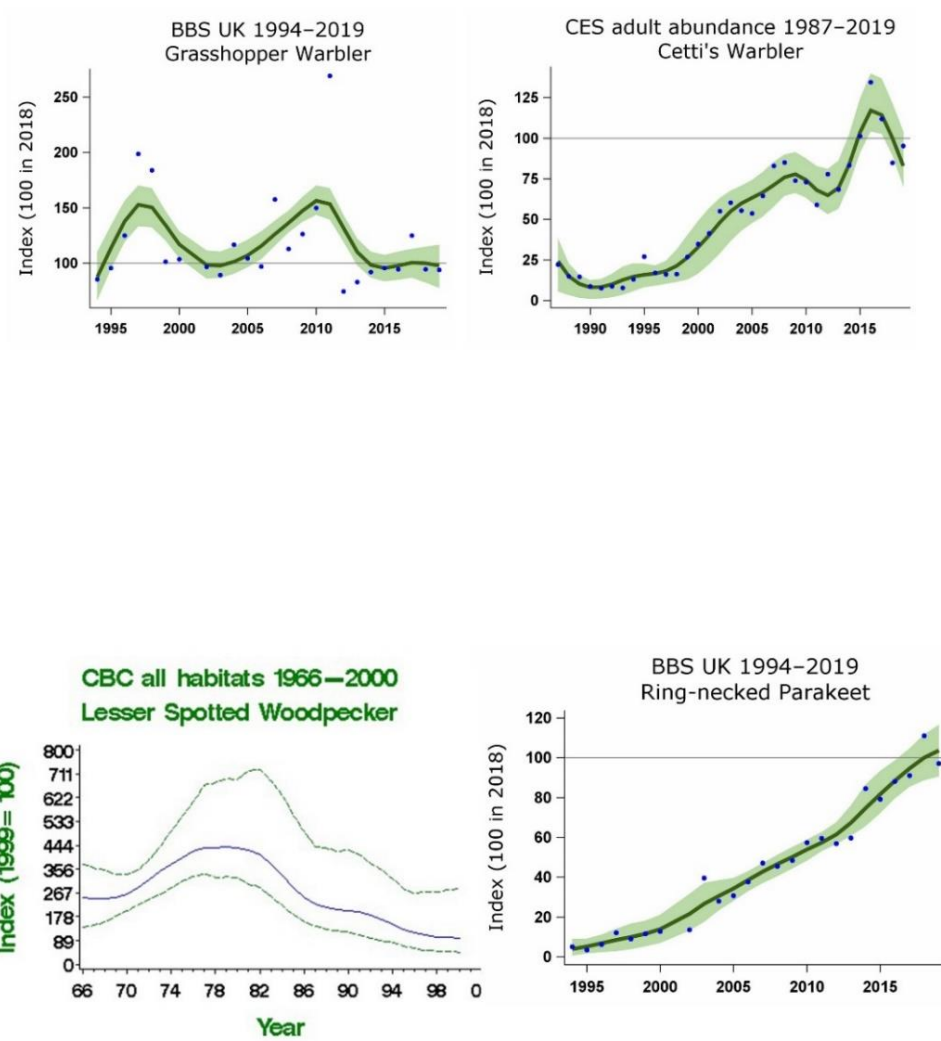
Figure 5-4 Temporal population trends for four UK bird species (Urban Indicators) (figure sourced from the BTO, Woodward et al., 2020). Data for grasshopper warbler and ring-necked parakeet were taken from the BBS, while Cetti's warbler were from CES (Constant Effort Sites scheme, Peach et al., 1996). For data summaries see legend of Figure 5-3.

Other species that were identified as urban indicators were Cetti's Warbler and ring-necked parakeet; both of whose populations have been constantly increasing over time in the UK (Fig. 5-4; Woodward et al., 2020). Cetti's warbler (*Cettia cetti*) is a recent colonist to the UK (first colonised Kent in the 1970s) and is associated with scrubby vegetation in proximity to aquatic habitats, often being found along waterways and damp areas close to wetlands (Robinson et al., 2007). As such, it is another species that, while being identified as an urban indicator, is not a true urban specialist. In contrast, ring-necked parakeet (*Psittacula krameri*) is more of a true urban bird, at least in the UK (Newson et al., 2011). The species is non-native, and is the UK's only naturalised parrot. It is now abundant in numerous towns and cities in the south east, particularly in suburban and urban parks, although it has also spread outside of cities and its distribution is believed to be shifting north (Menchetti et al., 2016; Heald et al., 2020). Therefore, a high associated relationship with urban areas does not necessarily mean successful adaptation to these kinds of environments. A good example of a human-commensal species, the house sparrow (*Passer domesticus*), which is also an urban exploiter, has been found to have been declining all over Europe over the past decades, although the reasons for its decline are not well understood (Mohring et al., 2021).

Overall, there were fewer species classified as urban indicators than rural indicators (Table 5-1). A limited number of species have successfully adapted to and established colonies in urban areas and other environments that have been affected by human activity. As most of the rural indicators were declining, it is reasonable to surmise that urbanization is negatively affecting the great majority of bird species in the UK during last 40 years. Increasing urbanization often results in simplified habitats with reduced possibilities for nesting, less diverse and less available food and increased predation (Evans

et al. 2011). They are then frequently dominated by abundant generalist species (Marzluff et al. 2008). Although some species are "urban exploiters", this does not guarantee their success in the cities (Tryjanowski et al., 2022). This phenomenon cannot be explained by one simple theory, but is related to all aspects of urbanization and further analysis of specific species is needed.

5.4.2 Winners and losers

By comparing temporal change dynamics for individual bird species, it was possible to classify species as either winners and losers (Tables 5-2 and 5-3). In general, the urban winner species were also increasing all over the UK (i.e. not just in urban area), while the loser species were decreasing nationwide. Thus, the species doing well in urban areas are typically the species doing well everywhere. This could be due to the fact that the UK is a post-perturbation system, with very few large areas of natural habitat remaining (Wayman et al., 2022). Thus, if a species is adapted to human disturbance, it is able to do well in large parts of the country and not just the major cities.

