

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

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29  
30 *Data Accessibility:* The Willow flycatcher genome and annotations are available through NCBI  
31 (accession number: PWAB00000000) and population-level RAD-Seq data are available through NCBI's  
32 Sequence Read Archive (<http://www.ncbi.nlm.nih.gov/bioproject/453612>). All code necessary to  
33 recreate the results is available at DOI: 10.5281/zenodo.4656570.

34

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

## 51 **Introduction**

52 The increasing pace of species extinctions has placed new urgency on the need to understand factors  
53 regulating vulnerability to climate change (Dawson et al., 2011; Pacifici et al., 2015; Urban, 2015;  
54 Walther et al., 2002; Warren et al., 2013). Recent advances in the field of conservation genomics support  
55 the idea that locally adapted populations can vary significantly in their response to environmental change,  
56 particularly when species distributions span multiple distinct ecological regions (Bay et al., 2018; Chen et  
57 al., 2011; Rugg et al., 2018; Yackulic et al., 2011). A species' ecological niche, defined as the sum of  
58 the habitat requirements and behaviors that allow a species to persist within an environment (Grinnell,  
59 1917), can be a key predictor of how they will respond to environmental change (Thuiller et al., 2005;  
60 Walther et al., 2002). For example, specialists whose niches are defined by a narrow set of climate  
61 parameters are thought to be more vulnerable to climate change impacts than generalists that occupy a  
62 wide range of climate conditions (Clavel et al., 2011; Lurgi et al., 2012; Moritz & Agudo, 2013). While  
63 species-level ecological niche models are widely used to quantify niche breadth, models that incorporate  
64 information below the level of species are often more accurate because locally adapted populations can  
65 vary in climate tolerances (Hällfors et al., 2016; Ikeda et al., 2017; Valladares et al., 2014). As a result,  
66 an important and unexplored next step in improving predictions of species responses to future climate  
67 change is to assess the relationship between niche breadth and past demographic change within locally

68 adapted populations.

69 Recent reports suggest that 2.9 billion birds have been lost from North America since the 1970s  
70 (Rosenberg et al., 2019), but reasons behind such declines remain unclear. Migratory animals represent a  
71 unique challenge for understanding the interaction between niche breadth and population vulnerability  
72 because their highly mobile life history strategies make it difficult to quantify the extent of exposure to  
73 climate conditions across time and space. The ability to track environmental conditions across seasons  
74 may facilitate the evolution of niche specialization if natural selection occurs in similar directions on  
75 breeding and wintering areas (Webster & Marra, 2004). Alternatively, the ability to switch niches at each  
76 stage of the annual cycle may facilitate the evolution niche generalization if natural selection across  
77 seasons is contrasting (Robinson et al., 2009). While understanding the extent to which birds track or  
78 switch their niche across seasons has important implications for understanding the evolution of niche  
79 breadth, results of niche tracking studies are often contradictory. Some studies suggest species switch  
80 niches (Gómez et al., 2016a; Joseph & Stockwell, 2000; Martínez-Meyer et al., 2004; Nakazawa et al.,  
81 2004), while others suggest species track niches to varying degrees, depending on factors such as range  
82 size, migration distance, and breeding latitude (Boucher-Lalonde et al., 2014; Laube et al., 2015; Zurell et  
83 al., 2018). A potential limitation of previous work is the focus on species-level migration rather than  
84 intraspecific migration which may obfuscate the extent of niche overlap across seasons if distinct  
85 populations follow divergent migratory pathways and winter in different areas (Ruegg & Smith, 2002;  
86 Turbek et al., 2018; but see Fandos et al 2020). While previous technological limitations made  
87 quantifying seasonal niche overlap below the species level challenging, new methodological  
88 breakthroughs in genomics and animal tracking technology have made it possible to map population-  
89 specific migratory routes (Ruegg et al., 2014). Here we move beyond previous work by investigating the  
90 relationship between seasonal niche overlap, niche breadth, and past population declines in genetically  
91 distinct populations of a migratory songbird, the willow flycatcher, *Empidonax traillii*.

92 The willow flycatcher is an important species for exploring the relationship between niche breadth and  
93 population vulnerability because understanding the factors behind population declines have important  
94 implications for its conservation. The willow flycatcher is currently divided into four subspecies across  
95 the continental USA (SI Fig. 1) which vary in status from not threatened (Pacific Northwestern form, *E. t.*  
96 *brewsteri*; Western Central form, *E. t. adastus*; and Eastern form, *E. t. traillii*) to Endangered  
97 (Southwestern form *E. t. extimus*). The southwestern subspecies, *E.t. extimus*, was listed as federally  
98 endangered following steep population declines through the first half of the 20th Century (Sogge et al.,  
99 1997; Unitt, 1987) and while there has been some controversy surrounding the subspecies designation of  
100 the southwestern willow flycatcher (Zink, 2015), recent data supports its genetic and ecological

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

114 In order to investigate the relationship between realized niche breadth, local adaptation, and regional  
115 population trends, we begin by mapping genetically distinct populations of willow flycatcher across  
116 breeding and wintering areas. We identify population structure across the breeding range using an  
117 analysis of genome-wide genetic data and then screen an additional 393 breeding samples and 363  
118 wintering individuals collected across breeding and wintering areas using a subset of SNP markers.  
119 Using genetic stock identification methods co-opted from fisheries management (Satterthwaite et al.,  
120 2015), we assign wintering individuals back to their most likely breeding population of origin and use the  
121 resulting assignments to build a map of population-specific migratory connections. To quantify niche  
122 breadth within each genetically distinct group, we then apply kernel smoothers to densities of occurrences  
123 in environmental space and calculate the total niche area across breeding and wintering grounds as well as  
124 the extent of seasonal niche overlap (Broennimann et al., 2012). Lastly, to assess the extent to which  
125 niche breadth within genetically distinct populations is associated with past population declines, we  
126 analyze population survey data from 1968 to 2015, stratified by genetic group (Sauer et al., 2017).

## 127 **Materials and Methods**

### 128 *Sample collection and DNA extraction*

129 We compiled a collection of 931 willow flycatcher blood or tissue samples, 568 samples from 37  
130 locations across the breeding range and 363 samples from 64 locations across the wintering range using a  
131 combination of samples from previous studies (Paxton, 2000), museum donations, and new field  
132 collections (SI Tables 1 & 2). A subset of 175 individuals previously sequenced using RAD-seq (Ruegg  
133 et al., 2018) were reanalyzed here to assess patterns of population structure across the breeding range and

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

139

#### 140 *Genome scan*

141 Genome scans were previously conducted by Ruegg et al (2018) on 219 individuals following the  
142 BestRAD library preparation protocol with some modifications (Ali *et al.* 2016). After visualizing the  
143 tradeoff between discarding SNPs with low coverage and discarding individuals with missing genotypes  
144 using the R package *genoscapeRtools* (DOI: [10.5281/zenodo.848279](https://doi.org/10.5281/zenodo.848279)) the final number of 105,000 SNPs  
145 and 175 individuals became the foundation for genome-wide analyses herein (Code and Data available at  
146 DOI: [10.5281/zenodo.4656570](https://doi.org/10.5281/zenodo.4656570)). From these SNPs, 289 were removed as likely paralogs due to  
147 aberrantly low homozygote genotype frequencies in samples from the Interior West. A further 85 SNPs  
148 that were monomorphic amongst the samples were also removed. Within the remaining dataset, of  
149 104,626 SNPs all 175 individuals were missing genotypes at fewer than 15.6% of SNPs and no SNP was  
150 missing a genotype in more than 7.5% of individuals (mean fraction of missing data=2.3%). *SNPrelate*  
151 (Zheng et al., 2012) was used visualize patterns of genome-wide population structure via Principal  
152 Components Analysis (SI Fig. 1). Based upon a preliminary evaluation of the population clustering on  
153 PC1 and PC2, we identified 7 main clusters which corresponded with geography, including (SI Fig. 1):  
154 Pacific Northwest, White Mountain, South Southwest, Interior Northwest, Kern, Southern California, and  
155 East. *SNPrelate* was then used to calculate genome-wide, pairwise  $F_{STs}$  between the seven main clusters.

