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Running Head: Environment in new world sparrow song

Authors: Kaiya L. Provost1,2*, Jiaying Yang2,3, Bryan C. Carstens2

1: Department of Biology, Adelphi University, One South Avenue, Garden City NY, 11530 USA.
2: Museum of Biological Diversity and Department of Evolution, Ecology and Organismal Biology, The Ohio State University, 1315 Kinnear Rd., Columbus OH, 43212 USA.
3: Biological Science Department, Vanderbilt University, 2201 West End Ave, Nashville, TN 37235 USA.

* Corresponding author: kprovost@adelphi.edu

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Abstract

One of the most obvious traits of birds is the astonishing array of songs that are produced by most species. The diversity and functions of bird vocalizations have been studied across many facets of biology, but variation in song is often assumed to be determined by sexual or social selection, rather than natural selection acting in the context of the landscape. Here we use deep machine learning to investigate multiple co-distributed species in the New World Sparrows. We leverage existing bioacoustic and genetic repositories and environmental data to identify the processes that structure variation in bird song within a community, and to determine how this variation corresponds to genetic and phenotypic patterns. Automated processing of these data at the family level has allowed us to synthesize at deep phylogenetic scales. Analysis of these data using a multiple matrix regression with randomization indicate that song variation in ~40% of species can be explained by environmental and stochastic factors. Genetic variation is explained by similar factors in ~30% of the species. This suggests that across a community and global scale, the action of natural selection on the evolution of song is at least as impactful as it is on other genetically-determined traits.

Introduction

Bird song (i.e., long and complex vocalizations associated with mating) is extremely important for avian reproduction and therefore their Darwinian fitness. Field investigations have indicated that song is used to mediate territorial disputes (e.g., de Kort et al 2009) and to advertise to potential mates (e.g., Eriksson et al 1986). Bird song also plays an important role in premating reproductive isolation (e.g., Brambilla et al 2008). Given how important song is to reproduction, sexual and social selection are assumed to be the predominant forces shaping song evolution (e.g., Catchpole 1987). This has led to a relative lack of attention to how landscape level variation affects bird songs within species in large part because sexual and social selection are expected to act as a homogenizing force (without the evolution of differences in preference) if the function of the trait (i.e., song) is to maintain species boundaries, as commonly assumed (e.g., Slabbekoorn and Smith 2002). Even in species where song is used by females to evaluate the quality of potential mates, sexual selection should act to maintain the songs of males near the fitness optimum. For example, Catchpole (et al 1984) shows that in sedge warblers, more complex songs get more copulation solicitations from potential mates, and as such there is a selective pressure for songs to become more complex through time, before hitting the performance maximum. While there is a general expectation that sexual selection should lead to a reduction in spatial variation of bird song across a species the obvious presence of spatial variation within species necessitates in the form of dialects indicate that other forces act in opposition to sexual selection to produce diversification. Dialects, which are regional variations of communication, exist in bird species in the form of variation in songs through space and time (Trainer 1989). Some dialect variations are associated with subspecific variation (e.g., Parker et al 2018), but in others they do not have clear boundaries (e.g., Wright and Dahlin 2017). The formation of dialects has numerous proposed causes.

One potential factor leading to the evolution of dialects is natural selection. This factor has been suggested to influence intraspecific song variation by the relationship between habitat and song in the ovenbird family (Furnariidae; Derryberry et al 2018). Dialect evolution may be caused by environmental constraints, as songs in urban environments differ in their bandwidth and frequency from rural environments, which may be an adaptation to avoid anthropogenic noise (Derryberry et al 2016) but could potentially result from phenotypic plasticity (Derryberry

et al 2020). Indirect effects may also play a role due to constraints on other features; for example Furnariids show a strong relationship between morphological variation and song (Derryberry et al 2018). Whether direct or indirect, natural selection should act as a diversifying process at the landscape scale (Cardoso and Price 2010) so long as the abiotic aspects contained within a species' range are variable.

In contrast to natural selection, there are stochastic processes that could potentially influence song evolution. For example, since song production has a genetic basis (Jarvis et al 1998, Scharff and Adam 2013), if the genomic DNA evolves due to genetic drift in violation of Hardy-Weinberg expectations these changes may have an effect on song production. Several investigations have suggested that species which exhibit more genetic differentiation also tend also to be more acoustically differentiated (Freeman et al 2017, Freeman et al 2022). Additionally, social learning, which occurs in many species of birds but particularly the Oscines or "Songbirds", may be important. In such species, young individuals must learn songs from the adults in the population (Slater 1989). Since this learning is imperfect, it can result in a phenomenon known as cultural drift where songs change from are different from year to year (e.g., Derégnaucourt and Gahr 2013). Since birds do not have infinite dispersal capabilities, any differences that emerge due to cultural drive are likely to be localized in space. The presence of song learning is known to influence the cadence at which song evolves (Mason et al 2016). Finally, in any species population structure may also play a role. For example, decades of phylogeographic results have suggested that species often persisted in multiple glacial refugia during the Pleistocene (e.g., Brown Harrigan Lavretsky 2022, Pârâu and Wink 2021). Even in the presence of selective constraints, song differentiation via these stochastic processes could eventually lead to differentiation of song in different glacial refugia (e.g., Dingle et al 2010; Provost et al 2018; Lipshutz et al 2018). Even after the retreat of the glaciers and the post-glacial expansion of bird populations there is likely to be a remnant of intraspecific variation from this process.

While each of the aforementioned factors (i.e., sexual and social selection, natural selection, cultural drift) may influence the evolution of bird song, it is often assumed that the major influence on the evolution of song has been sexual and social selection (e.g., Catchpole 1987). However, we lack a comprehensive understanding of the extent to which natural selection and stochastic cultural drift matter. A major challenge in determining the impact of any factor on song evolution is designing an investigation that can ascertain the relative influence of these factors. Unlike genetic data, which are now easily collected (e.g., McCormack et al. 2013), and environmental data, which are available in databases such as WorldClim (Fick et al 2017), data on intraspecific variation in bird songs are challenging to obtain. The challenge is not so much in obtaining the song data, as bird song recordings in bioacoustic databases cover much of the globe, existing as combinations of citizen science efforts (e.g., eBird, Xeno-Canto), museum-curated collections (e.g., Borror Lab of Bioacoustics, Macaulay Library), or *ad hoc* individual recordings (e.g., uploads on Flickr, YouTube). However, these databases typically contain repositories of the recordings themselves, rather than summaries of the variation in the songs. Extraction of data from these recordings has traditionally been a challenging endeavor.