Among the winners is Cetti's warbler (*Cettia cetti*), which was also listed as one of the urban indicators, while no absolute rural indicator was observed to be a winner (Wotton et al., 1998; Robinson et al., 2007; Hiley et al., 2013). Many of the other winners were associated with aquatic habitats, and these species were not significantly affected by changes in land use type (Woodward et al., 2020). While aquatic habitats may not be the first thing that comes to mind when we think of urban areas, many cities include a range of aquatic habitats, including ponds in city parks, large water supply reservoirs city margins (e.g. around the western edge of Greater London), storage reservoirs for canals, former mill ponds, and canals and rivers. It appears that these habitats are being exploited by a number of bird species that can be

considered winners, and thus may represent important habitats for conservation and the persistence of urban biodiversity moving forward (Wilby & Perry, 2006; Recuero et al, 2010; Palta et al., 2017).

As for the losing species, 5 rural indicators were included in the "loser" species list and they all exhibited a significant loss in the number of sites. These 5 species (whinchat, redstart, wood warbler, tree pipit and spotted flycatcher; see Fig. 5-3) have all declined massively and consistently since the start of the BTO's records (Woodward et al., 2020). The main reason for their loss was the reduction of preferred habitat (Gregory & Baillie, 1998; Benton et al., 2003; Hewson & Noble, 2009), particularly the reduction of deciduous woodlands. For example, one study by Smart et al. (2007) suggested that the loss of oak trees could be a determinant factor for wood warbler decreases. Another study found that agricultural activities on grassland habitats generally threaten whinchat nesting, cause mortality of incubating females and indirectly increasing the danger of exposure to predators (Gruebler et al. 2008). Consequently, anthropogenic activities could be considered as the main negative factor causing declines in these "losers". The replacement of many losing species by a relatively small fraction of widespread winners will likely produce a much more spatially homogenized biosphere (Mckinney et al. 1999).

The "rural indicator" species showed strong preferences for forest and grassland habitats which are particularly disturbed through the process of urbanization but have also been impacted by intensification of farming systems. Analysis of the land use change data indicates that, although the percentage of urban land cover did not change too much during the last 40 years, the composition of rural areas was very different, with more grassland and arable land and less woodland (Kuemmerle et al., 2016). The loss of

woodland likely significantly impacted the performance of these sensitive species, leading many of them to become extirpated and replaced by other species.

5.4.3 Nationwide trends

Following the results that the general pattern for both winners and losers was positively related with the baseline trend, it can be concluded that the increase of winners in urban areas mirrors their national increase, while the loss of losers similarly mirror national declines. There was no strong evidence for any species presenting an opposite trend to the nationwide tendency, but there were differences in the magnitude of increases and decreases. Some of the species increasing nationally were observed to increase at a much higher rate in urban areas, for example gadwall *(Mareca strepera)* and buzzard *(Buteo buteo)* although this parallels the trajectories in the UK as a whole.

It was necessary to note that some of the observed patterns may have been affected by sampling artefact issues. Some of the bird species identified as indicators and winners/losers are quite rare in the UK and it is possible that their presence might have been missed in certain study squares, potentially biasing the observed patterns. The selection of study squares may also have impacted results, particularly for the rural squares given only 100 squares were selected which may not be fully representative of UK rural areas. Finally, the data structure should also be considered: the lack of abundance data may have impacted results.

Chapter 6

Synthesis

6.1 Summary

Summary

This study has examined the changes in bird distribution and functional ecology in multiple UK cities. Trends and changes in species richness between 1970 and 2010 show significant differences between urban and rural bird communities. The rural bird communities have lost species while urban bird species richness increased during the same time period, although the average changes were very small. More importantly, temporal beta-diversity was larger in urban areas compared to rural ones (Chapter 2). In terms of the environmental variables driving structural changes, different metrics of temperature had important influences on species richness and beta-diversity at the temporal scale, whereas the amount land use change was less important than expected. Overall species richness (urban and rural) increased slightly from 1970 to 2010, and both the richness and turnover response is strongly linked the initial baseline 1970 data (Chapter 3). The data also show that rural bird communities are significantly different from urban ones, supporting a greater range of species and having a higher variability in composition. The urban sites are more homogenised than rural sites, which agrees with the hypothesis that urbanization is threatening bird species richness and beta-diversity (Chapter 4). By looking into the winners and losers among bird species, it was found that all the winner species were increasing all over the UK while loser species were experiencing decrease according to the baseline, as one would expect. Generalist species were less sensitive to habitat change and performed better than their rural counterparts, which usually preferred woodland habitat.

6.2 Urban sites vs rural sites

The global trend towards urbanization has raised a number of ecological issues concerning species diversity. Many studies have shown that the rapid expansion of urbanization has led to structural changes in bird communities (McKinney, 2002). Globally, avian species population density is negatively related with urban landcover (Aronson et al., 2014). In this study, the change in the total number of species was not significant during the past 40 years according to the average value of richness, with the overall difference in urban sites only slightly higher than that in rural areas. Overall, bird richness in the UK shows no clear responses to urbanization, but this conclusion changes when the temporal change and spatial difference in beta-diversity is analysed. Some empirical studies have found that environmental heterogeneity is the core cause for beta-diversity (Harrison et al., 1992, Spencer et al., 2002, Winter et al., 2010), whereas other researchers have named geographic distance as the most important predictor (Tuomisto et al., 2003, Qian et al., 2005). The results here indicate the situation is more complex and a combination of drivers is seemingly important.

6.2.1 Temporal variation

Land use change transforms habitats directly, creating fragmented habitats and artificial environments. At regional levels of study, it is one of the most relevant environmental changes influencing temporal variations of biological communities (Baselga et al., 2015; Maxwell et al., 2016). In this study, however, the temporal models (GLMMs) indicate that over the 40-year time period land use change was less important than temperature and human disturbance (see models in Chapter 3; Table 3-2 to 3-5). This may lead to the hypothesis that, at a regional scale, the temporal impact of land use type is not as significant as

climate change so long as the percentage urbanization remains below a certain level (Chapter 1, 1.4.1). Most studies agree that the consequence of community change is a synergistic phenomenon related to climate and land use, but the importance level of these two aspects remains unclear (Allen et al., 2000; Jetz et al., 2007). A recent study based in Southern Quebec provides a good view, suggesting that land use changes are a key driver in bird population changes at a regional scale (Regos et al., 2018). To better understand the importance level of different factors including climate and land use, more detailed studies (at different scales) are necessary with careful interpretation of the interactions between each combination of factors (Keil et al., 2012). Overall, the most important driver of temporal change in UK bird assemblages was the initial site richness, with the results implying that richer sites are more buffered against disturbance, and change less through time. This finding has important implications for the study of ecological community resilience and its links to diversity. Interestingly, the urban–rural classification variable was less important than HI in general, indicating that the effect of urbanisation on temporal composition change is likely better captured by HI than a simple urban–rural dichotomy.

