



LETTER

Broad-scale seasonal climate tracking is a consequence, not a driver, of avian migratory connectivity

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Abstract

Tracking climatic conditions throughout the year is often assumed to be an adaptive behaviour underlying seasonal migration patterns in animal populations. We investigate this hypothesis using genetic markers data to map migratory connectivity for 27 genetically distinct bird populations from 7 species. We found that the variation in seasonal climate tracking across our suite of populations at a continental scale is more likely a consequence, rather than a direct driver, of migratory connectivity, which is primarily shaped by energy efficiency—i.e., optimizing the balance between accessing available resources and movement costs. However, our results also suggest that regional-scale seasonal precipitation tracking affects population migration destinations, thus revealing a potential scale dependency of ecological processes driving migration. Our results have implications for the conservation of these migratory species under climate change, as populations tracking climate seasonally are potentially at higher risk if they adapt to a narrow range of climatic conditions.

KEYWORDS

climate change, genoscape, migratory connectivity, optimal migration, seasonal climate tracking

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INTRODUCTION

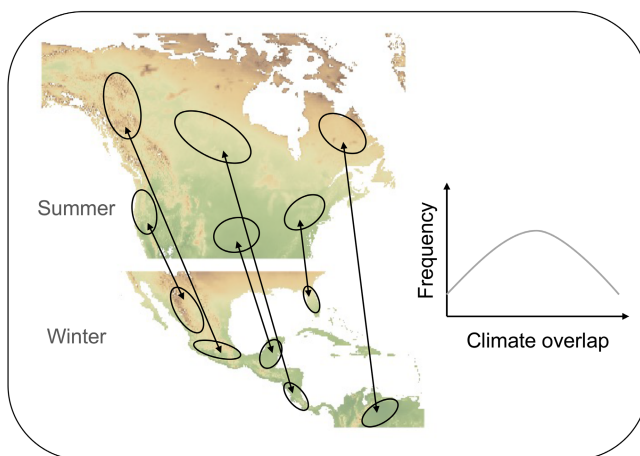
Migratory birds are declining fast (Rosenberg et al., 2019), and climate change is suspected to be one of the leading causes of this decline (Both et al., 2010; Rosenberg et al., 2019; Saino et al., 2011). Climate constitutes an important constraint on species distributions (Pigot et al., 2010; Tingley et al., 2009), and understanding how it shapes seasonal migration patterns is crucial to anticipate better how migratory species respond to ongoing anthropogenic climate change. Previous studies have found that the migratory avifauna is composed of both species that track favourable climatic conditions throughout the year (climate niche trackers) and species that switch climatic conditions seasonally (climate niche switchers) (Boucher-Lalonde et al., 2014; Gómez et al., 2016; Laube et al., 2015; Martínez-Meyer et al., 2004; Nakazawa et al., 2004; Somveille et al., 2019). However, patterns at the species level could be misleading if the drivers of bird migration operate at the population level.

Bird migration is a phenomenon that exhibits a great diversity of individual behaviours and strategies (Newton, 2008). Within species, migratory movements shape patterns of spatiotemporal linkages of populations between seasons, referred to as migratory connectivity (Webster et al., 2002), which are being increasingly revealed by novel technologies documenting differences in migratory behaviour (DeSaix et al., 2023; Faaborg et al., 2010; Finch et al., 2017; Gómez et al., 2021; Ruegg et al., 2014). These migratory patterns have important consequences for a species' broader ecology and evolution as they can affect population dynamics via

seasonal carry-over effects (Marra et al., 1998; Sillit & Holmes, 2002; Taylor & Norris, 2010). Seasonal climate tracking is often assumed to be an adaptive behaviour underlying migration patterns (e.g., Gutiérrez Illán et al., 2022; Thorup et al., 2021; Figure 1), and previous population-specific studies found evidence of seasonal climate tracking at population level (Fandos et al., 2020; Fandos & Tellería, 2020; Gutiérrez Illán et al., 2022). If seasonal climate tracking is a driver of migration patterns, migratory populations are expected to modify their migration patterns to track changing climate, which has been suggested in some migratory species (Dufour et al., 2021; Thorup et al., 2021; Van Doren et al., 2021), and climate change would thus be a direct driver of the evolution of migration routes within species. Under this scenario, migratory populations might be less vulnerable to climate change as they are more likely to track it by modifying their migratory behaviour and routes (Thorup et al., 2021).

An alternative hypothesis is that the variation in seasonal climate tracking among populations might result from how other processes shape migration patterns. A recent study found that migratory connectivity is broadly driven by optimizing the balance between accessing resources available in the environment and the cost of movement without directly using climate information (Somveille et al., 2021). Migratory connectivity resulting from resource availability and migration cost could then result in a mixture of climate-tracking and climate-switching populations whose distribution is shaped by geographical accident rather than direct causality (Figure 1). The question of whether migratory connectivity shapes the variation in seasonal climate tracking in migratory birds has, to our

