

Joint effects of species traits and environmental preferences on range edge shifts of British birds

Lucie Thompson¹  | Konstans Wells¹  | Núria Galiana²  | Miguel Lurgi¹ 

¹Department of Biosciences, Swansea University, Swansea, UK

²Department of Biogeography and Global Change, National Museum of Natural Sciences (CSIC), Madrid, Spain

Correspondence

Miguel Lurgi, Department of Biosciences, Swansea University, Singleton Park, Swansea SA2 8PP, UK.
Email: miguel.lurgi@swansea.ac.uk

Funding information

H2020 Marie Skłodowska-Curie Actions, Grant/Award Number: 101025471

Handling Editor: Sarah Supp

Abstract

Aim: Despite the strong evidence of species range shifts as a response to environmental change, attempts to identify species traits that modulate those shifts have been equivocal. We investigate the role of species traits and environmental preferences on birds' range shifts in Great Britain, an island where dispersal is limited by the English Channel and the North Sea.

Location: Great Britain (England, Scotland and Wales).

Taxa: Birds (*Aves*).

Time Period: 1968–2011.

Methods: Using 404,949 occurrence records from two time periods, we investigated the potential drivers of leading and rear range edge shifts of breeding birds using phylogenetic linear mixed models. We hypothesized that shifts are influenced by species' trophic and morphological traits, dispersal abilities and environmental preferences, but also by the geographical boundaries of Great Britain.

Results: Geographical boundaries—the distance from the northern or southern boundaries of Britain—accounted for most of the variability in range edge shifts. Species traits and environmental preferences emerged as relevant drivers of range shifts only for northern and Passeriform species. Northern habitat specialist, those with more predators and those sensitive to precipitation were more likely to shift their rear edge poleward. For Passeriformes, habitat generalists, species with smaller dispersal capabilities, under higher predatory pressure or associated with forest and grassland were more likely to shift their rear edge poleward.

Main Conclusions: While geographical boundaries impose constraints on range shifts in British birds, the subtle effects of species traits and environmental preferences emerge as relevant predictors for Northern and passeriform species' rear edge shifts. This highlights the importance of accounting for geographical boundaries when predicting species responses to global change. Differential range shifts of species across different trophic levels could result in the reorganization of biotic interactions, with consequences for ecosystem structure and stability.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2023 The Authors. *Global Ecology and Biogeography* published by John Wiley & Sons Ltd.

KEYWORDS

body size, dispersal, food webs, geographical barriers, migratory behaviour, northern species, passeriform species, phylogeny, southern species

1 | INTRODUCTION

Climate change has prompted a global trend of species geographical range shifts, with the largest shifts occurring in areas with highest levels of warming, including temperate regions (Chen et al., 2011; Parmesan & Yohe, 2003). The majority of species seem to shift their range poleward along latitudinal gradients or upward along elevational gradients (see Lenoir & Svenning, 2015 for a global review). However, some species have contracted their ranges (Bradshaw et al., 2014; Chen et al., 2011) or have differentially shifted their leading and rear range edges (Taheri et al., 2016), while others have maintained stable ranges (Parmesan & Yohe, 2003; Taheri et al., 2016). This creates a complex picture of range edge shifts across species and geographical regions. Considering both abiotic and biotic factors when investigating the drivers of range edge shifts can improve our understanding and prediction of the effects of those changes on biodiversity. This is of utmost importance given the compositional re-organization of communities that ensues, with concomitant effects on the persistence of species (Cahill et al., 2013; Thomas et al., 2004), biotic interactions (Lurgi, López, & Montoya, 2012a, b), and biodiversity-driven ecosystem services.

The three main factors determining species range shifts in response to environmental change are: exposure, vulnerability, and colonization abilities (Comte et al., 2014). Exposure relates to the intensity of climate and land cover change, vulnerability refers to the sensitivity of a species to these changes, whereas colonization is linked to their capacity to disperse and establish in novel abiotic and biotic conditions. A main constraint that limits species' responses to change are geographical boundaries, such as large bodies of water, which limit species capacity to disperse. While smaller geographical barriers, such as small expanses of water (e.g. the English Channel) or small mountain ranges, may be overcome; larger barriers can simply prevent species from colonizing new areas. If geographical boundaries rather than exposure, vulnerability or resilience drive range shift distance, assessing observed range shifts and their potential drivers, without accounting for those boundaries would inaccurately capture species vulnerability to global change.

On islands such as Great Britain, where terrestrial species are constrained to a narrow extent of land, geographical boundaries may limit their realized range edge shifts either completely, as would be the case of the North Sea, or partly as would be the case for the English Channel and small expanses of water separating the mainland from Great Britain's northern islands. Regardless of species traits or environmental preferences, we can expect southern species to benefit from more colonizable habitat to shift poleward. On the other hand, northern species are constrained in their capacity for

poleward range edge shifts due to their geographical context (Huntley et al., 2006). Similarly, widespread species would also suffer from a lack of colonizable habitat (Atkins & Travis, 2010). Only after geographical constraints (i.e. geographical boundaries and range size) have been accounted for, can we expect to observe the fingerprint of exposure, species vulnerability to change and resilience capacity on range edge shifts.

Species' vulnerability can be related to their level of habitat and/or diet specialization and position in the food web (i.e. trophic level). Top predators, especially raptors, are under higher stress from climate and land-use change, experiencing declining populations (Lurgi et al., 2012b; McClure & Rolek, 2020) and thus may be less able to track their abiotic and biotic niches. Lower consumers, on the other hand, may be able to track climate change better and benefit from trophic release from recently declining raptor populations (McClure & Rolek, 2020). This can create spatial mismatches in prey and predator populations, and the corresponding ecological interactions (Gilman et al., 2010). Changes in the phenology of some predators could alternatively increase top-down control on prey (as observed in black bear, coyote and caribou food webs in Bastille-Rousseau et al., 2018), inciting them to shift to places with weaker biotic interactions. Thus, overall, species under higher predatory pressure (i.e. with more predators) are expected to shift their ranges faster.

Similarly, species' diet breadth and habitat generality can strongly determine species response to environmental change given that changes in food availability have been identified as one of the leading causes of climate-led extinction (Cahill et al., 2013). Trophic and habitat generalists, as well as species with larger phenological and phenotypic plasticity, benefit from a wider choice of suitable resources and habitats (Buckley & Kingsolver, 2012; Diamond, 2018). This allows them to survive under changing conditions, thus reducing their need to shift their range (Tekwa et al., 2022). Trophic specialists, on the other hand, may be forced to shift their ranges in case of displacement or reduction of their food source (Buckley & Kingsolver, 2012).

Taheri et al. (2021) found that rear edge shifts of Northern British birds were correlated with climatic changes, whereas leading edge shifts of Southern British birds were correlated with land-use changes. This could be due to differences in environmental requirements across species and local adaptations, either in terms of land cover or climate in the North and South of Britain (Bradshaw et al., 2014; Pearce-Higgins et al., 2015). Thus, even within single species' ranges, different dynamics are expected at the leading and rear edges. At the rear (i.e. warmer) range edge, limiting factors are usually biotic interactions through predation and competition (Paquette & Hargreaves, 2021). Thus, at their rear edge, traits related to species' trophic interactions are expected to

be most important. At the leading (i.e. colder) range edge on the other hand, colonization and dispersal capacities are expected to be key (Angert et al., 2011; Comte et al., 2014). We would thus expect species that shift their leading edge poleward to be those with increased dispersal abilities, either thanks to larger body size (Lurgi et al., 2012b) and/or hand-wing index (a proxy for dispersal capabilities and migratory behaviour (Sheard et al., 2020), especially if they have geographical barriers to cross (e.g. crossing to an island).

Despite all these expectations, past studies relating range edge shift to species traits have yielded equivocal results. For instance, Angert et al. (2011) and Auer and King (2014) respectively found that diet breadth can be both, positively and negatively, correlated with poleward shifts in North American birds. Mixed trends have also been found on the effect of movement habits on range edge shifts. Hockey et al. (2011) and Laube et al. (2013) found that latitudinal shifters are more likely migrants and nomad birds, whilst Tingley et al. (2012) found similar results for resident birds. Lastly, Brommer (2008) found negligible impact of migratory strategy on Finnish birds shifts compared to other traits such as body size, diet composition and habitat specificity. Such seemingly inconsistent results from trait-based approaches have also been drawn for other terrestrial taxa like insects, mammals and plants (Beissinger & Riddell, 2021).

In contrast to these disparate results, biogeographical aspects of species ranges, such as range area (Pacifi et al., 2020) or geographical barriers (White, 2016), have been identified as better predictors of dispersal and/or range shifts than species traits. Given the observed influences of geography, environment and species traits on range shifts highlighted above, we contend that recent range edge shifts of British birds are modulated by species' trophic and morphological traits, as well as dispersal capabilities and environmental factors. However, given the elongated island topography of Great Britain, geographical constraints need to be accounted for, both to ensure accurate detection of the role of species traits, and assessing the vulnerability of species to global change.

