The Historical Biogeography of the New World Black Birds (Icteridae)

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Authors contribution statements

Axel Arango: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Software (equal); Writing – original draft (equal); Writing –review and editing (equal). **Chaitanya S. Gokhale:** Funding acquisition (equal); Project administration (equal); Supervision (equal); Writing – review and editing (equal).

AI use statement

No AI tools were used for the writing, coding or analysis of the data.

Data Accessibility Statement

Data and code to conduct all presented analyses are available from the Figshare Repository: https://figshare.com/s/2116486ba44c02cd9615

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Abstract

The New World blackbirds (Icteridae) are a widely distributed, ecologically diverse avian family whose biogeographic history remains poorly understood. Competing hypotheses have proposed Neotropical or Nearctic origins, while the relative roles of dispersal, *in situ* speciation, and range evolution as diversification drivers have remained unresolved. Here, we reconstruct the historical biogeography of Icteridae by integrating phylogenetic bioregionalization, probabilistic ancestral range estimation, biogeographic stochastic mapping (BSM), and Geographic Hidden State Speciation and Extinction (GeoHiSSE) modelling. We identified six phylogenetically distinct biogeographic regions and compared 18 models of range evolution across three dispersal hypotheses. The best-supported model strongly supported a Nearctic origin, with subsequent stepwise southward colonization beginning with Mesoamerica (~7.99 Ma), followed by the Isthmus-Andes (~6.36 Ma), Amazonas (~5.95 Ma), Southern South America (~4.93 Ma), and finally Patagonia (~2.79 Ma). The earliest dispersal from North to South America predates the closure of the Isthmus of Panama, coinciding instead with a documented dispersal wave of the Great American Biotic Interchange and open habitat expansion in northern South America. Dispersal was the dominant mode of range evolution, while *in situ* speciation was the primary cladogenetic process. The best-fit GeoHiSSE model revealed that geographic range alone does not fully explain diversification rate heterogeneity, with observed geographic states and unmeasured hidden rate classes jointly shaping macroevolutionary dynamics. Model-averaged speciation rates were comparable across regions. Together, these results support a Nearctic origin and stepwise southward colonization of the Americas by Icteridae, while demonstrating that lineage splitting is governed primarily by unmeasured biological factors within bioregions rather than geography per se.

Highlights:

- Six distinctive evolutionary regions were identified for Icteridae using phylogenetic bioregionalization.
- Strong support for Icteridae's Nearctic origin with subsequent southward step-wise colonization that predates the closure of the Panama Isthmus, instead of Mayr's proposed south American origin.
- Icteridae's expansion appears to be connected to the historical expansion of C4 grasses in the Americas.
- Speciation in Icteridae is not driven by geographical features, instead it might be linked to other biological or ecological traits in the lineage, such as ecological specialization or sexual selection.
- Icteridae seems to be following its parent clade (Emberizoidea) pattern of within region *in situ* speciation.

Keywords:

Dispersal, GABI, Passeriformes, Range Evolution, Speciation rates, SSE Models, Colonization

Introduction

The New World blackbirds (Icteridae) are among the most extensively studied avian clades in ecological, behavioral, and morphological research (Powell et al. 2014). This passerine family comprises approximately 106 extant species widely distributed throughout the Americas, from Alaska to Tierra del Fuego (Fraga 2008). Encompassing well-known groups such as orioles, grackles, cowbirds, and meadowlarks, Icterids exhibit remarkable diversity in evolutionarily important traits, including plumage, vocalizations, social behavior, and foraging strategies (Jaramillo and Burke 1999). As a result, members of this clade occupy nearly all major ecosystems in the New World, ranging from boreal forests and temperate grasslands to tropical rainforests, savannas, shrublands, and wetlands (Winkler et al. 2020). It is therefore reasonable to expect that their ecological and phenotypic diversity is closely tied to their biogeographic history, with the clade's origin and subsequent dispersal across the Americas driving distinct distributional patterns and adaptive specializations in response to diverse environmental pressures (Ricklefs 2006a; Simões et al. 2016). Nevertheless, despite the clade's prominence as a model system in ecological studies, its biogeographic history remains both controversial and understudied.

In 1946, Ernst Mayr theorized that the current distribution of Icteridae resulted from continuous colonization from South America, even before the Panama isthmus closed (Mayr 1946). Thus, despite being Pan-American, Icteridae was established as a clade of Neotropical origins. This hypothesis remained widely accepted until a recent study by Barker et al. (2015), wich placed Icteridae unequivocally of North American origin. Although this study provided robust and compelling evidence for a North American origin of Icteridae, their broad approach prevented a more detailed understanding of the clade's biogeographic history (Powell et al. 2014). As a result, key evolutionary processes, such as within-continental dispersal and *in situ* diversification, remain unresolved (Daru et al. 2017). For instance, it is still unclear whether the group's expansion followed a stepwise pattern through adjacent regions, as Mayr originally proposed, or whether dispersal was more opportunistic and unconstrained, consistent with the high dispersal ability and migratory behavior of many Icterid species (Kondo and Omland 2007; Arango et al. 2022). Similarly, the extent to which these dynamics and geographic barriers have shaped diversification across the Americas remains highly debated (Ricklefs 2006b; Machac 2020).

To better understand biodiversity patterns, it is crucial to define the biogeographical boundaries that reflect historical processes (Olson et al. 2001; Kreft and Jetz 2010). Incorporating evolutionary information into boundary delimitation reveals both the spatial and evolutionary structure of species distributions (Daru et al. 2016, 2017; Kennedy et al. 2017), and sheds light on the mechanisms driving these patterns (Leprieur et al. 2012; Daru et al. 2017). Therefore, by identifying clusters of lineages that diversified within shared biogeographic contexts, evolutionarily informed bioregionalizations offer insights into spatial aspects of evolutionary history, such as dispersal and *in situ* diversification (Baselga and Orme 2012; Daru et al. 2017). This perspective is particularly important for clades like Icteridae, which exhibit high ecological versatility and broad distributions across heterogeneous landscapes (Winkler et al. 2020).

