Genetic variation reveals individual-level climate tracking across the full annual cycle of a migratory bird

Rachael A. Bay[1], Daniel S. Karp[2], James F. Saracco[3], William R.L. Anderegg[4], Luke Frishkoff[5], David Wiedenfeld[6], Thomas B. Smith[7*], Kristen Ruegg[8*]

[1]Department of Evolution and Ecology, University of California Davis, Davis, CA 95616

[2]Department of Wildlife, Fish, and Conservation Biology, University of California Davis, Davis, CA 95616

[3]The Institute for Bird Populations, Petaluma, CA 94952

[4]School of Biological Sciences, University of Utah, Salt Lake City, UT 84112

[5]Department of Biology, University of Texas at Arlington, Arlington, TX 76019

[6]American Bird Conservancy, The Plains, VA 20198

[7]Institute of the Environment and Sustainability and Department of Ecology and Evolution, University of California Los Angeles, Los Angeles, CA 90024

[8]Department of Biology, Colorado State University, Fort Collins, CA 80523

*These authors contributed equally to this work

Abstract

Adaptation across climate gradients can provide the raw material needed for evolutionary response to climate change. In migratory species, studies of local climate adaptation are made challenging by seasonal movement, where it is unclear to what extent individuals track their local climate niches across the annual cycle. In the migratory songbird yellow warbler (*Setophaga petechia*), we test the hypothesis that individuals track similar climates between their breeding and wintering ranges. Further, we examine whether adaptation to local climate might lead to morphological differences among populations and different demographic responses to temporal climate variability. We find a correlation between wintering and breeding precipitation but not temperature regimes at the level of the individual bird. Specifically, birds from the driest wintering regions migrate to the driest breeding regions. Additionally, we find an association between bill size and breeding season precipitation which, given documented climate-associated genomic variation, suggests adaptation to local precipitation gradients might exist on the breeding grounds. Finally, we show geographic variation in the effect of precipitation on demography, with higher precipitation associated with population increases in some regions and declines in others. Taken together, our results suggest that variation in climate optima exists across the breeding range of yellow warblers and provide a potential mechanism for parallel selection across the annual cycle.

Intraspecific variation in climate-associated traits constitutes the raw material needed for species to adapt to ongoing climate change. Local adaptation has been investigated as a force maintaining such variation across environmental gradients (1-3). However, while local adaptation might provide a mechanism for the maintenance of standing variation at the species level, narrow population-level climate niches may simultaneously make particular populations more vulnerable to rapid environmental change, leaving them maladapted (4). While it is becoming increasingly clear that for some species persistence through the next century will require evolution (5, 6), much remains to be understood about the distribution and maintenance of putatively adaptive variation across contemporary climate gradients.

Investigations of local adaptation across climate gradients are particularly challenging for migratory species, which face selective constraints on both their breeding and wintering grounds. Selection on wintering grounds could either reinforce or counteract selection on breeding grounds. The question of whether species experience similar or different environmental conditions during different migratory stages has been asked by assessing the role of climate in setting distributional limits of migratory species (7-9). Some species, classified as ‘niche switchers,’ have been shown to migrate between areas with very different climates. Others, classified as ‘niche trackers,’ migrate between regions that share more similar climatic conditions than would be expected by chance. The biotic and abiotic environmental components of a species niche are extremely broad, however, much of the niche-tracking literature focuses on the particular role of climate in determining the ranges migratory species (10). Though the relative frequency of niche tracking versus switching across migratory species is still debated (8, 10, 11), niche tracking has been proposed as a mechanism explaining the evolution of migration, where species migrate to escape seasonality. In New World warblers (Parulidae), for example, migratory species tend to have more similar breeding and wintering niches than resident species (10).

To date, analyses of potential climatic constraints on the seasonal distributions of migratory species have focused nearly entirely on the species level with little consideration of such patterns within species. Could individuals also be tracking their climate niches such that, for example, birds from the hottest regions of the wintering range migrate to the hottest areas of the species' breeding range? Previously, investigation of this question was limited by the requirement for range-wide, individual-level definitions of migratory connections between the breeding and wintering ranges. Geolocator studies, for example, provide individual-level information, but suffer from small sample sizes due to their cost and the fact that they require

individuals to be recaptured after migrating (12, 13). Similarly, stable isotope analysis provides individual-level information but not at high-enough resolution to link climatic conditions between an individual's breeding and wintering grounds (14, 15). Finally, genetic sequencing and assignment can provide higher resolution maps of migratory connectivity, but these approaches have historically focused on the population or subspecies level (16). Fortunately, recent technological and analytical advances now make it possible to take advantage of isolation by distance signals in genetic data in order to estimate an individual's breeding location with high accuracy (17).

We leverage such advances to ask whether there is evidence for individual-level climate tracking in the Neotropical migratory songbird yellow warbler (*Setophaga petechia*) and how such a phenomenon, coupled with evidence of local adaptation on the breeding range, might affect demographic responses to climate change. On the species level, there is a high degree of overlap between breeding and wintering precipitation regimes, but less so for temperature (10). Our previous work has shown that there is genetic variation associated with precipitation across the species' breeding range and that mismatches between climate and genotype may have contributed to population declines over the last half century (18). Here, we use genomic data to describe migratory connectivity across the full annual cycle of the yellow warbler. We then use this information to test whether individuals track similar climates across their annual cycles. Finally, we examine the causes and consequences of local adaptation by testing for associations between climate and morphology and by analyzing how climate covaries with population trajectories over the past 50 years.

Results

We identified five yellow warbler breeding populations in North America within strong patterns of isolation by distance (Figure 1). Principle components analysis of 104,711 SNPs derived from RAD-Seq data for 197 breeding individuals (Fig S1, Table S1) showed clear associations with longitude and latitude (Figure S2; PC1 vs longitude: R^2=0.86,p<0.001; PC3 vs. latitude: R^2=0.43,p<0.001). RAD-Seq data were used to identify a set of 157 SNPs which we genotyped in 224 additional breeding birds to produce a spatial map of population structure. Bayesian hierarchical clustering in the software STRUCTURE identified K=2 as the optimal number of populations, but we still see obvious geographic patterns at higher values of K, likely driven by strong isolation by distance (19). The highest K value at which each group has individuals with majority ancestry is K=5 (Figure S3). Although the K=2 scenario may more

correctly identify barriers to gene flow, the K=5 scenario provides higher resolution for defining migratory connectivity and demographic patterns while still accurately assigning individuals to breeding groups. For this reason, we conducted subsequent analyses with K=5.

