

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

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33 genetic analyses; M.S. lead the climate tracking analysis, M.W. and
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36

37 *Data Accessibility:* The Willow flycatcher genome and annotations are
38 available through NCBI (accession number: PWAB00000000) and
39 population-level RAD-Seq data are available through NCBI's Sequence
40 Read Archive (<http://www.ncbi.nlm.nih.gov/bioproject/453612>). All
41 code necessary to recreate the results is available at DOI:
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43

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

68 **Introduction**

69 The increasing pace of species extinctions has placed new urgency on
70 the need to understand factors regulating vulnerability to climate
71 change (Dawson et al., 2011; Pacifici et al., 2015; Urban, 2015;
72 Walther et al., 2002; Warren et al., 2013). Recent advances in the
73 field of conservation genomics support the idea that locally adapted
74 populations can vary significantly in their response to environmental
75 change, particularly when species distributions span multiple distinct
76 ecological regions (Bay et al., 2018; Chen et al., 2011; Ruegg et al.,
77 2018; Yackulic et al., 2011). A species' ecological niche, defined as
78 the sum of the habitat requirements and behaviors that allow a species
79 to persist within an environment (Grinnell, 1917), can be a key
80 predictor of how they will respond to environmental change (Thuiller
81 et al., 2005; Walther et al., 2002). For example, specialists whose
82 niches are defined by a narrow set of climate parameters are thought
83 to be more vulnerable to climate change impacts than generalists that
84 occupy a wide range of climate conditions (Clavel et al., 2011; Lurgi
85 et al., 2012; Moritz & Agudo, 2013). While species-level ecological
86 niche models are widely used to quantify niche breadth, models that
87 incorporate information below the level of species are often more
88 accurate because locally adapted populations can vary in climate
89 tolerances (Hällfors et al., 2016; Ikeda et al., 2017; Valladares et
90 al., 2014). As a result, an important and unexplored next step in
91 improving predictions of species responses to future climate change is
92 to assess the relationship between niche breadth and past demographic
93 change within locally adapted populations.

94 Recent reports suggest that 2.9 billion birds have been lost from
95 North America since the 1970s (Rosenberg et al., 2019), but reasons
96 behind such declines remain unclear. Migratory animals represent a
97 unique challenge for understanding the interaction between niche
98 breadth and population vulnerability because their highly mobile life
99 history strategies make it difficult to quantify the extent of
100 exposure to climate conditions across time and space. The ability to
101 track environmental conditions across seasons may facilitate the
102 evolution of niche specialization if natural selection occurs in

103 similar directions on breeding and wintering areas (Webster & Marra,
104 2004). Alternatively, the ability to switch niches at each stage of
105 the annual cycle may facilitate the evolution niche generalization if
106 natural selection across seasons is contrasting (Robinson et al.,
107 2009). While understanding the extent to which birds track or switch
108 their niche across seasons has important implications for
109 understanding the evolution of niche breadth, results of niche
110 tracking studies are often contradictory. Some studies suggest
111 species switch niches (Gómez et al., 2016a; Joseph & Stockwell, 2000;
112 Martínez-Meyer et al., 2004; Nakazawa et al., 2004), while others
113 suggest species track niches to varying degrees, depending on factors
114 such as range size, migration distance, and breeding latitude
115 (Boucher-Lalonde et al., 2014; Laube et al., 2015; Zurell et al.,
116 2018). A potential limitation of previous work is the focus on
117 species-level migration rather than intraspecific migration which may
118 obfuscate the extent of niche overlap across seasons if distinct
119 populations follow divergent migratory pathways and winter in
120 different areas (Ruegg & Smith, 2002; Turbek et al., 2018; but see
121 Fandos et al 2020). While previous technological limitations made
122 quantifying seasonal niche overlap below the species level
123 challenging, new methodological breakthroughs in genomics and animal
124 tracking technology have made it possible to map population-specific
125 migratory routes (Ruegg et al., 2014). Here we move beyond previous
126 work by investigating the relationship between seasonal niche overlap,
127 niche breadth, and past population declines in genetically distinct
128 populations of a migratory songbird, the willow flycatcher, *Empidonax*
129 *traillii*.

130 The willow flycatcher is an important species for exploring the
131 relationship between niche breadth and population vulnerability
132 because understanding the factors behind population declines have
133 important implications for its conservation. The willow flycatcher is
134 currently divided into four subspecies across the continental USA (SI
135 Fig. 1) which vary in status from not threatened (Pacific Northwestern
136 form, *E. t. brewsteri*; Western Central form, *E. t. adastus*; and

137 Eastern form, *E. t. traillii*) to Endangered (Southwestern form *E. t.*
138 *extimus*). The southwestern subspecies, *E.t. extimus*, was listed as
139 federally endangered following steep population declines through the
140 first half of the 20th Century (Sogge et al., 1997; Unitt, 1987) and
141 while there has been some controversy surrounding the subspecies
142 designation of the southwestern willow flycatcher (Zink, 2015), recent
143 data supports its genetic and ecological distinctiveness (Mahoney et
144 al., 2020; Theimer et al., 2016). More specifically, our previous
145 work using ecological genomics investigated the link between a suite
146 of climate and landscape variables and genome-wide genetic signatures
147 and found strong support for an association between genetic variation,
148 temperature and precipitation, but not landscape variables. In
149 particular, we found highly significant correlations between allele
150 frequencies in genes linked to thermal tolerance and the intensity of
151 summer heat waves in the southwest (Ruegg et al., 2018). Further, the
152 mismatch between current and future predicted gene-environment
153 correlations supported the idea that the Southwestern population would
154 be the most vulnerable to future climate change, but this work focused
155 exclusively on the breeding grounds. Here we expand on past work by
156 investigating the extent to which locally adapted breeding populations
157 track similar environmental conditions across seasons. Such
158 information can be used to help understand the extent to which niche
159 breadth within locally adapted populations of the willow flycatcher
160 across seasons may help explain past population declines as well as
161 future population- and subspecific-level resilience to environmental
162 change.