(a) Energy efficiency → Migratory connectivity



(b) Climate tracking → Migratory connectivity

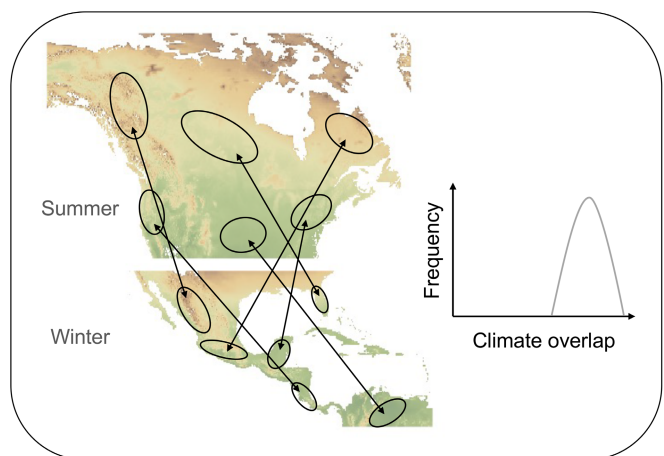


FIGURE 1 Conceptual plots showing the different expectations under the two main hypotheses regarding the causal relationship between seasonal climate tracking and migratory connectivity. (a) Hypothesis 1: Energy efficiency drives migratory connectivity, which then shapes the variation in seasonal climate tracking across populations; (b) Hypothesis 2: Seasonal climate tracking is a direct driver of migratory connectivity. The background colour scheme of the maps indicates the geographical variation of a hypothetical climate variable; oval shapes indicate the seasonal distribution of populations of a given migratory species; arrows indicate the connectivity of seasonal populations via migration; and the diagrams on the right of the maps indicate the expected distribution of seasonal climate tracking (i.e. climate overlap) across populations.

knowledge, never been investigated despite its important evolutionary and conservation implications. If the variation in seasonal climate tracking across populations is a consequence of migratory connectivity, then populations that, by chance, track climate could have adapted over time to a narrow climatic niche and, therefore, be highly vulnerable to changing climate.

Previous studies investigating seasonal climate tracking at the population level (Fandos et al., 2020; Fandos & Tellería, 2020; Gutiérrez Illán et al., 2022) have used tracking and banding data, which makes it difficult and somewhat arbitrary to define distinct populations. In contrast, advances in genomics make it possible to delineate genetically distinct populations across a species and map their seasonal destinations (DeSaix et al., 2023; Ruegg et al., 2014). A recent study using genetic markers for the Willow Flycatcher, *Empidonax traillii*, for example, found a combination of climate tracking and climate switching across populations of the species (Ruegg et al., 2021) but did not explore whether such tracking was a cause or consequence of migratory connectivity.

Here, we use data on population-level migratory connectivity derived from genetic markers for genetically distinct populations from seven different migratory species to investigate how these populations track climate throughout the annual cycle. We test whether population-level seasonal climate tracking is a driver or a consequence of broad-scale migratory connectivity by first examining if simulation models of migratory connectivity based on (i) the balance between access to available energy and the cost of migratory movements (a process hereafter called *energy efficiency*) or (ii) optimizing the tracking of climatic conditions throughout the year, can explain empirical variations in seasonal climate tracking across populations (Figure 1). As migratory connectivity patterns are scale-dependent (González-Prieto et al., 2016) and the underlying drivers might be as well—e.g., seasonal climate tracking could be affecting migration destinations at one scale but not at another—we also examine whether migratory populations track climate conditions at a regional scale better than if they re-distributed randomly around the most energy efficient destinations. Overall, this work provides an explicit test of whether seasonal climate tracking is a consequence or driver of migratory connectivity at both broad and regional geographic scales, contributing key insights for the conservation of migratory species.

METHODS

Bird data

We collated data for seven North American migratory species for which analysis has been previously conducted to identify genetically distinct populations:

Willow Flycatcher (*Empidonax traillii*; WIFL), Yellow Warbler (*Setophaga petechia*; YEWA), Wilson's Warbler (*Cardellina pusilla*; WIWA), Common Yellowthroat (*Geothlypis trichas*; COYE), American Redstart (*Setophaga ruticilla*; AMRE), Painted Bunting (*Passerina ciris*; PABU) and Hermit Thrush (*Catharus guttatus*; HETH). These species exhibit a variety of migration patterns, ranging from the relatively short-distance migration of HETH and PABU to the intermediate-distance migration of WIFL and COYE to the long-distance migration of YEWA, which are typical migration patterns for North American migratory birds where the bulk of migratory species breed between 30° and 60° North and spend the nonbreeding season in Mexico and Central America (Somveille et al., 2015). A total of 3829 genetic samples were available and distributed widely across these species' breeding and wintering ranges (Figures S1–S7).

Migratory connectivity was estimated using high-resolution genetic markers data compiled by the Bird Genoscape Project (www.birdgenoscape.org). Data and methodology for mapping migratory connectivity using genetic markers are described in detail in a set of species-specific papers (Alvarado et al., 2022; Bay et al., 2021; Bobowski et al., in review; DeSaix et al., 2023; Rueda-Hernández et al., 2023; Ruegg et al., 2014, 2020, 2021). Briefly, for each species, DNA was sampled from individuals across the species' breeding ground, and RAD-seq (WIFL, YEWA, PABU, and WIWA) or whole genome sequencing data (COYE, AMRE, and HETH) were used for an initial estimate of population structure. For all species except AMRE, a subset of 96–158 SNPs were identified for each species that could accurately assign individuals to the breeding population using population assignment tests (Moran & Anderson, 2018). These subsets of SNPs were used to genotype additional birds from the breeding grounds and individuals sampled across the wintering grounds. For the whole genome sequencing, genome-wide SNPs were identified that could accurately assign individuals to breeding populations, and the genotype likelihoods of these data were used for population assignment (DeSaix et al., 2024). Taking advantage of the population structure and isolation by distance signals on the breeding ground, we estimated the breeding location for each wintering sample.

This procedure resulted in 30 genetically distinct breeding populations, whose seasonal distributions are shown in Figures S1–S7. We removed populations with low-quality data (i.e., with fewer than 10 sampled individuals or fewer than 4 distinct locations for sampled individuals), thus removing 3 populations: YEWA East (Figure S2d), COYE California (Figure S4b) and PABU Louisiana (Figure S6b). Analyses were performed using the remaining 27 genetically distinct populations.