We used assignment to the five breeding populations to describe patterns of migratory connectivity across the breeding, wintering, and migratory stages of the annual cycle (Figure 1). Assignment to these populations, based on a set of 96 SNPs genotyped using Fluidigm SNPtype assays, was robust; 87.4% of breeding samples were correctly assigned. We were able to assign 189 wintering and 247 migrating birds (scaled likelihood > 0.9) to the five breeding populations. Birds from the four westernmost populations all winter broadly across Central America. There are slight differences between each populations' range; for example, the wintering range of the Western US population extends further north within Mexico than do the other populations. The Central population was found not only throughout Central America, but also in South America. Birds from the Eastern US populations were only found wintering in South America (not in Central America). Use of the four migratory flyways by the five breeding groups mirror longitudinal breeding distributions, with no evidence for crosswise migration at this level of resolution (Figure 1; Table S2).

In addition to the broad population assignments shown in Figure 1, we also estimated predicted breeding locations (*i.e.,* latitude and longitude) for each wintering individual to test the idea that individuals track their climate niches. Overall, we were able to predict breeding locations with a median error of 389.5km (Figure S4). We calculated a "Climate Matching Index" (CMI), defined as the degree to which wintering and inferred breeding climate were more similar (CMI>0) or less similar (CMI<0) than expected given a null model accounting for migratory distance. We found that birds migrated between areas with similar precipitation regimes, specifically areas with similar amounts of monthly precipitation when the species is present (Table S3; Figure 2A,C). This pattern was largely driven by birds wintering in the driest regions of Central America and breeding in the driest regions of North America (Table S4; Figure 2B). These results were robust to the choice of climate dataset (CRU vs. Worldclim; Table S3, S4; Figure S5). We did not find any evidence of individual-level tracking for mean, maximum, or minimum temperature or when temperature and precipitation were calculated over the entire year (*i.e.,* including periods when the species is absent; Table S3; Figure S6).

The existence of genetic variation associated with precipitation across the breeding range, as well as strong correlations between breeding and wintering precipitation regimes, suggest that local adaptation to precipitation could persist across the full annual life cycle of

yellow warblers. This led us to test which traits might differ in their optima across climate gradients. We reanalyzed a previously published dataset on male yellow warbler morphology within museum collections to test whether morphological traits varied with precipitation, potentially suggesting selection for different trait optima. We found that in specimens collected across the breeding range (n=145), bill length (adjusted p=0.001) and bill depth (adjusted p=0.025) were correlated with breeding season precipitation (Figure 3). Specifically, birds with longer, deeper bills were found breeding in wetter regions. No other morphological traits were correlated with breeding precipitation (Figure S7).

Adaptation to local climate gradients could also make populations vulnerable to year-to-year variability and longer-term shifts in climate. We used the North American Breeding Bird Survey (BBS) to test whether relative abundance was associated with temporal variation in precipitation anomaly (deviance from mean) from the prior one-two years (Figure 4). The four populations (the Arctic population was omitted due to limited data) showed different abundance trajectories, with the two western populations in decline throughout the survey period. The relationship between abundance and precipitation was complex (Table S5). The Western US population, the population encompassing the driest part of the breeding range, exhibited a positive relationship with precipitation, whereby wetter years yielded higher relative abundances one and two years later (Figure 4H). The Western Canada population, which is quite heterogeneous in terms of precipitation regime, showed a negative relationship with precipitation in the prior year (Figure 4G). Similarly, the Eastern US population, one of the wettest populations, showed a marginal negative relationship with precipitation with a two-year lag (Figure 4J).

Discussion

Predictions of species response to climate change will require understanding the extent to which local adaptation within a species confines the ranges of individuals and populations (18, 20). For migratory species, this is especially challenging. Overlap between climate niches on breeding and wintering grounds at the species level can be examined using observational data, but similarity among breeding and wintering climates at the individual level requires the ability to pinpoint breeding and wintering locations accurately for many individuals from across the range. We capitalize on innovations in genetic sequencing and analysis to accomplish this level of resolution, showing that yellow warbler individuals track similar precipitation (but not temperature) regimes between the breeding and wintering seasons. Coupled with evidence of

local adaptation across the breeding grounds, including associations between precipitation and both morphological (Figure 3) and genetic (18) variation, our results indicate that selection might reinforce local adaptation across the annual cycle.

A prerequisite for continued, reinforced natural selection across the annual cycle is site fidelity. If individuals move to new breeding or non-breeding locations each year then signals of selection might be lost. Our study and others have found strong isolation by distance in the breeding range (21), suggesting that individuals migrate to the same regions year after year. Previous multi-annual bird banding studies also support this observation (22). In the wintering range, we find substantial mixing of our five assignable populations, but also some sorting, with western populations wintering farther north in Mexico and eastern populations only found in South America. These findings support previous microsatellite and stable isotope studies of migratory connectivity in yellow warbler, which have reported segregation between eastern and western lineages on their wintering grounds (23, 24). Unlike a recent geolocator study (25), we find little evidence for crosswise migration. Although the combination of evidence for adaptation to precipitation gradients across the breeding range and climate tracking across the annual cycle suggests that local adaptation might also exist on the wintering grounds, data on the distribution of adaptive genetic and phenotypic variation and the relationship of such traits to climate during the wintering period is still needed.