When song data are analyzed in research investigations, ornithologists have traditionally annotated spectrograms of the recorded song by hand to extract data on intraspecific variations (e.g., Latimer 1977, Wonke and Wallschläger 2009; see also Kvsn et al 2020), and taken precautions to ensure that songs from different individuals are annotated in a consistent manner (e.g., Duc et al 2021). However, it is not the case that songs from one study are annotated in the

same manner as a different set of songs from a different investigation, which makes it difficult to conduct something like a meta-analysis using the results of many independent investigations. The sheer time required to annotate a single bioacoustic recording when combined with the challenges involved with comparing across studies have to date inhibited efforts to investigate bird songs across broader scales. However, recent advances in artificial intelligence (AI) methods for annotation of bird song (e.g., Cohen et al 2022) have enabled automated extraction of summary statistics from bird song recordings that produce accurate data that are directly comparable across species (e.g., Provost et al. 2022). These technological developments enable a broader investigation into the factors that influence intraspecific variation bird songs.

Here, we seek to investigate the factors that potentially explain song diversity in one focal group, the New World Sparrows (Family: Passerellidae). We test two hypotheses, which are not mutually exclusive. First, we hypothesize that environmental selection will be an important factor driving evolution across the New World Sparrow radiation, specifically that climate, habitat type, and urbanization act to influence intraspecific variation in song. This hypothesis predicts that, within a species, environmental distances will be correlated with intraspecific differences in bird songs. A corollary is also tested, by evaluating the extent to which morphological variation is correlated with intraspecific differences in song. The second hypothesis predicts that stochastic cultural drift has influenced intraspecific variation in sparrow song. Within a species, this hypothesis predicts that intraspecific variation in song is correlated with the physical or temporal distance among individuals. Since neutral genetic variation is predicted to vary in a similar manner, we also establish the extent to which there is genetic isolation by distance in the Passerellidae.

Methods

Focal System: Passerellidae

Our work adopts the IOC taxonomy for determining species designations (Gill et al 2023). Under this framework, the New World Sparrows include 30 genera, 138 species, and 419 named subspecies (Gill et al 2023; Klicka et al 2014, Barker et al 2015, Bryson et al 2016). The clade is distributed throughout the entirety of North and South America, save for the northernmost latitudes, and occupying a broad range of habitats therein (Winkler et al 2020). Phylogenetic relationships within this group vary, though taxa generally fall into eight major clades (i.e., Klicka et al 2014). We use one recent phylogeny (Bryson et al 2016) at the genus level to visualize phylogeographic patterns. Since some genera were missing from the Bryson et al. phylogeny, their placement followed two previous phylogenies (Barker et al 2015, Klicka et al 2014). The genus *Xenospiza* was placed as sister to *Centronyx*, which was in turn sister to *Melospiza*. The genus *Torreornis* was placed as sister to *Pezopetes*, and similarly *Oreothraupis* as sister to *Chlorospingus* and *Amphispizopsis* as sister to *Amphispiza*.

Acoustics

We downloaded all 10,836 songs of the family Passerellidae from Xeno-Canto (XC) on 5 July 2022. We supplemented these recordings with 12,145 songs from the Borror Lab of Bioacoustics (BLB) collection. In both cases, previous studies had annotated songs from these repositories (Provost el al 2022); we used those annotations to supplement our analysis. The few individuals who were described in the metadata as hybrids were eliminated from the analysis.

Songs were converted to mono WAV format and to a sample rate of 48,000 Hz using the resamp function in the seewave 2.2.0 package in R version 4.2.1 (Suer et al 2008; R Core Team 2022).

We used a machine learning model (i.e., TweetyNet; Cohen et al 2022) to identify the locations of individual syllables in each recording . A model that had been previously trained on nine species, including non-Passerellids (i.e., 9SppBalanced; Provost et al 2022) was applied to the new analysis of recordings three ways. First, the model was used to identify syllables without making any changes to the model. Second, we fine-tuned the model on only Passerellidae species with annotations from another study (Provost et al 2022) and used that version to identify syllables. Lastly, we fine-tuned the model again on all annotated Passerellidae that we had generated as part of the present study. After each set of predictions of syllables had been made, we extracted as syllables anything that the model had identified across any of the three sets of predictions. We removed all syllables that were less than 0.05 seconds in length as spurious.

In a similar manner to how phenotypic traits are measured within samples before being included in a quantitative analysis we extracted summary data from the song syllables. This was accomplished using the warbleR package version 1.1.28 (Araya-Salas and Smith-Vidaurre 2017) in R version 4.2.1. We calculated summary statistics based off of spectrograms using the function spectro_analysis. The summary statistics included metrics of song duration; mean and standard deviation of frequency; quantiles (including median, 25%, and 75%, and the interquartile distance) of frequency; quantiles of time duration; skew and kurtosis of the frequency spectrum; entropy measurements (spectral entropy, time entropy, and overall entropy); spectral flatness; dominant frequency calculations (mean, minimum, maximum, range, and value at start and end of sound); modulation index and slope of dominant frequency; peak frequency; and mean peak frequency. We also calculated fundamental frequency time series using the function freq_ts, which allowed us to get the frequency at each time bin. This lets us calculate the number of inflections, slopes, and mean slope per sound.

After generating these summary statistics, we extracted five for further analysis: bandwidth, as the IQR of frequency; time duration, as the IQR of the time; center, as the median frequency; inflections, as the number of fundamental frequency inflection points; and slope, as the mean fundamental frequency slope. From these five summary statistics we calculated values for each syllable, then generated a centroid value for each individual across all syllables. We performed a principal components analysis (PCA) on these data for downstream analyses (see Supplement).

Once centroid values for the five summary statistics were calculated for all individuals, we calculated euclidean distances between all individuals across all species. These euclidean distances were used as representation of song variation as the predictor variable of the song (see below). We then created subsets of these euclidean distances for each genus, species, and subspecies across Passerellidae. Unless otherwise specified, we only report results for the species distance matrices below -- for other analyses see Supplement. Finally, to serve as a proxy for the overall distances represented within each taxon, we took the mean and standard deviation of euclidean distance for each.

Recording quality varied across taxa, with some being of high quality (e.g., Xeno-Canto quality A), low quality (e.g., Xeno-Canto quality E) or unknown quality (e.g., the BLB recordings). We tested the impact of recording quality by repeating MMRR analyses (see below) on subsets of homogenous recording quality for *Zonotrichia leucophrys*, which had the most recordings (see Supplement).

Genetics

We downloaded geospatially labeled genetic data for all birds from GenBank using the phylogatR framework (Pelletier et al. 2022) on 7th December 2020. Of the 9,338,693 sequences present for all birds, Passerellidae make up 29,030 of those sequences representing 36 species. The overwhelming majority of the genes were CO1, so we restricted our analyses to that gene only.