Extracting climate

We obtained mean monthly temperature (in°C) and total monthly precipitation (in millimetres) data from CHELSA version 2.1 (raster of data of ~1 km resolution; Karger et al., 2021) between 2000 and 2018. Seasonal temperature and precipitation were obtained by averaging the climate data for each ~1 km pixel over the breeding (June–July) and wintering (December–February) seasons over the 19 years of climate data. We focused on the core months of the breeding and wintering periods for our migratory species, as this is when their geographical ranges are most likely to be seasonally static. We averaged climate over a multi-year period to best capture the predictable seasonal variation in climate that migratory birds are susceptible to track, and we chose these 19 years as they approximate the temporal extent of the eBird citizen-science program (Sullivan et al., 2014), whose data is used in the estimation of species' climate niches (see 'Methods' below). Seasonal temperature and precipitation were normalized using the z-score across the entire study region (i.e., Western Hemisphere).

Because most bioclimatic variables are specific to particular times of the year and we wanted our analysis to be generally applicable across seasons in temperate and tropical areas (Ruegg et al., 2021), we selected more general temperature and precipitation variables. These variables, i.e., mean seasonal temperature and accumulated precipitation over a season, are linked to physiological limitations for birds and are highly correlated with bioclimatic variables derived from temperature and precipitation data (Ruegg et al., 2018). Furthermore, these variables were previously used together to estimate both species-level and population-level seasonal climate overlap (Ruegg et al., 2021; Zurell et al., 2018).

We overlaid the locations of genetic samples onto a dataset of terrestrial ecoregions covering the Americas (Dinerstein et al., 2017; Figure S8) to estimate the seasonal, geographic distributions of genetically distinct populations and minimize spatial biases due to the specific sampling locations. Ecoregions are areas containing distinct assemblages of species and biotic characteristics (Dinerstein et al., 2017; Smith et al., 2018), and birds have been shown to exhibit strong fidelity to ecoregion boundaries (Smith et al., 2018). We assumed that if an ecoregion contains at least one sample, it is occupied seasonally (depending on whether it is a breeding or a wintering sample) by the population indicated by the sample's population assignment result. As the realized climate niche of a population is the combination of the climate experienced by all its individuals, and that we assumed that all individuals contributed equally, we weighted the contribution of ecoregions to a given population j based on the relative abundance of the species and how much of this relative abundance belongs to this population. We assigned for each ecoregion k occupied by population j of a given species the following weight:

$$W_{j,k} = A_k \frac{S_{j,k}}{\sum_{i=1}^p S_{i,k}},$$

where A_k is the relative abundance of the species in ecoregion k ; $S_{j,k}$ is the number of individual samples in ecoregion k that are assigned to population j ; and p is the total number of populations of the species.

Species' relative abundance in ecoregions across the study region was estimated using predictions from spatiotemporal exploratory models (STEMs) based on observation data from the eBird citizen-science program (Fink, Auer, Johnston, Strimas-Mackey, et al., 2020; Sullivan et al., 2014). The survey completeness of eBird is particularly good in the broad region where the species used in the study are located (La Sorte & Somveille, 2020). Estimates of relative abundance for the breeding and wintering seasons were obtained from eBird Status and Trends products (Fink, Auer, Johnston, Ruiz-Gutierrez, et al., 2020; 2022 version), downloaded in raster format of 9 km resolution via the R package *ebirdst*. For each ecoregion, we extracted relative abundance values within the geographical boundaries of the ecoregion and then summed them to obtain ecoregion-level relative abundance estimates.

Estimating species' climatic niches

For each season (i.e., breeding and wintering) and each population (i.e., using only individuals genetically assigned to that population), we estimated the realized climate niche by projecting the occurrences into a climate space defined by temperature and precipitation, thus obtaining a cloud of points. Temperature and precipitation values for population j and for a given season were obtained by sampling 10,000 points randomly across the seasonally occupied ecoregions, each ecoregion k weighted by $W_{j,k}$.

Following Broennimann et al. (2012), we then used a kernel density function on a 50×50 pixel grid superimposed onto the two-dimensional climate space to estimate niche density. This analysis was conducted using the 'kde2d' function in R, with a bandwidth of 1 and only keeping the top 95% of the density kernel, setting the rest of the pixels to 0. Niche overlap across seasons for a given population was computed using Schoener's D metric, which varies between 0 (no overlap) and 1 (complete overlap; Broennimann et al., 2012).

We also estimated the population's realized niche along single climate axes, i.e., the thermal and precipitation niches. To estimate these one-dimensional niche densities, we used Gaussian density kernels with a bandwidth of 0.25 (see Figures S1–S7). Niche overlap for a population was calculated as the area of overlap between the breeding and wintering density kernels divided by the total combined area of these kernel

densities, which varies between 0 (no overlap) and 1 (complete overlap).

Migration distance

Migration distance for population j was calculated in a similar way to previous studies as the great circle distance between the centroids of occupied ecoregions during the breeding and wintering seasons (Gilroy et al., 2016; La Sorte et al., 2013; Somveille et al., 2019). As the relative abundance of populations is not homogeneously distributed spatially, we calculated the seasonal centroids as the weighted mean latitude and weighted mean longitude of occupied ecoregions, given weights $W_{j,k}$ (the weight of ecoregion k occupied by population j).

Simulating energetically optimal wintering destinations

We used the optimal redistribution simulator (ORSIM) to simulate species' migratory connectivity based on energy optimization (Somveille et al., 2021). This model was developed to simulate an ideal optimal redistribution of individuals between a species' breeding and wintering grounds, balancing the minimization of energetic costs associated with relocating between seasonal grounds and the maximization of energy assimilation given the distribution of resources and intraspecific competition. Model predictions were found to accurately capture empirical migratory connectivity patterns for 25 avian species across the Americas. Here, ORSIM is calibrated using species' relative abundance in ecoregions over the study region (see details above), and the energetic cost was solely based on migration distance between sites. Thus, no climate information was used in the model. ORSIM uses a solution to the transportation problem from linear programming to simulate migratory connectivity, which is implemented in a Python wrapper of the FastEMD algorithm (Pele & Werman, 2008, 2009). A detailed description of the model can be obtained in Somveille et al. (2021).

