

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 behavior underlying seasonal migration patterns in animal populations. In this study, we investigate this hypothesis using genetic markers data to map migratory connectivity for 22 genetically distinct bird populations across 6 species. We found that the variation in seasonal climate tracking at a continental scale is more likely a consequence, rather than an underlying driver, of migratory connectivity, which is itself largely shaped by energy efficiency – i.e. optimizing the balance between accessing available resources and the cost of movement. However, our results also suggest that regional-scale seasonal precipitation tracking affects migration destinations, thus revealing a potential scale-dependency of ecological processes driving migration. Our results have implications for the conservation of migratory species under climate change, as populations that track climate seasonally are potentially at higher risk if they adapt to a narrow range of climatic conditions.

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; Saino *et al.* 2011; Rosenberg *et al.* 2019). Climate constitutes an important constraint on species distributions (Tingley *et al.* 2009; Pigot *et al.* 2010) and understanding how it shapes seasonal migration patterns is crucial to better anticipate how migratory species respond to ongoing anthropogenic climate change. Previous studies have found that the migratory avifauna is composed of both species that are tracking favorable climatic conditions throughout the year (climate niche trackers) and species that are switching 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 behaviors 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 behavior (Faaborg *et al.* 2010; Finch *et al.* 2017; Gómez *et al.* 2021; Ruegg *et al.* 2014; DeSaix *et al.* 2023a). These migratory patterns have important consequences for the broader ecology and evolution of a species as it can affect population dynamics via seasonal carry-over effects (Marra *et al.* 1998; Sillett & Holmes 2002; Taylor & Norris 2010). Seasonal climate tracking is often assumed to be an adaptive behavior underlying migration patterns (e.g., Thorup *et al.* 2021; Gutiérrez Illán *et al.* 2022), and previous population-specific studies found evidence of seasonal climate tracking at population level (Fandos & Telleria 2020; Fandos *et al.* 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 (Van

Doren *et al.* 2021; Dufour *et al.* 2021; Thorup *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 behavior and routes (Thorup *et al.* 2021).

An alternative hypothesis is that the variation in seasonal climate tracking among populations might be a consequence of 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 information on climate (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. The question of whether migratory connectivity shapes the variation in seasonal climate tracking in migratory birds has, to our 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 & Telleria 2020; Fandos *et al.* 2020; Gutiérrez Illán *et al.* 2022) have used tracking and banding data which makes it difficult and rather 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 (Ruegg *et al.* 2014). A recent study using genetic markers for 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 6 different migratory species to investigate the extent to which 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. 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 the first explicit test of whether seasonal climate tracking is a consequence or driver of migratory connectivity at both broad and regional geographic scales.

Methods

Bird data

We collated data for 6 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*; YEWL), Wilson’s Warbler (*Cardellina pusilla*; WIWA), Common Yellowthroat (*Geothlypis trichas*; COYE), American Redstart (*Setophaga ruticilla*; AMRE), and Painted Bunting (*Passerina ciris*; PABU). A total of 3326 genetic samples were available and distributed widely across the breeding and wintering ranges of these species (Figs. S1–S6).

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 is described in detail in a set of species-specific papers (Bay *et al.* 2021; DeSaix *et al.* 2023a; Rueda-Hernández *et al.* 2023; Ruegg *et al.* 2014, 2020, 2021, Bobowski *et al.* *in review*). 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 and AMRE) 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 breeding population using population assignment tests (Moran & Anderson 2018). These subsets of SNPs were used to genotype additional birds from the breeding grounds as well as 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.* 2023b). Taking advantage of the population structure and isolation by distance signals on the breeding ground, we estimated breeding location for each wintering sample.

This procedure resulted in 26 genetically distinct breeding populations, whose seasonal distributions are shown in Figs. S1–S6. We removed populations with low quality data (i.e. with fewer than 10 sampled individuals, or fewer than 3 distinct locations for sampled individuals, or fewer than 2 occupied ecoregions during at least one season), thus removing 4 populations: YEWA East, COYE California, AMRE Mid-West and PABU Louisiana. Analyses were performed using the remaining 22 genetically distinct populations.

Extracting climate

We obtained monthly temperature and precipitation data from CHELSA version 2.1 (raster of data of ~1 km resolution; Karger *et al.* 2021) between 2000–2018. Seasonal temperature and precipitation were obtained by averaging the climate data for each ~1km pixel over 3-month seasons – June–July for breeding and December–February for wintering – and over the 19 years of data. Seasonal temperature and precipitation were normalized using the z-score across the entire study region (i.e., Western Hemisphere).

