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Song evolution, speciation, and vocal learning in passerine birds

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Phenotypic divergence can promote reproductive isolation and speciation, suggesting a possible link between rates of phenotypic evolution and the tempo of speciation at multiple evolutionary scales. To date, most macroevolutionary studies of diversification have focused on morphological traits, whereas behavioral traits—including vocal signals—are rarely considered. Thus, although behavioral traits often mediate mate choice and gene flow, we have a limited understanding of how behavioral evolution contributes to diversification. Furthermore, the developmental mode by which behavioral traits are acquired may affect rates of behavioral evolution, although this hypothesis is seldom tested in a phylogenetic framework. Here, we examine evidence for rate shifts in vocal evolution and speciation across two major radiations of codistributed passerines: one oscine clade with learned songs (Thraupidae) and one suboscine clade with innate songs (Furnariidae). We find that evolutionary bursts in rates of speciation and song evolution are coincident in both thraupids and furnariids. Further, overall rates of vocal evolution are higher among taxa with learned rather than innate songs. Taken together, these findings suggest an association between macroevolutionary bursts in speciation and vocal evolution, and that the tempo of behavioral evolution can be influenced by variation in developmental modes among lineages.

KEY WORDS: Bird song, diversification, learning, macroevolution, sexual selection.

The tempo of speciation and phenotypic evolution varies dramatically among lineages. Some clades have undergone rapid speciation or phenotypic evolution, while others have diversified slowly (Simpson 1944; Harmon et al. 2003; Simões et al. 2016). We may expect lineages diversifying rapidly in phenotypic dimensions to also exhibit accelerated speciation rates if phenotypic divergence is linked to ecological divergence, assortative mating, and reproductive isolation (Ricklefs 2004; Rundle and Nosil 2005; Ingram 2011). Alternatively, rates of speciation and phenotypic evolution can be decoupled in "cryptic" species complexes or nonadaptive radiations (Gittenberger 1991; Kozak et al. 2006; Rundell and Price 2009). Previous macroevolutionary studies have found that rates of phenotypic evolution and speciation are correlated in some clades or traits (Rabosky and Adams 2012; Rabosky et al. 2013; Puttick et al. 2015; Price et al. 2016; Ramírez-Barahona et al. 2016) and uncorrelated in others (Adams et al. 2009; Venditti et al. 2012; Burbrink et al. 2012; Bapst et al. 2012; Zelditch et al. 2015; Lee et al. 2016), suggesting that both of these patterns may be widespread in nature.

To date, the debate has centered mainly on morphological traits, with behavioral and cultural traits receiving comparatively little attention. Yet behavioral traits are thought to play an important role in evolutionary diversification (Plotkin 1988; Wcislo 1989; Huey et al 2003; Duckworth 2009), particularly as they often function in mate choice and reproductive isolation (Andersson 1994; Catchpole and Slater 2008). Thus, theoretically, divergence in behavioral phenotypes may have a disproportionate effect as prezygotic barriers to gene flow, ultimately leading to speciation (West-Eberhard 1983; Wilkins et al. 2013). Developmental or mechanistic changes underlying the production or reception of behavioral traits involved in mate choice have been associated with variation in the tempo of speciation in certain systems (Carlson et al. 2011; Maia et al. 2013), but the extent to which rates of behavioral evolution and speciation are linked remains largely unknown.

Rates of behavioral evolution may vary among lineages due to numerous factors, including differences in the strength and mode of sexual selection (Ritchie 2007; Kraaijeveld et al. 2011; Seddon et al. 2013; Servedio and Bürger 2015), and variation in developmental processes (Lovette et al. 2002; Pfennig et al. 2010; Moczek et al. 2011), such as the prevalence of phenotypic plasticity and the degree to which behaviors are learned or innate. Learned traits are socially transmitted and are therefore subject to imprecise copying with reduced effective generation times, which can quickly generate novel phenotypes, accelerate rates of phenotypic evolution, and promote population divergence (Mundinger 1980; Cavalli-Sforza and Feldman 1981; Baldwin 1986; Paenke et al. 2007; Pfennig et al. 2010). Learning, however, may also impede rates of phenotypic evolution and population divergence if predispositions to learn one particular sexual signal over another are weak (Olofsson et al. 2011). Empirical examples of phenotypic plasticity reducing gene flow (Pfennig and Murphy 2002; Haavie et al. 2004; Dukas 2004; Huber et al. 2007) and promoting population connectivity (Grant and Grant 1997; Hughes et al. 1999; Crispo and Chapman 2008) illustrate the context-dependent effects of plasticity and learning on rates of phenotypic evolution and speciation (Pfennig et al. 2010; Verzijden et al. 2012).

