

## TECHNICAL ADVANCE

# Discriminating climate, land-cover and random effects on species range dynamics

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## Abstract

Species are reportedly shifting their distributions poleward and upward in several parts of the world in response to climate change. The extent to which other factors might play a role driving these changes is still unclear. Land-cover change is a major cause of distributional changes, but it cannot be discarded that distributional dynamics might be at times caused by other mechanisms (e.g. dispersal, ecological drift). Using observed changes in the distribution of 82 breeding birds in Great Britain between three time periods 1968–72 ( $t_1$ ), 1988–91 ( $t_2$ ) and 2007–2011 ( $t_3$ ), we examine whether observed bird range shifts between  $t_1$ – $t_2$  and  $t_1$ – $t_3$  are best explained by climate change or land-cover change, or whether they are not distinguishable from what would be expected by chance. We found that range shifts across the rear edge of northerly distributed species in Great Britain are best explained by climate change, while shifts across the leading edge of southerly distributed species are best explained by changes in land-cover. In contrast, at the northern and southern edges of Great Britain, range dynamics could not be distinguished from that expected by chance. The latter observation could be a consequence of boundary effects limiting the direction and magnitude of range changes, stochastic demographic mechanisms neither associated with climate nor land-cover change or with complex interactions among factors. Our results reinforce the view that comprehensive assessments of climate change effects on species range shifts need to examine alternative drivers of change on equal footing and that null models can help assess whether observed patterns could have arisen by chance alone.

## KEYWORDS

breeding bird survey, climate change, land-use or land-cover, northward shift, null model, species range dynamic

## 1 | INTRODUCTION

Assessments of climate change effects on species distributions are largely driven by observational studies relating to changes in species distributional shifts with geographic or climatic gradients (Chen et al., 2011; Pecl et al., 2017). When distributional shifts match expected gradients, it is assumed that climate change is the likely driver of such shifts. Besides issues with data quality, which often pervade

under-replicated studies across spatial and temporal dimensions, there are two potential problems with such an approach. The first is one of pattern detection. How can one be sure that the observed patterns would not have arisen by chance? The second is one of attribution. How can one be sure that the hypothesized drivers are the ones driving the observed pattern?

These are classical problems of inference based on correlations, and no easy solutions exist. Nevertheless, problems of pattern

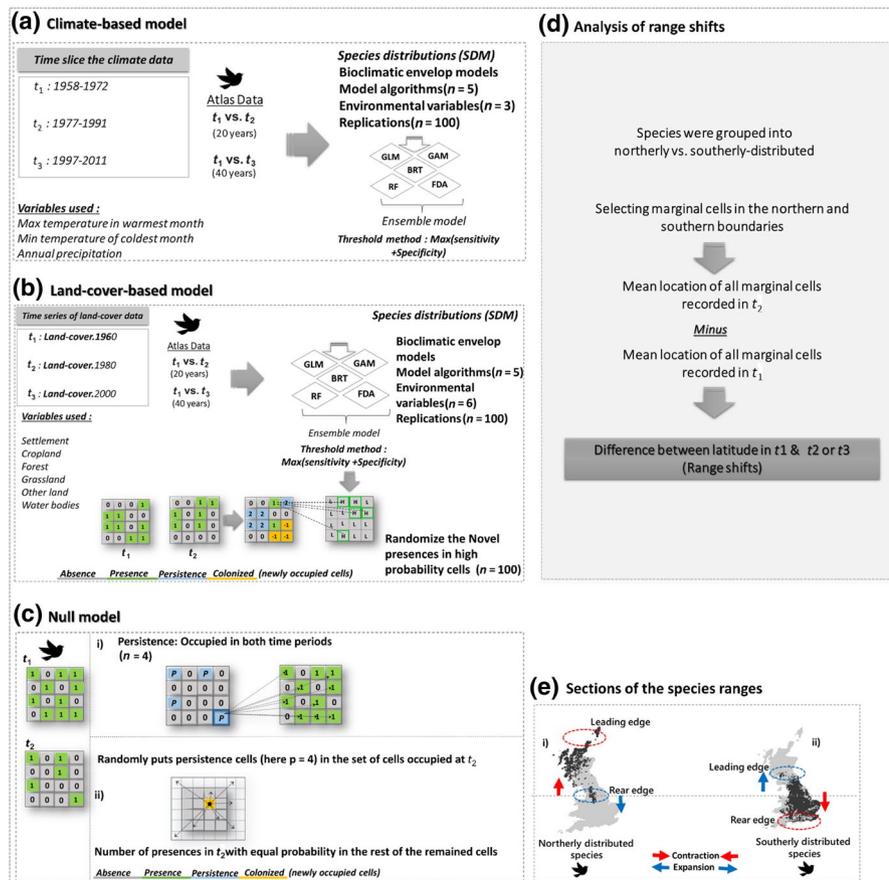
detection can often be handled within a null modelling framework that seeks to assess whether observed patterns in any given response variable (e.g. a species distributional change) could have arisen by chance (Gotelli & Graves, 1996). Null models are commonly used for testing ecological theory, but they are notoriously uncommon in studies assessing species distributional shifts and their underlying drivers (Taheri et al., 2021). Such models typically involve the use of randomized ecological data subject to sets of constraints and are designed to produce a pattern expected in the absence of a particular ecological mechanism. The generated (random) pattern can be compared with the real pattern of interest (Gotelli & McGill, 2006). Conceptually, null models help discern patterns in the data but they do not necessarily reveal the underlying causal mechanisms (Peres-Neto et al., 2001).

