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Disentangling the relative roles of climate and land cover change in driving the long-term population trends of European migratory birds

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Abstract

Aim: Global declines in the populations of migratory species have been attributed largely to climate change and anthropogenic habitat change. However, the relative contribution of these factors on species' breeding and non-breeding ranges is unclear. Here, we present the first large-scale assessment of the relative importance of climatic conditions and land cover on both the breeding and non-breeding grounds in driving the long-term population trends of migratory species.

Location: Europe and Africa.

Methods: We use data on the long-term population trends of 61 short- and 39 long-distance migratory species of European breeding birds. We analyse these population trends in relation to changes in climate and land cover across species' breeding and non-breeding ranges over a 36-year period, along with species' migratory behaviour.

Results: The population trends of European migratory birds appear to be more closely related to changes in climate than changes in land cover on their breeding grounds, but the converse is true on their non-breeding grounds. While improvements in climate suitability across the breeding ranges of short-distance migrants led to increasing population trends, the same was not true for long-distance migrants. The combined effects of changes in climate and land cover account for approximately 40% of the variation in migratory species' population trends, suggesting that factors other than climate and land cover as we have measured them, such as habitat quality, also affect the population trends of migrant birds.

Main Conclusions: Over recent decades, population trends of most migrant species are most strongly related to climatic conditions on the breeding grounds but land cover change on the non-breeding grounds. This suggests that management to stem the declines of migrant birds requires an integrated approach that considers all processes affecting migrant birds across their dynamic distributions throughout the year.

*This is the authors' preferred name and is currently unable to change it in ScholarOne.

KEYWORDS
Africa, avian migration, breeding, climate, Europe, habitat, non-breeding, population trends

1 | INTRODUCTION

Increasingly, climate change is implicated in an emerging global trend whereby migratory species are experiencing more rapid rates of population decline than their resident counterparts (Runge et al., 2015; Studds et al., 2017; Wilcove & Wikelski, 2008). With large numbers of the world's vertebrates making long-distance movements (Somveille, Rodrigues, & Manica, 2018), the decline of migrant species poses a serious threat to global biodiversity and associated ecosystem services (Bairlein, 2016; Vickery et al., 2014). Understanding the causes of these declines is complicated by the dependence of migrants on multiple habitats, including on their breeding and non-breeding grounds, as well as at stopover sites (Robinson et al., 2009; Zurell, Graham, Gallien, Thuiller, & Zimmermann, 2018). The dependence of migrants on conditions in multiple areas, and on the phenology of events in these areas, renders them more vulnerable to environmental changes than their resident counterparts (Finch, Pearce-Higgins, Leech, & Evans, 2014; Runge, Martini, Possingham, Willis, & Fuller, 2014). Elucidating drivers of their population change is further complicated by the need to understand in which of the various parts of the annual life cycle the population is critically limited (Ockendon, Hewson, Johnston, & Atkinson, 2012). Both climate change and anthropogenic habitat change are potential drivers of declines, alongside other factors such as increased persecution and hunting (Both, Bouwhuis, Lessells, & Visser, 2006; Jiguet et al., 2010; Kirby et al., 2008; Stephens et al., 2016; Studds et al., 2017; Vickery et al., 2014).

Afro-Palaearctic long-distance migratory birds, which breed across Europe and spend the non-breeding season in sub-Saharan Africa, are declining significantly faster than European breeding-resident and short-distance migrant birds (Cresswell, 2014; Gregory, Skorpilova, Vorisek, & Butler, 2019; Sanderson, Donald, Pain, Burfield, & van Bommel, 2006; Vickery et al., 2014). Many of these long-distance migrants have shown continent-wide patterns of sustained, often severe, decline since *circa* 1970. By contrast, many of their resident counterparts have undergone little or no decline during the same period (Sanderson et al., 2006; Vickery et al., 2014). Detailed monitoring in western Europe has provided a clear understanding of how changes in climate affect the populations of European breeding birds (Gregory et al., 2007; Thaxter, Joys, Gregory, Baillie, & Noble, 2010). Moreover, long-term trends in population sizes of birds in Europe have been related to climate trends on their breeding grounds (Stephens et al., 2016). Population declines in migratory species may be a consequence of asynchronous responses to changes in climate, resulting in phenological mismatch between, for example, the timing of breeding of insectivorous birds and their prey availability (Both et al., 2010; Møller, Rubolini, & Lehikoinen, 2008). Additionally, warmer winters may have improved the overwinter survival rates of resident species, increasing competition for breeding resources, to the detriment of those migratory species that arrive at the breeding grounds last (Berthold, Fiedler, Schlenker, & Querner, 1998; Pearce-Higgins, Eglington, Martay, & Chamberlain, 2015). Climatic conditions on species' non-breeding grounds have also been linked to long-term trends in the populations of migrant birds. In particular, rainfall across the Sahel region of Africa has been shown to affect overwinter survival (Peach, Baillie, & Underhill, 1991) and to influence the conditions of European breeding birds when they depart on spring migration, with potential carry-over effects on reproductive success (Ockendon, Leech, & Pearce-Higgins, 2013; Saino et al., 2011; Zwarts, Bijlsma, & van der kamp, & Wymenga, 2009). Land use change is also recognized as an important driver of population trends for some bird species (Sanderson et al., 2006, 2016; Sullivan, Newson, & Pearce-Higgins, 2015). For example, across Europe, birds associated with farmland habitats have declined steeply since the 1950s, which has been largely attributed to the intensification of agricultural practices (Donald, Sanderson, Burfield, & van Bommel, 2006; Gregory et al., 2019). However, little is currently known about the role of land use changes at non-breeding grounds on population trends (Beresford et al., 2019; Cresswell, Wilson, Vickery, Jones, & Holt, 2007; Wilson & Cresswell, 2006). It has been suggested that between 1970 and 1990, Afro-Palaearctic migrants dependent on dry, open habitats on their non-breeding grounds declined significantly more than other migratory birds (Atkinson et al., 2014; Sanderson et al., 2006). This was linked to an extended drought across the Sahel during this period, which probably impacted the shallow-rooted vegetation that dominates these open habitats (Atkinson et al., 2014). The similarities in population trends among species with shared habitat affinities imply that changes to land cover can drive population declines. However, the relative effects on the populations of European long-distance migrants of long-term climatic and land cover changes on breeding and non-breeding grounds remain uncertain (Ockendon et al., 2012; Vickery et al., 2014).

Here, we explore the potential contribution of long-term trends in (1) climate suitability and (2) land cover, on both breeding and non-breeding grounds, with the population trends of European breeding birds with different migratory strategies and habitat affinities. First, we associate the breeding and non-breeding distributions of these birds, at a continental scale, with long-term mean climate data. Based on those associations, we identify temporal trends in climate suitability for individual species, separately across their breeding and non-breeding ranges. We then calculated the trend in the extent of suitable land cover for each species on their breeding and non-breeding ranges. In order to determine the degree to which trends in breeding bird population sizes across Europe are directly attributable to changes in climate and land cover, we analyse the relationship between these climate suitability trends (CSTs), and land cover suitability trends (LCSTs), with long-term avian population

trends. Within this analysis, we control for species' habitat affinities because similar trends among species with shared habitat associations may indicate that processes affecting the condition of specific habitats that are not captured within the LCSTs, for example agricultural intensification, are also affecting populations. By analysing these effects separately for long- and short-distance migrants, we evaluate whether the drivers of population changes differ for different types of migrant birds.

2 | METHODS

2.1 | Species data

Annual indices of abundance for 133 species of European migratory breeding birds, as defined by Snow, Perrins, Hillcoat, Gillmor, and Roselaar (1997), were taken from the Pan-European Common Bird Monitoring Scheme (PECBMS, http://www.ebcc.info/pecbm.html) for the period 1980–2016. Of these, we excluded species for which population monitoring commenced post-2000, along with any species for which there had been a period of limited geographical coverage in population monitoring. We further excluded species whose European breeding populations migrate primarily to non-breeding areas outside of our Europe–Africa study area (i.e. Asia). This left 100 migratory species with long-term population trends calculated from breeding ground monitoring across 28 European countries (see Appendix S1 in the Supporting Information, Table S1.1). Multinational population trends were calculated as the coefficients of log-linear Poisson regressions of the annual index of the size of a species' European population across the 28 countries against calendar year (Gregory et al., 2005). To account for potential sampling error in the estimation of species' population trends in subsequent analyses, we also took the standard error of these regression coefficient values. Additional details on the calculation of population trends are provided in Appendix S1 in the supporting information. In addition, we calculated a multispecies population index separately for both short- and long-distance migrants (see below for definitions). Using the annual indices of population size, we took a geometric mean for each year as the annual population index for all species within each group, giving each species an equal weight in the analysis (Gregory et al., 2005).

Trait data for the 100 species were obtained principally from Gregory et al., (2009), who derived logged mean mass data from Cramp (1977–1994) and migratory strategy from Snow et al. (1997). Species were classified into two groups according to their migratory behaviour: (1) short-distance migrants, which migrate principally to different parts of Europe and North Africa in the non-breeding season; (2) and long-distance migrants, which spend the non-breeding season entirely in sub-Saharan Africa (see Appendix S1 in the Supporting Information, Table S1.2 for classifications). Each species' principal breeding range habitat was classified as farmland, woodland, wetland or other, following the classification of PECBMS (http://www.ebcc.info/pecbm.html). Non-breeding range habitat associations were taken principally from Atkinson et al. (2014), and for omitted species from Barshep, Erni, Underhill, and Altwegg (2017) and Cramp (1977–1994), and were classified as open country, shrub/woodland, wetland or other (see Table S1.2 for classifications and their source). We also calculated a continuous measure of migratory dispersion for each species following the methods of Gilroy, Gill, Butchart, Jones, and Franco (2016). Migratory dispersion is measured as the relative difference in size between a species' breeding and non-breeding ranges and, previously, has been linked to population declines in migratory species (Koleček, Procházka, Ieronymidou, Burfield, & Reif, 2018). This measure indicates the ability of a species to utilize a wider range of areas during the non-breeding season, which may confer increased population-scale resilience to area-specific threats (Gilroy et al., 2016; Runge et al., 2014).