Bird song has become a model system for comparative studies of behavioral evolution and speciation (Slabbekoorn and Smith 2002; Wilkins et al. 2013) as well as of variation in learning and cognitive plasticity (Brenowitz and Beecher 2005). Within the avian order that includes roughly half of all birds (Passeriformes), vocal learning predominates in the largest suborder (Passeri or "oscines") but not in its sister clade (Tyranni or "suboscines"; Beecher and Brenowitz 2005). Despite long-standing interest in the potential role of song in passerine diversification (Fitzpatrick 1988; Baptista and Trail 1992), we know little about how vocal evolution, and in particular the degree of cultural transmission, influences macroevolutionary rates of speciation, rates of song evolution, and possible associations between these processes at deeper evolutionary time scales.

To explore this issue, we quantify macroevolutionary patterns of avian vocal evolution and speciation in two large, diverse families of Neotropical passerines: the tanagers (Thraupidae) and the ovenbirds and woodcreepers (Furnariidae). These families are geographically codistributed and highly diverse, together comprising ~10% of all passerine birds. Thraupids are oscines that learn their songs (Isler and Isler 1999), whereas furnariids are tracheophone suboscines that develop vocal displays without conspecific tutors (Tobias et al. 2012; Touchton et al. 2014). Leveraging a large-scale comparative dataset of these two clades, we address three questions regarding the macroevolutionary dynamics of avian vocalizations and diversification: (1) are rates of speciation associated with rates of song evolution; (2) does vocal learning affect macroevolutionary associations between rates of speciation and vocal evolution; and (3) do rates of song evolution vary among avian lineages that differ in the degree of vocal learning involved in song development?

Methods

SPECIES AND CHARACTER SAMPLING

We gathered vocalization data from 4474 recordings of 581 species of tanagers and ovenbirds. The methods used to collect these data are described in detail elsewhere (thraupids: Mason et al. 2014; Mason and Burns 2015; furnariids: Tobias et al. 2014). We analyzed 2648 songs of 305 species of tanagers (mean number of songs ± standard deviation species $= 8.68 \pm 7.32$) and 1826 songs of 276 species of ovenbirds (6.61 ± 5.36). These two datasets shared eight vocal characters, including minimum frequency, maximum frequency, peak frequency, song frequency range, note count, note rate, song length, and vocal performance (i.e., residual values extracted from a linear model comparing song frequency range and note rate *sensu* Podos 2001). Because many vocal characters are correlated with body size in these taxa (Mason and Burns 2015), we acquired body mass data (Dunning 2007) and tested each character for a correlation with mass using the Pagel's λ model within a phylogenetic generalized least squares framework (Grafen 1989; Harvey and Pagel 1991; Martins and Garland 1991; Freckleton et al. 2002). We found correlations between six out of eight vocal characters and body mass (Supplementary Table S1). For those characters correlated with mass, we extracted residuals while accounting for phylogenetic nonindependence among species for subsequent comparative analyses (Revell 2009).

We also performed a phylogenetic principal component analysis (pPCA) on scaled data (mean $= 0$ and standard deviation $= 1$ for each character) using the Pagel's λ model (Revell 2009; Supplementary Table S2). A recent study raised concerns that pPCA analyses can introduce a spurious pattern of decreasing evolutionary rates through time in highly dimensional datasets (Uyeda et al. 2015). However, we note that these statistical artifacts appear most pronounced when pPCA analyses are performed under a Brownian motion model that deviates substantially from true underlying evolutionary processes and when only the first few components axes are considered (Uyeda et al. 2015). Here, we use the Pagel's λ model to generate pPCA axes and examine patterns among six pPCA axes, totaling 95% of the total phenotypic variance. Nonetheless, with the statistical biases of pPCA axes and interpretability in mind, we focus on downstream comparative analyses of individual song characters in the main text, but also present results with pPCA axes in the supplementary materials.

DIVERSIFICATION ANALYSES

Both Thrapuidae and Furnariidae have robust, comprehensive, multilocus phylogenies readily available (Derryberry et al. 2011; Burns et al. 2014). We built a supertree of tanagers and ovenbirds by combining maximum clade credibility trees from Burns et al. (2014) and Derryberry et al. (2011) using functions from the APE package (Paradis et al. 2004). We used the Jetz et al. (2012) phylogeny to calibrate the age of the node uniting Thrapuidae and Furnariidae. We used Bayesian Analyses of Macroevolutionary Mixtures (BAMM v2.5.0; Rabosky 2014; Rabosky et al. 2014; Shi and Rabosky 2015) to assess evidence for rate heterogeneity in speciation and rates of trait evolution for each of the eight vocal characters considered here (scaled to mean = 0 and standard deviation = 1) and the pPCA axes. For our speciation rate analysis, we accounted for incomplete taxonomic sampling by setting the globalSamplingFraction parameter equal to 581 out of 677 total taxa (375 thraupids + 302 furnariids) in accordance with current taxonomies (Clements et al. 2015). We set the poissonRatePrior to 0.5 and note that while concerns have been raised regarding the independence of posterior distributions from prior settings within BAMM (Moore et al. 2016), recent versions of BAMM ($\geq$ v2.5) generate posterior distributions for the number of inferred rate shifts that are largely independent of prior parameter settings (http://bamm-project.org/prior.html). The concerns raised by Moore et al. (2016) are therefore unlikely to affect the analyses performed here that were conducted with the most current working version of BAMM. For each BAMM analysis, we ran four separate metropolis-coupled MCMC chains with a temperature setting of deltaT = 0.01 and swapPeriod = 1000 for 10^6 generations and discarded the first 10^5 generations as burn-in. We confirmed that effective sample sizes of log-likelihoods, evolutionary rate parameters, and the number of processes all exceeded 300 using the CODA package (Plummer et al. 2006). We also visually inspected log-likelihood scores and the number of evolutionary rate regimes to confirm MCMC runs had converged.