Using a global dataset of terrestrial ecoregions (Olson *et al.* 2001), which represent regions with distinct biotic characteristics, we assumed that ecoregions containing at least one sample of a given breeding population was occupied by this population. For ecoregions on the wintering ranges, individuals’ population assignment results were used to determine the association of ecoregions with breeding populations. 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 eBird citizen-science program (Sullivan *et al.* 2014; Fink *et al.* 2020a). 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 *et al.* 2020b), downloaded in raster format of 2.96 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 niche and the precipitation niche. To estimate these one-dimensional niche densities, we used Gaussian density kernels with a bandwidth of 0.25 (see Figs. S1–S6). 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 as the great circle distance between the centroids of occupied ecoregions during the breeding and wintering seasons, which are calculated 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 the breeding and wintering grounds a species. It balances the minimization of energetic costs associated with relocating between seasonal grounds and the minimization of intraspecific competition for access to resources. ORSIM was 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. 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. Climate was extracted and seasonal niche overlap was calculated in the same way as for the observed wintering distributions, but the weight assigned to each simulated wintering ecoregion was the relative number of individuals coming from the empirical breeding distribution of the population.

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. Climate was extracted and seasonal niche overlap was calculated in the same way as for the observed wintering distributions.

Null model

To test whether migratory populations are tracking climate conditions at 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 in 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 we 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, 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. 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 in the same way as for the observed wintering distributions. We then calculated the rank of the observed seasonal niche overlap among the 1000 simulated ones. Ranks were rescaled between 0–1 and their distribution was tested for skewness towards low values (indicating seasonal niche tracking) by one-sample Kolmogorov-Smirnov tests against a uniform distribution.

Results

The genetically distinct bird populations analyzed in this study exhibit a wide variation in seasonal climate overlap. For the two-dimensional climatic niche (temperature + precipitation), overlap varies between 0.086–0.895 (Fig. 1b). 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 distribution in the south-west and south-central parts of North America (Fig. 1b). Similar variation is obtained for seasonal overlaps in temperature and precipitation separately, albeit with a smaller extent of overall variation (Fig. 1c,d). For temperature, seasonal overlap is lower for populations migrating either short or long distances, and it is higher for intermediate migration distances (Fig. 1c). For precipitation, no peak in overlap is observed at intermediate migration distance but overlap tends to decrease with distance ($r=-0.52$; $P=0.013$; Fig. 1d). 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 (Fig. 1d).

ORSIM – the model simulating migratory connectivity based on energy efficiency – captures the broad migratory connectivity pattern formed by the populations considered in this study (Fig. 1a,e). The model predicts variations in climate overlap (two-dimensional, thermal only, and precipitation only) with migration distance that are matching the observed patterns (Fig. 1). Specifically, it predicts that thermal overlap peaks at intermediate migration distance (Fig. 1g), that precipitation overlap generally decreases with migration distance (Fig. 1h), and that populations from north-west North America tend to have the lowest overlap while populations from south-west and south-central North America tend to have the highest overlap (Fig. 1f). The model also explains the distribution of migration distances across populations with a very high predictive power ($r=0.940$; $P<0.001$; Fig. 2a).

ORSIM predicts the variation in thermal overlap with a relatively high correlation between predictions and observations ($r=0.469$; $P=0.028$; Fig. 2c). ORSIM predictions for seasonal overlap also show some positive correlation with observations for precipitation ($r=0.277$; $P=0.212$; Fig. 2d) and two-dimensional climate ($r=0.295$; $P=0.183$; Fig. 2b) although these correlations are not statistically significant. Deviation of empirical seasonal climate overlap from ORSIM predictions is not significantly skewed to the right of a normal distribution centered around 0 and with a standard deviation equal to the observed distribution of errors (one-sample K-S test for two-dimensional climate niche: $P=0.150$; thermal tracking: $P=0.735$; precipitation tracking: $P=0.136$), 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 pattern of variation in climate overlap (two-dimensional, thermal only, and precipitation only) with migration distance (Fig. 1), and it is also the case for the models simulating migratory connectivity based on thermal and precipitation tracking separately (Fig. S7). In addition, the two-dimensional climatic tracking model was not able to predict the empirical variation in population climate

overlap (two-dimensional climate: $r=-0.173$; $P=0.44$; temperature only: $r=0.203$; $P=0.364$; precipitation only: $r=-0.009$; $P=0.969$), which was also the case for the models simulating migratory connectivity based on thermal and precipitation tracking separately.