Local climate can impact bird populations through multiple pathways; for example, by directly affecting physiology or through indirect effects on resources. We find a correlation between bill size (both length and depth) and precipitation trends. There are several potential mechanisms through which different precipitation regimes could select for different bill sizes. One possibility is that larger bills more efficiently dissipate heat (26, 27). Although this has largely been explored in connection with temperature, there is some evidence that larger bill sizes may be adapted to more humid environments where evapotranspiration is less efficient (28). Another hypothesis is that variation in bill size is a response to food availability. Evolutionary responses of bill size to food resources have been observed in a wide variety of avian taxa (29-33). As precipitation can structure the size distribution of insect communities (34), this might lead to different optimal bill morphologies. Interestingly, in the resident subspecies of yellow warbler found in Costa Rica, the mangrove warbler (*S. petechia xanthotera*), bill size also increases with precipitation (35). Further mechanistic studies are needed to disentangle the drivers of the relationship between precipitation and bill size.

Selective drivers can affect demographic trends through spatial and temporal variation in mortality and fecundity. For example, there is mounting evidence suggesting climatic effects on insect prey abundance can drive population trends. For example, Sillet et al. (36) found lower fecundity of black-throated blue warblers (*Setophaga caerulescens*) in El Niño years in the eastern US, and fecundity was correlated with prey biomass. Similarly, yellow warbler populations in Manitoba, Canada had lower survival and reproduction during El Niño years (37). The opposite pattern was observed in a study across 10 landbird species in the Pacific Northwest, with higher reproductive success in El Niño years (38) and models suggest that El Niño years are associated with higher survival in this region (39). These studies highlight not only the effects of climate on survival and reproduction in migratory birds, but also the potential geographical variation in demographic effects of climate anomalies. We found that while precipitation anomaly was associated with abundance in some populations, those relationships are not constant across the species range. In the western US population, which experiences the driest breeding climates, we found that wetter years were followed by years with higher yellow warbler abundance. This along with the marginal negative relationship between precipitation and abundance in the eastern US (a wetter population) might reflect negative effects of extreme precipitation in both directions. On the other hand, we also observed a marginal negative effect of precipitation was observed in the Pacific Northwest. Geographic variation in the relationship between abundance and climate could be due to spatial variation in El Niño effects and the mechanistic links between climate and fitness. For example, Nott et al. (38) suggests that the finding of higher reproductive success during El Niño years could be attributable to the fact that those birds winter Mexico where El Niño leads to favorable migration conditions. Additionally, spatial differences in the climate/abundance relationship could be a product of different populations having different climate optima.

Our results suggest that individuals sort non-randomly across breeding and wintering ranges so as to minimize differences in precipitation regimes. On the species level, this “niche tracking” has been suggested as an explanation for the evolution of migration – as an escape from seasonality (11). It is not clear how a similar explanation would play out at an individual or population level. We propose that for species that have already established migratory life histories, it may be beneficial that selection on traits that are adaptive in one part of the life cycle be reinforced across all seasons. One might imagine that birds with traits that allow them to persist in the driest breeding conditions then become the most fit in the driest wintering regions if the mechanisms of selection are either the same or parallel across both regions. Coupled with strong migratory connectivity, this would lead to intraspecific correlations between climate on

the breeding and wintering grounds, as we observe here. Taken to the extreme, we could imagine this parallel selection playing a role in the hard-wiring of specific migratory routes.

In conclusion, our study provides evidence that precipitation regimes (but not temperature) structure genetics and morphology, migratory connections, and population trajectories in a widespread migratory bird species. Such information about the ecological and evolutionary responses to changes in precipitation regime will be essential for understanding and predicting response to future global change.

Methods

Sampling: We assembled a collection of 903 yellow warbler blood, tissue, and feather samples taken across the breeding and wintering ranges as well as during migration (Figure S1, Table S1). These samples constitute a collection from previous studies (23, 24), tissue from museum collections, and blood or feathers taken at banding stations. DNA was extracted from all samples using the Qiagen DNeasy Blood and Tissue Kit. Blood and tissue samples from the breeding range were used to create RAD-Seq libraries and the remainder of samples were genotyped using custom Fluidigm SNPtype assays as described below.

Genotyping: Single nucleotide polymorphisms (SNPs) from RAD-Seq data generated for Bay et al. (18) were used to examine population structure across the breeding range. Detailed methods on read processing and SNP calling can be found in that paper. Briefly, we used the bestRAD protocol (40) to create libraries for 229 individuals from across the breeding range, which were sequenced on an Illumina HiSeq 4000. Paired end 150bp reads were quality filtered using scripts from the STACKS pipeline (41) and aligned to the yellow warbler genome (18) using bowtie2 (42). We called SNPs with GATK following best practices (www.broadinstitute.org). Using the R package genoscapeRtools, we discarded low coverage SNPs and low coverage individuals, resulting in a final dataset of 104,711 SNPs across 197 individuals. Within this dataset, all individuals had less than 25% missing data (mean=3.8%) and each SNP had less than 10% missing genotypes (mean=3.8%). We also discarded SNPs with minor allele frequency less than 1%.

RAD-Seq data was used to select a panel of SNPs that could be used to assign individuals to their breeding population. We used four different analyses: 1) F_{ST} between easternmost (Newfoundland, Nova Scotia, New Brunswick) and westernmost (British Columbia, Washington) locations, 2) F_{ST} between northernmost (Alaska locations and Churchill, Manitoba) and southernmost (Oregon, Pennsylvania, Michigan) locations, 3) Standard linear models

comparing allele frequency to latitude, and 4) Standard linear models comparing allele frequency to longitude. Per locus F_{ST} was calculated using the Weir and Cockerham method (43) in the R package hierfstat (44). For each of these metrics, we took the top ranked SNPs, for a total of 192 SNPs to be tested for genotyping. We developed Fluidigm SNPtype assays for these 192 SNPs and used these assays to genotype 231 feather samples from 28 new locations across the breeding range. These data were used to determine a final set of 96 SNPs based on the quality of the genotyping assay as well as linear correlations with latitude and longitude. These 96 SNPs were genotyped in 203 birds from across the wintering range as well as 275 birds caught during migration (Figure S1; Table S1). Only individuals with at least 80% of SNPs genotyped were used in downstream analysis.