We summarized the output from each BAMM analysis using BAMMtools v2.1 (Rabosky et al. 2014). We calculated the posterior probability associated with each possible number of evolutionary rate shifts for each trait. For each analysis, we extracted the credible set of rate shifts using a threshold of 20 Bayes Factors, and visualized the set of rate shifts with the highest posterior probability. We used Structured Rate Permutations on Phylogenies (STRAPP; Rabosky and Huang 2015) within BAMMtools to test for monotonic relationships between rates of speciation (rather than diversification, which requires estimating extinction as well as speciation) and rates of trait evolution. Briefly, STRAPP first requires speciation rates to be estimated with no knowledge of character states, as described above. Then, a test statistic (i.e., Spearman's rank correlation, or ρ) is computed that quantifies the association between speciation rate estimates and trait evolution rate estimates at the tips of the tree. Finally, the value of the test statistic is compared to a null distribution that is created by structured permutations of evolutionary rates across the tree, which accounts for the nested inheritance of rate shifts from "parent" to "offspring" lineages (Rabosky and Huang 2015). Thus, we first obtained instantaneous estimates of rate evolution for each tip using the getTipRates() function in BAMM and took the mean rate across the posterior for each vocal character and principal component axis. We then calculated Spearman's rank correlation coefficient and performed a one-tailed statistical test for positive correlations between estimated speciation rates and rates of trait evolution for all eight vocal characters and pPC1–pPC6. We visualized associations between speciation rates and rates of trait evolution using scatterplots and plotted loess-smoothed regression lines to visualize trends for significant, nonparametric associations. Finally, we performed the BAMM pipeline on the combined dataset of thraupids and furnariids as well as on each family independently to determine if vocal learning influences associations between rates of speciation and vocal evolution.

To test for clade-specific differences in rates of vocal evolution, we quantified phenotypic evolutionary rates (after controlling for correlations with body mass when present) via a multivariate method that leverages the evolutionary rate matrix (Adams 2014). Rather than scaling characters as we did for the BAMM analysis, we log transformed characters that had frequency as units (i.e., minimum frequency, maximum frequency, peak frequency, and song frequency range) in order to account for differences in scale between characters while maintaining interpretability, as suggested by previous studies (Felsenstein 1985; O'Meara et al. 2006; Adams 2013). Next, we calculated multivariate evolutionary rate estimates for thraupids ($\sigma^2_{\text{Thraupidae}}$) and furnariids ($\sigma^2_{\text{Furnariidae}}$). We then calculated the ratio between these two rates, which serves as a summary statistic that is compared to a null distribution of possible rates simulated under the assumption that there is a single multivariate evolutionary rate for both thraupids and furnariids (Adams 2014).

We also used two jackknifing strategies to test whether estimates of multivariate evolutionary rates based on the Adams (2014) method were biased by certain taxa. First, we performed 100 jackknife iterations in which we randomly removed 10% of the tips from both Thraupidae (30 tips removed) and Furnariidae (27 tips removed). We then recalculated the ratio of multivariate evolutionary rates between Thraupidae and Furnariidae ($\sigma^2_{\text{Thraupidae}}/\sigma^2_{\text{Furnariidae}}$) and calculated the mean as well as the approximate 95% confidence intervals of the resulting set of summary statistics. Second, to determine if taxa that exhibited accelerated speciation rates affected multivariate macroevolutionary rate estimates, we also calculated $\sigma^2_{\text{Thraupidae}}/\sigma^2_{\text{Furnariidae}}$ after removing any taxa that belonged to macroevolutionary diversification regimes identified by BAMM that differed from background speciation rates.