Range extent data (used to fit species distribution models [SDMs]—see below) for breeding and non-breeding distributions for each species were obtained from BirdLife International and NatureServe (2016) for the 100 species. The distribution maps of each species' breeding range were overlaid with a 0.5° x 0.5° grid covering both Europe and the part of Africa north of 20°N. A species was considered present in a 0.5° grid cell if ≥10% of the cell intersected with the species' breeding distribution. The non-breeding ranges of the 39 long-distance migrants were similarly overlaid with a 0.5° grid and converted to presence–absence data for the part of Africa south of 20°N. For the 61 species of short-distance migrants (the non-breeding ranges for some of which extend into Africa), the non-breeding ranges were gridded for both Europe and all of Africa.

2.2 | Climate data

Data for three climatic variables, mean monthly temperature, precipitation and percentage cloud cover from 1951 to 2000 (the period during which the majority of data underlying the species' range extent maps were collected), were obtained from the CRU TS 3.25 0.5° dataset (Harris, Jones, Osborn, & Lister, 2014). These data were used in conjunction with soil water capacity data and formulations, both from Prentice et al., (1992), to calculate five bioclimatic variables, at 0.5° resolution, for all of Europe and Africa. Separate sets of bioclimatic variables were calculated for the breeding and non-breeding seasons. Mean temperature of the warmest month (MTWA), mean temperature of the coldest month (MTCO) and total precipitation (TP) were assessed over months chosen to coincide as closely as possible with the times that the majority of species spend on their breeding (March–September) and non-breeding (August–February) ranges (Ponti, Arcones, Ferrer, & Vieites, 2019). We also included annual measures of seasonality of temperature (ST) and precipitation (SP). This was to account for the role of significant variations in climate that may affect underlying habitat conditions, for example the periodicity of precipitation across the Sahel or seasonal variability across Europe. These variables have been shown to be informative in describing both breeding and non-breeding range extents (Doswald et al., 2009; Thuiller, Araujo, & Lavorel, 2004) and abundance

patterns (Green et al., 2008; Gregory et al., 2009; Howard, Stephens, Pearce-Higgins, Gregory, & Willis, 2014, 2015) of European breeding birds. We calculated the mean values of these bioclimatic variables for the period 1950–2000, as well as annual values from 1980 to 2016, to match the species' population monitoring period.

2.3 | Modelling species' distributions

To model the relationship between the 1950 and 2000 mean bioclimatic variables and species distributions, we used an ensemble modelling framework, combining four widely applied techniques: generalized linear models (GLMs), generalized additive models (GAMs), generalized boosted regression models (GBMs) and random forests (RFs). These methods have all been shown to produce models that perform well when used in an ensemble SDM approach (Bagchi et al., 2013; Elith et al., 2006). Separate SDMs were built for a species' breeding range and non-breeding range using the range-specific bioclimatic variables. To ensure that model evaluation is robust to potential spatial autocorrelation (SAC), we used a "blocking" method (Bagchi et al., 2013), whereby we split the data into ten sampling blocks based on ecoregions (Olson et al., 2001; http://www.worldwildlife.org/science/data; Bagchi et al., 2013). We fitted the models to nine of the ten sampling blocks and tested model performance on the omitted block. We repeated this ten times for each of the four SDM approaches to produce 40 models for both the breeding and non-breeding ranges for each of the 100 species. Model fit was assessed using the area under the curve (AUC) of the receiver operating characteristic (ROC) plot (Brotons, Thuiller, Araujo, & Hirzel, 2004; Manel, Williams, & Ormerod, 2001). Additional details of the four SDM approaches, the methods utilized to account for SAC and our approach to assessing model fit can be found in Appendix S1 in the supporting information.

2.4 | Calculating trends in climate suitability

We applied the 40 SDMs for each species (10 block models x 4 modelling techniques) to the annual bioclimatic data from the CRU TS 3.25 0.5° dataset (Harris et al., 2014) to project climate suitability for each species for the years 1980 to 2016, for both breeding and non-breeding ranges. We then calculated an annual median projected climate suitability for each species for both the breeding and non-breeding ranges, using the projections from all 40 SDMs. Given that all SDMs performed well, with AUC > 0.7 for all species (see results), all projections were included in the calculations of median climate suitability. For the breeding range, this meant suitability from the 40 models was calculated across all cells of a species' breeding range within the area covered by PECBMS (the region for which we have population trend data; Table S1.1). For some species, there is evidence of a high level of dispersal during the non-breeding season (Finch, Butler, Franco, & Cresswell, 2017). Therefore, when evaluating climate suitability across the non-breeding ranges, we took the median climate suitability across species' entire European and African non-breeding ranges.

After calculating median annual climate suitability for each species, we used a generalized linear regression model, with a binomial error structure and a logit link, to regress climate suitability against year. This was restricted to the same time period for which population index data were available for each species. The slope from this regression was termed the climate suitability trend (CST: following Stephens et al., 2016), which indicates the overall trend in climate suitability for a species. CST was evaluated separately for the breeding and non-breeding grounds for each species, hereafter referred to as CST_b and CST_{nb}, respectively.

As with the population trends, we calculated the mean climate suitability for both short- and long-distance migrants. We first standardized CST values to have a value of 100 in 1980. We then took the geometric mean of all annual climate suitability values for each group of species, again giving each species an equal weight within the analysis. We calculated this metric separately for species' breeding and non-breeding grounds.

2.5 | Land cover suitability trend (LCST)

To quantify trends in the amount of suitable land cover within both species' breeding and non-breeding ranges, we first obtained information on species' habitat preferences from BirdLife International. For each species, we identified the suitability of nine broad habitat categories (shrubland, grassland, cropland, broadleaved forest, needle-leaved forest, wetlands and water bodies, urban, bare areas and sparsely vegetated), for both the breeding and non-breeding grounds (see Appendix S2 in the Supporting Information, Tables S2.1 and S2.2). We then calculated the area of land cover within a species' range classified as suitable. To do this, we obtained global land cover data from the European Space Agency Climate Change Initiative (2017) (ESA CCI: https://www.esalandcover-cci.org/?q=node/1). These data are available at a spatial resolution of 300 m and consist of 24 annual maps of land cover from 1992 to 2015, with each map comprising 22 land cover classes. We aggregated these land cover classes to align with the nine broad habitat categories used to classify species habitat preferences (Tables S2.1 and S2.2). Then, for each year, we calculated the proportion of land cover within a species' range classified as suitable. Finally, we used a generalized linear regression model, with a binomial error structure and a logit link, to regress the proportion of suitable land cover against year. The slope from this regression was termed the land cover suitability trend (LCST) and indicates the overall trend in the amount of suitable land cover within a species range. We evaluated LCST separately for both species' breeding and non-breeding grounds ($LCST_b$ and $LCST_{nb}$, respectively). For species, for which population index data were only available after 1992, the calculation of LCST was restricted to the same time period. Although these annual measures of land cover do not fully encompass the period of interest, they are, as far as we are aware, the best available at this

scale. To assess the potential impact on our results of evaluating LCSTs over a shorter time period, we repeated all following analyses using trend data restricted to the period between 1992 and 2015. Finally, we calculated mean land cover suitability values for both short- and long-distance migrants. We first standardized LCST values to have a value of 100 in 1992. We then took the geometric mean of all annual land cover suitability values for each group of species each year, giving each species an equal weight within the analysis. We evaluated this metric separately for species' breeding and non-breeding grounds.

2.6 | Accounting for variable sampling effort

Given the inevitable discrepancy between recording efforts in many infrequently visited non-breeding regions and the well-monitored breeding grounds, there is the potential for bias between models based on breeding and non-breeding grounds due to more complete occurrence datasets from breeding grounds. To control for this, we developed an additional series of analyses, incorporating a random bootstrapped sampling approach to control for potential discrepancies in recording effort. We used the total number of point occurrence records from the non-breeding range for a given species from the Global Biodiversity Information Facility database (GBIF: GBIF.org, 2018; using all records up to 2016) to guide the size of a subsample of cells to utilize in calculating CSTs and LCSTs for both the breeding and non-breeding ranges. Using the number of point occurrence records from across a species' non-breeding range as our sample size (x), we randomly sampled x cells from each of a species' breeding and non-breeding range. We then took the median climate suitability across the subsampled cells to recalculate CST_b and CST_{nb}. We also recalculated $LCST_b$ and $LCST_{nb}$ using the subsampled cells. We repeated this process 100 times to give 100 bootstrapped estimates of CST_b, CST_{nb}, $LCST_b$ and $LCST_{nb}$ for each species, which we then used to repeat our assessment of the relationship between species' population trends and both CSTs and LCSTs, described below.