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 for the two-dimensional climate niche (one-sample K-S test; $P=0.032$), marginally significantly skewed towards low values for precipitation (one-sample K-S test; $P=0.061$) and not significantly different from the null expectation for temperature (one-sample K-S test; $P=0.675$). For precipitation and two-dimensional climate niche, the variation in seasonal tracking seems to be driven by a set of populations that are tracking precipitation particularly well (i.e. relatively high overlap, underestimated by ORSIM and low rank amongst null values) versus a few populations that appear to be climate switchers for precipitation (i.e. relatively low overlap, overestimated by ORSIM and high rank amongst null values; Fig. 2b,d). Some species appear consistent in their results across their populations. In particular, all populations of Yellow Warbler are apparent precipitation switchers while all populations of American Redstart are apparent precipitation trackers (Fig. 2d).

Discussion

Contrary to a commonly held assumption, our results 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 largely responsible for intraspecific variation in broad-scale patterns of migratory connectivity (Figs. 1 and 2a). 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 (Fig. 1). 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.

Populations with high thermal overlap tended to migrate at intermediate distances, while the extent of precipitation overlap between populations decreased with migration distance. 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 (Fig. 1), 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 thermal tracking across populations can be largely explained by the model simulating energetically optimal wintering destinations (Fig. 2c). Moreover, populations do not track temperature more than what would be expected by randomizing wintering destinations in regions around these energetically optimal sites (Fig. 2c). In contrast to the commonly held belief that seasonal climate tracking drives migration patterns, our findings propose that avian populations do not actively follow temperature patterns, either on a regional or continental scale. Instead, the variability in thermal tracking among populations is primarily shaped 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 (Figs. 1 and 2; Somveille *et al.* 2021).

As energy efficiency drives avian migration patterns at broad scale, our results also reveal a potential scale-dependency of ecological processes, with precipitation tracking acting at a more regional scale to shape intra-specific migration patterns. In contrast with temperature, we found that the variation in seasonal precipitation tracking is not well explained by broad-scale migratory connectivity predicted under energy efficiency, but that populations appear to track precipitation favorably when compared to the null expectation of randomizing wintering destinations around the energetically optimal wintering destinations. These results open up a new avenue for research as better understanding 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 few migratory bird populations found that population-level seasonal climate

tracking is a bottom-up process that emerges from individual-level weather-tracking behavior (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 as we found that migratory bird populations tend to track precipitation regionally, meaning that while energy efficiency structures species' migratory connectivity, individuals might additionally be tracking precipitation conditions throughout the year leading to the emergence of population-level seasonal precipitation tracking. As precipitation regimes shape habitat quality and the type of available resources for birds (Smith *et al.* 2010; Rockwell *et al.* 2017), 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 favor seasonal precipitation tracking at regional scales.

The extent of seasonal precipitation tracking however varies by species. In particular, Yellow Warbler seems to consistently not track precipitation across its populations, with all populations appearing to be niche switchers for precipitation (i.e. relatively low overlap, overestimated by ORSIM and high rank amongst null values; Fig. 2d). This could be due to sampling for Yellow Warbler that is not well representative of the overall realized precipitation niche of the species for the wintering season, with a bias towards drier areas (Fig. S9d) as most sampled regions for this species are located on the western slopes of Central America (Fig. S2) where the dry season is very pronounced. This bias, combined with a sampling bias on the breeding grounds towards the western and northern parts of the range (Fig. S2) – in particular, the south-western and eastern/north-eastern parts of the range for this species were not included in the analysis (the eastern population was removed due to insufficient data on the wintering grounds), might explain the consistent niche switching for the populations of this species. If Yellow Warbler is removed from the analysis, then the distribution of ranks compared to the null expectations of randomizing wintering destinations around the energetically optimal wintering destinations becomes highly skewed towards low values for precipitation (one-sample K-S test; $P=0.003$), thus reinforcing the finding that populations are tracking a precipitation regime regionally.

In contrast with Yellow Warbler, American Redstart appears to have seasonal precipitation overlap consistently higher than the energetically optimal expectation and higher than most of the null random expectations for all its populations (Fig. 2d). Such consistent seasonal precipitation tracking across the populations of a migratory species could be either due to a direct physiological effect of precipitation leading to the species not being able to have a broad precipitation niche, and therefore its populations having to track a narrow precipitation regime throughout seasons, or due to indirect effects of precipitation on habitat and resources to which population are adapted, which in turn affects seasonal precipitation tracking. Studies on American Redstart have shown that winter precipitation affects survival and body conditions (Studds & Marra 2007) as well as spring departure (Studds & Marra 2011), indicating that populations of this species might be particularly adapted to precipitation regimes. In addition, range-wide population trends in American Redstart are not affected by temperature but have an association with winter plant productivity (Wilson *et al.* 2011), which in turn is influenced by precipitation.

Our analysis did not explicitly consider resource availability for the species investigated (e.g. insect density) due to the lack of available data at continental scale. Instead, we used seasonal 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). As climate is likely shaping the spatio-temporal availability of resources and the abundance distribution of species, it could still be an indirect determinant of migratory connectivity. Future studies using data on the specific distribution of resources for species could investigate the extent to which climate shape resource availability and thus indirectly affect migration patterns, which is important for predicting the impact of climate change on migratory birds.

