Evolution, 2025, **0**(**0**), 1–10
https://doi.org/10.1093/evolut/qpaf226
Advance access publication 4 November 2025
Original Article

OXFORD

The effects of the dispersal ability in the diversification dynamics of Emberizoidea (Aves: Passeriformes)

Axel Arango[1,2], Jesús Pinto-Ledezma[3], Octavio Rojas-Soto[2], Fabricio Villalobos[2]

[1]Center for Computational and Theoretical Biology, Univeristät Würzburg, Würzburg, Germany
[2]Red de Biología Evolutiva, Instituto de Ecología A.C., Xalapa, México
[3]Department of Ecology, Evolution & Behavior, University of Minnesota, Minneapolis, United States

Corresponding authors: Center for Computational and Theoretical Biology, Klara-Oppenheimer-Weg 32, Campus Hubland Nord, 97074 Würzburg, Germany. Email: axlarango@gmail.com; Laboratorio de Macroecologi´a Evolutiva, Red de Biologi´a Evolutiva, Instituto de Ecologi´a, A.C., Carretera antigua a Coatepec 351, El Haya, 91070 Xalapa, Veracruz, Mexico. Email: fabricio.villalobos@gmail.com

Abstract

Understanding how ecological and evolutionary forces shape biodiversity is a core pursuit in macroevolutionary research. Species' dispersal ability significantly impacts their colonization chances and geographic isolation, profoundly influencing species ecology and evolution. Our study delved into the relationship between dispersal ability and speciation rates within Emberizoidea, a diverse group of passerine birds. We used the Hand-Wing Index (HWI) as a morphological proxy for dispersal ability and phylogenetic data for 749 species of Emberizoidea (~90% of all recognized species for the clade) using trait-dependent diversification models, including continuous-state (QuaSSE) and hidden-states (SecSSE) models. We also applied the correlated speciation and trait rates simulation (Cor-STRATES) framework to assess correlation between HWI evolution and speciation rates. Our findings revealed that speciation in Emberizoidea was not significantly influenced by dispersal ability as estimated by HWI. While QuaSSE models suggested a peak in speciation rates at intermediate HWI values, the best-fit SecSSE model indicated that speciation was driven by unmeasured trait(s) rather than HWI. Moreover, HWI evolution and speciation rates were not correlated, suggesting that wing shape evolution is unrelated to cladogenetic events in Emberizoidea's evolutionary history. Our study challenges the notion that dispersal ability and wing shape drive diversification in birds, particularly in Emberizoidea.

Keywords: diversification rates, phenotypic evolutionary rates, oscine birds, state-dependent diversification models, dispersal ability

Introduction

The importance of the interactions between ecological and evolutionary processes in the origin of biodiversity is still one of the central questions in macroevolution (Imfeld & Barker, 2022). In fact, it is thought that the relationship between ecologically important traits and the rate at which new species arise explains major patterns of species distribution and diversity (Cooney & Thomas, 2021; Crouch & Ricklefs, 2019). Dispersal ability is a trait that directly influences the colonization likelihood of populations and the rate at which they develop geographical isolation from each other, promoting faster species divergence (Kennedy et al., 2016). Accordingly, dispersal ability is regarded as a significant trait with consequences for the ecology and evolution of species (Arango et al., 2022; Burgess et al., 2016; Claramunt, 2021).

The significance of dispersal ability for species generation is such that increases in diversity over time have frequently been associated to access of new regions of geographic or ecological space (Benton, 2009). Indeed, the ability to move to these new spaces is the central idea of the geographic radiations (Simões et al., 2016). According to this idea, species that have the capability to spread out and establish themselves in new environments would experience relief from various challenges like parasites and competitors (Ricklefs, 2011). At the same time, such species would be exposed to new ecological opportunities (Simpson, 1953) and different landscapes and topography (Cracraft, 1985). These factors would facilitate rapid speciation and specialization (Belmaker et al., 2012). Additionally, at the metapopulation level, the ability to disperse plays a crucial role in determining how quickly new areas are colonized and how many new individuals join existing populations. This process helps regulate gene flow and can potentially lead to genetic isolation (Kokko & Lopez-Sepulcre, 2006), which is often considered a necessary condition for speciation (Mayr, 1942; Rabosky, 2016).

Traits with ecological and/or evolutionary relevance (such as dispersal ability) can influence the rate at which lineages diversify, with certain trait states or values being associated with higher or lower speciation rates (Herrera-Alsina, 2019; Jablonski, 2008). Beyond the effect of trait states, it has also been proposed that speciation rates may correlate with the evolutionary rates of the traits themselves, that is the speed at which traits change over time (Reznick & Ricklefs, 2009; Shi et al., 2021; Stanley, 1998). This idea is particularly relevant in the context of adaptive radiations, where rapid trait evolution can promote increased lineage splitting (Schluter, 2000). Disentangling these potential drivers of diversification thus requires the combined evaluation of trait variation as well as trait evolutionary rate and their effect on diversification dynamics.

Received January 17, 2024; revisions received October 9, 2025; accepted October 27, 2025
Associate Editor: Alejandro Gonzalez-Voyer; Handling Editor: Hélène Morlon

In birds, dispersal ability is regarded as a crucial trait driving diversification, but the direction of this relationship remains unclear (Claramunt et al., 2012). While high dispersal ability is thought to be linked to higher reproductive isolation given that broadly distributed lineages are prone to be interrupted by barriers to dispersal (Mayr, 1963), it would also enable gene flow among populations, preventing genetic differentiation (Kisel & Barraclough, 2010). Conversely, low dispersal ability would limit gene flow among populations, aiding their reproductive isolation (Gavrilets, 2003). However, lineages with low dispersal abilities would maintain more genetic cohesion by not being able to geographically separate (Claramunt et al., 2012), slowing their divergence rates (Gavrilets & Vose, 2005). To reconcile this conflicting relationship between dispersal ability and speciation, an intermediate dispersal model has been proposed (Claramunt et al., 2012; Price & Wagner, 2004). This model considers that species with intermediate dispersal abilities have higher speciation rates by providing more opportunities of range expansion, but also of geographic isolation, avoiding genetic cohesion among populations and aiding genetic differentiation (Claramunt et al., 2012).

Dispersal ability is strongly influenced by flight efficiency, which in turn is closely linked to wing morphology (Claramunt, 2021; Sheard et al., 2020; Weeks et al., 2022). A widely used morphological proxy for flight efficiency, and by extension, dispersal ability, is the Hand-Wing Index (HWI), which is related to the wing's aspect ratio and represents its elongation by comparing the length of the hand-wing relative to total wing length (Arango et al., 2022; Claramunt et al., 2012). Higher HWI values generally correspond to more elongated wings, which reduce energy expenditure during flight and are associated with greater natal and adult dispersal distances (Claramunt, 2021). Conversely, species with lower HWI values tend to have less elongated wings, more suited to maneuverability in dense habitats but less efficient for long-distance movement. While morphological indices are imperfect proxies, HWI has been repeatedly validated against direct measures of dispersal (Bastidas-Urrutia et al., 2025; Claramunt, 2021; Weeks et al., 2022), making it a suitable trait for macroevolutionary analyses of dispersal in birds.