From these genetic data we calculated genetic distances between individuals using the dist.gene function in the ape package version 5.7 in R. After that, we used those genetic distances as the predictor variable (see below). We also calculated mean genetic distance within species by taking the average pairwise across all individuals. We chose to do genetic analyses as a parallel because the song data and genetic data were not always collected from the same localities and as such cannot be directly compared in the same model. Instead we chose to compare and contrast the two models to see if similar patterns emerge.

Traits

Morphological differentiation, and phenotypic differentiation more broadly, is one major way that species adapt to their environment. In birds, bill morphology is thought to be selected with respect to diet (Soons et al 2015, Tokita et al 2017), song (Huber et al 2006), nest building (Sheard et al 2023), and thermoregulation (Greenberg et al 2012, Tattersall et al 2017), and constrained by phylogeny (Bright et al 2016). Like in other vertebrates, body size is a key factor for thermoregulation (Weathers 1981, Ryeland et al 2017), and is also important in influencing song (e.g., Demery et al 2021). To assess the impact of morphological measures on our data, we downloaded data from AVONET (Tobias et al 2022, Ecol Letters), which has measures of beak length (to nares and culmen), beak width, beak depth, tarsus length as a proxy for body size, primary and secondary feather length, tail length, the hand-wing index, and Kipp's distance.

This dataset contained 127 Passerellidae species across all 30 genera (missing: *Arremon basilicus, A. costaricensis, A. perijanus, A. phaeoplerus, Atlapetes meridae, At. nigrifrons, Junco bairdi, Passerella megarhyncha, P. unalaschcensis,* and *Pipilo naufragus*). There were 1,177 measurements taken across the family. We used the average value for each species as a factor when looking at the genetic and song MMRR results. We also calculated the average value for each genus. We evaluated whether morphology explained our results by using ANOVA and Tukey's Honest Significant Difference tests (Miller 1981; Yandell 1997). We evaluated significance using an alpha value of 0.05.

Spatial and Temporal Features

To examine the impact of the environment, we downloaded rasterized data from multiple sources representing various environmental features; climate, land cover, habitat type, topography, soil features, urbanization, geographic distance, and temporal distance (Fick et al 2017, Buchorn et al 2015, EROS 2018, Farr et al 2007, Poggio et al 2021, Ellis et al 2021). After removing variables that were invariable in our dataset, this resulted in 48 total variables. Geographic distance (latitude and adjusted longitude) and temporal distance (year of recording) were separated out as representing the stochastic processes of isolation-by-distance and cultural drift, respectively. Note that year of recording was only available for the song data. The remaining variables were used as representations of environmental data. We performed a PCA on the environmental data, centering and scaling the variables and imputing missing data such

that any missing values were assigned the mean. We did this using the prcomp function in the stats package in R. We chose to retain five of the resulting PCs as they explained over 50% of the variation across the 48 original variables, and these were used to represent environmental distance. We calculated a euclidean distance matrix of geographic distance, temporal distance, and environmental distance between all individuals in both the genetic and song datasets.

Synthesis

We examined biases in sampling in XC, BLB, and GenBank data for Passerellidae using the locational and temporal metadata associated with each. We performed a multiple matrix regression with randomization (MMRR) analysis to test our hypotheses (Wang, 2013).MMRR estimates the coefficients of relationships between multiple distance matrices, controlling for the impact of all of the variables in the dataset, and then uses a randomization technique to estimate a *p*-value of significance. When an MMRR analysis is conducted with the same input matrices, all of the returned coefficients are identical except for *p*-values. We conducted MMRR comparisons multiple times for each dataset, randomizing each 1000 times, and then averaged the *p*-values accordingly. For the song models each were set up so that song distance was being predicted by environmental distance, geographic distance, and temporal distance. Because we did not have temporal information for our genetic data, those models were set up so that genetic distance was predicted by environmental and geographic distance only. If the environmental selection hypothesis is supported, the MMRR will return a significant value *p*-value (using an alpha value of 0.05) for the environmental distance matrix. If the stochastic cultural drift hypothesis is supported, the MMRR will return a significant p-value either geographic distance, temporal distance, or both. Both hypotheses may also be supported simultaneously.

MMRRs were performed at four levels: family, genus, species, and subspecies. We performed these analyses at these different taxonomic levels to evaluate the impact of each factor on progressively larger populations. Results other than species-level are found in the supplemental material. We then compared taxa that were significant in environment or geography for both song and genetics with their morphological measurements. We also compared this significance with the absolute differences present in genetics and song across species. We look at the phylogenetic relationships as well to see whether there is evidence that these patterns are phylogenetically conserved.

Results

Data Summary

Sampling of the Passerellidae is uneven across North and South America in both song and genetics (Figure 1). The western coast of North America, and Ohio, are highly sampled, whereas much of the Amazon, central North America, and the Caribbean are undersampled. The recordings vary in terms of time recorded as well (Figure 2). The BLB is a historical collection and substantially older recordings (range 1948-2014, mean 1979) than XC (range 1976-2022, mean 2013). Both databases also have peak recording from April to July, which corresponds to the breeding season for most species. 80.0% of BLB songs were recorded during these months, whereas 56.3% of XC songs were recorded during these months. Across space, sampling between the recording data and the genetic data is significantly correlated though the correlation is weak (log-corrected, p=0.030, adjR2 = 0.038).