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 to populations that happen to track climate to have evolved traits and behavior to adapt to a narrow set of climate conditions. This local adaptation could potentially lead to genetic differentiation, but it could also make seasonal climate tracking populations potentially more vulnerable to climate change. With changing climate, these populations are more likely to face new climate conditions that are outside their relatively narrow climate niche and since their migration patterns are not driven by seasonal climate tracking, particularly for temperature, these populations might not be able to adapt to climate change via change in their migration behavior. We found that populations migrating intermediate distances tend to have higher thermal overlap and therefore are potentially at higher risk under climate change. 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.

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Figure legends:

Fig. 1: 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), (e) and (i) show the connections between population migration destinations (i.e. migratory connectivity), and the other panels show the relationship between migration distance and (b,f,j) two-dimensional climate (temperature + precipitation), (c,g,k) thermal overlap (temperature only), and (d,h,l) 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.

Fig. 2: 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 0–1). The figure shows that a model based on energy efficiency explains most of the empirical variation in migration distance and thermal overlap, but for precipitation it seems to be more affected by regional precipitation tracking.

Fig. 1:

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Fig. 2:

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Supplementary Material

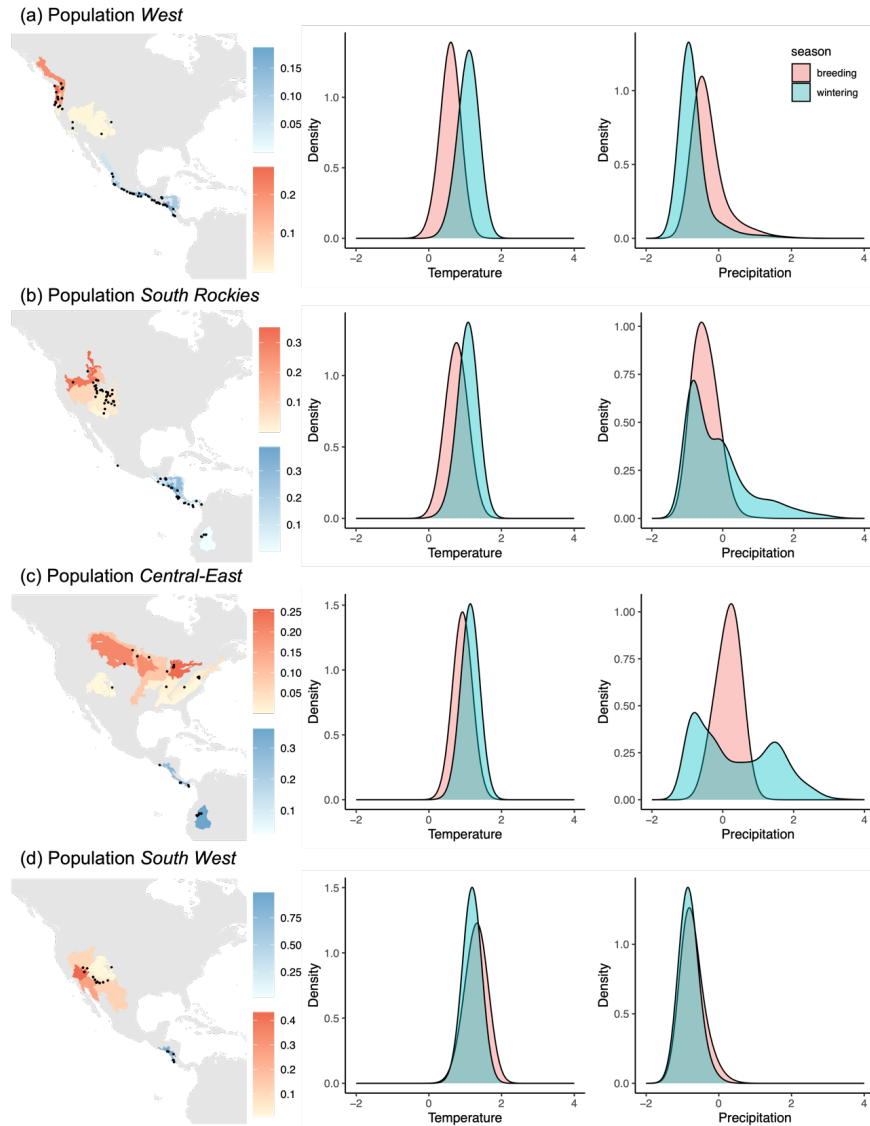


Figure S1 : Seasonal distribution and climate overlap of populations of Willow Flycatcher. In red: ecoregions occupied during the breeding season; in blue: ecoregions occupied during the wintering season. Darker the colour, higher the weight assigned to the ecoregion.