Here, we examined the relationship between dispersal ability and speciation rates in the Emberizoidea superfamily, a large clade of passerine birds (c. 832 spp; Barker et al., 2013) whose species have inspired important ecological and evolutive questions, from Darwin's finches to MacArthur's wood warblers. The clade Emberizoidea has been regarded as part of an important adaptive radiation (Barker et al., 2013; Lefebvre et al., 2016). This clade occurs in almost all the New World and parts of the Old World, exhibiting a wide range of ecological, behavioral, and morphological diversity (Curson, 1994; Forshaw, 1991; Holmes, 1990; Lowther, 1975), in addition to an evident variation in species diversity, with clades comprising around 400 species such as Thraupidae to monotypic clades such as Rhodinocichlidae (Barker et al., 2013, 2015). Their ubiquitous distribution in the New World, both in mainland and islands, as well as their colonization of the Old World and Galapagos are a testimony of this clade's dispersal abilities (Barker et al., 2015). The contrasting dispersal abilities and diversity within clades of Emberizoidea provide an ideal system to test the effects of dispersal ability on diversification dynamics.

We used the HWI to evaluate the potential influence of dispersal ability on speciation rates through two complementary approaches. First, we applied trait-dependent diversification models (quantitative state speciation and extinction [QuaSSE] and state-dependent speciation and extinction [SecSSE]) to test if speciation rates were influenced by HWI values. We included hidden state models to account for potential heterogeneity in speciation rates not captured by HWI, thus avoiding spurious associations between our focal trait and diversification. Second, we used the correlated speciation and trait rates simulation (Cor-STRATES) framework to examine if speciation rates were correlated with the evolutionary rate of HWI, thus capturing different aspects of trait-speciation dynamics. Finally, we performed a Bayesian multilevel regression model to test whether the observed relationship between evolutionary rate of HWI and speciation rate was consistent across the families within Emberizoidea.

Materials and methods

Dispersal ability data

We used HWI as a morphological proxy for dispersal ability (Arango et al., 2022; Bastidas-Urrutia et al., 2025; Claramunt, 2021; Sheard et al., 2020; Weeks et al., 2022). We compiled a dataset comprising a total of 749 spp (∼90% of the total species of Emberizoidea), based primarily on the wing measurements from Arango et al. (2022; 490 spp), which we then completed with additional species from the AVONET database (Tobias et al., 2022; 259 spp).

HWI data in the Arango et al. (2022) dataset were measured following Claramunt et al. (2012): $HWI = 100(\frac{WL-SL}{WL})$, using the standard length of the closed wing (WL) and the distance from the carpal joint to the tip of the first secondary feather (SL). AVONET states that their calculation of HWI used Kipp's distance instead of the difference between WL and SL, resulting in: $HWI = 100(\frac{Kipp's\ distance}{WL})$. To validate the combination of measurements, we compared HWI values from both datasets using their shared species and found a strong correlation ($n = 258$; $r = 0.83$; Figure S1), confirming that the AVONET data were comparable and could be reliably integrated with our measurements for subsequent analyses.

Phylogenetic data

We used Barker et al. (2015) maximum credibility clade (MCC) tree. This phylogeny is the most comprehensive species-level phylogeny for Emberizoidea, with 791 emberizoid species of an approximate 832 (95%). This phylogeny was estimated using a planned supertree method. This required assembling time-calibrated tree posteriors previously generated on a planned backbone. See Barker et al. (2015) for details of phylogenetic reconstruction. We pruned the MCC phylogeny to correspond with the species with HWI data. Although other avian mega phylogenies with a broader taxonomic scope are available, they are less suitable for their use with the Emberizoidea clade because they either have unresolved relationships among the clades of interest within Emberizoidea, such as an outdated backbone for the clade separation of Passerellidae and Emberizidae, lack resolution at the species level relationships, especially within Parulidae, are synthetically constructed (e.g., Jetz et al., 2012), or were

Table 1. QuaSSE model selection. Best-fitting model in bold.

Model	lnLik	K	AIC	ΔAIC	AICw
CONSTANT	−3,068.1	3	6,142.2	26.3	0
LINEAR	−3,066.7	4	6,141.4	25.5	0
lINEAR + dRIFT	−3,066.7	5	6,141.4	25.5	0
Sigmoidal	−3,062.2	6	6,138.4	22.5	0
SIGMOIDAL + DRIFT	−3,061.6	7	6,137.2	21.3	0
Unimodal	−3,055.5	6	6,123	7.1	0.03
Unimodal + DRIFT	**−3,051**	7	**6,115.5**	0	**0.97**

not specifically designed for this clade (e.g., Oliveros et al., 2019).

Dispersal ability and speciation

To test the effect of dispersal ability on speciation, we used QuaSSE models. This approach allows us to test and compare a board array of possible evolutionary hypotheses that would reflect the general trends affecting patterns of diversification (FitzJohn, 2010; Fitzjohn, 2012). We fitted models representing the potential relationships between dispersal ability (approximated by HWI) and speciation (i.e., linear, sigmoidal, and hump-shaped functions), which we then tested against a constant model (this model indicates that the trait holds no relationship with speciation), performing a model comparison based on the Akaike Information Criterion (AIC) and Akaike weights (AICw). We tested a total of seven different scenarios of how dispersal ability might have affected speciation in Emberizoidea (Table 1); these being: (1) a constant relationship (dispersal ability does not have an effect on speciation), (2) a linear relationship (an increase on dispersal ability results in either an increase or decrease of speciation), (3) a sigmoidal relationship (dispersal ability values have an inflexion point in where constant speciation increases or decreases), (4) a unimodal relationship (dispersal ability values have an optimum in which speciation maximizes), and (5–7) the same linear, sigmoidal, and unimodal models but incorporating a drift parameter, which allows for directional trends in trait evolution (Figure S2; Table 1).

In these models, trait drift represents the directional tendency of a continuous trait to increase or decrease over time, which may be driven by selection or any other process that has directional tendency (FitzJohn, 2010). In this case, the drift parameter allows to test whether there was an evolutionary trend in HWI values across Emberizoidea. A negative drift estimate would indicate a tendency for HWI to decrease over time, producing less elongated wings, and potentially reducing dispersal ability. In contrast, positive drift would indicate a tendency of HWI to increase over time, producing more elongated wings, and potentially enhancing dispersal ability. Thus, incorporating a trait drift term enables the detection of scenarios where traits evolve directionally over time, due to selection or other processes, even toward values that may be associated with reduced diversification (Clauset & Erwin, 2008; FitzJohn, 2010).

While traditional SSE models are prone to elevated Type 1 error rates (Rabosky & Goldberg, 2015), more recent implementations that incorporate the effect of hidden or unmeasured traits have substantially improve their robustness (Herrera-Alsina, 2019). Therefore, to corroborate the effects of HWI on Emberizoidea speciation when considering potential unmeasured traits, we compared four SSE models that contemplate the possibility that diversification may not be related to the focal trait but rather to some other unknown/unmeasured trait. Given that these hidden state speciation extinction models have not yet been developed for continuous traits, we used a model that considers discrete trait states, namely the several examined and concealed SecSSE model (Herrera-Alsina et al., 2019). For this, we classified HWI into three categories: low (6.4–18.1), intermediate (18.1–25.8), and high (25.8–39.4), using the natural breaks method. Natural breaks (Jenks) classification is a clustering technique that divides a dataset into a specified number of uniform attribute groups. It works by maximizing the variation between different groups while minimizing the variation within each group (Jenks, 1967). Using uniform discrete categories has been recently applied for SecSSE models (e.g., Hill et al., 2023) as it minimizes the known bias of SSE models caused by overrepresentation of one trait state and thus maximizes the power of the analysis (Davis et al., 2013).

We tested four scenarios using the SecSSE framework: (i) diversification rates are influenced by HWI (EDT1); (ii) diversification rates are not influenced by HWI but by concealed (unmeasured) traits (CDT1); (iii) diversification rates are influenced by HWI, which also has a directional evolutionary trend (i.e., wings become more or less elongated through time; EDT2); (iv) diversification rates are influenced by unmeasured traits that also have directional evolutionary trends (CDT2); and (v) diversification rates are constant across trait states (CR). We tested the fit of all models based on AIC and AICw.