6.2.2 Spatial variation

One of the most important findings in this study is to confirm the positive relationship between beta-diversity and site distance, which agrees with the "distance-decay effect" (Chapter 4). This effect was first proposed by Tobler (1970), describing the decrease in similarity of two observations with the increase in distance, and has been used in many spatial variation analyses of communities (Nekola and White 1999). Furthermore, the slope in the declining trend is flatter for urban sites in this study, leading to the deduction that the homogenization level of UK bird communities is higher in urban than in rural

areas, and this deduction possibly results in uniform urban bird communities in all cities (Jokimaki et al., 1996). With higher levels of urbanization, bird communities are expected to be more similar (Blair, 2001). This leads to the next topic, "winners" and "losers" in the human disturbed environment, when looking into dynamics of individual species. Besides the homogenization trend within a single city, the similarity of species composition occurs in all cities because of relatively similar landscape structure (Luck & Smallbone, 2011). This hypothesis assumes that the cities have been subjected to similar land use changes as they urbanised and are occupied by identical combinations of species with tolerance for the particular constraints of artificial habitat, enhancing the trend towards homogenization (McKinney, 2002, 2006, Clergeau et al., 2006).

6.2.3 Winners and losers

McKinney and Lockwood (1999) suggested that habitat modification caused by urbanization had led to changes in species composition with some species with low tolerance of human disturbance moving away from the urban environment ("urban avoiders") while some other species dominate the community ("urban adapters") and even expand their geographical extent. Theoretically, the "winners" which are proved to be well adapted to the urban habitat, seem to occupy the niches and resources and thrive in population and density in cities. Consequently, a few winner species are usually dominant in urban bird communities (Beissinger & Osborne, 1982, Bezzel, 1985, Marzluff, 2001). In this study, it is interesting to find that, although the population trends are declining (with fluctuations) during the last several decades, grasshopper warbler and lesser spotted woodpecker were classified as "urban indicators", which suggests that they are highly associated with urbanised areas. Rather than "urban adapters", these two species are more likely to be defined as "urban

avoiders", just as other sensitive "loser species" which are more associated with rural areas. It may cause the general declining trend across the whole country (Barnes et al., 2021, Stanbury et al., 2021).

6.2.4 Filtering species on traits?

Different groups of species, urban adapter or avoider, share some common biological traits related to tolerance patterns, including nesting, diet, flexibility, and behavioural habit (McClure, 1989, Lim, 2004, Clergeau et al. 2006, Kark et al., 2007). Kark et al. (2007) and Croci et al. (2008) suggested that whether a species is a potential urban avoider or adapter is linked to a combined set of trait modalities. This leads to the theory that cities can act as a filter, attracting adapters while rejecting avoiders with certain types of habits. This is the case for a previous study on bee communities, in which urbanized landscape filters specific ecological features facilitating bee's colonization of the city centre (Banaszak-Cibicka et al., 2012). A highly urbanized habitat is supposed to filter birds with their diets, e.g., carnivore guild species (Kettel et al. 2018) and species with scavenging diets (Evans et al. 2011). Further study on this topic is focused on species functional traits, which are the characteristics of organisms with demonstrable links to the organism's fitness (Cornelissen et al., 2003).

6.2.5 Cities as habitats

In this study, urban sites demonstrate increasing richness as well as turnover rate over the 40 years to a greater extent than in the rural areas over the same period. This result shows that, although human influence on bird diversity is often presented in a negative way (e.g., noise, contamination, light disturbance, habitat fragmentation), urban habitat holds attractions for some bird species. Previous studies have shown that some features of city ecosystem, such as

vegetation heterogeneity, landscape connectivity, urban green spaces, waterbodies, exotic ornamental plants etc., can positively influence species richness and diversity in urban areas (e.g., Faeth et al., 2011; Suri et al., 2017; Rodrigues et al., 2018). One case study based on The African Bird Atlas Project (Ostrich, 2021), analysing historical records of African birds, suggests that the urban landscape is valuable for African birds. Another study (Facundo et al., 2018) also suggests that the urbanized habitat sustains taxonomic diversity and functional diversity for birds with no major loss in 30 years. However, the support highly urbanized landscapes provide for the generalists and exotic species did not fully compensate for the loss caused by urbanization (Sol et al., 2017). There are also studies linking socio-economic features of cities with bird diversity (Luck et al., 2013), including city sizes, human population, and income levels.

6.3 Biases

6.3.1 The ornithological data and environmental data

The quality of atlas data is an important consideration for studies of this nature. Usually, atlas projects should provide adequate information concerning data quality to help researchers authenticate the appropriateness of the data for their analysis and take limitations into consideration during analysis.

Well-designed atlas projects, including for example The Atlas of Breeding Birds in Britain and Ireland, are designed to minimise biases within the data. These two datasets have been compiled by skilled volunteer surveyors and have been thoroughly validated and verified (see Chapter 1 for more details). They provide carefully designed protocols to ensure that data are of a high standard (BTO). This atlas project is designed to have approximately 20-year

intervals and data collection over 3 periods, 1968-1972, 1988-1991 and 2007-2011. Considering the recording effort of atlas data with the Frescalo analysis (Hill, 2012), it is suggested that the amount of effort put into BA1970 (1968-1972 breeding season) and BA2010 (2007-2011 breeding season) is comparable which supporting the study of breeding season distribution changes to be based on the BA1970 to BA2010 comparison.

6.3.2 Limitations of ornithological atlas data

The patterns of bird diversity show variability at different scales, both spatial and temporal. The quality of the data is restricted by the limitations of spatial scale, temporal resolution, and sampling bias.