Here, using Phylogenetic Generalized Linear Mixed Models, we explore the role of species traits in modulating range edge dynamics, and the extent to which the propensity to shift is a phylogenetically conserved trait (Davis et al., 2010; Diamond, 2018). We define range shift as the distance by which leading (Northern) and rear (Southern) range edges shifted between 1968 and 2011. We consider two main families of ecological features responsible for modulating shift: (1) species traits including trophic characteristics, body mass and dispersal capabilities and (2) environmental preferences that include climate and land cover. We study range shifts across the continuous landmass of Great Britain (England, Scotland, and Wales), as well as across the extended Great Britain, including the Northern islands of the Orkney and Shetland archipelagos. We additionally considered range size, and Northern and Southern geographical boundaries (quantified as the distance from northern and southern range edges to the corresponding geographical boundary of Great Britain) in our

analyses to account for the influence of geographical constraints, and the availability of habitat, on species' range shifts.

2 | METHODS

2.1 | Species distributions data and study areas

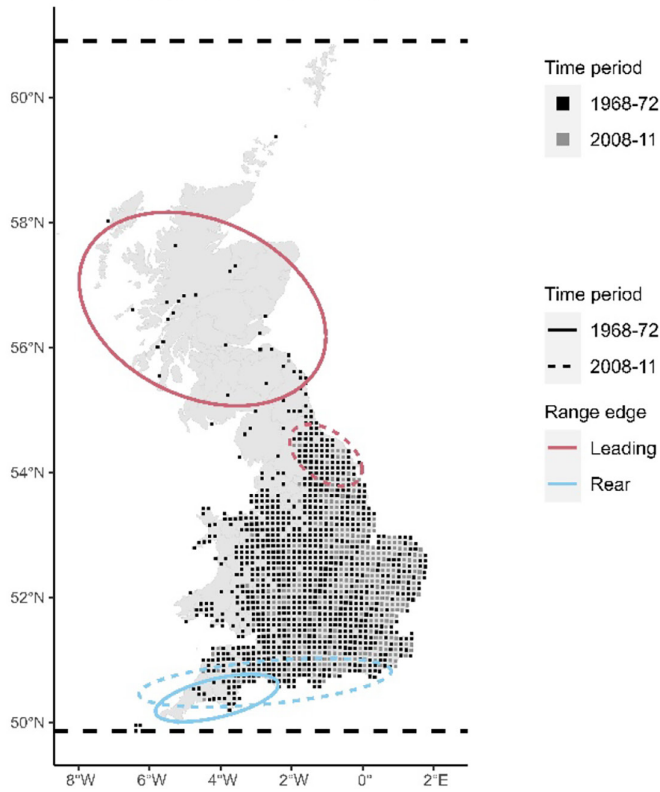
We extracted geographical distribution data at a 10×10 km spatial resolution for 311 breeding bird species across Great Britain (England, Scotland and Wales), excluding Ireland as well as the Channel Islands (Figure 1), from the British Trust for Ornithology's (BTO) British Breeding Survey scheme. The BTO provides a systematic survey of the distribution of all breeding species in Britain. Surveys were conducted by volunteers inside 10×10 km grid cells during the breeding period. The entire spatial extent was divided into subareas within regions of varying size depending on the time period (P1 and P3) with a set effort aimed at visiting all available habitat within each region (for more information on the survey protocols defined by the BTO, see text in Supplementary material 2 and Gillings et al., 2019). Records were obtained for the first and last time periods P1: 1968–1972 and P3: 2008–2011.

An accurate assessment of species' range shift requires similar survey effort across time periods. This was assessed for the BTO data by Gillings et al. (2019), who approximated survey effort using Frescalo (FREquency SCAling LOcal; Hill, 2012), that works by “identifying a neighbourhood of environmentally similar grid cells around each focal grid cell and determining the percentage of so-called benchmark species (locally common and widespread species) found in the focal square as a proxy of recording effort.” (Gillings et al., 2019). They found that P1 and P3 were similar in terms of homogeneity of survey effort across Britain (around 93% of well surveyed grid cells in both time periods).

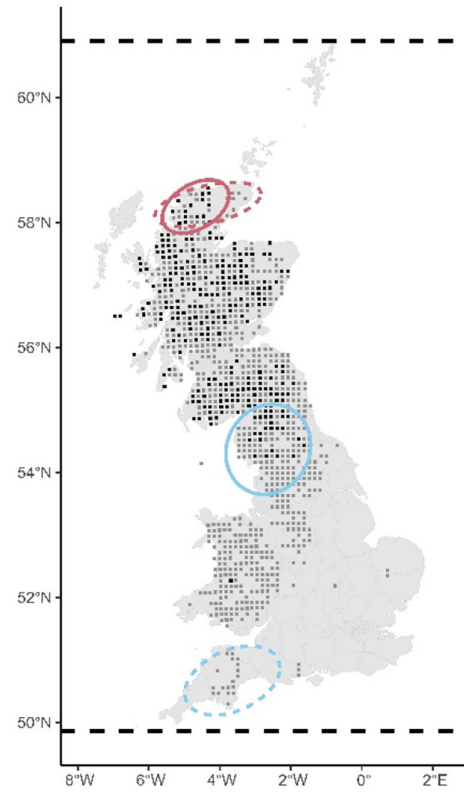
In addition, to assess the role of geographical barriers such as small expanses of water on species' realized range-edge shifts; we considered two separate study areas—the mainland: a continuous landmass excluding the Orkney and Shetland archipelagos, and the whole area which included the mainland as well as the two archipelagos (see Figure 1 for illustration).

From both study areas, we selected only those species recorded on at least 50 grid cells for each time period (P1 and P3). This threshold was chosen to ensure that species would have enough occurrences for them to have distinct leading and rear range edges (see below). We removed species constrained to coastal grid cells across the whole area (over 75% of presence cells within 20 km from the coastline) as their ranges are less likely to be described by many of the environmental variables explored here (as in Bradshaw et al., 2014; Taheri et al., 2021). In addition, we removed the northern pintail (*Anas acuta*), a northern species whose breeding range comprises the northernmost latitudes of Europe (including Siberia) and North America, close to the Arctic. In addition to rarely breeding in the UK, this species' range shift was inaccurately captured in the mainland study (leading edge shift = −236 km for the mainland study,

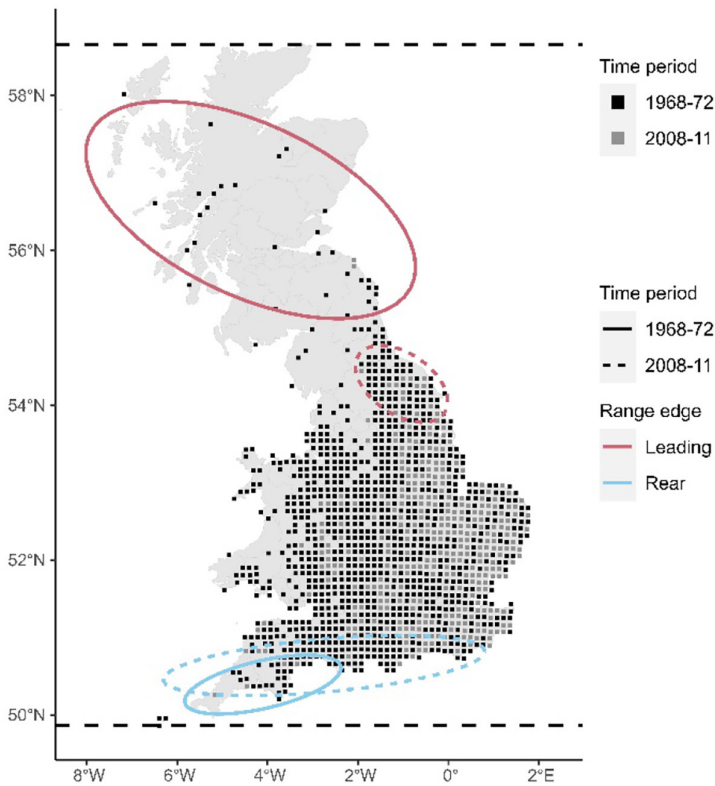
Southern species - Whole study



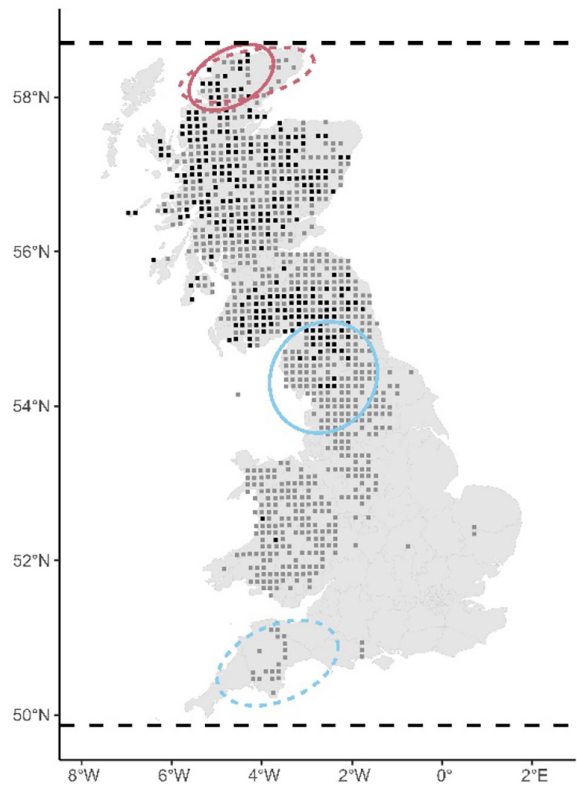
Northern species - Whole study



Southern species - Mainland



Northern species - Mainland



leading edge shift=1km for the whole study area). The mainland study (and more generally Great Britain) is a poor representation of this species' distribution. No other species suffered from such large

contrast in range shift direction and magnitude between both study areas. This resulted in 404,949 occurrence records for a final count of 135 terrestrial breeding birds (see Table S1 for the list of species).