163 In order to investigate the relationship between realized niche
164 breadth, local adaptation, and regional population trends, we begin by
165 mapping genetically distinct populations of willow flycatcher across
166 breeding and wintering areas. We identify population structure across
167 the breeding range using an analysis of genome-wide genetic data and
168 then screen an additional 393 breeding samples and 363 wintering
169 individuals collected across breeding and wintering areas using a
170 subset of SNP markers. Using genetic stock identification methods co-

171 opted from fisheries management (Satterthwaite et al., 2015), we
172 assign wintering individuals back to their most likely breeding
173 population of origin and use the resulting assignments to build a map
174 of population-specific migratory connections. To quantify niche
175 breadth within each genetically distinct group, we then apply kernel
176 smoothers to densities of occurrences in environmental space and
177 calculate the total niche area across breeding and wintering grounds
178 as well as the extent of seasonal niche overlap (Broennimann et al.,
179 2012). Lastly, to assess the extent to which niche breadth within
180 genetically distinct populations is associated with past population
181 declines, we analyze population survey data from 1968 to 2015,
182 stratified by genetic group (Sauer et al., 2017).

183 **Materials and Methods**

184 *Sample collection and DNA extraction*

185 We compiled a collection of 931 willow flycatcher blood or tissue
186 samples, 568 samples from 37 locations across the breeding range and
187 363 samples from 64 locations across the wintering range using a
188 combination of samples from previous studies (Paxton, 2000), museum
189 donations, and new field collections (SI Tables 1 & 2). A subset of
190 175 individuals previously sequenced using RAD-seq (Ruegg et al.,
191 2018) were reanalyzed here to assess patterns of population structure
192 across the breeding range and identify a subset of genetic markers
193 that could be used for population assignment. The remaining 393
194 breeding individuals and all of the overwintering individuals were
195 genotyped at a subset of genetic markers (see below for marker
196 selection methods) to identify population-specific wintering
197 locations. DNA from all samples was purified using the Qiagen™ DNeasy
198 Blood and Tissue extraction kit and quantified using the Qubit® dsDNA
199 HS Assay kit (Thermo Fisher Scientific).

200

201 *Genome scan*

202 Genome scans were previously conducted by Ruegg et al (2018) on 219
203 individuals following the BestRAD library preparation protocol with
204 some modifications (Ali et al. 2016). After visualizing the tradeoff

205 between discarding SNPs with low coverage and discarding individuals
206 with missing genotypes using the R package `genoscapeRtools` ([DOI:
207 10.5281/zenodo.848279](https://doi.org/10.5281/zenodo.848279)) the final number of 105,000 SNPs and 175
208 individuals became the foundation for genome-wide analyses herein
209 (Code and Data available at DOI: 10.5281/zenodo.4656570). From these
210 SNPs, 289 were removed as likely paralogs due to aberrantly low
211 homozygote genotype frequencies in samples from the Interior West. A
212 further 85 SNPs that were monomorphic amongst the samples were also
213 removed. Within the remaining dataset, of 104,626 SNPs all 175
214 individuals were missing genotypes at fewer than 15.6% of SNPs and no
215 SNP was missing a genotype in more than 7.5% of individuals (mean
216 fraction of missing data=2.3%). `SNPrelate` (Zheng et al., 2012) was
217 used visualize patterns of genome-wide population structure via
218 Principal Components Analysis (SI Fig. 1). Based upon a preliminary
219 evaluation of the population clustering on PC1 and PC2, we identified
220 7 main clusters which corresponded with geography, including (SI Fig.
221 1): Pacific Northwest, White Mountain, South Southwest, Interior
222 Northwest, Kern, Southern California, and East. `SNPrelate` was then
223 used to calculate genome-wide, pairwise F_{STs} between the seven main
224 clusters.

225

226 *SNP Genotyping*

227 To select a subset of SNPs with the most power for identifying
228 individuals to genetically identifiable populations, we ranked SNPs by
229 the probability of correct assignment for different population-level
230 comparisons, following Clemento et al. (2014, p. 118; see Github
231 repository DOI: 10.5281/zenodo.4656570). To determine if the selected
232 SNPs were convertible to SNPtype Assays based on GC content and the
233 amount of flanking sequence we used the R package `SNPS2ASSAYS` (DOI:
234 10.5281/zenodo.44692435). The resulting 174 SNPs for population
235 assignment were combined with 18 climate associated SNPs from Ruegg et
236 al (2018) to increase our power for population assignment. 192 SNPs
237 were then converted into SNPtype Assays (Fluidigm Inc.) for subsequent
238 genotyping of 393 breeding individuals on a Fluidigm™ 96.96 IFC
239 controller following manufacturer guidelines. Ten SNPs that could not

240 be reliably genotyped were eliminated to yield a final panel of 182.
241 After the initial screening, the SNP panel was further reduced to a
242 set of 96 SNPs based upon the power for population assignment and the
243 96-SNP panel was screened in 363 wintering individuals (SI Table 2).
244 Individuals with < 80% of SNPs successfully genotyped were removed
245 from downstream analyses.