For each population, we kept the empirical breeding destinations (i.e., occupied ecoregions during the breeding season), and ORSIM generates a simulated set of occupied ecoregions during the wintering season. Seasonal climate overlap and migration distance were calculated similarly for the observed wintering distributions, except that the weight assigned to each ecoregion was the relative number of individuals predicted to arrive there by ORSIM.

Simulating wintering destinations based on seasonal climate tracking

To simulate species' migratory connectivity based on optimizing population tracking of climatic conditions

throughout the year, we selected for each breeding ecoregion occupied by the species the wintering ecoregion occupied by the species that is the most similar in terms of climate. We estimated climate similarity as the distance between the mean climate of the ecoregions based on two-dimensional climate, temperature only, and precipitation only. For each population, we kept the empirical breeding destinations (i.e., ecoregions occupied by the population during the breeding season), and the model generates a simulated set of occupied ecoregions during the wintering season. Seasonal climate overlap and migration distance were calculated similarly for the observed wintering distributions without weighing the ecoregions.

Null model

To test whether migratory populations track climate conditions at a finer scale (i.e., regionally), we devised a null model against which seasonal climate overlaps (two-dimensional, thermal, and precipitation) were compared. This null model consists of randomized sampling around energetically optimal wintering destinations. For each genetically distinct population, we kept the empirical breeding destinations (i.e., occupied ecoregions during the breeding season) and sampled wintering destinations as follows. We randomly sampled N distinct ecoregions among the set of ecoregions satisfying the condition: $d_O < \frac{1}{2}d_{\max}$, where d_O is the geographic distance to the centroid of the set of occupied ecoregions during the wintering season simulated by ORSIM (the centroid was calculated as the weighted mean latitude and weighted mean longitude of occupied ecoregions, with weights based on the species' relative abundance in ecoregions), and d_{\max} is the maximum distance separating any pair of ecoregions occupied by the population during the wintering season simulated by ORSIM, and N is the observed number of ecoregions occupied by the population during the wintering season. If $N = 1$, which is only the case for two populations, then d_{\max} was set to 1500 km. The distance separating pairs of ecoregions was calculated as the great circle distance between the ecoregions' centroids.

Statistical analysis

The random sampling procedure in the null model was repeated 1000 times, thus generating 1000 simulated wintering distributions for each population. Each time, climate was extracted, and seasonal niche overlap was calculated similarly for the observed wintering distributions. We then calculated the observed seasonal niche overlap rank among the 1000 simulated ones. Ranks were rescaled between 0 and 1, and their distribution was tested for skewness towards low values (indicating

seasonal niche tracking) using one-sample Kolmogorov–Smirnov tests against a uniform distribution.

RESULTS

The genetically distinct bird populations analysed in this study exhibit a wide variation in seasonal climate overlap. For the two-dimensional climatic niche (temperature+precipitation), overlap varies between 0.11 and 0.83 (Figure 2c). Some geographical pattern is apparent in the distribution of seasonal climate overlap: populations with the lowest overlap are distributed in the north-west of North America and populations with the highest niche overlap are distributed in the south-west and south-central parts of North America (Figure 2c). Similar variation is obtained for seasonal overlaps in temperature and precipitation separately, albeit with a smaller extent of overall variation (Figure 2d,e). For temperature, seasonal overlap is lower for populations migrating either short or long distances, and it is higher

for intermediate migration distances (Figure 2d). For precipitation, no peak in overlap is observed at intermediate migration distance but overlap tends to decrease with distance (Pearson's correlation: $r = -0.506$; $p = 0.007$; Figure 2e). Populations migrating short distances and having relatively high precipitation overlap tend to be distributed in south-west of North America, while populations migrating long distances and having relatively low precipitation overlap tend to be distributed in the north-west of North America (Figure 2e).

ORSIM—the model simulating migratory connectivity based on energy efficiency—captures the broad migratory connectivity pattern formed by the populations considered in this study (Figure 2a vs. Figure 2f). The model explains the distribution of migration distances across populations with very high predictive power (Pearson's correlation: $r = 0.937$; $p < 0.005$; Figure 3a). In addition, model predictions for the frequency distribution of seasonal climate overlap across populations, and how this varies with migration distance. Both match the observed patterns (Figure 2). Specifically, ORSIM