2.7 | Assessing correlates of species' population trends

We used Markov Chain Monte Carlo generalized linear mixed models from the "MCMCglmm" R package (Hadfield, 2010) to assess the relationship between species' population trends and potential explanatory variables. This analysis was performed at a pan-European scale because, despite having national indices of abundance during the breeding season, we currently lack data on where different European populations spend the non-breeding season. MCMCglmm takes a Bayesian approach to fitting generalized linear mixed models. It can account for the non-independence between species that can arise from common ancestry, by including a phylogenetic variance–covariance matrix as a random effect. To account for sampling error in the estimation of species' population trends, we also included the standard error of the trend estimates as an additional random effect. In addition to the random effects of phylogeny and population trend standard error, fixed effects within the model included terms for each species to control for differences in body size (logged mean mass of a species), migratory strategy (short- or long-distance), migratory dispersion and primary habitat association. As species' primary breeding and non-breeding range habitat associations were significantly associated with each other for both short- ($X^2 = 157.2$, $df = 9$, $p < .01$) and long-distance migrants ($X^2 = 31.6$, $df = 9$, $p < .01$), we only included species' primary breeding habitat associations as an explanatory variable. We included interactions between CST_b, CST_{nb}, $LCST_b$ and $LCST_{nb}$, and migratory strategy, as we were interested in the potential for differing contributions of climate and land cover suitability to the population trends of short- and long-distance migrants. We assumed that the response variable had a Gaussian error distribution and used non-informative priors with an inverse Wishart distribution ($V = 1$, $\nu = 0.002$). Model outcomes were insensitive to the specification of the non-informative priors. We ran the model for 220,000 iterations, with a burn-in period of 20,000 and a sampling interval of 20. Approximately 1,000 independent samples were generated for each model. We used Gelman–Rubin statistics and diagnostic plots to check for convergence of model chains and the independence of samples.

Rather than using one phylogenetic tree, and assuming this tree was error-free, we instead randomly selected 100 trees from birdtree.org (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) and fitted the model to each of these trees. We then combined the posterior outputs of the resulting 100 MCMCglmms to provide estimates of model coefficients that incorporate phylogenetic uncertainty. For each model, we calculated the percentage of variance explained by each of the fixed effects and assessed model performance using marginal R^2, following the methods described in Nakagawa and Schielzeth (2013). All analyses were performed in R version 3.5.0 (R Core Team, 2019).

3 | RESULTS

3.1 | Species distribution models

SDMs fitted to the breeding and non-breeding ranges of all short- (61 species) and long-distance (39 species) migrants produced robust models for all species using all four SDM approaches. Model fit was very good across the breeding ranges (AUC on validation data: median = 0.98, IQR = 0.85 – 0.99; see Appendix S1 in the Supporting Information, Table S1.3 for individual model technique results). SDMs for species' non-breeding ranges were also good, though median fit was slightly lower than for the breeding range models (AUC on validation data: median = 0.96, IQR = 0.78 – 0.99; Table S1.3). There was no significant difference in SDM performance between short- and long-distance migrants for either the breeding (*t* test, $t_{96.5} = 0.07$, $p = .94$) or non-breeding grounds (*t* test, $t_{73.60} = 1.30$, $p = .20$). The mean annual projections from these models were used to calculate CST values for both the breeding and non-breeding grounds for all 100 species.

3.2 | Predictors of population trends

On average, the populations of short-distance migrants have remained relatively stable since 1980, while those of long-distance migrants have declined steadily over the same period (Figure 1a). There was no difference in average climate suitability between short- and long-distance migrants on either their breeding or non-breeding grounds (Figure 1b and c). However, while climate suitability within species' breeding grounds has declined steadily since 1980, the same cannot be said for species' non-breeding grounds, with climate suitability remaining relatively constant over time (Figure 1b and c). For both short- and long-distance migrants, the extent of suitable land cover across their breeding ranges has increased steadily since 1992 (Figure 1d). Across species non-breeding ranges, however, while

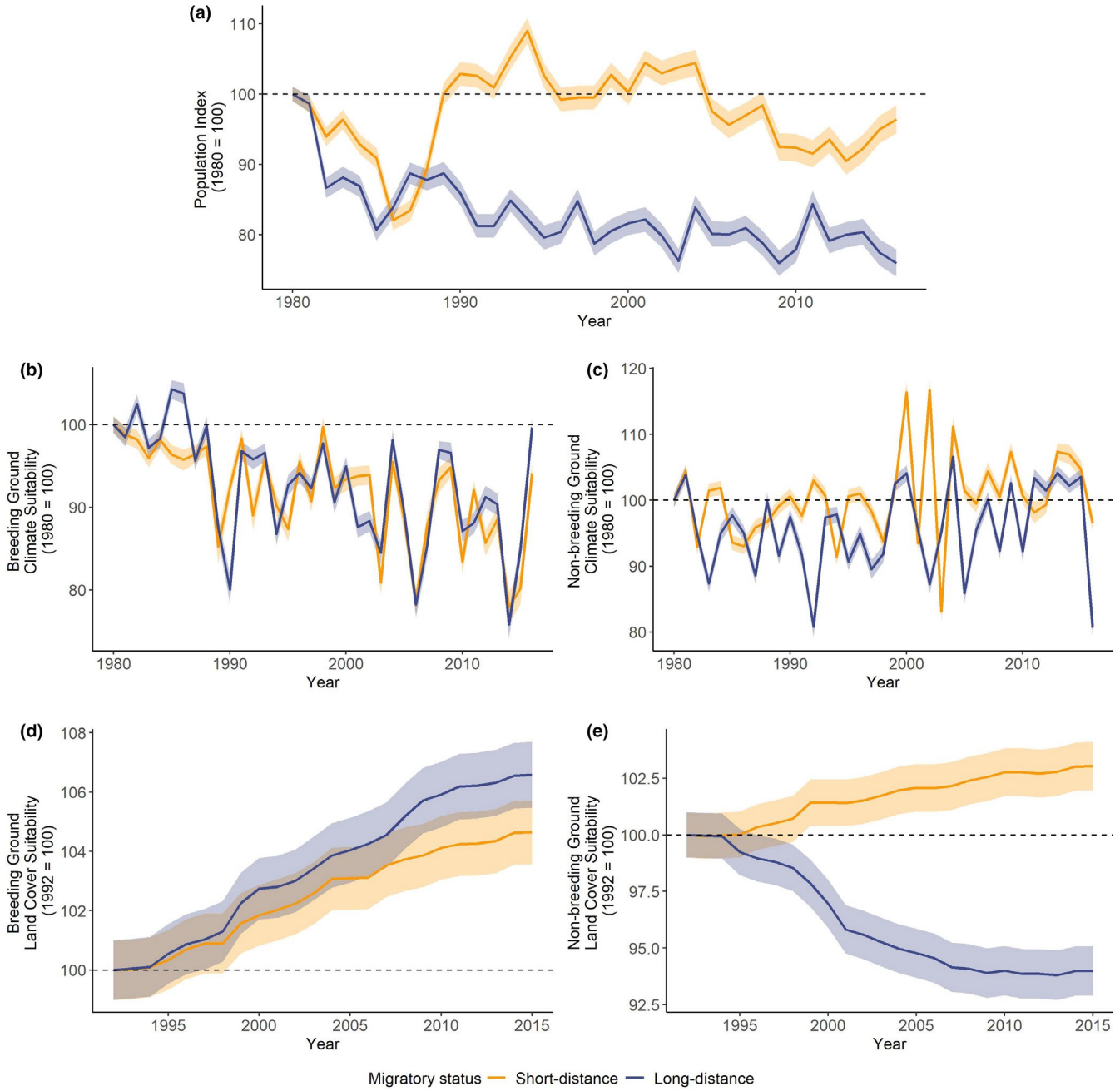

FIGURE 1 Changes in populations and climatic suitability for 61 species of short-distance (yellow lines) and 39 species of long-distance (blue lines) migratory European breeding birds between 1980 and 2016. Changes in Pan-European population indices are shown in (a), while changes in climate suitability are shown for both breeding grounds (b) and non-breeding grounds (c), and changes in the extent of suitable land cover are shown for both breeding grounds (d) and non-breeding grounds (e). For all panels, solid lines indicate the geometric mean, and shading indicates the standard deviation. For both groups of species in panels a- c, values for 1980 are arbitrarily set to 100. In panels d and e, for both groups of species values for 1992 are arbitrarily set to 100. The horizontal dashed lines at values of 100 show the expectation if there is no trend

there have been increases in land cover suitability for short-distance migrants, the suitability of land cover for long-distance migrants has steadily declined (Figure 1e).

Phylogenetically informed linear mixed models explained the population trends of the 100 European breeding migratory birds reasonably well (marginal R^2 = .40, S.D. ±0.02). When considered separately, the model-averaged parameter estimates explained the population trends of long-distance migrants less well than those of short-distance migrant species (R^2 = .15 and R^2 = .37, respectively). Our models indicated that higher CST_b and $LCST_{nb}$, greater body mass and increased dispersion during the non-breeding season were all positively related to species' population trends (Figure 2). In contrast, an association with farmland and open habitats had a negative effect on species' population trends (Figure 2). There was a significant interaction between CST_b and migratory strategy (Figure 2). CST_b was positively related to the population trends of short-distance migrants with a coefficient that was significantly greater than zero (β = 0.48, 95% credible intervals = 0.18 – 0.79, Figure 3). The relationship between CST_b and the population trend of long-distance migrants, however, was non-significant (with a coefficient that overlapped zero; β = −0.03, 95% CI = −0.33 – 0.28, Figure 3). None of CST_{nb}, $LCST_b$ or the interactions between CST_{nb}, $LCST_b$ and $LCST_{nb}$, with migratory strategy, were identified as significant predictors of species' population trends. The results from the analysis using 100 bootstrap estimates of CST_b, CST_{nb}, $LCST_b$ and $LCST_{nb}$ were qualitatively similar to those of the main analysis (see Appendix S1, Figure S1.1), but the model had less explanatory power (marginal R^2 = .29, S.D. ±0.01). The results from the analysis using data restricted to the period between 1992 and 2015 were also qualitatively similar to those in the main analysis (see Appendix S1, Figure S1.2), but again, the model had less explanatory power (marginal R^2 = .31, S.D. ±0.07).