Dispersal-ability evolution and speciation

To test the correlation between speciation rates and the evolutionary rate of HWI as an approximation of dispersal ability, we applied the Cor-STRATES framework (Cooney & Thomas, 2021). This approach allowed us to compare the observed correlation between the speciation rate and the rate of trait evolution with a null set of correlations generated by simulations. To do so, we first used the Bayesian cladogenetic diversification rate shift (ClaDS) model (Maliet et al., 2019) to calculate speciation rates (λ_{ClaDS}). This calculation was performed using the PANDA (Maliet & Morlon, 2022) package for julia (Bezanson et al., 2017) taking the appropriate sampling fraction and subsequently processed with the help of the RPANDA (Morlon et al., 2016) package for R. ClaDS provides high-resolution, branch-specific estimates of speciation rates by modeling gradual, lineage-specific rate changes, offering a more realistic and statistically robust alternative to models that assume rare, abrupt diversification shifts (Maliet et al., 2019). Subsequently, we calculated Pagel's λ on the observed HWI data and used the values of λ to rescale the Emberizoidea pruned tree using the package "geiger" for R (Harmon et al., 2009). This rescaling is done to adjust for the phylogenetic signal in trait data, which helps accounting for potential nonphylogenetic variation in trait values and thus reduces the chance for spurious correlations between rates (Cooney & Thomas, 2021). To calculate the rates of trait evolution of our observed HWI data, we used the lambda rescaled tree and fitted a trait evolution model using the Bayesian Analysis of Macroevolutionary Mixture (BAMM) (Rabosky, 2014). We used the setBAMMpriors function to establish the evolutionary priors, and to calculate the per-branch estimates of evolutionary rate (β_{BAMM}) we used the "getMeanBranchLengthTree" function from the R package BAMMtools 2.1.7 (Rabosky et al., 2014).

We calculated the observed correlation of the per-lineage speciation rate with the estimates of trait evolutionary rate using Spearman's rank correlation (ρ). Spearman's rank correlation is used in this case given the nonnormal distribution of both speciation and phenotypic evolutionary rates (Cooney & Thomas, 2021). Note that this analysis is not directly corrected for phylogeny, but instead the statistical significance of the observed correlation is assessed by contrasting it against a null distribution of correlation values derived from a null model in which the trait of interest evolves neutrally, hence intrinsically considering phylogenetic relatedness. For the calculation of the null correlations, we first fitted a Brownian motion model on the observed HWI data using the rescaled phylogeny, acquiring an estimated value of diffusion rate (σ^2). Then, we constructed 100 datasets with simulated trait data using the σ^2 value. Afterwards, we recalculated the per-branch trait evolution for each simulated dataset by using BAMM with the same approach as the observed rates of trait evolution and estimated the null correlations (ρNull) between each of the simulated rates of trait evolution with the observed lineage speciation rate. Finally, we computed a two-tailed p value for the observed correlation against the null correlations. This framework tests whether the observed correlation between speciation rate and trait evolutionary rate is stronger than expected under a phylogenetically structured, but neutral, evolutionary process.

Furthermore, to test whether the observed relationship between HWI evolutionary rate and speciation rate was consistent across the Emberizoidea superfamily, we performed a multilevel regression model using the "brms" R package and default priors (Bürkner, 2017). We used branch-specific estimates of HWI evolutionary rates, derived from the BAMM model of phenotypic evolution with a lambda-transformed tree, and branch-specific speciation rates estimated using the ClaDS model for all branches in the phylogeny. To account for the phylogenetic nonindependence and capture potential differences among subclades within Emberizoidea, we modeled taxonomic families, which are themselves monophyletic, as a grouping factor. This approach allowed us to investigate the effect of taxonomic hierarchy (family-specific effect) in the relationship between HWI evolutionary rates and speciation rates across Emberizoidea. This model was fit using four No-U-Turn Sampler (NUTS) sampling chains for 5,000 generations, discarding 20% of each run as burn-ins.

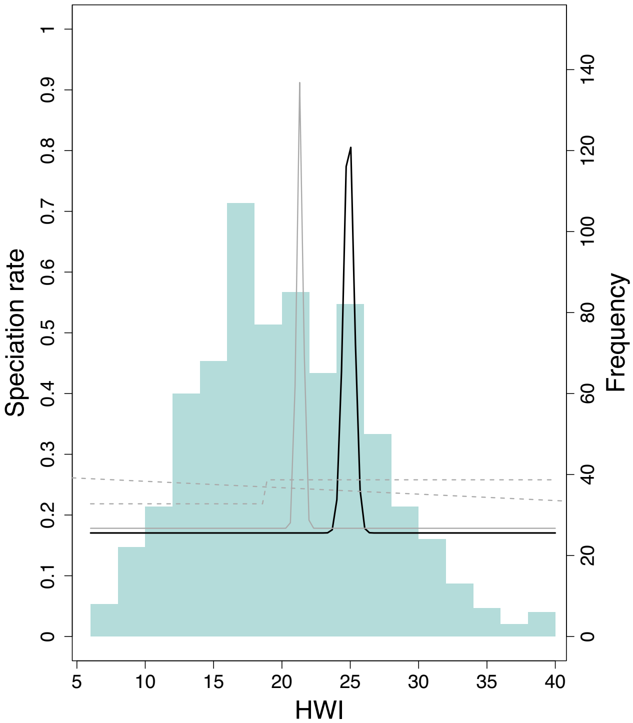

Figure 1. Relationships between dispersal ability and speciation rates in the Emberizoidea clade inferred from QuaSSE models. The histogram (y-axis = number of species per Hand-Wing Index [HWI] bin) shows the distribution of HWI values across the clade. The gray line represents the unimodal model, and the black line represents the best-fitting unimodal + drift model. Dashed lines represent the other models.

Results

Dispersal ability and speciation

The best-fitting QuaSSE model was the unimodal + drift relationship ($\chi^2 = 64.4$, $df = 7$; Table 1; Figure 1). The unimodal + drift model suggests that the optimal HWI values are around 24 and 26, while HWI itself shows a trend of decreasing over time (drift = −0.49).

In the SecSSE models, when not considering unmeasured traits (i.e., ETD models), the higher speciation rates were still attributable to intermediate HWI (0.289 sp/My) in comparison to low HWI (0.208 sp/My) and high HWI (0.198 sp/My). However, the best-fitting SecSSE model (CTD2) implied that speciation rate variation could not be attributed to HWI variation but to other, hidden/unmeasured traits (Table 2). Additionally, model selection further supports an evolutionary trend toward less elongated wings in Emberizoidea, with a higher transition rate to decreasing HWI (0.196) than to an increase (0.038). A sensitivity analysis using only AVONET data produced qualitatively similar results (Tables S1 and S2; Figure S3).