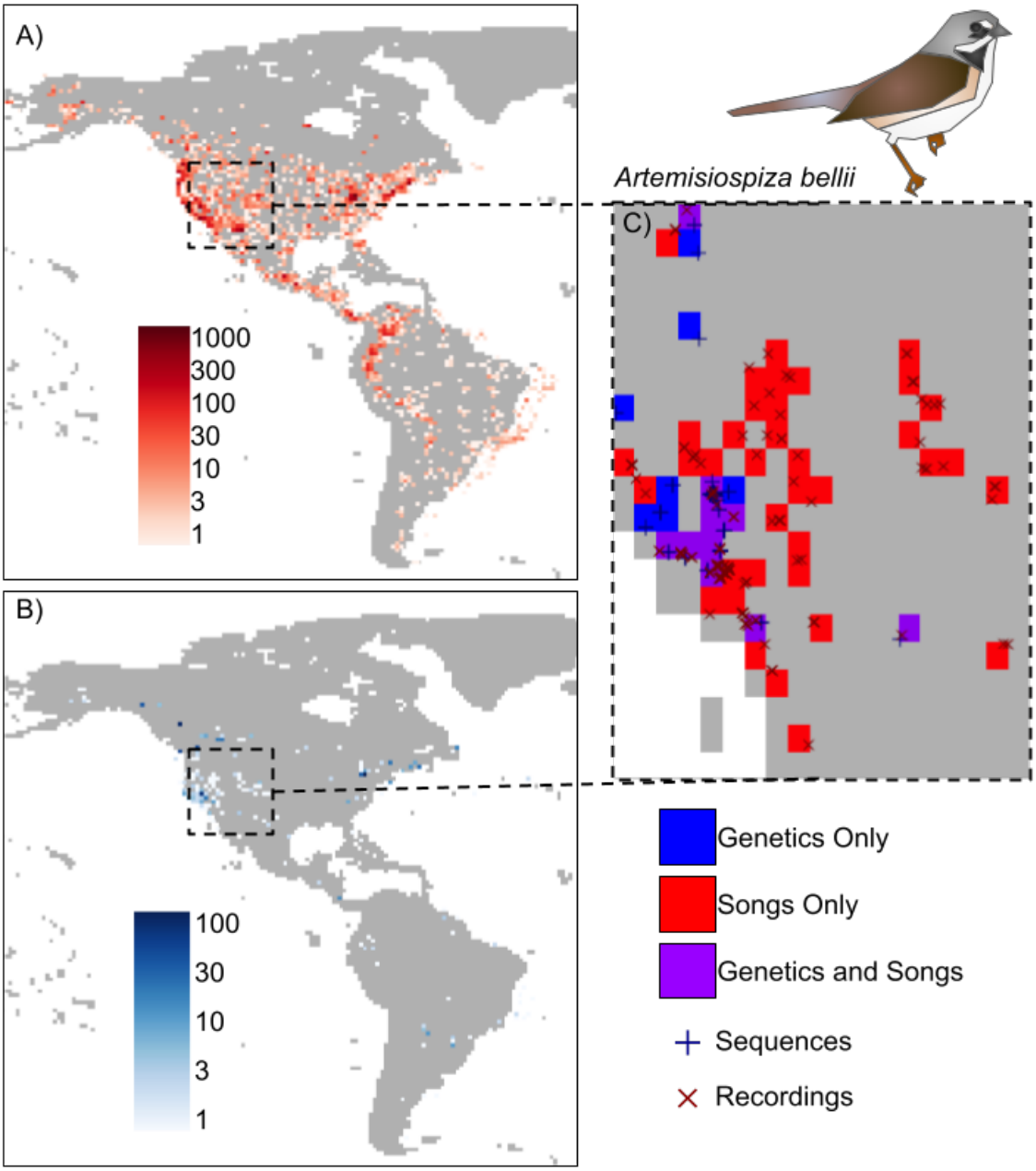

Figure 1: Song and genetic sampling rarely overlap within species. A) Song sampling from Xeno-Canto of all Passerellidae species. Color indicates density of recordings on a log scale, with lighter reds showing areas with few recordings, darker reds showing areas of many recordings, and gray showing areas with no recordings. Cells are one-degree latitude by one-degree longitude. B) Genetic sampling from phylogatR of all Passerellidae species. Color indicates density of recordings on a log scale, with lighter blues showing areas with few sequences, darker blues showing areas of many sequences, and gray showing areas with no sequences. Cells are one-degree latitude by one-degree longitude. C) Exemplar overlap for one species, *Artemisiospiza bellii*. Points show individual sequences (blue cross) or song recordings (red X). Color beneath shows whether the cell contains genetic data only (blue), song data only (red), or both genetic and sign data (purple). Cells are one-degree latitude by one-degree longitude.

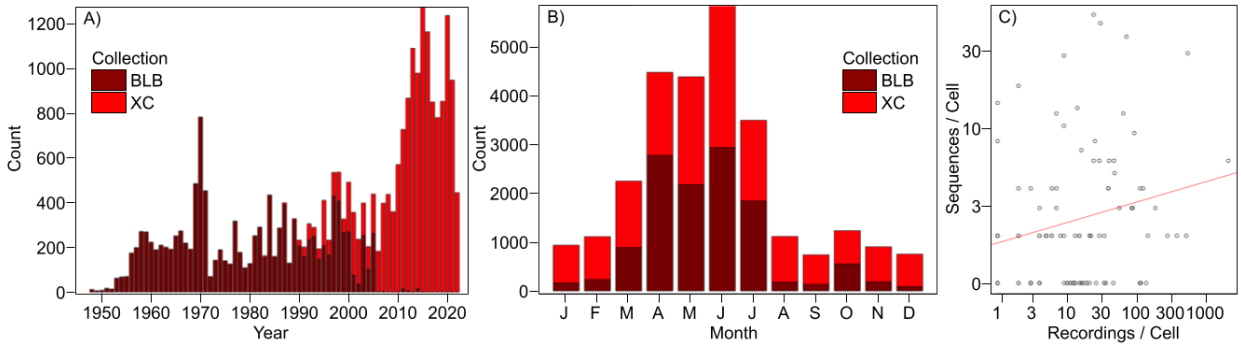

Figure 2: A) Recordings in the Borror Laboratory of Bioacoustics database (BLB, dark red) and Xeno-Canto (XC, red) across years. B) Recordings in the BLB (dark red) and XC (red) across months of the year. C) Recordings per cell vs sequences per cell across range of Passerellidae.

Acoustics and Genetics

After processing all song recordings through the TweetyNet model (Cohen et al 2022), our data consisted of 26,169 recordings and 513,617 annotated syllables. This comprised all 30 genera, 134 species, and 316 subspecies. All but one recording had latitude and longitude information, and 23,544 had date information. Taxa ranged in terms of their overall song differentiation. At the species level, the range was from 0.00 (*Chlorospingus inornatus*) to 4.32 (*Atlapetes personatus*). Quantitative data were extracted using summary statistics from each species, which are available in Supplemental Table 3.

For our PCA on song variables, we retained all five PCs for downstream analyses (Table 1). Syllables with high values of PC1 were long, with numerous inflection points, and narrow bandwidth. Syllables with high values of PC2 were high-frequency, wide-bandwidth. Syllables with high PC3 had negative slopes and high frequencies. Syllables with high PC4 had narrow bandwidths and positive slopes. Syllables with high PC5 had low frequencies, were short, and had numerous inflection points.

Table 1: Principal components analysis on five song variables extracted from Passerellidae syllables. Importance of each PC and loadings/rotation of each variable given.