Population structure: We used principle components analysis (PCA) and Bayesian hierarchical clustering to visualize population structure across the yellow warbler breeding range. PCA was conducted using the R package SNPrelate (45). We ran PCAs for all SNPs in the RAD dataset as well as for the subset of 96 SNPs used for population assignment in wintering and migrating birds. To define breeding populations, we ran the program STRUCTURE (46) on all high-quality SNPs from the 192 SNP panel, combining both Fluidigm and RAD-Seq genotypes. We ran a range of K values (1-6) using the following STRUCTURE parameters (BURNIN=50000, NUMREPS=100000, LOCPRIOR=1). For each K value, we performed 5 replicate runs and used the Evanno method to identify the best-fit K value. For display purposes, we show one run for each K value (Figure S3).

Population assignment and migratory connectivity: We used population structure across North America as a baseline to assign wintering and migratory birds to breeding populations. We used the R package rubias (47) to first investigate how reliable our markers were to assign individuals to breeding populations using leave-one-out self assignment. We then assigned each non-breeding sample back to a pre-defined breeding population (PofZ>0.8). Migrating birds were categorized into four flyways based on regions defined by US Fish and Wildlife (fws.gov/birds/management/flyways.php). We considered a breeding population to be using a given flyway if at least 10% of birds caught along that flyway were assigned to that breeding population (Table S2).

Probability surfaces for breeding locations: For each wintering bird, we generated a probability surface to predict breeding location using the R package OriGen (48). Using the 96 SNP panel, OriGen creates continuous allele frequency surfaces, which it then combines to estimate the probability of an individual belonging to each grid cell on the map. We used 423 known breeding

individuals to train the OriGen model (MaxGridLength=70, RhoParameter=10) and then estimated the breeding location for 203 wintering samples. This produced a 70 x 23 pixel grid across North America with probabilities based on inferred breeding locations for each bird. We trimmed the map output from OriGen to the actual breeding range for yellow warbler and then scaled the remaining probability values to sum to 1 (See example Figure S8). To estimate potential error in this analysis, we used leave-one-out cross validation with the breeding samples from known locations.

Climate Data: We obtained climate information from WorldClim (49) and CRU (50) for every bird capture site and every grid point encapsulated in the predicted breeding probability surfaces. Specifically, we averaged total annual precipitation and average annual temperature across the years 1970-2000 (Worldclim) and 1966-2015 (CRU: selected to cover the full BBS record). Over the same time periods, we also obtained monthly estimates of total precipitation and monthly average, maximum, and minimum temperatures. We averaged monthly climate values across the Yellow Warbler's breeding (June and July) and wintering (Nov.- Feb.) seasons (51).

Climate Matching: To calculate the expected breeding climate for each captured, wintering bird (N=203), we multiplied the climate values at each grid point across the breeding region by the predicted probability of occurrence (output by OriGen) at that grid point and then summed over all grid points. To calculate climate dissimilarity between breeding and wintering sites, we first calculated the absolute value of the difference in climate values between the wintering site where the bird was captured and each site in breeding grid. Then, as before, we multiplied the climate difference values by the predicted probabilities of occurrence at each grid point and summed over all grid points.

Next, we calculated the null expectation for each bird's breeding climate, controlling for the bird's expected migration distance. To do so, we first calculated the geographic distance of each breeding grid point to the wintering site where each bird was captured. Then, we used the probability surfaces generated from genomic data to create a probability distribution of each bird's migration distance (see example Figure S8). Next, for each wintering bird, we multiplied the climate values of each grid point in the breeding range by the probability that the bird migrated that distance and then summed over all grid points to ultimately arrive at the null expected breeding climate value. We used the same procedure to also calculate a null expected climate difference between the wintering and breeding sites. Finally, we computed each individual's 'Climate Matching Index' by subtracting our predicted climate distance (between the wintering and breeding locations) from the null expected climate distance.

Climate Matching Index values greater than 0 indicated that an individual migrated between locations with more similar breeding and wintering climates compared to the null expectation (controlling for geographic distance). We used linear mixed models (LMMs) to determine whether the climate matching index for each climate variable was greater than 0 (*i.e.,* the intercept was significantly larger than 0). We included a random intercept of wintering location, as multiple samples often originated from the same site.

Of all the climate variables (annual total precipitation, annual average temperature, and monthly precipitation, average temperature, maximum temperature, and minimum temperature), we only found evidence that average precipitation values at breeding sites (during June and July) and wintering sites (during Nov.— Feb.) were more similar than the null expectation. To determine which birds were most likely to match monthly precipitation values between breeding and wintering sites, we added linear and quadratic effects of 'winter site monthly precipitation' to our model. For all models, we verified residuals were normally distributed and did not exhibit heteroskedasticity.

Morphological variation: We used a previously published dataset (52) to examine correlations between morphology and climate across the breeding range. This dataset includes measurements on yellow warbler museum specimens from across the entire range. For our purposes, we extracted only North American breeding individuals (n=145) and assigned a breeding population based on our spatial map. Morphological measurements taken were: bill length, bill width, bill depth, tail length, tarsus length, sixth primary (distance from bend of wrist to the tip of sixth primary), and ninth primary ("wing length"). Although body size was not available for all specimens, tarsus length has been shown to be a reasonable proxy (53). We therefore scaled all other measurements by tarsus length by calculating residuals from simple linear regressions. We used a generalized least squared model to examine correlations between each of these morphological measurements and precipitation with an exponential correlation structure accounting for longitude and latitude (*i.e.,* spatial autocorrelation). P-values were adjusted for multiple tests using a false discovery rate correction.

Population trends: To examine recent population trends and temporal relationships between precipitation and abundance for each of the inferred breeding populations, we used data from the North American Breeding Bird Surveys (BBS) (54). Using our spatial map of population structure in the breeding range, we identified the breeding population for each BBS route for which at least one individual had been observed. We used hierarchical models as described in (55), with the exception of a negative binomial used to model count data and our genetically-

inferred breeding population as strata. For each route, we calculated the deviation from the mean precipitation for each year. We then used precipitation deviation in the year prior to the BBS survey as a covariate in the model. We chose to use annual precipitation from the prior year as BBS surveys are done in the summer and thus same-year precipitation would include conditions not yet experienced. Because there can be lag effects of climate on demography, we also included precipitation from two years prior as a covariate. Mean and 90% credible intervals were calculated from the posteriors for abundance index the precipitation effects.