Dispersal ability evolution and speciation

Using the Cor-STRATES framework, we calculated the lineages' speciation rate (λ_{ClaDS}; min = 0.04 sp/my [log −3.02], max = 5.18 sp/my [log 1.6], mean = 0.45 sp/my [log −1.17]; Figure 2A; Figure S4). Lineage-specific speciation rates estimated with BAMM, as suggested by Cooney and Thomas (2021), were strongly correlated to those calculated by ClaDS, ensuring consistency across methods (Figure

Table 2. SecSSE model selection. Best-fitting model in Bold

Model	LNLIK	K	AIC	ΔAIC	AICw
ETD1	−2,482.89	6	4,977.79	140.2	0
CTD1	−2,447.71	6	,4907.43	69.84	0
ETD2	−2,477.78	6	4,967.56	129.98	0
CTD2	**-2,412.79**	**6**	**4,837.58**	**0**	**1**
CR	−2,490.9	3	4,987.8	150.21	0

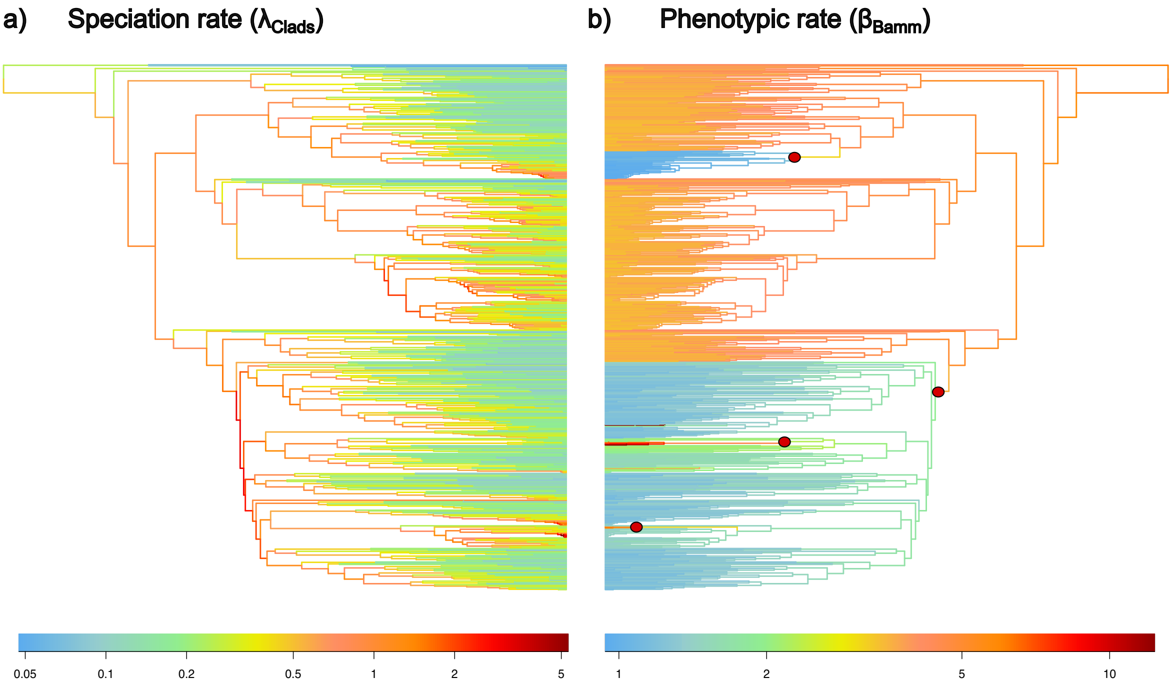

Figure 2. (A) Speciation rate (λ_{ClaDS}) inferred from cladogenetic diversification rate shift (ClaDS) using the time-calibrated Emberizoidea phylogeny. (B) Hand-Wing Index (HWI) evolutionary rate (β_{BAMM}) inferred from Bayesian Analysis of Macroevolutionary Mixture (BAMM) using the lambda rescaled Emberizoidea phylogeny. Circles in the nodes are indicative of a rate shift for phenotypic rates, from top to bottom: *Atlapetes–Melozone* common ancestor, Thraupidae family crown, *Nesospiza–Melanodera* common ancestor, *Tangara chilensis*.

S5). Pagel's λ for the observed HWI (dispersal ability) used to rescale the MCC phylogeny showed a high and significant phylogenetic signal ($\lambda = 0.83$, $p < 0.01$). This rescaled phylogeny was used to calculate the lineages' mean rate of trait evolution, where we found that the evolutionary rate of HWI had two predominant rates (β_{BAMM} ~3.6 HWI/my [log 1.3] and ~1.5 HWI/my [log 0.4]; Figure S6). The low-rate value comes from two lineage-wide decelerations at the Thraupidae family crown and the *Atlapetes–Melozone* common ancestor, as well as two accelerations in the *Nesospiza–Melanodera* common ancestor and in *Tangara chilensis* (β_{BAMM}; min = 0.95 HWI/my [log −0.051], max = 12.19 HWI/my [log 2.5], mean = 2.33 HWI/my [log 0.84]; Figure 2B). Although we detected a positive significant correlation between speciation rates and HWI evolutionary rates using Spearman's rank correlation ($\rho = 0.216$, $p < 0.01$; Figure 3), there was no significant difference between the null correlations (ρ_{NULL}; min = −0.54, max = 0.45, mean = -0.35) and the observed ρ with the ρ_{NULL} distributions (p = 0.27, [−0.51:0.39, 95% confidence intervals (CI)], SES = 2.64; Figure 4). Since the critical test in Cor-STRATES is whether observed correlations are different than what would be expected under neutral trait evolu-

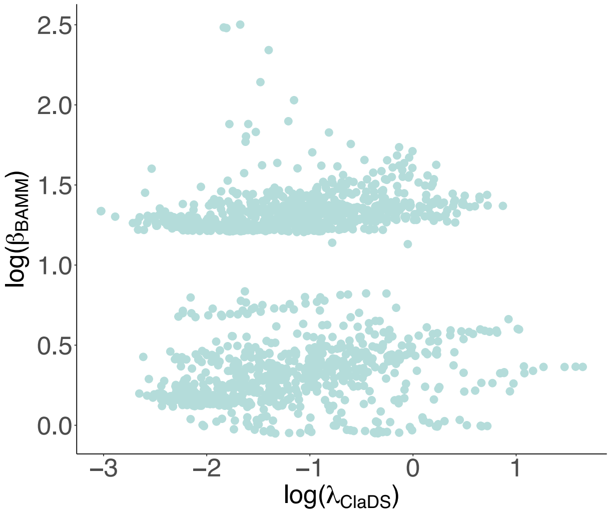

Figure 3. Correlation between lineage speciation rates (λ_{ClaDS}) and lineage Hand-Wing Index (HWI) evolutionary rates (β_{BAMM}) of Emberizoidea.

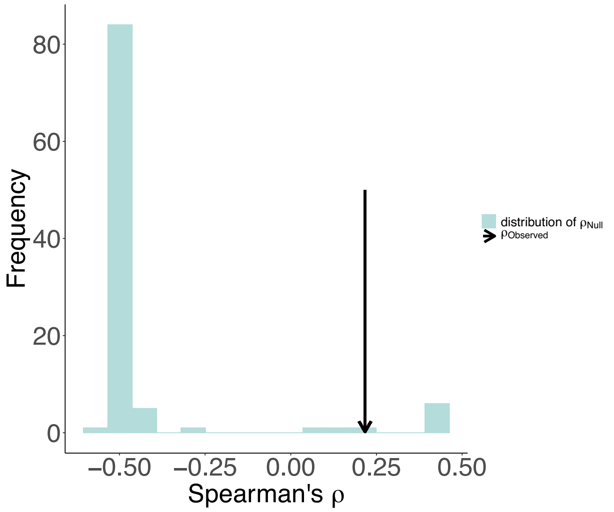

Figure 4. Correlation coefficient of the observed relationship between speciation rates and Hand-Wing Index (HWI) evolutionary rates (arrow) in relation to a null distribution of correlation coefficients calculated from 100 simulated datasets.

tion, this finding suggests that the association between HWI evolutionary rate and speciation rate is not stronger than expected under neutral trait evolution, thus not supporting a biologically meaningful link between dispersal trait dynamics and diversification in Emberizoidea.