As such, incorporating these evolutionarily informed bioregions into parametric models of range evolution can deepen our understanding of how geography and range evolution have shaped the diversification of lineages (Matzke 2013). This approach provides a more comprehensive view of the patterns, processes, and historical events that underlie present-day biodiversity distributions (Leprieur et al. 2012; Matzke 2014; Arango et al. 2025; Lima et al. 2025). Moreover, geography can also influence macroevolutionary dynamics by mediating speciation and extinction rates across regions that might differ in area, connectivity, ecological heterogeneity, and isolation (Goldberg et al. 2011; Rolland et al. 2014; Beaulieu and O'Meara 2016). In the case of Icteridae, North and South America could differ markedly in their biogeographic histories, climatic regimes, and habitat diversity, with differential diversification rates between the two regions, further highlighting the main processes shaping the clade's biodiversity (Ricklefs 2006b; Smith et al. 2014).

In this study, we reconstruct the historical biogeography of Icteridae and assess how geography shaped its diversification by integrating phylogenetic bioregionalization with comparative modeling. We first delineate evolutionarily coherent bioregions across the New World using a Phylogenetic Bioregionalization framework (Daru et al. 2020), providing biologically meaningful units for ancestral range estimation with BioGeoBEARS (Matzke 2014). We compare the most common models of range evolution across three different hypotheses: an unconstrained model with equal dispersal among regions, a dispersal-restricted model incorporating geographic connectivity, and a directional model allowing asymmetric movement between North and South America, to later use Biogeographic Stochastic Mapping (BSMs) to reconstruct the biogeographic events of the clade. To evaluate geography's impact on diversification rates, we apply Geographic Hidden State Speciation and Extinction (GeoHiSSE) models (Beaulieu and O'Meara 2016), which estimate speciation and extinction across regions. Together, these approaches clarify how geography, dispersal, and regional dynamics have shaped the evolutionary history of Icteridae.

Methods

Geographic and Phylogenetic data

We obtained the geographical distributions for Icterid species from the BirdLife international range maps V.2024 (BirdLife International and Handbook of the Birds of the world 2024), comprising 103 out of 106 recognized species as per 2025 according to the Clements checklist (Clements et al. 2019). We acquired the phylogenetic relationships of these 103 species by pruning the Icteridae clade from the Maximum Credibility Clade (MCC) phylogeny by Barker et al. (2015). The remaining three species were excluded from the analyses due to data protection for endangered species.

Phylogenetic Biogeographical regionalization

To reconstruct the biogeographical history of Icteridae, we first delimited the pertinent biogeographical regions for the clade. To delimit such regions, we applied a phylogenetic bioregionalization. This method identifies evolutionary distinct biogeographical regions by taking into consideration the evolutionary relatedness of species in the geography (Daru et al. 2017).

To perform the bioregionalization, we first transformed the breeding distribution maps of Icteridae species into a 1 x 1° presence-absence matrix. Using this matrix, we calculated the phylogenetic turnover between assemblages with Simpson's Phylogenetic Index of dissimilarity

($p\beta_{Sim}$). This index measures turnover based on shared branch lengths among grid cells and is particularly suited for biogeographic applications due to its insensitivity to differences in species richness (Kreft and Jetz 2013; Daru et al. 2016; Gross et al. 2025).

We then evaluated several hierarchical clustering methods to determine which best captured the structure of the phylogenetic dissimilarity matrix. These included complete linkage, UPGMA (unweighted pair-group method using averages), UPGMC (using centroids), WPGMA (weighted averages), WPGMC (weighted centroids), Ward's minimum variance, and the divisive method DIANA. Model performance was assessed using the cophenetic correlation coefficient (Sokal and Rohlf 1962).

To determine the optimal number of clusters (k), we applied the 'elbow' method (Salvador and Chan 2004), which identifies the point beyond which adding more clusters yields increases in explained variance no higher than 0.01 (Daru et al. 2020). While cluster selection is often considered arbitrary (Kreft and Jetz 2013),the elbow method provides a more objective criterion by identifying where the explained variance of the phylogenetic matrix levels off (Salvador and Chan 2004).

Finally, we performed non-metric multidimensional scaling (NMDS) based on the distance matrix derived from the best-performing clustering algorithm (UPGMA) and the optimal number of clusters. The result was a set of spatially coherent, phylogenetically distinct biogeographic regions for the Icteridae superfamily.

Biogeographic Modeling

We used the previously delimited biogeographical regionalization to evaluate distinct models of ancestral area reconstruction employing the BioGeoBEARS R package (Matzke 2014) to reconstruct the historical range evolution of Icteridae. BioGeoBEARS allows for the comparative evaluation of multiple likelihood-based biogeographic models under a common statistical framework (Matzke 2013).

We tested three widely used models of range evolution (DEC, DIVA, and BAY AREA), each with and without the addition of the founder-event speciation parameter (+J), resulting in a total of six candidate models per hypothesis. The models were informed by a discrete biogeographic dataset based on the results of our phylogenetic bioregionalization, with each species assigned to one or more of the identified bioregions.

To account for the geographic structure and varying connectivity between regions, we incorporated a geodesic distance matrix representing pairwise great-circle distances between the boundaries of each bioregion (See Table S1). Furthermore, we used different dispersal matrices to modify the dispersal probability multipliers between regions under different hypotheses of range evolution (See Table S2). Specifically, we tested three hypotheses: A) an unconstrained dispersal model in which all regions were assumed to have equal pairwise dispersal probabilities; B) a dispersal-restricted model, in which probabilities were inversely scaled by geographic distance, reflecting reduced dispersal likelihood over longer distances; and C) a directional dispersal model, in which asymmetries in dispersal rates were introduced to simulate biased movement from North to South America, consistent with a hypothesized southward expansion of the clade.

Each model was fit to the empirical range data and the maximum clade credibility tree using likelihood optimization. Model fit was evaluated based on log-likelihood (lnL) and corrected Akaike Information Criterion (AICc) scores. Comparisons among models were used to identify the best-fitting biogeographic scenario and assess the relative importance of dispersal constraints and founder-event speciation in shaping the distribution of Icteridae.

