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No Consistent Effect of Migration on Speciation Rates in Two Avian Superfamilies: A Check on the Robustness of Trait-Dependent Diversification Methods

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Abstract.—Seasonal migration is performed by taxonomically diverse groups across the planet's oceans and continents. Migration has been hypothesized to promote speciation through a variety of mechanisms that may initiate reproductive isolation and population divergence, such as temporal or spatial migratory divides, migration "falloffs," or the colonization of new, geographically isolated breeding areas. Migration has also been implicated in recent population divergence within a handful of bird species; however, it is unknown whether migration is generally associated with higher speciation rates. We sought to test this question in two large clades of New World birds with diverse migratory phenotypes, the suboscines and the Emberizoidea, employing three state-of-the-art comparative methods of trait-based diversification: estimates of tip speciation rates using 1) BAMM, 2) ClaDS, and 3) hidden-state speciation extinction models. Our results differed across methods and across taxonomic scales, suggesting an acute need to corroborate inferences across different frameworks and data sets prior to concluding that a given trait has, in fact, promoted diversification. Overall, and based upon the majority of results across different methods, we conclude that there is no methodologically consistent evidence of faster speciation in migratory lineages in these groups. We discuss the biological implications of this finding, as well as the challenges of inference posed by current tramigration-based diversification methods. [birds; comparative phylogenetics; diversification; migration; speciation.]

Migration—here defined as seasonal, reversible movements of individuals between locations (Dingle 2014)—is undertaken by roughly 20% of birds (Dufour et al. 2020), but also arthropods, fishes, turtles, and mammals (Milner-Gulland et al. 2011; Dingle 2014). The evolutionary contexts of these species are shaped by perilous journeys and the environments on either side (Hansson and Åkesson 2014): migration often imposes strong selection, for example, due to increased predation and mortality (Sabal et al. 2021), physiological and metabolic demands (Weber 2009), and the need for navigational and timekeeping systems (Bingman and Cheng 2005; Rappole 2013). Local selection may differ between the breeding and non-breeding environments and along the major migratory pathways (von Rönn et al. 2016). To the extent that migration determines the spatio-temporal pool of mates arriving at the breeding grounds, it circumscribes the assortment of potential mates, in addition to setting the environmental context of mating activities. Importantly, through its effect on breeding ranges and timing, migration can shape population structure. Studies in birds suggest that, through its effects on population structure, migration can induce reproductive isolation, promote population divergence, and possibly thereby initiate the speciation process (Rolland et al. 2014; Turbek et al. 2018; Gómez-Bahamón et al. 2020; Scordato et al. 2020). Below, we discuss mechanisms by which migration may initiate speciation, but whether, or to what extent, these processes have shaped macroevolutionary patterns of species richness is an open question. Here, we test the hypothesis that migratory lineages have elevated speciation rates in two superfamilies of Passerine birds.

Migration has been hypothesized to initiate premating isolation when migrating individuals colonize a new breeding region that is sufficiently isolated from other breeding regions to preclude gene flow (Rolland et al. 2014; Hemstrom et al. 2022). This is similar to a typical allopatric speciation process following the establishment of an isolated population, except that 1) long-distance migration may increase the probability of dispersal to new or isolated areas and 2) the newly isolated populations may continue to share a non-breeding range and thereby continue to interact and share a selective environment for part of the year (Winker 2010). Alternatively, migration can result in reproductive isolation between populations whose breeding ranges are not geographically isolated. For example, populations may arrive at breeding grounds at consistently different times if they take different migration routes (Bearhop et al. 2005). This can preclude mating between early and late arrivers (or in species that brood multiply in a season, reduce rather than preclude interbreeding). Migratory divides—broadly defined as divergence in migratory phenotypes (e.g., routes or timing) between populations in contact—can split populations spatially (Battey et al. 2017; Turbek et al. 2018, 2022) and/or temporally (Friesen et al. 2007; Turbek et al. 2022).

Although divergent migratory destinations or routes might initiate premating isolation as described above, a loss of migration by some populations could also be isolating. Migration fall-offs (a loss of migration by a population in a migratory species) separate breeding populations geographically if the breeding and (previously) nonbreeding regions are disjunct (Zhan et al. 2014; Winkler et al. 2017; Dufour et al. 2024). In American Barn Swallows (*Hirundo rustica erythrogaster*), a migration fall-off has resulted in a population of year-round residents in Argentina, whereas all other populations of this subspecies breed in North America (Winkler et al. 2017). This Argentine population has also switched their breeding period from the northern-hemisphere summer (May–September) to southern-hemisphere summer (October–February in Argentina: Winkler et al. 2017), resulting in allochrony. Thus, loss of migration in this population has prevented mating with the rest of the subspecies through both geographic and temporal isolation.

Migration can also contribute to post-mating isolation if interbreeding between migratory phenotypes produces lower-fitness offspring. When migration direction is genetically controlled, matings between individuals with different migration phenotypes can result in offspring with inferior migration routes (Alvarado et al. 2014; Delmore and Irwin 2014; Justen et al. 2021). If populations' different migratory routes or overwintering grounds are substantially ecologically different, divergent selection could cause phenotypic divergence (Rolshausen et al. 2009; von Rönn et al. 2015, 2016) resulting in low-fitness hybrids (Blain et al. 2024). Pre- and post-mating isolation mechanisms could work in tandem: if migratory phenotypes are incompletely geographically or temporally separated, post-mating selection against hybridization may further reduce gene flow where the two migratory phenotypes come into contact (Winker et al. 2013; Louder et al. 2024).

Although the potential of migration to initiate reproductive isolation has been suggested in the handful of empirical examples cited above, the generality of this phenomenon is unknown. The tendency of migration to increase dispersal distance (Paradis et al. 1998; Dawideit et al. 2009) and reduce spatial population structure (Everson et al. 2019) could be a more common or more important effect than that of divergence due to migratory divides or fall-offs. For instance, speciation rates were lower for species with high dispersal in the Furnariidae (Claramunt et al. 2011) and in Northern Melanesian avifauna (Weeks and Claramunt 2014), and phenotypic variation within North American bird species tends to be greater for nonmigratory or shorter-distance migrants (Montgomery 1896). The probability that any reproductive isolation caused by migration would result in speciation is also unknown and depends on the strength and persistence of that isolation, among other factors. In clades where it has originated at least once, migration is a particularly labile trait (Green 2021) and can be gained or lost very rapidly, as evidenced by extensive migratory polyphenism within some species (Zhan et al. 2014), direct observations of gains of novel migratory phenotypes (Berthold et al. 1992) or migratory losses (Winkler et al. 2017) within a few generations, and comparative work in salmonoids (Mcdowall 1997), bats (Bisson et al. 2009), and birds (Voelker et al. 2013; Dufour et al. 2020; Gómez-Bahamón et al. 2020). If transitions between migratory phenotypes are typically very rapid relative to the speciation rate, divergent migratory phenotypes may be lost before they complete speciation.

There are thus multiple pathways by which migratory phenotypes and/or lability of migratory states could influence speciation, raising questions about the extent to which variation in migratory character states has influenced broader patterns of biological diversity. If migratory states are associated with differential speciation rates, and if those character states themselves change slowly relative to the timescale of speciation (e.g., "conserved" character states), then we should be able to see the effect of those states on phylogenetic tree structure (Hey 1992; Barraclough et al. 1998; Stadler 2013). A variety of "trait-dependent" diversification methods have been developed to test the relationship between traits or processes occurring at directly observable or ecological timescales and macroevolutionary patterns (Maddison et al. 2007; Beaulieu and O'Meara 2016; Rabosky and Huang 2016; Maliet et al. 2019). Such approaches typically relate traits or proxies of ecological (e.g., range size: Hay et al. 2022; niche properties: Barreto et al. 2023) or evolutionary processes (e.g., indices of reproductive isolation: Rabosky and Matute 2013; sexual dimorphism: Cally et al. 2021) to geographic or temporal patterns of diversity. State-based speciation extinction (SSE) models (Maddison et al. 2007; Beaulieu et al. 2013) incorporate trait data to infer speciation rates for lineages conditioned on traits, which can then be compared (Hugall and Stuart-Fox 2012; Onstein et al. 2017; Corush 2019; Hardy and Otto). Alternatively, lineage-specific speciation rates can be inferred agnostic to traits ("tip" rates; Jetz et al. 2012; Rabosky 2014; Maliet et al. 2019; Title and Rabosky 2019) and then compared among groups of species according to trait values in a phylogenetically corrected statistical test (Jetz et al. 2012; Price-Waldman et al. 2020; Amado et al. 2021; Burbrink et al. 2023). If migration is a significant driver of reproductive isolation and speciation, we would expect to see a signal of elevated speciation rates in migratory lineages compared with non-migratory lineages. However, if migration rarely initiates reproductive isolation, or if such isolation rarely proceeds to speciation, we expect no association between speciation rate and migration.

In this article, we tested the hypothesis that migration promotes diversification in two clades of passeriform birds: the suboscines and the Emberizoidea. Together, these superfamilies comprise roughly 10–15% of all bird species. Within birds, the Passeriformes are the largest group in which migration is prevalent (the other major migratory clades being the Anseriformes and the Charadriiformes). The suboscines and Emberizoidea were chosen among other groups of Passeriformes because 1) they are some of the larger clades in which migratory lineages are common (Supplementary Fig. S1) and 2) they have high-resolution, low-uncertainty species-level phylogenies available (Barker et al. 2015a; Harvey et al. 2020). Given disagreement about the backbone of Aves (Jetz et al. 2012; Prum et al. 2015; Brown et al. 2017; Reddy et al. 2017) and the importance of high-resolution phylogenetic sampling for speciation rate methods (Chang et al. 2020; Craig et al. 2022), these superfamilies were the best compromise between taxonomic scale and resolution.