6.3.2.1 Spatial scale

Spatial scale is one of the fundamental aspects when using atlas data. It has two components: extent and grain (Whittaker et al., 2005). Spatial extent refers to the region of the map or geographical area where the atlas project is set and the atlas data collected. Grain, or spatial resolution, refers to the size of the sampling unit for conducting a single observation. The size of the grain is usually associated with the size of spatial extent. Atlas projects with smaller spatial extents have finer spatial resolution, while atlas projects with larger extent tend to have a coarser resolution (Dunn & Weston, 2008).

Atlas data at different spatial scales can be used to answer different research questions. The fineness of the spatial resolution can severely affect the types of research questions. The patterns of diversity can be different when the grid cell fineness varies, even with the same atlas dataset (Whittaker et al., 2005). For atlas data with fine resolution, the patterns of diversity can be assembled to reveal the patterns of coarse resolution data. This study used

atlas data of coarser resolution and larger extent, for example the BTO atlas data 1970 and 2010, where the grid size is 10 km and the spatial extent covers the whole of the UK. This dataset is capable of addressing topics for general trend of bird distribution and turnover changes on a regional scale, but is not suitable for such issues as species richness comparison at individual level. A finer scale resolution is also needed to understand the combined regional effects of climate and land use change (De Chazal & Rounsevell, 2009). Some recent studies discussing bird distribution changes use coarse resolution atlas data (the first European Breeding Bird Atlas, EBBA1) as background information, always accompanied by other fine resolution data (Herrando et al., 2019).

From the perspective of perusing more detailed and more informative datasets, data of larger spatial extent and finer resolution is always to be preferred. However, spatial resolution can be limited by the number of observers and the geographical area covered by the investigation (Gibbons et al., 2007). Considering the spatial extent of atlas projects, samples within each 10km square are collected at a finer tetrad scale, 25 in total combined with record of tetrad (2 times surveyed). Inclusion in the dataset is based on the number of tetrads surveyed to ensure that records are collected in particularly vulnerable areas to provide more complex and sensitive coverage than other part of the mapped region (Donald & Fuller, 1998).

6.3.2.2 Limitations in the environmental covariates

The main approach of this study is connecting the ornithological atlas data with environmental data, which generates interesting insights into the relationships between birds and the environment. In this study, the BTO atlas data in 1970 and 2010 were collected at a resolution of 10 km grid squares and only presence/absence counts were recorded. The quality of these atlas data is

better for assessing the effects of environmental change on avian distribution shifts at national or landscape scales than for the detailed study of habitat preference at individual bird level. However, suitable environmental data are rarely available at the same geographical scale as the atlas data, which is a significant obstacle when seeking to analyse the association between bird communities and environmental change.

As the use of Geographical Information System (GIS) increases, the possibility of producing applicable habitat data through GIS data products for appropriate ornithological data at the same geographical scale is growing (Leyequien et al., 2007). Deriving the environmental information, including current and historical patterns of habitat, topography and climate, directly from GIS products is one of the most accurate methods in generating precise environmental data at the required spatial scale. One of the best-known remote sensing products, Landsat, usually contains high quality data at a fine resolution of 30 metres grid (Tucker et al., 2004; Hansen et al., 2012). This dataset is suitable for individual bird level data with a resolution of 1 km square grid and below but it can processed up to larger scales. Landsat data has a number of known problems that require considerable preprocessing, such as atmospheric corrections, data loss because of scan lines (in Landsat 7 data) and cloud removal. Removing clouds from the map remains one of the knottiest issues when using remote sensing data in research (Martinuzzi et al., 2007; Shen et al., 2014). However, for most ecological purposes there are several professionally prepared datasets that are available.

6.3.2.3 Temporal resolution

For the temporal analysis of atlas data, the length of time between samples (i.e. the interval) is an important consideration and potential source of bias. Most atlas projects start with collecting data over a discrete time period, and follow

this with another phase at a later date in which the same sampling strategy is used with equal sampling effort (Harrison et al., 2008). Many examples of studies proved the feasibility of studying bird diversity range changes by comparing atlas datasets from different years (Donald & Fuller 1998). This study used the BTO atlas data project repeated for 3 phases with a time interval of 20 years. However, given the known issues with the 1990 BTO data (Gillings et al., 2019), the research presented here focused primarily on comparing the atlas data in 1970 with the data in 2010. Using a time interval of this magnitude (i.e., 40 years) could obscure lots of changes that have occurred during this period (e.g., species going extinct and re-colonising).

6.3.2.4 Sampling bias

Sampling bias is a major problem in atlas datasets (e.g., Dennis et al., 1999) and in the collection of any type of occurrence/abundance data (Funk & Richardson, 2002). Sampling bias includes spatial bias, temporal bias and taxonomic bias (Funk & Richardson, 2002). Spatial bias occurs when the sampling effort is uneven across the geographical spatial scale, which means some of the sampling units are visited less. Temporal bias happens when the sampling effort varies along the temporal scale, which means records are concentrated in one season or certain times of the year (Funk & Richardson, 2002). The BTO atlas data set contains two periods of sampling time: breeding season and winter. Therefore, the result of this study, which is based on the breeding data, should take temporal bias into consideration and care should be taken over its interpretation if extrapolating to other seasons.

Besides spatial and temporal sampling bias, taxonomic bias is also very important for atlas data; it occurs when the identification of species is not 100% correct. Taxonomic bias also happens when some species may be over-represented because they are more conspicuous, while some other species are

under-represented as they are rare and/or inconspicuous (Dennis et al., 2006). At the same time, low sampling effort may also cause taxonomic bias, due to the possibility of lack of records of rarer species in certain sampling units (Robertson et al., 1995). These elements of bias are well controlled for in the BTO Atlas data but issues still exist. Gillings et al. (2008) assigned a detection score evaluating the sampling effort, which reveals that the likelihood of missing a species was significantly positively correlated to its detection score. Given the coarse size of the grid squares and the use of multiple observers within each square, it is believed that taxonomic bias is minimised in the BTO atlas data, but some sampling issues may be present, particularly in difficult to sample squares (e.g., in rural Scotland).