Data availability: Raw reads from RAD-Seq data are available through the NCBI Sequence Read Archive (PRJNA421926). Filtered SNP datasets from SNPtype assays and scripts used for analyzing data are available at https://github.com/rachaelbay/Yellow-Warbler-Climate-Tracking

Acknowledgements

We thank many people who assisted in sample collection, especially M. Boulet, R. Dawson, E. Milot, K. Hobson, H. L. Gibbs, B. Keith, the University of Washington Burke Museum, S. Albert, T. Kita, and the many Institute for Bird Populations and MAPS volunteers for providing or assisting with collection of samples. This work used the Extreme Science and Engineering Discovery Environment (XSEDE), which is supported by National Science Foundation grant ACI-1548562. This work was made possible by an NSF Postdoctoral Fellowship to R.A.B, and support from NSF Rules of Life EAGER to R.A.B. (1837940), National Geographic to K.R. (WW-202R-17), California Energy Commission to K.R. (EPC-15-043), NSF CAREER to K.R. (1942313) and First Solar Incorporated.

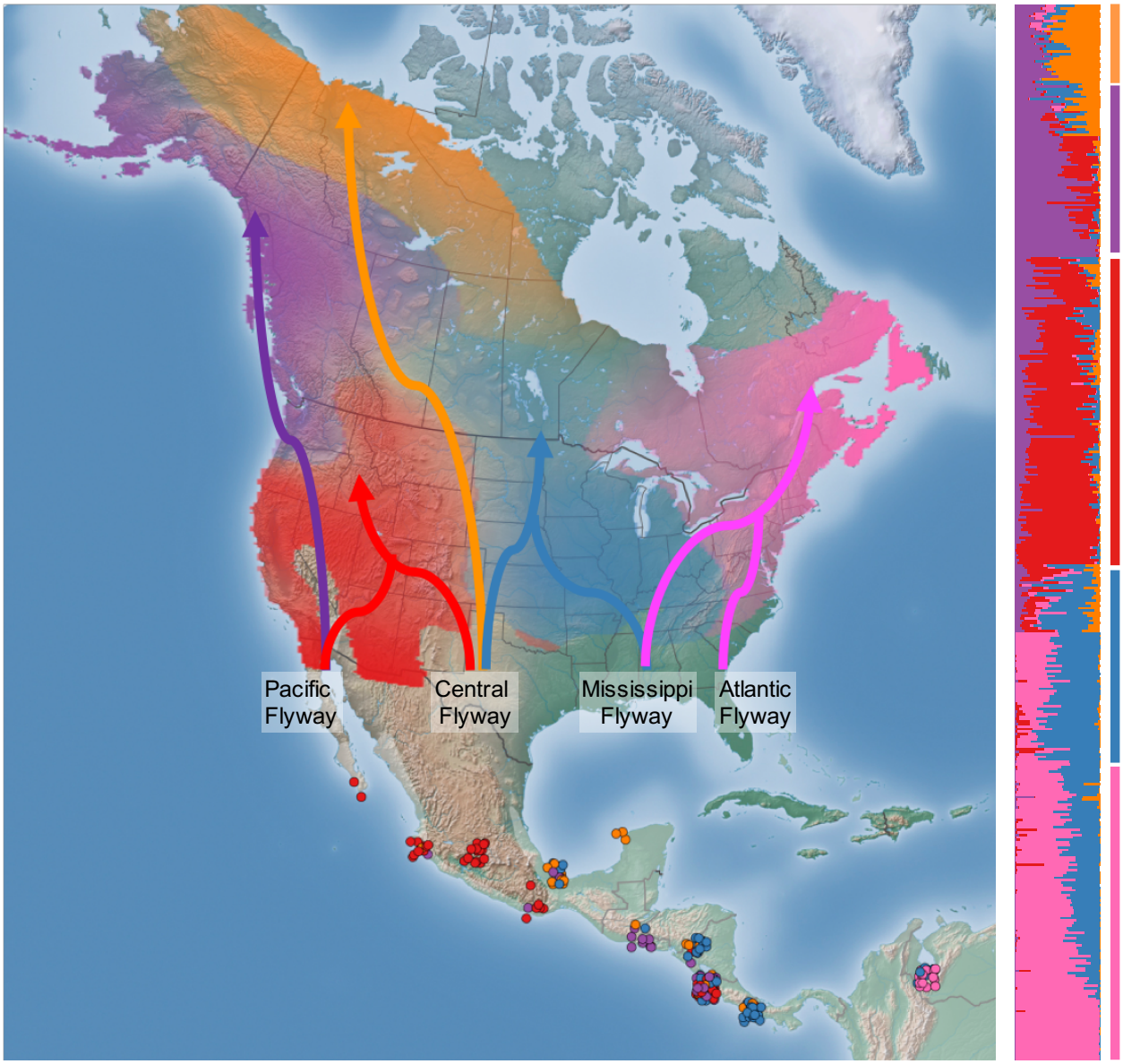

Figure 1. Migratory connectivity in yellow warbler. North American breeding range shows the five populations inferred by STRUCTURE (K=5). The barplot on the right shows the structure ancestry plot. Transparency reflects the posterior probability of group membership. Points on wintering grounds are colored based on breeding population assignment. Arrows indicate breeding population assignments for birds caught during migration.