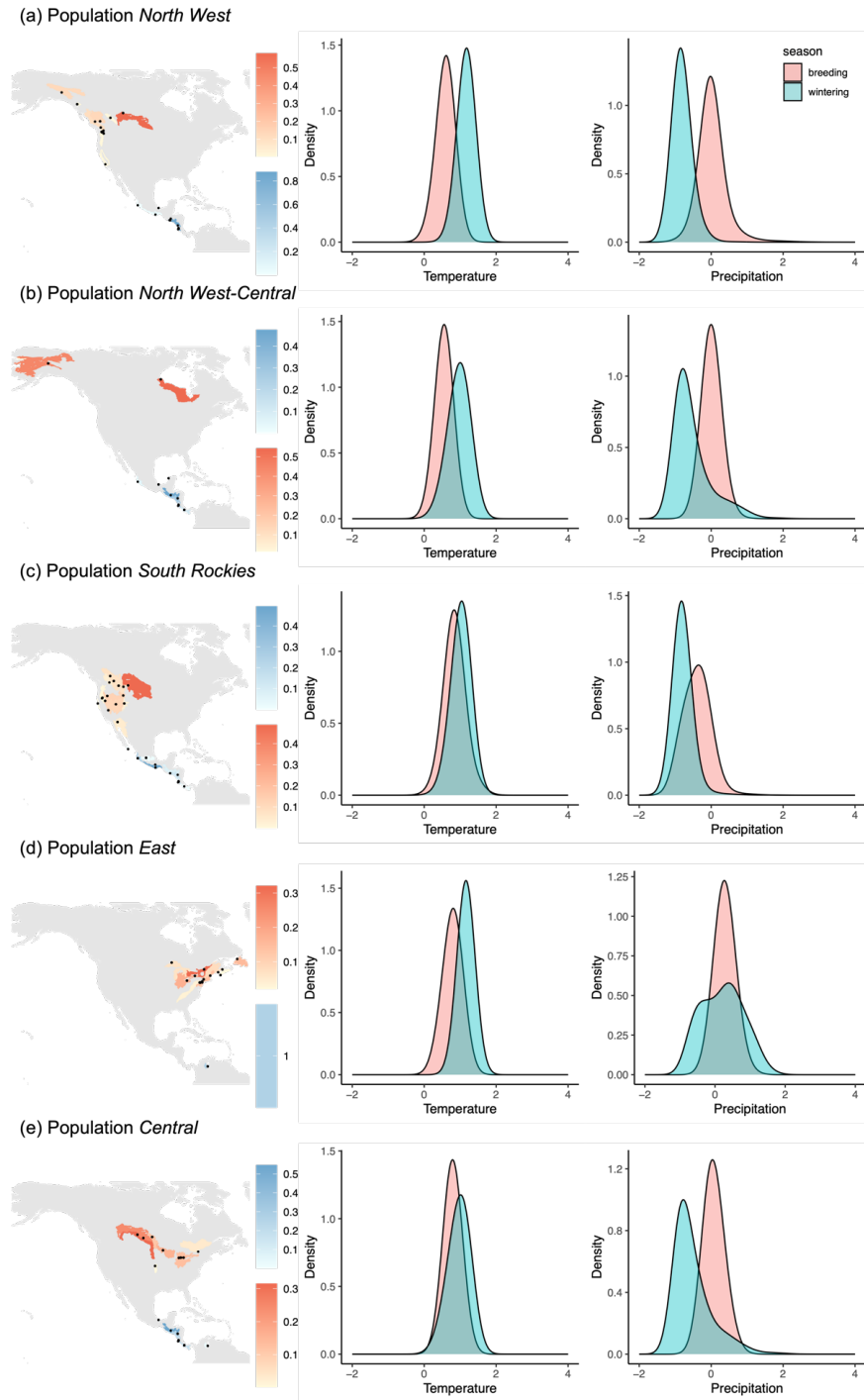


Figure S2 : Seasonal distribution and climate overlap of populations of Yellow Warbler. In red: ecoregions occupied during the breeding season; in blue: ecoregions occupied during the wintering season. Darker the colour, higher the weight assigned to the ecoregion.