		PC1	PC2	PC3	PC4	PC5
Importance	St. Dev.	1.245	1.023	0.994	0.990	0.660
	Prop. Of Variance	0.310	0.209	0.198	0.196	0.087
	Cumulative Prop.	0.310	0.519	0.717	0.913	1.000
Rotation	Bandwidth	-0.296	0.573	-0.304	-0.628	0.311
	Time	0.610	-0.001	-0.241	-0.465	-0.594
	Center	0.146	0.702	0.641	0.149	-0.228
	Inflection	0.710	0.023	0.061	0.004	0.701
	Slope	0.121	0.421	-0.659	0.606	-0.083

After compiling all of the genetic data, we ended up with 428 COI sequences across 20 genera and 36 species. There was no subspecific information available to us. Genetic differentiation also ranged across taxa. At the species level, mean genetic distance ranged from 0.00 (*Chlorospingus flavopectus*) to 164.19 (*Arremon taciturnus*).

Spatial and Temporal Features

After performing our PCA of environmental variables, we retained the first five PCs as they explained 53% of the data (Table 2, Table 3). High values of PC1 were associated with regions that were dry, cold, had relatively narrow daily temperature but high annual temperature ranges, and high temperature seasonality. High values of PC2 were associated with regions that were cold and wet, with narrow daily temperature and yearly precipitation ranges, acidic sandy soils, and lots of trees to the exclusion of shrubs, bare cover, grazing land, and irrigated land. High values of PC3 were associated with more urbanized areas, high in croplands and agriculture, with lots of seasonal water, low terrain ruggedness, and shallow slopes. High values of PC4 were associated with cold summers, rough terrain, and lots of permanent water. Lastly, high values of PC5 were associated with high population areas with lots of built up concrete, low elevations, and low relief.

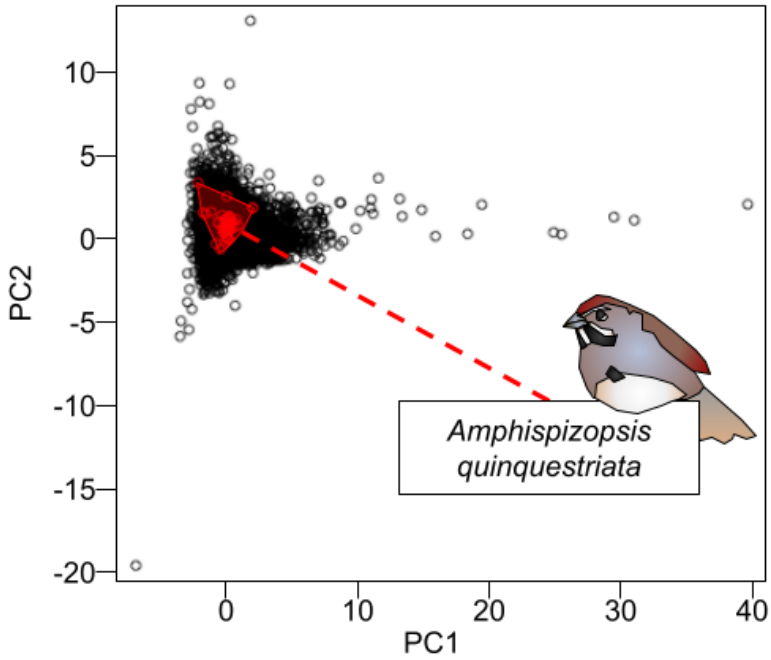

Figure 3: Breadth of syllable types across Passerellidae with one focal species highlighted. X-axis and y-axis depict PC1 and PC2, respectively, of five song variables (Table 1). Each point is an individual recording, with value showing the centroid across all syllables in that recording. Highlighted in red is one species, *Amphispizopsis quinquestriata*, with all recordings and their area given.

Table 2: Importance of first five PCs in a principal components analysis on environmental variables.

	PC1	PC2	PC3	PC4	PC5
Standard deviation	3.10	2.39	2.00	1.93	1.56
Proportion of Variance	0.20	0.12	0.08	0.08	0.05
Cumulative Proportion	0.20	0.32	0.40	0.48	0.53

Table 3: Rotation/loadings of first five PCs in a principal components analysis on environmental variables. Variables are categorized by general type.

		PC1	PC2	PC3	PC4	PC5
Land Cover %	Bare	0.076	-0.115	-0.060	0.039	-0.110
	Built Up	0.008	-0.004	0.083	0.159	0.330
	Crops	0.029	-0.026	0.163	-0.090	-0.016
	Grasses	0.116	-0.114	-0.052	-0.028	-0.273
	Moss/Lichens	0.013	0.021	-0.015	0.018	-0.042
	Permanent Water	0.029	0.024	0.059	0.065	0.006
	Seasonal Water	0.017	-0.011	0.054	0.007	-0.014
	Shrubs	0.018	-0.231	-0.163	-0.028	-0.137
	Trees	-0.136	0.197	-0.050	-0.089	0.015
Climate	Mean Annual Temp.	-0.234	-0.245	0.095	-0.092	0.097
	Mean Diurnal Temp. Range	0.137	-0.220	-0.134	-0.184	-0.071
	Isothermality	-0.264	-0.123	-0.103	0.044	-0.123
	Temp. Seasonality	0.276	0.110	0.097	-0.138	0.039
	Max Temp. Warmest Month	0.005	-0.267	0.139	-0.282	0.134
	Min Temp. Coldest Month	-0.282	-0.176	0.019	0.037	0.054
	Annual Temp. Range	0.284	0.046	0.049	-0.174	0.011
	Mean Temp. Warmest Quarter	-0.106	-0.176	0.196	-0.223	0.046
	Mean Temp. Driest Quarter	-0.202	-0.214	-0.072	0.052	0.064
	Mean Temp. Warmest Quarter	-0.072	-0.244	0.206	-0.245	0.168
	Mean Temp. Coldest Quarter	-0.272	-0.210	0.010	0.006	0.045
	Annual Precip.	-0.270	0.163	0.084	-0.062	-0.077
	Precip. Wettest Month	-0.282	0.076	0.018	0.002	-0.058
	Precip. Driest Month	-0.136	0.241	0.185	-0.171	-0.079
	Precip. Seasonality	-0.060	-0.252	-0.170	0.200	0.079
	Precip. Wettest Quarter	-0.279	0.091	0.024	0.006	-0.055
	Precip. Driest Quarter	-0.149	0.242	0.182	-0.167	-0.086
	Precip. Warmest Quarter	-0.204	0.100	0.124	-0.189	-0.141
	Precip. Coldest Quarter	-0.200	0.165	0.023	0.083	-0.006
Urbanization (by decade)	% Cropland	0.056	-0.061	0.242	-0.148	-0.040
	% Grazing Land	0.009	-0.207	0.005	-0.074	-0.206
	% Rice Cover	-0.001	-0.001	0.009	-0.003	-0.005
	Census Population	-0.002	-0.016	0.055	0.103	0.297
	% Land Irrigated	0.003	-0.117	0.057	-0.026	-0.031
	% Urban Landcover	0.017	-0.017	0.104	0.158	0.381
Habitat Classifications	Biosphere-Atmosphere Transfer Scheme	-0.009	0.002	0.088	0.112	-0.070
	International Geosphere Biosphere Programme	0.018	-0.069	0.363	0.238	-0.140
	USGS Land Use System	-0.033	0.121	-0.202	0.031	-0.143
	Olson Global Ecosystem	-0.001	-0.133	0.055	-0.111	-0.218
	Simple Biosphere 2 Model 2	0.072	-0.106	0.287	0.268	-0.234