FIGURE 1 Example of a northern (Goosander, *Mergus merganser*) and southern (European turtle dove, *Streptopelia turtur*) species range when considering the whole study area (top panels) and Great Britain mainland only (bottom panels). Black squares on the map represent grid cells where the species was recorded (BTO Breeding Bird Surveys). Horizontal dashed lines show the boundaries of Great Britain (northernmost and southernmost points—note that the Northern boundary changes when we extend the study area to the Orkney and Shetland islands) used to calculate boundary effects. Ellipses encompass the 20 grid cells used to calculate range edges. The mean latitude of the points within the red (blue) ellipse were used to quantify the leading (rear) edge. Continuous and dashed ellipses represent range edges in periods P1 (1968–72) and P3 (2008–11), respectively. See [Figure S2.1](#) for two other examples of species distribution changes for species that shifted to the Orkney and Shetland islands.

Leading and rear edges of species ranges were defined as the average latitude of the 20 northern- and southern-most grid cells in the species distribution maps, respectively ([Figure 1](#)). This allowed an accurate representation of range edges while avoiding overlap between edges in the species with the smallest ranges (50 cells as defined above). Range edge shifts were calculated independently for each edge as the distance between a given edge at time period P1 versus the same edge at P3. Lastly, range expansion was computed as the difference between leading and rear edge shift. Positive values representing expansion, and negative values representing contraction.

2.2 | Geographical constraints

We included geographical constraints hypothesized to influence species capacity to shift their range edges into our analyses. This allowed us to account for the influence of exogenous geographical factors on range edge shifts, as well as the fact that our data is only a subset of species' entire ranges (which often expand beyond Great Britain). We considered (1) a coarse measure of range size, quantified as the number of grid cells where the species was recorded in P1 and (2) distance to geographical boundaries. The latter was quantified as the distance from each species' leading edge to the northernmost point of the mainland (latitude of 58.70 decimal degrees, [Figure 1](#)) for the mainland study or to the northernmost point of the Shetland islands for the whole study (latitude of 60.90 decimal degrees); and as the distance from the rear edge to the southern tip of Great Britain (latitude of 49.86 decimal degrees, [Figure 1](#)).

2.3 | Species traits

2.3.1 | Diet diversity

A first measure of diet diversity [DD1] was based on diet categories extracted for each species from the Elton Traits database (Wilman et al., 2014). Elton Traits provide information on the fraction (out of 100) of the following ten categories in each species diets: (1) Invertebrates, (2) endotherm (3) ectotherm, (4) unknown vertebrates, (5) fish, (6) fruit, (7) nectar, (8) seed, (9) plant (other than 6, 7, and 8) and (10) scavenger. We used the Shannon measure of entropy (Equation 1) to quantify diet diversity of species j ,

$$DD1_j = \left(- \sum_{i=1}^N (P_{ij} \times \log_{10}(P_{ij})) \right) \quad (1)$$

where N is the total number of categories in the set (in this case diet categories) and P_i is the proportion of the diet category i in species j diet.

2.3.2 | Normalized indegree

An alternative measure of diet breadth [DD2] was quantified as the number of prey in each species diet, normalized by the total number of species in the food web from which the number of prey was quantified (see definition of the food web below):

$$DD2_j = \sum_{i=1}^N (P_{ij}) / N \quad (2)$$

with N the number of species in the British food web and P_{ij} equals 1 if species i is consumed by j or 0 if not. The British food web was extracted by sub-setting the European-wide food web compiled in the TetraEU 1.0 database (Maiorano et al., 2020), comprising trophic interactions for all tetrapod vertebrates in Europe extracted from observations, literature sources and expert knowledge. Using the geographical distribution data for all species included in the TetraEU food web (Maiorano et al., 2013) we selected only the species that overlapped the map of Great Britain from the 'rnatuarearth' R package (South, 2017). The British food web thus obtained comprised 282 tetrapod species and 4186 trophic interactions. However, since only tetrapods are resolved to the species level in this network, basal tetrapods that consume insects, plants and carrion resources have a null normalized indegree (Equation 2). To compare diet breadth across all species in the network, we replaced the null values of normalized indegree obtained for basal species with the DD1 diet diversity measure (a normalized quantity) defined above. Thus, DD2 is a combination of (1) the normalized indegree for non-basal species ([Equation 2](#)) and (2) DD1 of the basal species.

2.3.3 | Trophic position and number of predators

Two additional measures were extracted from the British food web: (1) the number of predators that consume each species and (2) the trophic position, calculated for each species as its average position across all food chains (i.e. paths between basal resources and the consumer species) containing the species, using the 'cheddar' R package (Hudson et al., 2013).

2.3.4 | Body mass

Body mass is a fundamental species trait that covaries with other traits such as dispersal capacity, trophic level, population abundance and reproductive behaviour (Lurgi et al., 2012b). As such, it is expected to have a central role on influencing species' responses to environmental change. We extracted body mass (g) from the Elton Traits database for all the species in our dataset (Wilman et al., 2014).

2.3.5 | Dispersal abilities

Hand-wing index—a morphological metric linked to wing aspect ratio has been widely used as a single-parameter proxy of avian flight efficiency and dispersal ability (Sheard et al., 2020). We included hand-wing index (obtained from Sheard et al., 2020) to test whether species' range shift correlated with dispersal capabilities.

2.4 | Species' environmental preferences

To quantify the relationship between the range edge shifts of species and their environmental preferences, we assessed the environmental niche of the studied species in Great Britain (whole study area including Orkney and Shetland islands) during P1 based on climatic and land cover variables. Climatic variables considered included the mean temperature and precipitation during both, the winter (January and February) and spring (March, April and May) seasons extracted for each 10×10km grid cell within Great Britain from 1963 to 1972 (P1) (Harris et al., 2020). Land cover variables included the proportion forest, grassland, cropland and settlements (i.e. urbanized areas) for each cell in 1960 (P1), extracted from the Historic Land Dynamics Assessment (HILDA) land use change database (1×1km) (Fuchs et al., 2015) (see Figures S2.2 and S2.3 for changes in climate and land cover across time periods). We assessed the relative importance of climatic and land cover variables on the presence-absence of breeding records from P1 using an ensemble of five different Species Distribution Models (SDMs) (glm, gam, fda, svm, gbm) within the “*sdm*” R package (Naimi & Araújo, 2016). We used a randomization procedure with 10 runs of subsampling replications with 30% of the data reserved for testing.

Species environmental preferences (climatic and land cover) were extracted by collapsing the Area Under the Curve (AUC) measures independently for each of the 4 climatic and 4 land cover variables from the SDMs into 4 overall summary components using Principal Component Analysis (PCA). We ran two independent PCAs: one using the 4 land cover variables and another one using the 4 climatic variables. We extracted the values for the centred and scaled rotated data for each data point (i.e. species) for the dimensions (i.e. axes) with eigenvalues larger than 1 (Tables S2.1 and S2.2). This yielded 4 summary environmental variables (2 from each PCA). Of the 2 summary environmental variables extracted from the climatic PCA, one showed a negative correlation to spring and winter precipitation whereas the second was positively correlated to spring and winter temperatures (Tables S2.1

and S2.3). From the land cover PCA one variable was negatively correlated to forest and grassland while the other was positively correlated to cropland and urban areas (Tables S2.2 and S2.4). These were used as measures of the importance of each environmental factor in the comparative analysis of range shifts.

As a further measure of species environmental preference, habitat generality was calculated using the Shannon diversity index (Equation 1), over the 8 climatic and land cover variables described above, with N being the total number of categories (climate and land cover) and P_i the mean relative contribution of the category i to the SDMs. Thus, species with homogeneous contribution of all environmental dimensions will have a higher diversity than species who exhibit disproportionate preference for a single environmental dimension. Hence larger values for the Shannon index were assumed to represent stronger habitat generality.

2.5 | Bird phylogeny

To incorporate species phylogenetic relatedness into our analyses, we used a widely adopted bird consensus phylogeny from the Big Bird dataset (Burleigh et al., 2015), which includes 6714 species. We pruned this tree to obtain a subtree comprising only the 135 species considered in this study.

2.6 | Species subgroups

To compare species traits among subgroups of species with potentially different local adaptation capacities and spatial distributions, we performed two independent splits of the dataset according to: (1) geographic position of the distribution core and (2) taxonomy. We split species into northern ($N=44$) and southern ($N=91$) species (Figure 1) based on the average latitude of the species distribution in P1 relative to the geographical centre of Great Britain (54.24 decimal degrees). To compare our results with studies of, for example Angert et al. (2011), we also considered the split between Passeriformes ($N=67$) and other species, using the taxonomy from the Elton Traits database (Wilman et al., 2014) (see Table S1).

2.7 | Statistical analyses

As exploratory analysis, we (1) quantified the proportion of species that showed statistically significant shifts in either direction (poleward, southward or stable) and (2) looked for differences in shifts between northern and southern species and between leading and rear edge shifts for each group. For these analyses, given that our range shift data did not conform with the normality assumption required to conduct “standard” Student t tests (checked with Shapiro tests), we used their non-parametric equivalent, two-sided Wilcoxon tests, which ranks the values in each sample and compares the distribution of the difference between ranks of

each sample to its null distribution. Effectively, this compares the median between each sample. We adopted a significance level of 0.05. For (1), we carried out one-sided Wilcoxon signed rank tests. For each species, this test compared the median latitude of the 20 cells comprising their leading and rear edges between P1 and P3. If the median latitude of the cells in P3 was significantly greater or smaller than in P1 ($p < 0.05$), then we concluded that the species shifted significantly poleward. For (2), using one-sided Wilcoxon rank sum tests, we compared the magnitude of all the leading and rear edge shifts between northern versus southern birds, as well as the magnitude of all leading versus rear edge shifts among southern and northern birds.