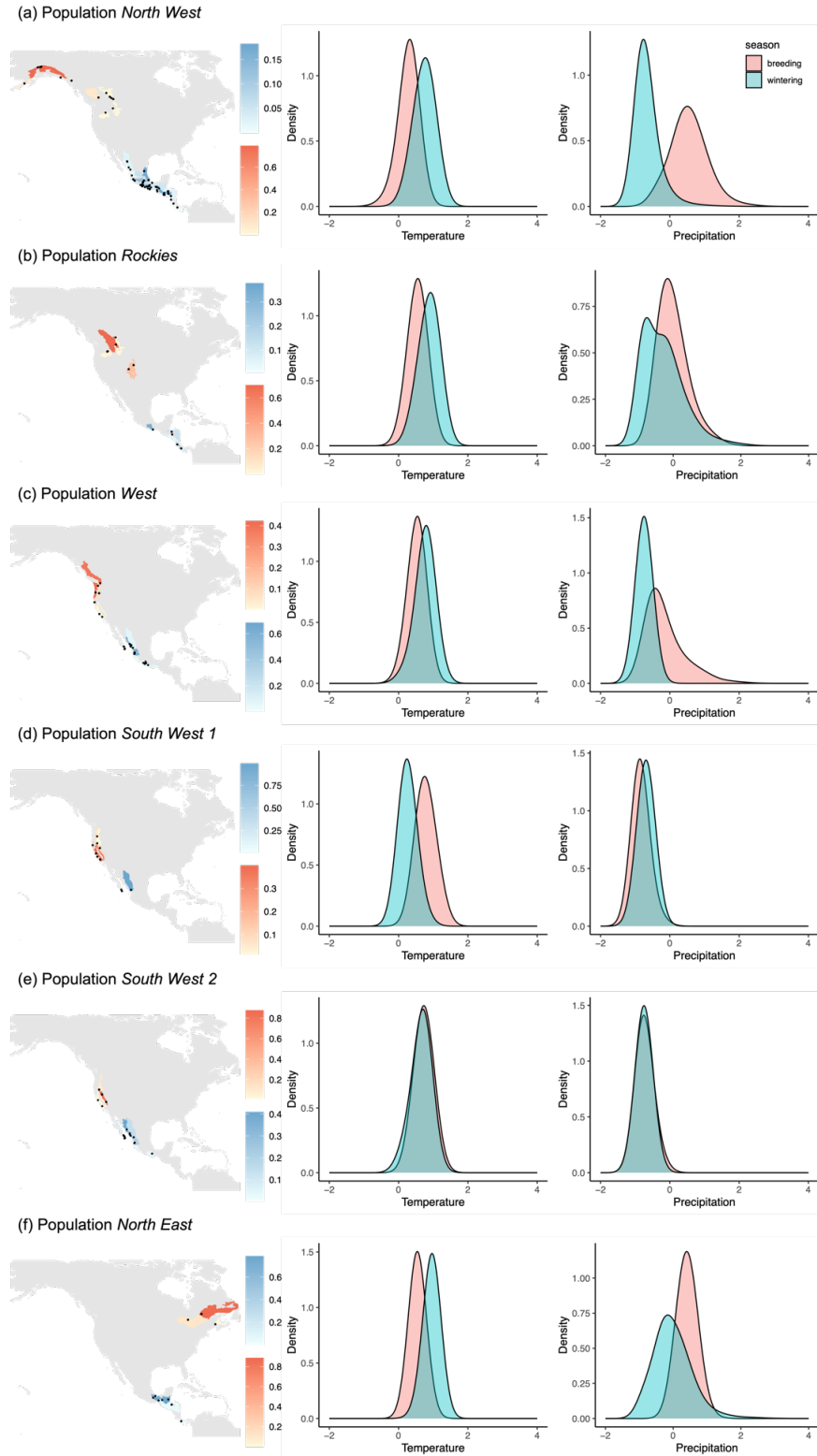


Figure S3 : Seasonal distribution and climate overlap of populations of Wilson's Warbler. In red: ecoregions

occupied during the breeding season; in blue: ecoregions occupied during the wintering season. Darker the colour, higher the weight assigned to the ecoregion.