	Simple Biosphere Model 1	0.052	-0.068	0.304	0.297	-0.224
	Running Vegetation Lifeforms	0.017	-0.050	0.269	0.225	-0.219
Topography	Elevation	-0.003	-0.036	-0.267	-0.038	-0.311
	Relief	-0.031	0.006	-0.013	0.024	-0.044
	Roughness	-0.071	0.018	-0.002	0.357	0.120
	Ruggedness Index	-0.149	-0.031	-0.214	0.129	-0.074
	Slope	-0.063	-0.022	-0.158	0.103	-0.005
Soil	Acidity	-0.165	0.244	0.026	-0.050	-0.015
	Texture Classification	0.143	0.154	-0.008	0.068	0.027

Synthesis: MMRR

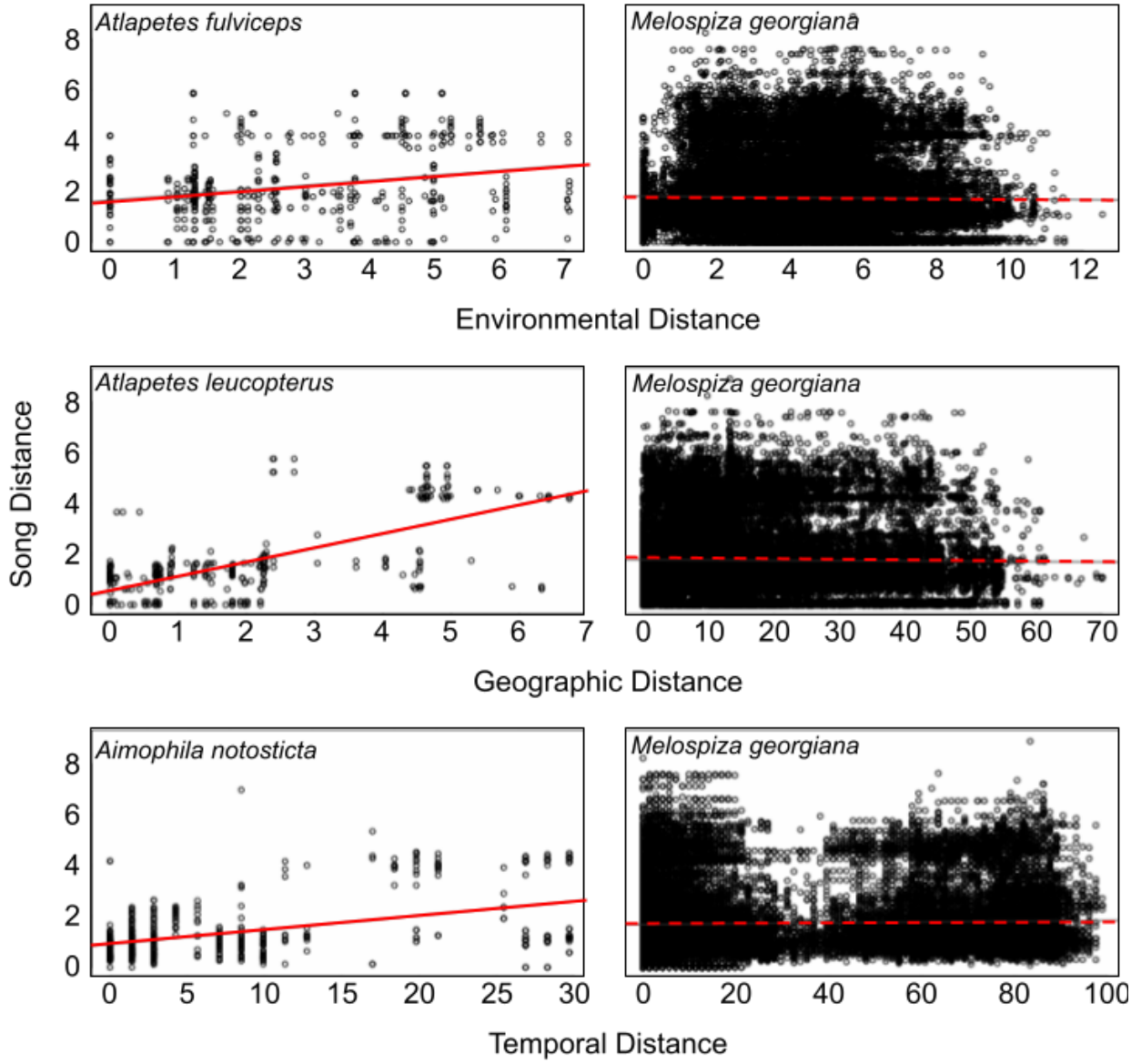

Figure 4: relationship between song distance (y-axis) and spatiotemporal variables (x-axes) in four species. Top two panels show song vs environmental distance, middle two panels show song vs geographic distance, and bottom two panels show song vs temporal distance. Left column shows three species where the relationship is significant (solid red line), the right column shows one species where relationships are always non-significant (dashed red line).

Acoustics MMRR

For the MMRRs using song data there are 30 genera, 125 species, and 171 subspecies with sufficient information to test the significance of environment, geography, and time (Figure 3, Supplementary Table 1, Supplementary Table 2). At the species level (Figure 4), 76/125 species showed no significant relationships between our spatial factors and song differentiation.

Of the rest, 37/125 had one factor significant: 16/125 were environment, 14/125 were time, and 7/125 were geography. An additional 11/125 had two factors significant: 5/125 for environment and geography, 4/125 for geography and time, and 2/125 for environment and time. The remaining one species had all three significant. This thus resulted in 24/125 species having the environment being significant in some way, 21/125 having time significant, and 17/125 having geography significant. Overall, this suggests that the environmental hypothesis is supported in 19.2% of species and the stochastic hypothesis in 26.4% of species.