156

#### 157 *SNP Genotyping*

158 To select a subset of SNPs with the most power for identifying individuals to genetically identifiable  
159 populations, we ranked SNPs by the probability of correct assignment for different population-level  
160 comparisons, following Clemento et al. (2014, p. 118; see Github repository DOI:  
161 [10.5281/zenodo.4656570](https://doi.org/10.5281/zenodo.4656570)). To determine if the selected SNPs were convertible to SNPtype Assays based  
162 on GC content and the amount of flanking sequence we used the R package *SNPS2ASSAYS* (DOI:  
163 [10.5281/zenodo.44692435](https://doi.org/10.5281/zenodo.44692435)). The resulting 174 SNPs for population assignment were combined with 18  
164 climate associated SNPs from Ruegg et al (2018) to increase our power for population assignment. 192  
165 SNPs were then converted into SNPtype Assays (Fluidigm Inc.) for subsequent genotyping of 393  
166 breeding individuals on a Fluidigm™ 96.96 IFC controller following manufacturer guidelines. Ten SNPs  
167 that could not be reliably genotyped were eliminated to yield a final panel of 182. After the initial

168 screening, the SNP panel was further reduced to a set of 96 SNPs based upon the power for population  
169 assignment and the 96-SNP panel was screened in 363 wintering individuals (SI Table 2). Individuals  
170 with < 80% of SNPs successfully genotyped were removed from downstream analyses.

171

#### 172 *Structure analysis and genoscape construction*

173 To map the geographic distribution of genetically identifiable populations across the breeding range (*i.e.*  
174 create the genoscape), we combined genotypes generated via the Fluidigm and RAD-Seq pipelines for all  
175 568 individuals at 182 loci and used the resulting dataset to run the program STRUCTURE (Pritchard et  
176 al., 2000). We ran 5 replicates for K values ranging from 3-9 using the following parameter values:  
177 BURNIN=50000, NUMREPS=100000. To confirm that results were consistent between the Fluidigm and  
178 RAD-Seq analysis pipelines and that there was no ascertainment bias associated with our SNP selection  
179 procedure (Anderson, 2010), we visualized the structure results by genotyping method within each  
180 sampling location (SI Fig. 2). To simplify the comparison of results, the program CLUMPP (Jakobsson  
181 & Rosenberg, 2007) was used to reorder the cluster labels between runs, and individual *q* values  
182 (proportion of an individual's ancestry inferred from each cluster) were plotted using the program  
183 Distruct (N. A. Rosenberg, 2004).

184

185 To build the genoscape, the *q* values from each individual in STRUCTURE were smoothed across space  
186 via a kriging algorithm and visualized as transparency levels of different colors overlaid upon a base map  
187 from Natural Earth (naturalearthdata.com). The results were clipped to the breeding range using a  
188 shapefile (NatureServe 2012), making use of the R packages *sp*, *RGDAL*, *raster*, and *TESS3* (Caye et al.,  
189 2016; Bivand et al., 2014; Hijmans et al., 2020; Pebesma et al., 2020). The transparency of colors within  
190 each genetic group was scaled so that the highest posterior probability of membership in the group  
191 according to STRUCTURE is opaque and the smallest is transparent, creating a spatially-explicit map of  
192 genomic clustering, or the genoscape.

193

#### 194 *Panel validation and identification of population-specific wintering areas*

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

201

202 *Seasonal niche breadth and overlap*

203 We modeled the realized seasonal climatic niches of the willow flycatcher as a whole as well as for each  
204 of the four main genetically distinct groups (Southwest, Pacific NW, Interior West, and East) separately  
205 (Code and data available at: DOI:10.5281/zenodo.4656570). The three additional genetically identifiable  
206 groups in the Kern, Southern CA, and the White Mountains, lacked sufficient data to characterize niche  
207 breadth and were therefore removed from subsequent analyses. Total niche area as well as the degree of  
208 overlap between breeding and wintering grounds was calculated using the modeling framework described  
209 in (Broennimann et al., 2012). Selection of climate variables for the present study was directly informed  
210 by the results of Ruegg et al (2018) who tested the association between 24 different temperature,  
211 precipitation, and landscape variables and found that genetic variation across the breeding range was most  
212 strongly associated with temperature and precipitation (mean temperature of the coldest quarter, max  
213 temperature of the warmest month, and precipitation of the driest quarter), but not landscape. Because  
214 several of the climate variables in Ruegg et al (2018) were specific to particular times of the year and we  
215 wanted our analysis to be more generally applicable across season in temperate and tropical areas (Janzen  
216 1967), we selected more general temperature and precipitation variables that were highly correlated with  
217 those used in Ruegg et al (2018). More specifically, we obtained monthly temperature and precipitation  
218 data from WorldClim 2.0 (Fick & Hijmans, 2017) for breeding months (June–August) and wintering  
219 months (November–April) associated with locations of genetically assigned individuals with a posterior  
220 probability > 0.8. We selected dates for the wintering period based upon Koronkiewicz et al (2006), but  
221 also tested the effect of narrower bounds (Dec – Feb) on the wintering period to ensure that our results  
222 were robust to variation in the definition of the wintering period. Climate data was extracted on a grid of  
223 equal-area hexagons ~55km wide (Sahr et al., 2003), covering the Western Hemisphere (>30°W). In each  
224 hexagon containing a genetically identified individual, we computed the average climate values and  
225 obtained summer climate by taking the mean values between June and August, and winter climate by  
226 taking the mean values between November and April. Seasonal temperature and precipitation were  
227 normalized using the z-score across the whole of the study region (i.e. Western Hemisphere). For each  
228 season (i.e., breeding and wintering) and each subspecies (i.e., using only individuals genetically assigned  
229 to that subspecies) as well as the entire species, we estimated the realized climate niche by projecting the  
230 occurrences into a climate space defined by temperature and precipitation, thus obtaining a cloud of  
231 points. Following Broennimann *et al.* (2012), we then used a kernel density function on a 50 x 50 pixel  
232 grid super-imposed onto the two-dimensional climate space to estimate niche density. This analysis was  
233 conducted using the ‘kde2d’ function in R, with a bandwidth of 1 and only keeping the top 95% of the  
234 density kernel, setting the rest of the pixels to 0. To assess whether these choices of parameter values  
235 influence the results, we performed a sensitivity analysis of the kernel density estimation. Specifically,

236 we varied two parameters: the bandwidth of the seasonal density kernel function, and the threshold above  
237 which pixels of the density kernel were set to 0, and we assessed the effect of the variation on the results  
238 for breeding and wintering niche sizes as well as for seasonal niche overlap. Further, to assess whether  
239 our results were significantly influenced by wintering ground sample size, which varies between  
240 populations, we performed randomization tests in which we set the total number of samples for the  
241 Pacific Northwest, the Interior Northwest and the East to  $n=12$ , which is the number of samples available  
242 for the Southwest.

243  
244 To calculate the total realized niche size as a proxy for niche breadth within each subspecies, we calculated  
245 the number of pixels across climate space whose density was above 0 for each season. Niche overlap within  
246 a subspecies across seasons as well as between subspecies was computed using Schoener's D metric, which  
247 varies between 0 (no overlap) and 1 (complete overlap) (Broennimann *et al.* 2012). To assess the  
248 relationship between seasonal niche overlap and migration distance we calculated the average migration  
249 distance as the great circle distance between the mean location of breeding individuals (i.e. mean latitude  
250 and mean longitude across individuals) and the mean location of wintering individuals for that population.  
251 To assess the relationship between the seasonal niche overlap and breeding range size we calculated the  
252 number of total number of hexagons within the genetically defined breeding range of each subspecies as  
253 depicted in Fig. 1.

