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Linking climate niches across seasons to assess population vulnerability in a migratory bird

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Abstract

Global loss of biodiversity has placed new urgency on the need to understand factors regulating species response to rapid environmental change. While specialists are often less resilient to rapid environmental change than generalists, species-level analyses may obscure the extent of specialization when locally adapted populations vary in climate tolerances. Until recently, quantification of the degree of climate specialization in migratory birds below the species level was hindered by a lack of genomic and tracking information, but recent technological advances have helped to overcome these barriers. Here we take a genome-wide genetic approach to mapping population-specific migratory routes and quantifying niche breadth within genetically distinct populations of a migratory bird, the willow flycatcher (*Empidonax traillii*), which exhibits variation in the severity of population declines across its breeding range. While our sample size is restricted to the number of genetically distinct populations within the species, our results support the idea that locally adapted populations of the willow flycatcher with narrow climatic niches across seasons are already federally listed as endangered or in steep decline, while populations with broader climatic niches have remained stable in recent decades. Overall, this work highlights the value of quantifying niche breadth within genetically distinct groups across time and space when attempting to understand the factors that facilitate or constrain the response of locally adapted populations to rapid environmental change.

KEYWORDS
climate change, ecological genomics, migratory connectivity, niche tracking

1 | INTRODUCTION

The increasing pace of species extinctions has placed new urgency on the need to understand factors regulating vulnerability to climate change (Dawson et al., 2011; Pacifici et al., 2015; Urban, 2015; Walther et al., 2002; Warren et al., 2013). Recent advances in the field of conservation genomics support the idea that locally adapted populations can vary significantly in their response to environmental change, particularly when species distributions span multiple distinct ecological regions (Bay et al., 2018; Chen et al., 2011; Ruegg et al., 2018; Yackulic et al., 2011). A species' ecological niche, defined as the sum

of the habitat requirements and behaviors that allow a species to persist within an environment (Grinnell, 1917), can be a key predictor of how they will respond to environmental change (Thuiller et al., 2005; Walther et al., 2002). For example, specialists whose niches are defined by a narrow set of climate parameters are thought to be more vulnerable to climate change impacts than generalists that occupy a wide range of climate conditions (Clavel et al., 2011; Lurgi et al., 2012; Moritz & Agudo, 2013). While species-level ecological niche models are widely used to quantify niche breadth, models that incorporate information below the level of species are often more accurate because locally adapted populations can vary in climate tolerances (Hällfors

et al., 2016; Ikeda et al., 2017; Valladares et al., 2014). As a result, an important and unexplored next step in improving predictions of species responses to future climate change is to assess the relationship between niche breadth and past demographic change within locally adapted populations.

Recent reports suggest that 2.9 billion birds have been lost from North America since the 1970s (Rosenberg et al., 2019), but reasons behind such declines remain unclear. Migratory animals represent a unique challenge for understanding the interaction between niche breadth and population vulnerability because their highly mobile life-history strategies make it difficult to quantify the extent of exposure to climate conditions across time and space. The ability to track environmental conditions across seasons may facilitate the evolution of niche specialization if natural selection occurs in similar directions on breeding and wintering areas (Webster & Marra, 2004). Alternatively, the ability to switch niches at each stage of the annual cycle may facilitate the evolution niche generalization if natural selection across seasons is contrasting (Robinson et al., 2009). While understanding the extent to which birds track or switch their niche across seasons has important implications for understanding the evolution of niche breadth, results of niche tracking studies are often contradictory. Some studies suggest species switch niches (Gómez et al., 2016; Joseph & Stockwell, 2000; Martínez-Meyer et al., 2004; Nakazawa et al., 2004), whereas others suggest species track niches to varying degrees, depending on factors such as range size, migration distance, and breeding latitude (Boucher-Lalonde et al., 2014; Laube et al., 2015; Zurell et al., 2018). A potential limitation of previous work is the focus on species-level migration rather than intraspecific migration which may obfuscate the extent of niche overlap across seasons if distinct populations follow divergent migratory pathways and winter in different areas (Ruegg & Smith, 2002; Turbek et al., 2018; but see Fandos et al., 2020). While previous technological limitations made quantifying seasonal niche overlap below the species-level challenging, new methodological breakthroughs in genomics and animal tracking technology have made it possible to map population-specific migratory routes (Ruegg et al., 2014). Here we move beyond previous work by investigating the relationship between seasonal niche overlap, niche breadth, and past population declines in genetically distinct populations of a migratory songbird, the willow flycatcher, *Empidonax traillii*.

The willow flycatcher is an important species for exploring the relationship between niche breadth and population vulnerability because understanding the factors behind population declines has important implications for its conservation. The willow flycatcher is currently divided into four subspecies across the continental USA (Figure S1) which vary in status from not threatened (Pacific Northwestern form, *E. t. brewsteri*; Western Central form, *E. t. adastus*; and Eastern form, *E. t. traillii*) to Endangered (Southwestern form *E. t. extimus*). The southwestern subspecies, *E.t. extimus*, was listed as federally endangered following steep population declines through the first half of the 20th century (Sogge et al., 1997; Unitt, 1987) and while there has been some controversy surrounding the subspecies designation of the southwestern willow flycatcher (Zink,

2015), recent data support its genetic and ecological distinctiveness (Mahoney et al., 2020; Theimer et al., 2016). More specifically, our previous work using ecological genomics investigated the link between a suite of climate and landscape variables and genome-wide genetic signatures and found strong support for an association between genetic variation, temperature, and precipitation, but not landscape variables. In particular, we found highly significant correlations between allele frequencies in genes linked to thermal tolerance and the intensity of summer heat waves in the southwest (Ruegg et al., 2018). Furthermore, the mismatch between current and future predicted gene–environment correlations supported the idea that the Southwestern population would be the most vulnerable to future climate change, but this work focused exclusively on the breeding grounds. Here we expand on past work by investigating the extent to which locally adapted breeding populations track similar environmental conditions across seasons. Such information can be used to help understand the extent to which niche breadth within locally adapted populations of the willow flycatcher across seasons may help explain past population declines as well as future population- and subspecific-level resilience to environmental change.