246

247 *Structure analysis and genoscape construction*

248 To map the geographic distribution of genetically identifiable
249 populations across the breeding range (*i.e.* create the genoscape), we
250 combined genotypes generated via the Fluidigm and RAD-Seq pipelines
251 for all 568 individuals at 182 loci and used the resulting dataset to
252 run the program STRUCTURE (Pritchard et al., 2000). We ran 5
253 replicates for K values ranging from 3-9 using the following parameter
254 values: BURNIN=50000, NUMREPS=100000. To confirm that results were
255 consistent between the Fluidigm and RAD-Seq analysis pipelines and
256 that there was no ascertainment bias associated with our SNP selection
257 procedure (Anderson, 2010), we visualized the structure results by
258 genotyping method within each sampling location (SI Fig. 2). To
259 simplify the comparison of results, the program CLUMPP (Jakobsson &
260 Rosenberg, 2007) was used to reorder the cluster labels between runs,
261 and individual q values (proportion of an individual's ancestry
262 inferred from each cluster) were plotted using the program Distruct
263 (N. A. Rosenberg, 2004).

264

265 To build the genoscape, the q values from each individual in STRUCTURE
266 were smoothed across space via a kriging algorithm and visualized as
267 transparency levels of different colors overlaid upon a base map from
268 Natural Earth (naturalearthdata.com). The results were clipped to the
269 breeding range using a shapefile (NatureServe 2012), making use of the
270 R packages *sp*, *RGDAL*, *raster*, and *TESS3* (Caye et al., 2016; Bivand et
271 al., 2014; Hijmans et al., 2020; Pebesma et al., 2020). The
272 transparency of colors within each genetic group was scaled so that
273 the highest posterior probability of membership in the group according

274 to STRUCTURE is opaque and the smallest is transparent, creating a
275 spatially-explicit map of genomic clustering, or the genoscape.

276

277 *Panel validation and identification of population-specific wintering*
278 *areas*

279 The accuracy of our baseline for assignment of individuals to the 7
280 genetically identifiable using the 96-SNP panel was evaluated via
281 *leave-one-out* cross validation in RUBIAS (Moran & Anderson, 2018). We
282 then used RUBIAS to identify the most likely breeding population of
283 origin for wintering samples. Assignments of wintering individuals
284 with high certainty (a posterior probability > 0.8) were color coded
285 by genetic group, mapped to the genoscape (with jittering to avoid
286 overprinting), and used in the downstream analysis of seasonal niche
287 breadth.

288

289 *Seasonal niche breadth and overlap*

290 We modeled the realized seasonal climatic niches of the willow
291 flycatcher as a whole as well as for each of the four main genetically
292 distinct groups (Southwest, Pacific NW, Interior West, and East)
293 separately (Code and data available at: DOI:10.5281/zenodo.4656570).
294 The three additional genetically identifiable groups in the Kern,
295 Southern CA, and the White Mountains, lacked sufficient data to
296 characterize niche breadth and were therefore removed from subsequent
297 analyses. Total niche area as well as the degree of overlap between
298 breeding and wintering grounds was calculated using the modeling
299 framework described in (Broennimann et al., 2012). Selection of
300 climate variables for the present study was directly informed by the
301 results of Ruegg et al (2018) who tested the association between 24
302 different temperature, precipitation, and landscape variables and
303 found that genetic variation across the breeding range was most
304 strongly associated with temperature and precipitation (mean
305 temperature of the coldest quarter, max temperature of the warmest
306 month, and precipitation of the driest quarter), but not landscape.
307 Because several of the climate variables in Ruegg et al (2018) were
308 specific to particular times of the year and we wanted our analysis to

309 be more generally applicable across season in temperate and tropical
310 areas (Janzen 1967), we selected more general temperature and
311 precipitation variables that were highly correlated with those used in
312 Ruegg et al (2018). More specifically, we obtained monthly
313 temperature and precipitation data from WorldClim 2.0 (Fick & Hijmans,
314 2017) for breeding months (June–August) and wintering months
315 (November–April) associated with locations of genetically assigned
316 individuals with a posterior probability > 0.8. We selected dates for
317 the wintering period based upon Koronkiewicz et al (2006), but also
318 tested the effect of narrower bounds (Dec – Feb) on the wintering
319 period to ensure that our results were robust to variation in the
320 definition of the wintering period. Climate data was extracted on a
321 grid of equal-area hexagons ~55km wide (Sahr et al., 2003), covering
322 the Western Hemisphere (>30°W). In each hexagon containing a
323 genetically identified individual, we computed the average climate
324 values and obtained summer climate by taking the mean values between
325 June and August, and winter climate by taking the mean values between
326 November and April. Seasonal temperature and precipitation were
327 normalized using the z-score across the whole of the study region
328 (i.e. Western Hemisphere). For each season (i.e., breeding and
329 wintering) and each subspecies (i.e., using only individuals
330 genetically assigned to that subspecies) as well as the entire
331 species, we estimated the realized climate niche by projecting the
332 occurrences into a climate space defined by temperature and
333 precipitation, thus obtaining a cloud of points. Following
334 Broennimann et al. (2012), we then used a kernel density function on a
335 50 x 50 pixel grid super-imposed onto the two-dimensional climate
336 space to estimate niche density. This analysis was conducted using the
337 'kde2d' function in R, with a bandwidth of 1 and only keeping the top
338 95% of the density kernel, setting the rest of the pixels to 0. To
339 assess whether these choices of parameter values influence the
340 results, we performed a sensitivity analysis of the kernel density
341 estimation. Specifically, we varied two parameters: the bandwidth of
342 the seasonal density kernel function, and the threshold above which
343 pixels of the density kernel were set to 0, and we assessed the