254  
255 To test whether the degree of niche tracking for each population was significantly different from random,  
256 we used a niche similarity analysis adapted from niche similarity tests proposed by Broennimann *et al.*  
257 (2012). Specifically, we compared the observed seasonal niche overlap metric (D) with seasonal niche  
258 overlap metrics simulated for alternative migration destinations. This was done by shifting randomly the  
259 population's breeding ground within the species' breeding range and computing the resulting D metric  
260 between the observed winter niche and the breeding niche of the shifted breeding ground. To shift the  
261 breeding ground, we first selected an individual  $i$  randomly sampled among all the breeding individuals  
262 available in our dataset. Then we selected  $N$  individuals ( $N$  corresponding to the observed number of  
263 breeding individuals for that population) using the probability of being sampled  $P_s = 1/\text{rank}(d_{iN_j})^2$ ,  
264 where  $N_j$  is individual  $j$  among the  $N$  individuals sampled;  $d_{iN_j}$  is the great circle distance between  
265 individual  $i$  and individual  $N_j$ ; and  $\text{rank}(d_{iN_j})$  is the rank of  $d_{iN_j}$  among all  $d_{iN}$ . This sampling procedure  
266 ensures that the breeding individuals sampled are clustered together in space to form a realistic simulated  
267 breeding ground of the population. We shifted the breeding ground of populations while keeping their  
268 wintering ground as observed because (i) the wintering range of Willow Flycatcher is much more restricted



269 than its breeding range and contains a significantly smaller pool of individuals to sample from, and (ii) it  
270 follows how observed migratory connectivity was determined, i.e. by assigning wintering individuals to  
271 genetically distinct populations on the breeding ground. We repeated the procedure of shifting the  
272 population's breeding ground 1000 times, each time recording the simulated D metric. To assess statistical  
273 significance, i.e. whether the population is tracking its climatic niche more than random, we computed a p-  
274 value investigating whether the observed niche overlap  $D_{obs}$  is higher than 95% of the simulated niche  
275 overlaps  $D_{sim}$ . We also calculated the standardized effect size  $E_D = \frac{D_{obs} - \text{mean}(D_{sim})}{sd(D_{sim})}$  associated with the p-  
276 value.

277

### 278 *Demographic analysis*

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

286

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

293

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

295

$$296 \quad n_{i,t} = z_i \exp(S_i + \beta_i(t - t^*) + \gamma_{i,t})$$

297

298 where  $S_i$ ,  $\beta_i$ , and  $\gamma_{i,t}$  are the intercept, slope, and year effects for a particular stratum and  $z_i$  is the proportion  
299 of routes on which the species has been observed. This metric cannot be compared across stratum, but  
300 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  
301 overall abundance index, we summed stratum totals across the four populations, assuming that  
302 contributions from very small genetic populations would be negligible.

303

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

306

$$307 \quad B_i = \left\{ \frac{N_{i,t_b}}{N_{i,t_a}} \right\}^{1/(t_b-t_a)}$$

308

## 309 **Results**

### 310 *Genome-wide population genetic structure*

311 PCA analysis of 175 breeding individuals at 104,626 SNP loci revealed support for genetic differentiation  
312 between the 4 main subspecies, *E. t. extimus* (Southwest), *E. t. brewsteri* (Pacific Northwest), *E. t.*  
313 *adastus* (Interior Northwest), and *E. t. trailli* (East; SI Fig. 1). Further, our analysis supports the existence  
314 of sub-differentiation within the currently defined range of *E. t. extimus*, with the White Mountains, Kern,  
315 San Diego and being more closely aligned with *E. t. brewsteri* and *E. t. adastus* than the remainder of the  
316 Southwest (SI Fig. 1). Because downstream genoscape construction was based on a subset of highly  
317 divergent SNPs which do necessarily not reflect genome wide patterns of gene flow, we calculated  
318 pairwise  $F_{ST}$  between the seven groups apparent within the PCA using the genome-wide data. Pairwise  $F_{ST}$   
319 analyses suggest that highest degree of genetic divergence was between the East and all other pairwise  
320 comparisons (Table 1;  $F_{ST}$  range = 0.064 – 0.09), apart from between East and Interior Northwest which  
321 was lower ( $F_{ST} = 0.036$ ). Comparisons between the White Mountains and the Southwest ( $F_{ST} = 0.067$ ),  
322 Kern and the Southwest ( $F_{ST} = 0.066$ ), and the White Mountains versus Kern and Southern California ( $F_{ST}$   
323 = 0.058 and 0.059, respectively) were the next most divergent. The Southwest was also strongly  
324 differentiated from the Pacific Northwest and to a lesser degree the Interior Northwest ( $F_{ST} = 0.059$  and  
325 0.048, respectively), with the lowest levels of divergence found between the Interior Northwest and all  
326 other pairwise comparisons ( $F_{ST}$  range = 0.009 – 0.032).

327

### 328 *Structure analysis and genoscape construction*

329 The willow flycatcher genoscape for this study was created using a subset of SNPs specifically designed  
330 to accentuate groups of individuals within geographic areas that are genetically distinguishable from other  
331 genetically groups for the purpose of linking wintering breeding populations, and therefore the groupings  
332 within the genoscape do not necessarily reflect historic patterns of gene flow across the genome. While  
333 our STRUCTURE analysis revealed that a K value of 4, 5, 6, and 7 populations were biologically realistic  
334 hypotheses for the number of groups within the species (SI Fig. 2), the goal of our analysis was not to  
335 find the most likely value of K, but to identify spatially explicit genetic groups that could be tracked

336 across the full annual cycle, similar to fisheries stock management (McKinney et al., 2019). Thus, we set  
337 the number of groups to 7 based on concordance between spatially informative genetic clusters identified  
338 in the genome-wide PCA (SI Fig. 1), the STRUCTURE runs based on a limited set of loci (Fig. 1), and  
339 the power to assign individuals to groups at  $k=7$  using RUBIAS (SI Table 1). The 7 genetically  
340 distinguishable groups, 4 of which were roughly concordant with previously defined subspecies  
341 boundaries, were distributed across North America as follows (Fig. 1): Pacific Northwest (green, 1 - 3)  
342 corresponded with *E. t. brewsteri*, Kern (red, 4) fell within the current boundary for *E. t. extimus*,  
343 Southern California (yellow, 6 and 7) fell within the current boundary for *E. t. extimus*, Interior Northwest  
344 (purple, 8-18) fell within the current boundary for *E. t. adastus*, Southwest (orange, 19-27), White  
345 Mountain (sky blue, 28) fell within the current boundary for *E. t. extimus* and East (dark blue, 29-37) fell  
346 within the current boundary for *E. t. trailli*. From here on we will refer to genetic groups by their  
347 geographic rather than subspecies name unless a direct comparison with the subspecies is needed.  
348 Sampling location 5, Owen's River at Bishop, did not fall clearly into any one genetic cluster and rather  
349 represented a mixture between Interior Northwest, Southern California, and Southwestern groups.  
350 Further, a comparison between genetic assignments generated using SNPs from the RADseq and  
351 Fluidigm pipelines were concordant suggesting no significant ascertainment bias associated with SNP  
352 sub-setting (SI Fig. 2).

353

#### 354 *Identification of population specific wintering areas*

355 Leave-one-out cross validation of our genetic baseline in RUBIAS revealed that the power to assign  
356 individuals to groups was high, with the Pacific Northwest having the highest probability of correct  
357 assignment (99.7%), followed by the Southwest (98.6%), the East (97.5%), the Interior West (91%), the  
358 Kern (80%) and Southern California (78%), and the White Mountains (70%) (SI Table 3). The majority  
359 of the incorrect assignments in the White Mountains were to the surrounding populations in the  
360 Southwest, while the majority of the incorrect assignments in Southern California and the Kern were from  
361 neighboring populations in the Kern and Pacific Northwest, respectively. Higher mis-assignment rates in  
362 the Kern, Southern California and the White Mountains are likely due to admixture with neighboring  
363 groups, indicating these may be areas of hybridization between subspecies. Subsequent assignment of  
364 wintering individuals to genetically distinct breeding groups using RUBIAS indicated that Pacific  
365 Northwest birds winter from western Mexico to Costa Rica, Interior West breeders winter from  
366 Guatemala south to Panama, Eastern breeders winter from Costa Rica to Ecuador, and Southwestern  
367 breeders are restricted to Costa Rica and Nicaragua (Fig. 1b; SI Table 2). We did not detect any Kern,  
368 White Mountain, or Southern California breeders on their wintering grounds which is not surprising given

369 the low population sizes in those regions and the correspondingly low probability of detection outside of  
370 the breeding range.