Using the multilevel regression model, we found that the estimated standard deviation (σ) of the relationship between the evolutionary rate of HWI and speciation rate varied substantially (mean $\sigma = 0.56$ [0.31:0.99; 95% CI]). Further exploration of the parameter estimations indicated that the families Thraupidae and Passerellidae have a strong negative effect on the association between the rates of trait evolution and speciation. In contrast, Emberizidae and Cardinallidae show a positive effect—although the 95% credible intervals overlap with zero (Figure S7).

Discussion

Our results suggest that the speciation in Emberizoidea is not driven by wing shape, described by HWI and considered as a proxy of dispersal ability. Accordingly, we can infer that the ability to enter new ecological and geographical spaces through dispersal did not have a noticeable effect in the clade's diversification dynamics (Arango et al., 2025; Claramunt et al., 2012). HWI itself appears to be decreasing over time, implying that more recent species in Emberizoidea may have lower dispersal ability, possibly due to selective pressures or trait drift along the history of the clade. Previous work has shown that HWI evolution in Emberizoidea follows an Ornstein–Uhlenbeck pattern (Arango et al., 2022), which is consistent with a tendency toward an adaptive optimum, though the underlying processes remain uncertain. Moreover, we found no evidence that the evolutionary rate of HWI is more strongly linked to speciation rates than what would be expected under a null model of neutral trait evolution (i.e., Brownian motion), suggesting that species divergence in Emberizoidea were not followed or caused by the evolutionary dynamics of HWI and thus dispersal ability.

While HWI can in principle promote speciation by enabling colonization of new environments through dispersal ability, where divergence would occur due to geographic isolation (Gavrilets & Vose, 2005), our analyses indicate that this role is limited in Emberizoidea. Our results provide evidence that speciation across Emberizoidea seems to be driven instead by other unmeasured traits, even when certain lineages with intermediate values of HWI may be associated with higher speciation rates. In fact, there is evidence for some Neotropical taxa within this superfamily such as *Geothlypis aeoquinoctalis* and *Emberizoides herbicola* where vicariance and dispersal ability appear to play a minor role in divergence, with lineage histories instead reflecting ecological dynamics of the habitats they inhabit (van Els et al., 2021). Similarly, low divergence across large geographic distances in taxa with poor dispersal ability (Bates et al., 2003) and the importance of the lineages' intrinsic ability to persist in the landscape (i.e., local adaptation), without invoking dispersal ability (Smith et al., 2014), point to ecological or behavioral mechanisms, rather than dispersal per se, as drivers of speciation. Although certain species within Emberizoidea, such as *Leistes militaris* and *Leistes superciliaris*, may have resulted from divergence through dispersal events associated with seasonal migratory straying, thus highlighting gene flow and isolation effects linked to migratory behavior (Gomez-Bahamón et al., 2020; van Els et al., 2021), other species such as the song sparrow (*Melospiza melodia*) could be differentiating through ecological divergence rather than dispersal per se, highlighting the role of adaptation to distinct environments (Patten, 2010). Together this evidence suggests that dispersal ability may facilitate population separation, but other traits such as ecological specialization or species behavior likely interact with it to shape lineage divergence. For example, for Icteriade, Passerellidae, and Thraupidae, beak shape closely related to dietary specialization has been correlated with their speciation rates (Conway & Olsen, 2019). Similarly, traits related to plumage and song evolution have been suggested as evolutionary drivers of Emberizoidea clades (Cicero et al., 2020; Price & Eaton, 2014; Price-Waldman, 2019).

This limited role of HWI in driving diversification in Emberizoidea contrasts with patterns observed in another major avian clade. In furnariids, for example, low dispersal ability is closely related to isolation and diversification (Claramunt et al., 2012). Emberizoidea, by contrast, spans a wider geographic range and includes a higher number of migratory species across several biographic realms (i.e., Neotropics, Afrotropic, Nearctic, and Palearctic; Barker et al., 2015), yet dispersal ability, as estimated by HWI, has only a minor influence on the clade's diversification. Instead, our best-fitting model indicates that heterogeneity in speciation rates is not explained by HWI. While we cannot determine the specific causes of this heterogeneity in our analysis, it may potentially involve ecological specializations, behavioral syndromes, life-history strategies, or other unmeasured traits, as drivers of lineage diversification. Recently, similar results were found when considering migratory behavior for Emberizoidea and the suboscines, with no consistent relationship between migration and speciation at higher taxonomic levels (Calabrese et al., 2025).

The observed pattern of HWI decrease overtime reinforces this interpretation. Dispersal ability in birds tends to be reduced when species adapt to specialized foraging strategies (Forstmeier & Keßler, 2001; Jocque et al., 2010; Weeks et al., 2022) or predator avoidance behaviors (Swaddle & Lockwood, 2003). For example, in starling (*Sturnus vulgaris*) populations, HWI decreased by ~3.8% within 120 years after the colonization of new habitats (Bitton & Graham, 2015). In Emberizoidea, diversification and functional evolution are considerably faster than expected by birth–death processes (Imfeld & Barker, 2022), consistent with ecological adaptation fostering speciation. Neotropical Emberizoids, in particular, display remarkable ecological versatility, exploiting diverse dietary and habitat niches, fostering speciation (Conway & Olsen, 2019; Lefebvre et al., 2016; Vinciguerra & Burns, 2021). Some appear to be limiting their species by habitat preference (D'Horta, 2009) or other behavioral traits such as feeding specialization (Phillimore et al., 2006) rather than geographical barriers like rivers or landscape processes (Bates et al., 2003; Naka et al., 2022; van Els et al., 2021).

Clade-specific patterns further highlight the complexity of the relationship of HWI with speciation. In Thraupidae (Figure S8), a clade mostly confined to the Neotropics (Winkler et al., 2020), we observed deceleration in HWI evolution, which together with their intense ecological adaptation through feeding specialization and innovations (Lefebvre et al., 2016; Vinciguerra & Burns, 2021), could suggest that specialization may reduce the relevance of dispersal ability causing evolutionary stasis in HWI (Eldredge et al., 2005). Yet, the importance of dispersal ability may reemerge in island taxa in certain *Nesospiza* and *Melanodera* migrant species (Del Hoyo, 2020), where gene flow and isolation pressures would recover the usefulness for dispersal ability, breaking its evolutionary stasis (Eldredge et al., 2005). In the *Atlapetes*–*Melozone* lineage (Figure S9), HWI deceleration coincides with the *Atlapetes* speciation rate acceleration, though it is unclear whether this relationship is indicative of exploitation of ecological opportunities during the Andean uplift (Weir, 2006) or a reflection of Pleistocene isolation and drift (García-Moreno & Fjeldså, 2000; Sánchez-González et al., 2015). These examples suggest that the role of dispersal ability in diversification may vary substantially across taxonomic scales and evolutionary history of particular clades, helping to explain why its overall relationship with diversification has remained elusive (Calabrese et al., 2025; Claramunt et al., 2012; Phillimore et al., 2006).

Comparisons with other taxa further illustrate this point. In furnariids high dispersal ability inhibits speciation (Claramunt et al., 2012); in Corvids wing morphology is linked to both range size and diversification potential, although the strength and direction of these associations vary geographically (Kennedy et al., 2016). Outside birds, the link between dispersal and diversification is equally context-dependent, shaped by habitat structure and life-history traits (Burgess et al., 2016; Jablonski, 2008). Thus, the impact of dispersal ability on speciation may be strongly shaped by clade-specific ecological and evolutionary contexts, and broad generalizations may obscure this important variation. Altogether, these findings highlight the need to evaluate different proxies of dispersal ability and their influence on diversification at different phylogenetic scales.