Results

ACCELERATED BURSTS OF SPECIATION AND VOCAL EVOLUTION COINCIDE

We inferred substantial rate heterogeneity in the evolution of vocal displays and speciation among 581 species of tanagers and ovenbirds (Fig. 1 and Supplementary Fig. S1 for detail). We observed similar patterns of speciation rate heterogeneity compared to previous studies of the same taxa with respect to the number and location of diversification rate shifts in the phylogeny (e.g., Derryberry et al. 2011; Burns et al. 2014). Specifically, we found diversification rate shifts corresponding to Darwin's finches, the subfamily Sporophilinae, and members of the genus *Cranioleuca* and closely related species (Fig. 1). The number of evolutionary rate shifts varied substantially among vocal characters (Fig. 1; Supplementary Fig. S2) and pPCA axes (Supplementary Fig. S3; Supplementary Fig. S4): some characters, such as song length, had approximately 65 rate shifts, while others, such as vocal performance, had closer to 25 macroevolutionary regimes. Using the combined dataset of Thraupidae and Furnariidae, we uncovered monotonic, positive correlations between speciation rate and four vocal characters: minimum frequency, maximum frequency, peak frequency, and song length (Fig. 2). We also uncovered positive correlations between speciation rates and evolutionary rates for four out of six pPCA axes (Supplementary Fig. S5). When each family was considered separately, however, we found no significant correlations between rates of speciation and evolutionary rates of any of the eight vocal characters, although correlation coefficients were generally higher in thraupids with learned song compared to furnariids with innate song (Fig. 2).

VOCAL DISPLAYS EVOLVE FASTER AMONG TAXA WITH LEARNED SONG

We found significant differences in multivariate rates of vocal evolution between thraupids and furnariids. Specifically, vocal displays evolve roughly 1.4× faster in thraupids with learned song compared to furnariids with innate song ($\sigma^2_{\text{Thraupidae}} = 28.64$; $\sigma^2_{\text{Furnariidae}} = 20.30$; $\sigma^2_{\text{Thraupidae}}/\sigma^2_{\text{Furnariidae}} = 1.41$; $p_{\text{sim}} = 0.002$). When we jackknifed our dataset, we found that the mean of the resulting pseudo values was $\sigma^2_{\text{Thraupidae}}/\sigma^2_{\text{Furnariidae}} = 1.38$ (95% confidence intervals = 1.26–1.50). Furthermore, after removing taxa that belonged to evolutionary regimes with speciation rates that differed from background diversification rates, we found that thraupids still have faster rates of vocal evolution compared to furnariids ($\sigma^2_{\text{Thraupidae trim}}/\sigma^2_{\text{Furnariidae trim}} = 1.78$; $p_{\text{sim}} = 0.002$). Together, these findings suggests that the higher rates of multivariate vocal evolution among tanagers inferred with the complete dataset is a generalized pattern that is not driven by a few taxa of large effect.

Discussion

Our analyses reveal coincident bursts in rates of speciation and various song characters at multiple nodes within Furnariidae and Thraupidae (Fig. 2). When we combined phylogenetic and bioacoustic data from both these families, we found correlations between speciation and frequency related (i.e., minimum frequency, maximum frequency, peak frequency; Fig. 2) as well as structural aspects of song (i.e., song length; Fig. 2). These correlations are driven in large part by coincident rate shifts in two thraupid clades (Darwin's finches and Neotropical seedeaters and seed finches) and one furnariid clade (spinetails and their allies). We also uncovered faster overall rates of vocal evolution among thraupids, which have learned song, compared to furnariids, which have innate song. These patterns may be driven by multiple, nonexclusive biological processes.

POSITIVE ASSOCIATIONS BETWEEN RATES OF SPECIATION AND TRAIT EVOLUTION

One possible explanation of the positive association between rates of vocal evolution and speciation is that acoustic divergence may occur late in the speciation process (Wilkins et al. 2013). In this scenario, songs diverge relatively slowly in allopatry. On secondary contact, once speciation is complete, song differences then rapidly increase, as expected under a model of reinforcement (Servedio 2004; Olofsson et al. 2011). Rather than rapid vocal evolution promoting speciation, selection against hybrids between diverged lineages is driving character displacement of mating signals. Character displacement of songs appears unlikely, however, at least in furnariids. Work in this radiation suggests that character displacement may only occur in earlier stages of