To investigate the relationship between realized niche breadth, local adaptation, and regional population trends, we begin by mapping genetically distinct populations of willow flycatcher across breeding and wintering areas. We identify population structure across the breeding range using an analysis of genome-wide genetic data and then screen an additional 393 breeding samples and 363 wintering individuals collected across breeding and wintering areas using a subset of Single nucleotide polymorphism (SNP) markers. Using genetic stock identification methods co-opted from fisheries management (Satterthwaite et al., 2015), we assign wintering individuals back to their most likely breeding population of origin and use the resulting assignments to build a map of population-specific migratory connections. To quantify niche breadth within each genetically distinct group, we then apply kernel smoothers to densities of occurrences in environmental space and calculate the total niche area across breeding and wintering grounds as well as the extent of seasonal niche overlap (Broennimann et al., 2012). Lastly, to assess the extent to which niche breadth within genetically distinct populations is associated with past population declines, we analyze population survey data from 1968 to 2015, stratified by genetic group (Sauer et al., 2017).

2 | MATERIALS AND METHODS

2.1 | Sample collection and DNA extraction

We compiled a collection of 931 willow flycatcher blood or tissue samples, 568 samples from 37 locations across the breeding range and 363 samples from 64 locations across the wintering range using a combination of samples from previous studies (Paxton, 2000), museum donations, and new field collections (Tables S1 and S2). A subset of 175 individuals previously sequenced using RAD-seq (Ruegg et al., 2018) were reanalyzed here to assess patterns of population

structure across the breeding range and identify a subset of genetic markers that could be used for population assignment. The remaining 393 breeding individuals and all of the overwintering individuals were genotyped at a subset of genetic markers (see below for marker selection methods) to identify population-specific wintering locations. DNA from all samples was purified using the Qiagen™ DNeasy Blood and Tissue extraction kit and quantified using the Qubit® dsDNA HS Assay kit (Thermo Fisher Scientific).

2.2 | Genome scan

Genome scans were previously conducted by Ruegg et al. (2018) on 219 individuals following the BestRAD library preparation protocol with some modifications (Ali et al., 2016). After visualizing the tradeoff between discarding SNPs with low coverage and discarding individuals with missing genotypes using the R package genoscapeRtools (https://doi.org/10.5281/zenodo.848279), the final number of 105,000 SNPs and 175 individuals became the foundation for genome-wide analyses herein (code and data available at https://doi.org/10.5281/zenodo.4656570). From these SNPs, 289 were removed as likely paralogs due to aberrantly low homozygote genotype frequencies in samples from the Interior West. A further 85 SNPs that were monomorphic among the samples were also removed. Within the remaining dataset, of 104,626 SNPs all 175 individuals were missing genotypes at fewer than 15.6% of SNPs and no SNP was missing a genotype in more than 7.5% of individuals (mean fraction of missing data = 2.3%). SNPrelate (Zheng et al., 2012) was used visualize patterns of genome-wide population structure via principal components analysis (Figure S1). Based upon a preliminary evaluation of the population clustering on PC1 and PC2, we identified seven main clusters which corresponded with geography, including (Figure 1) Pacific Northwest, White Mountain, South Southwest, Interior Northwest, Kern, Southern California, and East. SNPrelate was then used to calculate genome-wide, pairwise F_{STs} between the seven main clusters.

2.3 | SNP genotyping

To select a subset of SNPs with the most power for identifying individuals to genetically identifiable populations, we ranked SNPs by the probability of correct assignment for different population-level comparisons, following Clemento et al. (2014, p. 118; see Github repository https://doi.org/10.5281/zenodo.4656570). To determine whether the selected SNPs were convertible to SNPtype Assays based on GC content and the amount of flanking sequence, we used the R package SNPS2ASSAYS (https://doi.org/10.5281/zenodo.44692435). The resulting 174 SNPs for population assignment were combined with 18 climate-associated SNPs from Ruegg et al. (2018) to increase our power for population assignment. In all, 192 SNPs were then converted into SNPtype Assays (Fluidigm Inc.) for subsequent genotyping of 393

breeding individuals on a Fluidigm™ 96.96 IFC controller following manufacturer guidelines. Ten SNPs that could not be reliably genotyped were eliminated to yield a final panel of 182. After the initial screening, the SNP panel was further reduced to a set of 96 SNPs based upon the power for population assignment and the 96-SNP panel was screened in 363 wintering individuals (Table S2). Individuals with <80% of SNPs successfully genotyped were removed from downstream analyses.

2.4 | Structure analysis and genoscape construction

To map the geographic distribution of genetically identifiable populations across the breeding range (i.e., create the genoscape), we combined genotypes generated via the Fluidigm and RAD-Seq pipelines for all 568 individuals at 182 loci and used the resulting dataset to run the program STRUCTURE (Pritchard et al., 2000). We ran five replicates for K values ranging from 3 to 9 using the following parameter values: BURNIN = 50,000, NUMREPS = 100,000. To confirm that results were consistent between the Fluidigm and RAD-Seq analysis pipelines and that there was no ascertainment bias associated with our SNP selection procedure (Anderson, 2010), we visualized the structure results by genotyping method within each sampling location (Figure S2). To simplify the comparison of results, the program CLUMPP (Jakobsson & Rosenberg, 2007) was used to reorder the cluster labels between runs, and individual q values (proportion of an individual's ancestry inferred from each cluster) were plotted using the program Distruct (Rosenberg, 2004).

To build the genoscape, the q values from each individual in STRUCTURE were smoothed across space via a kriging algorithm and visualized as transparency levels of different colors overlaid upon a base map from Natural Earth (naturalearthdata.com). The results were clipped to the breeding range using a shapefile (NatureServe Bia, 2012), making use of the R packages *sp*, *RGDAL*, *raster*, and *TESS3* (Caye et al., 2016; Keitt et al., 2014; Hijmans et al., 2020; Pebesma et al., 2020). The transparency of colors within each genetic group was scaled so that the highest posterior probability of membership in the group according to STRUCTURE is opaque and the smallest is transparent, creating a spatially explicit map of genomic clustering, or the genoscape.