Our aim was to examine the relationship between migration and macroevolutionary patterns of speciation. We employed a set of widely used trait-based diversification methods (which are rarely used in conjunction within a study) in order to assess the sensitivity of our results to the choice of method and thereby build support for our inferences. Some previous work has found that speciation rates were higher for migratory birds (compared with non-migratory; Rolland et al. 2014; in the Tyrannidae family specifically: Gómez-Bahamón et al. 2020), whereas others have found that dispersal ability—which may be correlated with migration in some cases—had a negative association with speciation rate (Claramunt et al. 2011). These results are difficult to interpret because the studies employed types of SSE models that can, in some cases, provide misleading inferences about the relationship between traits and diversification (Rabosky and Goldberg 2015; Beaulieu and O'Meara 2016; Helmstetter et al. 2023). We tested the effect of migration state on speciation using a class of SSE models that reduces the mis-attribution of speciation rate heterogeneity to associations with traits (relative to other types of SSE models), as well as tip-based methods. We also assessed the extent to which our results were consistent across phylogenetic scale. Given recent concerns over the reliability of trait-dependent diversification inferences (Rabosky and Goldberg 2015; Harvey and Rabosky 2018; Scott 2018), we explored several post-hoc assessments as a robustness check on our results. Overall, we found no consistent evidence of elevated speciation rates in migratory lineages at this macroevolutionary scale. In addition to raising biological questions about the importance of migration for speciation, our results illustrate the value of corroborating inferences across multiple methods in order to understand how traits influence diversification.

Materials and Methods

Analyses were conducted in R version 4.3.1 (R Core Team 2023). We used the following R packages in plotting: ggplot2 (Wickham 2016), scales (Wickham 2018), ape (Paradis and Schliep 2019), phytools (Revell 2024), and circlize (Gu et al. 2014).

Phylogenies and Trait Data

We used Harvey et al.'s (2020) suboscine phylogeny, specifically the T400F alignment Howard and Moore/AOS species tree (Harvey 2020), and Barker et al.'s (Barker et al. 2015a) maximum clade credibility Emberizoidea phylogeny (Barker et al. 2015b). We pruned these trees of taxa that have since been re-classified as sub-species ($n = 3$ suboscine and $n = 6$ emberizoid taxa) and of one duplicated suboscine species (see Supplementary Methods). We used migration data from Dufour et al. (2020; see Supplementary Methods), following their categorical classification of species as either resident (all individuals occur within the breeding range year-round), strict migrant (all individuals move between geographically disjunct breeding and wintering areas), or partial migrants (both resident and migrant phenotypes are present in the species). Although more recent databases of migratory phenotypes exist (e.g., Tobias et al. 2022), the criteria for categorizing migratory phenotype used by Dufour et al. were most relevant to the hypothesized mechanisms by which migration promotes speciation as discussed in the introduction. Because uncertainties in trait data can bias diversification analyses (Alves et al. 2017), we assessed the sensitivity of our results to the choice of migration data (see Supplementary Methods and Results).

Migration data were available for all 1282 species of suboscines but were not available for two emberizoid species (one extinct and one recently described; see Supplementary Methods). We restricted the analysis to the 783 (of 785) emberizoid species with migration data by pruning the tree of these tips.

In addition to migratory phenotype, we also tested the association between breeding latitude and speciation rate in these superfamilies, because speciation rate may exhibit latitudinal patterns in some taxa (Weir and Schluter 2007; Rabosky et al. 2018), and latitude can be correlated with migratory phenotype in birds (Somveille et al. 2013). We used latitudes of the centroid of the breeding and nonbreeding ranges of each species, collected from digitized range maps acquired from BirdLife International in February 2019 (BirdLife International 2019). Latitudinal data were available for

1236 suboscine species (96.4%) and 772 emberizoid species (98.6%). Breeding-range latitude was used as a covariate in PGLS models of tip speciation rates described below, whereas nonbreeding-range latitude was used in plotting but not analyzed.

Ancestral Character Reconstruction

We reconstructed the evolution of migration across ancestral states using package corHMM (Beaulieu et al. 2013). In addition to fitting a model with constant transition rate between trait states (e.g., resident → strict migrant) for the entire tree, corHMM uses hidden Markov models that incorporate a "hidden" state category to allow for heterogeneity in a given transition rate across the tree (e.g., fitting a resident → strict migrant rate for hidden state A and fitting a separate resident → strict migrant rate for hidden state B). We fit models with and without hidden states and compared their fits using AIC scores. We fit an all-rates-different model for transitions between migration phenotypes, but within the hidden state category, we used an all-rates-equal model (Supplementary Fig. S2). We set symmetric transition rates between the observed and hidden state categories. We fit models with migration as a stepwise process, in which partial migrant was a necessary intermediate between resident and strict migrant phenotypes (Supplementary Fig. S2a), as well as models in which this assumption was dropped, and direct transitions were allowed between all migratory phenotypes (Supplementary Fig. S2b). All models were fit with 100 random restarts to increase the probability of finding the maximum likelihood solution.

Trait-Based Speciation Analyses

We provide an overview of our main methods for trait-based speciation analyses in Figure 1. Whether extinction rates from phylogenies can be reliably estimated from phylogenies that vary in diversification rates is an area of ongoing controversy (Rabosky 2010, 2016; Beaulieu and O'Meara 2015; Marshall 2017; Louca and Pennell 2021). Therefore, we did not assess how migration affects extinction rates.

We estimated tip speciation rates for each tree separately using three model-based methods (Fig. 1a): BAMM (Rabosky 2014), CLaDS (Maliet et al. 2019), and MiSSE (Vasconcelos et al. 2022). All three methods are more accurate than non-model-based approaches (Maliet et al. 2019; Title and Rabosky 2019; Vasconcelos et al. 2022), and they are complementary in that BAMM is most accurate at identifying broad rate regimes underlying large parts of the phylogeny, whereas ClaDS can more accurately detect rate variation when there are many small changes in rate across the phylogeny (Maliet et al. 2019; see Vasconcelos et al. 2022 for comparison), and rates estimated by MiSSE tend to have higher heritability than ClaDS but more heterogeneity than BAMM (Vasconcelos et al. 2022). Critically, we note that BAMM will generally fail to detect fine-grained rate variation when it does exist, whereas CLaDS estimates will suggest the presence of fine-grained rate variation when it does not exist (Vasconcelos et al. 2022).

We used BAMM version 2.5 (bamm-project.org), running for 200 million generations, with priors (λ_{initial}, $\mu_{\text{initial},}$ and $\mu_{\text{shift}} = 1$; $\lambda_{\text{shift}} = 0.05$) used in Harvey et al.'s (2020) biogeographic analysis of suboscine diversification. We used BAMMtools (Rabosky et al. 2014) to assess convergence and discard 10% burn-in from the event data, after which we extracted the mean tip speciation rate for each species and identified the areas of the tree with the most support for a substantial change in speciation rate (the "best shift set"). To calculate ClaDS tip speciation rates, we used the PANDA package version 0.0.7 (Maliet and Morlon 2022) and RCall (Lai et al. 2024) in Julia version 1.9.1 (Bezanson et al. 2017). We ran the MCMC until the Gelman statistic dropped below 1.05 and extracted the maximum a posteriori tip rates after discarding 25% burn-in. Results were analyzed in R using package RPANDA (Morlon et al. 2016). To estimate MiSSE tip rates, we fixed extinction fraction to 0 such that only the speciation rate parameter was estimated (net turnover = speciation rate when extinction fraction = 0; equivalent to a pure-birth model), as we did for the other SSE-type models (see below) but not for the BAMM and ClaDS tip-rate models. For each clade, we fit MiSSE models with up to 15 speciation rate parameters and performed marginal reconstructions on each model. We selected the best set of models for each clade (set of models with ΔAIC < 2 compared with lowest-AIC model) and obtained the model-averaged tip speciation rates from marginal reconstructions of that best set.

To test for an association between migration state and speciation rate, or breeding latitude and speciation rate, we used structured rate permutation tests on the log of BAMM-estimated tip speciation rates (STRAPP: Rabosky and Huang 2016; package BAMMtools: Rabosky et al. 2014) with 10,000 permutations, using a Kruskal-Wallis rank sum statistic (migration phenotype) or a Spearman correlation coefficient (breeding latitude). We also applied ANOVA to a phylogenetic least squares model (pgls function in package caper: Orme et al. 2018) to test whether migration phenotype, breeding latitude, or their interaction were significantly associated with the log of tip speciation rates (for BAMM-, ClaDS-, and MiSSE-estimated rates).

We employed SSE models to test the association between migration and speciation rate (Fig. 1b), specifically MuHiSSE, which employs hidden states to account for speciation rate heterogeneity that is not associated with character (migration) states (package "hisse"; Beaulieu and O'Meara 2016). We fit both a CD model and an equally complex CID model to reduce the potential for spurious inferences on trait-dependent diversification (Beaulieu and O'Meara 2016). For the character-