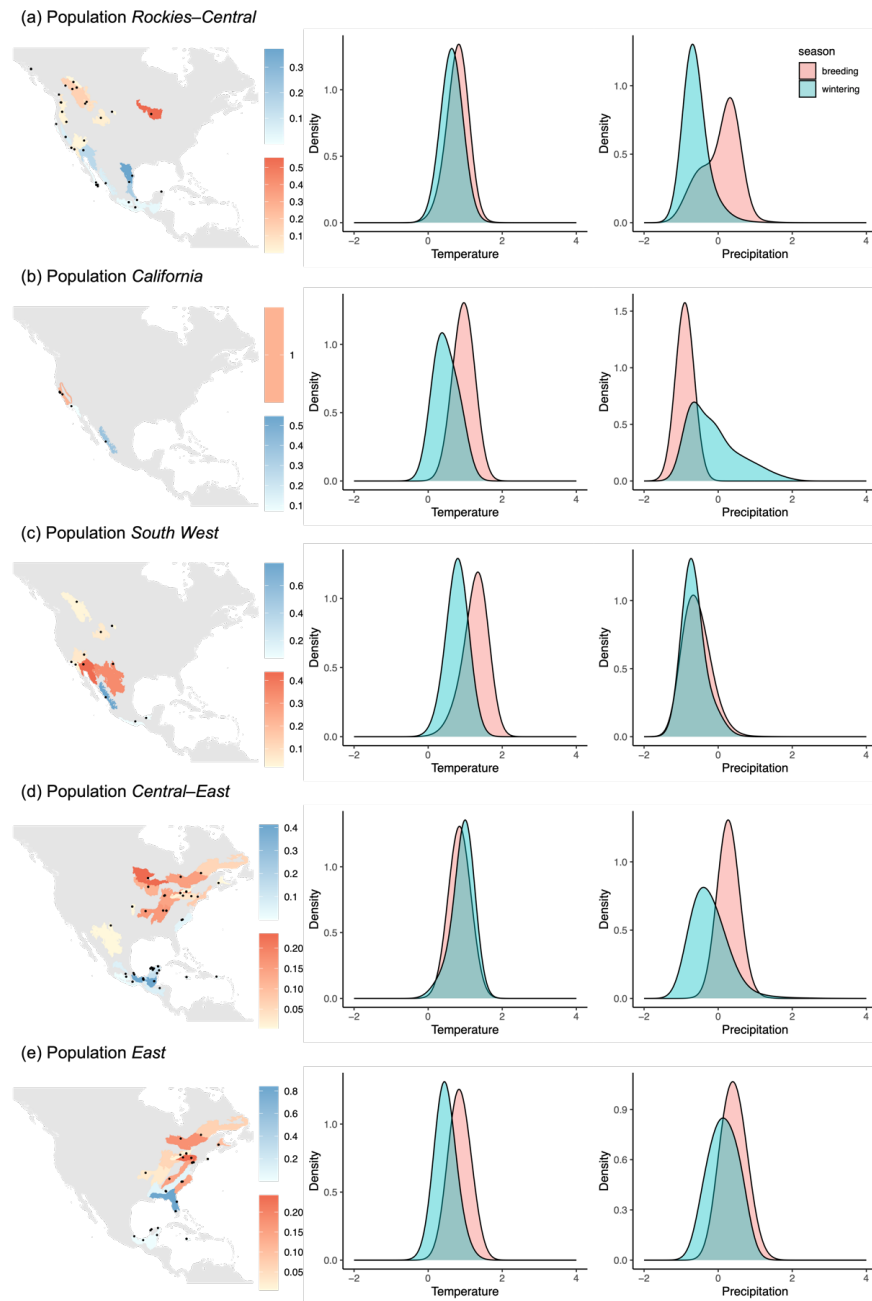


Figure S4 : Seasonal distribution and climate overlap of populations of Common Yellowthroat. In red: ecoregions occupied during the breeding season; in blue: ecoregions occupied during the wintering season. Darker the colour, higher the weight assigned to the ecoregion.