371

### 372 *Seasonal climate niche breadth and overlap*

373 An analysis of seasonal climate niche breadth revealed that while breeding niches within the willow  
374 flycatcher are similar in size, wintering niches sizes are more variable (Fig. 2; Table 2). Specifically, the  
375 wintering niche of the Eastern group is around twice as large the wintering niche of the Southwest and  
376 Pacific Northwest group (Fig. 2; Table 2). This is mainly driven by long-distance migratory individuals  
377 of the Eastern group found as far south as Ecuador, generating wide variation along the precipitation axis.  
378 We acknowledge that sampling gaps on the wintering grounds limit our ability to fully characterize the  
379 wintering niche of Interior Northwest and Easter populations which likely winter in unsampled areas of  
380 the northern Andes. This being the case, we also acknowledge that inclusion of additional samples from  
381 these regions would either maintain or increase the wintering niche size for each of these groups and  
382 would not significantly change the interpretation of our results. Calculation of niche overlap revealed that  
383 while the willow flycatcher as a species tracked its climate niche rather closely throughout the year  
384 (Schoener's  $D = 0.53$ ; Fig. 2d; Table 2), there was variation in the amount of niche overlap below the  
385 species level. In particular, the Southwestern group demonstrated the highest niche overlap between  
386 breeding and wintering areas (Schoener's  $D = 0.65$ ; Fig. 2d; Table 2), the Eastern group demonstrated the  
387 lowest niche overlap across seasons (Schoener's  $D = 0.06$ ), and the Interior Northwest and Pacific  
388 Northwest groups fell in between the upper and lower extremes (Schoener's  $D = 0.22$  for both). These  
389 results were robust to variations in parameter values associated with the kernel density estimation (SI Fig  
390 3a), as well as to variations in boundaries set on the length of the wintering period (SI Fig 4). Further  
391 randomization tests in the Pacific Northwest, Interior West, and East confirmed that niche overlap was  
392 not significantly influence by wintering ground sample size (SI Fig 3b).

393

394 Comparison of niche breadth (calculated as the total niche area on breeding and wintering grounds) to the  
395 degree of niche overlap revealed an inverse relationship, with higher niche overlap between breeding and  
396 wintering areas found in populations with lower overall niche breadth like the Southwest (Table 2). In  
397 addition, migration distance and breeding range size also varied by genetic group, with migration distance  
398 and the breeding range being inversely correlated to the degree of seasonal niche overlap across genetic  
399 groups (Table 2; SI Fig. 5a&b). In addition, niche similarity tests show that the southwest population is  
400 tracking its climatic niche throughout the year better than random given the availability of climate across  
401 the species distribution (Table 2). However, the niche similarity tests also show that the three other  
402 populations are not significantly tracking their climatic niche throughout the year, and have negative

403 effect sizes. The east and interior northwest populations in particular have relatively high negative effect  
404 sizes indicating that they tend to be closer to being niche switchers rather than niche trackers, while the  
405 interior west population falls somewhere in between.

406

#### 407 *Demographic analysis*

408 Overall, the demographic analysis revealed that while the species as a whole has been declining,  
409 abundance trends vary by genetically distinct group. In particular, a comparison in the % change between  
410 1968 and 2015 suggests that while species as a whole has declined slightly (-1.26, CI: -1.60% to -0.94%),  
411 there has been no significant change in the Eastern population (0.36%, CI -0.02% to 0.75%), a significant  
412 decrease in the Interior NW (-1.83%, CI -2.50% to -1.16%) and the Pacific NW (-2.01%, CI: -2.53 to -  
413 1.51%), and no detectable difference in the endangered Southwestern group which had already declined  
414 prior to the start of the survey in 1968 (Fig. 2c). A comparison between population trends and niche  
415 breadth support the idea that groups with narrower niches across seasons have been declining more  
416 dramatically or, in the case of the Southwest group had previously declined to the point of being federally  
417 endangered, while groups with broader niche across seasons have remained stable.

418

#### 419 **Discussion**

420

421 Recent research suggests over ~2.9 billion birds have been lost from North America since the 1970's  
422 (Rosenberg et al., 2019), representing a staggering and largely unexplained loss of biological diversity.  
423 While advances in migrant tracking technology have provided new insights into geographic regions  
424 important to population declines in some migratory birds (Kramer et al., 2018), we still lack basic  
425 knowledge of how fundamental aspects of avian ecology may interact with other stressors to promote  
426 resiliency to environmental change. Here we demonstrate how mapping niche breadth across seasons  
427 within genetically distinct populations of a migratory bird yields important insights into the relationship  
428 between climate specificity and threatened status. Our results show that genetically distinct populations  
429 of the willow flycatcher with narrower total climate niches demonstrate high climate niche overlap  
430 between breeding and wintering areas, while genetically distinct populations with broader total niches  
431 have low climate niche overlap across seasons. Remarkably, when paired with population-specific  
432 demographic trend data since the late 1960s, we find that populations with narrower climate niches across  
433 seasons are already endangered or steeply declining, while populations with broader climate niches across  
434 seasons have remained stable in recent decades; a pattern that would have been masked by a species-level  
435 only analysis. While further work across species and populations is needed to assess the generality of our  
436 findings, this work highlights the importance of quantifying niche breadth within species across the

437 annual cycle when attempting to understand the factors that facilitate or constrain the response of locally  
438 adapted migratory populations to rapid environmental change.

439

#### 440 *Niche tracking and ecological divergence across seasons*

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

457

458 In addition to providing a framework for understanding the relationship between niche tracking and local  
459 adaptation, the increased clarity provided by our population-level analysis of niche tracking suggests that  
460 mixed evidence regarding the extent to which species track or switch their niche across seasons may in  
461 part be due to a failure to match the appropriate tracking tool with the spatial scale of the question. On  
462 one end of the spectrum, species level analyses may be too coarse in scale to quantify niche breadth when  
463 genetically distinct populations vary in climate tolerances (Boucher-Lalonde et al., 2014; Gómez et al.,  
464 2016b; Joseph & Stockwell, 2000; Laube et al., 2015; Martínez-Meyer et al., 2004; Nakazawa et al.,  
465 2004; Zurell et al., 2018). On the other end of the spectrum, fine scale movement data provided by GPS  
466 tags (Fandos et al., 2020) may lack the genetic backdrop necessary identify how individual movements fit  
467 within the context of locally adapted populations. Alternatively, our results suggest that a genomic  
468 approach to mapping seasonal climate niches can illuminate key linkages between climate tracking, local  
469 adaptation, and niche breadth that can be used to help shed light on the evolution of climate specialization  
470 across the annual cycle.

471

472 *Niche breadth and vulnerability to climate change*

473 The willow flycatcher is an excellent model for exploring the relationship between niche breadth and  
474 population level vulnerability to climate change because past work provides support for the existence of  
475 local adaptation to climate across the breeding range (Ruegg et al 2018), but the present study provides  
476 the first demonstration of a method for quantifying the climate niche of locally adapted populations across  
477 breeding and wintering grounds. Thuiller (2005) highlights four main hypotheses regarding which groups  
478 should be more sensitive to climate change, including groups with: (1) marginal distributions outside of  
479 the mean climate conditions (Swihart et al 2003), (2) narrow niche breadth (specialist species) (Brown  
480 1995), (3) restricted distributions (Johnson et al 1998), and (4) distributions within regions strongly  
481 exposed to climate change. Here we find that the endangered southwestern willow flycatcher fits all 4  
482 climate sensitivity criteria – previous work demonstrated that genetic diversity is significantly associated  
483 with climate variables that fall outside of the mean climate conditions (Ruegg et al 2018; Figure 2a), its  
484 highly fragmented breeding range is at the edge of the species distribution where the intensity of summer  
485 heat waves is most pronounced (Smith et al., 2013), and here we show it has the narrowest total niche  
486 breadth of the 4 main genetic groups across breeding and wintering grounds. In contrast, the Eastern  
487 population of the willow flycatcher demonstrates the characteristics of a climate resilient population –  
488 previous work demonstrated that genetic diversity is significantly associated with mean climate variables  
489 (Ruegg et al 2018; Figure 2a), its broad, northern distribution is predicted to be less susceptible to intense  
490 summer heat waves (Smith et al, 2013), and here we show it has the broadest total niche breadth of the 4  
491 main groups across seasons. As a result, sensitivity to climate change may help explain why population  
492 numbers have remained low in the southwest, despite concentrated recovery efforts over the last decade,  
493 while population numbers in the east have not changed significantly. Indeed, while we only have 4  
494 populations and cannot test whether the relationship between niche breadth and population trends are  
495 statistically significant, it remains striking that across the four main groups where niche breadth could be  
496 calculated, we see a trend toward steeper declines or, in the case of the already endangered southwestern  
497 willow flycatcher, greater vulnerability, with increasing climate specialization. The trend towards greater  
498 vulnerability to climate change in the southwestern willow flycatcher mirrors the results from Ruegg et al  
499 (2018) which predicted significantly higher mismatches between current and future gene-environment  
500 relationships in the southwestern population. Thus, in combination with other anthropogenic disturbances  
501 such as loss of critical breeding habitat, having a narrow range of climate optima may further exacerbate  
502 losses in already vulnerable populations. Overall, this work more generally highlights the importance of  
503 understanding the extent of climate specificity within genetically distinct populations across time and  
504 space when attempting to prioritize conservation in a rapidly changing world. Future work will focus on