344 effect of the variation on the results for breeding and wintering
345 niche sizes as well as for seasonal niche overlap. Further, to assess
346 whether our results were significantly influenced by wintering ground sample size, which varies between
347 populations, we performed randomization tests in which we set the total number of samples for the
348 Pacific Northwest, the Interior Northwest and the East to $n=12$, which is the number of samples available
349 for the Southwest.

350
351 To calculate the total realized niche size as a proxy for niche breadth
352 within each subspecies, we calculated the number of pixels across climate
353 space whose density was above 0 for each season. Niche overlap within a
354 subspecies across seasons as well as between subspecies was computed
355 using Schoener's D metric, which varies between 0 (no overlap) and 1
356 (complete overlap) (Broennimann *et al.* 2012). To assess the relationship
357 between seasonal niche overlap and migration distance we calculated the
358 average migration distance as the great circle distance between the mean
359 location of breeding individuals (i.e. mean latitude and mean longitude
360 across individuals) and the mean location of wintering individuals for
361 that population. To assess the relationship between the seasonal niche
362 overlap and breeding range size we calculated the number of total number
363 of hexagons within the genetically defined breeding range of each
364 subspecies as depicted in Fig. 1.

365
366 To test whether the degree of niche tracking for each population was
367 significantly different from random, we used a niche similarity analysis
368 adapted from niche similarity tests proposed by Broennimann *et al.* (2012).
369 Specifically, we compared the observed seasonal niche overlap metric (D)
370 with seasonal niche overlap metrics simulated for alternative migration
371 destinations. This was done by shifting randomly the population's
372 breeding ground within the species' breeding range and computing the
373 resulting D metric between the observed winter niche and the breeding
374 niche of the shifted breeding ground. To shift the breeding ground, we
375 first selected an individual i randomly sampled among all the breeding
376 individuals available in our dataset. Then we selected N individuals (N
377 corresponding to the observed number of breeding individuals for that

378 population) using the probability of being sampled $P_s = 1/\text{rank}(d_{iN_j})^2$, where
379 N_j is individual j among the N individuals sampled; d_{iN_j} is the great
380 circle distance between individual i and individual N_j ; and $\text{rank}(d_{iN_j})$ is
381 the rank of d_{iN_j} among all d_{iN} . This sampling procedure ensures that the
382 breeding individuals sampled are clustered together in space to form a
383 realistic simulated breeding ground of the population. We shifted the
384 breeding ground of populations while keeping their wintering ground as
385 observed because (i) the wintering range of Willow Flycatcher is much
386 more restricted than its breeding range and contains a significantly
387 smaller pool of individuals to sample from, and (ii) it follows how
388 observed migratory connectivity was determined, i.e. by assigning
389 wintering individuals to genetically distinct populations on the
390 breeding ground. We repeated the procedure of shifting the population's
391 breeding ground 1000 times, each time recording the simulated D metric.
392 To assess statistical significance, i.e. whether the population is
393 tracking its climatic niche more than random, we computed a p-value
394 investigating whether the observed niche overlap D_{obs} is higher than 95%
395 of the simulated niche overlaps D_{sim} . We also calculated the standardized
396 effect size $E_D = \frac{D_{obs} - \text{mean}(D_{sim})}{\text{sd}(D_{sim})}$ associated with the p-value.

397

398 *Demographic analysis*

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

409

410 To estimate trends in relative abundance since 1968, we used the
 411 Bayesian hierarchical model presented in Link and Sauer (2002). This
 412 model includes a random effect to account for observer bias. Link and
 413 Sauer used physiographic 'strata' as regional units within which they
 414 calculate abundance indices and populations trends. We substituted
 415 these strata with our four genetically-informed populations. The BBS
 416 data is then fit using Markov chain Monte Carlo methods and abundance
 417 indices and trends are calculated from the model's parameters.

418
 419 Annual stratum-specific abundance index (n) in strata i at time t is
 420 estimated as:

$$421 \quad n_{i,t} = z_i \exp(S_i + \beta_i(t - t^*) + \gamma_{i,t})$$

422
 423 where S_i , β_i , and $\gamma_{i,t}$ are the intercept, slope, and year effects for a
 424 particular stratum and z_i is the proportion of routes on which the
 425 species has been observed. This metric cannot be compared across
 426 stratum, but indices for stratum totals can be calculated by
 427 multiplying by the stratum area ($N_{i,t} = A_{i,t}n_{i,t}$). To obtain an overall
 428 abundance index, we summed stratum totals across the four populations,
 429 assuming that contributions from very small genetic populations would
 430 be negligible.