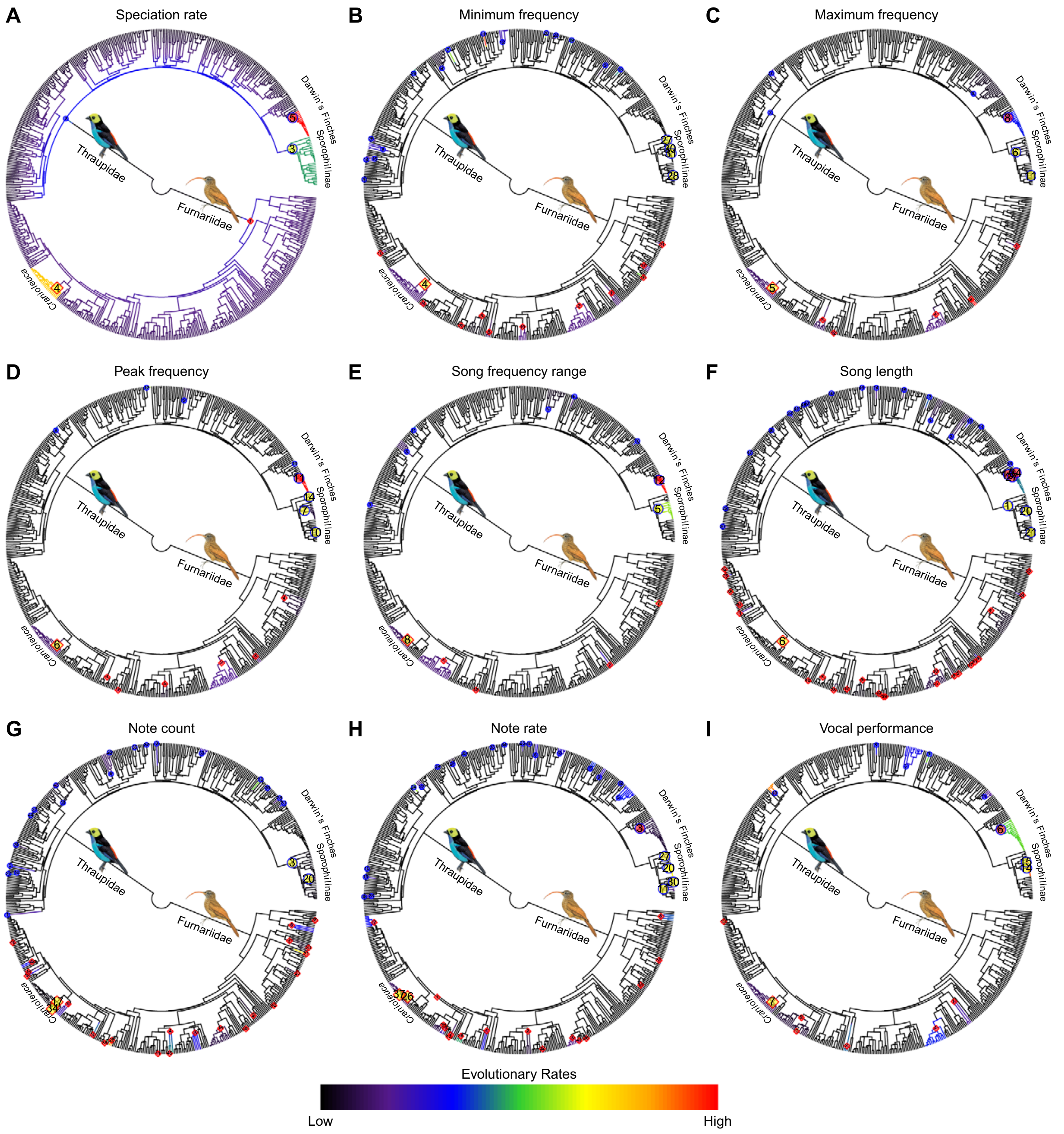

Figure 1. Relative rates of speciation or vocal evolution mapped onto the combined MCC phylogenies of Thraupidae and Furnariidae. Colors at each point in time along branches indicate the relative instantaneous rate of speciation or phenotypic evolution. Evolutionary rates are averaged across all evolutionary regimes sampled from the posterior. The evolutionary rate shift configuration with the highest posterior probability is shown for each character, in which the position of rate accelerations and decelerations are indicated with symbols that respond to different speciation regimes. Blue-filled circles with blue outlines pertain to the background thraupid speciation regime. Red-filled circles with blue outlines correspond to Darwins Finches. Yellow-filled circles with blue outlines pertain to Sporophilinae. Red-filled diamonds with red outlines correspond to the background furnariid speciation regime. Yellow-filled diamonds with red outlines pertain to *Cranioleuca* and allies. Rate shifts are numbered according to their relative node depth; smaller numbers indicate rate shifts that occur on deeper nodes in the phylogeny. Evolutionary bursts of speciation and vocal evolution often coincide in these two lineages. Illustrations reproduced with the permission of Lynx Edicions.