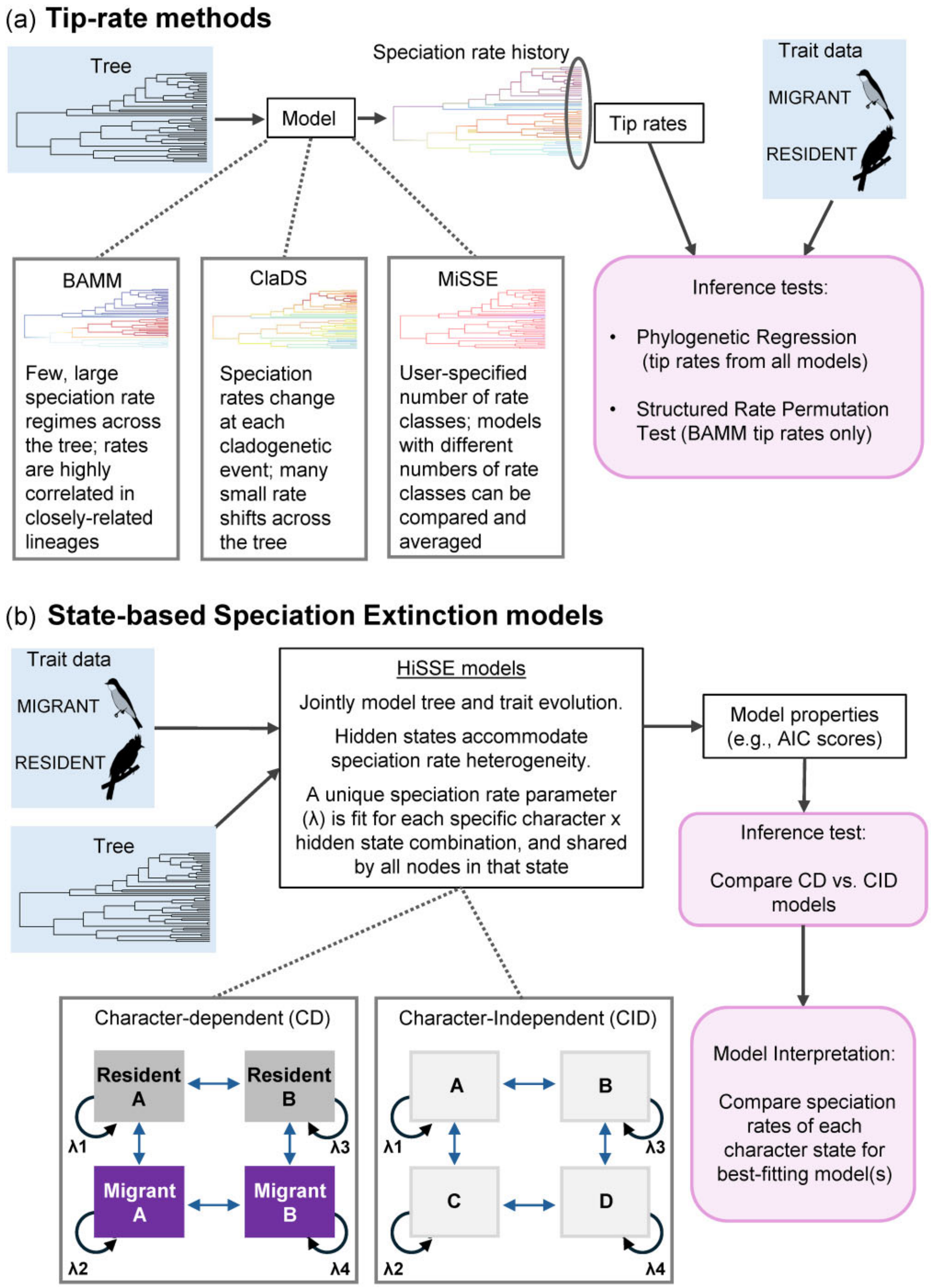

Figure 1. An overview of model-based methods used to infer trait-dependent speciation. (a) For tip-rate methods, a time-calibrated phylogeny is provided as input data to an evolutionary model, which then fits estimates of speciation rates across the tree. The models we used include BAMM, ClaDS, and MiSSE, and selected assumptions and properties of these models are given. The speciation rates at the tips of the tree ("tip rates") estimated by the model are then combined with trait data (migration state for each species) for inference tests. (b) HiSSE and MuHiSSE jointly model the evolution of the tree, characters (observed traits), and "hidden" states, where hidden states are included to accommodate rate heterogeneity that is unattributed to the trait of interest. These character-dependent (CD) models fit a unique speciation rate (λ) for each combination of observed and hidden states. Character-Independent (CID) models assume that observed states (e.g., migratory, resident) do not confer different diversification rates upon lineages but may nonetheless differ in evolutionary rate due to unobserved hidden states that are unlinked to the focal state of interest. Equally complex CD and CID models are fit (in this example, 4 unique rate parameters, λ1-λ4) and compared. If CD models are found to fit better than CID models, the rate parameters associated with each state are then compared with determine directionality and importance of effects of the focal trait on speciation rates and to assess the possibility of false positives. Results from (a) and (b) were then compared with those from sister clade contrasts (Fig. 5) and the time-slice contrast count (TSCC) (Fig. 6). Illustration of *Xolmis pyrope* by Edwin Price, shared under CC BY 4.0 license; silhouette of *Myiarchus* species by Ferran Sayol.

dependent model, we parameterized different speciation rates for resident, partial, and strict migrants in each of two hidden state categories, for a total of six different speciation rate parameters. For the character-independent model, we allowed six hidden state categories, also resulting in six different speciation rate parameters. For all models, the sampling fraction was set to 1; we also set the extinction fraction to 0 for all states such that the model only estimated speciation rates to vary across the states. To assess the significance of migration on speciation rate, we compared model fits of CD versus CID hidden state models using log likelihood and AIC scores.

Robustness Checks

Our whole-tree approaches to state-dependent diversification revealed discordance among methods, and we therefore interrogated the data further by repeating analyses across several subsets of the suboscine phylogeny. In particular, we analyzed the Tyrannidae subtree (301 species) within the suboscines separately, because migratory species were concentrated in this family (84% of suboscine migrants are Tyrannids), and therefore it was likely driving any positive associations between migration and speciation rate identified by the models. As an additional check on the robustness of state-dependent inferences, we compared species richness among sister clades that differed in whether each was predominately migratory or nonmigratory in the Tyrannids. Sister clade analyses (Slowinski and Guyer 1993; Vamosi and Vamosi 2005; Paradis 2012; Käfer and Mousset 2014) typically compare richness of sister clades that are each monomorphic for an opposing trait value. However, almost all clades in the suboscines are polymorphic for migration: disregarding sister dyads, there are only 13 sets of sister clades that are monomorphically migratory versus non-migratory, and 12 of these consisted of one of the sister clades having $N = 1$ species. Therefore, we identified clades that were predominately migratory (over 50% of tip species were either partial or strict migrants) that were sister to clades that were predominately nonmigratory (over 50% of tip species were residents) and counted the number of tip species in each clade. This set of 5 pairs of sister clades included 93 out of 301 Tyrannid species (31%) and contained 49 migratory species (64% of migrant Tyrannids; 54% of migrant suboscines). We also performed sister clade analyses on the 13 monomorphic sister pairs (see Supplementary Material).

We also developed a non-parametric method to assess the reliability of formal state-dependent diversification tests using tip rate methods, which we refer to as the Time Slice Contrast Count (TSSC; Fig. 2). Unlike sister clade analyses, it specifically examines patterns of lineage-specific speciation rates among character states. For example, sister clades with identical numbers of species could nonetheless show marked differences in speciation rate; visually, such a pattern would likely be evident in the branch length distributions for the two clades, with the faster-speciating clade showing proportionately shorter branches closer to the present relative to the slower-speciating clade. TSSC is designed to capture such differences, thus complementing formal sister clade comparisons by facilitating contrasts in tip speciation rates without requiring that clades differ in species richness or that sister clades be fixed for different states. The approach is conservative in that it provides independent evidence for associations between character states and speciation rates without requiring any model-based inference on character evolution.

Consider a rooted phylogenetic tree where tip speciation rates have been estimated independently of character state histories using information in the phylogenetic tree only, as provided by BAMM, CLaDS, MiSSE, or DR (Jetz et al. 2012). Given a set of character states at the tips of the tree, we can compute the mean speciation rate for all species having character state 0 (e.g., “nonmigratory”) versus state 1 (“migratory”). Denote the difference in these mean rates by Δ_λ, where $\Delta_\lambda = \lambda_1 - \lambda_0$, with λ_1 and λ_0 denoting the mean speciation rates for all tips in states 1 and 0, respectively. Minimally, Δ_λ represents a single phylogenetically independent data point: provided that there is variation in states within the tree, we can be certain that there has been at least one independent state change since the root.

The logic underlying TSSC is to decompose a given phylogeny into a series of independent subtrees as described above, such that Δ_λ can be computed for each subtree. Provided the subtrees are independent, each Δ_λ will also be independent, since each rooted subtree will be descended from a single ancestral node that is unshared with any other such subtree. Because each rooted subtree represents the descendants of a single ancestral node, any state-associated rate differences Δ_λ will necessarily reflect character state shifts that are independent of those occurring in any other subtrees. We obtained sets of independent subtrees by choosing a “slice time” τ, which can be visualized as a vertical slice cutting the phylogeny at τ time units before the present. Each branch bisected by the slice time τ defines a unique subclade, and the “tipward” descendant clade from each is statistically independent of all other clades—as delimited by a particular time slice—with respect to the Δ_λ metric (Fig. 1). Note that some branches bisected by the slice time will not lead to valid clades for the computation of Δ_λ: specifically, any valid descendant clade needs to contain variation in character state.

Consider a set of K clades—each with variation in state—defined by the slice at time τ. Under the null hypothesis (no state-dependent speciation), we expect to observe roughly equal numbers of subclades with $\Delta_\lambda < 0$ and $\Delta_\lambda > 0$. On the other hand, if state 1 results in faster speciation, we should observe an excess of subclades with $\Delta_\lambda > 0$. We recognize that this approach