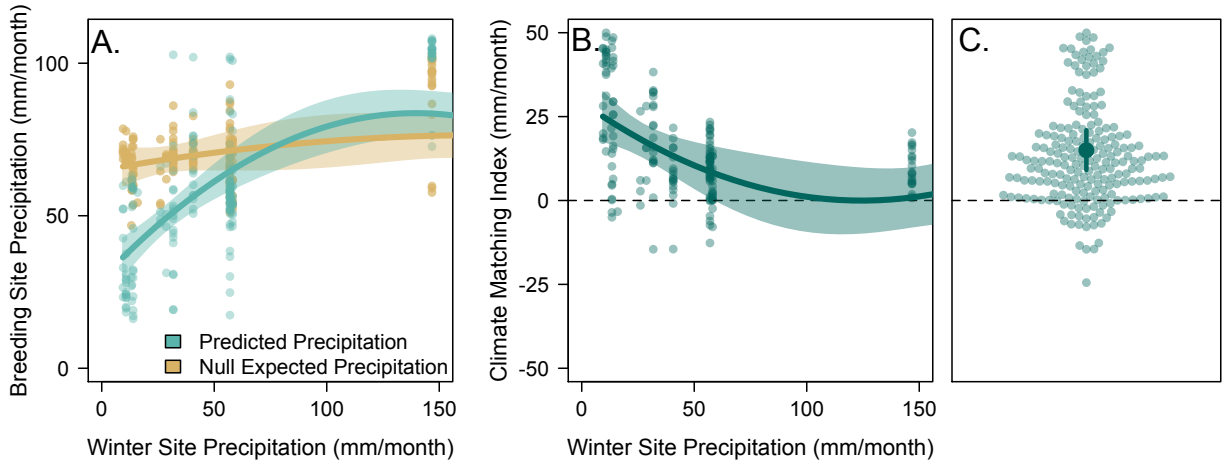

Figure 2. Individual climate tracking in yellow warblers caught in the wintering range. (A) Individuals captured at drier wintering sites were predicted to breed at drier sites (based on genetic analyses; blue points and lines). This trend that did not occur under the null expectation, in which breeding locations were only constrained by migration distances (brown points and lines). (B) After accounting for migration distances, the Climate Matching Index (see methods) indicates similarity between breeding and wintering climate is highest for birds in dry regions. (C)The Climate Matching Index was significantly greater than 0, providing evidence for individual-level climate tracking of precipitation regimes. Precipitation values were calculated from CRU data. In (A) and (B), lines represent predictions from mixed-effects models, shaded regions are 95% confidence intervals, points are individual birds. In (C), transparent points are individual birds, the solid point is the mean estimated Climate Matching Index, and the line is the 95% confidence interval.

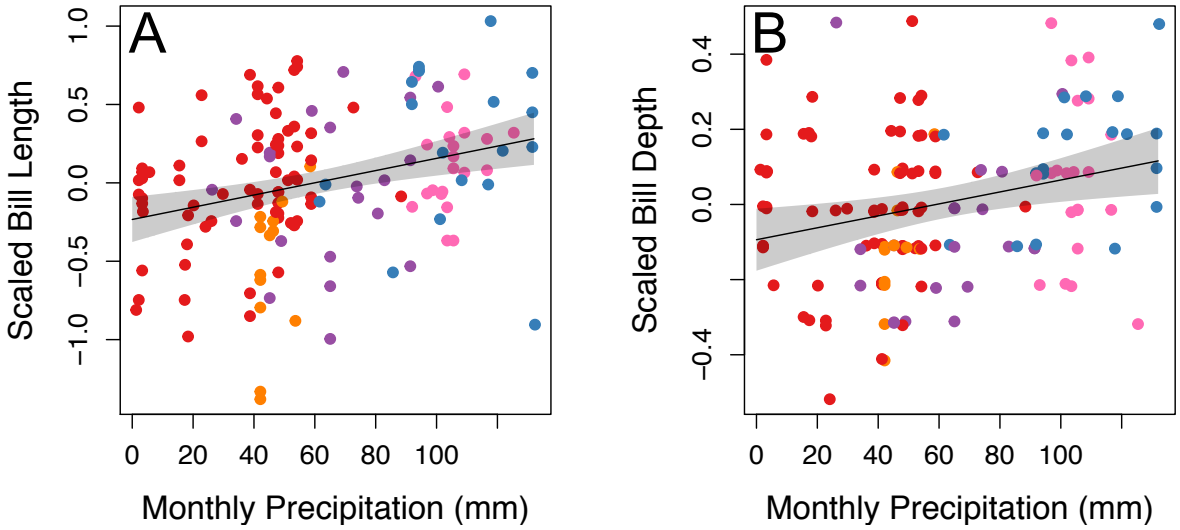

Figure 3. Correlation between bill length (A) and bill depth (B) and precipitation for birds sampled across the breeding range. Measurements were scaled by tarsus length as a proxy for body size. Morphological data are from Weidenfeld (1991). Precipitation values were calculated as average precipitation during the breeding season, extracted from the CRU dataset. Points (individual birds) are colored according to the five yellow warbler populations depicted in Figure 1.