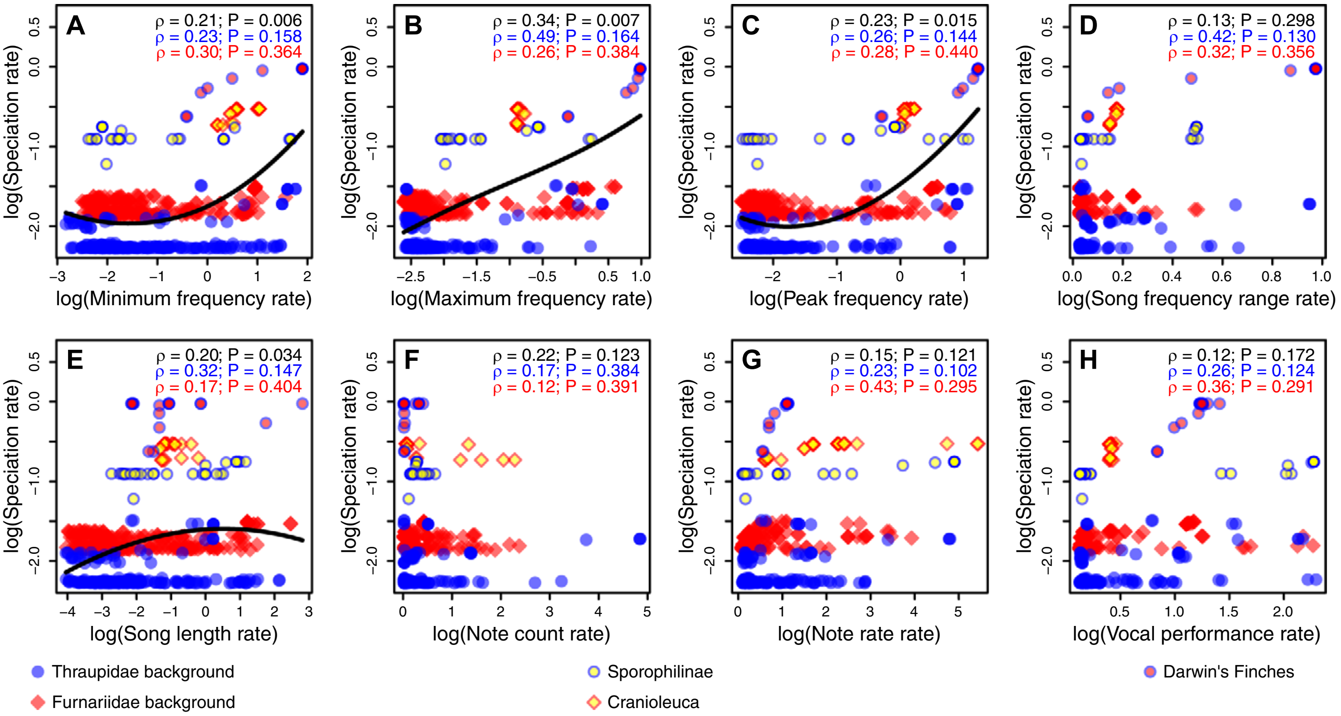

Figure 2. Scatterplots of speciation rates and instantaneous evolutionary rates for each of eight vocal characters. Oscines (Thraupidae) are indicated with blue outlines, while suboscines (Furnariidae) are indicated with red outlines. Within each of these groups, taxa assigned to evolutionary regimes that are distinct from the background regime (i.e., the regime with the greatest number of taxa), are distinguished with different colored symbols, as shown in the key at the bottom right. The Spearman's correlation coefficients and the corresponding *P* values are displayed for each comparison. When the *P* value is statistically significant (i.e., below 0.05) a Loess-smoothed trend line is displayed.

adaptive radiations; apparently high levels of character divergence between sympatric taxa may simply reflect time since divergence without invoking character displacement (Tobias et al 2014). Careful examinations of the association between acoustic divergence and neutral genetic distance are needed to assess whether acoustic divergence is occurring earlier or later in the speciation process.

An alternative explanation is that the evolution of vocal traits is promoting the speciation process. Vocal diversification could promote speciation if divergence in vocal characters is associated with divergence in mating preferences such that vocal traits are acting as premating barriers to gene flow (West-Eberhard 1983; Price 1998). Accrual of differences in secondary sexual characters linked to mate choice—such as bird song—could shape patterns of gene flow among populations, subsequently increasing the pace of speciation (Slater 1986; Grant and Grant 1996). Accelerated song evolution within a lineage may therefore represent a shift to a distinct evolutionary regime that promotes the rapid appearance and fixation of vocal differences and associated mate preferences among populations and species.

Models of vocal evolution suggest that periods of allopatry promote drift in mating preferences and signal content (Lachlan and Servedio 2004), and evolutionary processes that reduce population sizes may further accelerate song divergence by increasing the effects of drift (Lynch and Baker 1994; Grant and Grant 1996). Island archipelagos or biogeographic histories characterized by repeated range fragmentations and reductions in population size offer plausible scenarios that may promote accelerated vocal evolution and speciation (Hewitt 1996; Grant and Grant 1996; Lovette 2005; Losos and Ricklefs 2009). Among the taxa considered here, we observe accelerated vocal evolution and speciation among Darwin's finches, which have a storied history of colonization and diversification in the Galápagos archipelago (Grant 1986; Sato et al. 2001). Meanwhile, seedeaters and seed-finches in the subfamily Sporophilinae inhabit grasslands in Central and South America, which have undergone numerous periodic contractions and expansions in response to glacial cycles (Cracraft and Prum 1988; Clapperton 1993; Mason and Burns 2013); furthermore, various lineages in this subfamily—such as the southern capuchinos—have undergone recent bouts of speciation in short evolutionary timeframes (Campagna et al. 2012, 2015). Finally, rapid and recent diversification among spinetails in the genus *Cranioleuca* and closely related species is characterized by a complex biogeographic history involving numerous small, allopatric distributions in the Andes and Amazonian lowlands (Garcia-Moreno 1999; Derryberry et al. 2011). Taken together, evolutionary scenarios that favor repeated partitioning of geographic distributions and population contractions may accelerate vocal evolution as well as corresponding mate preferences, thereby rapidly generating reproductively isolated lineages and augmenting the tempo of speciation and trait evolution.