431
 432
 433 Population trend for each population as well as for the whole species
 434 is calculated as $100(B_i - 1) \%$ between 1968 (t_a) and 2015 (t_b):

$$435 \quad B_i = \left\{ \frac{N_{i,t_b}}{N_{i,t_a}} \right\}^{1/(t_b - t_a)}$$

436 437 438 **Results**

439 *Genome-wide population genetic structure*

440 PCA analysis of 175 breeding individuals at 104,626 SNP loci revealed
 441 support for genetic differentiation between the 4 main subspecies, *E.*
 442 *t. extimus* (Southwest), *E. t. brewsteri* (Pacific Northwest), *E. t.*

443 *adastus* (Interior Northwest), and *E. t. trailli* (East; SI Fig. 1).
444 Further, our analysis supports the existence of sub-differentiation
445 within the currently defined range of *E. t. extimus*, with the White
446 Mountains, Kern, San Diego and being more closely aligned with *E. t.*
447 *brewsteri* and *E. t. adastus* than the remainder of the Southwest (SI
448 Fig. 1). Because downstream genoscape construction was based on a
449 subset of highly divergent SNPS which do necessarily not reflect
450 genome wide patterns of gene flow, we calculated pairwise F_{ST} between
451 the seven groups apparent within the PCA using the genome-wide data.
452 Pairwise F_{ST} analyses suggest that highest degree of genetic divergence
453 was between the East and all other pairwise comparisons (Table 1; F_{ST}
454 range = 0.064 - 0.09), apart from between East and Interior Northwest
455 which was lower ($F_{ST} = 0.036$). Comparisons between the White Mountains
456 and the Southwest ($F_{ST} = 0.067$), Kern and the Southwest ($F_{ST} = 0.066$),
457 and the White Mountains versus Kern and Southern California ($F_{ST} =$
458 0.058 and 0.059, respectively) were the next most divergent. The
459 Southwest was also strongly differentiated from the Pacific Northwest
460 and to a lesser degree the Interior Northwest ($F_{ST} = 0.059$ and 0.048,
461 respectively), with the lowest levels of divergence found between the
462 Interior Northwest and all other pairwise comparisons (F_{ST} range =
463 0.009 - 0.032).

464 *Structure analysis and genoscape construction*

466 The willow flycatcher genoscape for this study was created using a
467 subset of SNPs specifically designed to accentuate groups of
468 individuals within geographic areas that are genetically
469 distinguishable from other genetically groups for the purpose of
470 linking wintering breeding populations, and therefore the groupings
471 within the genoscape do not necessarily reflect historic patterns of
472 gene flow across the genome. While our STRUCTURE analysis revealed
473 that a K value of 4, 5, 6, and 7 populations were biologically
474 realistic hypotheses for the number of groups within the species (SI
475 Fig. 2), the goal of our analysis was not to find the most likely
476 value of K, but to identify spatially explicit genetic groups that
477 could be tracked across the full annual cycle, similar to fisheries

478 stock management (McKinney et al., 2019). Thus, we set the number of
479 groups to 7 based on concordance between spatially informative genetic
480 clusters identified in the genome-wide PCA (SI Fig. 1), the STRUCTURE
481 runs based on a limited set of loci (Fig. 1), and the power to assign
482 individuals to groups at $k=7$ using RUBIAS (SI Table 1). The 7
483 genetically distinguishable groups, 4 of which were roughly concordant
484 with previously defined subspecies boundaries, were distributed across
485 North America as follows (Fig. 1): Pacific Northwest (green, 1 - 3)
486 corresponded with *E. t. brewsteri*, Kern (red, 4) fell within the
487 current boundary for *E. t. extimus*, Southern California (yellow, 6 and
488 7) fell within the current boundary for *E. t. extimus*, Interior
489 Northwest (purple, 8-18) fell within the current boundary for *E. t.*
490 *adastus*, Southwest (orange, 19-27), White Mountain (sky blue, 28) fell
491 within the current boundary for *E. t. extimus* and East (dark blue, 29-
492 37) fell within the current boundary for *E. t. trailli*. From here on
493 we will refer to genetic groups by their geographic rather than
494 subspecies name unless a direct comparison with the subspecies is
495 needed. Sampling location 5, Owen's River at Bishop, did not fall
496 clearly into any one genetic cluster and rather represented a mixture
497 between Interior Northwest, Southern California, and Southwestern
498 groups. Further, a comparison between genetic assignments generated
499 using SNPs from the RADseq and Fluidigm pipelines were concordant
500 suggesting no significant ascertainment bias associated with SNP sub-
501 setting (SI Fig. 2).