4 | DISCUSSION

Until now, the relative contribution of changes in climate and land cover on the breeding and non-breeding grounds to the declines of European breeding long-distance migrants has been poorly understood (Sanderson et al., 2006; Vickery et al., 2014). Here, we discuss our results in the light of three key findings: 1) the long-term population trends of migratory birds are more closely associated

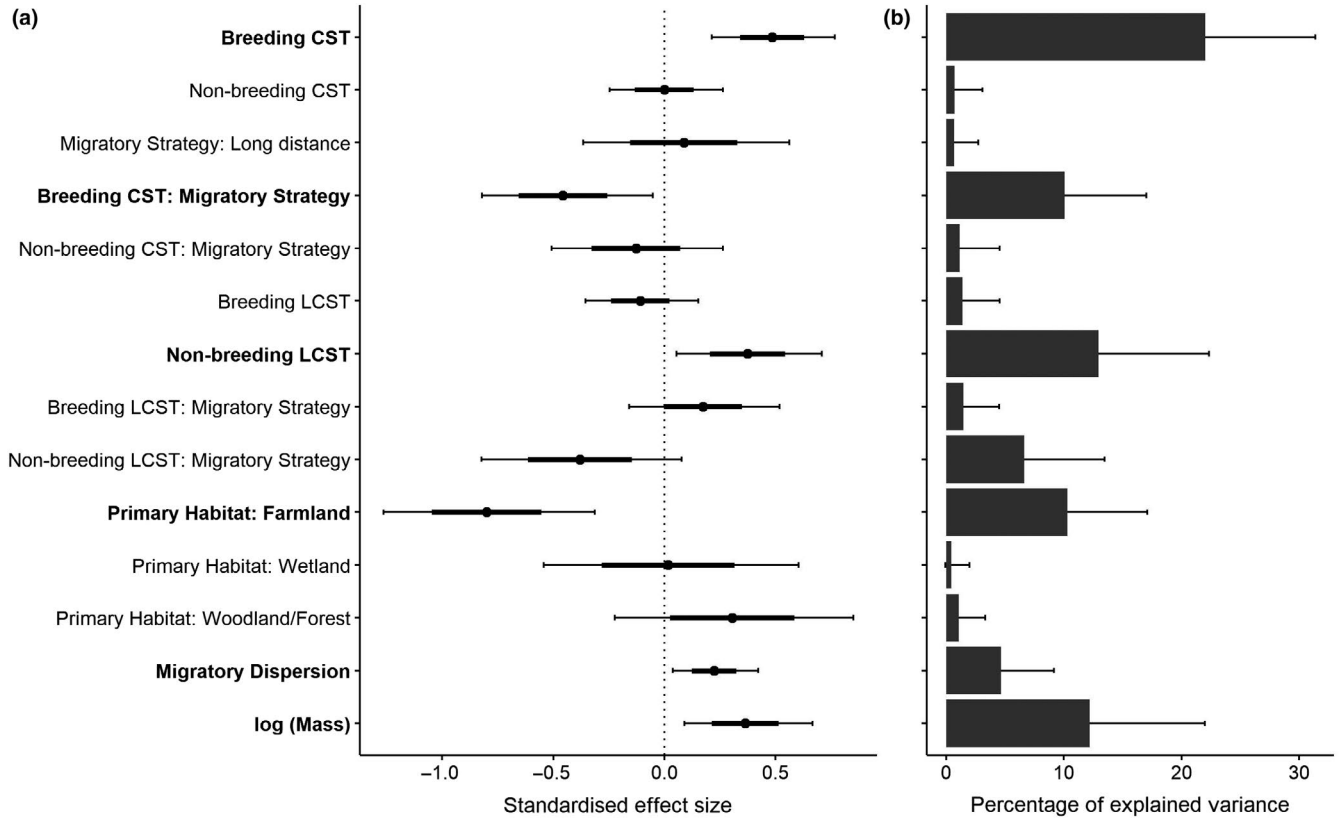

FIGURE 2 Standardized coefficients (a) and percentage of variance explained (b) from MCMC generalized linear mixed models of the population trends of 100 European migratory birds since 1980 (marginal R^2 = 0.40, S.D. ±0.02). In (a), the centre point indicates the mean, the thick bars indicate the posterior standard deviations, and the thin lines indicate the 95% credible intervals of the coefficient values produced by averaging 100 separate MCMCglmms. To standardize coefficient values, all predictors were z-transformed. The reference level for categorical variables includes "short-distance" for migratory strategy and "other" for both breeding and non-breeding habitat association. Overlap of CIs with the dashed line at zero indicates that the effect of the parameter is not statistically significant (i.e. $p > .05$). In (b), bars indicate the mean percentage of variance explained that is attributable to each variable, while thin lines indicate the standard deviation. Significant terms are also indicated in bold on the shared y-axis

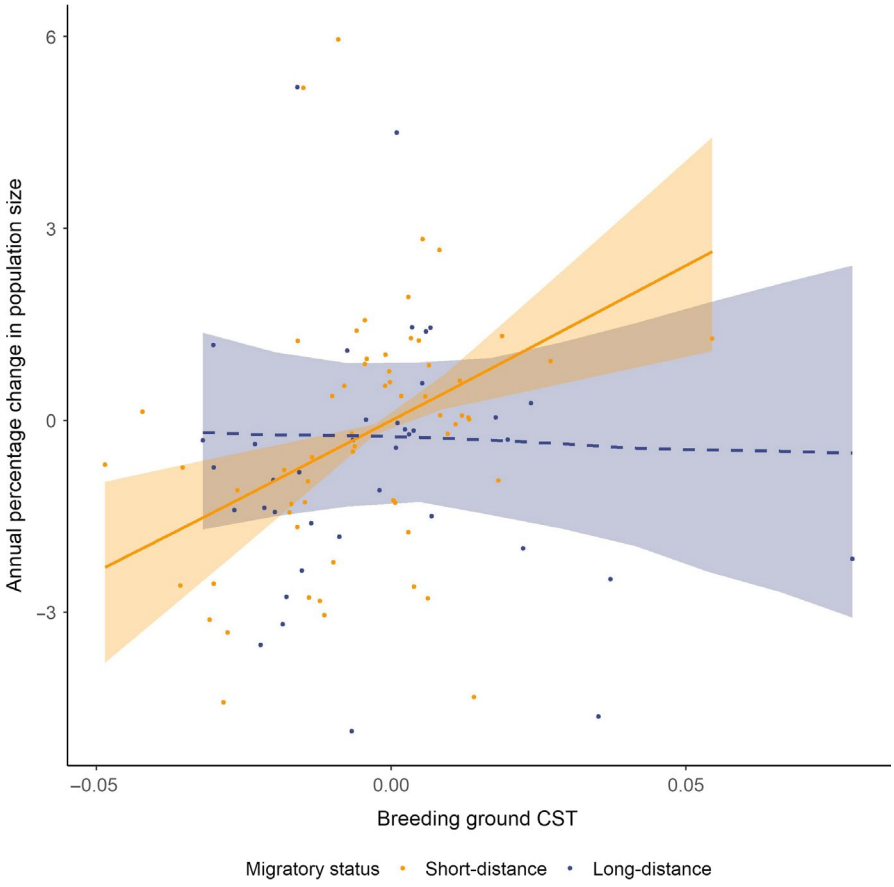

FIGURE 3 Relationship between the annual percentage change in population size and trend in climate suitability (CST) across the breeding ground ranges of 61 short-distance migrant species and 39 long-distance migrant species. Lines indicate the mean non-standardized effect size from across the 100 separate MCMC generalized linear mixed models, while shaded areas indicate the 95% credible intervals. Solid line indicates a relationship that is significantly different from zero (i.e. $p < .05$), while dashed line indicates a relationship non-significantly different from zero

with changes in climate than changes in land cover on their breeding grounds, but the converse is true on their non-breeding grounds; 2) climate trends on the breeding grounds explain more variation in long-term population trends for short-distance migrants than for long-distance migrants; and 3) our ability to explain species' population trends depends on their migratory strategy but nonetheless still only explains about 40% of observed variation in population trends. We discuss these three key findings in turn below.

4.1 | Importance of environmental conditions on the breeding and non-breeding grounds

This is the first large-scale assessment of the relative importance of climate and habitat, as measured by land cover on both the breeding and non-breeding grounds for populations of migratory birds. We have demonstrated that the variables of greatest importance for driving the long-term population trends of migratory species differ between their breeding and non-breeding grounds. Our results highlight the importance of climatic conditions on species' breeding grounds, with a positive relationship between population trend and breeding ground CST, even after accounting for phylogeny, migratory behaviour, body mass and habitat. These results corroborate previous research demonstrating that interspecific variation in the recent population trends of European birds is correlated with climatic trends on species' breeding grounds (Green et al., 2008; Stephens et al., 2016). By contrast, population trends on the breeding grounds were not related to land cover change, at least at the scale as which we assessed this (see below). This is despite the fact that since the 1950s, there have been large-scale changes in both the extent and management intensity of land use across Europe. Particularly notable have been the increases in the extent of forested and urban areas alongside intensification of agricultural practices (Kuemmerle et al., 2016). By contrast, our results suggest that on species' non-breeding grounds, large-scale land cover change is of greater importance. Our finding that there has been an approximately 5% reduction in the extent of suitable land cover across long-distance migrants, sub-Saharan non-breeding ranges, but an approximately 2.5% increase for short-distance migrants, indicates that this results may be partially driven by extensive land cover change across Africa. Since the 1970s, there have been extensive changes in land management and land cover across Africa, but in particular the Sahel region (Cour, 2001), with large-scale expansion and intensification of agriculture, loss of wetlands as a consequence of dam construction and irrigation, and deforestation from clearance for agriculture, wood fuel and grazing (Adams, Small, & Vickery, 2014). Previously, it has been widely assumed that these large-scale changes in land cover are linked to the population declines of Afro-Palaearctic migrant birds on their breeding grounds (Adams et al., 2014; Vickery et al., 2014). Until now, however, evidence for this has been mixed and largely limited to smaller-scale field studies (Adams et al., 2014). Our results provide evidence for a link between large-scale changes

in land cover across migratory species' non-breeding ranges and their breeding population trends.