Problems of attribution are also inherent to the use of correlations for inferring causation. Confidence in the inferences with correlative methods comes from accumulation of evidence and, ideally, from accumulation of evidence arising from multiple (and diverse) sources (e.g. Araújo et al., 2019). For any particular analysis, the problem is particularly challenging when multiple candidate predictors covary, which limits the ability to discern the variables truly driving observed patterns or, more subtly, how they interact to conform the observed pattern (Dormann, 2007). Testing model inferences requires independent replication but empirical data in many ecological problems are notoriously under-replicated (Lemoine et al., 2016). One approach to deal with uncertainty brought by covarying candidate predictors is to compare, on

equal footing, inferences made with alternative sets of predictors (Burnham & Anderson, 2004). While such an approach is familiar in ecology (e.g. Araújo et al., 2008; Eglinton & Pearce-Higgins, 2012; Rangel et al., 2018), it is seldom used for studying mechanisms driving observed species distributional dynamics (e.g. Rich & Currie, 2018). For example, a recent study demonstrated that previous analysis examining climate change signals on the distributional shift of British birds (Thomas & Lennon, 1999), overestimated these signals by failing to examine distributional changes across multiple dimensions (Taheri et al., 2016).

The matter of fact is that shifts in range edges toward higher latitude or elevation are often interpreted as a response of species to warming climate (e.g. Chen et al., 2011; Hickling et al., 2006; Parmesan et al., 1999). However, variation in magnitude and direction of such range shifts suggests that climate, particularly temperature, might not be the sole driver (e.g. Fei et al., 2017; Taheri et al., 2016). Shifts in geographic distributions of species may also reflect natural population dynamics (Bradshaw et al., 2014), or complex interactions with other factors such as human-mediated land-use change (e.g. Guo et al., 2018; Lehikoinen et al., 2013), dispersal limitations (Anderson et al., 2009) competition (Marion & Bergerot, 2018), biological invasions (Sax & Gaines, 2008), disease (Hof et al., 2011) and interactions among several factors (e.g. Vicente et al., 2019).

Understanding range dynamics and their underlying causes thus requires more sophisticated analysis than is typically performed. In this study, we illustrate these issues by examination of