We modelled the relationship between the observed leading/rear edge shifts and the centred and scaled (i.e. subtracting the mean and dividing by the standard deviation) species traits, environmental preferences and geographical constraints described thus far using phylogenetic linear mixed models with a Gaussian distribution (*phyr* R package (Li et al., 2020)). Variables used as predictors in our models did not display high levels of correlation (Figure S2.4). Allowing for a correlation structure among phylogenetically related birds enabled us to account for the potential lack of independence in responses between related species (Diamond, 2018). We employed the same model structure (i.e. including all species traits, environmental preferences and geographical constraints) for all species groups analysed. To quantify the variance explained by the phylogenetic signal alone, we measured the difference in variance explained by the phylogenetic models versus equivalent linear models that do not account for phylogeny. We assessed goodness of fit with an R^2 that measures the relative sum of square errors for a full and reduced model using the “*rr2*” package (Ives, 2019).

For all models, we considered effects of each explanatory variable to be ‘significant’ if their p -value was below 0.05 and “marginally significant” if their p -values were between 0.05 and 0.1. For the entirety of this study, the poleward shift is the “expected” shift, so when we state that a covariate has a significant “positive effect” on the shift of either the leading or rear edge we mean it is significantly correlated with poleward shift of the said edge. The model estimates are reported in their scaled form to interpret their magnitude as well as their sign. We also occasionally report the non-scaled results which are obtained by multiplying the scaled estimate by the standard deviation of the original (non-scaled) variables. Non-scaled estimates can be interpreted as the shift in kilometres resulting from one unit increase in the variable of interest.

All analysis were conducted in R version 4.1.2 (R Core Team, 2021).

3 | RESULTS

In the following, results reported refer to the mainland study unless stated otherwise.

Between the late 1960s and 2011, 50% and 53% of the 135 British breeding birds considered here displayed stable rear and leading edges, respectively. Meanwhile, 30% shifted their leading edge significantly poleward by 62 ± 73 km (mean and SD) and 30% shifted their rear edge poleward by 37 ± 60 km. Finally, 19% of species shifted their rear-edge southward by -45.61 ± 75.54 km and 17% of species shifted their leading edge southward by -50.83 ± 60.43 km.

Northern species shifted their leading edge significantly less than Southern species (Wilcoxon rank sum test, $W = 1568$, $p = 0.02$), with a mean leading-edge shift of -1.54 ± 6.91 km for Northern and 14.83 ± 73.6 km for Southern species. The same was not true for rear edge shifts ($W = 1978$, $p > 0.05$, mean rear edge shift of 3.36 ± 93 km for Northern species and 2.05 ± 18.66 km for Southern species).

Expectedly, after accounting for boundary effects, southern species, Passeriformes and all species together whose leading edge was further from the northern boundary of the study area experienced more poleward shifts in their leading edge (southern species: number of species (N) = 91, model estimate (e) = 39.81, $p < 0.01$; Passeriformes: $N = 67$, $e = 38.92$, $p < 0.001$; all species: $N = 135$, $e = 27.99$, $p < 0.001$) (Figure 2b–d and see Figures S2.5–S2.8 for conditional regression graphs). For example, converted into its original (non-scaled) units, this means that for 1 km increase in distance between the northern boundary and the species' southern leading edge, southern species shifted 0.23 km further north (0.25 km for northern species and 0.19 km for all species; see Table S3.2 for all coefficients in km). Similarly, southern species, northern species and all species together further from the southern boundary were biased toward southward shift in their rear edge (southern species: $N = 91$, $e = -12.86$, $p < 0.001$; northern species: $N = 44$, $e = -49.15$, $p < 0.05$; all species: $N = 135$, $e = -14.26$, $p < 0.05$) (see Table S3 and Figure 2).

On the contrary, northern species whose leading edge was further away from the northern boundary of Great Britain experienced a smaller shift in their leading edge ($N = 44$, $e = -3.38$, $p < 0.01$). Converted into its original (non-scaled) units, this means that for one unit increase in distance between a species leading edge and the island's northern boundary, species shifted 0.19 km (standard error [SE] = 0.09 km) further north.

Range size however, only had a strong positive effect on Passeriformes' leading-edge shifts ($N = 67$, $e = 24.06$, $p < 0.05$) (Figure 2c).

3.1 | Geographical barriers change the importance of species traits on leading-edge shift

When comparing results for the mainland only and those for the whole study area (including the Orkney and Shetland islands; Figure 1), we found that, for all species subgroups, the effect size of species traits on leading-edge shift increased strongly between the models for mainland only (mean effect size of 4.03, $SD = 4.00$) to those considering the whole study area (mean effect size of 9.70,

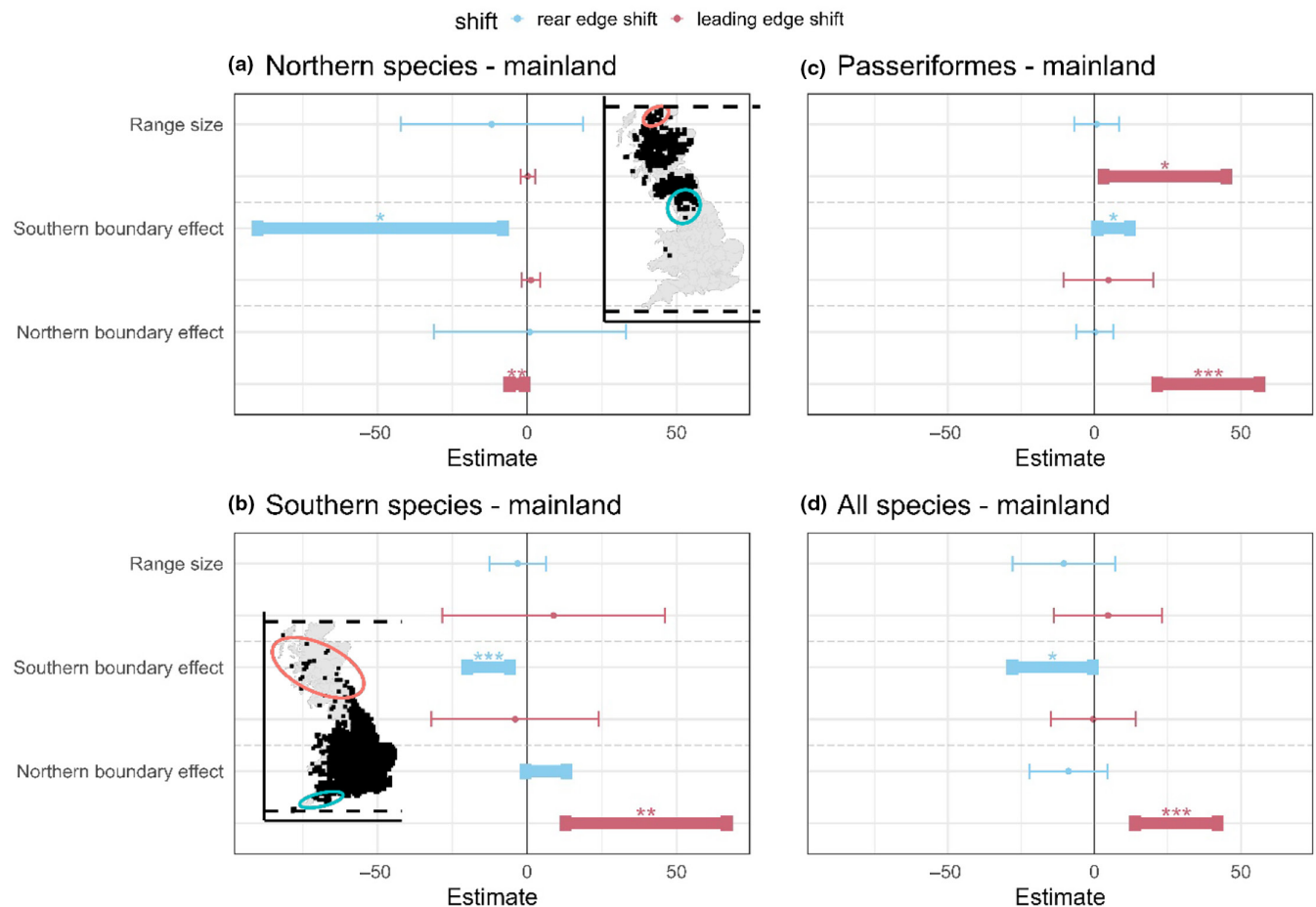


FIGURE 2 Geographical barriers constrain range edge shifts in British breeding birds. Effect sizes (shown with 95% CIs) of geographical constraints on leading (red) and rear (blue) range edge shifts of British birds as determined by phylogenetic generalized linear mixed models (results for the whole study are very similar and presented in Figure S2.9). A positive effect means that the variable is positively correlated with a poleward range edge shift. Each plot corresponds to a subgroup of species: (a) northern species, (b) southern species, (c) Passeriformes and (d) all species. Significant and marginally significant effects of species traits are highlighted with thicker error bars. The significant effects' confidence intervals do not overlap zero, they only seem to from the enlarged error bars. Significance codes (p -values): <0.1 ; * <0.05 ; ** <0.01 ; and *** <0.001 .