6.4 Future prospective

While this thesis has provided a range of novel findings, many unsolved problems remain. For example, how does a change in land use correlate with other environmental factors (i.e., an interaction) in its influence on species richness and beta-diversity? Keil et al. (2012) emphasised the importance of geographical scale and grain size when interpreting the impact of different factors on beta-diversity, because all the relationships between distance and beta-diversity depend on grain size and spatial extent. Due to the spatial resolution of this study using atlas data (10 km grid), the general patterns of bird diversity presented are at the regional scale. The detailed condition of bird communities in individual UK cities at local scales is not known and cannot be derived from these general patterns. It is likely that many sensitive groups of species are associated with both local level and landscape level habitat features, and thus the former will have been missed in the present research. Other studies have demonstrated support for landscape-level effects on birds in urban areas and have concluded that urbanization around forest patches and

riparian areas affects bird diversity and abundance within these areas (e.g., Munyenyembe et al., 1989, Smith & Schaefer, 1992, Bolger et al., 1997, Germaine et al., 1998, Saab, 1999). However, results from multiple-scale studies have not consistently shown that these effects are significant (Berry and Bock, 1998, Clergeau et al., 1998). Although landscape-level studies detect and predict patterns, local-level and demographic studies are necessary to determine many of the mechanisms involved in avian population and community change. Therefore, for further research aiming to construct a detailed profile of UK bird diversity and make predictions about the future trend of bird communities, a multiscale approach is required.

Another unsolved question is why would urban winners fail to produce larger populations? This question needs information not only from climate and land cover data, but also about target species feeding, nesting and breeding behaviour and interactions with other species on a local scale, e.g., competition within the species and with other species as well as small predators like domesticated cats (Fischer et al., 2012). In addition, the fundamental aspects of vegetation, environmental structural complexity, ecological carrying capacity and the knowledge of species physiological mechanisms, all require further study (Evans et al., 2009c, Bonier, 2012, Huang et al., 2015).

Studies on the gradient between urban and rural areas also frequently oversimplify cities (Theobald, 2004, Alberti, 2008). Instead of growing in a linear gradient, cities in the real world develop quickly, intricately, non-linearly, and expansively. In light of this, it is possible to make mistakes when using categorical or quantitative measures of geographic linear distance in urban ecological investigations. Numerous studies using urban land-use types and landscape metrics can partially capture some of the non-linear heterogeneity and complexity of cities, but they still oversimplify urban environments because

they frequently predigest complex environmental drivers into a small number of aggregated variables used in study design and data analysis (Alberti et al., 2003). The complicated growth and dynamic nature of modern cities in the context of a rapidly urbanising world must be taken into account in further work.

6.5 Conservation implications

The findings of the present work have conservation implications at multiple levels, both in terms of the metrics used and operationally in terms of conservation practice in urban areas.

6.5.1 Methodological considerations

Beta-diversity can offer important insights into the fundamental processes underlying community assembly, diversity and dynamics (Myers & LaManna, 2016). Understanding the consequences of land use changes on taxonomic diversity and establishing the connections between biodiversity and human-induced disturbances remains a pressing issue. This research provides support for the efficacy of beta-diversity in informing conservation strategies and activities related to ecologically vulnerable regions or biodiversity hotspots.

Beta-diversity plays an important part in discerning the primary land-use categories that contribute to the development of functional landscape heterogeneity (Fahrig et al., 2011). The observed high beta diversity may be linked to species replacement, which suggests that the implementation of habitat conservation efforts will likely be effective (Hill et al., 2017). In cases where disparities of richness influence beta diversity, conservation strategies tend to focus on areas of higher taxonomic richness rather than sites with high

beta diversity. This arises because high beta-diversity sites are essentially subsets of locations characterised by high taxonomic richness, so have little impact on the regional species pool (Hill et al., 2021). It is important to acknowledge that higher levels of beta-diversity do not always correspond to an increased conservation value (Socolar et al., 2016). The use of temporal fluctuations in beta-diversity to evaluate biodiversity patterns requires an assessment of the implications associated with these alterations. Specifically, the association between high levels of beta-diversity and adverse conservation results in places characterized by low-intensity activities should be acknowledged (Santana et al., 2017).

While Beta-diversity serves as a valuable tool for disentangling the processes involved in community assembly, there are important challenges that occur when one tries to link processes to patterns (Myers and LaManna, 2016). One further concern with the use of beta-diversity is its scale dependency, necessitating a systematic evaluation at several scales before it is applied to a conservation problem. Spatial heterogeneity and beta-diversity must be evaluated and used for conservation objectives at appropriate scales in relation to the target organism or habitat (e.g. Báldi & Batáry, 2011).

6.5.2 Conservation practice in urban areas

The findings of this work suggest that over time in the UK avian communities have become more homogenised, a pattern common to many such studies (e.g. McKinney & Lockwood, 1999, Clergeau., et al. 2006). The process is likely a result of trait filtering removing species that are highly sensitive to land use change due their specific habitat requirements Homogenisation is frequently seen as a negative but highly urbanized landscapes provide for generalists and exotic species which offer opportunities for people to engage with wildlife in

cities (Cox and Gaston, 2015), although it is clear that this does not fully compensate for the loss caused by urbanization (Sol et al., 2017).

Moreover, studies illustrate that some features of a city ecosystem, such as vegetation heterogeneity, landscape connectivity, urban green spaces, waterbodies, exotic ornamental plants etc., can be managed to positively influence avian species richness and diversity in urban areas (e.g., Faeth et al., 2011, Suri et al., 2017, Rodrigues et al., 2018). This work has also shown that in terms of enhancing the potential for urban avoiders woodland conservation should be a key priority for conservation planning in city landscapes.