505 assessing the relationship between niche breadth and population trends in a multi-species comparative  
506 framework in order to test the generality of patterns observed herein.

507

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

527

## 528 *Conclusions*

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



539 understand factors that facilitate or constrain the response of locally adapted populations to rapid  
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748 **Figure Legends**

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750 **Figure 1. Willow Flycatcher Genoscape.** Population genetic structure in Willow Flycatchers across the  
751 breeding grounds and corresponding population specific wintering locations. A) STRUCTURE analysis  
752 revealed support for the existence of 7 genetically distinct groups across the breeding range. Numbers at  
753 the top of the STRUCTURE plot correspond to locations on map and in Table 1. Numbers in the SSW  
754 population are not consecutive because data generated using RADseq and SNP genotyping were lumped  
755 together to test for consistent results (SI Figure 2). B) The posterior probability of group membership  
756 from STRUCTURE was visualized as transparency levels of different colors overlaid upon a base map  
757 from Natural Earth (naturalearthdata.com) and clipped to the species breeding range using a shapefile  
758 (NatureServe 2012). Wintering individuals are color coded based upon assignments to breeding group  
759 using the program RUBIAS. Points on the wintering grounds are jiggered for visualization purposes.  
760 Wintering sample location details and associated assignments can be found in SI Table 1.

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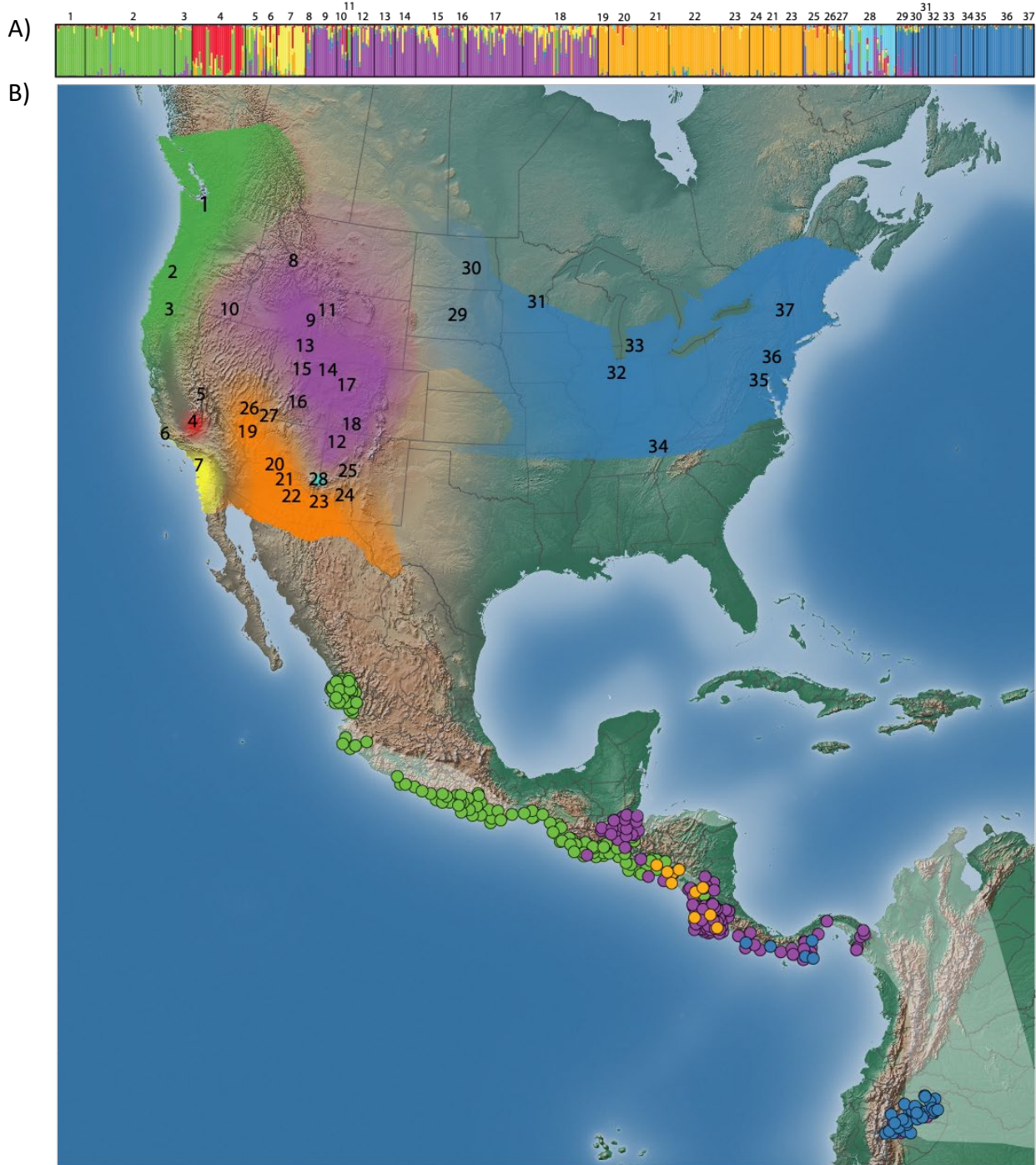
763 **Figure 2. Realized Climate Niche and Population Trends for the Willow Flycatcher.** A) Maps of the  
764 sampling distribution for the species and each of the 4 main genetically defined groups separately.  
765 Geographic regions on the breeding grounds were defined according the genoscape map in Figure 1.  
766 Triangles indicate samples that were identified to each genetically distinct group, but fell outside of the  
767 genoscape boundaries, while circles fell within the genoscape boundaries. B) The realized climate niche  
768 occupied by each group on its breeding and wintering range as well as across both seasons. C)  
769 Demographic trends estimated with BBS data showing declines in the Pacific NW and Interior NW, but  
770 no significant change in the East. The Endangered Southwestern group is reported to have declined prior  
771 to the start of the survey. D) Niche overlap for the species as well as each genetically distinct group.