SD=13.35). Thus, Passeriformes showed significant effects of logged body mass ($N=67$, $e=-28.61$, $p<0.05$) and habitat generality ($e=-28.03$, $p<0.05$) and marginally significant effect of sensitivity to precipitation ($e=-15.93$, $p<0.1$) on their leading edge shifts for the whole study. However, none of these effects were significant for the mainland study area (logged body mass: $e=-12.06$, $p>0.1$; habitat generality: $e=-7.17$, $p>0.1$; precipitation: $e=-10.58$, $p>0.1$).

3.2 | Northern species and Passeriformes presented most evidence for species' traits-led rear-edge shift

Southern birds only showed a significant effect for one species trait: number of predators, where species with more predators were more likely to shift their rear edge poleward ($N=91$, $e=4.61$, $p<0.05$). For all birds together in the mainland study, none of the species' traits we tested here succeeded at explaining range shifts.

Overall, species traits were only significantly related to shifts among northern and Passeriform species (Figure 3 and Table 1), and mostly for rear-edge shifts. The following results thus focus on these subgroups (but see Table S3 for full results).

3.3 | Trophic traits relate to northern and Passeriform species' rear-edge shifts

The number of predators was found to be positively related to rear edge shifts in northern species ($N=44$, $e=49.85$, $p<0.05$), being the most relevant trait tested here. Thus, species with many predators shifted their rear edge poleward by 6.03 km (SE = 3.04 km) per added predator on average. In addition, trophic position had a marginally significant negative effect on rear-edge shift of Passeriform species ($N=67$, $e=-7.02$, $p<0.1$), meaning that species at lower trophic position were more likely to shift their rear-edge poleward.

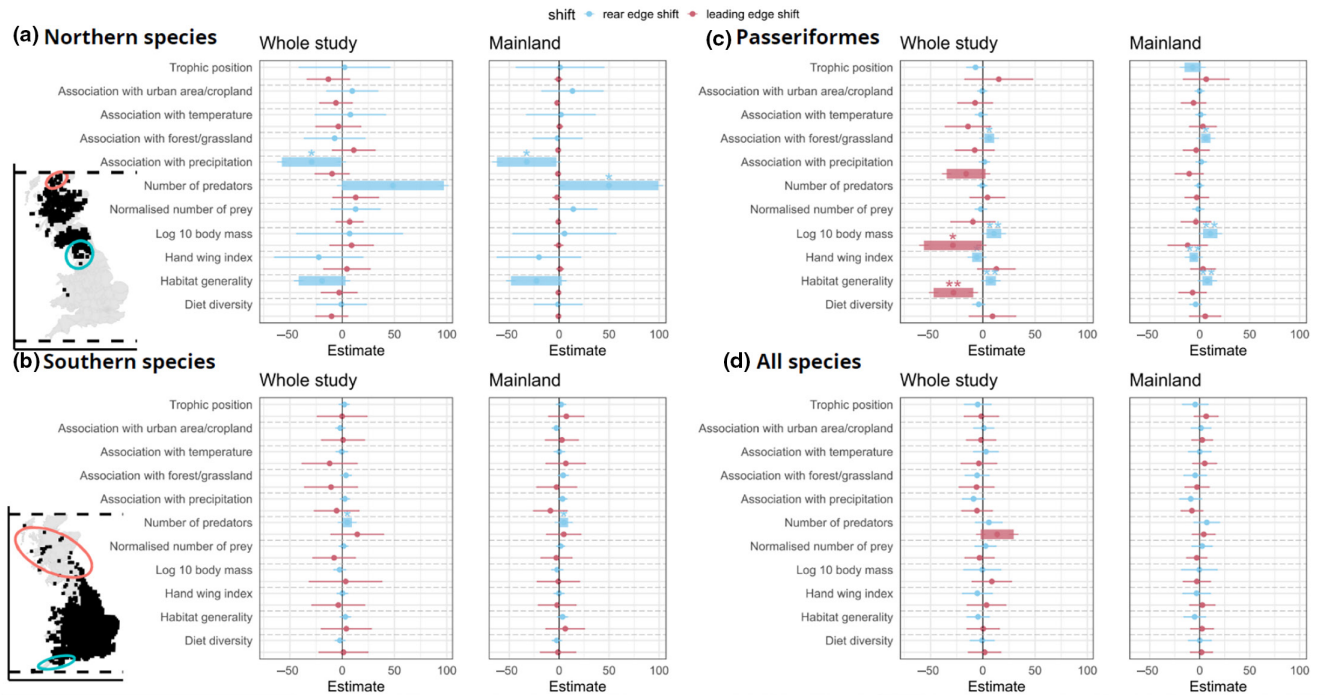


FIGURE 3 Species traits and environmental preference as determinants of range edge shifts in British breeding birds. Effect sizes (shown with 95% CIs) of species-specific traits and environmental preferences on leading (red) and rear (blue) range edge shifts of British birds as determined by phylogenetic generalized linear mixed models (results for the full models are presented in Figure S2.1). A positive effect means that the variable is positively correlated with a poleward range edge shift. Each plot corresponds to a subgroup of species: (a) northern species, (b) southern species, (c) Passeriformes and (d) all species. Southern species and all species together (bottom plots b and d) show no significant results. For each species subgroup (Northern, Southern, Passeriformes, all species) the plots depicts the models results for the whole study area and the mainland only. Maps illustrate the ranges of a northern (Goosander, *Mergus merganser*) and a southern species (European turtle dove, *Streptopelia turtur*), respectively (see Figure 1 for larger figure). Significant and marginally significant effects of species traits (highlighted error bars) on range edge shifts were mostly observed for northern species and Passeriformes (a, c). The effect size of species traits on leading edge shifts decreased strongly on the mainland dataset when compared to the results from the whole study area. The significant effects' confidence intervals do not overlap zero, they only seem to from the enlarged error bars. Significance codes (p -values): <0.1; * <0.05; ** <0.01; and *** <0.001.

3.4 | Body size and dispersal ability influence rear-edge shifts in Passeriform species

Body mass was a strong driver of Passeriform species' rear-edge shift: larger species displayed further poleward rear-edge shifts ($N=67$, $e=10.54$, $p<0.01$). Surprisingly, Passeriformes with larger hand-wing index also displayed the mostly southward rear-edge shifts ($e=-5.89$, $p<0.01$).

Neither body mass and hand-wing index nor diet diversity revealed any relationship with range edge shifts for northern species.

3.5 | Environmental preferences affect rear-edge shifts differentially across species subgroups

Species environmental preferences influenced rear-edge shifts differently for Passeriform and northern species. Among Passeriformes, habitat generalists were more likely to shift their rear edge poleward ($N=67$, $e=7.56$, $p<0.01$). On the other hand, northern habitat generalists were less likely to shift their rear edge poleward (rear edge: $N=44$, $e=-22.74$, $p<0.1$).

In addition to the coarse measure of habitat generality, we investigated whether some species who relied on specific land cover types or climatic conditions were more susceptible to shift. We found that forest and grassland Passeriform species shifted their rear edges more poleward than species with other environmental preferences ($N=67$, $e=6.04$, $p<0.05$). Thus, species avoiding human landscapes seemed to shift their rear-edge further. Additionally, northern species with distributions driven by precipitation were more prone to shift their rear edge poleward than those with other environmental affinities ($N=44$, $e=-35.7$, $p<0.05$) (because the second PCA axis is negatively correlated to precipitation).

3.6 | Range expansion is determined by the same factors as edge shifts

To paint a complete picture of species range shifts, we looked at how species traits affected overall species range expansion or contraction (see Table S3). Model outputs for the effect of geographical boundaries on range expansion were similar to those observed in models of leading edge dynamics for all species together

TABLE 1 Effects of species traits and environmental preferences on mainland range shifts in British breeding birds.