To test such dispersal hypothesis models that better explain Icterid biogeographic events, we performed likelihood ratio tests between the best models of each hypothesis. Following model selection, we implemented biogeographic stochastic mapping (BSM) under the best-supported model to estimate the number, direction, and timing of historical dispersal, extinction, and range-switching events. We generated 1000 stochastic maps to summarize the frequency and spatial pattern of inferred events across the phylogeny, providing a probabilistic view of the processes that have shaped Icteridae current distribution.

Geographic diversification

To evaluate the role of geography in shaping diversification rates within Icteridae, we implemented a series of geography-dependent diversification models using the GeoHiSSE framework (Caetano et al. 2018). To do so, we classified species as endemic of North America (NA), endemic of South America (SA) or Widespread (WS).

We compared four classes of models to test whether geographic occupancy is associated with differences in speciation, extinction, or transition rates. First, we fitted a null model in which diversification is independent of geography, assuming equal rates across continents. Second, we tested the canonical GeoSSE model, in which speciation, extinction, and range transition rates are allowed to differ between lineages restricted to different regions and those occupying multiple areas. Third, we applied a null model with hidden states, which maintains geographic independence but allows diversification rates to vary across unobserved (hidden) character states, thus accounting for potential rate heterogeneity unrelated to geography. Finally, we tested a set of GeoHiSSE models that incorporate both observed geographic states and hidden rate classes, allowing for complex diversification dynamics structured by geography as well as unmeasured biological or ecological factors.

By comparing the fit of these models using AIC, we assessed whether the observed geographic distribution of lineages is associated with shifts in diversification rates, while controlling for background rate heterogeneity. This approach provides a robust framework to evaluate whether regional occupancy has had a significant impact on the diversification of Icteridae. Furthermore, to evaluate each region’s contribution to the speciation of Icteridae, we averaged the resulting parameters of each model at the tips, weighted by their AICw using a harmonic mean, as suggested by Caetano et al., 2018.

Results

Phylogenetic Biogeographical regionalization

The best performing cluster algorithm for the Icteridae phylogenetic turnover was UPGMA (see Table S3). According to the "elbow" method, the optimal number of regions (k) was 6, based on the convergence, low level of stress, and explained variance (Figure S1; Table S4).

Accordingly, the NMDS ordination defined six phylogenetic biogeographical regions for Icteridae (Figure S2): Nearctic (A), Isthmus-Andes (B), Amazonas (C), Southern South America (D), Patagonia (E), and Mesoamerican-Caribbean (F; Figure 1a)

Biogeographic modelling

Model comparisons revealed that the best-fitting model under the unconstrained dispersal hypothesis was BAYAREA, which assumed widespread sympatry and frequent range expansions without penalizing geographic distance. Under the adjacent-area dispersal hypothesis, both DEC and DEC+J models performed similarly, supporting stepwise dispersal between neighboring regions. In contrast, the best-fitting model for the gradual directional dispersal hypothesis was DEC+J, which incorporates distance-based dispersal probabilities and founder-event speciation (Table 1).

Given that the best fitting model for the unconstrained hypothesis was largely outperformed by the best fitting models for both the adjacent and the gradual hypothesis, we excluded it from the likelihood ratio test. Furthermore, since the likelihood ratio test showed no difference between the DEC and DEC+J model in the adjacent hypothesis, we decided to use the model with less parameters (DEC) for its comparison with the gradual hypothesis best fitting model (DEC+J). The likelihood ratio test comparing the best adjacent-area model (DEC) and the best gradual model (DEC+J) showed that the gradual model provided a significantly better fit (Table S5).

Ancestral area reconstruction under the best-fit gradual DEC+J model strongly supported a Nearctic origin for the clade, with the highest marginal probability concentrated in bioregion A (Figure 1b). Accordingly, the Biogeographic Stochastic Mappings (BSMs) under the gradual DEC+J revealed strong support for directional dispersal from Icteridae's ancestral area in the Nearctic into Neotropical regions.

Across 1000 BSMs, it was shown that the main mode of range evolution for Icteridae was dispersal, with an average number of anagenetic dispersal events of 163.57 (±7.96), whereas range contraction was significantly lower (43.43 ± 6.97). Most of the cladogenetic events in the clade were *in situ* events, with an average of 49.91 (±4.47), followed by range expansion cladogenesis with an average of 29.24 (±4.59) events. Although rarer, vicariant events were also present, with an average of 14.42(±3.17). Founder event speciation were the rarer events, with an average of 9.41 (±2.8), indicating that the main mode of cladogenesis was within region speciation (Table S6; Figure S3).

The BSMs reconstructed the origin of Icteridae in the Nearctic region (A), from which the clade subsequently expanded across the Americas in a southward progression. Then, the BSMs showed that the earliest dispersal event occurred approximately 7.99 (±1.52) Ma, when lineages colonized the Mesoamerican-Caribbean region (F). The Isthmus-Andes region (B) was reached shortly thereafter, around 6.36 (±1.45) Ma, followed by the Amazonas region (C) at approximately 5.95 (±1.68) Ma. Colonization continued southward, with lineages establishing in Southern South America (D) around 4.93 (±1.41) Ma and ultimately reaching the southernmost extent of the family's range, the Patagonian region (E), around 2.79 (±1.52) Ma (Figure 2a; Table S7).

Biogeographic stochastic mapping revealed a clear directionality in the dispersal history of Icteridae, consistent with a Nearctic origin and progressive southward colonization of the Neotropics. The highest dispersal flow out of the Nearctic was directed toward Mesoamerica (24.66 ± 5.04 events), which itself functioned as a major stepping-stone toward South America, dispersing extensively into the Isthmus-Andes (21.54 ± 3.06) and Amazonas (11.18 ± 2.77). From the Isthmus-Andes, lineages continued to spread southward, with dispersal toward Amazonas (23.52 ± 4.81) and Southern South America (14.31 ± 3.48) substantially exceeding the reverse directions (12.13 ± 3.91 and 5.88 ± 2.33, respectively), reinforcing a net south-directed dynamic. Amazonas further contributed to the colonization of Southern South America (16.91 ± 4.25 vs. 8.97 ± 2.72 events in the opposite direction), representing the final major step in this continental progression. Patagonia emerged as a distal peripheral sink at the terminus of this colonization axis, receiving dispersal almost exclusively from Southern South America

(6.97± 1.54) with negligible backflow, and contributing little to outward dispersal across any route. Overall, the Nearctic and Mesoamerica were the dominant net source regions (net = +10.85 and +11.93 events, respectively), while Amazonas (−10.66), Southern South America (−9.87), and Patagonia (−6.75) functioned as net recipients, tracing a coherent south-directed colonization pathway from North America through the Isthmus into the heart of South America (Table S8-9; Figure 2b).