Differentiation in vocal signals may also be an indirect effect of divergence along ecological axes. Avian vocalizations coevolve with numerous ecological traits: bill size and shape (Podos 2001; Seddon 2005; Derryberry et al. 2011), body size (Tubaro and Mahler 1998; Mason and Burns 2015), and differences in the bioacoustics properties of vegetation structure among habitat types types (Morton 1975; Boncoraglio and Saino 2007; Tobias et al. 2010) can all impart selective constraints on the evolution of bird song (Podos et al. 2004). If lineages undergoing accelerated speciation are also rapidly and repeatedly diversifying into different habitat types or trophic niches, then vocal divergence may accumulate as a byproduct of ecological diversification. Bill size and shape play important roles in avian trophic ecology; bill morphology is correlated with frequency-related and temporal aspects of vocal displays in Darwin's finches (Podos 2001; Huber and Podos 2006) and woodcreepers (Derryberry et al. 2012), both of which are included in this study. Furthermore, rates of climatic niche evolution are correlated with species richness in both thraupids (Title and Burns 2015), furnariids (G. Seeholzer, pers. comm.), and birds more generally (Cooney et al. 2016). Thus, natural and sexual selection may act together to accelerate trait evolution and the generation of premating barriers to gene flow, as has been suggested in other taxa (Wagner et al. 2012; Safran et al. 2013).

When we considered associations between speciation rates and rates of vocal evolution within each family independently, we found no significant correlations (Fig. 2). Interpreting this null result is not possible as we lack the statistical power to determine whether learning influences macroevolutionary links between rates of vocal evolution and speciation by comparing analyses performed on each clade independently. Comparative studies that aim to document macroevolutionary rate variation in speciation and phenotypic evolution typically require many hundreds—if not thousands—of taxa to reach sufficient statistical power (Rabosky et al. 2013; Rabosky and Huang 2015); such comparisons are inherently limited by the number of diversification rate shifts that characterize the evolutionary history of a given clade. As datasets from other taxa with learned songs (i.e., hummingbirds, parrots) or innate songs (i.e., most nonpasserines) are accumulated, we can better determine if learning influences associations between rates of vocal evolution and speciation by increasing the number of evolutionary regimes under consideration.

RATES OF BEHAVIORAL EVOLUTION AND DEVELOPMENTAL MODES

We also observed faster rates of vocal evolution among species with learned song than those with unlearned song among the taxa considered here. This observation was robust to jackknifing our dataset by randomly removing a subset of taxa and also by removing taxa that differed from background rates. Together, these jackknifing results suggest that faster rates of vocal evolution among thraupids is driven by higher overall rates across thraupids rather than a few taxa with exceptionally higher rates of vocal evolution. We note, however, that the multivariate method implemented in this study (Adams 2014) assumes a single evolutionary rate among the taxa assigned to each comparison group. Given that we observed multiple rate shifts for each song character in our study, this assumption is likely not true for our dataset and perhaps most datasets. Yet, we know of no multivariate method to estimate and compare evolutionary rates among different taxonomic groupings; developing a methodological framework that allows multivariate comparisons of trait evolution while allowing rates to vary within comparison groups would be a valuable contribution to the comparative phylogenetic toolbox. Accepting these methodological caveats, we suggest possible biological mechanisms that may underlie faster vocal evolution in Thraupidae compared to Furnariidae.

Our findings support the hypothesis that learning could promote evolvability of song. Learning is a form of phenotypic plasticity, which has long been predicted to accelerate trait evolution (Plotkin 1988; West-Eberhard 2005). Unlike many other plastic responses, learned behaviors can be transferred across generations. Cultural transmission of learned behaviors, such as song in oscines, can rapidly generate new selective environments and persistence of novel behaviors across generations (reviewed in Duckworth 2009). The effects of plasticity vary, however, when lineages come into secondary contact and depend on reaction norms, the degree of plasticity, and inheritability for a given trait (Lachlan and Servedio 2004; Pfennig et al. 2010). Yet in allopatry, models consistently predict that phenotypic plasticity—specifically learning—should accelerate trait evolution (Baldwin 1986; Irwin and Price 1999; Lachlan and Servedio 2004). Allopatric speciation through vicariance and dispersal has played a large part in the evolutionary history of Neotropical avifauna (Cracraft and Prum 1988; Smith et al. 2014). We therefore speculate that accelerated rates of vocal evolution among taxa with learned song may reflect a macroevolutionary signature of the rapid generation and fixation of novel vocal phenotypes among populations and species of oscines through song learning and cultural evolution in allopatry.