Shift	Subgroup	N	R ²	R ² of phylogenetic signal	Distance to northern boundary	Distance to southern boundary	Hand-wing index	Range size	Habitat generality	Logged body mass	Number of predators	Precipitation	Grassland and forest	Trophic position
Leading edge shift	Northern	44	0.37	0.1	-3.38*	1.28	0.88	0.24	-0.67	-0.46	-2.11	-1.05	-0.94	-0.62
	Passeriformes	67	0.39	0	38.92***	4.81	3.29	24.06*	-7.17	-12.06	-2.97	-10.58	-3.51	6.45
	Southern	91	0.25	0	39.81**	-4.00	-1.96	8.84	6.06	-0.79	4.62	-8.75	-2.47	7.18
	All species	135	0.23	0	27.99***	-0.42	2.60	4.65	2.29	-2.90	4.01	-7.82	-2.70	6.43
Rear edge shift	Northern	44	0.42	0.2	0.89	-49.15*	-20.22	-11.88	-22.74	5.36	49.85*	-32.48*	-1.48	0.88
	Passeriformes	67	0.32	0	0.26	6.55*	-5.89**	0.75	7.56**	10.54**	-0.50	1.48	6.04*	-7.02
	Southern	91	0.24	0	6.34	-12.86***	-0.09	-3.17	3.40	-1.91	4.61*	3.34	3.99	1.89
	All species	135	0.1	0.03	-8.86	-14.26*	-3.12	-10.42	-5.06	-0.40	6.96	-9.03	-4.58	-4.54
Expansion	Northern	44	0.43	0.22	-4.27	50.44*	21.10	12.12	22.07	-5.83	-51.96*	31.43*	0.54	-1.51
	Passeriformes	67	0.35	0	38.66***	-1.74	9.19	23.31	-14.72	-22.60	-2.47	-12.06	-9.55	13.47
	Southern	91	0.2	0	33.47*	8.87	-1.88	12.01	2.66	1.12	0.02	-12.09	-6.46	5.28
	All species	135	0.14	0	38.51***	13.24	9.16	16.27	9.13	-3.80	-0.98	3.02	1.72	9.34

Note: Subset of the outputs from phylogenetic linear mixed models relating range edge shift to species traits, environmental preferences and geographical constraints for the mainland study. For legibility, this table only present results of geographical constraints, species traits and environmental preferences with a significant effect on range edge shifts. A table with the full set of results is available in Table S3.1. All variables were centred (i.e. subtracting the mean) and scaled (i.e. dividing by the standard deviation) for non-scaled output see Table S3.2. Each row corresponds to one model per type of shift (leading/rear edge shift, or expansion) and species subgroup (northern, southern, Passeriformes, all species). The R² for the phylogenetic signal was obtained as the relative variance explained by the PGLMM versus that of the equivalent linear model with no phylogenetic random effect. Significance codes (p-values): <0.1; *<0.05; **<0.01; and ***<0.001.

and for southern species (Table 1). This was expected given the considerably larger leading versus rear edge shifts in the majority of species. Interestingly, northern birds constituted a notable exception. In their case, the number of predators was related to range contraction ($N=44$, $e=-51.96$, $p<0.05$), whereas precipitation was, on the other hand, related to range expansion ($N=44$, $e=31.43$, $p<0.05$).

3.7 | Effects of phylogenetic relatedness on range edge shifts are negligible

Phylogenetic signal on species range shifts was weak overall. The strongest signal was found in the model of rear edge shifts for northern species, with 20% of the model variance explained by phylogeny ($p<0.001$) (Table 1 and Table S3). As a comparison, the phylogenetic signal for the rear edge shifts when considering all species together only explained 3% of model variation ($p=0.04$). No other models showed significant phylogenetic signal, suggesting that within the subset of species analysed here, range shift was unaffected by species relatedness.

4 | DISCUSSION

We investigated the relationship between recent (from 1968 to 2011) geographical range edge shifts of 135 British breeding birds and their trophic and morphological traits, as well as dispersal capabilities and environmental preferences, while accounting for geographical features that are known to constrain these shifts. Due to their recognized importance in species responses to environmental change, we only considered latitudinal shifts in this study (but see e.g. Taheri et al. (2016) for longitudinal range dynamics). We found varying magnitudes of shifts for northern and southern birds. Our results suggest that on islands like Great Britain, it is important to control for geographical barriers to range edge shift as they had a strong role in constraining the direction and magnitude of shifts. Species traits had a limited effect compared to the constraints imposed by these geographical features. Nonetheless, northern species, which have been deemed more vulnerable to environmental change (Huntley et al., 2006; Lindström et al., 2013; Pearce-Higgins et al., 2015) appear to have shifted their leading edge the least. An association of trophic traits and environmental preferences seemed to partly describe rear-edge shifts observed in northern species and Passeriformes but not those of all species together nor for Southern species. Interestingly, leading-edge shifts only showed effect of species' traits when we included the northern islands of the Orkney and Shetland archipelagos, thus introducing some geographical barriers in our latitudinal gradient. Northern and Passeriform species with many predators were more likely to shift their rear edge poleward. This suggests an imbalance in shift across trophic levels, with species at lower trophic levels more likely to shift their ranges compared to top predators. In addition, northern and Passeriform species with specific land cover

preferences shifted more: habitat specialists, species sensitive to precipitation or avoiding anthropized land cover were more likely to shift their rear edges poleward.

4.1 | Geographical boundaries

It has recently been reported that range edge shifts at the northern or southern boundaries of Great Britain cannot be distinguished from what would be expected from random processes operating on range dynamics (Taheri et al., 2021). This observation might be a consequence of the geography Great Britain, due to a limited amount of colonizable area at both the northern and southern edges of the island. This issue is accentuated by the fact that Great Britain comprises only a subset of the entire geographical range of its resident bird species, which extend beyond British boundaries. Thus, due to the nature of the geographical scope, we only capture species' local range shifts. Most northern species in Great Britain are at the lower end of their entire range, while the opposite holds for southern species. Given that most species range edges do not align between Great Britain and Europe, our results might be difficult to extrapolate to the continent. For instance, environmental preferences of British birds might not necessarily reflect those of mainland Europe. Similarly, the direction and magnitude of range shifts in Great Britain might not match shifts observed elsewhere, even for the same species considered here.

4.2 | The differential exposure to climate change between subgroups

Species traits seem to mostly influence range shifts in northern species—the species that shifted less in magnitude—and Passeriformes. In addition from being limited by available colonizable habitat, northern species are often exposed to faster climate change (Loarie et al., 2009), so their response may forecast future shifting behaviours for species at lower latitudes. Southern species are usually considered warm tolerant and have increased in abundance relatively to northern birds in recent decades across Europe (Huntley et al., 2006; Lindström et al., 2013). Conversely, northern birds and habitat specialists have shown decreasing population trends in a study of European birds response to warming (Pearce-Higgins et al., 2015). More recently, Antão et al. (2022) reported that northern species found themselves in suboptimal niches more often than southern species in light of recent climate change. Given that geographical barriers did not act as a major constraint on northern species, their higher susceptibility to climate change causing their population to decline could partly explain their smaller shifts. This paints a complicated picture where observed range edge shifts result from the response of species to exogeneous factors—like geographical boundaries and climate—which can also translate into changes in population trends, both ultimately modulated by species traits and the underlying environmental conditions.

This interplay between species' vulnerability and exposure to change (Comte et al., 2014) transpires in northern species, among whom habitat specialist and species sensitive to precipitation were more likely to shift their rear edge poleward. Indeed, contrary to generalist species, shifting for specialist species under high exposure to climate or land cover change may be a necessity if their range of tolerance is small (Huey et al., 2012), meaning that their "shifting" threshold is reached faster.

4.3 | Geographical barriers enhance the effect of species' traits on range shift

When comparing range shifts across a continuous landmass to those including species dispersing to the northern islands of Orkneys and Shetlands, we found that the effect sizes of species' traits on leading-edge shifts were much smaller in the mainland only study. This suggests that species' traits might emerge as relevant predictors of range shift in the presence of geographical barriers that filter the species that can or need to cross them. We would expect similar results for species dispersing across the English Channel from Europe to Great Britain for example. White (2016) found that dispersal ability interacted with geographical barriers to predict Himalayan bird's range size. Further analyses could be performed on the BTO data to assess the effect of geographical barriers on species distributions depending on their dispersal capabilities. For instance, developing a quantitative assessment of the extent of water bodies species have to cross in order to colonize new areas as a measure of the geographical barriers.

4.4 | Species' vulnerability as the main driver of some shifts

In our case however, the traits that were highlighted in species that overcame geographical barriers were not related to dispersal ability but rather to vulnerability: the species that dispersed to those islands were habitat specialists or smaller bodied species sensitive to precipitation. Again, this supports our hypothesis that the species shifting are more vulnerable to environmental change. However, the opposite set of traits were found to drive rear-edge shift in Passeriformes, suggesting that poleward leading- and rear-edge shift were realized by two distinct sets of Passeriformes that can be described by their body size and habitat generality. These two sets of results for the same subgroup of species suggests different mechanisms driving some Passeriformes to shift their rear edge while other Passeriformes shift their leading edge. It may be that one set of Passeriformes are shifting their leading edge by necessity to track their climatic or environmental niche (thus why traits related to vulnerability were most important), while another set of more generalist Passeriformes are shifting their rear edge opportunistically. This refutes our initial hypothesis that leading-edge

shifts would be driven by traits related to colonization and dispersal capabilities (Angert et al., 2011; Comte et al., 2014) while rear-edge shifts would be rather driven by species' biotic interactions and vulnerability, as it seems that vulnerability can play a role in both instances.

Another line of evidence against this hypothesis was the negative effect of dispersal ability (through hand-wing index (Sheard et al., 2020)) on Passeriformes' rear-edge shifts. An explanation for this unexpected result may be that hand-wing index is strongly related to migratory behaviour (Sheard et al., 2020). It has been suggested that migratory birds may be less able to disperse due to their high fidelity to breeding sites and constraints of having to evolve yet new adaptations to novel conditions in discontinuous habitats like their breeding and wintering grounds (Bensch, 1999).

4.5 | Trophic traits are important predictors of rear-edge shift

Our results suggest that measures of trophic traits such as number of predators are relevant in predicting range edge shifts of northern and southern birds too. This observation could arise from two processes: either predator (here raptor) species are declining (McClure & Rolek, 2020), thus releasing prey from top down control (Lurgi et al., 2012b) and prey species are better able to track climate change than their predators thus creating spatial mismatch in prey–predator population (Gilman et al., 2010) or climate and land use changes affect predator phenology (Bastille-Rousseau et al., 2018) subjecting prey to higher predatory pressure. In all cases, prey species exploited by a larger set of predator species are expected to shift their range to "predator free" grounds.