In sum, our results challenge the assumption that dispersal ability, as estimated from HWI, is a major driver of speciation in Emberizoidea. Instead, our best-fitting SecSSE model indicates that heterogeneity in speciation rates is not explained by HWI. While we cannot determine the specific causes of this heterogeneity, previous work in Emberizoidea points to ecological factors (e.g., diet, song, and plumage) as likely candidates (Cicero et al., 2020; Conway & Olsen, 2019; Price-Waldman, 2019; Vinciguerra & Burns, 2021). The observed decrease of HWI over time and the lack of correlation between its evolutionary rate and speciation further support this view, suggesting that other traits more related to specialization would have driven diversification (Conway & Olsen, 2019; Lefebvre et al., 2016; Salisbury et al., 2012; Vinciguerra & Burns, 2021) regardless of dispersal events (Arango et al., 2025). Together, these findings highlight the need to explore traits beyond dispersal ability, such as feeding and behavioral specialization, and to consider temporal dynamics (e.g., through stratified state-dependent diversification models) to better understand the drivers of Emberizoidea diversification.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

The data underlying this article are available in FigShare at https://doi.org/10.6084/m9.figshare.29148893.v1 and can be freely accessed.

Author contributions

A.A. and F.V. conceived the ideas and wrote the first draft. A.A. collected the data and conducted the analyses. All authors discussed and interpreted the results. All authors contributed to the final version of this manuscript.

Funding

Research was supported by the Consejo Nacional de Humanidades, Ciencia y Tecnología (CONAHCyT) providing F.V. with a Ciencia Basica project grant (A1-S-34563) and A.A. with a scholarship (# 838518).

Conflict of interest

The authors declare no conflict of interest.

Acknowledgments

We thank the Posgrado en Ciencias of Instituto de Ecología A.C. (INECOL). A.A. and F.V. acknowledge the support provided by the Consejo Nacional de Ciencia y Tecnología (CONACyT) for the scholarship (# 838518) and Ciencia Basica project (A1-S-34563) granted, respectively. J.P.-L. was supported in part by the University of Minnesota President's Postdoctoral Fellowship Program and by the U.S. National Science Foundation (DEB 2017843 grant to J.P.-L.). A.A. would like to thank Juliana Herrera Perez for the guidance in making the SecSSE models and the Theoretical Biology group, particularly Prof. Dr. Chaitanya Gokhale for the support.

References

Arango, A., Pinto-Ledezma, J., Rojas-Soto, O., Lindsay, A. M., & Mendenhall, C. D. (2022). Hand-Wing Index as a surrogate for dispersal ability: the case of the Emberizoidea (Aves: Passeriformes) radiation. *Biological Journal of the Linnean Society*, *137*(1), 137–144. https://doi.org/10.1093/biolinnean/blac071

Arango, A., Pinto-Ledezma, J., Rojas-Soto, O., & Villalobos, F. (2025). Broad geographic dispersal is not a diversification driver for Emberizoidea. *Proceedings of the Royal Society B: Biological Sciences*, *292*(2039), 20241965.

Barker, F. K., Burns, K. J., Klicka, J., Lanyon, S. M., & Lovette, I. J. (2013). Going to extremes: Contrasting rates of diversification in a recent radiation of new world passerine birds. *Systematic Biology*, *62*(2), 298–320. https://doi.org/10.1093/sysbio/sys094.

Barker, F. K., Burns, K. J., Klicka, J., Lanyon, S. M., & Lovette, I. J. (2015). New insights into new world biogeography: An integrated view from the phylogeny of blackbirds, cardinals, sparrows, tanagers, warblers, and allies. *The Auk*, *132*(2), 333–348. https://doi.org/10.1642/AUK-14-110.1

Bastidas-Urrutia, A. M., Biber, M. F., Böhning-Gaese, K., Fritz, S. A., & Kreft, H. (2025). Species traits and island biogeography: Wing metrics linked to avian dispersal ability predict species occurrence on remote islands worldwide. *Journal of Biogeography*, *52*, 350–361. https://doi.org/10.1111/jbi.15038

Bates, J. M., Tello, J. G., & Silva, J. M. C. (2003). Initial assessment of genetic diversity in ten bird species of South American Cerrado. *Studies on Neotropical Fauna and Environment*, *38*(2), 87–94. https://doi.org/10.1076/snfe.38.2.87.15924

Belmaker, J., Sekercioglu, C. H., & Jetz, W. (2012). Global patterns of specialization and coexistence in bird assemblages. *Journal of Biogeography*, *39*(1), 193–203. https://doi.org/10.1111/j.1365-2699.2011.02591.x

Benton, M. J. (2009). The Red Queen and the Court Jester: Species diversity and the role of biotic and abiotic factors through time. *Science*, *323*(5915), 728–732. https://doi.org/10.1126/science.1157719.

Bezanson, J., Edelman, A., Karpinski, S., & Shah, V. (2017). Julia: A fresh approach to numerical computing. *SIAM Review*, *59*(1), 65–98. https://doi.org/10.1137/141000671

Bitton, P. P., & Graham, B. A. (2015). Change in wing morphology of the European starling during and after colonization of North America. *Journal of Zoology*, *295*(4), 254–260. https://doi.org/10.1111/jzo.12200

Burgess, S. C., Baskett, M. L., Grosberg, R. K., Morgan, S. G., & Strathmann, R. R. (2016). When is dispersal for dispersal? Unifying marine and terrestrial perspectives. *Biological Reviews*, *91*, 867–882. https://doi.org/10.1111/brv.12198

Bürkner, P.-C. (2017). brms: An R Package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*(1), 1–28. https://doi.org/10.18637/jss.v080.i01

Calabrese, G. M., Delmore, K. E., Wolf, J. B. W., Safran, R. J., & Rabosky, D. L. (2025). No consistent effect of migration on speciation rates in two avian superfamilies: A check on the robustness of trait-dependent diversification methods. *Systematic Biology*, syaf068. https://doi.org/10.1093/sysbio/syaf068

Cicero, C., Mason, N. A., Benedict, L., & Rising, J. D. (2020). Behavioral, morphological, and ecological trait evolution in two clades of New World Sparrows (Aimophila and Peucaea, Passerellidae). *PeerJ*, *8*, e9249. https://doi.org/10.7717/peerj.9249

Claramunt, S. (2021). Flight efficiency explains differences in natal dispersal distances in birds. *Ecology*, *102*(9), e03442. https://doi.org/10.1002/ecy.3442

Claramunt, S., Derryberry, E. P., Remsen, J. V., & Brumfield, R. T. (2012). High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1733), 1567–1574. https://doi.org/10.1098/rspb.2011.1922

Clauset, A., & Erwin, D. H. (2008). The evolution and distribution of species body size. *Science*, *321*, 399–401https://doi.org/10.1126/science.1157534

Conway, M., & Olsen, B. J. (2019). Contrasting drivers of diversification rates on islands and continents across three passerine families. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1915), 20191757. https://doi.org/10.1098/rspb.2019.1757

Cooney, C. R., & Thomas, G. H. (2021). Heterogeneous relationships between rates of speciation and body size evolution across vertebrate clades. *Nature Ecology & Evolution*, *5*(1), 101–110. https://doi.org/10.1038/s41559-020-01321-y

Cracraft, J. (1985). Biological diversification and its causes. *Annals of the Missouri Botanical Garden*, *72*, 794–822. https://doi.org/10.2307/2399222

Crouch, N. M., & Ricklefs, R. E. (2019). Speciation rate is independent of the rate of evolution of morphological size, shape, and absolute morphological specialization in a large clade of birds. *The American Naturalist*, *193*(4), E78–E91. https://doi.org/10.1086/701630

Curson, J. (1994). *New world warblers*. A&C Black.