2.5 | Panel validation and identification of population-specific wintering areas

The accuracy of our baseline for assignment of individuals to the seven genetically identifiable using the 96-SNP panel was evaluated via *leave-one-out* cross validation in RUBIAS (Moran & Anderson, 2018). We then used RUBIAS to identify the most likely breeding population of origin for wintering samples. Assignments of wintering individuals with high certainty (a posterior probability > 0.8) were
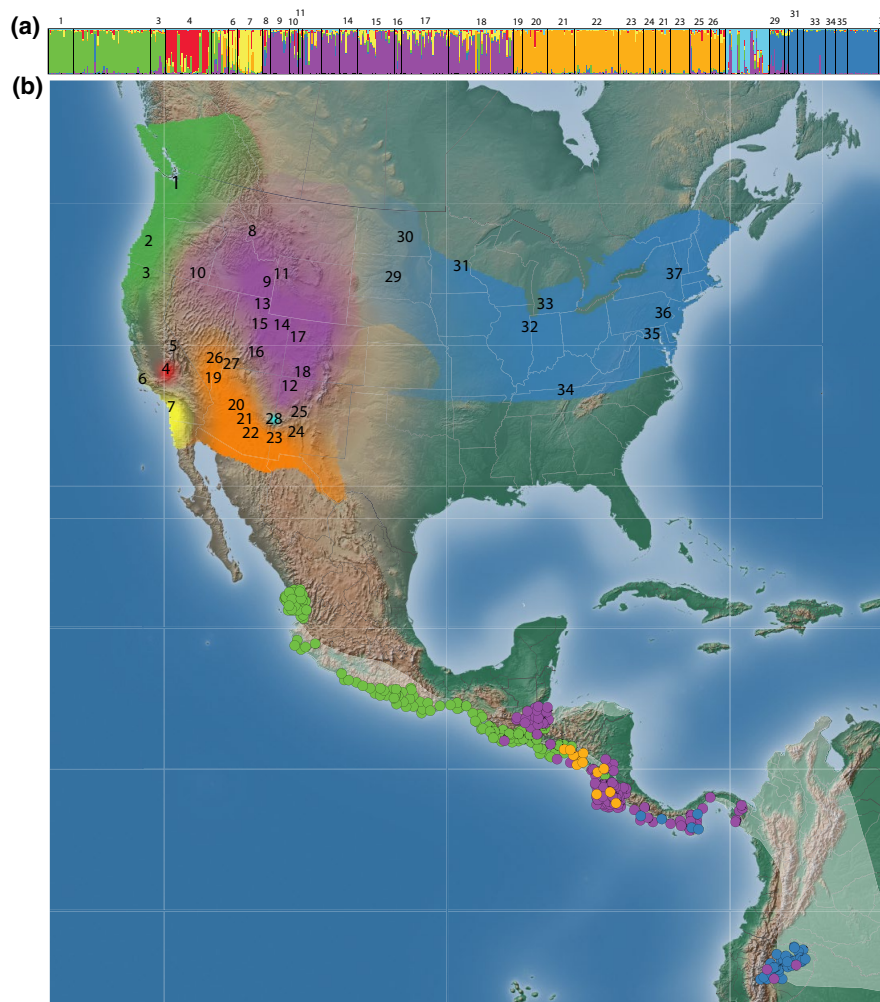
FIGURE 1 Willow Flycatcher genoscape. Population genetic structure in Willow Flycatchers across the breeding grounds and corresponding population-specific wintering locations. (a) STRUCTURE analysis revealed support for the existence of seven genetically distinct groups across the breeding range. Numbers at the top of the STRUCTURE plot correspond to locations on map and in Table 1. Numbers in the SSW population are not consecutive because data generated using RADseq and SNP genotyping were lumped together to test for consistent results (Figure S2). (b) The posterior probability of group membership from STRUCTURE was visualized as transparency levels of different colors overlaid upon a base map from Natural Earth (naturalearthdata.com) and clipped to the species breeding range using a shapefile (NatureServe Bia, 2012). Wintering individuals are color coded based upon assignments to breeding group using the program RUBIAS. Points on the wintering grounds are jiggered for visualization purposes. Wintering sample location details and associated assignments can be found in Table S1 [Colour figure can be viewed at wileyonlinelibrary.com]

color coded by genetic group, mapped to the genoscape (with jittering to avoid overprinting), and used in the downstream analysis of seasonal niche breadth.

2.6 | Seasonal niche breadth and overlap

We modeled the realized seasonal climatic niches of the willow flycatcher as a whole as well as for each of the four main genetically distinct groups (Southwest, Pacific NW, Interior West, and East) separately (Code and data available at: https://doi.org/10.5281/zenodo.4656570). The three additional genetically identifiable groups in the Kern, Southern CA, and the White Mountains lacked sufficient data to characterize niche breadth and were therefore removed from subsequent analyses. Total niche area as well as the degree of overlap between breeding and wintering grounds was calculated using the modeling framework described in Broennimann et al. (2012). Selection of climate variables for the present study was directly informed by the results of Ruegg et al. (2018) who tested the association between 24 different temperature, precipitation, and landscape variables and found that genetic variation across the breeding range was most strongly associated with temperature and precipitation (mean temperature of the coldest quarter, max temperature of the warmest month, and precipitation of the driest quarter), but not landscape. Because several of the climate variables in Ruegg et al. (2018) were specific to particular times of the year and we wanted our analysis to be more generally applicable across season in temperate and tropical areas (Janzen, 1967), we selected