In line with this observation, higher consumers among Passeriformes showed slightly smaller rear-edge shifts compared to lower trophic levels. Due to their high mobility and usually larger ranges, top predators may be equipped with better phenotypic and diet plasticity, able to adapt to changing conditions more easily (Diamond, 2018; Estrada et al., 2016). It may also be that predator population are decreasing faster than lower trophic level (McClure & Rolek, 2020), preventing those species to shift. This imbalance in shifts across trophic levels could result in important compositional changes of communities and alterations to local food web dynamics, including dietary shifts of consumers resulting from changes in abundance of prey (Lurgi, López, & Montoya, 2012a, b). For instance, shifts of species in lower trophic levels could induce changes in interaction strength inside source (from which species emigrate) and sink (to which species immigrate) communities. Higher trophic levels could find themselves tracking their prey and moving to sub optimal environments. For example, raptors are predicted to be particularly susceptible to these changes, as the occurrence of their prey is highly sensitive to environmental change (Kassara et al., 2017). An avenue for future research would be the investigation of whether predators have been able to track their prey across our study period.

4.6 | Weak evidence of the role of species traits overall

In our study, species traits only became significant within subsets of species, for birds that shifted less in magnitude and with higher exposure to change. Sub-setting our dataset among species reduces the number of observations used for inference, increasing chances for significant results to emerge by chance alone. Despite this, our conclusions agree with previous contrasting evidence of species' traits as reliable predictors of range shift in the literature (Beissinger & Riddell, 2021), which often stems from the dependency of these relationships on the species subgroup considered. For example, although trophic position has been found to be positively correlated to range shifts in marine species, this trend was mostly influenced by a handful of species, and when looking at subgroups comprised of fish species only, the trend was reversed (Sunday et al., 2015). Similarly, diet breadth was reported to have a positive effect on all North American birds and Passeriformes's shifts (Angert et al., 2011), but Auer and King (2014) who studied a subsample of Angert et al. (2011)'s bird assemblage reported the inverse result. Thus, species' traits seem to perform poorly in finding generalizable patterns that describe all species' range shifts.

Although we acknowledge that we did not consider all potentially relevant species traits in our analyses (e.g. traits defining reproduction strategies (Weil et al., 2022) or competition (Beissinger & Riddell, 2021)), we do not stand alone in finding that species' traits have weak explanatory power for range shift. Much evidence suggests that the power of generalization of species' traits is weak. The overall lack of support for species traits in explaining shifts was discussed by, for example Beissinger and Riddell (2021) and Estrada et al. (2016). Beissinger and Riddell (2021), for example, mentioned that species that inhabit the leading edge of a geographic range "often exhibit trait values that depart from the species mean due to unique selective pressures at the range edge". Species' traits are also not fixed. In fact, traits like body condition have varied substantially in European birds over the last decades as a result of warming temperatures (McLean et al., 2022). Other traits involved in phenotypic adaptation like egg-laying date and number of offspring have varied too (McLean et al., 2022). This suggests that there is a non-negligible role of phenotypic plasticity and adaptation in addition to range shift that intervene in response to changes in local conditions.

4.7 | Conclusion

The evidence of recent range shift as a response to climate change and other disturbances is undeniable (Chen et al., 2011; Parmesan & Yohe, 2003) and the attempts to discriminate among range expanders and contractors are numerous (e.g. Angert et al., 2011; Auer & King, 2014; Bradshaw et al., 2014; La Sorte & Thompson III, 2007; Sunday et al., 2015; Tingley et al., 2012; Yang et al., 2020). Our work differs from previous efforts to tease out the differences between these groups of species in that (1) it was set in a bounded environment,

where species are physically constrained in their shifts and (2) we accounted for geographical constraints, environmental preferences and species traits (including trophic characteristics) within the same analytical framework. We showed that species traits can account for small amounts of shift but fail to explain prominent variation in range shifts, especially if the geographical context is not considered. Once physical limitations to range shifts were accounted for, some species traits were found to be relevant for specific species subgroups. However, larger range shifts were best explained by boundary effects, which overshadowed species traits. Although compartmentalization is detrimental to generalization, our hypothesis that exposure to climate change and habitat availability, and their interplay with species traits, are responsible for some of the differences reported between subgroups (Bradshaw et al., 2014; Pearce-Higgins et al., 2015) revealed useful knowledge that can be incorporated into predictive frameworks to forecast future range shifts of species.

ACKNOWLEDGEMENTS

We thank Prof. Emily Shepard for her insight and suggestions throughout this study. LT was funded by Swansea University ECR BIOL postgraduate research scholarship. NG received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement BIO-FOODWEB (No 101025471).

CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

Breeding and wintering bird distributions in Britain and Ireland from citizen science bird atlases (Gillings et al., 2019) can be accessed at <https://www.bto.org/our-science/data/what-data-are-available>. Climatic data (Climatic Research Unit (CRU) time series v.4.01 from 1901 to 2016) (Harris et al., 2020) can be accessed at <https://catalogue.ceda.ac.uk/uuid/58a8802721c94c66ae45c3baa4d814d0>. Land cover changes in Europe (HILDA version 2.0 from 1900 to 2010) (Fuchs et al., 2015) can be accessed at <https://doi.pangaea.de/10.1594/PANGAEA.921846?format=html#download>. Phylogenetic tree (BigBird phylogeny 6714 taxa tree) (Burleigh et al., 2015) can be accessed at <https://datadryad.org/stash/dataset/doi:10.5061/dryad.r6b87>. Dispersal capabilities through the global hand-wing index (Sheard et al., 2020) can be accessed at <https://zenodo.org/record/3747657>. Species traits (diet composition, body mass - Elton traits) (Wilman et al., 2014) can be accessed at https://figshare.com/articles/Data_Paper_Data_Paper/3559887. European food web (TETRA EU 1.0) (Maiorano et al., 2020) <https://datadryad.org/stash/dataset/doi:10.5061/dryad.jm63xsj7b>.

CODE AVAILABILITY

R scripts to reproduce all analyses is available from the Zenodo repository: <https://doi.org/10.5281/zenodo.8205602> and from GitHub: <https://github.com/LucieTp/Range-shift-BTO-Breeding-birds-species-traits>.