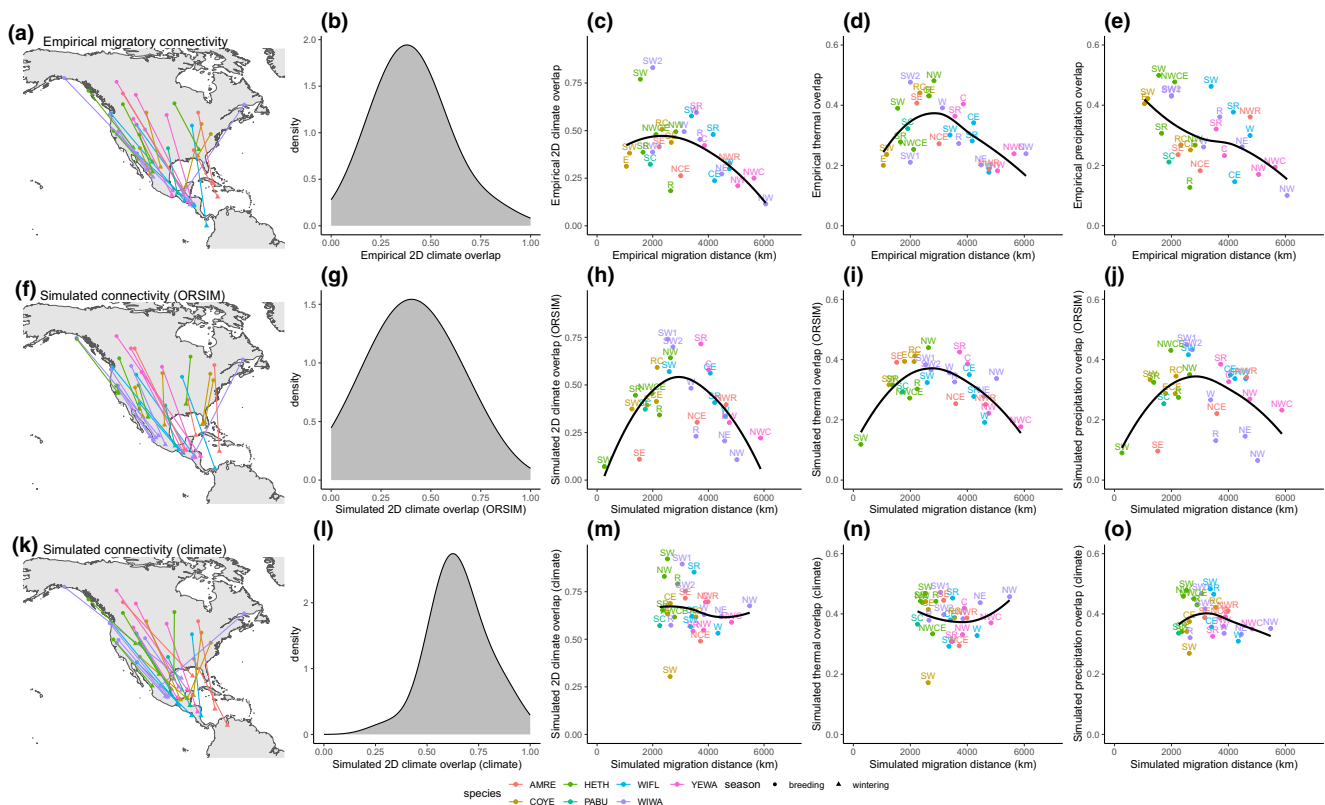


FIGURE 2 Patterns of empirical and simulated migratory connectivity and seasonal climate tracking. Empirical migratory connectivity and variation in seasonal climate tracking is better captured by a model based on energy efficiency than by the simulation model based on climate tracking. Top row: Empirical patterns; middle row: Patterns simulated by ORSIM; bottom row: Patterns simulated by the climate tracking model. Panels (a), (f) and (k) show the connections between population migration destinations (i.e. migratory connectivity); panels (b), (g) and (l) show the density distributions of climate overlap across populations; and the other panels show the relationship between migration distance and (c, h, m) two-dimensional climate overlap (temperature + precipitation), (d, i, n) thermal overlap (temperature only), and (e, j, o) precipitation overlap (precipitation only). Population acronyms are a combination of a latitudinal region: N=north and S=south; and a longitudinal region: W=west, R=Rockies, C=central and E=east. If no latitudinal letter is indicated in an acronym, it means that the population somewhat spans both north and south. If two longitudinal letters are indicated in an acronym, it means that the population somewhat spans both regions. Black curves are loess smooth splines with a span of 1.5.