more general temperature and precipitation variables that were highly correlated with those used in Ruegg et al. (2018). More specifically, we obtained monthly temperature and precipitation data from WorldClim 2.0 (Fick & Hijmans, 2017) for breeding months (June–August) and wintering months (November–April) associated with locations of genetically assigned individuals with a posterior probability >0.8. We selected dates for the wintering period based upon Koronkiewicz et al. (2006), but also tested the effect of narrower bounds (December–February) on the wintering period to ensure that our results were robust to variation in the definition of the wintering period. Climate data were extracted on a grid of equal-area hexagons ~55 km wide (Sahr et al., 2003), covering the Western Hemisphere (>30°W). In each hexagon containing a genetically identified individual, we computed the average climate values and obtained summer climate by taking the mean values between June and August, and winter climate by taking the mean values between November and April. Seasonal temperature and precipitation were normalized using the z-score across the whole of the study region (i.e., Western Hemisphere). For each season (i.e., breeding and wintering) and each subspecies (i.e., using only individuals genetically assigned to that subspecies) as well as the entire species, 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. Following Broennimann et al. (2012), we then used a kernel density function on a 50 × 50 pixel grid super-imposed 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. To assess whether these choices of parameter values influence the results, we performed a sensitivity analysis of the kernel density estimation. Specifically, we varied two parameters: the bandwidth of the seasonal density kernel function and the threshold above which pixels of the density kernel where set to 0, and we assessed the effect of the variation on the results for breeding and wintering niche sizes as well as for seasonal niche overlap. Furthermore, to assess whether our results were significantly influenced by wintering ground sample size, which varies between populations, we performed randomization tests in which we set the total number of samples for the Pacific Northwest, the Interior Northwest and the East to $n = 12$, which is the number of samples available for the Southwest.

To calculate the total realized niche size as a proxy for niche breadth within each subspecies, we calculated the number of pixels across climate space whose density was above 0 for each season. Niche overlap within a subspecies across seasons as well as between subspecies was computed using Schoener's D metric, which varies between 0 (no overlap) and 1 (complete overlap; Broennimann et al., 2012). To assess the relationship between seasonal niche overlap and migration distance, we calculated the average migration distance as the great circle distance between the mean location of breeding individuals (i.e., mean latitude and mean longitude across individuals) and the mean location of wintering individuals for that population. To assess the relationship between the seasonal niche overlap and breeding range

size, we calculated the number of total number of hexagons within the genetically defined breeding range of each subspecies as depicted in Figure 1.

To test whether the degree of niche tracking for each population was significantly different from random, we used a niche similarity analysis adapted from niche similarity tests proposed by Broennimann et al. (2012). Specifically, we compared the observed seasonal niche overlap metric (D) with seasonal niche overlap metrics simulated for alternative migration destinations. This was done by shifting randomly the population's breeding ground within the species' breeding range and computing the resulting D metric between the observed winter niche and the breeding niche of the shifted breeding ground. To shift the breeding ground, we first selected an individual i randomly sampled among all the breeding individuals available in our dataset. Then, we selected N individuals (N corresponding to the observed number of breeding individuals for that population) using the probability of being sampled $P_s = 1/$ rank (d_{iN_j}), where N_j is individual j among the N individuals sampled; d_{iN_j} is the great circle distance between individual i and individual N_j; and rank (d_{iN_j}) is the rank of d_{iN_j} among all d_{iN}. This sampling procedure ensures that the breeding individuals sampled are clustered together in space to form a realistic simulated breeding ground of the population. We shifted the breeding ground of populations while keeping their wintering ground as observed because (i) the wintering range of Willow Flycatcher is much more restricted than its breeding range and contains a significantly smaller pool of individuals to sample from and (ii) it follows how observed migratory connectivity was determined, that is, by assigning wintering individuals to genetically distinct populations on the breeding ground. We repeated the procedure of shifting the population's breeding ground 1000 times, each time recording the simulated D metric. To assess statistical significance, that is, whether the population is tracking its climatic niche more than random, we computed a p value investigating whether the observed niche overlap D_{obs} is higher than 95% of the simulated niche overlaps D_{sim}. We also calculated the standardized effect size $E_D = D_{obs} - \text{mean}(D_{sim})/\text{SD}(D_{sim})$ associated with the p value.

2.7 | Demographic analysis

We used data from the North American Breeding Bird Surveys (BBS; Sauer et al., 2017) to estimate population trends for each of the four subspecies with occurrences on the wintering grounds. Raw data were downloaded from https://pwrc.usgs.gov/BBS/RawData on July 10, 2019. We selected only observations that represented a single run per year, with no replicated efforts (RPID = 101) and conditions that meet BBS criteria (RunType = 1). Only routes in which at least one individual Willow Flycatcher was observed were used for analysis. A shapefile representing geographic boundaries for the four populations was used to assign each route to a population.

To estimate trends in relative abundance since 1968, we used the Bayesian hierarchical model presented in Link and Sauer (2002). This model includes a random effect to account for observer bias. Link and

Sauer used physiographic "strata" as regional units within which they calculate abundance indices and populations trends. We substituted these strata with our four genetically informed populations. The BBS data are then fit using Markov chain Monte Carlo methods and abundance indices and trends are calculated from the model's parameters.

Annual stratum-specific abundance index (n) in strata i at time t is estimated as:

$$n_{i,t} = z_i \exp(S_i + \beta_i(t - t*) + \gamma_{i,t}),$$

where S_i, β_i, and $\gamma_{i,t}$ are the intercept, slope, and year effects for a particular stratum, respectively, and z_i is the proportion of routes on which the species has been observed. This metric cannot be compared across stratum, but indices for stratum totals can be calculated by multiplying by the stratum area ($N_{i,t} = A_{i,t}n_{i,t}$). To obtain an overall abundance index, we summed stratum totals across the four populations, assuming that contributions from very small genetic populations would be negligible.