**FIGURE 1** Methodological framework. (a) Climate model, (b) Land-cover model, (c) Null model, (d) Analysis of range shifts. Presence/Absence map was generated for each species based on the three alternative models. The pattern of range shifts was compared with the observed data using the Wilcoxon signed-rank test. (e) Sections of the species ranges shows the different sections of the distributions. Leading and rear edges of southerly distributed species ( $n=47$ ), and rear and leading edge of northernly distributed species ( $n=35$ ) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

historical range dynamics among 82 bird species in Great Britain against three alternative models: climate change model, assuming that distributions changed following climate changes; land-cover change model, assuming that species distributions changed following land-cover changes; and a null model that, while keeping the same quantities of observed distributional changes (expansions and contractions), randomized the direction of the changes. Because drivers of species range shifts are unlikely to be equally important across different sections of species ranges and following previous studies of range shifts in Great Britain (e.g. Hickling et al., 2006; Thomas & Lennon, 1999), we independently examine four sections of species distributions: leading and rear edges of the southern and northernmost edges of southerly and northerly distributed species (Figure 1e). The analysis is repeated across a 20 year period (1968–72 vs. 1988–91) and a 40 year period (1968–72 vs. 2007–11).

## 2 | MATERIALS AND METHODS

### 2.1 | Species data

We used species distributional data from three Atlas of breeding Bird surveys compiled for Great Britain, providing presence and absence records at 10 × 10 km spatial resolution. The first atlas covered the period of 1968–72 ( $t_1$ ; Sharrock, 1976). The second covered the period of 1988–91 ( $t_2$ ; Gibbons et al., 1993). The third included records from 2007 to 2011 ( $t_3$ ; Balmer et al., 2013). The Atlases used the Ordnance Survey National Grid as a means of identifying location of bird records. These standard inventory-type surveys aimed at generating 'hectad' (10 × 10 km) resolution distribution maps, and incorporated fixed-effort data using timed visits to a sample of 'tetrads' (2 × 2 km squares) in each hectad (Gillings et al., 2019).

We digitized the distribution data from online-published sources (<https://www.bto.org/>). We excluded marine species and restricted-range species with less than 20 records in the first atlas data since small range changes in restricted-range species can have a great relative effect even if driven by stochastic factors. We also excluded wide-ranging species with more than 2000 records (ubiquitous species) in the first atlas ( $t_1$ ; Britain includes 2280 10 km grid cells), since the capacity to shift ranges biased towards range reduction. Using these criteria, we selected 82 species for analysis, involving species range comparisons between  $t_1$  and  $t_2$  (20 years) and  $t_1$  and  $t_3$  (40 years).

### 2.2 | Climate

We used a time series of changes in maximum and minimum temperatures and annual precipitation at a spatial resolution of 0.5 degrees from the updated version of the Climate Research Unit's database (<http://www.cru.uea.ac.uk>). The baseline covered the period of 1958–2011, and then we sliced climate data for a 15 year interval before the last census in each period. The climate slices are as follows:

For the  $t_1$  period, we used climate time series from 1958 to 1972; for  $t_2$ , from 1977 to 1991; and for  $t_3$ , from 1997 to 2011. We used 15 years of climate data for each atlas on the assumption that species' ranges respond to the long-term average of climate conditions.

The climatic variables were processed using R *BioCalc* function (Ramirez, 2009). They included Maximum Temperature of Warmest Month, Minimum Temperature of Coldest Month and Annual Precipitation. Our choice of variables reflects those known to impose general constraints on bird distributions in Europe (Lennon et al., 2000; Whittaker et al., 2007). We then downscaled climate data using Inverse Distance Weighting (IDW) following (Shepard, 1968) in raster package R (Hijmans et al., 2015). Inverse distance weighting (IDW) is a method of interpolation that estimates cell values by averaging the values of sample data points in the neighbourhood of each processing cell. The closer a point is to the centre of the cell being estimated, the more influence, or weight it has in the averaging process (Zhou & Zhang, 2014). The output cell size and other parameters of the new raster layers were matched to the 10\*10 km of bird's atlas dataset.

To examine the climate-based prediction, we developed ensemble species distribution models using the *sdm* package in R (Naimi & Araújo, 2016). We modelled each species presence/absence as a function of the three climate variables. We ran five different algorithms for modelling the presence/absence of birds using an ensemble modelling framework (Araújo & New, 2007): generalized linear models (GLM; McCullagh & Nelder, 1989), generalized additive models (GAM; Hastie & Tibshirani, 2017), random forest (RF; Breiman, 2001), mixed effect modelling (FDA; Hastie et al., 1994), boosted regression tree (BRT; Friedman, 2001; Figure 1a). In order to avoid biases to the parameter estimation, we used a bootstrapping method (Fielding & Bell, 1997; Hastie et al., 2009) with 100 random replications for each species and modelling technique. Bootstrapping repeats a sampling with replacement, each time a sample with equal size as the original data is drawn and used for training data. The observations that are not selected are used for the evaluation at each run. Then we generated a consensus model, using weighted average probability for each species, where weights were obtained from the area under the curve (AUC) in evaluation data (Garcia et al., 2012; Marmion et al., 2009).