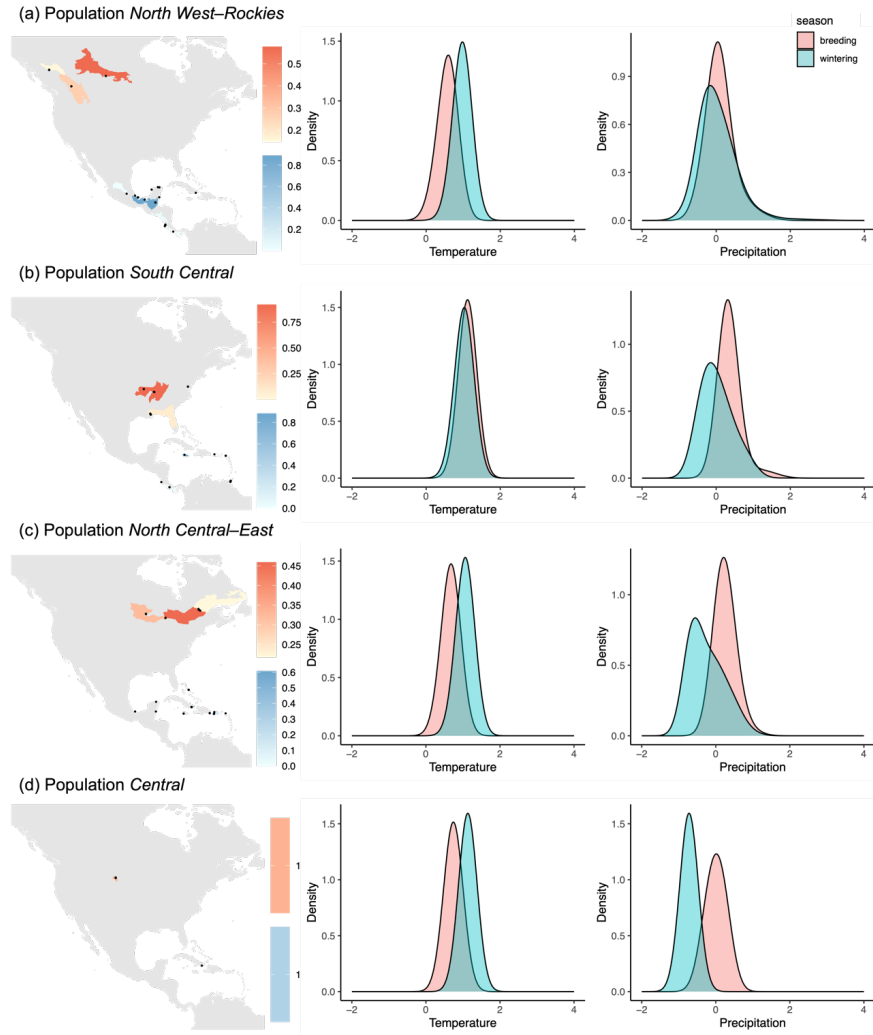


Figure S5 : Seasonal distribution and climate overlap of populations of American Redstart. In red: ecoregions occupied during the breeding season; in blue: ecoregions occupied during the wintering season. Darker the colour, higher the weight assigned to the ecoregion.

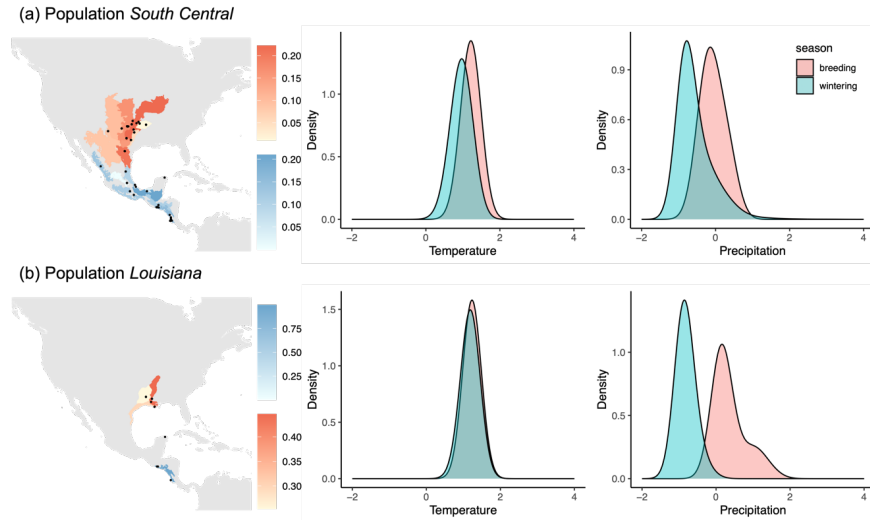


Figure S6 : Seasonal distribution and climate overlap of populations of Painted Bunting. In red: ecoregions occupied during the breeding season; in blue: ecoregions occupied during the wintering season. Darker the colour, higher the weight assigned to the ecoregion.

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Figure S7: Patterns of empirical and simulated migratory connectivity and seasonal climate tracking. Top row: empirical patterns; second row: patterns simulated by ORSIM; third row: patterns simulated by the thermal tracking model; bottom row: patterns simulated by the precipitation tracking model;. Panels (a), (e), (i) and (m) show the connections between population migration destinations (i.e. migratory connectivity), and the other panels show the relationship between migration distance and (b,f,j,n) two-dimensional climate (temperature + precipitation), (c,g,k,o) thermal overlap (temperature only), and (d,h,l,p) 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.

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Figure S8 : Comparing densities of climate values between the entire species breeding range and the breeding sample sites . Plots on the left-hand side indicate densities along temperature axis (z-scored) and plots on the right-hand side indicate densities along precipitation axis (z-scored). Climate values were extracted for each occupied ecoregion as the mean values across the ecoregion. In red: climate values extracted across the entire breeding range of the species; in blue: climate values extracted for ecoregions where breeding samples are located.

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Figure S9 : Comparing densities of climate values between the entire species wintering range and the wintering sample sites . Plots on the left-hand side indicate densities along temperature axis (z-scored) and plots on the right-hand side indicate densities along precipitation axis (z-scored). Climate values were extracted for each occupied ecoregion as the mean values across the ecoregion. In red: climate values extracted across the entire wintering range of the species; in blue: climate values extracted for ecoregions where wintering samples are located.