Population trend for each population as well as for the whole species is calculated as $100 (B_i - 1)$ % between 1968 (t_a) and 2015 (t_b):

$$B_i = \left\{ \frac{N_{i,t_b}}{N_{i,t_a}} \right\}^{1/(t_b - t_a)},$$

3 | RESULTS

3.1 | Genome-wide population genetic structure

Principle components analysis (PCA) of 175 breeding individuals at 104,626 SNP loci revealed support for genetic differentiation between the four main subspecies, *E. t. extimus* (Southwest), *E. t. brewsteri* (Pacific Northwest), *E. t. adastus* (Interior Northwest), and *E. t. traillii* (East; Figure S1). Furthermore, our analysis supports the existence of sub-differentiation within the currently defined range of *E. t. extimus*, with the White Mountains, Kern, San Diego and being more closely aligned with *E. t. brewsteri* and *E. t. adastus* than the remainder of the Southwest (Figure 1). Because downstream genoscape construction was based on a subset of highly divergent SNPs which do necessarily not reflect genome-wide patterns of gene flow, we calculated pairwise F_{ST} between the seven groups apparent within the PCA using the genome-wide data. Pairwise F_{ST} analyses suggest that highest degree of genetic divergence was between the

East and all other pairwise comparisons (Table 1; F_{ST} range = 0.064–0.09), apart from between East and Interior Northwest which was lower (F_{ST} = 0.036). Comparisons between the White Mountains and the Southwest (F_{ST} = 0.067), Kern and the Southwest (F_{ST} = 0.066), and the White Mountains versus Kern and Southern California (F_{ST} = 0.058 and 0.059, respectively) were the next most divergent. The Southwest was also strongly differentiated from the Pacific Northwest and to a lesser degree the Interior Northwest (F_{ST} = 0.059 and 0.048, respectively), with the lowest levels of divergence found between the Interior Northwest and all other pairwise comparisons (F_{ST} range = 0.009–0.032).

3.2 | Structure analysis and genoscape construction

The willow flycatcher genoscape for this study was created using a subset of SNPs specifically designed to accentuate groups of individuals within geographic areas that are genetically distinguishable from other genetically groups for the purpose of linking wintering breeding populations, and therefore the groupings within the genoscape do not necessarily reflect historic patterns of gene flow across the genome. While our STRUCTURE analysis revealed that a K value of 4, 5, 6, and 7 populations were biologically realistic hypotheses for the number of groups within the species (Figure 2), the goal of our analysis was not to find the most likely value of K, but to identify spatially explicit genetic groups that could be tracked across the full annual cycle, similar to fisheries stock management (McKinney et al., 2019). Thus, we set the number of groups to 7 based on concordance between spatially informative genetic clusters identified in the genome-wide PCA (Figure 1), the STRUCTURE runs based on a limited set of loci (Figure 1), and the power to assign individuals to groups at $k = 7$ using RUBIAS (Table S1). The seven genetically distinguishable groups, four of which were roughly concordant with previously defined subspecies boundaries, were distributed across North America as follows (Figure 1): Pacific Northwest (green, 1–3) corresponded with *E. t. brewsteri*, Kern (red, 4) fell within the current boundary for *E. t. extimus*, Southern California (yellow, 6 and 7) fell within the current boundary for *E. t. extimus*, Interior Northwest (purple, 8–18) fell within the current boundary for *E. t. adastus*, Southwest (orange, 19–27), White Mountain (sky blue, 28) fell within the current

Population	Interior NW (8–18)	Kern (4)	Pacific NW (1–3)	Southern CA (6 & 7)	Southwest (20–27)	White MT (28)
East (29–37)	0.037	0.078	0.064	0.077	0.091	0.065
Interior NW	—	0.029	0.010	0.033	0.049	0.031
Kern	—	—	0.027	0.051	0.067	0.059
Pacific NW	—	—	—	0.040	0.059	0.041
Southern CA	—	—	—	—	0.048	0.060
Southwest	—	—	—	—	—	0.068

TABLE 1 Pairwise genome-wide FST between genetically distinct groups calculated with all 105,000 SNP loci. Numbers after population names refer to location in Figure 1 and details in Table S1
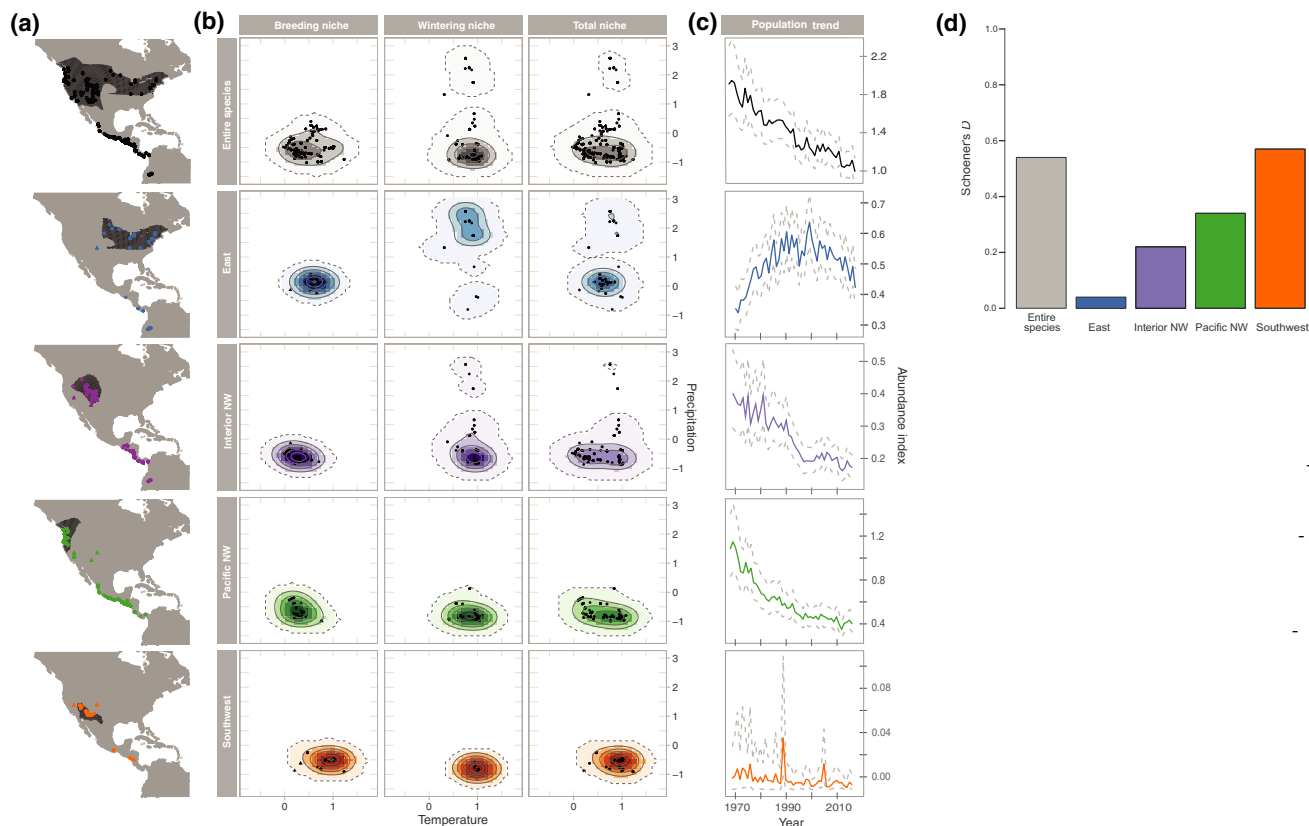
FIGURE 2 Realized climate niche and population trends for the Willow Flycatcher. (a) Maps of the sampling distribution for the species and each of the four main genetically defined groups separately. Geographic regions on the breeding grounds were defined according the genoscape map in Figure 1. Triangles indicate samples that were identified to each genetically distinct group, but fell outside of the genoscape boundaries, while circles fell within the genoscape boundaries. (b) The realized climate niche occupied by each group on its breeding and wintering range as well as across both seasons. (c) Demographic trends estimated with Breeding Bird Survey data showing declines in the Pacific NW and Interior NW, but no significant change in the East. The Endangered Southwestern group is reported to have declined prior to the start of the survey. (d) Niche overlap for the species as well as each genetically distinct group [Colour figure can be viewed at wileyonlinelibrary.com]