To assess habitat suitability based on climate constraints, we converted probabilistic output to presence/absence using one of the recommended threshold techniques: Max (Sensitivity + Specificity; Liu et al., 2005). Values above or equal to the threshold are classified as predicted species presences, while values below the threshold are classified as predicted absences. When the presence/absence map was provided for each species, we measured the range shift and compared the results of climate related range shifts with observed range shifts.

### 2.3 | Land-cover

We used land-cover change estimates from the Laboratory of Geo-information Sciences and Remote Sensing at the University of Wageningen (HILDA version 2.0). The HILDA dataset is available at a 1 km spatial resolution from 1900 to 2010 for the whole of Europe

(Fuchs et al., 2012, 2015). The temporal resolution of the dataset is decadal (10 years) and contains six land-cover classes:

1. Settlement (incl. green urban areas);
2. Cropland (incl. orchards and agroforestry);
3. Forest (incl. transitional shrub and woodlands, tree nurseries, reforested areas for forestry purposes);
4. Grassland (incl. natural grassland, wetlands, pasture and Mediterranean shrub vegetation);
5. Other land (incl. glaciers, sparsely vegetated areas, beaches, bare soil);
6. Water (incl. water bodies, sea, streams).

We considered three decadal land-cover survey periods approximately matching species atlas surveys: 1960; 1980; and 2000. The proportion of individual land-cover classes present within each 10 km Bird Atlas grid cell (Figure 1b) was then calculated. In order to determine the signal of land-cover changes on species range shifts, we run the same species modelling techniques used for climate but with land-cover variables instead (Thuiller et al., 2004). Specifically, we modelled each species presence/absence as a function of the six land-cover predictors. Following the procedure used with climate variables, we ran five different algorithms to model the presence and absence of bird species within an ensemble modelling framework. We used the land-cover predictors for the 1960s ( $t_1$ ) as baseline. Then, we projected distributions using land-cover predictors in 1980s (1960 vs. 1980, 20 years) and 2000s (1960 vs. 2000, 40 years). Like with the climate models, we generated 100 random replications using bootstrapping (sampling with replacement) for each species and modelling technique. We used AUC in evaluation data, to obtain the probability of distribution for each species and used the same threshold method implemented with the climate model to convert the probabilities generated from the land-cover model into presence and absences.

To address the link between the magnitude of the land-cover change and species range shifts, we first selected all persistence cells (cells where species remained present from the first to the second survey (Presence in  $t_1 \cap$  Presence in  $t_2$  or  $t_3$ ). Then, we treated all persistence cells as static, while randomizing newly occupied cells in  $t_2$  or  $t_3$  within the potential cells that had a high probability of occurrence as projected by the ensemble models using the land-cover predictors. Here, the constrained randomization ensures that each novel presence has an equal chance of occupying any of the suitable sites predicted by the land-cover model. In order to estimate the variability of the results, we replicate the randomization process 100 times for each species. We used the average of these replications to measure the range shifts constrained by land-cover and compared the results with observed range shifts.

## 2.4 | Null model

We developed a patch-occupancy null model to infer expected range shifts in the absence of climate change or land-cover change

but with the geographical constraints imposed by the geometry of Great Britain, while maintaining the observed rates of expansion or contraction of the 82 species in the intervals  $t_1$ - $t_2$  and  $t_1$ - $t_3$ . In a given interval, the model computes the null expected range shift of each species as follows.