Range contraction events (Table S10), reflecting local extinction or range shrinkage within areas, were also unevenly distributed across regions. Mesoamerica exhibited the highest mean number of range contractions (mean = 11.20 ± 3.05), exceeding all other areas and suggesting high lineage turnover despite its role as a major dispersal corridor and center of *in situ* diversification. The Isthmus-Andes (8.25 ± 2.73), Amazonas (7.70 ± 2.77), and the Nearctic (7.23 ± 2.28) showed intermediate and similar contraction counts, indicating comparable levels of range loss across these core areas. Southern South America had somewhat fewer contractions (6.28 ± 2.47), while Patagonia showed markedly lower range contraction rates (2.82 ± 1.61), consistent with its very low lineage diversity and limited overall involvement in Icteridae biogeographic dynamics. For all areas, most extirpation events happened from 2.54 Ma onwards, while being heavily skewed to the present (Figure S4).

In situ speciation events were unevenly distributed across the six biogeographic areas, reflecting both the antiquity and the diversification potential of each region (Table S11). Mesoamerica (F) showed the highest mean number of within-area speciation events (mean = 11.80 ± 3.74), followed closely by the Nearctic (A; 10.80 ± 3.88) and the Isthmus-Andes (B; 9.87 ± 3.87), suggesting that these regions not only served as sources of dispersal but also as important centers of *in situ* diversification. Amazonas (C; 8.39 ± 4.64) and Southern South America (D; 8.94 ± 2.67) showed intermediate speciation counts, though Amazonas exhibited notably higher variance, possibly reflecting heterogeneity in diversification dynamics across the distribution of SBMs. Patagonia (E) stood in stark contrast to all other regions, with an almost absent *in situ* speciation signal (mean = 0.019 ± 0.137), consistent with its role as a peripheral sink colonized too recently or too sporadically to have accumulated substantial *in situ* diversification.

In terms of timing, *in situ* speciation events in the Nearctic were on average the oldest (mean = 5.26 ± 3.07Ma), indicating that diversification within this ancestral area began earlier than in any other region and predates the major southward colonization pulses. Speciation events in Southern South America (2.76 ± 1.24 Ma) were somewhat more recent on average, consistent with a later arrival of lineages at the southern end of the colonization axis. The remaining regions: Mesoamerica (2.55 Ma), the Isthmus-Andes (2.53 ± 1.59 Ma), and Amazonas (2.37 ± 1.41 Ma), showed similar and relatively recent mean speciation times, suggesting a roughly contemporaneous burst of *in situ* diversification across the Neotropics during the Pliocene–Pleistocene (Table S12; Figure 2c). In Patagonia, only 19 SBMs recovered an *in situ* event, all of them at the common ancestor of *Amblyramphus holosericeus* and *Curaeus curaeus*, around 3.53 Ma.

Geographic diversification

Model comparison across GeoSSE, GeoHiSSE, and null models revealed that the full GeoHiSSE model provided the best fit to the data (Table 2), indicating that diversification dynamics in Icteridae are shaped by both observed geographic occupancy and unmeasured hidden states. This result suggests that geography alone does not fully capture the heterogeneity in speciation and extinction rates across the clade, and that at least one additional biological or ecological factor (not explicitly modeled here) contributes to diversification rate variation among lineages.

The two hidden rate classes reveal distinct macroevolutionary regimes. In hidden rate class A, turnover is low to moderate and geographically structured, with South American endemics showing the lowest values ($\tau = 0.084$ sp/My) and Widespread lineages the highest ($\tau = 0.48$ sp/My), followed by North American lineages ($\tau = 0.40$ sp/My). All ranges had negligible extinction fractions. In hidden rate class B, the geographic structure shows a completely different pattern, North American endemics show near-zero turnover, South American endemics had moderate values ($\tau = 0.41$ sp/My) while Widespread lineages show extraordinarily high values ($\tau = 7.740$ sp/My). Since extinction fractions were negligible across endemic states, all rate differences are driven by speciation variation rather than differential extinction. In the case of Widespread lineages, extinction fraction cannot be calculated since, for a lineage to get extinct first it needs to contract their range (become endemic). Because of this caveat, turnover in Widespread lineages represents the sum of three cladogenetic speciation components (within-NA, within-SA, and between-area vicariant speciation; Caetano et al. 2018), not a combination of speciation and extinction. The high turnover therefore reflects an elevated overall rate of cladogenetic events across all three ranges simultaneously, rather than high lineage turnover in the conventional sense. Concordantly, speciation rates when averaging all models were highest in South America (0.29 sp/My), followed Widespread lineages (0.24 sp/My) and North America endemics (0.21 sp/My), having similar rates of speciation. This reflects the highly transitory nature of Widespread lineages and the combined contribution of both hidden rate classes weighted by their marginal probabilities across the phylogeny (Table 3).

These results are congruent with a scenario in which Icteridae originated in the Nearctic and diversified primarily *in situ* within newly colonized regions, with sustained diversification in both North and South America over evolutionary time (Figure 3).

Discussion

This study sheds new light on the historical biogeography of Icteridae, a widespread and ecologically diverse New World avian clade. By combining phylogenetic bioregionalization, probabilistic inference of historical range evolution, and geography-dependent diversification modelling, we offer an integrated view of how biogeographic events shaped the evolutionary history of this family. Our findings support a Nearctic origin for Icteridae followed by a progressive southward expansion and *in situ* diversification across the Americas, refining and expanding upon prior hypotheses about the family's evolutionary trajectory and offering broader insights into the macroevolutionary mechanisms shaping New World avifauna.