boundary for *E. t. extimus* and East (dark blue, 29–37) fell within the current boundary for *E. t. traillii*. From here on we will refer to genetic groups by their geographic rather than subspecies name unless a direct comparison with the subspecies is needed. Sampling location 5, Owen's River at Bishop, did not fall clearly into any one genetic cluster and rather represented a mixture between Interior Northwest, Southern California, and Southwestern groups. Furthermore, a comparison between genetic assignments generated using SNPs from the RADseq and Fluidigm pipelines were concordant suggesting no significant ascertainment bias associated with SNP sub-setting (Figure S2).

3.3 | Identification of population-specific wintering areas

Leave-one-out cross-validation of our genetic baseline in RUBIAS revealed that the power to assign individuals to groups was high, with the Pacific Northwest having the highest probability of correct assignment (99.7%), followed by the Southwest (98.6%), the

East (97.5%), the Interior West (91%), the Kern (80%) and Southern California (78%), and the White Mountains (70%; Table S3). The majority of the incorrect assignments in the White Mountains were to the surrounding populations in the Southwest, while the majority of the incorrect assignments in Southern California and the Kern were from neighboring populations in the Kern and Pacific Northwest, respectively. Higher mis-assignment rates in the Kern, Southern California, and the White Mountains are likely due to admixture with neighboring groups, indicating these may be areas of hybridization between subspecies. Subsequent assignment of wintering individuals to genetically distinct breeding groups using RUBIAS indicated that Pacific Northwest birds winter from western Mexico to Costa Rica, Interior West breeders winter from Guatemala south to Panama, Eastern breeders winter from Costa Rica to Ecuador, and Southwestern breeders are restricted to Costa Rica and Nicaragua (Figure 1b; Table S2). We did not detect any Kern, White Mountain, or Southern California breeders on their wintering grounds which is not surprising given the low population sizes in those regions and the correspondingly low probability of detection outside of the breeding range.

TABLE 2 Climate niche characteristics, migration distance and breeding range size co-vary across genetically-distinct populations. Niche size is measured in number of occupied pixels in niche space (see Section 2 for details), niche overlap has no unit and vary between 0 and 1, migration distance is measured in km, and range size is measured in number of occupied hexagons (see Section 2 for details). The niche similarity test assesses whether the population is tracking its climatic niche better than random given the climate available throughout the species range. Values for the niche similarity test presented in the table indicate effect size (see Section 2 for how it is calculated), and stars represent significance levels at $p < 0.05$ (*), 0.01(**) or 0.001 (***)

Population	Breeding niche size	Wintering niche size	Niche breadth (total niche size)	Seasonal niche overlap	Migration distance	Breeding range size	Niche similarity test
Species	318	481	458	0.53	3520	2547	NA
East	175	470	456	0.06	4581	1003	−1.381
Interior W	183	401	409	0.22	4024	460	−1.391
Pacific NW	208	209	267	0.31	3871	309	−0.672
Southwest	199	152	200	0.65	3105	230	1.586*

3.4 | Seasonal climate niche breadth and overlap

An analysis of seasonal climate niche breadth revealed that while breeding niches within the willow flycatcher are similar in size, wintering niches sizes are more variable (Figure 2; Table 2). Specifically, the wintering niche of the Eastern group is around twice as large the wintering niche of the Southwest and Pacific Northwest group (Figure 2; Table 2). This is mainly driven by long-distance migratory individuals of the Eastern group found as far south as Ecuador, generating wide variation along the precipitation axis. We acknowledge that sampling gaps on the wintering grounds limit our ability to fully characterize the wintering niche of Interior Northwest and Easter populations which likely winter in unsampled areas of the northern Andes. This being the case, we also acknowledge that inclusion of additional samples from these regions would either maintain or increase the wintering niche size for each of these groups and would not significantly change the interpretation of our results. Calculation of niche overlap revealed that while the willow flycatcher as a species tracked its climate niche rather closely throughout the year (Schoener's $D = 0.53$; Figure 2d; Table 2), there was variation in the amount of niche overlap below the species level. In particular, the Southwestern group demonstrated the highest niche overlap between breeding and wintering areas (Schoener's $D = 0.65$; Figure 2d; Table 2), the Eastern group demonstrated the lowest niche overlap across seasons (Schoener's $D = 0.06$), and the Interior Northwest and Pacific Northwest groups fell in between the upper and lower extremes (Schoener's $D = 0.22$ for both). These results were robust to variations in parameter values associated with the kernel density estimation (Figure S3a), as well as to variations in boundaries set on the length of the wintering period (Figure S4). Further randomization tests in the Pacific Northwest, Interior West, and East confirmed that niche overlap were not significantly influence by wintering ground sample size (Figure S3b).