First, denote as  $P_{t1}$  the set of cells in which the species is present at the first atlas. Likewise,  $P_{t2}$  is the set of cells with presence of the species in the second census (either time  $t_1$  or  $t_2$ ). Further, denote as  $P_s$  the set of cells in which the species persists from the first to the second census, and with  $P_c$  the set of cells newly colonized by the species in the second census. Thus, the number of occupied cells in the second census is simply  $|P_{t2}| = |P_s| + |P_c|$  where the double bars indicate the cardinality of a set, i.e. the number of elements it contains. If the species has expanded its distribution,  $|P_{t2}| > |P_{t1}|$ , which implies  $|P_c| > 0$  but allows for  $|P_s|$  to reach 0, in the limit case in which a species changes its whole range between censuses. On the other hand, if the species has suffered a contraction between censuses, it means  $|P_{t2}| < |P_{t1}|$ , in this case implying  $|P_s| < |P_{t1}|$ .

The null model keeps the number of persisting occurrences and colonized cells of each species fixed, and simply distributes these quantities stochastically ( $|P_s|$  and  $|P_c|$ ) across the appropriate sets of cells. In particular, for each realization of the model for a given species, the first step is to assign the cells in which the species persist. Since we assume that all cells are equivalent, we expect species to persist with equal probability in any of the cells occupied in the first census. Therefore, we randomize the number of persisting cells,  $|P_s|$ , among the set of occupied cells at  $T1$ ,  $P_{t1}$ . Using set operations, the randomized  $P_s \subseteq P_{t1}$  (panel i) of Figure 1c. The second step is assigning the colonized cells,  $P_c$ . Again, as we assume no other constraints, any cell of the whole territory can be assigned a presence. Thus, if  $T$  is the set of cells of the whole territory, in each realization we randomize  $P_c \subseteq T$  (panel ii) of Figure 1c.

This approach accounts for expansions and contractions in the number of cells with persistent occurrences ( $t_1 = 0$ ,  $t_2 = 1$ ) or colonized cells ( $t_1 = 0$ ,  $t_2 = 1$ ), thus including the whole variability of range shifts observed. In this study, we generated 1000 draws of the null model for each one of the 82 bird species considered, totalizing 82,000 null model distributions. The final analysis of range shifts was carried out with averaged shifts across these 1000 replicates for each species.

## 2.5 | Analysis of range shifts

To relate observed species range shifts to our three alternative modelled shifts (constrained by climate, land-cover or random dynamics), and following Thomas and Lennon (1999), we first split species into northerly and southerly distributed depending on whether their distributional core lies to the north or to the south of the mean position of the all 100 km<sup>2</sup> grid cells in Great Britain respectively (Figure 1e; Table S4). Overall, we obtained 47 and 35 southerly and northerly distributed species respectively.

We then examined range changes along leading and rear edges. Shifts in range margins between two atlases were calculated as

the mean distance of 20 most marginal records in the southern and northern margins in  $t_2$  or  $t_3$  minus  $t_1$ ; positive values indicate a move toward the boundary (expansion) and negative values indicate a move toward the core of the distribution (contraction; Figure 1d). Then we provided Presence/Absence map for three alternative models (climate, land-cover, null) and compared shifts at the leading and rear edge with observed data using the Wilcoxon signed-rank test.

### 3 | RESULTS

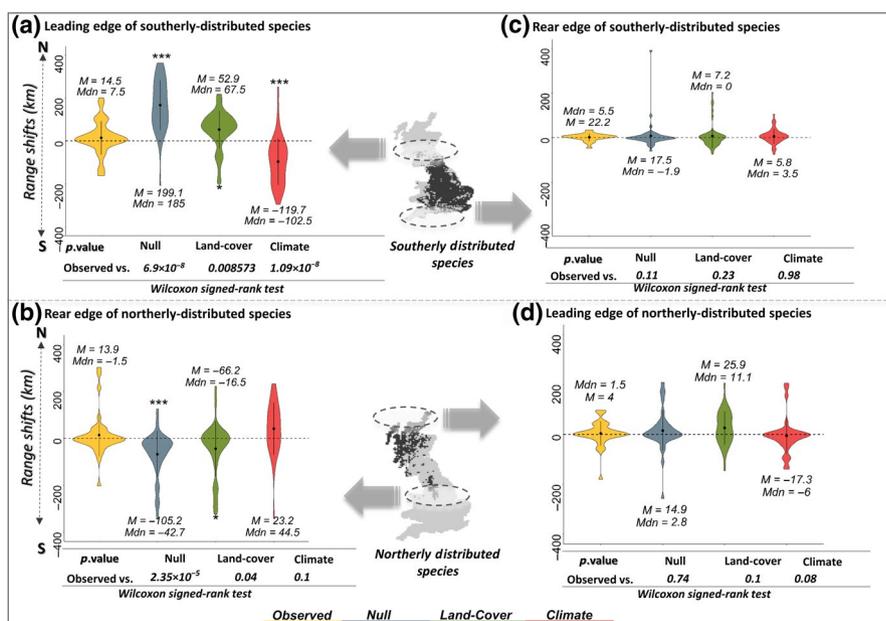
Comparison of observed range shifts with projections arising from the three alternative models revealed that determinants of species