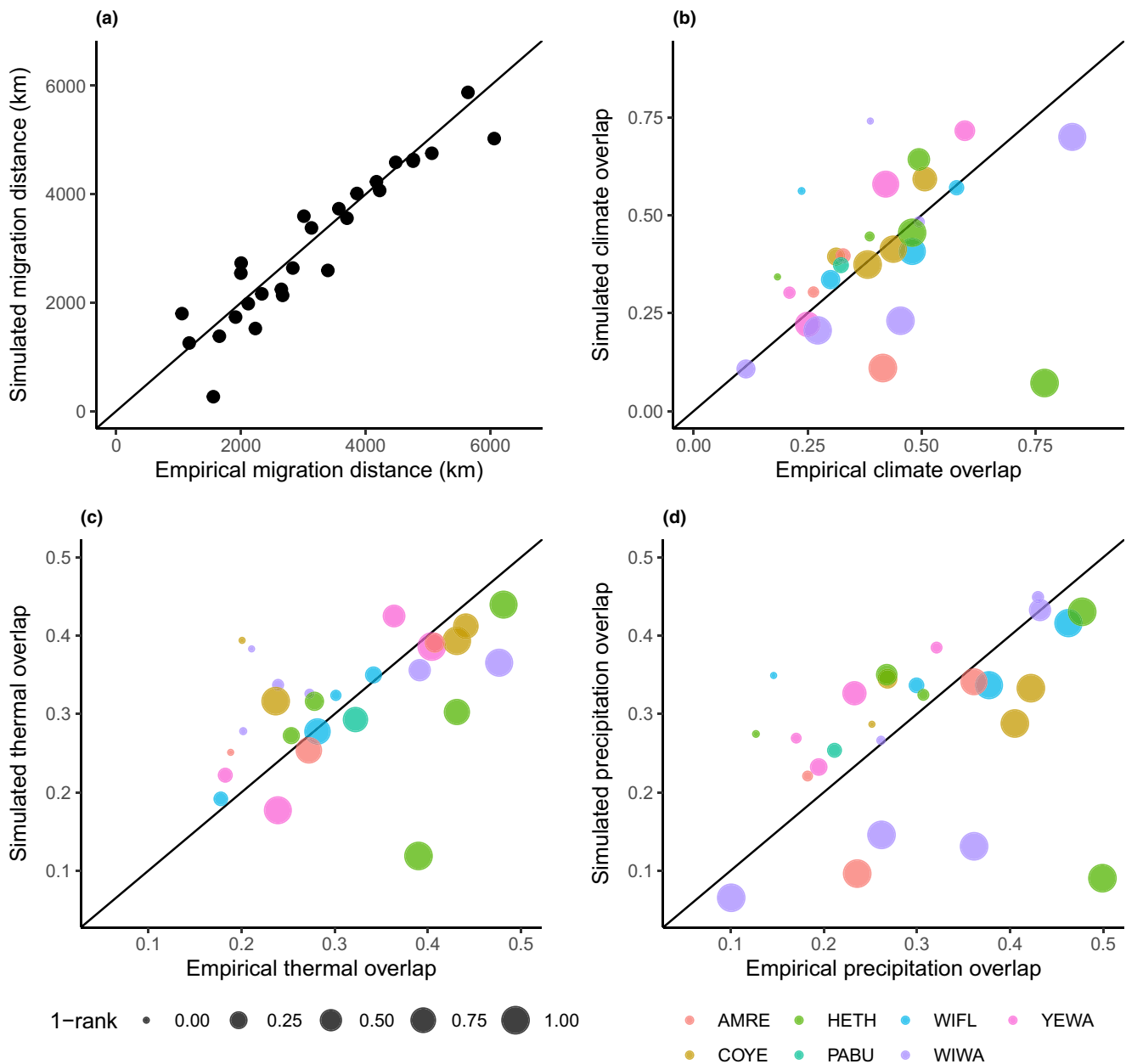


FIGURE 3 Relationship between empirical and simulated patterns. Expectation from energy efficiency simulated by ORSIM versus empirical (a) migration distance, and seasonal overlap of (b) two-dimensional climate, (c) temperature and (d) precipitation. Black lines indicate the 1:1 lines. Points below the 1:1 line in (b)–(d) indicate populations that seasonally track climate more than expected by ORSIM. Point size in (b)–(d) indicates the rank among values for the null model randomizing wintering destinations in regions around ORSIM expectation (1 minus scaled rank between 0 and 1): The bigger points indicate populations that are empirically tracking regional climate better than random (active regional climate trackers), the smaller points indicate populations that are empirically tracking regional climate worse than random (active regional climate switchers), and points of intermediate size indicate populations whose empirical tracking of regional climate is not different from random. The figure shows that a model based on energy efficiency explains most of the empirical variation in migration distance and in season climate overlap, which is particularly the case for temperature while for precipitation it seems to be also affected by regional precipitation tracking.

predicts a relatively wide frequency distribution of seasonal climate tracking that peaks in the middle (Figures 1a and 2g), which closely matches the observed data (two-sample K-S test: $D=0.148$, $p=0.936$). ORSIM also predicts that seasonal climate and thermal overlaps peak at intermediate migration distance (Figure 2h,i) and that populations from northwest North America

tend to have long migration distances and low climate overlap. In contrast, populations from south-west and south-central North America tend to migrate short distances and have relatively high climate overlap (with a notable exception for the south-west population of Hermit Thrush; Figure 2h). For seasonal precipitation overlap, ORSIM prediction matches the observation

only for populations migrating intermediate to long distances (Figure 2j).

ORSIM predictions for the variation in seasonal climate overlap are statistically significant or marginally significant, and with relatively high correlation coefficients when compared to observations (Pearson's correlations: two-dimensional climate: $r=0.377$, $p=0.052$, Figure 3b; temperature only: $r=0.481$, $p=0.011$, Figure 3c; precipitation only: $r=0.386$; $p=0.047$; Figure 3d). Deviation of empirical seasonal climate overlap from ORSIM predictions is not significantly skewed to the right of a normal distribution centred around 0 and with a standard deviation equal to the observed distribution of errors (one-sample K-S test for two-dimensional climate niche: $p=0.334$; thermal tracking: $p=0.674$; precipitation tracking: $p=0.345$), indicating that populations do not tend to have a higher seasonal climate overlap than predicted by ORSIM.

Contrary to ORSIM, the model simulating migratory connectivity based on tracking two-dimensional climatic conditions does not capture the observed frequency distribution of seasonal climate tracking (Figures 1b and 2b,i; two-sample K-S test: $D=0.778$, $p<0.005$), nor does it capture the pattern of variation in climate overlap (two-dimensional, thermal only, and precipitation only) with migration distance (Figure 2). In addition, correlations between the empirical variation in seasonal climate overlap and the one predicted by the two-dimensional climatic tracking model were not statistically significant (Pearson's correlations: two-dimensional climate: $p=0.123$; temperature only: $p=0.221$; precipitation only: $p=0.076$). The model simulating migratory connectivity based on seasonal thermal tracking only could not capture the empirical variation in seasonal thermal tracking (Pearson's correlation: $p=0.545$; Figure S9k). However, the model simulating migratory connectivity based on seasonal precipitation tracking only was able to capture well the empirical variation in seasonal precipitation tracking (Pearson's correlation: $r=0.591$; $p<0.005$; Figure S9p) but not the empirical variation in seasonal thermal tracking (Pearson's correlation: $p=0.172$; Figure S9o).

The distribution of the ranks of seasonal climate overlap among simulated values for the null model randomizing wintering destinations around ORSIM expectation is significantly skewed towards low values compared to a uniform distribution for precipitation only (one-sample K-S test; $p<0.005$) but not significantly different from the uniform expectation for the two-dimensional climate niche (one-sample K-S test; $p=0.064$) and temperature only (one-sample K-S test; $p=0.107$). The variation in seasonal tracking of climate variables seems to be driven by a set of populations that are tracking climate particularly well (i.e., relatively high overlap, underestimated by ORSIM and low rank among null values) versus a few populations that appear to be climate switchers (i.e.,

relatively low overlap, overestimated by ORSIM and high rank among null values; Figure 3b,d).