502

503 *Identification of population specific wintering areas*

504 Leave-one-out cross validation of our genetic baseline in RUBIAS
505 revealed that the power to assign individuals to groups was high, with
506 the Pacific Northwest having the highest probability of correct
507 assignment (99.7%), followed by the Southwest (98.6%), the East
508 (97.5%), the Interior West (91%), the Kern (80%) and Southern
509 California (78%), and the White Mountains (70%) (SI Table 3). The
510 majority of the incorrect assignments in the White Mountains were to
511 the surrounding populations in the Southwest, while the majority of
512 the incorrect assignments in Southern California and the Kern were

513 from neighboring populations in the Kern and Pacific Northwest,
514 respectively. Higher mis-assignment rates in the Kern, Southern
515 California and the White Mountains are likely due to admixture with
516 neighboring groups, indicating these may be areas of hybridization
517 between subspecies. Subsequent assignment of wintering individuals to
518 genetically distinct breeding groups using RUBIAS indicated that
519 Pacific Northwest birds winter from western Mexico to Costa Rica,
520 Interior West breeders winter from Guatemala south to Panama, Eastern
521 breeders winter from Costa Rica to Ecuador, and Southwestern breeders
522 are restricted to Costa Rica and Nicaragua (Fig. 1b; SI Table 2). We
523 did not detect any Kern, White Mountain, or Southern California
524 breeders on their wintering grounds which is not surprising given the
525 low population sizes in those regions and the correspondingly low
526 probability of detection outside of the breeding range.

527

528 *Seasonal climate niche breadth and overlap*

529 An analysis of seasonal climate niche breadth revealed that while breeding niches within the willow
530 flycatcher are similar in size, wintering niches sizes are more variable (Fig. 2; Table 2). Specifically, the
531 wintering niche of the Eastern group is around twice as large the wintering niche of the Southwest and
532 Pacific Northwest group (Fig. 2; Table 2). This is mainly driven by long-distance migratory individuals
533 of the Eastern group found as far south as Ecuador, generating wide variation along the precipitation axis.
534 We acknowledge that sampling gaps on the wintering grounds limit our ability to fully characterize the
535 wintering niche of Interior Northwest and Eastern populations which likely winter in unsampled areas of
536 the northern Andes. This being the case, we also acknowledge that inclusion of additional samples from
537 these regions would either maintain or increase the wintering niche size for each of these groups and
538 would not significantly change the interpretation of our results. Calculation of niche overlap revealed that
539 while the willow flycatcher as a species tracked its climate niche rather closely throughout the year
540 (Schoener's $D = 0.53$; Fig. 2d; Table 2), there was variation in the amount of niche overlap below the
541 species level. In particular, the Southwestern group demonstrated the highest niche overlap between
542 breeding and wintering areas (Schoener's $D = 0.65$; Fig. 2d; Table 2), the Eastern group demonstrated the
543 lowest niche overlap across seasons (Schoener's $D = 0.06$), and the Interior Northwest and Pacific
544 Northwest groups fell in between the upper and lower extremes (Schoener's $D = 0.22$ for both). These
545 results were robust to variations in parameter values associated with the kernel density estimation (SI Fig
546 3a), as well as to variations in boundaries set on the length of the wintering period (SI Fig 4). Further

547 randomization tests in the Pacific Northwest, Interior West, and East confirmed that niche overlap was
548 not significantly influence by wintering ground sample size (SI Fig 3b).

549
550 Comparison of niche breadth (calculated as the total niche area on breeding and wintering grounds) to the
551 degree of niche overlap revealed an inverse relationship, with higher niche overlap between breeding and
552 wintering areas found in populations with lower overall niche breadth like the Southwest (Table 2). In
553 addition, migration distance and breeding range size also varied by genetic group, with migration distance
554 and the breeding range being inversely correlated to the degree of seasonal niche overlap across genetic
555 groups (Table 2; SI Fig. 5a&b). In addition, niche similarity tests show that the southwest population is
556 tracking its climatic niche throughout the year better than random given the availability of climate across
557 the species distribution (Table 2). However, the niche similarity tests also show that the three other
558 populations are not significantly tracking their climatic niche throughout the year, and have negative
559 effect sizes. The east and interior northwest populations in particular have relatively high negative effect
560 sizes indicating that they tend to be closer to being niche switchers rather than niche trackers, while the
561 interior west population falls somewhere in between.

562

563 *Demographic analysis*

564 Overall, the demographic analysis revealed that while the species as a
565 whole has been declining, abundance trends vary by genetically
566 distinct group. In particular, a comparison in the % change between
567 1968 and 2015 suggests that while species as a whole has declined
568 slightly (-1.26, CI: -1.60% to -0.94%), there has been no significant
569 change in the Eastern population (0.36%, CI -0.02% to 0.75%), a
570 significant decrease in the Interior NW (-1.83%, CI -2.50% to -1.16%)
571 and the Pacific NW (-2.01%, CI: -2.53 to -1.51%), and no detectable
572 difference in the endangered Southwestern group which had already
573 declined prior to the start of the survey in 1968 (Fig. 2c). A
574 comparison between population trends and niche breadth support the
575 idea that groups with narrower niches across seasons have been
576 declining more dramatically or, in the case of the Southwest group had
577 previously declined to the point of being federally endangered, while
578 groups with broader niche across seasons have remained stable.