The apparent low importance of land cover suitability on species' breeding grounds may be a consequence of the high spatial and temporal heterogeneity in large-scale changes in land cover across Europe. Changes in the extent of broad habitat categories across Europe show distinct spatial patterns with, for example, hotspots of cropland decline occurring mostly in Eastern Europe but cropland expansion occurring mostly in North-West Europe (Kuemmerle et al., 2016). When assessed across a large scale, these contrasting patterns may counteract one another to reduce the apparent importance of large-scale land cover change in driving Europe-wide species' population trends. The spatial heterogeneity in the population monitoring periods, with most Eastern European countries having shorter monitoring periods than countries in the west, may further exacerbate these effects. In addition, our measure of land cover suitability only measures large-scale changes in broad habitat classifications and not changes in the intensity of land use management. Despite, as mentioned above, some large-scale changes in the extent of some land cover types, since the 1950s, land use change in Europe has predominantly occurred along intensification gradients (Kuemmerle et al., 2016; Rounsevell et al., 2012); these changes would not be reflected in our measure of land cover suitability.

The lack of a climate signal at non-breeding grounds on breeding populations may be influenced, in part, by the fact that some species in our analysis are somewhat itinerant during the non-breeding season, potentially overwintering in multiple discrete areas during different periods of the non-breeding season. For example, some sub-Saharan migrants, such as willow warblers (*Phylloscopus trochilus)*, move southwards through the non-breeding range over the course of the European winter (Cresswell, Boyd, & Stevens, 2008; Salewski & Jones, 2006). With such species only using non-breeding ranges transiently, mean climatic conditions across non-breeding areas for the entire period may provide misleading estimates of climate suitability. Further data on the intra-seasonal use of the non-breeding range by individual species are required to develop a more nuanced measure of changing climatic suitability in dynamic non-breeding ranges. Such data are not currently available for most species. Migratory connectivity, the extent to which migrant populations spread out and mix during the non-breeding season, may also have influenced this result. Low migratory connectivity, where individual populations of a species spread out and mix over a larger area during the non-breeding season, is common in long-distance migrants (Lemke et al., 2013). Low connectivity should provide greater resilience to climate change by facilitating rapid range shifts (Gilroy et al., 2016). However, if the extent of suitable habitat declines, the proportion of populations that spread out over a large area during the non-breeding season, and that reach the remaining suitable habitat, will also decline (Finch et al., 2017). This may, in turn, decouple the relationship between climate suitability trends on the non-breeding ranges and population trends. Currently, we lack the data required to model the precise relationship between population trends and migratory connectivity (Finch et al., 2017).

The weak evidence for a link between trends in non-breeding climate suitability and long-term population trends emerges despite the wealth of published evidence linking fluctuations in non-breeding grounds' weather conditions, particularly rainfall, to overwinter survival (Johnston et al., 2016) and population size (Ockendon, Johnston, & Baillie, 2014). Although events such as droughts have substantial impacts on species, their irregular occurrence means that the overall relationship between long-term climatic conditions on the non-breeding grounds and migrant population trends is weak (Nevoux et al., 2008a,2008b). In addition, given that we focus on breeding ground population trends, the relationship with conditions on the breeding ranges is likely to be stronger than with conditions on non-breeding ranges. Non-breeding ranges may encompass areas utilized by populations that breed outside of the area covered by PECBMS, and so, climate suitability evaluated across the entire non-breeding range may be less directly linked to trends in breeding populations. This relationship may be further diluted for species containing populations that demonstrate different migratory behaviours. In such cases, the likely stronger relationship between population trends and conditions on the breeding grounds for more resident populations may mask the relationship with conditions on the non-breeding grounds of migratory populations. This result may also, in part, be driven by our use of gridded species distribution data. Species' range maps are often derived from point observations and delineate broad range boundaries (extent of occurrence, sensu Gaston, 2003) rather than maps of occupancy. Given the discrepancies in recording efforts between Europe and Africa, there is an increased probability of false positives in species' gridded data across non-breeding grounds. However, by analysing our data at a relatively coarse scale, our characterizations of species' distributions are less prone to false positives (Hurlbert & Jetz, 2007). Furthermore, our results were also robust to the inclusion of sampling effort, suggesting that the weak relationship between non-breeding ground CST and the long-term population trends of European breeding migratory birds was not a consequence of variable sampling effort across species' ranges.

Conditions across the Sahel, a key environment in the non-breeding season for many long-distance trans-Saharan migrants, are intricately linked to seasonal precipitation (Ockendon et al., 2014; Vickery et al., 2014). When rainfall in the Sahel is higher, resources for migrant birds are more plentiful. From the 1960s, drought conditions predominated in the Sahel (Nicholson, 2000). Although rainfall across some of this region has increased since the 1990s (Fontaine, Roucou, Gaetani, & Marteau, 2011), there are strong regional differences in the extent and direction of this "re-greening" trend (Kaptué, Prihodko, & Hanan, 2015). Habitat changes resulting from the lengthy period of drought have been widely linked to population declines of long-distance migrant birds, observed since the 1970s (Sanderson et al., 2006). Improving conditions since the 1990s may have led to the stabilization of, and increases in, some populations (Baillie et al., 2010; Nevoux et al., 2008a,2008b). In addition, spatial heterogeneity in changes in climate across Africa may have resulted in contrasting directional population trends between species that

overwinter in different regions. For example, it has been shown that species that winter in the humid tropical zone have recently declined, while migrants that winter in the arid Sahelian zone show more stable population trends (Ockendon et al., 2012; Thaxter et al., 2010). These contrasting patterns may counteract one another to weaken the apparent relationship between the population trends of migratory birds and long-term trends in climate on their non-breeding grounds. Thus, while there is strong evidence that annual fluctuations or short-term trends in the abundance of migrants are linked to precipitation across the non-breeding grounds, our results suggest that the long-term population trends of most long-distance migrants are more strongly associated with long-term trends in climate suitability on their breeding ranges than on their wintering grounds.

4.2 | The effect of breeding ground climate suitability on trends of long-distance versus short-distance migrants

The relationship between CST across migrant species' breeding grounds and their population trends is strongly dependent upon migratory strategy. While improving trends in climate suitability across the breeding grounds correspond with increasing population trends for short-distance migrants, this was not the case for long-distance migrants. A number of mechanisms could underlie this pattern. Long-distance migrants are likely to be more susceptible to the potential effects of phenological mismatch upon their reproductive success than short-distance migrants (Møller et al., 2008; Saether & Engen, 2010). Because of the later breeding, and potentially slower rates of nesting advancement in some long-distance migrants, an increasing proportion of individuals appear to be mis-timing their breeding relative to peak availability of key prey species, which has advanced in response to warming spring conditions on the breeding grounds (Both et al., 2006, 2010; Mayor et al., 2017; Saino et al., 2011). However, the evidence for phenological mismatch driving large-scale declines in the breeding success of mismatched migrants is limited. This suggests that there is not a causal link between changes in migrant arrival times and long-term population trends or that any such link occurs through changes in post-breeding survival rates, rather than productivity (Franks et al., 2017). Climate change may also disrupt competitive relationships on the breeding grounds (Bohning-Gaese & Bauer, 1996; Vickery et al., 2014). It has been suggested that warmer winters may improve overwinter survival of short-distance migrants that remain in Europe, while warmer springs may also boost their productivity (Pearce-Higgins et al., 2015). This may account for the close relationship between climate suitability trends on the breeding grounds and short-distance migrant population trends, particularly given that the breeding and non-breeding ranges of short-distance migrants are closer than their long-distance migrant counterparts. Increases in resident and short-distance migrant populations may lead to long-distant migrants facing greater competition for resources in breeding areas (Both & Visser, 2001).