Comparison of niche breadth (calculated as the total niche area on breeding and wintering grounds) to the degree of niche overlap revealed an inverse relationship, with higher niche overlap between breeding and wintering areas found in populations with lower overall niche breadth like the Southwest (Table 2). In addition, migration distance and breeding range size also varied by genetic group, with migration distance and the breeding range being inversely correlated to the degree of seasonal niche overlap across genetic groups (Table 2; Figure S5a,b). In addition, niche similarity tests show that the southwest population is tracking its climatic niche throughout the year better than random given the availability of climate across the species distribution (Table 2). However, the niche similarity tests also show that the three other populations are not significantly tracking their climatic niche throughout the year, and have negative effect sizes. The east and interior northwest populations in particular have relatively high negative effect sizes indicating that they tend to be closer to being niche switchers rather than niche trackers, while the interior west population falls somewhere in between.

3.5 | Demographic analysis

Overall, the demographic analysis revealed that while the species as a whole has been declining, abundance trends vary by genetically distinct group. In particular, a comparison in the % change between 1968 and 2015 suggests that while species as a whole has declined slightly (−1.26, CI: −1.60% to −0.94%), there has been no significant change in the Eastern population (0.36%, CI −0.02% to 0.75%), a significant decrease in the Interior NW (−1.83%, CI −2.50% to −1.16%) and the Pacific NW (−2.01%, CI: −2.53 to −1.51%), and no detectable difference in the endangered Southwestern group which had already declined prior to the start of the survey in 1968 (Figure 2c). A comparison between population trends and niche breadth support the idea that groups with narrower niches across seasons have been declining more dramatically or, in the case of the Southwest group had previously declined to the point of being federally endangered while groups with broader niche across seasons have remained stable.

4 | DISCUSSION

Recent research suggests over ~2.9 billion birds have been lost from North America since the 1970s (Rosenberg et al., 2019),

representing a staggering and largely unexplained loss of biological diversity. While advances in migrant tracking technology have provided new insights into geographic regions important to population declines in some migratory birds (Kramer et al., 2018), we still lack basic knowledge of how fundamental aspects of avian ecology may interact with other stressors to promote resiliency to environmental change. Here we demonstrate how mapping niche breadth across seasons within genetically distinct populations of a migratory bird yields important insights into the relationship between climate specificity and threatened status. Our results show that genetically distinct populations of the willow flycatcher with narrower total climate niches demonstrate high climate niche overlap between breeding and wintering areas while genetically distinct populations with broader total niches have low climate niche overlap across seasons. Remarkably, when paired with population-specific demographic trend data since the late 1960s, we find that populations with narrower climate niches across seasons are already endangered or steeply declining, while populations with broader climate niches across seasons have remained stable in recent decades; a pattern that would have been masked by a species-level only analysis. While further work across species and populations is needed to assess the generality of our findings, this work highlights the importance of quantifying niche breadth within species across the annual cycle when attempting to understand the factors that facilitate or constrain the response of locally adapted migratory populations to rapid environmental change.

4.1 | Niche tracking and ecological divergence across seasons

Climate niche tracking across seasons provides the potential for the evolution of specialization to a narrow set of climate optima, but such hypotheses are difficult to investigate in migratory animals without genetic and tracking data below the level of species. We use a genome-wide genetic approach to quantifying breeding and wintering climate niches in the willow flycatcher and find that while the species as a whole occupies a broad breeding niche with relatively high levels of seasonal niche tracking, the degree of niche tracking within genetically distinct populations increases with increasing climate specialization. In particular, the Southwestern group has the smallest total niche breadth and the highest degree of seasonal niche overlap, while the Eastern group has the broadest total niche and the lowest degree of seasonal niche overlap. When combined with previous work showing that genome-wide genetic variation is more strongly tied to climate in the southwest than in the east (Ruegg et al., 2018), our results point to the idea that intraspecific variation in the extent of climate niche tracking across seasons may accelerate the process of ecological specialization in some groups while promoting ecological generalization in others. The work presented here represents an important first step toward studying the process of natural selection across the annual cycle by providing a framework for understanding the extent to which genetically

distinct breeding populations are exposed to similar or contrasting environmental conditions on their breeding and wintering grounds.

In addition to providing a framework for understanding the relationship between niche tracking and local adaptation, the increased clarity provided by our population-level analysis of niche tracking suggests that mixed evidence regarding the extent to which species track or switch their niche across seasons may in part be due to a failure to match the appropriate tracking tool with the spatial scale of the question. On one end of the spectrum, species-level analyses may be too coarse in scale to quantify niche breadth when genetically distinct populations vary in climate tolerances (Boucher-Lalonde et al., 2014; Gómez et al., 2016; Joseph & Stockwell, 2000; Laube et al., 2015; Martínez-Meyer et al., 2004; Nakazawa et al., 2004; Zurell et al., 2018). On the other end of the spectrum, fine-scale movement data provided by global positioning system (GPS) tags (Fandos et al., 2020) may lack the genetic backdrop necessary identify how individual movements fit within the context of locally adapted populations. Alternatively, our results suggest that a genomic approach to mapping seasonal climate niches can illuminate key linkages between climate tracking, local adaptation, and niche breadth that can be used to help shed light on the evolution of climate specialization across the annual cycle.