DISCUSSION

Contrary to a commonly held assumption, the results we obtained across the 27 populations we examined indicate that seasonal climate tracking is not a primary driver of intraspecific migration patterns on a broader scale. Instead, our work supports the idea that energy efficiency, specifically optimizing the balance between accessing environmental resources and the cost of movement, is mainly responsible for intraspecific variation in broad-scale patterns of migratory connectivity across these populations (Figures 1a, 2, and 3a). In turn, migratory connectivity underlies the significant variation in the degree of seasonal climate overlap observed between populations, with some populations having relatively high overlap while others have almost no overlap (Figure 2). In addition to energy efficiency at broad scale, our results also suggest that regional-scale seasonal precipitation tracking affects migration destinations, thus revealing a potential scale dependency of ecological processes driving migration.

The bird populations we examined have a relatively broad distribution of empirical climate overlap, which peaks at intermediate values. In addition, populations with high thermal overlap tend to migrate intermediate distances, while populations with high precipitation overlap tend to migrate long distances. Overall, these patterns align more closely with the predictions of a model based on selecting energetically optimal wintering destinations rather than climatically similar wintering destinations (Figures 1 and 2), thus supporting the hypothesis that seasonal climate tracking is a consequence, rather than a cause, of migratory connectivity. Additional evidence supporting this hypothesis is found in the observation that variation in seasonal climate tracking across populations can be explained mainly by the model simulating energetically optimal wintering destinations (Figure 3). Moreover, populations do not track temperature more than what would be expected by randomizing wintering destinations in regions around these energetically optimal sites. Therefore, in contrast to the commonly held assumption that seasonal climate tracking drives migration patterns, our findings propose that the seasonal geographical destinations of the migratory avian populations investigated here are not directly shaped by a similarity in thermal conditions. Instead, the variability in thermal tracking among populations is primarily determined by migratory connectivity patterns. These connectivity patterns are largely influenced by the delicate balance between maximizing energy acquisition from the environment and minimizing the energy costs associated with migratory movement (Somveille et al., 2021).

As energy efficiency drives avian migration patterns at broad scale (Somveille et al., 2018, 2021), our results also reveal a potential scale dependency of ecological processes, with precipitation tracking acting at a more regional scale to shape intraspecific migration patterns. In contrast with temperature, we found that populations appear to track precipitation favourably compared to the null expectation of randomizing wintering destinations around the energetically optimal wintering destinations. We also found that the variation in seasonal precipitation tracking is well explained by the model based on broad-scale tracking of precipitation regimes, but as this model cannot explain the variation in thermal tracking, it also suggests a rather complementary role of precipitation tracking to energy efficiency. These results open up a new avenue for research as a better understanding of the scale at which the drivers of migration play out is crucial for predicting how migratory birds will respond to global change. While previous high-resolution work focusing on a few migratory bird populations found that population-level seasonal climate tracking is a bottom-up process that emerges from individual-level weather-tracking behaviour (Fandos et al., 2020), we found that population-level seasonal climate tracking is also a top-down process shaped by how energy efficiency drives species' migratory connectivity. These two processes are not mutually exclusive. We found that migratory bird populations tend to track precipitation regionally, meaning that while energy efficiency structures species' migratory connectivity, individuals might also be tracking precipitation conditions throughout the year, leading to population-level seasonal precipitation tracking. As precipitation regimes shape habitat quality and the type of available resources for birds (Rockwell et al., 2017; Smith et al., 2010), precipitation likely determines habitat selection (Frishkoff et al., 2016; Frishkoff & Karp, 2019)—potentially more so than temperature does (Londoño et al., 2016). In turn, precipitation affects the composition of avian communities (Gomez et al., 2019) and selects for specific traits, such as beak morphology (Bay et al., 2021), thus potentially leading natural selection to favour seasonal precipitation tracking at regional scales.

There is one particularly noticeable outlier in our results: the 'southwest' population of Hermit Thrush. Our empirical genetic data indicates that this population occurs mainly in the coastal and inland mountains of California and Oregon during the breeding season and migrates a short distance to spend the winter in north-western Mexico (Figure S7e). These seasonal grounds have remarkably similar climatic conditions, and this population has the second highest climate overlap in our dataset (Figure 2c). ORSIM, however predicts that this population stay largely resident on its breeding ground, which results in very low seasonal climate overlap (the lowest climate overlap predicted by ORSIM across all the examined populations; Figure 2h) as these temperate

mountains experience a high degree of climatic seasonality. Although ORSIM's prediction is reasonably close to the observation (i.e., wintering in California versus north-western Mexico, respectively, for this relatively wide-ranging species), the discrepancy between observed and predicted climate overlap is very high (by far the highest across the examined populations). Being an extreme case (i.e., very high empirical climate overlap but very low predicted overlap), this population has an outsized influence on the results, and removing it from the analysis would substantially further increase the statistical predictive ability of ORSIM (Pearson's correlations: two-dimensional climate: $r=0.643$, $p<0.005$; temperature only: $r=0.655$, $p<0.005$; precipitation only: $r=0.595$; $p<0.005$). This population could be tracking precipitation regionally in addition to energy efficiency, as a short-distance relocation to track precipitation could explain its migration pattern.