579

580 **Discussion**

581

582 Recent research suggests over ~2.9 billion birds have been lost from North America since the 1970's
583 (Rosenberg et al., 2019), representing a staggering and largely unexplained loss of biological diversity.
584 While advances in migrant tracking technology have provided new insights into geographic regions
585 important to population declines in some migratory birds (Kramer et al., 2018), we still lack basic
586 knowledge of how fundamental aspects of avian ecology may interact with other stressors to promote
587 resiliency to environmental change. Here we demonstrate how mapping niche breadth
588 across seasons within genetically distinct populations of a migratory
589 bird yields important insights into the relationship between climate
590 specificity and threatened status. Our results show that genetically
591 distinct populations of the willow flycatcher with narrower total
592 climate niches demonstrate high climate niche overlap between breeding
593 and wintering areas, while genetically distinct populations with
594 broader total niches have low climate niche overlap across seasons.
595 Remarkably, when paired with population-specific demographic trend
596 data since the late 1960s, we find that populations with narrower
597 climate niches across seasons are already endangered or steeply
598 declining, while populations with broader climate niches across
599 seasons have remained stable in recent decades; a pattern that would
600 have been masked by a species-level only analysis. While further work
601 across species and populations is needed to assess the generality of
602 our findings, this work highlights the importance of quantifying niche
603 breadth within species across the annual cycle when attempting to
604 understand the factors that facilitate or constrain the response of
605 locally adapted migratory populations to rapid environmental change.

606

607 *Niche tracking and ecological divergence across seasons*

608 Climate niche tracking across seasons provides the potential for the
609 evolution of specialization to a narrow set of climate optima, but
610 such hypotheses are difficult to investigate in migratory animals
611 without genetic and tracking data below the level of species. We use a
612 genome-wide genetic approach to quantifying breeding and wintering
613 climate niches in the willow flycatcher and find that while the
614 species as a whole occupies a broad breeding niche with relatively
615 high levels of seasonal niche tracking, the degree of niche tracking

616 within genetically distinct populations increases with increasing
617 climate specialization. In particular, the Southwestern group has the
618 smallest total niche breadth and the highest degree of seasonal niche
619 overlap, while the Eastern group has the broadest total niche and the
620 lowest degree of seasonal niche overlap. When combined with previous
621 work showing that genome-wide genetic variation is more strongly tied
622 to climate in the southwest than in the east (Ruegg et al., 2018), our
623 results point to the idea that intraspecific variation in the extent
624 of climate niche tracking across seasons may accelerate the process of
625 ecological specialization in some groups, while promoting ecological
626 generalization in others. The work presented here represents an
627 important first step towards studying the process of natural selection
628 across the annual cycle by providing a framework for understanding the
629 extent to which genetically distinct breeding populations are exposed
630 to similar or contrasting environmental conditions on their breeding
631 and wintering grounds.

632
633 In addition to providing a framework for understanding the
634 relationship between niche tracking and local adaptation, the
635 increased clarity provided by our population-level analysis of niche
636 tracking suggests that mixed evidence regarding the extent to which
637 species track or switch their niche across seasons may in part be due
638 to a failure to match the appropriate tracking tool with the spatial
639 scale of the question. On one end of the spectrum, species level
640 analyses may be too coarse in scale to quantify niche breadth when
641 genetically distinct populations vary in climate tolerances (Boucher-
642 Lalonde et al., 2014; Gómez et al., 2016b; Joseph & Stockwell, 2000;
643 Laube et al., 2015; Martínez-Meyer et al., 2004; Nakazawa et al.,
644 2004; Zurell et al., 2018). On the other end of the spectrum, fine
645 scale movement data provided by GPS tags (Fandos et al., 2020) may
646 lack the genetic backdrop necessary identify how individual movements
647 fit within the context of locally adapted populations. Alternatively,
648 our results suggest that a genomic approach to mapping seasonal
649 climate niches can illuminate key linkages between climate tracking,
650 local adaptation, and niche breadth that can be used to help shed

651 light on the evolution of climate specialization across the annual
652 cycle.

653

654 *Niche breadth and vulnerability to climate change*

655 The willow flycatcher is an excellent model for exploring the relationship between niche breadth and
656 population level vulnerability to climate change because past work provides support for the existence of
657 local adaptation to climate across the breeding range (Ruegg et al 2018), but the present study provides
658 the first demonstration of a method for quantifying the climate niche of locally adapted populations across
659 breeding and wintering grounds. Thuiller (2005) highlights four main hypotheses regarding which groups
660 should be more sensitive to climate change, including groups with: (1) marginal distributions outside of
661 the mean climate conditions (Swihart et al 2003), (2) narrow niche breadth (specialist species) (Brown
662 1995), (3) restricted distributions (Johnson et al 1998), and (4) distributions within regions strongly
663 exposed to climate change. Here we find that the endangered southwestern willow flycatcher fits all 4
664 climate sensitivity criteria – previous work demonstrated that genetic diversity is significantly associated
665 with climate variables that fall outside of the mean climate conditions (Ruegg et al 2018; Figure 2a), its
666 highly fragmented breeding range is at the edge of the species distribution where the intensity of summer
667 heat waves is most pronounced (Smith et al., 2013), and here we show it has the narrowest total niche
668 breadth of the 4 main genetic groups across breeding and wintering grounds. In contrast, the Eastern
669 population of the willow flycatcher demonstrates the characteristics of a climate resilient population –
670 previous work demonstrated that genetic diversity is significantly associated with mean climate variables
671 (Ruegg et al 2018; Figure 2a), its broad, northern distribution is predicted to be less susceptible to intense
672 summer heat waves (Smith et al, 2013), and here we show it has the broadest total niche breadth of the 4
673 main groups across seasons. As a result, sensitivity to climate change may help explain why population
674 numbers have remained low in the southwest, despite concentrated recovery efforts over the last decade,
675 while population numbers in the east have not changed significantly. Indeed, while we only have 4
676 populations and cannot test whether the relationship between niche breadth and population trends are
677 statistically significant, it remains striking that across the four main groups where niche breadth could be
678 calculated, we see a trend toward steeper declines or, in the case of the already endangered southwestern
679 willow flycatcher, greater vulnerability, with increasing climate specialization. The trend towards greater
680 vulnerability to climate change in the southwestern willow flycatcher mirrors the results from Ruegg et al
681 (2018) which predicted significantly higher mismatches between current and future gene-environment
682 relationships in the southwestern population. Thus, in combination with other anthropogenic disturbances
683 such as loss of critical breeding habitat, having a narrow range of climate optima may further exacerbate
684 losses in already vulnerable populations. Overall, this work more generally highlights the importance of