Our ancestral area reconstructions strongly support a Nearctic origin for Icteridae, corroborating the molecular phylogenetic evidence of Barker et al. (2015) and refuting earlier ideas of a Neotropical origin put forward by Mayr (1946). The reconstructed colonization sequence, from the Nearctic into Mesoamerica (~7.99 Ma), then to the Isthmus-Andes (~6.35 Ma), Amazonas (~5.95 Ma), Southern South America (~4.93 Ma), and finally Patagonia (~2.79 Ma), traces a stepwise southward progression consistent with the gradual DEC +J model that provided the best fit to the data. This pattern is consistent with broader trends identified across New World birds, where avian lineages with Nearctic origins have repeatedly dispersed into the tropics and radiated throughout South America, while lineages of South American tropical origins remain largely restricted to the Neotropical region (Smith and Klicka 2010). The asymmetry in dispersal directionality we recovered for Icteridae, therefore, could reflect a broader macroevolutionary pattern of niche conservatism and southward ecological expansion that has shaped New World avifauna more generally (Hawkins et al. 2006; Smith and Klicka 2010; Smith et al. 2012).

Concordantly, most of the early speciation events in Icteridae, occurred during mid to late Pliocene, coinciding with the progressive expansion of open habitats (Anderson 2006), which appear to be the ancestral habitat for the family, as suggested by the preferences of their closest relative *Icteria virens* (McKibbin and Bishop 2010) and its earliest diverged species *Xanthocephalus xanthocephalus* (Twedt and Crawford 2020). Further expansion of these habitats and their displacement of woody ecotones as the planet became drier (Pagani et al. 1999; Osborne 2008) might have incentivized the expansion and dispersal of Icteridae, as its lineages were following their ancestral biome (Wiens and Donoghue 2004; Crisp et al. 2009).

As such, the timing of the earliest dispersal from North America to South America (~6.35 Ma) predates the traditionally accepted completion of the Isthmus of Panama (~3 Ma; Coates and

Stallard 2013), suggesting that early colonization of South America occurred via overwater dispersal or through pre or proto-isthmian land connections. This timing agrees with the expansion of open habitats in northern South America due to the Andean uplift around 9-6 Ma (Kirschner and Hoorn 2020). Moreover, the timing also coincides with growing biological evidence that the Great American Biotic Interchange (GABI) was a long and complex process beginning as early as the Oligocene–Miocene transition, with significant terrestrial organism's dispersal waves documented at approximately 20 and 6 Ma (Bacon et al. 2015). And, while following the suggested pattern of Northern colonization with subsequent speciation of South America (Smith and Klicka 2010), such events happened at least three million years before previously suggested, following more closely the timing of a dispersal wave (Bacon et al. 2015), than continuous dispersals after or during the isthmus closure 3 Ma (Weir et al. 2009; Smith and Klicka 2010; Barker et al. 2015).

Mesoamerica was both the first Neotropical region colonized from the Nearctics and the highest net source of dispersal events across the entire clade's history, while simultaneously exhibiting the greatest number of range contractions and *in situ* speciation events among all regions. This combination of high dispersal events, high speciation, and high lineage turnover suggest that Mesoamerica has acted as a highly dynamic biogeographic hub rather than a simple stepping-stone. As such, Mesoamerica harbors exceptionally high avian endemism generated by a complex geological and ecological history (Rocha-Méndez et al. 2019) and functions as a key relay in biotic interchange where topographic heterogeneity promotes both diversification and lineage turnover (McCormack et al. 2023). The peak of range contraction counts in Mesoamerica around 3 Ma (Figure S4) may also reflect competitive dynamics following land bridge closure, as newly arrived lineages displaced earlier colonists (Weir et al. 2009; Smith and Klicka 2010). At the same time, most *in situ* speciation events in the region occurred during the Pleistocene. Examples of these events are found by most *Quiscalus* and *Icterus* lineages, which already begun to diverge during the Pliocene (Powell et al. 2014). The timing of these cladogenetic events may be related to rapid diversification driven by this epoch's characteristic climatic oscillations, which caused extensive habitat fragmentation and ultimately allopatric speciation of already diverging lineages (Avise and Walker 1998; Avise et al. 1998; Weir 2006). In fact, such oscillations are well documented to isolate avian populations and generate the allopatric conditions necessary for speciation in Mesoamerica, particularly in open habitats (Barber and Klicka 2010; Castillo-Chora et al. 2021).

Within South America, the Isthmus-Andes region functioned as the primary continental entry point and dispersal hub to both Amazonas and Southern South America even early on, with the second highest mean *in situ* speciation after Mesoamerica. Its role as both a major source and recipient of dispersal events and as a center of *in situ* speciation mirrors patterns documented across closely related Neotropical passerine lineages such as Thraupids and New world Sparrows (Hazzi et al. 2018). For these clades the Andean uplift and mountain dispersal facilitated by temperature oscillations of the Pleistocene, generated new ecological opportunities and drove diversification (Smith et al. 2014; Hazzi et al. 2018).

Colonization proceeded southward, with Amazonas receiving the highest net inflow of lineages and contributing to the assembly of the Southern South American fauna. *In situ* speciation events were intermediate in both Amazonas and Southern South America. This pattern contrasts with that documented across many other Neotropical clades, for which Amazonas is recognized as the primary source of Neotropical biodiversity, providing over 2,800 lineages to other regions (Antonelli et al. 2018), but following other New World avian clades' biogeographical patterns (Smith and Klicka 2010). In Icteridae, Amazonas was a net recipient rather than a net source, likely reflecting the clade's non-Neotropical origins. Interestingly, both the Isthmus-Andean and Southern South America regions presented early *in situ* diversification during the Pliocene, which coincides with the firm establishment of open habitats (such as paramo, floodplains, and savannas) in South America (Kirschner and Hoorn 2020).

Patagonia stands out across all biogeographic metrics as a very distinct region. It received dispersal almost exclusively from Southern South America, harbored virtually no *in situ* speciation, and showed the lowest range contraction counts. These features seem consistent with a region that might have been colonized late, rarely, and sparsely (Vuilleumier 1991; Bukowski et al. 2024). The near-absent speciation signal is a pattern aligned with recent findings that colonization of new regions does not automatically generate elevated diversification (Kennedy et al. 2017; Arango et al. 2025).