4.3 | Explaining the population trends of short- and long-distance migrants

Breeding and non-breeding ground CST were better at explaining the population trends of short-distance migrants compared with long-distance migrants (our models explained only 15% of variation in trends for the latter). This may be suggestive of other factors driving population trends of long-distance migrants, or that our ability to detect the effect of CST on long-distance migrants was reduced by uncertainty over their winter distributions and their potentially more dispersed distribution at this time, as outlined above. Given the complexity of the annual cycle of long-distance migrants, it is perhaps unsurprising that CST and habitat only explained a small proportion of the variance in the population trends of these birds (Robinson et al., 2009). By using multiple landscapes throughout the annual cycle, long-distance migrants are more likely to be exposed to land use changes during at least part of the year than are other species (Runge et al., 2014). Furthermore, their use of stopover sites during migration can expose long-distance migrants to a greater number of location-specific threats, such as habitat degradation and hunting (Runge et al., 2014). Long-range movements made during extended migrations also increase the likelihood and associated risks of encountering new, unfamiliar environments (Rotics et al., 2017). The enhanced energetic costs of long-distance migration may also have a detrimental effect on the survival of Afro-Palaearctic migrants, with possible carry-over effects (Ryan Norris & Marra, 2007). Indeed, it has been suggested that there is an inverse relationship between energy expenditure and survival in birds (Sala, Wilson, & Quintana, 2015). Notably, some species, including Eurasian blackcap (Sylvia atricapilla) and common chiffchaff (Phylloscopus collybita), have shown changes in their migratory behaviours, with short-stopping and overwintering closer to breeding grounds becoming increasingly common (Elmberg, Hessel, Fox, & Dalby, 2014; Sutherland, 1998), often resulting in markedly improved population trends (Berthold & Terrill, 1988; Rotics et al., 2017; Visser, Perdeck, van Balen, & Both, 2009). It may also be that the variables included in our models are better proxies for the conditions experienced during migrations and on stopovers by short- rather than long-distance migrants. As noted above, the breeding and non-breeding ranges of short-distance migrants are closer together than those of long-distance migrants. Consequently, the conditions that short-distance migrants experience during migration may be, in part, captured by our measures of breeding and non-breeding ground climate suitability and land cover. In contrast, the same measures are less likely to encapsulate the conditions experienced by long-distance migrants during their migrations.

4.4 | Future directions

Detailed knowledge of the destinations of birds that migrate beyond Europe during the non-breeding season, and the specific habitats that they utilize, is currently lacking for the vast majority

of passerine species included in our analysis, especially in terms of linking specific breeding populations to non-breeding localities. Furthermore, we lack nuanced data on trends in the conditions of different habitat types, particularly on the non-breeding grounds. Consequently, population-specific drivers of migrant declines are little studied at present (Cresswell, 2014). Recent advances in tracking, remote sensing technology and the development of genoscapes are enhancing our understanding of migration by providing information on migrant non-breeding ranges, and on the connectivity of breeding and non-breeding sites (Finch et al., 2015; Renfrew et al., 2013; Robinson et al., 2010; Ruegg et al., 2014; Trierweiler et al., 2014), enabling migration routes to be linked to adult survival and population trends (Hewson et al. 2016). Currently, however, such data are available for only relatively small numbers of individuals, and for few species and populations. Expansion of this monitoring will enhance our understanding of specific habitat use on the non-breeding grounds and of linkages between migratory end-points (Vickery et al., 2014). Our pan-European analysis provides valuable insight into the large-scale drivers of the population trends of migratory breeding birds. Future linkage of population-specific breeding and wintering areas, migration routes and stopover locations, as well as improved data on trends in habitat conditions, will enable a better understanding of the mechanisms driving the declines of long-distance migrants at a finer scale (Ockendon et al., 2012).

We have demonstrated that, at a continental scale, the population trends of European breeding migratory birds are more closely associated with long-term climate change than land cover changes on their breeding grounds, but the converse is true on their non-breeding grounds. Importantly, we have shown that, in recent decades, long-distance migrants have benefited less than short-distance migrants from any improvements in climate suitability across their breeding grounds. Nonetheless, our understanding of the drivers of population trends of long-distance migrants remains incomplete because we lack crucial information on migration stopover locations (and associated threats) and on the linkages between breeding and non-breeding localities. Population-level studies into the use of non-breeding areas by migrant species are urgently required if we are to understand the drivers of migrant population dynamics and to prevent, or reverse, further declines.

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DATA AVAILABILITY STATEMENT

Population index data come from the Pan-European Common Bird Monitoring Scheme (PECBMS, http://www.ebcc.info/pecbm.html). Climate data were obtained from the CRU TS 3.2 0.5° dataset (NCAS British Atmospheric Data Centre: (http://catalogue.ceda.ac.uk/uuid/2949a8a25b375c9e323c53f6b6cb2a3a). Land cover data were obtained from the European Space Agency Climate Change Initiative (ESA CCI: https://www.esalandcover-cci.org/?q=node/1). Species distribution data were obtained from Birdlife International (http://datazone.birdlife.org/home).

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REFERENCES

Adams, W. M., Small, R. D. S., & Vickery, J. A. (2014). The impact of land use change on migrant birds in the Sahel. *Biodiversity*, *15*(2–3), 101–108. https://doi.org/10.1080/14888386.2014.931822

Atkinson, P. W., Adams, W. M., Brouwer, J., Buchanan, G., Cheke, R. A., Cresswell, W., … Vickery, J. A. (2014). Defining the key wintering habitats in the Sahel for declining African-Eurasian migrants using expert assessment. *Bird Conservation International*, *24*(04), 477–491. https://doi.org/10.1017/S0959270913000531

Bagchi, R., Crosby, M., Huntley, B., Hole, D. G., Butchart, S. H. M., Collingham, Y., … Willis, S. G. (2013). Evaluating the effectiveness of conservation site networks under climate change: Accounting for uncertainty. *Global Change Biology*, *19*(4), 1236–1248. https://doi.org/10.1111/gcb.12123

Baillie, S. R., Marchant, J. H., Leech, D. I., Joys, A. C., Noble, D. G., Barimore, C., Robinson, R. A. (2010). *Breeding Birds in the Wider Countryside: their conservation status 2009BTO Research Report No. 541*. BTO, Thetford. (https://www.bto.org/our-science/publications/birdtrends/breeding-birds-wider-countryside-their-conservation-status-2009).

Bairlein, F. (2016). Migratory birds under threat. *Science*, *354*(6312), 547 LP – 548.

Barshep, Y., Erni, B., Underhill, L. G., & Altwegg, R. (2017). Identifying ecological and life-history drivers of population dynamics of wetland birds in South Africa. *Global Ecology and Conservation*, *12*(Supplement C), 96–107. https://doi.org/10.1016/j.gecco.2017.09.001.

Beresford, A. E., Sanderson, F. J., Donald, P. F., Burfield, I. J., Butler, A., Vickery, J. A., & Buchanan, G. M. (2019). Phenology and climate change in Africa and the decline of Afro-Palearctic migratory bird populations. *Remote Sensing in Ecology and Conservation*, *5*(1), 55–69. https://doi.org/10.1002/rse2.89

Berthold, P., Fiedler, W., Schlenker, R., & Querner, U. (1998). 25-year study of the population development of central European songbirds: A general decline most evident in long-distance migrants. *Naturwissenschaften*, *85*(7), 350–353. https://doi.org/10.1007/s001140050514

Berthold, P., & Terrill, S. B. (1988). Migratory behaviour and population growth of Blackcaps wintering in Britain and Ireland: Some hypotheses. *Ringing & Migration*, *9*(3), 153–159. https://doi.org/10.1080/03078698.1988.9673939

BirdLife International and NatureServe. (2016). *Bird species distribution maps of the world*. Version 6.0. Cambridge, UK: BirdLife International.

BirdLife International, Cambridge, UK & NatureServe, Arlington, USA. Retrieved from http://www.birdlife.org/datazone/.

BohningGaese, K., & Bauer, H. G. (1996). Changes in species abundance, distribution, and diversity in a central European bird community. *Conservation Biology*, *10*(1), 175–187. https://doi.org/10.1046/j.1523-1739.1996.10010175.x

Both, C., Bouwhuis, S., Lessells, C. M., & Visser, M. E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature*, *441*(7089), 81–83. https://doi.org/10.1038/nature04539.

Both, C., Van Turnhout, C. A. M., Bijlsma, R. G., Siepel, H., Van Strien, A. J., & Foppen, R. P. B. (2010). Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1685), 1259–1266.

Both, C., & Visser, M. E. (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, *411*(6835), 296–298.

Brotons, L., Thuiller, W., Araujo, M. B., & Hirzel, A. H. (2004). Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography*, *27*(4), 437–448. https://doi.org/10.1111/j.0906-7590.2004.03764.x.

R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org/.

Cour, J. M. (2001). The Sahel in West Africa: Countries in transition to a full market economy. *Global Environmental Change*, *11*(1), 31–47. https://doi.org/10.1016/S0959-3780(00)00043-1

Cramp, S. (1977–1994). *Birds of the Western Palearctic: Handbook of the Birds of Europe, the Middle East and North Africa*. (S. Cramp, Ed.). Oxford, UK: Oxford University Press.

Cresswell, W. (2014). Migratory connectivity of Palaearctic-African migratory birds and their responses to environmental change: The serial residency hypothesis. *Ibis*, *156*(3), 493–510. https://doi.org/10.1111/ibi.12168

Cresswell, W., Boyd, M., & Stevens, M. (2008). *Movements of Palearctic and Afrotropical bird species during the dry season* (November-February) within Nigeria. In *Proceedings of the 12th Pan African Ornithological Congress* (pp. 18–28).

Cresswell, W., Wilson, J. M., Vickery, J., Jones, P., & Holt, S. (2007). Changes in densities of Sahelian bird species in response to recent habitat degradation. *Ostrich*, *78*(2), 247–253. https://doi.org/10.2989/OSTRICH.2007.78.2.20.100

Donald, P. F., Sanderson, F. J., Burfield, I. J., & van Bommel, F. P. J. (2006). Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. *Agriculture Ecosystems & Environment*, *116*(3–4), 189–196. https://doi.org/10.1016/j.agee.2006.02.007.

Doswald, N., Willis, S. G., Collingham, Y. C., Pain, D. J., Green, R. E., & Huntley, B. (2009). Potential impacts of climatic change on the breeding and non-breeding ranges and migration distance of European Sylvia warblers. *Journal of Biogeography*, *36*(6), 1194–1208. https://doi.org/10.1111/j.1365-2699.2009.02086.x.