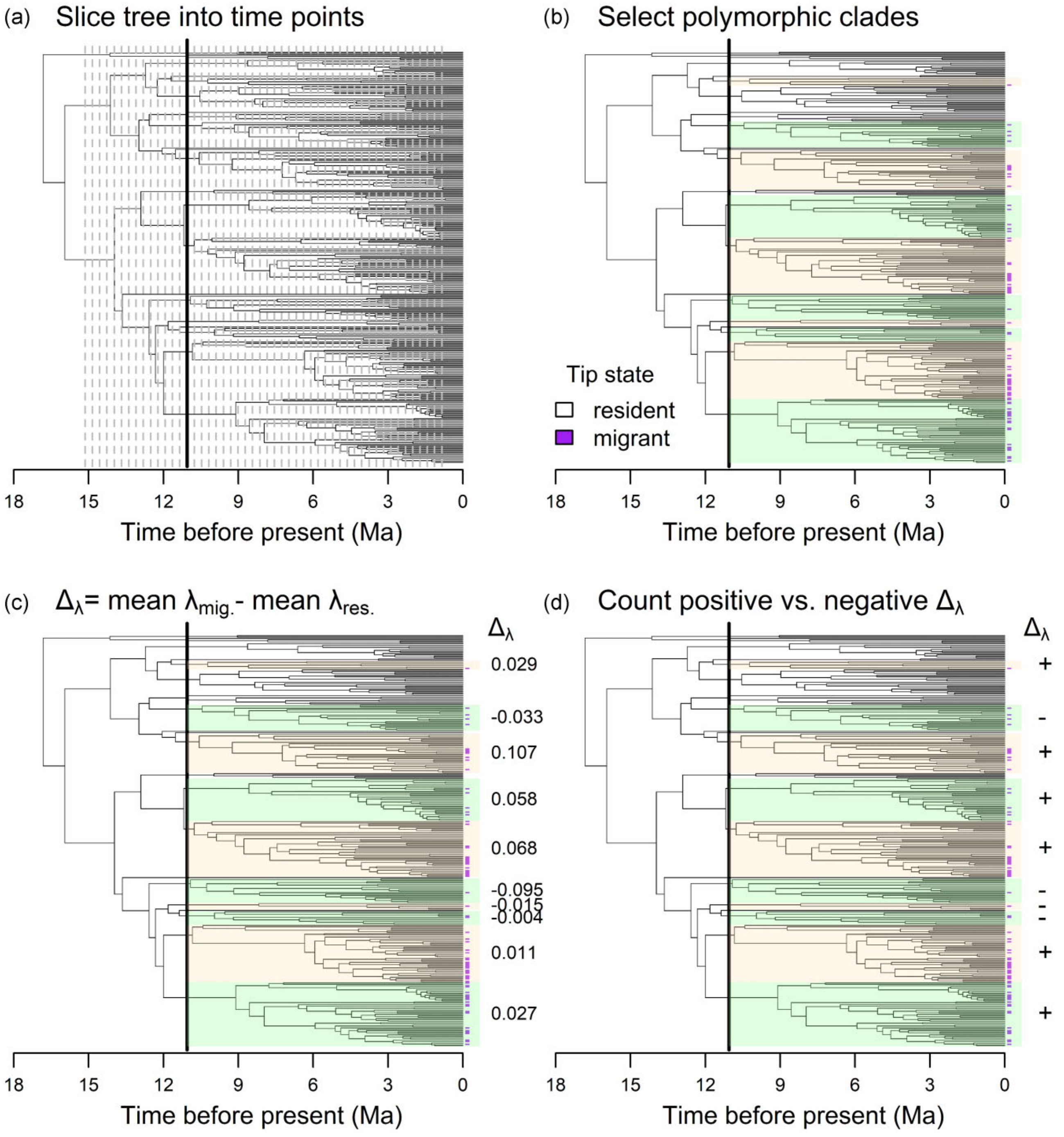

FIGURE 2. Illustration of the TSCC on the Tyrannidae tree. (a) The tree is subdivided into a series of equally spaced time points. (b) all rooted subtrees present at a single slice that include variation in tip character states are selected for analysis; qualifying clades are highlighted. (c) For each clade, calculate contrast, Δ_λ = mean tip speciation rate (λ) of migrant species—mean tip speciation rate (λ) of resident species. In this example, the DR statistic is used for the tip speciation rates. (d) Count the number of clades with positive and negative Δ_λ at the slice. In this example, at the 15th time slice, 6 clades had a positive contrast (migrants speciate faster than residents on average in those clades), whereas 4 clades had a negative contrast (residents speciate faster). Steps (b)–(d) are repeated across all time slices with ≥ 10 qualifying clades, and counts can then be plotted over time as in Figure 6.

is conservative, because it reduces each subclade to a single independent data point. However, we view this approach as an important check on the robustness of formal state-dependent analyses described in the previous section.

We sampled a series of time points (slices) throughout the history of each group (the suboscines: 200 slices, the tyrannid tree within the suboscines: 50 slices, and the Emberizoidea: 100 slices); see Figure 2 for a worked example. At each time slice τ, we assessed each of the largest monophyletic clades with at least one resident and one migrant tip (collapsing partial and strict migrants into one category), indicating one or more transitions within the clade. We omitted slices with fewer than 10 clades meeting these criteria. For each slice time, we counted the number of clades at a given time slice where the contrast (Δ_λ) was positive (migratory lineages speciate faster) versus negative (resident lineages speciate faster). Repeating this process across all time slices from the present to the common ancestor, we then plotted the contrast counts as a function of time. If positive contrasts were more common than negative contrasts, this would indicate migration is associated with higher speciation rates. Clearly, the Δ_λ statistics are not independent for different time slices applied to the same tree, and we do not treat them as such. However, by repeating the approach across equally spaced timepoints and plotting the results, we could ensure that results were not conditional on a single user-defined time slice. Our intention in applying the TSSC approach is not as a primary test for state dependence but as a secondary check on results obtained with other methods and as a complement to sister clade contrasts in species richness. We additionally applied the TSCC method to a binary metric of breeding latitude by categorizing species either tropical breeders (centroid of breeding latitude between 23.5° N and 23.5° S) or temperate breeders.

We focused on the DR statistic as the metric of tip speciation rates (Jetz et al. 2012) for the TSCC analysis, because the DR statistic generates identical results for symmetric subclades that differ in character state. Tip rates calculated with BAMM and ClaDS are subject to stochastic noise even for a fully symmetric phylogeny with identical branch lengths. However, we also applied the TSCC to BAMM and ClaDS tip rates (see Supplementary Results).

RESULTS

Migration and Breeding Latitude

In both clades, breeding at tropical latitudes was strongly associated with residency (90.2% of resident suboscines and 88% of resident Emberizoidea breed in the tropics). In the Emberizoidea, migrant species are typically temperate breeding (81% of partial and 99% of strict migrants), whereas migrant suboscines are more mixed (50% of partial migrants and 89% of strict migrants breed at temperate latitudes).

Ancestral Character Reconstruction

For suboscines, the stepwise-migration models had weakly better support than the comparable all-transitions models (ΔAIC ≥ 4), although they were equivalent for the Emberizoidea (ΔAIC < 2; Supplementary Table S1). The hidden-rates models were a substantially better fit than the models without hidden rates for both clades (ΔAIC > 10; Supplementary Table S1). The overall best model was stepwise migration with hidden rates (Supplementary Table S1; although for Emberizoidea, all transitions with hidden rates were equally supported); therefore, we describe and plot results of stepwise hidden-rates models for the remainder of the paper. These models fit two transition rate categories ascribed to the hidden states (Supplementary Fig. S3). Generally, migratory lineages were more commonly found in parts of the tree subject to the faster transition rate regime (Figs. 3a, b, 4a, b). The faster rate category applied to 340 suboscine tip species (27% of the tree) and 130 Emberizoidea tip species (17% of the tree). The common ancestor of the suboscines was likely resident (Fig. 3a), whereas the common ancestor of the Emberizoidea was likely a strict migrant (Fig. 4a).

Diversification Analyses

Overall, there was no consistent effect of migration on speciation rates, either across all clades or within any clade across the various speciation rate methods and analyses (Supplementary Table S2). The most common result was no detectable effect of migration on speciation rate in either direction. Comparing across clades within a method, the tip rate methods (BAMM, MiSSE, and ClaDS) yielded the same qualitative result (no association for BAMM or MiSSE and a positive association between migration and speciation rate for ClaDS) for all clades examined, whereas HiSSE models indicated elevated speciation rates for migrant lineages in the Tyrannidae only. Results were not sensitive to the choice of migration data source (Supplementary Results). The significance of the relationship between breeding latitude and tip speciation rates also differed across methods, in the same pattern as the migration results (no association between breeding latitude and BAMM or MiSSE tip rates for any clade; significant association between breeding latitude and ClaDS tip rates for both suboscines and Emberizoidea). We consider results for each method in more detail below.

BAMM—The BAMM best credible shift set included five major increases in speciation rate in the history of the suboscines (Fig. 3), all of which were in lineages that were likely residents according to our ancestral character reconstruction. These shifts were in lineages that produced no or very few migratory descendants,