Finally, the macroevolutionary analyses indicate that the full GeoHiSSE model provided the best fit, revealing that diversification dynamics in Icteridae are shaped by both observed geographic occupancy and unmeasured hidden traits. This implies that geography alone does not fully capture the heterogeneity in speciation and extinction rates across the clade (Caetano et al. 2018).

The two hidden rate classes reveal distinct macroevolutionary regimes that are coherent with the biogeographic history recovered by our BSM analyses. In hidden rate class A, cladogenetic rates are low to moderate and geographically structured. North American endemics show the highest within-area speciation, consistent with the deep early diversification recovered in the Nearctic by our BSMs, while South American endemics show the lowest values with a non-negligible extinction fraction, pointing to a more dynamic macroevolutionary regime in the Neotropics where speciation is partly offset by extinction as documented across other South American passerine radiations (Ricklefs 2006b). As such the elevated extinction fraction among South American Icterid endemics in hidden rate class A is consistent with the high range contraction rates recovered by our BSMs in Isthmus-Andean and Amazonian regions, suggesting that lineage-level turnover has been a persistent feature of Icteridae's South American history.

Widespread lineages in hidden rate class A show moderate cladogenetic rates, consistent with the ongoing intercontinental exchange documented in the BSMs and with the high dispersal ability and migratory behavior that characterize many Icterid lineages (Kondo and Omland 2007; Price et al. 2009; Arango et al. 2022). Moreover, the pattern of niche conservatism documented across Icterid lineages (Eaton et al. 2008) could suggest that these range expansions in hidden rate class A occurred between ecologically similar environments, consistent with biome tracking hypotheses that might explain the family's southward expansion.

In hidden rate class B, the relationship between geography and diversification is qualitatively different and decoupled from the pattern in class A. North American endemics show near-zero cladogenetic rates while South American lineages showed comparable than class A North American lineages, and widespread lineages showed the highest cladogenetic rate of any state combination. Due to parametrization, widespread lineages turnover reflects rapid cladogenesis across all three ranges at once rather than a conventional high turnover cycle of speciation and extinction (Goldberg et al. 2011; Caetano et al. 2018). These lineages therefore split rapidly into endemic daughter lineages on each continent, a pattern that mirrors at the intercontinental scale the dominance of cladogenetic range-splitting documented across the whole Emberizoid passerines (Arango et al. 2025).

This contrast demonstrate that geography does not drive diversification in isolation. Instead, the same geographic area yields distinct diversification rates depending on the hidden regime of the lineage, indicating that geography merely contributes to a more complex rate structure. Importantly, the near-zero subsequent diversification of North American endemics in hidden rate class B does not reflect a geographic constraint on diversification in North America per se as the Nearctic clearly supported substantial diversification in rate class A. This pattern likely shows that lineages in hidden rate class B which happen to end up as North American endemics do not subsequently radiate (Caetano et al. 2018).

As such, mean speciation rates were comparable between continents, suggesting that both regions contributed substantially to overall clade richness, while the rate of lineage splitting in Icteridae is predominantly governed by an unmeasured biological axis that does not covariate with neither continent nor range size. This finding resonates strongly with recent work on the closely related Emberizoidea superfamily, which showed that broad geographic dispersal is not a diversification driver for the group, and that cladogenetic events occur primarily within bioregions rather than between them, suggesting that ecological opportunity, habitat specialization, and interspecific relationships within cohesive bioregions drive speciation more than dispersal events between regions (Arango et al. 2025). Specifically, ecological specialization has been identified as a significant positive predictor of speciation rates across Emberizoidea at continental scales, including Icteridae (Conway and Olsen 2019), while dispersal ability shows no significant relationship with speciation rates in the clade (Arango et al. 2026). Moreover, sexual selection through plumage and song divergence is recognized as a critical process for speciation (Higashi et al. 1999). Particularly in Icteridae and allied groups, it has been shown that color evolution and dichromatism might drive species cladogenesis (Friedman et al. 2009; Price and Eaton 2014). These lines of evidence point toward ecologically driven within-region speciation that could be mediated by feeding specialization, social behavior, and sexual selection as the most likely biological axis underlying the hidden diversification regimes recovered by GeoHiSSE, rather than any geographically structured process. Formally testing this hypothesis will require integrating these traits directly into future diversification analyses of Icteridae.

Taken together, these results suggest that Icteridae's diversification history was shaped by the interplay between geography-mediated colonization, regional ecological opportunity, and different macroevolutionary regimes. With the Nearctic providing an ancient source of deep early diversification (Arango et al. 2025), Mesoamerica acting as a dynamic filter, relay, and site of Plio-Pleistocene *in situ* diversification (Barber and Klicka 2010; Castillo-Chora et al. 2021), and the core Neotropical regions accumulating diversity through a combination of immigration and *in situ* speciation (Smith and Klicka 2010; Harvey et al. 2020). While the macroevolutionary results establish that the rate of diversification is primarily governed by something other than geography, with a secondary geographic component that is consistent with (but does not strongly drive) the continental patterns recovered by the BSMs. These results not only corroborate the origin of Icteridae posited by Barker et al. (2015) but also support Mayr's stepwise colonization hypothesis, though our findings indicate the colonization occurred in the inverse direction.

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Table 1: BioGeoBEARS model selection across the three dispersal hypotheses. LnL= log-likelihood; n= number of parameters; d= dispersal rate; e= extirpation (or local extinction rate); and j = jump dispersal rate. Best fit models for each hypothesis are highlighed.