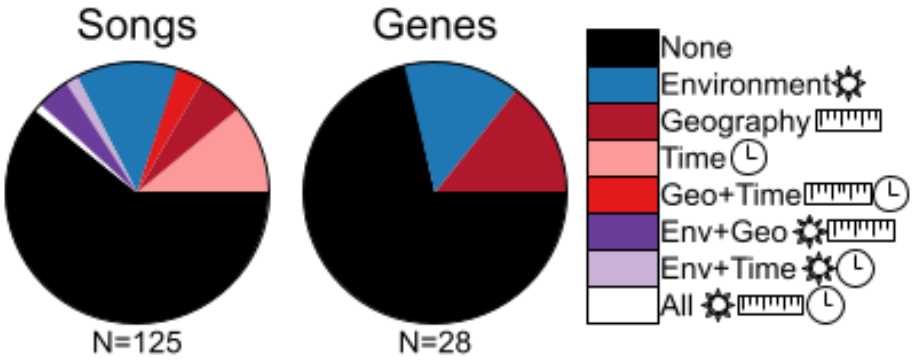

Figure 5: Pie charts displaying proportion of species whose traits are best predicted by different spatial and temporal features. Traits shown are songs (left) and genetics (center). Colors indicate the significant predictors (see legend, right) -- shades of red are stochastic features (geography, time), shades of blue are environmental features, purple/white indicate some combination, and black indicates no such feature. Sample sizes are given below each plot.

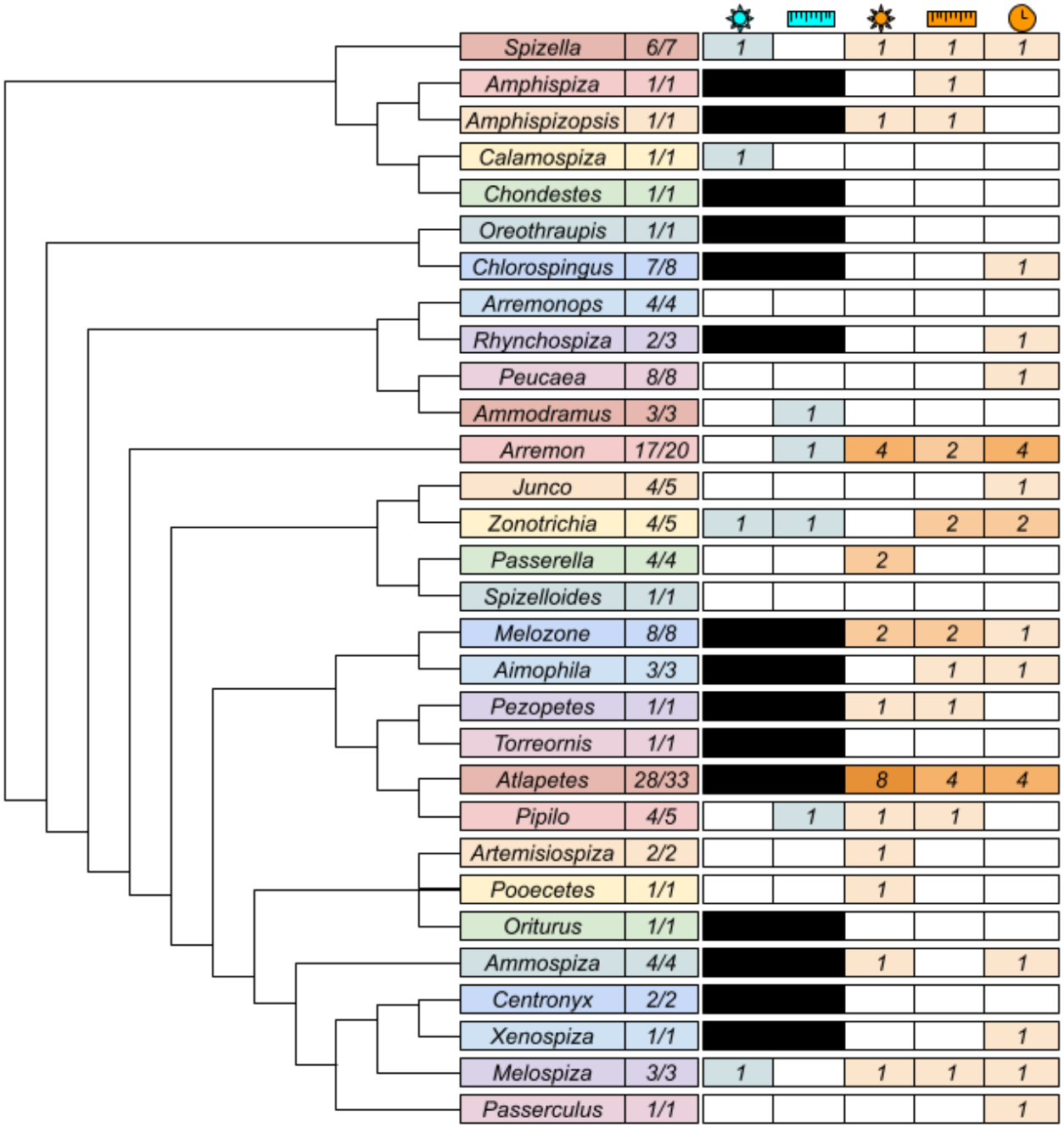

Figure 6: Best predictors of species-level differences in traits. Left: phylogeny at the generic level, with sample sizes of species sampled/total species. Right: heat map of number of species sampled that show significant differences in song (orange shades) and genetics (teal shades). Icons indicate spatial/temporal features tested: sun indicates environment, ruler indicates geographic distance, and clock indicates time. Shades of color correspond to the number of species where there are significant differences found, with darker shades showing more species and white showing no species. Black boxes indicate no genetic data are available. For genus-level and subspecies-level analyses, see Supplemental material.

Genetics MMRR

For the genetic MMRRs, there are 15 Passerellidae genera and 28 species with sufficient genetic information to test the significance of stochastic and environmental features (Figure 3, Supplemental Table 1, Supplemental Table 2). Only 8/28 species showed any influence of spatial factors on genetics: four with environment only, four with geography only. Overall, this suggests that the environmental hypothesis is supported in 14.2% of species and the stochastic hypothesis in 14.2% of species.

MMRR Comparisons

We compared whether song and genetics were explained by the same factors for the 28 species that had both genetic and song MMRRs (with the caveat that we did not evaluate genetic influence of time). For species, there were no taxa that had both gene and song explained by environment. However, 18/28 species had neither gene nor song explained by environment, with the remaining species being mismatched (four species with genes explained by environment, six species with song being explained). Likewise, there were no taxa that had both gene and song explained by geography. 20/28 species had neither gene nor song explained, the remaining eight were mismatched (four with genes being explained by geography, four with song being explained).