685 understanding the extent of climate specificity within genetically distinct populations across time and
686 space when attempting to prioritize conservation in a rapidly changing world. Future work will focus on
687 assessing the relationship between niche breadth and population trends in a multi-species comparative
688 framework in order to test the generality of patterns observed herein.

689
690 In addition to helping clarify the degree of climate specialization
691 across breeding and wintering grounds, a genomic approach to niche
692 tracking can also provide insights into the capacity for populations
693 to shift the location of breeding and wintering ranges in response to
694 climate change. Comparative analyses across many species using range
695 maps suggest that the extent to which birds track their niche between
696 breeding and wintering ranges depends largely on factors such as range
697 size, habitat specificity, and migration distance (Somveille et al.,
698 2019; Zurell et al., 2018). Here we find that niche breadth increases
699 with migration distance and breeding range size, supporting hypotheses
700 raised by Somveille et al (2019) that where birds migrate may result
701 from tradeoffs between the degree of specialization, the cost of
702 migration, and the availability of resources. Thus, while specialized
703 populations like the southwestern willow flycatcher may outcompete
704 generalists like the Eastern willow flycatcher for geographically
705 closer wintering ranges, this may come at the cost of reduced
706 flexibility to alter their ranges in the face of rapid environmental
707 change. In turn, while the Eastern willow flycatcher may have greater
708 access to resources in more southern wintering ranges as well as
709 greater flexibility in climate tolerances across the annual cycle,
710 this flexibility may come at the cost of a longer migratory journey.
711 Overall, differences in the degree of flexibility to alter breeding
712 and wintering ranges in the face of environmental change may help
713 explain why willow flycatchers in the east have remained stable in
714 recent decades while willow flycatchers in the southwest are
715 endangered. Future work looking at the frequency of changes in
716 migratory pathways within populations with different levels of
717 specialization would test the potential link between flexibility in
718 migratory routes and resilience to environmental change.

719
720 *Conclusions*

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

738
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753

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947 **Figure Legends**

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949 **Figure 1. Willow Flycatcher Genoscape.** Population genetic structure
950 in Willow Flycatchers across the breeding grounds and corresponding
951 population specific wintering locations. A) STRUCTURE analysis
952 revealed support for the existence of 7 genetically distinct groups
953 across the breeding range. Numbers at the top of the STRUCTURE plot
954 correspond to locations on map and in Table 1. Numbers in the SSW
955 population are not consecutive because data generated using RADseq and
956 SNP genotyping were lumped together to test for consistent results (SI
957 Figure 2). B) The posterior probability of group membership from
958 STRUCTURE was visualized as transparency levels of different colors
959 overlaid upon a base map from Natural Earth (naturalearthdata.com) and
960 clipped to the species breeding range using a shapefile (NatureServe
961 2012). Wintering individuals are color coded based upon assignments
962 to breeding group using the program RUBIAS. Points on the wintering
963 grounds are jiggered for visualization purposes. Wintering sample
964 location details and associated assignments can be found in SI Table
965 1.

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968 **Figure 2. Realized Climate Niche and Population Trends for the Willow**969 **Flycatcher.** A) Maps of the sampling distribution for the species and

970 each of the 4 main genetically defined groups separately. Geographic

971 regions on the breeding grounds were defined according the genoscape

972 map in Figure 1. Triangles indicate samples that were identified to

973 each genetically distinct group, but fell outside of the genoscape

974 boundaries, while circles fell within the genoscape boundaries. B)

975 The realized climate niche occupied by each group on its breeding and

976 wintering range as well as across both seasons. C) Demographic

977 trends estimated with BBS data showing declines in the Pacific NW and

978 Interior NW, but no significant change in the East. The Endangered

979 Southwestern group is reported to have declined prior to the start of

980 the survey. D) Niche overlap for the species as well as each

981 genetically distinct group.

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Table 1. Pairwise genome-wide F_{ST} between genetically distinct groups calculated with all 105,000 SNP loci. Numbers after population names refer to location in Figure 1 and details in SI Table 1.

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 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 methods for details), niche overlap has no unit and vary between 0–1, migration distance is measured in km, and range size is measured in number of occupied hexagons (see methods 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 methods 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*