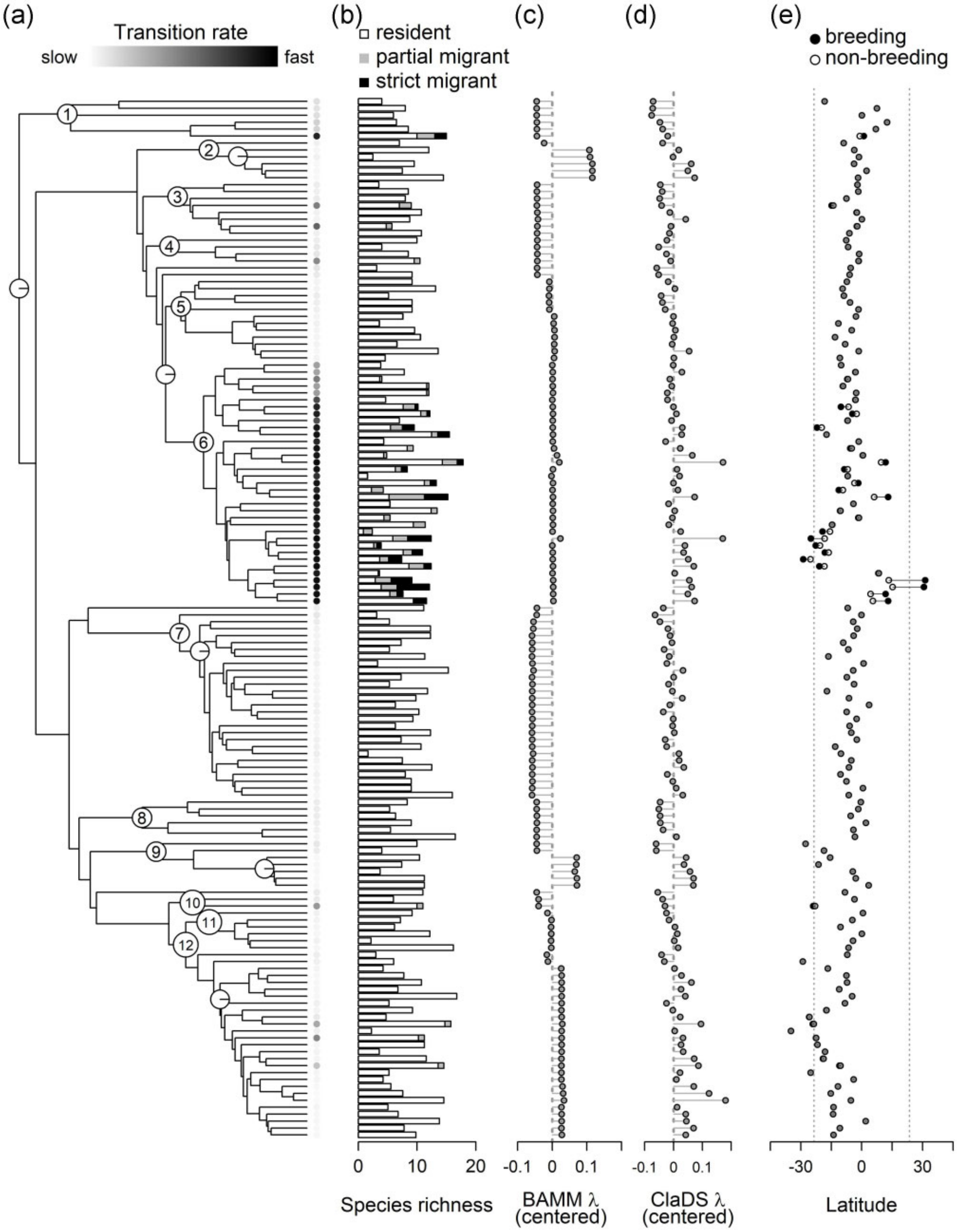

FIGURE 3. No relationship between migration phenotype and speciation rate in the suboscines. (a) A suboscine tree simplified to 150 tips (representing 1282 species) with major clades labeled at nodes: 1) Eurylaimides, 2) Pipridae, 3) Cotingidae, 4) Tityridae, 5) Rhynchocyclidae (after Harvey et al. 2020), 6) Tyrannidae, 7) Thamnophilidae, 8) Grallariidae, 9) Rhinocryptidae, 10) Scleruridae, 11) Dendrocolaptidae, 12) Furnariidae. Tip points show posterior probability of being in the "fast" rate category (Supplementary Fig. S3a) of transition rates between migration phenotypes. Pies at internal nodes show the posterior probability of migration phenotype (white = resident, gray = partial migrant, black = strict migrant) at the common ancestor and at the five nodes where BAMM speciation rates significantly increased (BAMM best shift set). (b) Bars show richness of species represented by each tip in the simplified tree, colored by migration phenotype. (c) BAMM and (d) ClaDS speciation rates are given for each tip in the simplified tree, centered around the tree-wide median rate. (e) Breeding and non-breeding latitudes connected by line segments for each tip in the simplified tree. Dashed vertical lines indicate tropical latitudes. Tip data (panel a: transition rate; panels c and d: speciation rates; panel e: latitudes) is the mean across the set of species represented by that tip in the simplified tree.

except for the shift in the common ancestor of the tyrannids and rhynchocyclids: migration is common in the tyrannids but absent in the rhynchocyclids (Fig. 3). Three of the four major increases in speciation rate in the Emberizoidea occurred in lineages that were likely residents and produced entirely or mostly resident descendent species (Fig. 4; shifts occurred in the common ancestor of the *Atlapetes and Piplio* within the Passerellidae and at the origins of the Darwin's Finches and *Sporophila* within Thraupidae). The fourth shift to faster

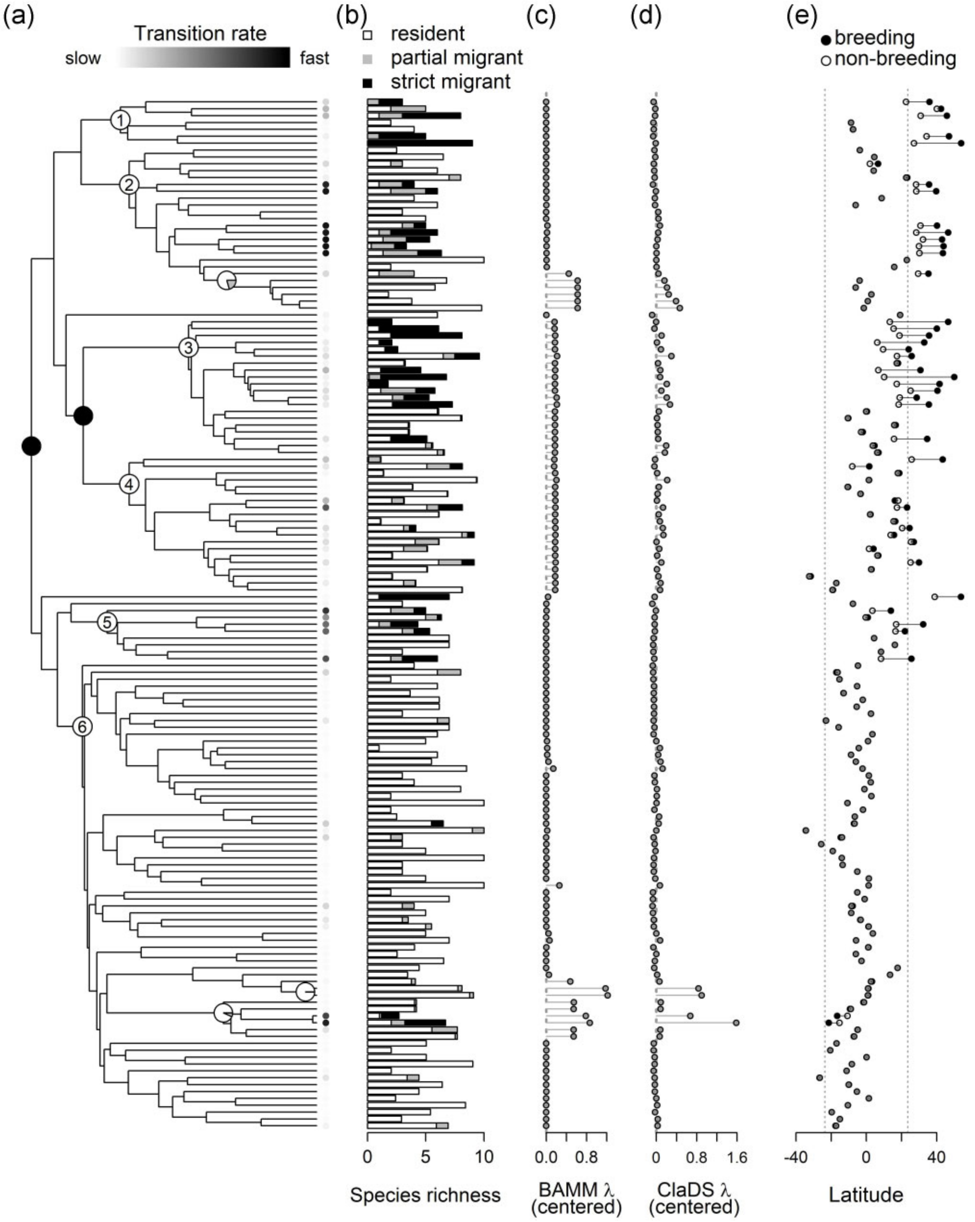

FIGURE 4. No relationship between migration phenotype and speciation rate in the Emberizoidea. (a) An Emberizoidea tree simplified to 150 tips (representing 783 species) with major clades labeled at nodes: 1) Emberizidae, 2) Passerellidae, 3) Parulidae, 4) Icteridae, 5) Cardinalidae, 6) Thraupidae. Tip points show posterior probability of being in the "fast" rate category (Supplementary Fig. S3b) of transition rates between migration phenotypes. Pies at internal nodes show the posterior probability of migration phenotype (white = resident, gray = partial migrant, black = strict migrant) at the common ancestor and at the 4 nodes where BAMM speciation rates significantly increased (BAMM best shift set). (b) Bars show richness of species represented by each tip in the simplified tree, colored by migration phenotype. (c) BAMM and (d) ClaDS speciation rates are given for each tip in the simplified tree, centered around the tree-wide median rate. (e) Breeding and non-breeding latitudes for each tip in the simplified tree. Tip data (panel a: transition rate; panels c and d: speciation rates; panel e: latitudes) is the mean across the set of species represented by that tip in the simplified tree.

speciation occurred in the likely strict-migrant ancestor of the parulids and icterids, and migration is more common in these clades (particularly the Parulidae; Fig. 4). Overall, these results do not support our hypothesis that migration promotes speciation but rather show that most increases in speciation rate regimes detected by BAMM happened in non-migratory species.

According to STRAPP permutation tests, BAMM-estimated speciation rates did not differ among migration phenotypes for either the suboscines ($P = 0.813$), the Tyrannidae specifically ($P = 0.928$), or the Ember-

TABLE 1. Speciation rate estimates for each migratory phenotype across methods.

Clade	Method	Resident	Partial migrant	Strict migrant
Suboscines	BAMM	0.1375	0.1431	0.1436
	ClaDS	0.1054	0.1498	0.1703
	MiSSE	0.1201	0.1426	0.1765
	MuHiSSE[a]	0.1030	0.1030	0.1030
Tyrannidae	BAMM	0.1432	0.1432	0.1437
	ClaDS	0.1188	0.1573	0.1799
	MiSSE	0.1475	0.1680	0.1898
	MuHiSSE	0.0767	0.2180	0.2213
Emberizoidea	BAMM	0.1378	0.1438	0.2952
	ClaDS	0.1534	0.1585	0.1636
	MiSSE	0.1708	0.1933	0.1728
	MuHiSSE	0.1502	0.1502	0.1502

Notes: [a]multistate hidden state-based speciation and extinction. For BAMM, ClaDS, and MiSSE, the median tip rate for each migration phenotype is reported; for MuHiSSE, the mean of migration-dependent speciation rates across the two hidden states in the best-fitting model (see Table 2) is reported. Averages of tip speciation rates by migratory phenotype do not control for clade-level differences in rates that are unlinked to the character state (BAMM, ClaDS, and MiSSE in particular): most dramatically, the fast BAMM rates in emberizoids largely reflect the fact that most migratory lineages occur in the fast-speciating Parulidae. For Emberizoidea and suboscines, speciation rates reported for MuHiSSE are the same for all three migration phenotypes because the character (i.e., migration)-independent model was the best fit; thus, the best-fitting model inferred only one speciation rate for all migration phenotypes.

izoidea ($P = 0.874$; Table 1). Speciation rate estimated with BAMM was also not correlated with breeding latitude for any clade according to the STRAPP permutation tests (suboscines: Spearman $r = -0.088$, $P = 0.523$; Tyrannidae only: Spearman $r = 0.0097$, $P = 0.899$; Emberizoidea: Spearman $r = 0.084$, $P = 0.927$); nor were BAMM tip-rates significantly associated with migration phenotype, breeding latitude, or their interaction according to the phylogenetic least squares analysis (Supplementary Table S3).