Davis, M. P., Midford, P. E., & Maddison, W. (2013). Exploring power and parameter estimation of the BiSSE method for analyzing species diversification. *BMC Evolutionary Biology*, *13*, 1–11. https://doi.org/10.1186/1471-2148-13-38

del Hoyo, J. (Ed.). (2020). *All the birds of the world*. Barcelona: Lynx Edicions. ISBN 978-84-16728-37-4.

D'Horta, F. M. (2009). *Filogenia molecular e filogeografia de espécies de passeriformes (Aves): História biogeográfica da regiao neotropical com ênfase na Floresta Atlântica*. Diss. Universidade de São Paulo.

Eldredge, N., Thompson, J. N., Brakefield, P. M., Gavrilets, S., Jablonski, D., Jackson, J. B. C., Lenski, R. E., Lieberman, B. S., McPeek, M. A., & Miller, W. (2005). The dynamics of evolutionary stasis. *Paleobiology*, *31*(S2), 133–145. https://doi.org/10.1666/0094-8373(2005)031%5b0133:TDOES%5d2.0.CO;2

FitzJohn, R. G. (2010). Quantitative traits and diversification. *Systematic Biology*, *59*(6), 619–633. https://doi.org/10.1093/sysbio/syq053

Fitzjohn, R. G. (2012). Diversitree: Comparative phylogenetic analyses of diversification in R. *Methods in Ecology and Evolution*, *3*(6), 1084–1092. https://doi.org/10.1111/j.2041-210X.2012.00234.x

Forshaw, J. M. (Ed.). (1991). *Encyclopedia of animals: Birds*. Merehurst Limited.

Forstmeier, W., & Keßler, A. (2001). Morphology and foraging behaviour of Siberian Phylloscopus warblers. *Journal of Avian Biology*, *32*(2), 127–138. https://doi.org/10.1034/j.1600-048X.2001.320205.x

García-Moreno, J., & Fjeldså, J. (2000). Chronology and mode of speciation in the Andean avifauna. *Bonner Zoological Monographs*, *46*, 25–46.

Gavrilets, S. (2003). Perspective: Models of speciation: What have we learned in 40 years?. *Evolution*, *57*(10), 2197–2215. https://doi.org/10.1111/j.0014-3820.2003.tb00233.x

Gavrilets, S., & Vose, A. (2005). Dynamic patterns of adaptive radiation. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(50), 18040–18045. https://doi.org/10.1073/pnas.0506330102

Gómez-Bahamón, V., Márquez, R., Jahn, A. E., Miyaki, C. Y., Tuero, D. T., Laverde-R, O., Restrepo, S., & Cadena, C. D. (2020). Speciation associated with shifts in migratory behavior in an avian radiation. *Current Biology*, *30*(7), 1312–1321.e6. https://doi.org/10.1016/j.cub.2020.01.064

Harmon, L., Weir, J., Brock, C., Glor, R., Challenger, W., & Hunt, G. (2009). *geiger: Analysis of evolutionary diversification*. R package version 1.3-1. https://doi.org/http://CRAN.R-project.org/package=geiger

Herrera-Alsina, L. (2019). *Species selection and the spatial distribution of diversit y*. [Thesis fully internal (DIV), University of Groningen]. University of Groningen. https://doi.org/10.33612/diss.99272986

Herrera-Alsina, L., Van Els, P., & Etienne, R. S. (2019). Detecting the dependence of diversification on multiple traits from phylogenetic trees and trait data. *Systematic Biology*, *68*(2), 317–328. https://doi.org/10.1093/sysbio/syy057

Hill, A., Jiménez, M. F. T., Chazot, N., Cássia-Silva, C., & Faurby, S. (2023). Apparent effect of range size and fruit colour on palm diversification may be spurious. *Journal of Biogeography*, *50*(10), 1724–1736. https://doi.org/10.1111/jbi.14683

Holmes, R. T. (1990). American warblers: An ecological and behavioral perspective. *Science*, *248*(4957), 901–902. https://doi.org/10.1126/science.248.4957.901.b

Imfeld, T. S., & Barker, F. K. (2022). Songbirds of the Americas show uniform morphological evolution despite heterogeneous diversification. *Journal of Evolutionary Biology*, *35*(10), 1335–1351. https://doi.org/10.1111/jeb.14084

Jablonski, D. (2008). Species selection: Theory and data. *Annual Review of Ecology, Evolution, and Systematics, 39*, 501–524. https://doi.org/10.1146/annurev.ecolsys.39.110707.173510

Jenks, G. F. (1967). The data model concept in statistical mapping. *International Yearbook of Cartography*, *7*, 186–190.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, *491*(7424), 444–448. https://doi.org/10.1038/nature11631

Jocque, M., Field, R., Brendonck, L., & De Meester, L. (2010). Climatic control of dispersal–ecological specialization trade-offs: A metacommunity process at the heart of the latitudinal diversity gradient?. *Global Ecology and Biogeography*, *19*(2), 244–252. https://doi.org/10.1111/j.1466-8238.2009.00510.x

Kennedy, J. D., Borregaard, M. K., Jønsson, K. A., Marki, P. Z., & Fjeldså, J. (2016). The influence of wing morphology upon the dispersal, geographical distributions and diversification of the Corvides (Aves; Passeriformes). *Proceedings of the Royal Society B: Biological Sciences*, *283*(1844), 20161922. https://doi.org/10.1098/rspb.2016.1922

Kisel, Y., & Barraclough, T. G. (2010). Speciation has a spatial scale that depends on levels of gene flow. *The American Naturalist*, *175*(3), 316–334. https://doi.org/10.1086/650369

Kokko, H., & Lo´pez-Sepulcre, A. (2006). From individual dispersal to species ranges: Perspectives for a changing world. *Science*, *313*(5788), 789–791. https://doi.org/10.1126/science.1128566

Lefebvre, L., Ducatez, S., & Audet, J. N. (2016). Feeding innovations in a nested phylogeny of neotropical passerines. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1690), 20150188. https://doi.org/10.1098/rstb.2015.0188

Lowther, P. E. (1975). Geographic and ecological variation in the family Icteridae. *The Wilson Bulletin*, *87*(4), 481–495.

Maliet, O., Hartig, F., & Morlon, H. (2019). A model with many small shifts for estimating species-specific diversification rates. *Nature Ecology & Evolution*, *3*(7), 1086–1092. https://doi.org/10.1038/s41559-019-0908-0

Maliet, O., & Morlon, H. (2022). Fast and accurate estimation of species-specific diversification rates using data augmentation. *Systematic Biology*, *71*(2), 353–366. https://doi.org/10.1093/sysbio/syab055

Mayr, E. (1942). *Birds collected during the Whitney South Sea Expedition. 48, Notes on the Polynesian species of Aplonis*. The American Museum of Natural History.