Appendices

Figures and tables

Chapter 1

Table A1 The dataset, for an exemplar set of sites

grid	NJ90	NS46	NS56	NS65	NS66	⋯
classify	urban	urban	urban	urban	urban	
city	Aberdeen	Glasgow	Glasgow	Glasgow	Glasgow	
population	196670	591620	591620	591620	591620	
X1970	76	79	63	64	63	
X2010	75	73	55	57	60	
Breed_1970.2010	-1	-6	-8	-7	-3	
beta.sim	0.2	0.150685	0.2	0.192982	0.233333	
beta.sne	0.005298	0.033526	0.054237	0.046687	0.018699	
beta.sor	0.205298	0.184211	0.254237	0.239669	0.252033	
cha_hil_gra	-9.25926	-15	0	-5	-4	
grass_70	25.92593	52	5	57	35	
urban_70	59.25926	44	77	40	31	
crop_70	14.81481	0	17	3	33	
forest_70	0	4	0	0	1	
grass_10	16.66667	37	5	52	31	
urban_10	72.22222	47	94	43	60	
crop_10	3.703704	1	0	0	4	
forest_10	7.407407	15	0	5	5	
prec_70	11563.84	24214.71	21808.58	23243.92	21409.57	
tavg_70	11.18365	12.46476	12.7513	11.79444	12.58612	
tmin_70	7.939506	8.320148	8.809946	7.899721	8.554318	
tmax_70	14.43602	16.59725	16.69924	15.72039	16.58797	
range_70	6.496512	8.277104	7.889295	7.820674	8.033651	
prec_10	10888.42	24477.36	23143.27	24546.65	22737.44	
tavg_10	12.38306	13.55628	13.86819	12.97679	13.74371	
tmin_10	9.140957	9.306572	9.82685	8.994206	9.629233	
tmax_10	15.60979	17.8091	17.94626	17.01047	17.86123	
range_10	6.468834	8.50253	8.119412	8.016263	8.231999	
HI	51.89004	57.92807	61.06409	46.53837	55.99472	
lon	-2.08424	-4.47766	-4.31807	-4.15348	-4.15844	
lat	57.13587	55.8532	55.85631	55.76943	55.85922	

Chapter 2
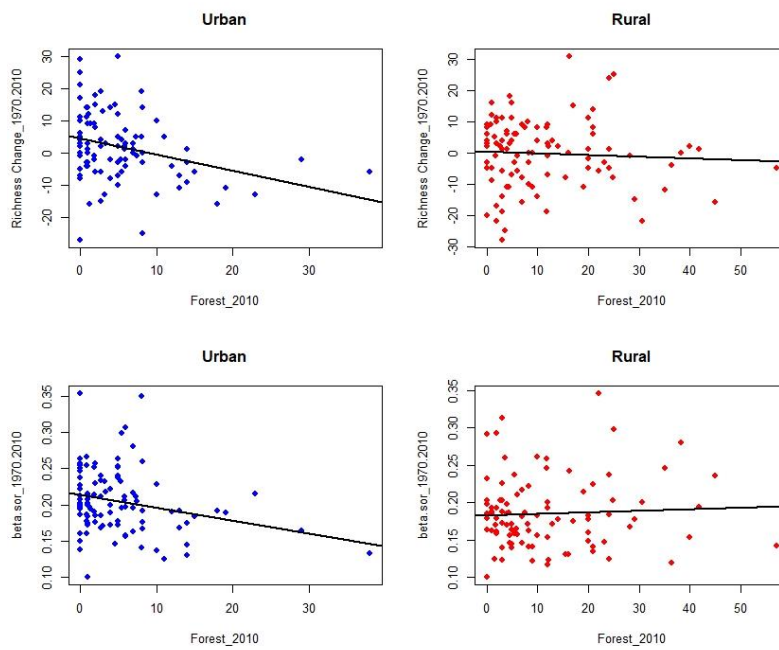
Fig A2-1

Relationships between forest land cover and richness change & beta diversity (between 1970 and 2010), for urban and rural squares. Black lines are least square regression fits.
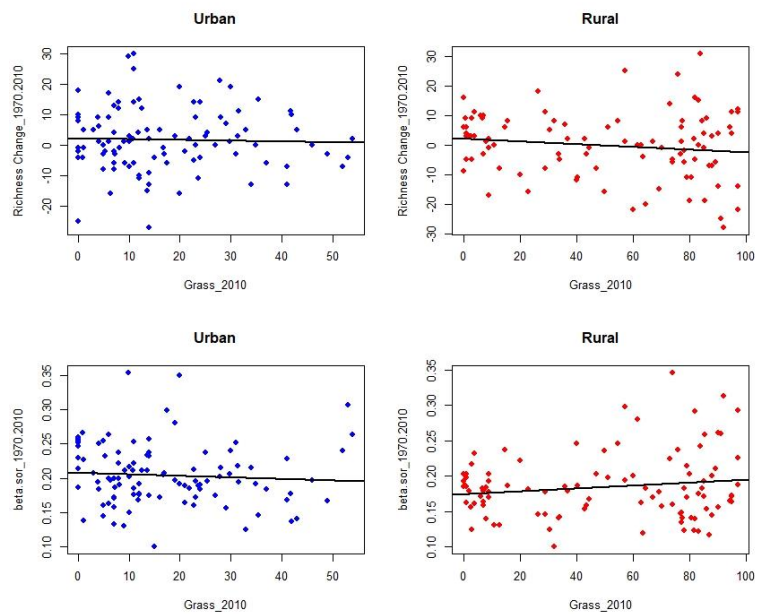
Fig A2-2

Relationships between grass land and richness change & beta diversity (between 1970 and 2010), for urban and rural squares.
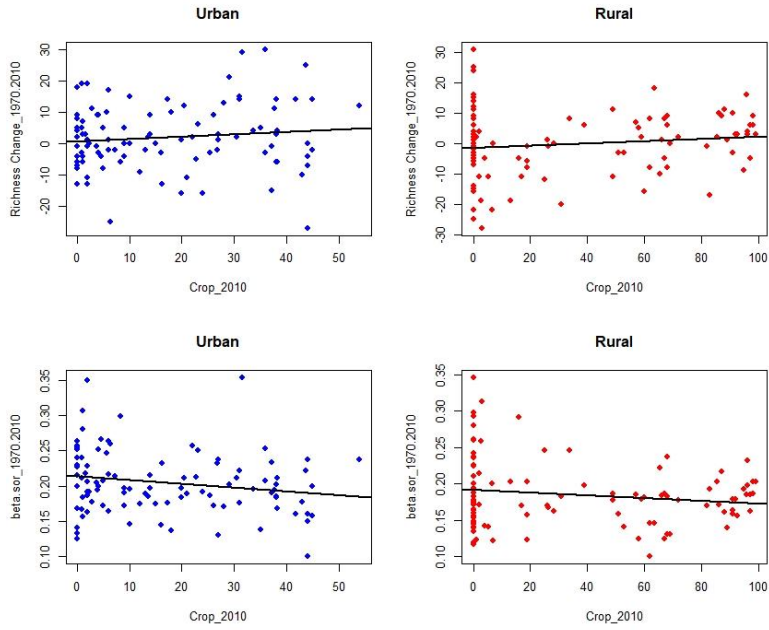
Fig A2-3