ClaDS—In contrast to BAMM, ClaDS-estimated tip speciation rates were significantly higher for migratory lineages and for lineages breeding at higher latitudes in both suboscines and Emberizoidea (Table 1; Supplementary Table S4). In the suboscines, strict migrants had the highest ClaDS speciation rates, followed by partial migrants (Table 1), and breeding latitude had an additive effect such that higher breeding latitude was associated with higher speciation rates (Supplementary Table S4). An effect of breeding latitude on speciation rate was not supported for the analysis restricted to the Tyrannidae family (Supplementary Table S4; ΔAIC < 2). In the Emberizoidea, breeding latitude interacted negatively with migration (Supplementary Table S4), indicating that the effect of breeding latitude on ClaDS speciation rate was weaker for migrants (alternatively, that the effect of migration on speciation rate was weaker for high latitude breeders; this interaction is likely reflective that breeding latitude is confounded with migration).

MiSSE—Median MiSSE tip speciation rates were higher for strict migrants than residents or partial migrants in the suboscines (and the Tyrannidae specifically), but partial migrants had the highest median tip rates in the Emberizoidea (Table 1). However, none of the PGLS models that included an effect of migration (or breeding latitude) were supported over intercept-only models in any clade (Supplementary Table S5).

State-based speciation models—For both the entire suboscine tree and the Emberizoidea, the CID speciation models were a better fit than the CD models (ΔAIC > 10; Table 2), indicating that speciation rates did not differ by migration phenotype. When we fit models to the Tyrannidae tree within the suboscines, the CD speciation model with stepwise transitions was the best overall fit (Table 2), indicating that speciation rates differ by migratory phenotype in Tyrannidae. This best-fitting model for Tyrannidae assigned the highest speciation rates to strict and partial migrants, ~2.8x faster than that of residents (Table 1).

Sister clades comparison in Tyrannidae—To interrogate conflicting results between the BAMM, MiSSE, ClaDS, and HiSSE approaches, we qualitatively examined species richness and migration phenotype among sister clades in the Tyrannidae (the family containing the most migratory species in the suboscines). Differences in species richness between predominately migratory clades and their predominately resident sisters were marginal (Fig. 5), even though these clades accounted for 64% of migratory species across the entire family, and despite the significantly faster rates in migratory (relative to resident) lineages estimated using MuHiSSE and ClaDS. Additional sister clade analyses performed on monomorphic clades also did not support greater species richness for migratory clades (Supplemental results, Supplementary Fig. S4).

Time Slice Contrast Count—There was no consistent evidence that faster speciation was more common for migrants for any of the groups (suboscines, Tyrannidae, Emberizoidea) examined (Fig. 6, Figs. S5, S6). For example, a time slice through the suboscine phylogeny 6 Myr before the present generated a set of 29 independent subclades that showed variation in migratory state (Fig. 6a). The mean speciation rate for migratory tips, relative to non-migratory, was faster in 14 of those subclades ($\Delta_\lambda > 0$); however, 12 subclades showed faster rates for

Table 2. HiSSE models support a relationship between migration and speciation only in the Tyrannidae.

Clade	Model	lnL[a]	ΔAIC[b]
Suboscines	Character-dependent, stepwise	−3811.41	47.04
	Character-dependent, all transitions	−3791.18	14.58
	Character-Independent, stepwise	**−3791.88**	**–**
	Character-Independent, all transitions	−3791.88	3.99
Tyrannidae	**Character-dependent, stepwise**	**−938.50**	**–**
	Character-dependent, all transitions	−940.57	12.14
	Character-Independent, stepwise	−955.90	26.79
	Character-Independent, all transitions	−955.90	30.79
Emberizoidea	Character-dependent, stepwise	−2136.26	28.36
	Character-dependent, all transitions	−2135.78	35.39
	Character-Independent, stepwise	−2126.92	1.68
	Character-Independent, all transitions	**−2124.08**	**–**

Notes: [a]log likelihood; [b]Akaike information criteria. The model with the lowest AIC score in each clade is indicated in bold; ΔAIC for other models within each clade are relative to this model. For the CD models, speciation rate was allowed to vary by the three migratory phenotypes (resident, partial migrant, and strict migrant) and the two hidden-state characters, for a total of 6 free speciation rate parameters. For the CID models, speciation rate did not differ between the migratory phenotypes but did vary across six hidden-state characters (a CID-6 model: Beaulieu and O'Meara 2016), such that CD and CID models were of equal complexity and could be directly compared. The "stepwise" models disallowed direct transitions between resident and strict migrant phenotypes (thereby specifying "partial migrant" as an intermediate evolutionary step), whereas the "all transitions" models allowed direct transitions between all three migratory phenotypes.

the non-migratory tips ($\Delta_\lambda < 0$), and 3 were identical ($\Delta_\lambda = 0$). Overall, regardless of clade and phylogenetic scale, any given partition of the phylogeny is likely to yield subclades where tip rates are essentially the same for migratory and non-migratory lineages. We note that tip rates appear faster for migratory suboscines for time slices early in the clade history when there are relatively few subclades (e.g., >13 Ma there are only 10 subclades generated by TSCC, and migrants speciate faster in 8 of those 10 clades in the average slice over that period). Tropical-breeding suboscines had faster speciation (DR statistic) than temperate-breeding suboscines (Fig. 6), although this pattern was not apparent within the Tyrannidae.

Discussion

Our objective was to assess whether migration was consistently associated with elevated rates of speciation in birds across different methods. We assessed the relationship between tip speciation rates and migration phenotype and additionally assessed trait-dependent speciation rates fit by SSE models in two passerine superfamilies in which migration is variable. We did not find robust or consistent evidence of a relationship between migration phenotype and speciation in either the suboscines or the Emberizoidea. Although there was discordance among the results from the various methods, a lack of a significant relationship in either direction was the most common result across clades and methods (Supplementary Table S2). These results differ from previous work that found elevated speciation rates for migrants across the broader avian phylogeny but sparse species-level sampling (Rolland et al. 2014). Our results could be explained by different biological scenarios, including that migration evolves too quickly to affect speciation or that migration both promotes and impedes speciation in different contexts. For instance, if migratory falloffs promote speciation in island taxa (Dufour et al. 2024), but migration decreases population structure and slows speciation in mainland-breeding taxa, these effects could counter each other. Indeed, it may be common for traits to have opposing effects on diversification in different ecological contexts (Anderson et al. 2023). Alternatively, migration could promote (or impede) speciation in these taxa without detection by our analyses. The disagreement we observed among the results of different methods limits definitive biological conclusions about our hypothesis.

Inconsistent Inferences among Diversification Rate Models

Disagreement among these methods is not necessarily unexpected, given their different underlying model assumptions. For instance, under some conditions, approaches that jointly model trait evolution and diversification rate shifts (such as MuHiSSE) have higher power to detect trait-associated diversification, compared with tests of correlations between traits and the diversification rates modeled independently of those traits (e.g., ClaDS, MiSSE, or BAMM; O'Meara et al. 2006). However, we note that the greatest discordance in our results was between the tip rate methods: inferences from ClaDS and BAMM differed for all clades, while MuHiSSE results aligned with BAMM for the suboscines and Emberizoidea and with ClaDS for the Tyrannidae (Supplementary Table S2). We also note that, although the inferences differed greatly between BAMM and ClaDS, the average speciation rates estimated for each character state were very similar between these methods in most cases (Table 1).

Differences in model assumptions between BAMM and ClaDS likely underly the very different outcomes