Mayr, E. (1963). *Animal species and evolution*. Belknap Press. https://doi.org/10.4159/harvard.9780674865327

Morlon, H., Lewitus, E., Condamine, F. L., Manceau, M., & Clavel, J. (2016). RPANDA: An R package for macroevolutionary analyses on phylogenetic trees. *Methods in Ecology and Evolution*, *7*(5), 589–597. https://doi.org/10.1111/2041-210X.12526

Naka, L. N., Costa, B. M., Lima, G. R., & Claramunt, S. (2022). Riverine barriers as obstacles to dispersal in Amazonian birds. *Frontiers in Ecology and Evolution*, *10*, 846975. https://doi.org/10.3389/fevo.2022.846975

Oliveros, C. H., Field, D. J., Ksepka, D. T., Barker, F. K., Aleixo, A., Andersen, M. J., Alström, P., Benz, B. W., Braun, E. L., Braun, M. J., Bravo, G. A., Brumfield, R. T., Chesser, R. T., Claramunt, S., Cracraft, J., Cuervo, A. M., Derryberry, E. P., Glenn, T. C., Harvey, M. G., & Faircloth, B. C. (2019). Earth history and the passerine superradiation. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(16), 7916–7925. https://doi.org/10.1073/pnas.1813206116

Patten, M. A. (2010). Evolution and historical biogeography of a Song Sparrow ring in western North America. In *Evolutionary biology–concepts, molecular and morphological evolution: 13th meeting 2009*(pp. 329–342). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-12340-5

Phillimore, A. B., Freckleton, R. P., Orme, C. D. L., & Owens, I. P. (2006). Ecology predicts large-scale patterns of phylogenetic diversification in birds. *The American Naturalist*, *168*(2), 220–229. https://doi.org/10.1086/505763

Price, J. J., & Eaton, M. D. (2014). Reconstructing the evolution of sexual dichromatism: Current color diversity does not reflect past rates of male and female change. *Evolution*, *68*(7), 2026–2037. https://doi.org/10.1111/evo.12417

Price, J. P., & Wagner, W. L. (2004). Speciation in Hawaiian angiosperm lineages: Cause, consequence, and mode. *Evolution*, *58*(10), 2185–2200. https://doi.org/10.1111/j.0014-3820.2004.tb01597.x

Price-Waldman, R. M. (2019). *Phylogenomics, trait evolution, and diversification of the tanagers (Aves: Thraupidae)*. Master's thesis, San Diego State University.

Rabosky, D. L. (2014). Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS ONE*, *9*, e89543. https://doi.org/10.1371/j ournal.pone.0089543

Rabosky, D. L. (2016). Reproductive isolation and the causes of speciation rate variation in nature. *Biological Journal of the Linnean Society*, *118*(1), 13–25. https://doi.org/10.1111/bij.12703

Rabosky, D. L., & Goldberg, E. E. (2015). Model inadequacy and mistaken inferences of trait-dependent speciation. *Systematic Biology*, *64*(2), 340–355. https://doi.org/10.1093/sysbio/syu131

Rabosky, D. L., Grundler, M., Anderson, C., Title, P., & Shi, J. J. (2014). BAMMtools: An R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods in Ecology and Evolution*, *5*(7), 701–707. https://doi.org/10.1111/2041-210X.12199

Reznick, D. N., & Ricklefs, R. E. (2009). Darwin's bridge between microevolution and macroevolution. *Nature*, *457*(7231), 837–842. https://doi.org/10.1038/nature07894

Ricklefs, R. E. (2011). A biogeographical perspective on ecological systems: Some personal reflections. *Journal of Biogeography*, *38*(11), 2045–2056. https://doi.org/10.1111/j.1365-2699.2011.02520.x

Salisbury, C. L., Seddon, N., Cooney, C. R., & Tobias, J. A. (2012). The latitudinal gradient in dispersal constraints: Ecological specialisation drives diversification in tropical birds. *Ecology Letters*, *15*(8), 847–855. https://doi.org/10.1111/j.1461-0248.2012.01806.x

Sánchez-González, L. A., Navarro-Sigüenza, A. G., Krabbe, N. K., Fjeldså, J., & García-Moreno, J. (2015). Diversification in the Andes: The Atlapetes brush-finches. *Zoologica Scripta*, *44*(2), 135–152. https://doi.org/10.1111/zsc.12088

Schluter, D. (2000). *The ecology of adaptive radiation*. Oxford University Press.

Sheard, C., Neate-Clegg, M. H. C., Alioravainen, N., Jones, S. E. I., Vincent, C., MacGregor, H. E. A., Bregman, T. P., Claramunt, S., & Tobias, J. A., &(2020). Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nature Communications*, *11*(1), 1–9. https://doi.org/10.1038/s41467-020-16313-6

Shi, J. J., Westeen, E. P., & Rabosky, D. L. (2021). A test for rate-coupling of trophic and cranial evolutionary dynamics in New World bats. *Evolution*, *75*, 861–875. https://doi.org/10.1111/evo.14188

Simões, M., Breitkreuz, L., Alvarado, M., Baca, S., Cooper, J. C., Heins, L., Herzog, K., & Lieberman, B. S. (2016). The evolving theory of evolutionary radiations. *Trends in Ecology & Evolution*, *31*(1), 27–34.

Simpson, G. G. (1953). *The major features of evolution*. Columbia University Press.

Smith, B. T., McCormack, J. E., Cuervo, A. M., Hickerson, M. J., Aleixo, A., Cadena, C. D., Pérez-Emán, J., Burney, C. W., Xie, X., Harvey, M. G., Faircloth, B. C., Glenn, T. C., Derryberry, E. P., Prejean, J., Fields, S., & Brumfield, R. T. (2014). The drivers of tropical speciation. *Nature*, *515*(7527), 406–409. https://doi.org/10.1038/nature13687

Stanley, S. M. (1998). *Macroevolution: Pattern and process*. Johns Hopkins University Press.

Swaddle, J. P., & Lockwood, R. (2003). Wingtip shape and flight performance in the European Starling Sturnus vulgaris. *Ibis*, *145*(3), 457–464. https://doi.org/10.1046/j.1474-919X.2003.00189.x

Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J. M., Yang, J., Sayol, F., Neate-Clegg, M. H. C., Alioravainen, N., Weeks, T. L., Barber, R. A., Walkden, P. A., MacGregor, H. E. A., Jones, S. E. I., Vincent, C., Phillips, A. G., Marples, N. M., Montaño-Centellas, F. A., Leandro-Silva, V., Claramunt, S., & Schleuning, M., …(2022). AVONET: Morphological, ecological and geographical data for all birds. *Ecology Letters*, *25*(3), 581–597. https://doi.org/10.1111/ele.13898

van Els, P., Zarza, E., Moreira, L. R., Gómez-Bahamón, V., Santana, A., Aleixo, A., Ribas, C. C., do Rêgo, P. C., Santos, M. P. D., Zyskowski, K., Prum, R. O., & Berv, J. (2021). Recent divergence and lack of shared phylogeographic history characterize the diversification of neotropical savanna birds. *Journal of Biogeography*, *48*(5), 1124–1137. https://doi.org/10.1111/jbi.14065

Vinciguerra, N. T., & Burns, K. J. (2021). Species diversification and ecomorphological evolution in the radiation of tanagers (Passeriformes: Thraupidae). *Biological Journal of the Linnean Society*, *133*(3), 920–930. https://doi.org/10.1093/biolinnean/blab042

Weeks, B. C., O'Brien, B. K., Chu, J. J., Claramunt, S., & Sheard, C. (2022). Morphological adaptations linked to flight efficiency and aerial lifestyle determine natal dispersal distance in birds. *Functional Ecology*, *36*, 1681–1689, https://doi.org/10.1111/1365-2435.14056

Weir, J. T. (2006). Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution*, *60*(4), 842–855. https://doi.org/10.1111/j.0014-3820.2006.tb01161.x

Winkler, D. W., Billerman, S. M., & Lovette, I. J. (2020). Tanagers and allies (Thraupidae), version 1.0. In S. Billerman, B. K. Keeney, P. G. Rodewald, & T. S. Schulenberg (Eds.), *Birds of the world*. Cornell Lab of Ornithology.https://doi.org/10.2173/bow

Received January 17, 2024; revisions received October 9, 2025; accepted October 27, 2025
Associate Editor: Alejandro Gonzalez-Voyer; Handling Editor: Hélène Morlon