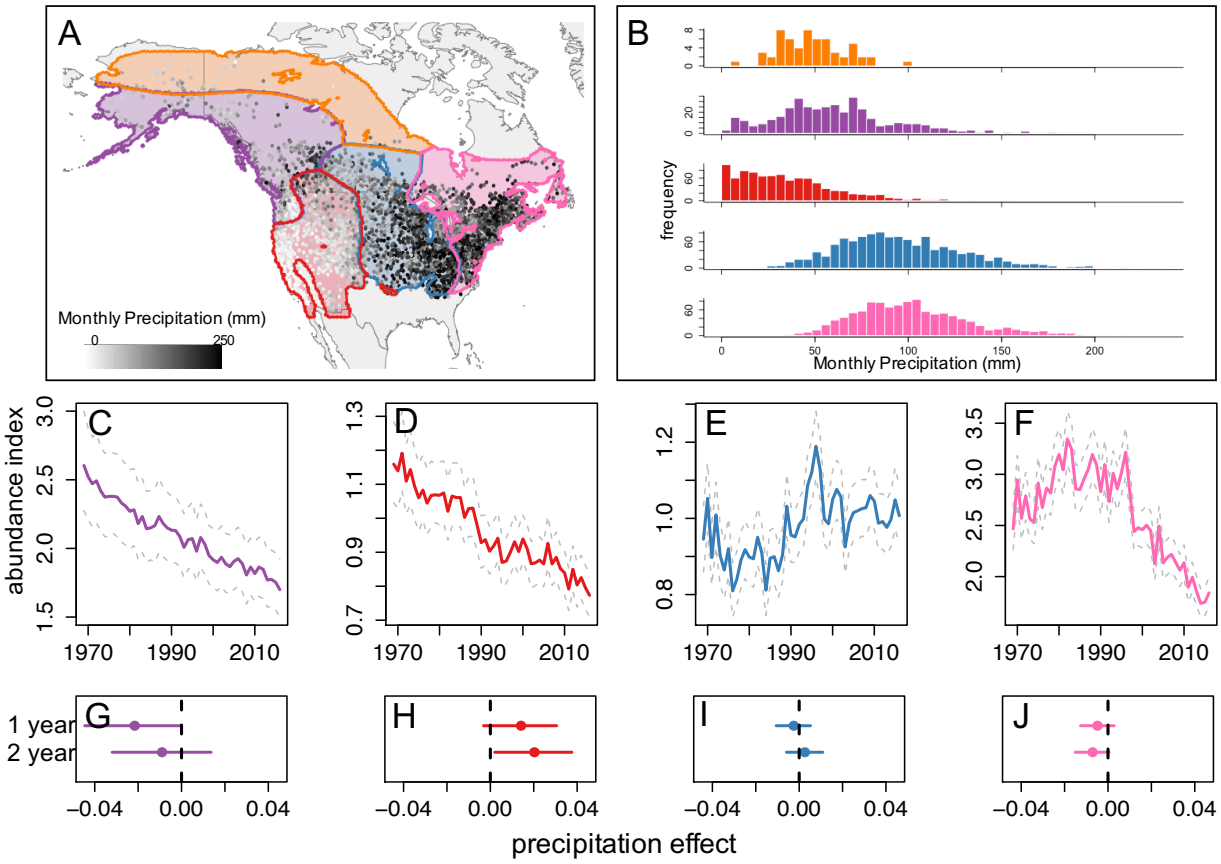

Figure 4. Associations between precipitation and abundance trends. (A-B) Breeding season precipitation values (average monthly precipitation from June to July) for each of the five yellow warbler populations. (C-F) Population trends for each population inferred from North American Breeding Bird Survey (BBS) data. We did not include the Arctic (orange) population in our analysis because there are very few BBS routes in that region. Dotted grey lines correspond to 90% credible intervals. (G-J) The effect of precipitation in the previous year and two years on relative abundance for each population. Mean and 90% credible intervals are shown for β values in the hierarchical model (positive values indicate a positive effect of precipitation on relative abundance) for precipitation in the year before the survey (1 year) and two years before the survey (2 year).

References

1. Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications* 1(1):95–111.

2. Bay RA, Palumbi SR (2014) Multilocus adaptation associated with heat resistance in reef-building corals. *Current Biology* 24(24):2952–2956.

3. Walters RJ, Berger D (2019) Implications of existing local (mal) adaptations for ecological forecasting under environmental change. *Evolutionary Applications* 12(7):1487–1502.

4. Brady SP, et al. (2019) Causes of maladaptation. *Evolutionary Applications* 12(7):1229–1242.

5. Jump AS, Penuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters* 8(9):1010–1020.

6. Rehfeldt GE, et al. (2002) Intraspecific responses to climate in Pinus sylvestris. *Glob Change Biol* 8(9):912–929.

7. Nakazawa Y, Peterson AT, Martinez-Meyer E, Navarro-Sigüenza AG (2004) Seasonal niches of Nearctic-Neotropical migratory birds: implications for the evolution of migration. *The Auk* 121(2):610–618.

8. Somveille M, Manica A, Rodrigues AS (2019) Where the wild birds go: explaining the differences in migratory destinations across terrestrial bird species. *Ecography* 42(2):225–236.

9. Zurell D, Gallien L, Graham CH, Zimmermann NE (2018) Do long-distance migratory birds track their niche through seasons? *J Biogeography* 45(7):1459–1468.

10. Gómez C, Tenorio EA, Montoya P, Cadena CD (2016) Niche-tracking migrants and niche-switching residents: evolution of climatic niches in New World warblers (Parulidae). *Proceedings of the Royal Society B: Biological Sciences* 283(1824):20152458.

11. Winger BM, Auteri GG, Pegan TM, Weeks BC (2019) A long winter for the Red Queen: rethinking the evolution of seasonal migration. *Biological Reviews* 94(3):737–752.

12. Bridge ES, et al. (2013) Advances in tracking small migratory birds: a technical review of light-level geolocation. *Journal of Field Ornithology* 84(2):121–137.

13. Arlt D, Low M, Pärt T (2013) Effect of geolocators on migration and subsequent breeding performance of a long-distance passerine migrant. *PLoS ONE* 8(12):e82316.

14. Kelly JF, Ruegg KC, Smith TB (2005) Combining isotopic and genetic markers to identify breeding origins of migrant birds. *Ecological Applications* 15(5):1487–1494.

15. Hobson KA (2005) Stable isotopes and the determination of avian migratory connectivity and seasonal interactions. *The Auk* 122(4):1037–1048.

16. Ruegg KC, et al. (2014) Mapping migration in a songbird using high-resolution genetic markers. *Mol Ecol* 23(23):5726–5739.

17. Rañola JM, Novembre J, Lange K (2014) Fast spatial ancestry via flexible allele frequency surfaces. *Bioinformatics* 30(20):2915–2922.

18. Bay RA, et al. (2018) Genomic signals of selection predict climate-driven population declines in a migratory bird. *Science* 359(6371):83–86.

19. Bradburd GS, Coop GM, Ralph PL (2018) Inferring continuous and discrete population genetic structure across space. *Genetics* 210(1):33–52.

20. Fitzpatrick MC, Keller SR (2015) Ecological genomics meets community-level modelling of biodiversity: mapping the genomic landscape of current and future environmental adaptation. *Ecology Letters* 18(1):1–16.

21. Gibbs HL, Dawson RJG, Hobson KA (2000) Limited differentiation in microsatellite DNA variation among northern populations of the yellow warbler: evidence for male-biased gene flow? *Mol Ecol* 9(12):2137–2147.