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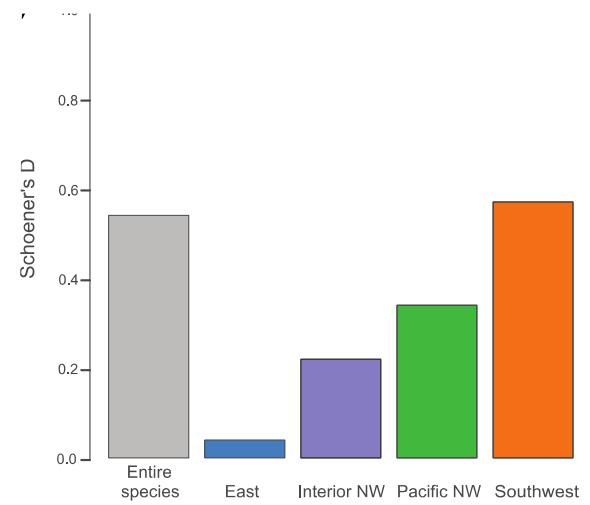
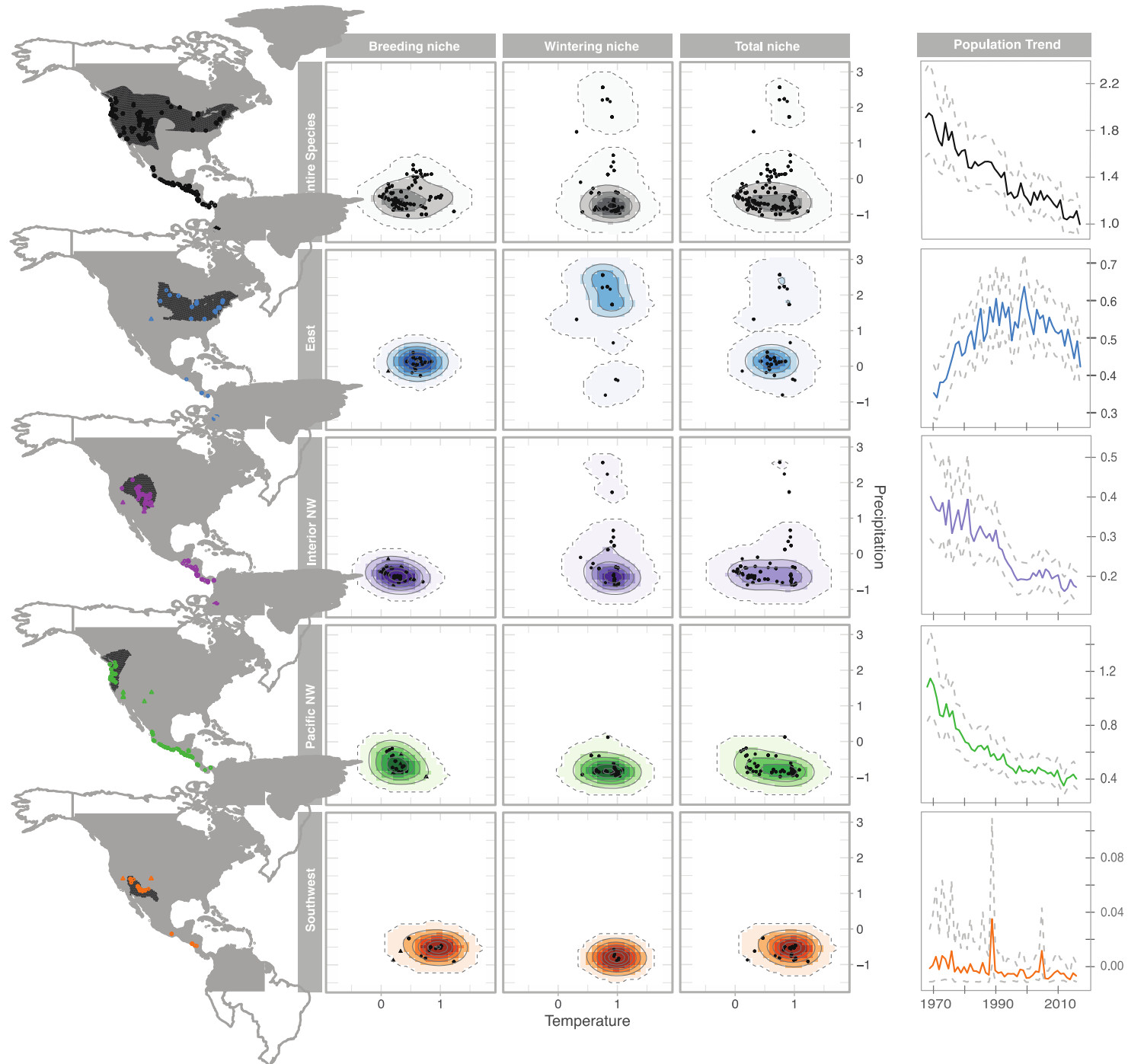






**Figure 1. Willow Flycatcher Genoscape.**

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 7 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 (SI Figure 2). 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](http://naturalearthdata.com)) and clipped to the species breeding range using a shapefile (NatureServe 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 SI Table 1.



**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 4 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 BBS 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.

**Table 1.** Location of breeding samples with number of individuals sequenced using RADseq and the number of individuals genotyped using SNP assays in each population. Map labels refer to the corresponding numbers on Figure 1.

Map label	Near Town	State	Latitude	Longitude	Num RADseq	Num SNP
1	Mirror Lake	WA	47.746	-122.857	11	6
2	Astoria Airport	OR	43.893	-123.259	19	33
3	Seiad Valley	CA	41.375	-122.143	6	4
4	South Fork Kern River	CA	35.659	-118.462	13	18
5	Owen's River at Bishop	CA	37.408	-118.480	0	12
6	Santa Ynez River	CA	34.617	-120.180	0	6
7	San Diego	CA	33.268	-117.165	6	11
8	Hamon Memorial	MT	46.070	-114.126	4	1
9	Mink Creek	ID	43.119	-111.856	13	0
10	Malheur NWR	OR	42.833	-118.867	6	0
11	Fall Creek	WY	43.339	-110.810	0	3
12	Shiprock	NM	35.733	-107.953	0	13
13	Logan Canyon	UT	41.766	-111.706	0	12
14	Stewart Lake	UT	40.314	-109.311	6	6
15	East Canyon Reservoir	UT	40.170	-111.347	11	14
16	Fish Lake	UT	38.498	-111.591	0	5
17	Arapahoe National Wildlife Ref	CO	39.610	-107.467	0	32
18	Clear Creek	CO	37.493	-106.878	0	44
19	Lower Colorado River	AZ	36.050	-114.733	0	5
20	Camp Verde	AZ	34.558	-111.841	0	17
21	Roosevelt Lake	AZ	33.767	-111.241	10	18
22	San Carlos Reservation	AZ	33.197	-110.440	0	30
23	San Pedro/Gila River confluence	AZ	32.975	-110.769	14	17
24	East Pima site	AZ	32.828	-109.705	0	8
25	Los Ojos/Parkerview Fish Hatchery	NM	33.379	-108.182	0	14
26	Pahrnagat Lake NWR	NV	37.317	-115.130	0	6
27	St. George	UT	37.108	-113.738	0	4
28	White Mountains	AZ	34.000	-109.000	13	17
29	Little White River Rec. Area	SD	44.062	-99.853	8	2
30	Arrowwood NWR	ND	47.213	-98.842	0	3
31	Elm Creek	MN	45.133	-93.450	2	4
32	Willow Slew	IN	40.983	-87.525	4	0
33	Vicksburg	MI	42.424	-85.344	4	11
34	Cross Creek	TN	36.455	-85.243	0	7
35	Lilypons	MD	39.268	-77.131	0	8
36	Bethlehem	PA	40.666	-75.505	21	0
37	Black Creek SWMA	NY	43.135	-73.812	4	2
<b>Total</b>					<b>175</b>	<b>393</b>