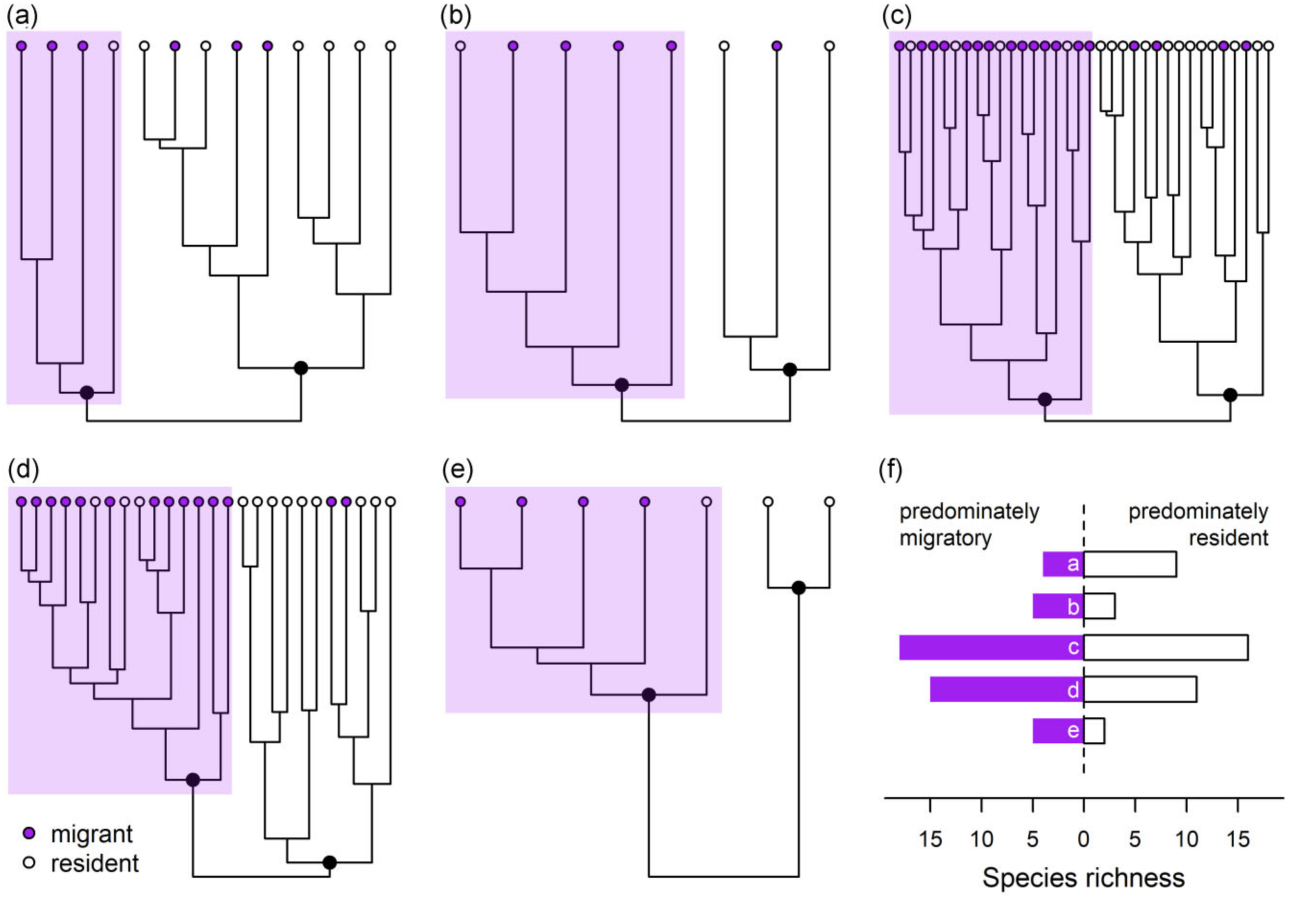

Figure 5. Sister clade comparison within the Tyrannidae does not support markedly more speciation in clades where migration is common. Pairs of sister clades (a–e) in which both clades contained > 1 tip species, one clade was predominately (>50%) migratory (highlighted box), and the other was predominately resident were compared. Migratory phenotype of tip species is indicated by filled circles. (a) left: *Xolmis* + *Neoxolmis*; right: *Myiotheretes* + *Agriornis*; (b) left: descendants of common ancestor of (*Muscisaxicola maclovianus* + *M. frontalis*); right: descendants of common ancestor of (*M. griseus* + *M. cinereus*); (c) left: *Empidonax* + *Sayornis*; right: *Contopus* + *Mitrephanes*; (d) left: *Tyrannus* + *Empidonomus*; right: descendants of common ancestor of (*Conopias* + *Myiodynastes*); (e) left: *Pseudocolopteryx*; right: *Serpophaga*. (f) Species richness of the predominately migratory (solid bar) and resident (white bar) clades are shown for each pair of sister clades in panels (a) through (e). Despite MuHiSSE-estimated speciation rates of migratory lineages ~2.8x faster than resident lineages (Table 1) and significantly elevated speciation for migrant lineages in ClaDS (Table 1, Supplementary Table S4), differences in species richness in (f) are marginal and not consistent in direction.

of the inference tests applied to these estimates. BAMM assumes speciation rates are highly correlated among closely related lineages and fits models with few changes in speciation rate regimes that are highly heritable (relative to other approaches such as ClaDS: Maliet et al. 2019). For our trees of ~1 K species, BAMM fits on the order of 5–10 regime shifts and thus may have relatively low power to detect a significant relationship between these regime shifts and trait phenotypes (Rabosky and Huang 2016). Indeed, we found no difference in BAMM speciation rates among migratory phenotypes in any clade, using either PGLS or STRAPP analyses. In contrast to BAMM, we found a positive association between ClaDS speciation rate and migration in all clades, which may be due to the greater power derived from tip rate variability under ClaDS: the ClaDS model assumes that rates undergo evolutionary change along every branch, and thus, that every species has a potentially unique rate. Indeed, comparing BAMM and ClaDS speciation rates for the Emberizoidea is instructive: BAMM speciation rates for strict migrants were > 2x greater compared with residents or partial migrants (Table 1), yet neither PGLS nor STRAPP inference tests found a significant relationship (Supplementary Table S2). In contrast, ClaDS speciation rates were very similar among migration phenotypes for Emberizoidea (Table 1; <7% difference between resident and strict migrant speciation rates), yet PGLS found that these modest differences were significant.

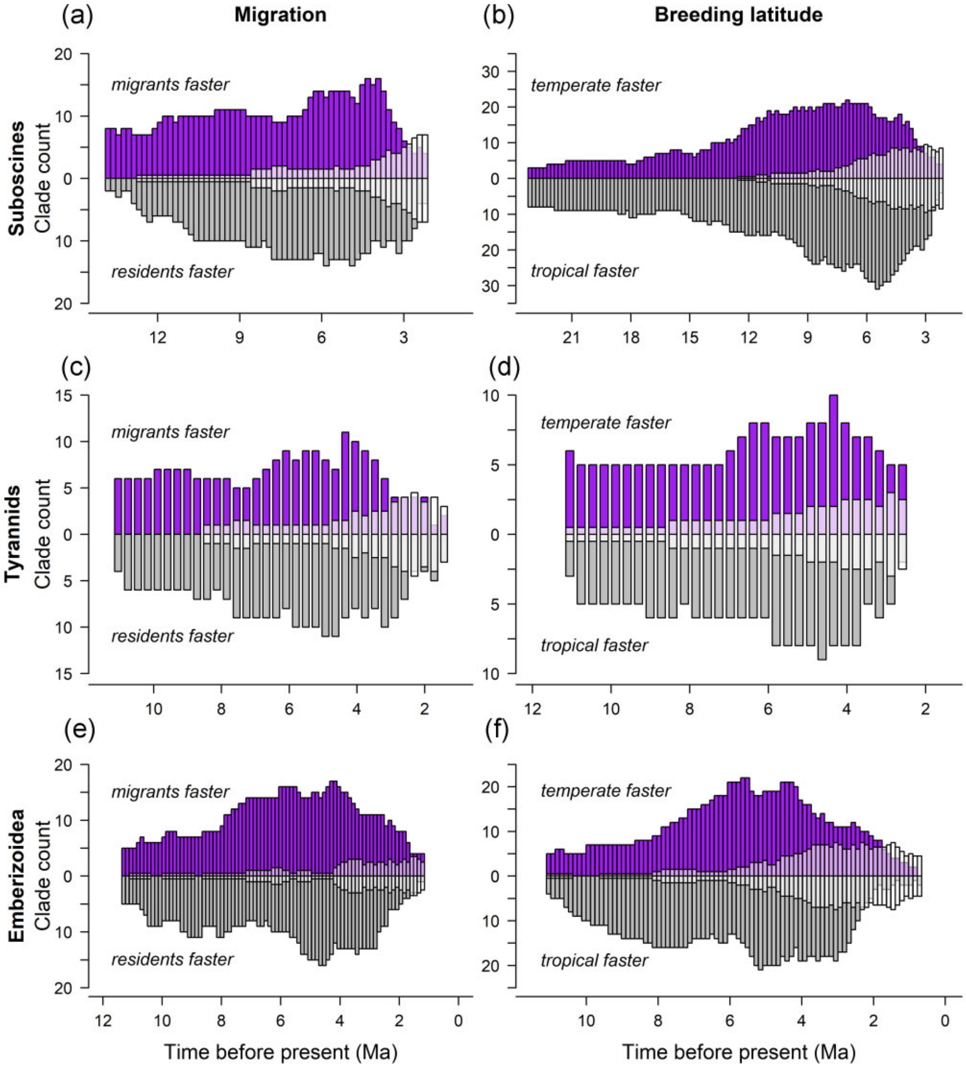

FIGURE 6. TSSC of DR statistics reveal no consistent effect of migratory state on speciation rate in suboscines (a), tyrannids (c), nor emberizoids (e). Clade count (y-axis) is the number of statistically independent "sliced clades" (see methods) where the focal character state (migratory: panels a, c, e; temperate breeding: panels b, d, f) shows faster (above zero) or slower (below zero) speciation rate (measured via DR statistic) relative to the alternative character state. Clades for which average speciation rates were equal for both character states within the clade are indicated by translucent white bars centered at zero. A pattern of faster speciation rates for tropical-breeding suboscines (compared with temperate-breeding suboscines) is seen in (b), where the below-zero area is greater than the above-zero area consistently across time.

Considerations for Implementing Trait-Based Diversification Analyses

Discordance in the results among the methods is perhaps unsurprising, given their different assumptions. However, the discordance is nonetheless significant: it highlights the sensitivity of an empiricist's conclusions to their choice among well-established trait-based diversification methods at the outset of their study. Many empiricists use only one such approach to test whether a trait is associated with increased (or decreased) diversification. Consider: had we executed this study using only ClaDS models, we would have concluded that speciation rates are higher for migrant lineages in both the suboscines and the Emberizoidea; had we instead used BAMM or MiSSE, we would have found no evidence that migration promotes speciation in either clade; and had we chosen the MuHiSSE framework, we would have found that migration is associated with elevated speciation rates in the Tyrannidae, but not in the suboscines more generally, nor in the Emberizoidea.

The performance of these and other trait-based diversification methods is typically tested and compared on simulated data (Beaulieu and O'Meara 2016; Rabosky et al. 2017; Maliet et al. 2019; Title and Rabosky 2019; Vasconcelos et al. 2022), and these simulations necessarily make many assumptions that differ from real phylogenetic histories. An empiricist does not know whether the true history of a clade involves many small rate shifts (indicating that the ClaDS model is a closer approximation to their data) or few large ones (in which case BAMM would be the more appropriate choice). Given these constraints, qualitative agreement in results across methods would be desirable as evidence supporting their reliability. In the following, we discuss some best practices for implementing individual diversification methods and make suggestions for comparing them.