Traits

We found that there were some differences in morphology between taxa that showed environmental and stochastic influences on their genetics and song. At the species level, both vocalization and genetic differences were associated with morphology. In species that showed significant differences in genetics across geographic distances, both hand-wing indices and Kipp's distances were much shorter ($p<0.029$), which generally indicates that these birds have rounder, less pointed wings. With respect to vocalization, species that had significant correlations between song distances and environmental distances had longer wings ($p=0.012$), longer tails ($p=0.0291$), and longer secondaries ($p=0.0275$). Body size was also larger, though not significantly so ($p=0.056$). This is consistent with these birds being larger.

We investigated whether or not absolute differences in our traits and spatiotemporal features influenced the final results. Means and standard deviations are correlated with each other for each variable (range r: 0.72-0.93). Because of this, we only examine significant associations between mean values. Geography and environment are also highly correlated with each other, as expected ($r=0.65$). All other variables are correlated with each other to lesser extents ($r<0.37$).

At the species level, we find that we are more likely to detect significant differences between song and environment when the absolute song differences were higher ($p=0.031$). Again, this is easily explained, as when there is little song variation whatsoever the likelihood of detecting differentiation is slim.

We found no correlation between sample size and whether or not genetic differentiation was significant ($p=0.751$). However, there is a strong correlation with song differentiation (both with and without log-correcting for sample size disparity) such that taxa with more recordings are more likely to have a significant correlation detected ($p<4.9\times10^{-6}$).

Discussion

Automatic processing of bioacoustic data at the family level has allowed us to address questions related to the factors that influence song evolution across a phylogenetic scale. In New World sparrows, stochastic factors such as geographic distance or temporal distance (i.e., cultural drift) are generally more important than environmental factors in structuring song diversity within species, although there are individual species where each factor is approximately equally important. Across species, environment explains variation in 19% of species and stochastic factors in 26% of species (13% geography, 16% time). In particular, cultural drift is at least as important to the evolution of bird song as genetic drift is to the evolution of intraspecific genetic diversity. Within genera, these numbers are 33% for environment and 43% for stochastic (23% geography, 33% time). This suggests to us that both stochastic drift and the environment play a large role in shaping sound at these two taxonomic levels.

For the taxa wherein neither of these factors is important in explaining song variation, there is still work to be done to determine what is influencing song evolution. Across many species, there appears to be little song variation. This could result from small sample size, but also could be an indication that song variation is not present. We believe this highlights the need for deeper sampling. At present, we did not incorporate recordings from other sources (e.g., Macaulay Library) due to concerns about processing time.

In contrast to taxa with little song variation, there are a few taxa that have high song variation that are not explained by stochastic or environmental factors (e.g., *Pipilo maculatus*). One explanation might be that these species do not occupy environmentally variable areas, perhaps due to very strict niche requirements. However, we don't find any evidence that absolute environmental differences are driving these patterns. Alternatively, sexual and social selection may cause this pattern; however our study is not set up to detect these processes. Sexual and social selection are generally thought to be important determinants of song evolution across Passerines and birds more broadly (Catchpole 1987). These processes were not included because the song data contained in existing repositories lack the requisite metadata required for such an analysis. For example, estimating the impact of sexual selection requires knowledge about mate choice or mate competition, and in many species even determining the sex of the individual during the recording process is difficult.

Phylogeny

No major patterns emerge from an examination of phylogenetic relationships within the context of the spatial analyses conducted here. While song production itself has a phylogenetic component (Ryan et al 1985), the impact of phylogeny on the specific attributes of bird song is unclear. Further, there is evidence that divergence at different taxonomic levels are not due to the same process (e.g., Read and Weary 1992). If phylogeny is a large driver of spatiotemporal features in bird songs, we would expect to find clades where one spatiotemporal feature was prominent in its impact. While we see this within some genera (e.g., *Atlapetes* has a high proportion of taxa whose song is associated with the environment), such a pattern does not appear at larger scales. Our results are thus consistent with phylogeny having some small effect on the evolution of bird song, but additional work is needed to explore higher level effects in comparative phylogenetic contexts. One note is that taxonomic uncertainty is a challenge to studies like the one conducted here. As a potential hedge against the analysis of cryptic species, we performed the same analyses using subspecies as our focal taxa (see supplement) and found similar results, though a smaller proportion of taxa have significant relationships between

spatiotemporal features and song likely due to sample size. That the patterns are similar suggests that our findings are robust to taxonomic uncertainty.

Genetics, behavior, and morphology

Genetic and behavioral patterns are fairly similar, with 43% of species having the exact same spatiotemporal factors explaining genes and song and an additional 50% having a partial match (note that this ignores the temporal aspect present only for song). This is in line with evidence that genetic distance and song distance in other species is correlated (e.g., Irwin 1988). Here, we found that morphology is associated with differences across species for both genetics and songs.

In songs, species whose vocalizations are associated with environmental adaptation tend to have longer flight feathers, which may represent larger body size. In contrast, at the generic level, genera with shorter beaks showed more influence of isolation-by-distance. For genetics, isolation-by-distance was associated with species having stubbier wings. Morphological differentiation in birds is often associated with different factors. Beak shape is a constraint on diet (Navalón et al 2019), song frequency and bandwidth (Derryberry et al 2012), and thermoregulation (Tattersall et al 2017, Ryeland et al 2017). In this study, birds whose song properties are likely to be influenced by geography are also likely to have shorter beaks, but whether or not this is due to direct selection on song properties or indirect selection on other beak-associated traits is presently unknown. Tarsus length is generally associated with body size in birds (Senar and Pascual 1997), although mass itself was not found to be associated with any of the MMRR results. Nevertheless, body size is also associated with song properties (e.g., Ryan et al 1985) and thermoregulation (via Allen's rule; Symonds and Tattersall 2010) and therefore the same conclusions apply as for beak size. Lastly, wing morphology is often used as a proxy for dispersal in birds (Shard et al 2020). Birds with smaller hand-wing index, therefore stubbier wings and less presumed dispersal ability, were more likely to have genetics explained by isolation-by-distance. This suggests that the influence of spatial factors on diversification within species (i.e., in songs or genetics) is particularly pronounced on birds with poorer dispersal ability.

Conclusion

The comparative analyses presented here are the first attempt to understand the factors that influence song evolution in birds on a phylogenetic scale. Our results indicate that spatial, temporal, and environmental factors exert a clear influence on song evolution within many species. In scale, they mirror our results that tested for an association between geographic and genetic distance. This suggests that cultural drift is at least as important to the evolution of bird song as genetic drift is to the evolution of intraspecific genetic diversity. As with their genomic variation (e.g., Armstrong et al. 2018), bird songs are likely influenced by both cultural drift and selection. Taken in aggregate, it appears that spatial-associated factors are at least as important in shaping the evolution of song within bird species as geographic distance is a factor in intraspecific genetic differentiation.

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