Our results contribute to the growing literature examining whether learning as a developmental mode affects the rate of vocal evolution. Previous studies have found accelerated rates of vocal evolution among oscines compared to suboscines at temperate, but not tropical, latitudes (Weir and Wheatcroft 2011). Another study on parrots found similar rates of evolution for learned vocal signals and morphological traits in parrots (Medina-García et al. 2015), which is not consistent with the hypothesis that learning accelerates vocal evolution. Methodological differences between these studies and ours preclude direct comparisons, but the patterns observed in this study may not be retained across all avian lineages and may vary among biogeographic regions.

LIMITATIONS OF OUR STUDY

Although our analysis leverages song data from thousands of individuals representing hundreds of species, our inference ultimately relies on a one-to-one comparison of lineages that vary in vocal ontogeny. Furnariids and thraupids vary in many aspects of their biology beyond their vocal development, which may also contribute to faster rates of vocal evolution among thraupids as representative oscines with song learning. For example, the syringeal anatomy of thraupids, and oscines more generally, is far more complex than furnariids, such that thraupids may be able to use their syrinx to produce a wider variety of vocal signals. This difference in syringeal morphology may therefore also affect the evolvability of song.

One additional caveat to our interpretations is that our findings could in part be explained by taxonomic sampling and inaccuracies in species delimitation. Comparative studies are contingent on an accurate species-level taxonomy (Isaac 2004). Although we followed a widely used and up-to-date taxonomy to guide our comparative analyses (i.e., Clements et al. 2015), many of the taxa included in our study have been the subject of taxonomic debates over species delimitation (Tobias et al. 2008; Mckay and Zink 2014). Further, song has become an important marker in identifying species, particularly cryptic species in tropical clades such as ours (Tobias et al. 2012). If taxonomists are more likely to identify species in lineages with more phenotypic variation associated with species identification, this could lead to a positive association between rates of phenotypic evolution and speciation (Rabosky et al. 2013). Some caution may therefore be required in interpreting rapid bursts of trait evolution and speciation in recent radiations. However, these caveats underline the advantage of focusing on two largely codistributed clades in the same order of birds, which reduces the influence of geographic and taxonomic biases in species delimitation.

CONCLUSION

In summary, we find evidence for coincident bursts in rates of vocal evolution and speciation when combining bioacoustics and phylogenetic data from two distantly related lineages of Neotropical passerine birds. We also uncover faster overall rates of vocal evolution among thraupids with learned song compared to furnariids with innate song. We propose that the accrual of premating barriers to gene flow observed in certain lineages may be propelled by accelerated vocal diversification through sexual selection driving cultural evolution as well as indirect effects of ecological diversification on bioacoustic displays. Alternatively, song diversification may follow speciation through the process of reinforcement. While recent studies have highlighted links between rates of morphological evolution and speciation (Rabosky and Adams 2012; Rabosky et al. 2013), our findings suggest that behavioral traits involved in mate choice and territoriality among individuals and populations also contribute to macroevolutionary patterns of species richness. Finally, our study suggests that ontogenetic differences in behavioral development—namely, the presence of learning as a form of phenotypic plasticity in bird song—may influence the tempo of phenotypic diversification at macroevolutionary scales.

DATA AVAILABILITY

We provide the phylogenies, phenotypic dataset, example input files, and R scripts used in this study through the Dryad Digital Repository (doi:10.5061/dryad.r99p7).

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Supplementary Table S1: Results from phylogenetic generalized least squares analysis using Pagel's λ model with body mass as the independent character.

Supplementary Table S2: Phylogenetic principal component axis loadings after extracting residuals for characters correlated with body mass.

Supplementary Figure S1: Speciation rates for tanagers and furnariids mapped onto the combined MCC phylogeny with tip labels shown for interpretability.

Supplementary Figure S2: Marginal distributions of the number of distinct macroevolutionary rate regimes exhibited by Thaupidae and Furnariidae combined for speciation rate and eight vocal traits.

Supplementary Figure S3: Marginal distributions of the number of distinct macroevolutionary rate regimes exhibited by Thaupidae and Furnariidae combined for speciation rate and six phylogenetic principal component axes.

Supplementary Figure S4: Relative rates of speciation or and rates of evolution for principal component axes mapped onto the combined MCC phylogenies of Thraupidae and Furnariidae.

Supplementary Figure S5: Scatterplots of speciation rate as a response variable and instantaneous evolutionary rates for each species derived from scores of six principal component axes as predictor variables with residuals extracted for characters correlated with body mass.