ORCID

Lucie Thompson  <https://orcid.org/0000-0001-7526-6231>

Konstans Wells  <https://orcid.org/0000-0003-0377-2463>

Núria Galiana  <https://orcid.org/0000-0001-7720-0615>

Miguel Lurgi  <https://orcid.org/0000-0001-9891-895X>

REFERENCES

- Angert, A. L., Crozier, L. G., Rissler, L. J., Gilman, S. E., Tewksbury, J. J., & Chunco, A. J. (2011). Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, *14*, 677–689.
- Antão, L. H., Weigel, B., Strona, G., Hällfors, M., Kaarlejärvi, E., Dallas, T., Opedal, Ø. H., Heliölä, J., Henttonen, H., Huitu, O., Korpimäki, E., Kuussaari, M., Lehtikainen, A., Leinonen, R., Lindén, A., Merilä, P., Pietiäinen, H., Pöyry, J., Salemaa, M., ... Laine, A.-L. (2022). Climate change reshuffles northern species within their niches. *Nature Climate Change*, *12*, 587–592.
- Atkins, K. E., & Travis, J. M. J. (2010). Local adaptation and the evolution of species' ranges under climate change. *Journal of Theoretical Biology*, *266*, 449–457.
- Auer, S. K., & King, D. I. (2014). Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds. *Global Ecology and Biogeography*, *23*, 867–875.
- Bastille-Rousseau, G., Schaefer, J. A., Peers, M. J. L., Ellington, E. H., Mumma, M. A., Rayl, N. D., Mahoney, S. P., & Murray, D. L. (2018). Climate change can alter predator-prey dynamics and population viability of prey. *Oecologia*, *186*, 141–150.
- Beissinger, S. R., & Riddell, E. A. (2021). Why are Species' traits weak predictors of range shifts? *Annual Review of Ecology, Evolution, and Systematics*, *52*, 47–66.
- Bensch, S. (1999). Is the range size of migratory birds constrained by their migratory program? *Journal of Biogeography*, *26*, 1225–1235.
- Bradshaw, C. J. A., Brook, B. W., Delean, S., Fordham, D. A., Herrando-Pérez, S., Cassey, P., Early, R., Sekercioglu, C. H., & Araújo, M. B. (2014). Predictors of contraction and expansion of area of occupancy for British birds. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20140744.
- Brommer, J. E. (2008). Extent of recent polewards range margin shifts in Finnish birds depends on their body mass and feeding ecology. *Ornis Fennica*, *85*, 109–117.
- Buckley, L. B., & Kingsolver, J. G. (2012). Functional and phylogenetic approaches to forecasting Species' responses to climate change. *Annual Review of Ecology, Evolution, and Systematics*, *43*, 205–226.
- Burleigh, J. G., Kimball, R. T., & Braun, E. L. (2015). Building the avian tree of life using a large-scale, sparse supermatrix. *Molecular Phylogenetics and Evolution*, *84*, 53–63.
- Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Yeong Ryu, H., Sbeglia, G. C., Spagnolo, F., Waldron, J. B., Warsi, O., & Wiens, J. J. (2013). How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20121890.
- Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*, 1024–1026.
- Comte, L., Muriene, J., & Grenouillet, G. (2014). Species traits and phylogenetic conservatism of climate-induced range shifts in stream fishes. *Nature Communications*, *5*, 5053.
- Davis, C. C., Willis, C. G., Primack, R. B., & Miller-Rushing, A. J. (2010). The importance of phylogeny to the study of phenological response to global climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 3201–3213.
- Diamond, S. E. (2018). Contemporary climate-driven range shifts: Putting evolution back on the table. *Functional Ecology*, *32*, 1652–1665.
- Estrada, A., Morales-Castilla, I., Caplat, P., & Early, R. (2016). Usefulness of species traits in predicting range shifts. *Trends in Ecology & Evolution*, *31*, 190–203.
- Fuchs, R., Herold, M., Verburg, P. H., Clevers, J. G. P. W., & Eberle, J. (2015). Gross changes in reconstructions of historic land cover/use for Europe between 1900 and 2010. *Global Change Biology*, *21*, 299–313.
- Gillings, S., Balmer, D. E., Caffrey, B. J., Downie, I. S., Gibbons, D. W., Lack, P. C., Reid, J. B., Sharrock, J. T. R., Swann, R. L., & Fuller, R. J. (2019). Breeding and wintering bird distributions in Britain and Ireland from citizen science bird atlases. *Global Ecology and Biogeography*, *28*, 866–874.
- Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology & Evolution*, *25*, 325–331.
- Harris, I., Osborn, T. J., Jones, P., & Lister, D. (2020). Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Scientific Data*, *7*, 109.
- Hill, M. O. (2012). Local frequency as a key to interpreting species occurrence data when recording effort is not known: A key to interpreting species occurrence data. *Methods in Ecology and Evolution*, *3*, 195–205.
- Hockey, P. A. R., Sirami, C., Ridley, A. R., Midgley, G. F., & Babiker, H. A. (2011). Interrogating recent range changes in South African birds: Confounding signals from land use and climate change present a challenge for attribution. *Diversity and Distributions*, *17*, 254–261.
- Hudson, L. N., Emerson, R., Jenkins, G. B., Layer, K., Ledger, M. E., Pichler, D. E., Thompson, M. S. A., O'Gorman, E. J., Woodward, G., & Reuman, D. C. (2013). Cheddar: Analysis and visualisation of ecological communities in R. *Methods in Ecology and Evolution*, *4*, 99–104.
- Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A. M., Jess, M., & Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: Roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 1665–1679.
- Huntley, B., Collingham, Y. C., Green, R. E., Hilton, G. M., Rahbek, C., & Willis, S. G. (2006). Potential impacts of climatic change upon geographical distributions of birds. *Ibis*, *148*, 8–28.
- Ives, A. R. (2019). R²s for correlated data: Phylogenetic models, LMMs, and GLMMs. *Systematic Biology*, *68*, 234–251.
- Kassara, C., Gangoso, L., Mellone, U., Piasevoli, G., Hadjikyriakou, T. G., Tsiopelas, N., Giokas, S., López-López, P., Urios, V., Figuerola, J., Silva, R., Bouten, W., Kirschel, A. N. G., Virani, M. Z., Fiedler, W., Berthold, P., & Gschwend, M. (2017). Current and future suitability of wintering grounds for a long-distance migratory raptor. *Scientific Reports*, *7*, 8798.
- La Sorte, F. A., & Thompson, F. R., III. (2007). Poleward shifts in winter ranges of north american birds. *Ecology*, *88*, 1803–1812.
- Laube, I., Korntheuer, H., Schwager, M., Trautmann, S., Rahbek, C., & Böhning-Gaese, K. (2013). Towards a more mechanistic understanding of traits and range sizes: Avian traits and range size. *Global Ecology and Biogeography*, *22*, 233–241.
- Lenoir, J., & Svenning, J.-C. (2015). Climate-related range shifts - a global multidimensional synthesis and new research directions. *Ecography*, *38*, 15–28.
- Li, D., Dinnage, R., Nell, L. A., Helmus, M. R., & Ives, A. R. (2020). phyr: An R package for phylogenetic species-distribution modelling in ecological communities. *Methods in Ecology and Evolution*, *11*, 1455–1463.
- Lindström, Å., Green, M., Paulson, G., Smith, H. G., & Devictor, V. (2013). Rapid changes in bird community composition at multiple temporal and spatial scales in response to recent climate change. *Ecography*, *36*, 313–322.

- Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*, 1052–1055.
- Lurgi, M., López, B. C., & Montoya, J. M. (2012a). Climate change impacts on body size and food web structure on mountain ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 3050–3057.
- Lurgi, M., López, B. C., & Montoya, J. M. (2012b). Novel communities from climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 2913–2922.
- Maiorano, L., Amori, G., Capula, M., Falcucci, A., Masi, M., Montemaggiore, A., Pottier, J., Psomas, A., Rondinini, C., Russo, D., Zimmermann, N. E., Boitani, L., & Guisan, A. (2013). Threats from climate change to terrestrial vertebrate hotspots in Europe. *PLoS One*, *8*, e74989.
- Maiorano, L., Montemaggiore, A., Ficetola, G. F., O'Connor, L., & Thuiller, W. (2020). TETRA-EU 1.0: A species-level trophic metaweb of European tetrapods. *Global Ecology and Biogeography*, *29*, 1452–1457.
- McClure, C. J. W., & Rolek, B. W. (2020). Relative conservation status of bird orders with special attention to raptors. *Frontiers in Ecology and Evolution*, *8*, 593941.
- McLean, N., Kruuk, L. E. B., van der Jeugd, H. P., Leech, D., van Turnhout, C. A. M., & van de Pol, M. (2022). Warming temperatures drive at least half of the magnitude of long-term trait changes in European birds. *Proceedings of the National Academy of Sciences of the United States of America*, *119*, e2105416119.
- Naimi, B., & Araújo, M. B. (2016). sdm: A reproducible and extensible R platform for species distribution modelling. *Ecography*, *39*, 368–375. <https://doi.org/10.1111/ecog.01881>
- Pacifici, M., Rondinini, C., Rhodes, J. R., Burbidge, A. A., Cristiano, A., Watson, J. E. M., Woinarski, J. C. Z., & Di Marco, M. (2020). Global correlates of range contractions and expansions in terrestrial mammals. *Nature Communications*, *11*, 2840.
- Paquette, A., & Hargreaves, A. L. (2021). Biotic interactions are more often important at species' warm versus cool range edges. *Ecology Letters*, *24*, 2427–2438.
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*, 37–42.
- Pearce-Higgins, J. W., Eglinton, S. M., Martay, B., & Chamberlain, D. E. (2015). Drivers of climate change impacts on bird communities. *Journal of Animal Ecology*, *84*, 943–954.
- R Core Team. (2021). R: A language and environment for statistical computing.
- Sheard, C., Neate-Clegg, M. H. C., Alioravainen, N., Jones, S. E. I., Vincent, C., MacGregor, H. E. A., Bregman, T. P., Claramunt, S., & Tobias, J. A. (2020). Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nature Communications*, *11*, 2463.
- South, A. (2017). *naturalearth*: World map data from natural earth.
- Sunday, J. M., Pecl, G. T., Frusher, S., Hobday, A. J., Hill, N., Holbrook, N. J., Edgar, G. J., Stuart-Smith, R., Barrett, N., Wernberg, T., Watson, R. A., Smale, D. A., Fulton, E. A., Slawinski, D., Feng, M., Radford, B. T., Thompson, P. A., & Bates, A. E. (2015). Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, *18*, 944–953.
- Taheri, S., García-Callejas, D., & Araújo, M. B. (2021). Discriminating climate, land-cover and random effects on species range dynamics. *Global Change Biology*, *27*, 1309–1317.
- Taheri, S., Naimi, B., & Araújo, M. B. (2016). Did British breeding birds move north in the late 20th century? *Climate Change Responses*, *3*, 5.
- Tekwa, E. W., Watson, J. R., & Pinsky, M. L. (2022). Body size and food-web interactions mediate species range shifts under warming. *Proceedings of the Royal Society B: Biological Sciences*, *289*, 20212755.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, *427*, 145–148.
- Tingley, M. W., Koo, M. S., Moritz, C., Rush, A. C., & Beissinger, S. R. (2012). The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology*, *18*, 3279–3290.
- Weil, S., Gallien, L., Lavergne, S., Börger, L., Hassler, G. W., Nicolai, M. P. J., & Allen, W. L. (2022). Chameleon biogeographic dispersal is associated with extreme life history strategies. *Ecography*, *2022*, e06323.
- White, A. E. (2016). Geographical barriers and dispersal propensity interact to limit range expansions of Himalayan birds. *The American Naturalist*, *188*, 99–112.
- Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals: Ecological archives E095-178. *Ecology*, *95*, 2027.
- Yang, X., Wang, Y., Si, X., & Feng, G. (2020). Species traits linked with range shifts of Chinese birds. *Global Ecology and Conservation*, *21*, e00874.

BIOSKETCH

Lucie Thompson is a PhD student at the Computational Ecology Lab under the supervision of Dr Miguel Lurgi. Her research interests focus on the drivers and consequences of recent changes in spatial distribution of terrestrial species. She investigates species responses to anthropogenic changes by integrating them into their network of ecological interactions, with the aim to better understand how community structure varies in space and time.

SUPPORTING INFORMATION

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

How to cite this article: Thompson, L., Wells, K., Galiana, N., & Lurgi, M. (2023). Joint effects of species traits and environmental preferences on range edge shifts of British birds. *Global Ecology and Biogeography*, *00*, 1–15. <https://doi.org/10.1111/geb.13752>