**Table 2.** Location of wintering ground samples and summary of population assignments at each site using RUBIAS.

Country	Location	Latitude	Longitude	East	Interior NW	Pacific NW	Southwest	Total
CR	Puerto Jimenez	8.516	-83.294	1	2	0	0	3
CR	Coto/Coto 44	8.562	-82.958	1	3	0	0	4
CR	Playa Caleta	9.759	-85.266	0	1	0	1	2
CR	Chomes	10.069	-84.899	0	27	2	0	29
CR	Solimar	10.291	-85.166	0	3	0	0	3
CR	Santa Cruz	10.329	-85.650	0	5	0	1	6
CR	Bolson	10.355	-85.420	0	31	5	1	37
EC	Jatun Sacha	-1.086	-77.616	2	0	0	0	2
EC	Jaguar Lodge	-1.070	-77.610	6	2	0	0	8
EC	Hacienda Johanna, Tena	-0.996	-77.813	6	1	0	0	7
EC	Yachana	-0.836	-77.221	2	0	0	0	2
EC	La Selva	-0.500	-76.370	4	1	0	0	5
EC	Sani	-0.476	-76.313	7	0	0	0	7
EC	Sacha	-0.470	-76.460	1	0	0	0	1
EC	Coca/Coca River	-0.456	-76.993	6	1	0	0	7
EC	Sani Lodge, Yuturi	-0.423	-76.285	3	2	0	0	5
EL	Jocotal E. (El Torre)	13.319	-88.243	0	0	2	0	2
EL	Jocotal W. (Desague S.)	13.326	-88.270	0	1	1	0	2
EL	Olomega RR	13.332	-88.020	0	0	1	0	1
EL	Nancuchiname	13.341	-88.719	0	0	6	0	6
EL	San Juan SE	13.368	-88.160	0	0	1	0	1
EL	La Barra de Santiago	13.692	-89.943	1	1	4	0	6
GUAT	Puerto San Jose	13.930	-90.913	0	0	14	0	14
GUAT	La Avallena	13.940	-90.440	0	0	2	0	2
GUAT	Finca Las Ojas, Chiquimulill	14.015	-90.393	0	0	2	0	2
GUAT	San Sebastian	14.574	-91.633	0	1	9	0	10
GUAT	Finca Nueva, Los Amates	15.247	-89.104	0	13	2	0	15
GUAT	Los Amates B	15.250	-89.050	0	1	0	0	1
GUAT	Los Amates C	15.260	-89.070	0	1	0	0	1
GUAT	Quiche	15.425	-90.863	0	2	0	0	2
GUAT	Finca La Cabana, El Estor	15.518	-89.300	0	10	4	0	14
MX	Lag. Pampa el Cabildo, Chis	14.723	-92.420	0	0	6	0	6
MX	San Isidro, Chis	15.703	-93.381	0	0	1	0	1
MX	Rio Copalita, Oax	15.793	-96.050	0	0	7	0	7
MX	Puerto Escodido, Oax	15.808	-97.002	0	0	1	0	1
MX	La Barra, Chis	15.890	-93.710	0	0	7	0	7
MX	Santa Rita, Oax	16.300	-94.505	0	0	1	0	1
MX	Cuanjinicuilapa, Gro	16.470	-98.413	0	0	6	0	6
MX	Rio Chila, Oax	16.500	-98.409	0	0	1	0	1
MX	Marquelia, Gro	16.583	-98.826	0	0	3	0	3
MX	Jose la Garzona	16.640	-96.656	0	0	4	0	4
MX	La Barra Vieja, Gro	16.721	-99.600	0	0	5	0	5
MX	L. de Piterro (near Tecpan)	17.175	-100.607	0	0	2	0	2



MX	Ixtapa, P. Linda, Gro	17.690	-101.640	0	0	3	0	3
MX	East Habillal, P Azul, Mich	18.018	-102.372	0	0	1	0	1
MX	Manzanillo Airport Marshe:	19.162	-104.559	0	0	2	0	2
MX	Rio Aguacate, Jalisco	19.220	-104.640	0	0	1	0	1
MX	Rio Cuixmala, Jalisco	19.398	-104.969	0	0	2	0	2
MX	San Blas - Crocodila, Nayari	21.528	-105.220	0	0	3	0	3
MX	Quimichi, Novillero, Nayarit	22.395	-105.550	0	0	38	0	38
NICA	Laguna la Tisma	12.086	-85.431	0	8	1	2	11
NICA	Laguna de Tisma west	12.100	-85.980	0	2	0	0	2
NICA	Reserva Natural Peninsula c	12.250	-86.340	0	1	1	1	3
NICA	Finca de San Miguel	12.798	-87.158	0	1	0	2	3
NICA	Cosiguina	12.880	-87.490	0	2	6	1	9
NICA	Caba" a los Pozo	12.887	-87.497	0	2	2	3	7
NICA	Potosi	12.950	-87.490	0	0	2	0	2
NICA	La Piscina, Cosiguina	12.955	-87.493	0	0	1	0	1
NICA	Lago de Apanas	13.190	-85.960	0	2	0	0	2
PA	Laguna Naranja	7.449	-80.376	2	4	0	0	6
PA	Pese	7.887	-80.541	1	6	0	0	7
PA	El Real	8.106	-77.723	0	5	0	0	5
PA	San Felix	8.173	-81.867	0	2	0	0	2
PA	Tocuman Marsh	9.071	-79.376	0	2	0	0	2
<b>Total</b>				<b>43</b>	<b>146</b>	<b>162</b>	<b>12</b>	<b>363</b>

**Table 3.** Pairwise genome-wide  $F_{ST}$  between genetically distinct groups calculated with all 105,000 SNP loci.

Population	Interior NW	Kern	Pacific NW	Southern CA	Southwest	White MT
East	0.0365	0.0779	0.0641	0.0774	0.0906	0.0645
Interior NW	-	0.0289	0.0096	0.0330	0.0488	0.0314
Kern	-	-	0.0272	0.0508	0.0669	0.0591
Pacific NW	-	-	-	0.0402	0.0594	0.0412
Southern CA	-	-	-	-	0.0479	0.0603
Southwest	-	-	-	-	-	0.0680

**Table4.** Niche Statistics for the species as a whole and each genetically distinct group.

Population	Breeding Niche Size	Wintering Niche Size	Niche Breath (total niche area)	Seasonal Niche Overlap	Migration distance	Breeding Range Size
Species	318	481	458	0.53	3520	2547
East	175	470	456	0.06	4581	1003
Interior West	183	401	409	0.22	4024	460
Pacific NW	208	209	267	0.22	3871	309
Southwest	199	152	200	0.65	3105	230

**Table5.** Niche overlap overall between populations across seasons.

	East	Interior NW	Pacific NW	Southwest
East	–	–	–	–
Interior NW	0.16	–	–	–
Pacific NW	0.14	0.87	–	–
Southwest	0.2	0.28	0.29	–

**SI\_Table1.** Assignment of Willow Flycatchers of known origin back to breeding population using rubias, with 96 SNPs. Population names are listed in Table 1 and the colors indicate the genetic group ( Fig. 1).

Population (Fig. 1, Table 1)	Pacific Northwest	Kern	Southern California	Interior West	Southwest	White Mountain	East
1	17	0	0	0	0	0	0
2	47	3	1	1	0	0	0
3	5	1	1	3	0	0	0
4	6	21	4	0	0	0	0
6	0	0	5	1	0	0	0
7	0	0	16	0	1	0	0
8	0	0	0	5	0	0	0
9	1	0	0	12	0	0	0
10	0	0	0	6	0	0	0
11	2	0	0	1	0	0	0
12	0	0	0	12	0	0	1
13	0	0	0	12	0	0	0
14	0	0	0	12	0	0	0
15	0	0	1	24	0	0	0
16	1	0	0	4	0	0	0
17	0	0	0	32	0	0	0
18	1	0	0	41	2	0	0
19	0	0	0	0	5	0	0
20	0	0	0	0	17	0	0
21	0	0	0	0	28	0	0
22	0	0	0	0	30	0	0
23	0	0	0	0	31	0	0
24	0	0	0	0	8	0	0
25	0	0	0	2	12	0	0
26	0	0	0	0	6	0	0
27	0	0	0	0	4	0	0
28	2	0	0	6	0	22	0
29	0	0	0	1	0	0	9
30	0	0	0	1	0	0	2
31	0	0	0	0	0	0	6
32	0	0	0	0	0	0	4
33	0	0	0	0	0	0	15
34	0	0	0	0	0	0	7
35	0	0	0	0	0	0	8
36	0	0	0	0	0	0	21
37	0	0	0	0	0	0	6



