range shifts were seemingly variable across each one of the four pre-defined sections of the range (Figure 1e).

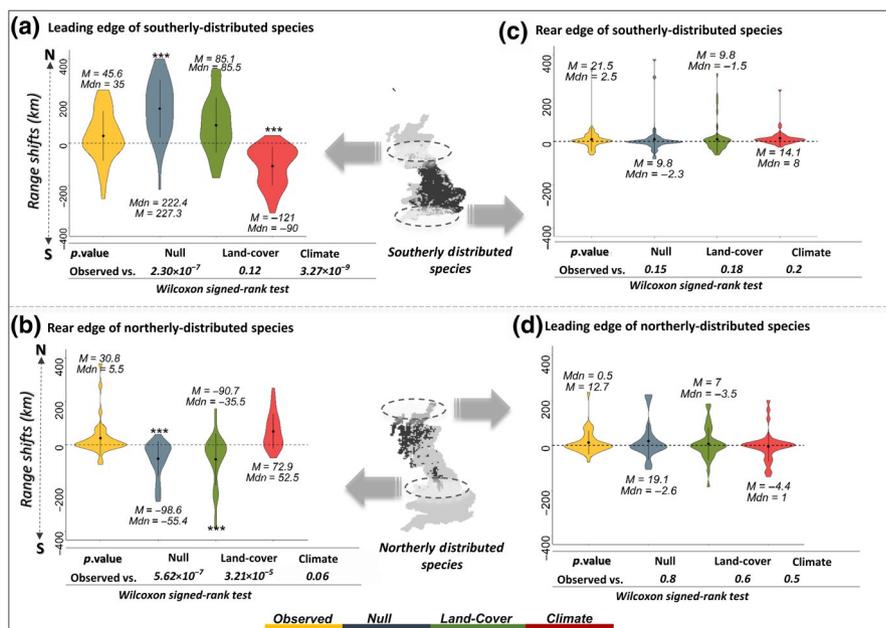
At both the southern and northern tips of Great Britain (i.e. the rear edge of southerly distributed species and the leading edge of northerly distributed species), observed range shifts were no different from expected by chance; this being true for both the  $t_1$  vs.  $t_2$  and  $t_1$  vs.  $t_3$  comparisons (Figures 2c,d and 3c,d). Observed trends were also no different than expected by chance with respect to both the climate and land-cover change models, making it difficult to attribute observed changes to any specific driver.

At the rear edge of northerly distributed species, observed range shifts were inconsistent with range changes obtained with the null model (Wilcoxon signed-rank test  $p < 0.001$ ; Figures 2b and 3b) as well as with the land-cover model ( $p < 0.01$  and