Relationships between crop land and richness change & beta diversity (between 1970 and 2010), for urban and rural squares.
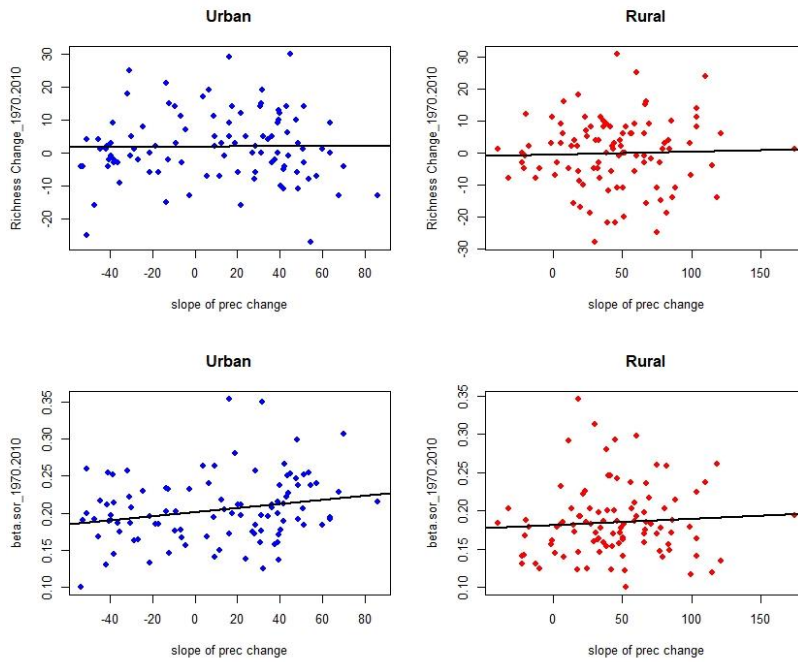
Fig A2-4

Relationships between precipitation change and richness change & beta diversity (between 1970 and 2010), for urban and rural squares.

Chapter 3

Table A2 Axis length of variables from DCA results

(environmental predictors vs functional traits)

	DCA1	DCA2	DCA3	DCA4
Axis lengths	0.17947	0.1069	0.1078	0.1078

("decorana" function in package"vegan" is used to calculate the axis length.)

Table A3 A selection of species data with the functional traits information from AVONET

grid	Latin Name	R/M	Family1	Order1	Mass	Habitat	Trophic.Level	Trophic.Niche
Red.throated.Diver	Gavia stellata	migrant	Gaviidae	Gaviiformes	1486.0	Wetland	Carnivore	Aquatic predator
Black.throated.Diver	Gavia arctica	migrant	Gaviidae	Gaviiformes	2251.1	Wetland	Carnivore	Aquatic predator
Little.Grebe	Tachybaptus ruficollis	resident	Podicipedidae	Podicipediformes	169.4	Wetland	Carnivore	Aquatic predator
Great.Crested.Grebe	Podiceps cristatus	resident	Podicipedidae	Podicipediformes	731.0	Wetland	Carnivore	Aquatic predator
Black.necked.Grebe	Podiceps nigricollis	migrant	Podicipedidae	Podicipediformes	412.4	Wetland	Carnivore	Aquatic predator
Bittern	Botaurus stellaris	resident	Ardeidae	Pelecaniformes	1319.5	Wetland	Carnivore	Aquatic predator
…								

(AVONET ref: Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J., Yang, J., Sayol, F., ... & Schleuning, M. (2022). AVONET: morphological, ecological and geographical data for all birds. Ecology Letters, 25(3), 581-597.

Table A4 GLM model selection results for four response variables: richness change, and then the three temporal beta diversity indices (Sne, Sim, Sor). For each, all models with delta AIC values < 2 are presented. Variable importance values (i.e., the sum of AIC weights across models in which a variable is found) are shown for all predictors.

Table A4-1 Richness change model

richness change	A3	cha_urb	classify	HI	lat	slope_prec	slope_tav	slope_tmin	x1970	AIC
1	1.88518	NA	NA	NA	1.385061	-1.08756	NA	1.810735	-5.32764	1448.713
2	1.899854	NA	NA	NA	1.129699	NA	NA	1.988042	-5.21128	1449.181
3	1.874302	NA	NA	NA	NA	NA	NA	1.454586	-5.4013	1449.433
4	1.924723	NA	NA	NA	1.403027	NA	2.112302	NA	-5.21061	1449.458
5	1.858832	NA	NA	NA	NA	-0.8227	NA	1.229242	-5.52181	1450.013
6	1.877274	-0.50908	NA	NA	1.445043	-1.22373	NA	1.827929	-5.42531	1450.268
7	1.904093	NA	NA	NA	1.462893	-0.80678	1.783549	NA	-5.29247	1450.319
8	1.874435	NA	+	NA	1.159728	NA	NA	1.960363	-5.16599	1450.445
9	1.881749	NA	NA	NA	NA	NA	1.307356	NA	-5.40908	1450.477
10	1.87852	NA	NA	0.526118	1.159218	NA	NA	1.917627	-5.15978	1450.638
11	1.824229	-1.21017	+	NA	1.268576	NA	NA	2.015055	-5.2998	1450.69
12	1.918969	NA	NA	NA	1.364905	NA	1.066194	1.183331	-5.21604	1450.701

Table A 4-2 Importance of predictors (richness change model)

	X1970	A3	Slope_tmin	lat	Slope_tav	Slope_prec	Cha_urban	classify	HI	Cha_forest
weights	1.00	1.00	0.64	0.59	0.44	0.44	0.35	0.33	0.30	0.26