22. Cilimburg AB, Lindberg MS, Tewksbury JJ, Hejl SJ (2002) Effects of dispersal on survival probability of adult Yellow Warblers (Dendroica petechia). *The Auk* 119(3):778.

23. Boulet M, Gibbs HL, Hobson KA (2006) Integrated analysis of genetic, stable isotope, and banding data reveal migratory connectivity and flyways in the northern yellow warbler (*Dendroica petechia: Aestiva* group). *Ornithological Monographs* 61:29–78.

24. Milot E, Gibbs HL, Hobson KA (2000) Phylogeography and genetic structure of northern populations of the yellow warbler (*Dendroica petechia*). *Mol Ecol* 9:667–681.

25. Witynski ML, Bonter DN (2018) Crosswise migration by Yellow Warblers, Nearctic-Neotropical passerine migrants. *Journal of Field Ornithology* 89(1):37–46.

26. Greenberg R, Danner R, Olsen B, Luther D (2012) High summer temperature explains bill size variation in salt marsh sparrows. *Ecography* 35(2):146–152.

27. Symonds MRE, Tattersall GJ (2010) Geographical Variation in Bill Size across Bird Species Provides Evidence for Allen's Rule. *American Naturalist, The* 176(2):188–197.

28. Gardner JL, et al. (2016) Spatial variation in avian bill size is associated with humidity in summer among Australian passerines. *Climate Change Responses* 3(1):11.

29. Grant R, Grant PR (1993) Evolution of Darwin's finches caused by a rare climatic event. *Proc Biol Sci* 251:111–117.

30. Bosse M, et al. (2017) Recent natural selection causes adaptive evolution of an avian polygenic trait. *Science* 358(6361):365–368.

31. Cattau CE, Fletcher RJ Jr, Kimball RT, Miller CW, Kitchens WM (2018) Rapid morphological change of a top predator with the invasion of a novel prey. *Nature ecology & evolution* 2(1):108–115.

32. Badyaev AV, Young RL, Oh KP, Addison C (2008) Evolution on a local scale: developmental, functional, and genetic bases of divergence in bill form and associated changes in song structure between adjacent habitats. *Evolution* 62(8):1951–1964.

33. Smith TB (1993) Disruptive selection and the genetic basis of bill size polymorphism in the African finch Pyrenestes. *Nature* 363(6430):618–620.

34. Janzen DH, Schoener TW (1968) Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49(1):96–110.

35. Chavarria Pizarro T, et al. (2019) Strong phenotypic divergence in spite of low genetic structure in the endemic Mangrove Warbler subspecies (Setophaga petechia xanthotera) of Costa Rica. *Ecol Evol*.

36. Sillett TS (2000) Impacts of a Global Climate Cycle on Population Dynamics of a Migratory Songbird. *Science* 288(5473):2040–2042.

37. Mazerolle DF, Dufour KW, Hobson KA, Haan den HE (2005) Effects of large-scale climatic fluctuations on survival and production of young in a Neotropical migrant songbird, the yellow warbler *Dendroica petechia*. *Journal of Avian Biology* 36:155–163.

38. Nott MP, DeSante DF, Siegel RB, Pyle P (2002) Influences of the El Niño/Southern Oscillation and the North Atlantic Oscillation on avian productivity in forests of the Pacific Northwest of North America. *Global Ecology and Biogeography* 11(4):333–342.

39. LaManna JA, George TL, Saracco JF, Nott MP, DeSante DF (2012) El Niño—Southern Oscillation influences annual survival of a migratory songbird at a regional scale. *The Auk* 129(4):734–743.

40. Ali OA, et al. (2016) RAD capture (Rapture): flexible and efficient sequence-based genotyping. *Genetics* 202(2):389–400.

41. Catchen J, Hohenlohe PA, Bassham S, Amores A, Cresko WA (2013) Stacks: an analysis tool set for population genomics. *Mol Ecol* 22(11):3124–3140.

42. Langmead B, Salzberg SL (2012) Fast gapped-read alignment with Bowtie 2. *Nature Methods* 9(4):357–359.

43. Weir BS, Cockerham CC (1984) Estimating F-Statistics for the Analysis of Population Structure. *Evolution* 38(6):1358.

44. Goudet J (2005) hierfstat, a package for R to compute and test hierarchical F-statistics. *Molecular Ecology Notes* 5:184–186.

45. Zheng X, et al. (2012) A high-performance computing toolset for relatedness and principal component analysis of SNP data. *Bioinformatics* 28(24):3326–3328.

46. Pritchard JK, Stephens M, Donnelly P (2000) Inference of Population Structure Using Multilocus Genotype Data. *Genetics* 155(2):945–959.

47. Anderson EC, Waples RS, Kalinowski ST (2008) An improved method for predicting the accuracy of genetic stock identification. *Can J Fish Aquat Sci* 65(7):1475–1486.

48. Rañola JM, Novembre J, Lange K (2014) Fast spatial ancestry via flexible allele frequency surfaces. *Bioinformatics* 30(20):2915–2922.

49. Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol* 37(12):4302–4315.

50. Harris I, Jones PD, Osborn TJ, Lister DH (2014) Updated high-resolution grids of monthly climatic observations–the CRU TS3. 10 Dataset. *Int J Climatol* 34(3):623–642.

51. Fink D, et al. (2018) Modeling avian full annual cycle distribution and population trends with citizen science data. *Ecological Applications*.

52. Wiedenfeld DA (1991) Geographical morphology of male yellow warblers. *The Condor* 93:712–723.

53. Senar JC, Pascual J (1997) Keel and tarsus length may provide a good predictor of avian body size. *ARDEA-WAGENINGEN-* 85:269–274.

54. Sauer JR, et al. (2017) The first 50 years of the North American Breeding Bird Survey. *The Condor: Ornithological Applications* 119(3):576–593.

55. Link WA, Sauer JR (2002) A hierarchical analysis of population change with application to cerulean warblers. *Ecology* 83(10):2832.