Our results suggest that migratory bird populations do not track climate directly and actively at broad scale, but climate could have an indirect effect by shaping the spatiotemporal availability of resource and habitat quality for species. In turn, this is expected to shape migratory connectivity and the variation in seasonal climate tracking across populations via energy efficiency as we found in this study. As we indeed observe some response of species' relative abundance estimates to climate for many species (Figure S10), and that previous studies found evidence of indirect climate effects on resource supply in migratory birds (e.g. Smith et al., 2010; Studds & Marra, 2011), it suggests that climate could have some indirect effect on migratory connectivity. In our analysis, we used seasonal species' relative abundance predicted by STEMs, which correlate citizen science occurrence data with land cover descriptors, assuming that it reflects the distribution of energy available to the species across their seasonal ranges (Somveille et al., 2021). Still, future studies using data on the specific distribution of resources for species (e.g., insect density) could investigate the extent to which climate shapes resource availability and thus indirectly affect migration patterns. Another assumption that might require further scrutiny is that ecoregions containing at least one sample assigned to a population are fully occupied by that population. This assumption was made in part to minimize geographical and climatic biases due to the specific sampling locations, and indeed, no evident bias was found in our sampled climate (Figures S11 and S12). This assumption that populations fully occupy ecoregions is not unrealistic since ecoregions represent distinct and relatively homogeneous biotic communities (Dinerstein et al., 2017; Smith et al., 2018), and that the species that we used in our analysis are relatively widespread and highly mobile, but it needs further examination.

Due to data availability, our analysis focuses on a restricted set of species, and as more genetic data is

becoming available for birds, extending this analysis to a larger fraction of the migratory avifauna will reveal the generalizability of our findings. Yet, the suite of populations that we used are from species whose migrations are reasonably well representative of the patterns of the North American bird migration system (Somveille et al., 2015). We therefore hypothesize that our results are robust and applicable to a broader range of migratory bird species, particularly ones with similar life histories to the species used in our analysis. Between species, the extent of variation in seasonal climate tracking appears relatively consistent in our analysis, with species typically comprising both climate-tracking and climate-switching populations. This apparent lack of species effect additionally supports a potential generalizability of our results to a broader migratory avifauna.

The results obtained in this study have implications for local adaptation and the conservation of migratory species. Our findings suggest that much of the variation in seasonal climate tracking is a consequence of how other ecological processes shape migration patterns, which could lead populations that track climate to have evolved traits and behaviours to adapt to a narrow set of climate conditions. This local adaptation could lead to genetic differentiation, but it could also make climate-tracking populations more vulnerable to climate change. With changing climate, these populations are more likely to face new climate conditions outside their relatively narrow climate niche. Suppose their migration patterns are not driven by seasonal climate tracking, particularly for temperature. In that case, these populations might not be able to adapt to a warming climate via change in their migration behaviour. A study on the Willow Flycatcher, one of the species in our dataset, found that populations closely tracking climate seasonally are experiencing a faster population decline than climate-switching populations with broad climatic niches, potentially due to their limited ability to adapt to climate change (Ruegg et al., 2021). Here, we found that populations migrating intermediate distances tend to have higher thermal overlap and are potentially at higher risk under climate change. We also found that precipitation tracking at a regional scale affects the migration destinations of the populations that we investigated, which indicates that these populations might be able to respond and track future changes in precipitation if there is a sufficient variation in these changes at a regional scale, but less so if these precipitation changes occur relatively uniformly over broader areas across the Americas. In addition, as migratory connectivity is largely driven by energy efficiency, anthropogenic change in the distribution of resources for migratory birds through land use change is likely to reshape migratory connectivity patterns, which would drive populations that are tracking climate seasonally to potentially experience new climate conditions for which they are not adapted.

AUTHOR CONTRIBUTIONS

M.S. and K.C.R. conceived and designed the study. M.S. performed the analysis with support from C.M.B. and M.G.D., and drafted the manuscript. All authors contributed critical input to the manuscript.

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PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14496>.

DATA AVAILABILITY STATEMENT

The eBird Status and Trends data products are open-access and free to use for research. They are downloadable through the R package *ebirdst*. The genetic data is archived in public repositories as follows. For Yellow Warbler, raw reads from RAD-Seq data are available through the NCBI Sequence Read Archive (PRJNA421926) and filtered SNP datasets from SNPtype assays and scripts used for analysing data are available at <https://github.com/rachaelbay/Yellow-Warbler-Climate-Tracking> or archived on zenodo (<https://doi.org/10.5281/zenodo.4473204>). For Painted Bunting, the genetic data and input files for population assignment to distinct genetic clusters can be found on Dryad <https://doi.org/10.5068/D1P96N>. For Common Yellowthroat, the genetic data is available at <https://datadryad.org/stash/share/xmCoXi1USvuuM5-83fhuRsI3XF84k43qv1jxi5PBoa0>. For Willow Flycatcher, the genome and annotations are available through NCBI (accession number: **PWAB00000000**), population-level RAD-Seq data are available through NCBI's Sequence Read Archive (<http://www.ncbi.nlm.nih.gov/bioproject/453612>), and all codes necessary to recreate the results are available at <https://doi.org/10.5281/zenodo.4656570>. For Wilson's Warbler, the data and scripts for population genomic analysis (from SNP selection to estimation of population genomic parameters) are available on GitHub (<https://github.com/eriqande/wiwa-popgen>) and Dryad (<http://doi.org/10.5061/dryad.j5d33>). For American Redstart, genomic data have been deposited in the Dryad repository <https://doi.org/10.5061/dryad.gmsbcc2td>, and all analysis scripts have been made available at <https://>

github.com/mgdesaix/amre-mc. For Hermit Thrush, genomic data have been deposited in the Dryad repository <https://doi.org/10.5061/dryad.n02v6wx50>. Finally, the computer code used for the analysis in this study is available at: <https://github.com/msommeille/seasonal-climate-tracking.git>.

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SUPPORTING INFORMATION

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