A phylogeny that is nearly fully sampled at the species level, and that was assembled with long alignments, is preferable for inferring trait-based diversification, as incompletely sampled phylogenies and low-information sequence alignments can lead to inference of spurious rate shifts (Chang et al. 2020; Craig et al. 2022; Helmstetter et al. 2023). BAMM generally infers few, large speciation rate regimes, giving it low power for inference of trait-dependent diversification on smaller trees. Generally, trees of at least ~500–1k taxa are desirable for assessing trait-dependent speciation (Rabosky and Huang 2016), but power also requires rate heterogeneity: even a large tree with little rate variation will have lower power. SSE models generally require phylogenies larger than 300 taxa (Davis et al. 2013), and the trait of interest should have arisen multiple times across the phylogeny. Although it has been recommended that the ratio among different tip states be less than 10:1 for SSE models (Davis et al. 2013), recent work suggests that inference is biased only at more extreme ratios (i.e., 100:1; Helmstetter et al. 2023).

Some classes of SSE models have hidden state implementations (HiSSE, MuHiSSE, GeoHiSSE, etc.), whereas others only model observed characters (BiSSE, ClaSSE, MuSSE, QuaSSE). When fitting and comparing SSE models, the candidate set of models should always include hidden state but otherwise "observed character"-independent models (CID), because those models can accommodate diversification rate heterogeneity that is unlinked to the (observed) character state of interest. Failing to include hidden states will generally lead to spurious associations between states and rates (Rabosky and Goldberg 2015; Beaulieu and O'Meara 2016) when rates vary through time or among lineages. Finally, Schwery et al. (2023) demonstrate that posterior predictive checks on model adequacy, using a range of summary statistics, have considerable potential for reducing false positives in state-dependent analyses.

Given our findings that results of trait-dependent diversification studies may be highly sensitive to the choice of a single method, we suggest that studies of trait-based speciation assess the concordance of results from multiple methods (Martínez-Gómez et al. 2024). Beyond assessing general robustness, results from multiple methods can provide context that may identify the nuances and interactions of factors driving diversification. For example, Alencar et al. (2024) demonstrate that both false positives and negatives in state-dependent analyses can be reduced by conditioning results on "background" (e.g., clade-wide) shifts in rates detected by BAMM and stateless MiSSE models. They found that Andean-distributed clades within South American lizards have elevated speciation rates; other traits that predominate in these specific clades were spuriously identified as having tree-wide associations with diversification by both state-dependent modeling and phylogenetic regression of tip rates (Alencar et al. 2024). In addition to comparing the results of multiple diversification methods, we also suggest the following robustness checks: isolate and analyze separately any subclades that appear likely to be driving results of the full tree (Beaulieu and O'Meara 2016; Alencar et al. 2024); employ at least one method that requires replication (e.g., sister clade comparisons or phylogenetic regression); and use visualizations to interrogate significant results (e.g., TSCC, sister clade comparisons: Fig. 5). Finally, there is a need for more meta-analyses or other studies that compare the results of trait-based diversification studies on empirical data—both comparing applications of the same method (as in Helmstetter et al. 2023), and across methods (as in Martínez-Gómez et al. 2024).

The methods we employed to estimate speciation rate do not model or test for any specific microevolutionary process that is hypothesized to underly trait-based diversification. Hypotheses for migration-associated speciation include colonization of new breeding ranges by migrants and subsequent allopatric speciation, divergence due to allochrony at migratory divides, and migratory fall-offs. General tests of association between speciation rates and migration phenotype are advantageous in that they may detect a signal if any one of these mechanisms, or all in combination, contribute to elevated speciation rates for migrants. However, each mechanism may result in a distinct macroevolutionary pattern. For example, speciation due to migratory fall-offs occurs when one population of a migratory species transitions to resident; in this scenario, transitions between migration phenotype may be sufficiently close to the resulting speciation event to be considered cladogenetic transitions (Rolland et al. 2014). In contrast, if higher speciation in migratory lineages occurs due to temporal isolation at migratory divides, the parent and both descendant lineages would be migratory, all else held equal, and cladogenetic transitions of migratory phenotype would not necessarily be common under this scenario. Methods that are agnostic to cladogenetic versus anagenetic transitions are general enough to test for a signal of elevated speciation rates in migratory lineages under both scenarios, but tests that are explicitly linked to microevolutionary mechanisms may provide more insight. None of our methods are capable of specifying cladogenetic versus anagenetic transitions between migration phenotypes (Fig. 1), and to our knowledge no appropriate method to do this is currently available. The ClaSSE framework (Goldberg and Igić 2012;

used in Rolland et al. 2014) specifically models cladogenetic and anagenetic trait evolution, but a hidden-state version of this model is not currently available (but see Tarasov and Uyeda 2024 for ongoing work in this area), and thus it is subject to inference problems discussed above. More generally, additional work is needed to develop trait-based diversification methods that identify signatures of explicit microevolutionary mechanisms of speciation on macroevolutionary patterns.

Migration and Speciation in the Tyrannidae

The Tyrannidae are the suboscine family in which migration is most common and the only suboscine family with intercontinental migrants to North America. Migration may directly promote speciation through various mechanisms that initiate reproductive isolation (e.g., migratory divides or fall-offs); it is also possible that migration may indirectly promote speciation, through the introduction of ecological opportunity in a newly colonized region, as in the Tyrannids breeding in North America. That said, a migratory fall-off is implicated in incipient speciation in of austral-breeding Fork-tailed Flycatchers (Gómez-Bahamón et al. 2020). Further, Tyrannid speciation rates are similar to those of their all-resident, tropical sister clade (the Rhyncocylcidae; Fig. 3), and speciation rates are much higher in other resident, tropical suboscine clades (e.g., the Pipridae, and *Scyatlopus*; Fig 3) compared with the Tyrannidae. Recent, rapid speciation in *Scytalopus* particularly has been attributed to their limited dispersal and use of habitat with many geographic barriers (Cadena et al. 2020). Thus, diversification patterns in the Tyrannids and the other suboscines are likely the result of complex interactions of biogeographic features and histories, as well as potential effects of migration, dispersal, and other life history traits.

We found faster speciation rates for migrants in the Tyrannidae using both ClaDS speciation rates and state-based speciation extinction modeling (MuHiSSE). This result is consistent with a previous study (Gómez-Bahamón et al. 2020) of Tyrannidae, which also found faster speciation rates for migrants, using a different type of SSE model (MuSSE, which does not allow for trait-independent rate heterogeneity and is thus subject to issues described in Rabosky and Goldberg 2015). The best-fitting MuHiSSE model in our study estimated that speciation in tyrannid strict migrants was nearly 3x faster than in residents (Table 1), a result that is inconsistent with the marginal differences in species richness across the predominantly migratory versus non-migratory clades (Fig. 5) that accounted for the majority of migratory species in the tyrannids. We also observe that the tyrannid species *not* shown in Figure 5 do not show clear patterns of increased speciation associated with migration: most of the migratory species not included in the sister clade analysis form dyads involving one migratory and one non-migratory species (e.g., *Attila phoenicurus* and *A. cinnamomeus*; *Elaenia spectabilis* and *E. ridleyana*). Further, there was no apparent pattern of speciation rate differences among Tyrannid migratory phenotypes in the TSCC analysis (Fig. 6).

CONCLUSIONS

Our most predominate result across methods and clades was a lack of relationship between migration phenotype and speciation rate in these passerine groups (Supplementary Table S2), which does not support (or refute) our initial hypothesis that migratory lineages speciate faster. Divergent migratory phenotypes have contributed to reproductive isolation and genetic divergence in extant bird species (Rolshausen et al. 2009; Delmore et al. 2015; Turbek et al. 2022). However, it is possible that migratory phenotypes transition too quickly to cause speciation, or that high trait lability reduces our ability to detect true trait-dependent effects. Indeed, populations of passerines have been observed to gain (Able and Belthoff 1998) and lose (Rolshausen et al. 2009; Winkler et al. 2017) a migratory phenotype that is novel within their species in a few dozen generations. If divergent migration phenotypes do initiate reproductive isolation, as has been observed in extant species, these phenotypes may rarely persist through the completion of the speciation process. Indeed, the evolution of reproductive isolation between populations more generally may be decoupled from macroevolutionary speciation in birds, perhaps because recently isolated populations rarely persist on geological timescales (Rabosky and Matute 2013; Veron et al. 2025).

It is also possible that migration promotes speciation in other bird groups: the two clades selected for analysis based on phylogenetic resolution are predominately New World, and it is possible that migratory evolution and diversification differ significantly in old-world birds. Additionally, the passerines are one of three major migratory clades in birds, the others being the Anseriformes and the Charadriiformes, both of which are deeply diverged from passerines and differ substantially in life history. Future studies could also test migration-associated speciation in non-avian groups in which migration is prevalent, such as ungulates or fish (Tsukamoto et al. 2002).

In recent years, novel migration phenotypes have been observed to evolve and initiate reproductive isolation within a human lifespan, whereas advances in speciation genomics have allowed us to detect divergence along older migratory divides. Together these developments have ushered in a spate of interest in the role of migration in speciation (Winger et al. 2012, 2014; Ruegg et al. 2014; von Rönn et al. 2016; Everson et al. 2019; Delmore et al. 2020; Gómez-Bahamón et al. 2020; Pegan and Winger 2020; Louder et al. 2024). Our study finds no robust relationship between migration and speciation at higher taxonomic levels, thereby raising important questions about both the fate of populations and subspecies diverging due to migration and our ability to study how traits contribute to speciation in a comparative framework.

Supplementary material

Data available from the Dryad Digital Repository: https://dx.doi.org/10.5061/dryad.[NNNN].

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Data Availability

All the data and scripts necessary to reproduce the analyses reported in this study can be accessed at the Dryad repository: https://doi.org/10.5061/dryad.9ghx3ffsj.

Conflict of Interest Statement

None declared.

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