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., … E. Zimmermann, N. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, *29*(2), 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Elmberg, J., Hessel, R., Fox, A. D., & Dalby, L. (2014). Interpreting seasonal range shifts in migratory birds: A critical assessment of 'short-stopping' and a suggested terminology. *Journal of Ornithology*, *155*(3), 571–579. https://doi.org/10.1007/s10336-014-1068-2

European Space Agency (ESA) (2017). Land Cover CCI Product User Guide Version 2. Tech. Rep. Available at: maps.elie.ucl.ac.be/CCI/viewer/download/ESACCI-LC-Ph2-PUGv2_2.0.pdf

Finch, T., Butler, S. J., Franco, A. M. A., & Cresswell, W. (2017). Low migratory connectivity is common in long-distance migrant birds. *Journal of Animal Ecology*, *86*(3), 662–673. https://doi.org/10.1111/1365-2656.12635

Finch, T., Pearce-Higgins, J. W., Leech, D. I., & Evans, K. L. (2014). Carry-over effects from passage regions are more important than breeding climate in determining the breeding phenology and performance of three avian migrants of conservation concern. *Biodiversity and Conservation*, *23*(10), 2427–2444. https://doi.org/10.1007/s10531-014-0731-5.

Finch, T., Saunders, P., Avilés, J. M., Bermejo, A., Catry, I., de la Puente, J., … Butler, S. J. (2015). A pan-European, multipopulation assessment of migratory connectivity in a near-threatened migrant bird. *Diversity and Distributions*, *21*(9), 1051–1062. https://doi.org/10.1111/ddi.12345

Fontaine, B., Roucou, P., Gaetani, M., & Marteau, R. (2011). Recent changes in precipitation, ITCZ convection and northern tropical circulation over North Africa (1979–2007). *International Journal of Climatology*, *31*(5), 633–648. https://doi.org/10.1002/joc.2108

Franks, S. E., Pearce-Higgins, J. W., Atkinson, S., Bell, J. R., Botham, M. S., Brereton, T. M., … Leech, D. I. (2017). The sensitivity of breeding songbirds to changes in seasonal timing is linked to population change but cannot be directly attributed to the effects of trophic asynchrony on productivity. *Global Change Biology*, *24*(3), 957–971. https://doi.org/10.1111/gcb.13960

Gaston, K. J. (2003). *The Structure and Dynamics of Geographic Ranges*. Oxford, UK: Oxford University Press.

GBIF.org. (2018). *GBIF Home Page*. Retrieved May 8, 2018, from https://www.gbif.org

Gilroy, J. J., Gill, J. A., Butchart, S. H. M., Jones, V. R., & Franco, A. M. A. (2016). Migratory diversity predicts population declines in birds. *Ecology Letters*, *19*(3), 308–317. https://doi.org/10.1111/ele.12569

Green, R. E., Collingham, Y. C., Willis, S. G., Gregory, R. D., Smith, K. W., & Huntley, B. (2008). Performance of climate envelope models in retrodicting recent changes in bird population size from observed climatic change. *Biology Letters*, *4*(5), 599–602. https://doi.org/10.1098/rsbl.2008.0052

Gregory, R. D., Skorpilova, J., Vorisek, P., & Butler, S. (2019). An analysis of trends, uncertainty and species selection shows contrasting trends of widespread forest and farmland birds in Europe. *Ecological Indicators*, *103*, 676–687. https://doi.org/10.1016/j.ecolind.2019.04.064

Gregory, R. D., van Strien, A., Vorisek, P., Meyling, A. W. G., Noble, D. G., Foppen, R. P. B., & Gibbons, D. W. (2005). Developing indicators for European birds. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *360*(1454), 269–288. https://doi.org/10.1098/rstb.2004.1602.

Gregory, R. D., Vorisek, P., Van strien, A., Gmelig meyling, A. W., Jiguet, F., Fornasari, L., … Burfield, I. J. (2007). Population trends of widespread woodland birds in Europe. *Ibis*, *149*, 78–97. https://doi.org/10.1111/j.1474-919X.2007.00698.x

Gregory, R. D., Willis, S. G., Jiguet, F., Vořišek, P., Klvaňová, A., van Strien, A., … Green, R. E. (2009). An indicator of the impact of climatic change on European bird populations. *PLoS One*, *4*(3), e4678. https://doi.org/10.1371/Journal.Pone.0004678

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, *33*(2), 1–22.

Harris, I., Jones, P. D., Osborn, T. J., & Lister, D. H. (2014). Updated high-resolution grids of monthly climatic observations–the CRU TS3.10 Dataset. *International Journal of Climatology*, *34*(3), 623–642.

Howard, C., Stephens, P. A., Pearce-Higgins, J. W., Gregory, R. D., & Willis, S. G. (2014). Improving species distribution models: The value of data on abundance. *Methods in Ecology and Evolution*, *5*(6), 506–513. https://doi.org/10.1111/2041-210X.12184

Howard, C., Stephens, P. A., Pearce-Higgins, J. W., Gregory, R. D., & Willis, S. G. (2015). The drivers of avian abundance: Patterns in the relative

importance of climate and land use. *Global Ecology and Biogeography*, *24*(11), 1249–1260. https://doi.org/10.1111/geb.12377

Hurlbert, A. H., & Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences*, *104*(33), 13384 LP – 13389. https://doi.org/10.1073/pnas.0704469104.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, *491*(7424), 444–448. https://doi.org/10.1038/Nature11631.

Jiguet, F., Gregory, R. D., Devictor, V., Green, R. E., Vorisek, P., Van Strien, A., & Couvet, D. (2010). Population trends of European common birds are predicted by characteristics of their climatic niche. *Global Change Biology*, *16*(2), 497–505. https://doi.org/10.1111/j.1365-2486.2009.01963.x.

Johnston, A., Robinson, R. A., Gargallo, G., Julliard, R., van der Jeugd, H., & Baillie, S. R. (2016). Survival of Afro-Palaearctic passerine migrants in western Europe and the impacts of seasonal weather variables. *Ibis*, *158*(3), 465–480. https://doi.org/10.1111/ibi.12366

Kaptué, A. T., Prihodko, L., & Hanan, N. P. (2015). On regreening and degradation in Sahelian watersheds. *Proceedings of the National Academy of Sciences*, *112*(39), 12133–12138. https://doi.org/10.1073/pnas.1509645112

Kirby, J. S., Stattersfield, A. J., Butchart, S. H. M., Evans, M. I., Grimmett, R. F. A., Jones, V. R., … Newton, I. (2008). Key conservation issues for migratory land-and waterbird species on the world's major flyways. *Bird Conservation International*, *18*(S1), S49–S73. https://doi.org/10.1017/S0959270908000439

Koleček, J., Procházka, P., Ieronymidou, C., Burfield, I. J., & Reif, J. (2018). Non-breeding range size predicts the magnitude of population trends in trans-Saharan migratory passerine birds. *Oikos*, *127*(4), 599–606. https://doi.org/10.1111/oik.04549

Kuemmerle, T., Levers, C., Erb, K., Estel, S., Jepsen, M. R., Müller, D., … Reenberg, A. (2016). Hotspots of land use change in Europe. *Environmental Research Letters*, *11*(6), 64020. https://doi.org/10.1088/1748-9326/11/6/064020

Lemke, H. W., Tarka, M., Klaassen, R. H. G., Akesson, M., Bensch, S., Hasselquist, D., & Hansson, B. (2013). Annual Cycle and Migration Strategies of a Trans-Saharan Migratory Songbird: A Geolocator Study in the Great Reed Warbler. *PLoS One*, *8*(10), e79209. https://doi.org/10.1371/journal.pone.0079209.

Manel, S., Williams, H. C., & Ormerod, S. J. (2001). Evaluating presence–absence models in ecology: The need to account for prevalence. *Journal of Applied Ecology*, *38*(5), 921–931. https://doi.org/10.1046/j.1365-2664.2001.00647.x

Mayor, S. J., Guralnick, R. P., Tingley, M. W., Otegui, J., Withey, J. C., Elmendorf, S. C., … Schneider, D. C. (2017). Increasing phenological asynchrony between spring green-up and arrival of migratory birds. *Scientific Reports*, *7*(1), 1902. https://doi.org/10.1038/s41598-017-02045-z

Møller, A. P., Rubolini, D., & Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(42), 16195–16200. https://doi.org/10.1073/pnas.0803825105.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Nevoux, M., Barbraud, J., & Barbraud, C. (2008a). Nonlinear impact of climate on survival in a migratory white stork population. *Journal of Animal Ecology*, *77*(6), 1143–1152. https://doi.org/10.1111/j.1365-2656.2008.01435.x

Nevoux, M., Barbraud, J.-C., & Barbraud, C. (2008b). Breeding experience and demographic response to environmental variability in the white stork. *The Condor*, *110*(1), 55–62. https://doi.org/10.1525/cond.2008.110.1.55

Nicholson, S. (2000). Land surface processes and Sahel climate. *Reviews of Geophysics*, *38*(1), 117–139. https://doi.org/10.1029/1999rg900014

Ockendon, N., Hewson, C. M., Johnston, A., & Atkinson, P. W. (2012). Declines in British-breeding populations of Afro-Palaearctic migrant birds are linked to bioclimatic wintering zone in Africa, possibly via constraints on arrival time advancement. *Bird Study*, *59*(2), 111–125. https://doi.org/10.1080/00063657.2011.645798