**FIGURE 2** Violin plots depicting the frequency distribution of range shifts between (1968–72 and 1988–91) among leading (a) and rear (c) edges of southerly distributed species ( $n = 47$ ), and rear (b) and leading edge (d) of northerly distributed species ( $n = 35$ ). The degree of mismatch between observed shifts (yellow) and range shifts predicted by the null model (blue), land-cover model (green) and climate model (red). The black dots inside the violin plots show the median and the vertical line shows the deviation from the mean. \*\*\* and \* indicate if there is any significant difference from observed shifts  $p < 10^{-3}$  and  $p < 0.05$  respectively using (Wilcoxon sign rank test). Maps in the centre show different sections of the distribution and are an example of leading and rear edges of southerly and northerly distributed species [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 3** Violin plots depicting the frequency distribution of range shifts between (1968–72 and 2007–11) among leading (a) and rear (c) edges of southerly distributed species ( $n = 47$ ), and rear (b) and leading edge (d) of northerly distributed species ( $n = 35$ ). The degree of mismatch between observed shifts (yellow) and range shifts predicted by the null model (blue), land-cover model (green) and climate model (red). The black dots inside the violin plots show the median and the vertical line shows the deviation from the mean. \*\*\* and \* indicate if there is any significant difference from observed shifts  $p < 10^{-3}$  and  $p < 0.05$  respectively using (Wilcoxon sign rank test). Maps in the centre show different sections of the distribution and are an example of leading and rear edges of southerly and northerly distributed species [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



$p < 0.001$  for the 20 years and 40 years comparison respectively; Figures 2b and 3b), which predicted a shift of opposite direction as observed. Observed range shifts were, in turn, consistent with that estimated with the climate model (Figures 2b and 3b). Such consistency between observation and modelled shifts can be interpreted as indicating the existence of a climate change signal in species distributional dynamics in this geographical section of the range. More specifically, observed data showed a general tendency for northward shift with a mean of 14 km (median = -1.5) during the 20 years comparison and a mean of 30.8 km (median = 5.5) during the 40 years comparison. Climate models projected a northward range shift of greater magnitude with a mean of 23 km (median = 44.5; Figure 2b) during the 20 years and a mean of ~72.9 km (median = 52.5; Figure 3b) during the 40 years.

At the leading edges of southerly distributed species, range dynamics were again inconsistent with the null model ( $p < 0.001$ ; see Figures 2a and 3a) and with the climate model projections ( $p < 0.001$ ; Figures 2a and 3a), which predicted shifts of opposite direction as observed. The land-cover model generated, in contrast, projections that were consistent with observed range shifts (Figures 2a and 3a). Specifically, observed trends indicate a northward shift by average of 14.4 km (median = 7.5) during the 20 years and 45.6 km (median = 35) during the 40 years. The land-cover model inferred the same trend of northward expansion by 52.9 km (median = 67.5; Wilcoxon signed-rank test,  $p = 0.008$ , Figure 2a) during the 20 years and 85 km during the 40 years (median = 86.5; Wilcoxon signed-rank test,  $p = 0.1$ ; Figure 3a) respectively.

## 4 | DISCUSSION

We show that different mechanisms are likely implicated in shaping bird range dynamics across Great Britain and that the importance of such mechanisms (e.g. climate change versus land-cover change) varies across sections of species ranges. While rear edges of northerly distributed species have shifted consistently with projections from a climate-driven model, shifts at the leading edge of southerly distributed species carry a stronger imprint of land-cover change. In contrast, shifts at the leading edges of northerly distributed species and the rear edges of southerly distributed species—that is, distributions at both the northern and southern tips of Great Britain—were no different from that expected by chance.

One question arising when interpreting range shifts in a geographically bounded area, such as Great Britain, is the extent to which the magnitude and direction of range changes are constrained by the geometry of the region (see Gillings et al., 2014; Groom, 2013). For example, suppose that a species is distributed in the easternmost corner of the Island and that climate change would drive species to expand north. Since north of that region there is boundary with the sea, the species would be blocked from moving north having to first move west and then north. Such constraints

could have played a role in species distributional dynamics at the leading margins of northerly distributed species and rear margins of southerly distributed species, where the northern and southern terrestrial boundary of Great Britain restricts movement. In addition to the shape of the boundary, there can be other natural boundaries (e.g. mountain ranges, rivers, fragmented habitats) that prevent dispersal and reduce the rate of species adaptation to climate change through shifting ranges.

Geometric constraints on the spatial distribution of species is not an entirely new topic (see Colwell & Lees, 2000). For example, Keith et al. (2011) showed that physical barriers have restricted dispersal of pelagic larvae in the south coast of England. Another study showed that the absence of *Mecistogaster modesa* in South America is strongly related to physical barriers such as the Andes mountain range and oceanic barriers (Amundrud et al., 2018).