4.2 | Niche breadth and vulnerability to climate change

The willow flycatcher is an excellent model for exploring the relationship between niche breadth and population-level vulnerability to climate change because past work provides support for the existence of local adaptation to climate across the breeding range (Ruegg et al., 2018), but the present study provides the first demonstration of a method for quantifying the climate niche of locally adapted populations across breeding and wintering grounds. Thuiller et al. (2005) highlights four main hypotheses regarding which groups should be more sensitive to climate change, including groups with (1) marginal distributions outside of the mean climate conditions (Swihart et al., 2003), (2) narrow niche breadth (specialist species; Brown, 1995), (3) restricted distributions (Johnson et al., 1998), and (4) distributions within regions strongly exposed to climate change. Here we find that the endangered southwestern willow flycatcher fits all four climate sensitivity criteria—previous work demonstrated that genetic diversity is significantly associated with climate variables that fall outside of the mean climate conditions (Ruegg et al., 2018; Figure 2a), its highly fragmented breeding range is at the edge of the species distribution where the intensity of summer heat waves is most pronounced (Smith et al., 2013), and here we show it has the narrowest total niche breadth of the four main genetic groups across breeding and wintering grounds. In contrast, the Eastern population of the willow flycatcher demonstrates the characteristics of a climate resilient population—previous work demonstrated that genetic diversity is significantly associated with mean climate variables (Ruegg et al., 2018; Figure 2a), its broad, northern distribution is predicted

to be less susceptible to intense summer heat waves (Smith et al., 2013), and here we show it has the broadest total niche breadth of the four main groups across seasons. As a result, sensitivity to climate change may help explain why population numbers have remained low in the southwest, despite concentrated recovery efforts over the last decade, while population numbers in the east have not changed significantly. Indeed, while we only have four populations and cannot test whether the relationship between niche breadth and population trends are statistically significant, it remains striking that across the four main groups where niche breadth could be calculated, we see a trend toward steeper declines or, in the case of the already endangered southwestern willow flycatcher, greater vulnerability, with increasing climate specialization. The trend toward greater vulnerability to climate change in the southwestern willow flycatcher mirrors the results from Ruegg et al. (2018) which predicted significantly higher mismatches between current and future gene–environment relationships in the southwestern population. Thus, in combination with other anthropogenic disturbances such as loss of critical breeding habitat, having a narrow range of climate optima may further exacerbate losses in already vulnerable populations. Overall, this work more generally highlights the importance of understanding the extent of climate specificity within genetically distinct populations across time and space when attempting to prioritize conservation in a rapidly changing world. Future work will focus on assessing the relationship between niche breadth and population trends in a multi-species comparative framework in order to test the generality of patterns observed herein.

In addition to helping clarify the degree of climate specialization across breeding and wintering grounds, a genomic approach to niche tracking can also provide insights into the capacity for populations to shift the location of breeding and wintering ranges in response to climate change. Comparative analyses across many species using range maps suggest that the extent to which birds track their niche between breeding and wintering ranges depends largely on factors such as range size, habitat specificity, and migration distance (Somveille et al., 2019; Zurell et al., 2018). Here we find that niche breadth increases with migration distance and breeding range size, supporting hypotheses raised by Somveille et al. (2019) that where birds migrate may result from tradeoffs between the degree of specialization, the cost of migration, and the availability of resources. Thus, while specialized populations like the southwestern willow flycatcher may outcompete generalists like the Eastern willow flycatcher for geographically closer wintering ranges, this may come at the cost of reduced flexibility to alter their ranges in the face of rapid environmental change. In turn, while the Eastern willow flycatcher may have greater access to resources in more southern wintering ranges as well as greater flexibility in climate tolerances across the annual cycle, this flexibility may come at the cost of a longer migratory journey. Overall, differences in the degree of flexibility to alter breeding and wintering ranges in the face of environmental change may help explain why willow flycatchers in the east have remained stable in recent decades while willow flycatchers in the southwest are endangered. Future work looking at the frequency of changes in migratory pathways within populations with different levels of specialization would test the potential link between flexibility in migratory routes and resilience to environmental change.

5 | CONCLUSIONS

The extent to which migratory animals track climate conditions across the annual cycle has important consequences for understanding the link between climate specificity and population vulnerability. Here we show that genetically distinct populations of the willow flycatcher that are declining or already endangered occupy narrow climate niches across seasons while genetically distinct populations that have remained stable in recent decades occupy broad climate niches across seasons. While increased niche specialization may help individuals defend more geographically proximate wintering locations, it may also reduce a population's flexibility to alter migratory routes in the face of global environmental change. By linking ecological genomics with population-specific migratory tracking, we provide important first step in the ability to study the process of natural selection across the annual cycle. Overall, this work highlights the value of a genomic approach to mapping migratory pathways when the goal is to understand factors that facilitate or constrain the response of locally adapted populations to rapid environmental change.

AUTHOR CONTRIBUTION

Kristen Ruegg, Mary Whitfield, Eben H. Paxton, and Thomas B. Smith conceived of the study; Rachael A. Bay assembled and annotated the genome ; Eric C. Anderson, Rachael A. Bay, and Kristen Ruegg contributed to the population genetic, Breeding Bird Survey (BBS), and landscape genetic analyses; Marius Somveille lead the climate tracking analysis; Mary Whitfield and Eben H. Paxton contributed the samples and biological expertise; Kristen Ruegg wrote the paper with contribution from all authors.

DATA AVAILABILITY STATEMENT

The Willow flycatcher genome and annotations are available through NCBI (accession number: PWAB00000000) and population-level RAD-Seq data are available through NCBI's Sequence Read Archive (http://www.ncbi.nlm.nih.gov/bioproject/453612). All codes necessary to recreate the results are available at https://doi.org/10.5281/zenodo.4656570.

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SUPPORTING INFORMATION

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

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