Ockendon, N., Johnston, A., & Baillie, S. (2014). Rainfall on wintering grounds affects population change in many species of Afro-Palaearctic migrants. *Journal of Ornithology*, *155*(4), 905–917. https://doi.org/10.1007/s10336-014-1073-5

Ockendon, N., Leech, D., & Pearce-Higgins, J. W. (2013). Climatic effects on breeding grounds are more important drivers of breeding phenology in migrant birds than carry-over effects from wintering grounds. *Biology Letters*, *9*(6), 20130669. https://doi.org/10.1098/rsbl.2013.0669

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., … Kassem, K. R. (2001). Terrestrial Ecoregions of the World: A New Map of Life on Earth A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience*, *51*(11), 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Peach, W., Baillie, S., & Underhill, L. (1991). Survival of British Sedge Warblers Acrocephalus schoenobaenus in relation to west African rainfall. *Ibis*, *133*(3), 300–305. https://doi.org/10.1111/j.1474-919X.1991.tb04573.x

Pearce-Higgins, J. W., Eglington, S. M., Martay, B., & Chamberlain, D. E. (2015). Drivers of climate change impacts on bird communities. *Journal of Animal Ecology*, *84*(4), 943–954. https://doi.org/10.1111/1365-2656.12364

Ponti, R., Arcones, A., Ferrer, X., & Vieites, D. R. (2019). Seasonal climatic niches diverge in migratory birds. *Ibis*, *162*(2), 318–330. https://doi.org/10.1111/ibi.12784

Prentice, I. C., Cramer, W., Harrison, S. P., Leemans, R., Monserud, R. A., & Solomon, A. M. (1992). A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography*, *19*(2), 117–134. https://doi.org/10.2307/2845499.

Renfrew, R. B., Kim, D., Perlut, N., Smith, J., Fox, J., & Marra, P. P. (2013). Phenological matching across hemispheres in a long-distance migratory bird. *Diversity and Distributions*, *19*(8), 1008–1019. https://doi.org/10.1111/ddi.12080

Robinson, R. A., Crick, H., Learmonth, J. A., Maclean, I., Thomas, C. D., Bairlein, F., … Visser, M. E. (2009). Travelling through a warming world: Climate change and migratory species. *Endangered Species Research*, *7*(2), 87–99. https://doi.org/10.3354/esr00095

Robinson, W. D., Bowlin, M. S., Bisson, I., Shamoun-Baranes, J., Thorup, K., Diehl, R. H., … Winkler, D. W. (2010). Integrating concepts and technologies to advance the study of bird migration. *Frontiers in Ecology and the Environment*, *8*(7), 354–361. https://doi.org/10.1890/080179

Rotics, S., Turjeman, S., Kaatz, M., Resheff, Y. S., Zurell, D., Sapir, N., … Nathan, R. (2017). Wintering in Europe instead of Africa enhances juvenile survival in a long-distance migrant. *Animal Behaviour*, *126*, 79–88. https://doi.org/10.1016/j.anbehav.2017.01.016

Rounsevell, M. D. A., Pedroli, B., Erb, K.-H., Gramberger, M., Busck, A. G., Haberl, H., … Wolfslehner, B. (2012). Challenges for land system science. *Land Use Policy*, *29*(4), 899–910. https://doi.org/10.1016/j.landusepol.2012.01.007

Ruegg, K. C., Anderson, E. C., Paxton, K. L., Apkenas, V., Lao, S., Siegel, R. B., … Smith, T. B. (2014). Mapping migration in a songbird using high-resolution genetic markers. *Molecular Ecology*, *23*(23), 5726–5739. https://doi.org/10.1111/mec.12977

Runge, C. A., Martini, T. G., Possingham, H. P., Willis, S. G., & Fuller, R. A. (2014). Conserving mobile species. *Frontiers in Ecology and the Environment*, *12*(7), 395–402. https://doi.org/10.1890/130237.

Runge, C. A., Watson, J. E. M., Butchart, S. H. M., Hanson, J. O., Possingham, H. P., & Fuller, R. A. (2015). Protected areas and global conservation of migratory birds. *Science*, *350*(6265), 1255–1258. https://doi.org/10.1126/science.aac9180

Ryan, N. D., & Marra, P. P. (2007). Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor*, *109*(3), 535–547. https://doi.org/10.1093/condor/109.3.535

Saether, B., & Engen, S. (2010). Population consequences of climate change. In A. P. Moller, W. Fiedler, & P. Berthold (Eds.), *Effects of Climate Change on Birds*. United States: Oxford University Press Inc.

Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Hüppop, K., … Sokolov, L. (2011). Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B-Biological Sciences*, *278*(1707), 835–842. https://doi.org/10.1098/rspb.2010.1778.

Sala, J. E., Wilson, R. P., & Quintana, F. (2015). Foraging effort in Magellanic penguins: Balancing the energy books for survival? *Marine Biology*, *162*(3), 501–514. https://doi.org/10.1007/s00227-014-2581-9

Salewski, V., & Jones, P. (2006). Palearctic passerines in Afrotropical environments: A review. *Journal of Ornithology*, *147*(2), 192–201. https://doi.org/10.1007/s10336-006-0057-5

Sanderson, F. J., Donald, P. F., Pain, D. J., Burfield, I. J., & van Bommel, F. P. J. (2006). Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation*, *131*(1), 93–105. https://doi.org/10.1016/j.biocon.2006.02.008.

Sanderson, F. J., Pople, R. G., Ieronymidou, C., Burfield, I. J., Gregory, R. D., Willis, S. G., … Donald, P. F. (2016). Assessing the performance of EU nature legislation in protecting target bird species in an era of climate change. *Conservation Letters*, *9*, 172–180. https://doi.org/10.1111/conl.12196

Snow, D. W., Perrins, C. M., Hillcoat, B., Gillmor, R., & Roselaar, C. S. (1997). *The birds of the Western Palearctic*. Oxford: Oxford University Press.

Somveille, M., Rodrigues, A. S. L., & Manica, A. (2018). Energy efficiency drives the global seasonal distribution of birds. *Nature Ecology & Evolution*, *2*(6), 962–969. https://doi.org/10.1038/s41559-018-0556-9

Stephens, P. A., Mason, L. R., Green, R. E., Gregory, R. D., Sauer, J. R., Alison, J., … Willis, S. G. (2016). Consistent response of bird populations to climate change on two continents. *Science*, *352*(6281), 84–87. https://doi.org/10.1126/science.aac4858

Studds, C. E., Kendall, B. E., Murray, N. J., Wilson, H. B., Rogers, D. I., Clemens, R. S., Fuller, R. A. (2017). Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. *Nature Communications*, *8*, 14895. Retrieved from doi: https://doi.org/10.1038/ncomms14895.

Sullivan, M. J. P., Newson, S. E., & Pearce-Higgins, J. W. (2015). Using habitat-specific population trends to evaluate the consistency of the effect of species traits on bird population change. *Biological Conservation*, *192*, 343–352. https://doi.org/10.1016/j.biocon.2015.10.009

Sutherland, W. J. (1998). Evidence for Flexibility and Constraint in Migration Systems. *Journal of Avian Biology*, *29*(4), 441–446. https://doi.org/10.2307/3677163

Thaxter, C. B., Joys, A. C., Gregory, R. D., Baillie, S. R., & Noble, D. G. (2010). Hypotheses to explain patterns of population change among breeding bird species in England. *Biological Conservation*, *143*(9), 2006–2019. https://doi.org/10.1016/j.biocon.2010.05.004.

Thuiller, W., Araujo, M. B., & Lavorel, S. (2004). Do we need land-cover data to model species distributions in Europe? *Journal of Biogeography*, *31*(3), 353–361. https://doi.org/10.1046/j.0305-0270.2003.00991.x

Trierweiler, C., Klaassen, R. H. G., Drent, R. H., Exo, K.-M., Komdeur, J., Bairlein, F., & Koks, B. J. (2014). Migratory connectivity and population-specific migration routes in a long-distance migratory bird. *Proceedings of the Royal Society of London B: Biological Sciences*, *281*(1778), 20132897. https://doi.org/10.1098/rspb.2013.2897.

Vickery, J. A., Ewing, S. R., Smith, K. W., Pain, D. J., Bairlein, F., Škorpilová, J., & Gregory, R. D. (2014). The decline of Afro-Palaearctic migrants and an assessment of potential causes. *Ibis*, *156*(1), 1–22. https://doi.org/10.1111/ibi.12118

Visser, M. E., Perdeck, A. C., van Balen, J. H., & Both, C. (2009). Climate change leads to decreasing bird migration distances. *Global Change Biology*, *15*(8), 1859–1865. https://doi.org/10.1111/j.1365-2486.2009.01865.x

Wilcove, D. S., & Wikelski, M. (2008). Going, going, gone: Is animal migration disappearing? *Plos Biology*, *6*(7), 1361–1364. https://doi.org/10.1371/journal.pbio.0060188

Wilson, J. M., & Cresswell, W. (2006). How robust are Palearctic migrants to habitat loss and degradation in the Sahel? *Ibis*, *148*(4), 789–800. https://doi.org/10.1111/j.1474-919X.2006.00581.x

Zurell, D., Graham, C. H., Gallien, L., Thuiller, W., & Zimmermann, N. E. (2018). Long-distance migratory birds threatened by multiple independent risks from global change. *Nature Climate Change*, *8*(11), 992–996. https://doi.org/10.1038/s41558-018-0312-9

Zwarts, L., Bijlsma, R., van der kamp, J., & Wymenga, E. (2009). *Living on the edge: Wetlands and birds in a changing Sahel*. Zeist, The Netherlands: KNNV publishing.

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SUPPORTING INFORMATION

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

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