Despite previous insights on geometrical constraints, only a few studies have compared observed species distributional changes with null models to discriminate between directional patterns of range change and non-directional ones (e.g. potentially arising from stochastic processes). One such examples involves the use of Monte Carlo simulations to generate distributions of species across elevation under the null hypothesis (Forero-Medina et al., 2011). In that study, the authors found that by chance alone, 55 birds in Peruvian mountains could have moved on average ~40 m upward in elevation during 40 years.

Although a great deal of research on species range shifts has focused on climate change and its signals (e.g. Hanberry et al., 2011; Hickling et al., 2005; Parmesan et al., 1999; Thomas & Lennon, 1999) population declines have also been linked to agricultural intensification and fragmentation, fertilizer application or pesticide use through time (Chamberlain et al., 2000; Eglinton & Pearce-Higgins, 2012; Reino et al., 2018). There is also evidence that land-cover or agricultural practices can cause varying types of range shifts depending on behavioural and trophic characteristics of the species (e.g. Gaüzère et al., 2020; Reino et al., 2018). For example, *Spiza americana*, a grassland bird from North America, displayed northward expansions during 1960–1980 owing to changes in winter food supply associated with changing agricultural practices from rice growing to cattle raising (MacArthur, 1972).

In our study, we had no detailed information on agricultural practices at the cell level and analyses were based on patterns of change across six broad types of land-cover classes. Including more detailed information on agricultural practices can provide a more reliable estimation of the magnitude of species range shifts under land-use (rather than coarse land-cover) change. Our results are consistent with previous studies showing that expansions at leading edges of species ranges can arise as a consequence of land-cover change (Groom, 2013; Lima et al., 2007). In the Italian Alps, for example, the upward shifts of 21 bird species between 1982 and 2017 have been attributed to shrub and forest cover expansion (Bani et al., 2019), and range expansion among 10 out of 23 birds in the Czech Republic seems to be affected by habitat change (Reif et al., 2010).

We have considered the independent role of individual models (climate, land-cover and null) by comparing their outputs against observed trends, on equal footing. However, global change drivers do not act independently from each other. Indeed, some recent studies detected these synergistic and antagonistic interactions between climate change and human disturbances or land-use change (e.g. Dainese et al., 2017; Elsen et al., 2020; Guo et al., 2018). Although a detailed analysis of the synergistic effects among different drivers is beyond the scope of this paper, we examined the presence of potential interactions between climate and land-cover change using an ANOVA framework and found significant interaction effects (Supplementary material; Figure S1). At the rear edge of northerly distributed species, for example, maximum temperature interacts with forest loss and may be underlie northward shifts, while maximum temperature in interaction with forest gain covaries with southward shifts (Figure S2c). Another example of interaction effects was between open-lands and minimum temperature at the leading edge of southerly distributed species. The results show that minimum temperature interacts with open-lands loss and potentially drives species to move further to the north with higher magnitude (Figures S2a and S3a). Such post hoc analysis of interactions among drivers of range change reveals that, although we could successfully identify variation in the main drivers contributing to range shifts of birds in Great Britain, the interaction among predictor variables should be also taken into account when possible.

To our knowledge, we provide the first empirical assessment of alternative mechanisms underlying range changes in different sections of the species ranges, on equal footing. Moving forward to assess the where and when of climate change effects on biodiversity is crucial to guide the timing and magnitude of human adaptation strategies for biodiversity. We highlight the substantial need for methods that are able to distinguish between directional and non-directional changes, thus being able to help tease apart distributional changes driven by natural population dynamics from changes driven by external forcing (climatic or non-climatic).

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## AUTHOR CONTRIBUTION

S.T., D.G.-C., M.B.A. conceived the study. S.T. wrote the scripts for climate and landcover model, and D.G.-C. wrote the scripts for the null model. S.T. undertook the analyses and prepared the figures. S.T. and M.B.A. wrote the manuscript with contributions from D.G.C.

## DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study are available within the article [and/or] its supplementary material.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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