Hypothesis	*Model*	*LnL*	*n*	*d*	*e*	*j*	*AIC*
Unconstrained	DEC	-373.6	2	0.087	0.16	0	751.2
	DEC+J	-373.4	3	0.095	0.2	1.00E-05	752.8
	DIVALIKE	-401.8	2	0.074	3.50E-08	0	807.6
	DIVALIKE+J	-399.5	3	0.07	1.00E-12	0.012	805.1
	BAYAREALIKE	-351.6	2	0.048	0.2	0	707.3
	BAYAREALIKE+J	**-348**	**3**	**0.033**	**0.16**	**0.011**	**702.1**
Adjacent	**DEC**	**-302.5**	**2**	**0.18**	**0.12**	**0**	**609.2**
	DEC+J	-302.1	3	0.16	0.065	0.024	610.4
	DIVALIKE	-319.6	2	0.17	1.00E-12	0	643.4
	DIVALIKE+J	-317.2	3	0.16	1.00E-12	0.032	640.7
	BAYAREALIKE	-318.7	2	0.069	0.14	0	641.5
	BAYAREALIKE+J	-308.3	3	0.11	1.00E-07	0.12	622.9
Gradual	DEC	-301.5	2	0.3	0.04	0	607.1
	DEC+J	**-298.3**	**3**	**0.36**	**0.12**	**0.064**	**602.9**
	DIVALIKE	-317.7	2	0.33	1.00E-12	0	639.5
	DIVALIKE+J	-314.7	3	0.31	1.00E-12	0.083	635.5
	BAYAREALIKE	-312.5	2	0.15	0.13	0	629.2
	BAYAREALIKE+J	-303.4	3	0.19	0.011	0.25	613

Table 2: Model selection of State-dependent Speciation and Extinction (SSE) models. Null is a model of diversification independent of geography; GeoSSE model is the canonical GeoSSE model where diversification is dependent of the geography; Hidden Null is a model where diversification is independent of the geography but related to unmeasured traits; and GeoHiSSE model, where diversification is affected both by the geography and an unmeasured trait.

model	*LnL*	*AICc*	*AICw*
Null	-300.10	606.44	5.84E-02
GeoSSE	- 298.45	607.52	4.00E-04
Hidden Null	- 294.22	599.06	0.026
GeoHiSSE	**- 284.62**	**594.12**	**0.97**

Table 2: Parameter estimates from the best-fit GeoHiSSE model (AICw = 0.97) for Icteridae. For each combination of geographic state and hidden rate class, turnover (τ = speciation + extinction) and extinction fraction (ε = extinction/speciation) are reported from the maximum likelihood solution. The speciation column (λ) reports model-averaged rates across all candidate models at the tips of the phylogeny, weighted by AICc weights, and represents the primary summary statistic for geographic diversification differences. NA = North America endemic; SA = South America endemic; WS = Widespread. Both hidden rate classes (A and B) are unobserved and unmeasured states estimated by the model; and do not correspond to the observed geographic distribution of species.

	Hidden Class Rate A		***Hidden Class Rate B***		
Region/Parameter	Turnover (τ)	Extinction fraction (ε)	Turnover (τ)	Extinction fraction (ε)	Speciation (λ)
NA Endemic	0.40	7.24E-08	2.06E-09	7.24E-08	0.213
SA Endemic	0.08	7.24E-08	0.41	7.24E-08	0.292
Widespread	0.48	—	7.74	—	0.248