2330-99720	2330-99720	fluidigm	Feather	MX	Rv#o Copalit	15.79279	-96.0488	Wintering	PNW	mixture	2004	FEB	23	Mary Whitfield	
2240-04328	2240-04328	fluidigm	Feather	MX	Rio Cuixmala	19.39757	-104.969	Wintering	PNW	mixture	2002	FEB	3	Mary Whitfield	
2330-99740	06N30205	2330-99740	fluidigm	Feather	MX	San Blas, Coc	22.39511	-105.55	Wintering	PNW	mixture	2006	FEB	28	Mary Whitfield
2240-94392	06N30208	2240-94392	fluidigm	Feather	MX	SE San Blas, P	22.39511	-105.55	Wintering	PNW	mixture	2006	FEB	28	Mary Whitfield
2330-99744	06N30204	2330-99744	fluidigm	Feather	MX	SE San Blas, P	22.39511	-105.55	Wintering	PNW	mixture	2006	FEB	27	Mary Whitfield
2330-99795	06N30222	2330-99795	fluidigm	Feather	MX	SE San Blas, P	22.39511	-105.55	Wintering	PNW	mixture	2006	FEB	27	Mary Whitfield
2330-99796	06N30223	2330-99796	fluidigm	Feather	MX	SE San Blas, P	22.39511	-105.55	Wintering	PNW	mixture	2006	FEB	27	Mary Whitfield
2330-99797	06N30224	2330-99797	fluidigm	Feather	MX	SE San Blas, P	22.39511	-105.55	Wintering	PNW	mixture	2006	FEB	28	Mary Whitfield
2230-99721	2230-99721	fluidigm	Feather	MX	La Barra Vieje	16.72081	-99.6002	Wintering	PNW	mixture	2004	MAR	7	Mary Whitfield	
2230-99722	2230-99722	fluidigm	Feather	MX	La Barra Vieje	16.72081	-99.6002	Wintering	PNW	mixture	2004	MAR	7	Mary Whitfield	
2240-94377	2240-94377	fluidigm	Feather	MX	La Barra Vieje	16.72081	-99.6002	Wintering	PNW	mixture	2004	MAR	6	Mary Whitfield	
2240-94379	2240-94379	fluidigm	Feather	MX	La Barra Vieje	16.72081	-99.6002	Wintering	PNW	mixture	2004	MAR	7	Mary Whitfield	
2240-94380	2240-94380	fluidigm	Feather	MX	La Barra Vieje	16.72081	-99.6002	Wintering	PNW	mixture	2004	MAR	7	Mary Whitfield	
2240-94375	2240-94375	fluidigm	Feather	MX	Marquella, G	16.58252	-98.8259	Wintering	PNW	mixture	2004	MAR	4	Mary Whitfield	
2240-94376	2240-94376	fluidigm	Feather	MX	Marquella, G	16.58252	-98.8259	Wintering	PNW	mixture	2004	MAR	4	Mary Whitfield	
2240-94381	06N30217	2240-94381	fluidigm	Feather	MX	NW San Blas,	22.39511	-105.55	Wintering	PNW	mixture	2006	MAR	3	Mary Whitfield
2240-94387	06N30214	2240-94387	fluidigm	Feather	MX	NW San Blas,	22.39511	-105.55	Wintering	PNW	mixture	2006	MAR	3	Mary Whitfield
2240-94388	06N30213	2240-94388	fluidigm	Feather	MX	NW San Blas,	22.39511	-105.55	Wintering	PNW	mixture	2006	MAR	3	Mary Whitfield
2240-94391	06N30212	2240-94391	fluidigm	Feather	MX	NW San Blas,	22.39511	-105.55	Wintering	PNW	mixture	2006	MAR	3	Mary Whitfield
18N00309	18N00309	224094389	fluidigm	Feather	NICA	Cosiguina	12.89	-87.49	Wintering	PNW	mixture	2018	FEB	8	Mary Whitfield
18N00310	18N00310	224094389	fluidigm	Feather	NICA	Cosiguina	12.89	-87.49	Wintering	PNW	mixture	2018	FEB	8	Mary Whitfield
18N00313	18N00313	233099924	fluidigm	Feather	NICA	Cosiguina	12.89	-87.49	Wintering	PNW	mixture	2018	FEB	10	Mary Whitfield
18N00314	18N00314	233099925	fluidigm	Feather	NICA	Cosiguina	12.89	-87.49	Wintering	PNW	mixture	2018	FEB	10	Mary Whitfield
18N00327	18N00327	233099922	fluidigm	Feather	NICA	Cosiguina	12.88	-87.49	Wintering	PNW	mixture	2018	FEB	11	Mary Whitfield
18N00397	18N00397	233099798	fluidigm	Feather	NICA	Cosiguina	12.88	-87.49	Wintering	PNW	mixture	2016	FEB	9	Mary Whitfield
18N00328	18N00328	233099800	fluidigm	Feather	NICA	Potosi	12.95	-87.49	Wintering	PNW	mixture	2018	FEB	11	Mary Whitfield
18N00329	18N00329	233099799	fluidigm	Feather	NICA	Potosi	12.95	-87.49	Wintering	PNW	mixture	2018	FEB	11	Mary Whitfield
18N00324	18N00324	233099915	fluidigm	Feather	NICA	Reserva Natu	12.25	-86.34	Wintering	PNW	mixture	2018	FEB	1	Mary Whitfield
241067774	241067774	fluidigm	Feather	NICA	CabaOa los P	12.887293	-87.49636	Wintering	PNW	mixture	2017	JAN	27	Mary Whitfield	
241067728	241067728	fluidigm	Feather	NICA	CabaOa los P	12.887084	-87.497	Wintering	PNW	mixture	2017	JAN	18	Mary Whitfield	
241067776	241067776	fluidigm	Feather	NICA	La Piscina, Cc	12.955452	-87.4932	Wintering	PNW	mixture	2017	JAN	28	Mary Whitfield	
224094390	224094390	fluidigm	Feather	NICA	Laguna la Tisi	12.085834	-85.43054	Wintering	PNW	mixture	2017	JAN	26	Mary Whitfield	
96N2148	96N2148	NA	fluidigm	OAX	Jose la Garzo	16.64003	-96.6556	Wintering	PNW	mixture	1996	DEC	20	BM	
96N2171	96N2171	NA	fluidigm	OAX	Jose la Garzo	16.64003	-96.6556	Wintering	PNW	mixture	1996	DEC	21	BM	
96N2189	96N2189	NA	fluidigm	OAX	Jose la Garzo	16.64003	-96.6556	Wintering	PNW	mixture	1996	DEC	19	BM	
96N2205	96N2205	NA	fluidigm	OAX	Jose la Garzo	16.64003	-96.6556	Wintering	PNW	mixture	1996	DEC	20	BM	
2150-26574	2150-26574	fluidigm	Feather	CR	Playa Caleta	9.759	-85.266	Wintering	SSW	mixture	2000	FEB	11	Eben Paxton	
1710-46345	1710-46345	fluidigm	Feather	CR	Bolson	10.3552	-85.4195	Wintering	SSW	mixture	2001	JAN	1	Eben Paxton	
1710-20353	1710-20353	fluidigm	Feather	CR	Santa Cruz	10.329	-85.6495	Wintering	SSW	mixture	1999	MAR	18	Eben Paxton	
18N00396	18N00396	233099920	fluidigm	Feather	NICA	Cosiguina	12.88	-87.49	Wintering	SSW	mixture	2016	FEB	9	Mary Whitfield
241067724	241067724	fluidigm	Feather	NICA	CabaOa los P	12.887293	-87.49636	Wintering	SSW	mixture	2017	JAN	15	Mary Whitfield	
241067753	241067753	fluidigm	Feather	NICA	CabaOa los P	12.887084	-87.497	Wintering	SSW	mixture	2017	JAN	18	Mary Whitfield	
241067755	241067755	fluidigm	Feather	NICA	CabaOa los P	12.887084	-87.497	Wintering	SSW	mixture	2017	JAN	18	Mary Whitfield	
241067727	241067727	fluidigm	Feather	NICA	Finca de San	12.798346	-87.1575	Wintering	SSW	mixture	2017	JAN	17	Mary Whitfield	
241067750	241067750	fluidigm	Feather	NICA	Finca de San	12.798346	-87.1575	Wintering	SSW	mixture	2017	JAN	17	Mary Whitfield	
241067732	241067732	fluidigm	Feather	NICA	Laguna la Tisi	12.085834	-85.43054	Wintering	SSW	mixture	2017	JAN	25	Mary Whitfield	
241067771	241067771	fluidigm	Feather	NICA	Laguna la Tisi	12.085834	-85.43054	Wintering	SSW	mixture	2017	JAN	26	Mary Whitfield	
18N00394	18N00394	233099913	fluidigm	Feather	NICA	Reserva Natu	12.25	-86.34	Wintering	SSW	mixture	2016	JAN	31	Mary Whitfield