Table A4-3 Beta.sim model

	cha_crop	cha_forest	cha_urb	classify	HI	lat	slope_tav	slope_tmin	x1970	AIC
1	-0.00553	NA	NA	NA	0.009927	0.015938	0.008078	NA	-0.00685	-652.531
2	-0.00546	NA	NA	+	NA	0.016106	0.009227	NA	-0.00707	-652.461
3	-0.00622	-0.00473	NA	+	NA	0.015889	0.00867	NA	-0.00634	-652.198
4	NA	NA	NA	+	NA	0.014613	0.009172	NA	-0.00667	-652.152
5	NA	NA	NA	NA	0.011016	0.014405	0.007903	NA	-0.00642	-652.146
6	-0.00627	-0.00449	NA	NA	0.008707	0.015762	0.007709	NA	-0.00619	-652.053
7	NA	-0.00377	NA	+	NA	0.014273	0.008722	NA	-0.00604	-651.231
8	NA	-0.00349	NA	NA	0.010183	0.014108	0.007598	NA	-0.00586	-651.03
9	NA	NA	0.004376	NA	0.008058	0.014038	0.008022	NA	-0.006	-650.957
10	-0.00576	NA	NA	NA	0.009608	0.01617	0.012587	-0.00501	-0.00687	-650.951
11	-0.00658	-0.00517	NA	+	NA	0.016154	0.014225	-0.00628	-0.00629	-650.926
12	-0.00593	-0.00544	NA	NA	0.009156	0.016834	0.007244	NA	NA	-650.906
13	-0.00589	-0.00574	NA	+	NA	0.017004	0.008258	NA	NA	-650.88
14	-0.00535	NA	NA	NA	0.01136	0.011302	NA	NA	-0.0065	-650.879
15	-0.00569	NA	NA	+	NA	0.016333	0.013679	-0.00499	-0.00709	-650.876
16	NA	NA	0.004215	+	NA	0.014207	0.008969	NA	-0.0062	-650.857
17	-0.00664	-0.00494	NA	NA	0.008184	0.016035	0.013321	-0.00628	-0.00615	-650.779
18	-0.00618	-0.00494	NA	NA	0.009948	0.011341	NA	NA	-0.0058	-650.748
19	NA	NA	NA	NA	0.012385	0.009915	NA	NA	-0.00609	-650.677
20	NA	NA	NA	NA	0.011665	0.015738	0.007506	NA	NA	-650.676
21	-0.00543	NA	NA	+	0.005445	0.015992	0.008553	NA	-0.00692	-650.589
22	-0.00497	NA	NA	NA	0.010726	0.017194	0.00764	NA	NA	-650.565
23	-0.00494	NA	0.002131	NA	0.008602	0.015597	0.008118	NA	-0.0066	-650.561

Table A4-4 Importance of predictor (beta.sim model)

	lat	X1970	Slope_tav	HI	Cha_crop	classify	Cha_forest	Cha_urb	Slope_tmin	Slope_prec	A4
weight	0.99	0.65	0.65	0.54	0.51	0.48	0.47	0.37	0.34	0.31	0.27

Table A4-5 Beta.sne model

beta.sne	A5	cha_crop	cha_forest	cha_urb	HI	slope_prec	slope_tav	slope_tmin	x1970	AIC
1	-2.20682	NA	NA	NA	NA	NA	-0.00677	NA	-0.00653	-699.504
2	-2.15477	0.004211	NA	NA	NA	NA	-0.00603	NA	-0.00614	-699.388
3	-2.2035	NA	NA	-0.00358	NA	NA	-0.00644	NA	-0.00718	-698.842
4	-2.22214	0.004356	NA	NA	NA	NA	NA	-0.00512	-0.00637	-698.264
5	-2.2854	NA	NA	NA	NA	NA	NA	-0.00589	-0.0068	-698.255
6	-2.11787	0.004506	0.002398	NA	NA	NA	-0.00575	NA	-0.00658	-697.888
7	-2.27837	NA	NA	-0.00386	NA	NA	NA	-0.00569	-0.00746	-697.832
8	-2.16324	0.003348	NA	-0.00237	NA	NA	-0.00597	NA	-0.00664	-697.803
9	-2.18122	NA	0.001846	NA	NA	NA	-0.00659	NA	-0.0069	-697.764
10	-2.27229	NA	NA	-0.0062	0.003993	NA	-0.00718	NA	-0.00722	-697.678
11	-2.20556	NA	NA	NA	NA	0.001723	-0.00599	NA	-0.00634	-697.649
12	NA	0.004408	NA	NA	NA	NA	-0.0061	NA	-0.00638	-697.647
13	NA	NA	NA	NA	NA	NA	-0.00687	NA	-0.0068	-697.59

Table A4-6 Importance of predictors (beta.sne model)

	X1970	A5	Slope_tav	Cha_cro	Slope_tmin	Cha_urb	Slope_prec	HI	Cha_forest	lat	classify
weight	0.81	0.72	0.57	0.47	0.39	0.38	0.32	0.30	0.30	0.28	0.28

Table A4-7 Beta.sor model

beta.sor	A6	cha_crop	cha_forest	cha_urb	classify	HI	lat	x1970	AIC
1	NA	NA	NA	NA	NA	0.010685	0.013624	-0.01325	-714.8
2	0.74045	NA	NA	NA	NA	0.010381	0.013994	-0.01332	-713.576
3	NA	NA	-0.00148	NA	NA	0.01031	0.013572	-0.01302	-712.926
4	NA	NA	NA	-0.00156	NA	0.011729	0.013779	-0.0134	-712.838

Table A4-8 Importance of predictors (beta.sor model)

	X1970	lat	HI	classify	A6	Cha_forest	Slope_tav	Cha_urb	Slope_tmin	Cha_crop	Slope_prec
weight	1.00	1.00	0.79	0.40	0.35	0.29	0.28	0.28	0.27	0.27	0.26

Chapter 4

Table A5 Axis length of variables from DCA results
(environmental predictors vs bird species)

	DCA1	DCA2	DCA3	DCA4
Axis lengths	1.8938	1.1188	0.9817	1.3614

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Chapter 2

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Chapter 3

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