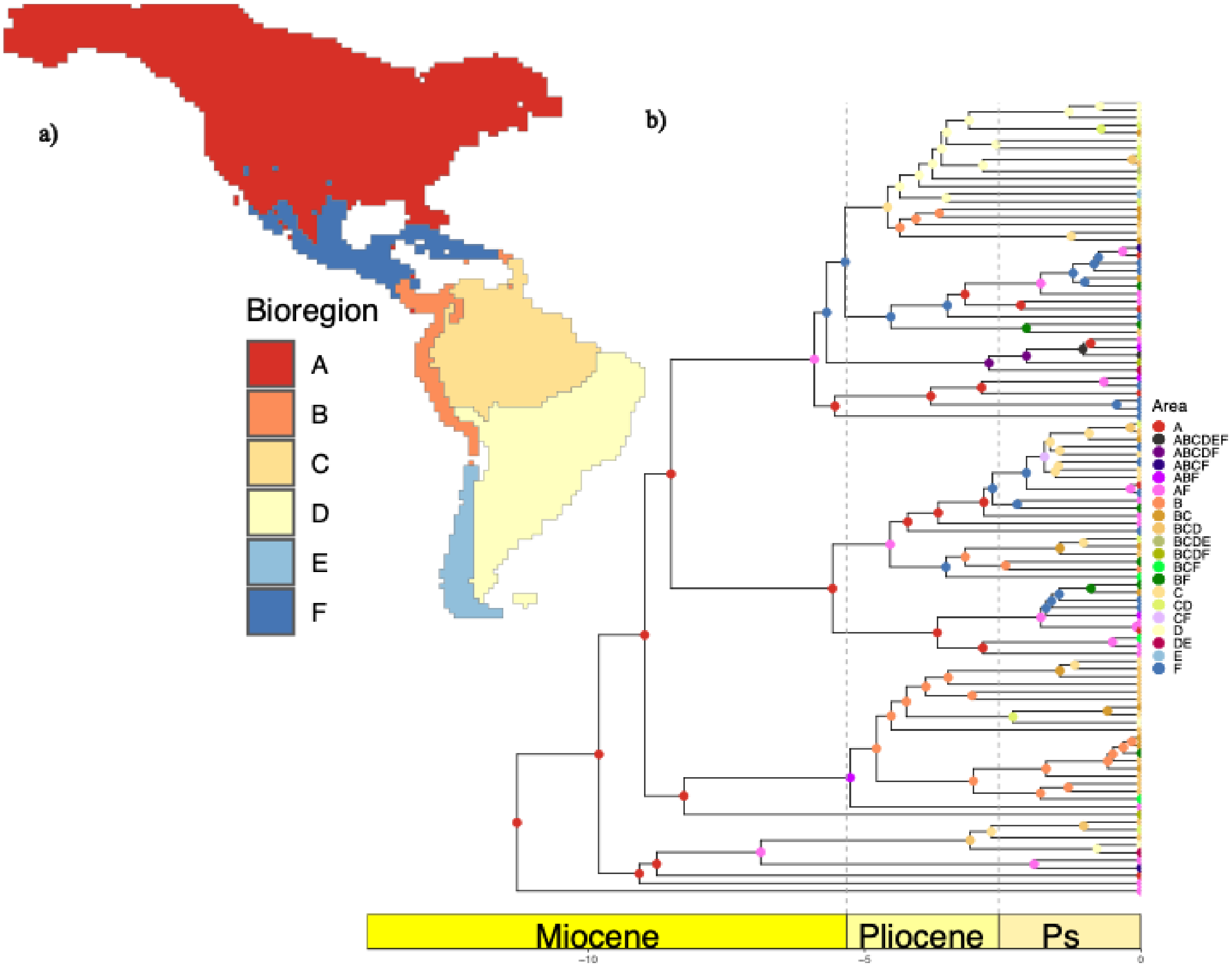

Figure 1: a) Bioregionalization of Icteridae according to the phylogenetic distance clusters provided by non-metric multidimensional scaling (NMDS). Nearctic (A); Ithsmus-Andes (B); Amazonas (C); Southern South America (D); Patagonia (E); Mesoamerica (F). b) Most probable ancestral state estimates under gradual DEC+J model (dispersal = 0.36, extinction = 0.12, j = 0.064, log-likelihood (LnL) = −298.3) on the Icteridae. Colors with single letters correspond to bioregions from a), while colors with multiple letters represent an area resulting from the combination of the said bioregions (e.g. AF represents a region formed by the Nearctic and Mesoamerica); Ps= Pleistocene.

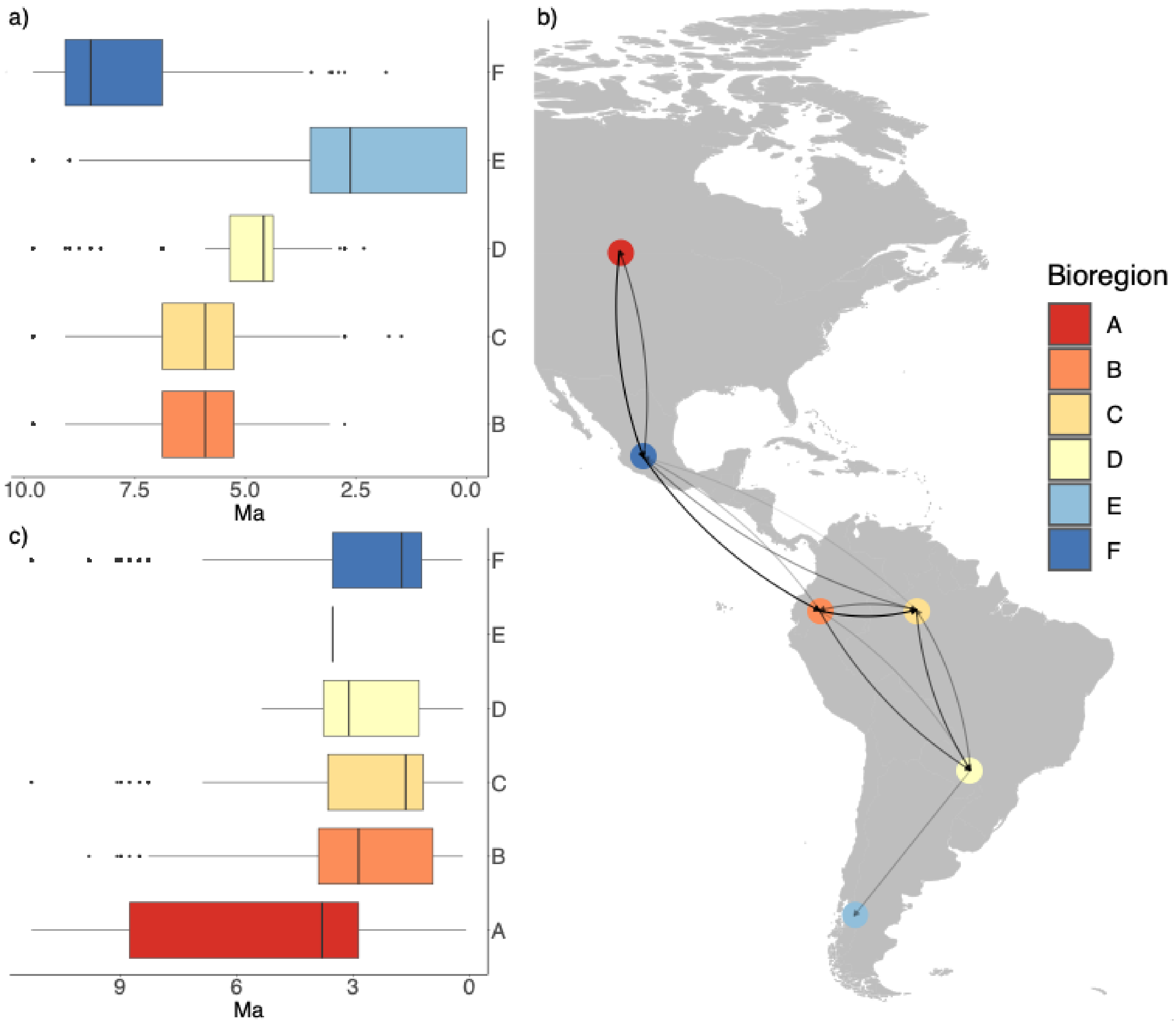

Figure 2: a) Timing of first colonization events for each region (except for ancestral region A) according to the 1000 BSMs; B (median= 5.91 Ma [IQR=5.26; 5.88]); C (median= 5.91 Ma [IQR= 5.26; 6.88]); D (median= 4.59 Ma [IQR= 4.37; 5.35]); E (median= 2.62 Ma [IQR=0; 3.53]); F (median=8.5 Ma [IQR=6.88; 9.08]). b) Dispersal direction and intensity between regions, according to the mean number of dispersal events per region, averaged using the 1000 BSMs, bolder arrows indicate higher intensity (see table S8-9). c) Distribution of *in situ* speciation events timing per region, calculated by the 1000 BSMs; A (median= 3.8 Ma [IQR= 2.86; 8.76]); B (median= 2.86 Ma [IQR= 0.94; 3.86]); C (median= 1.65 Ma [IQR= 1.20; 3.65]);

D (median= 3.11 Ma [IQR= 1.3; 3.67]); E (median= 3.53 Ma [IQR= 3.53; 3.53]); F (median=1.75 Ma [IQR= 1.23; 3.53]).

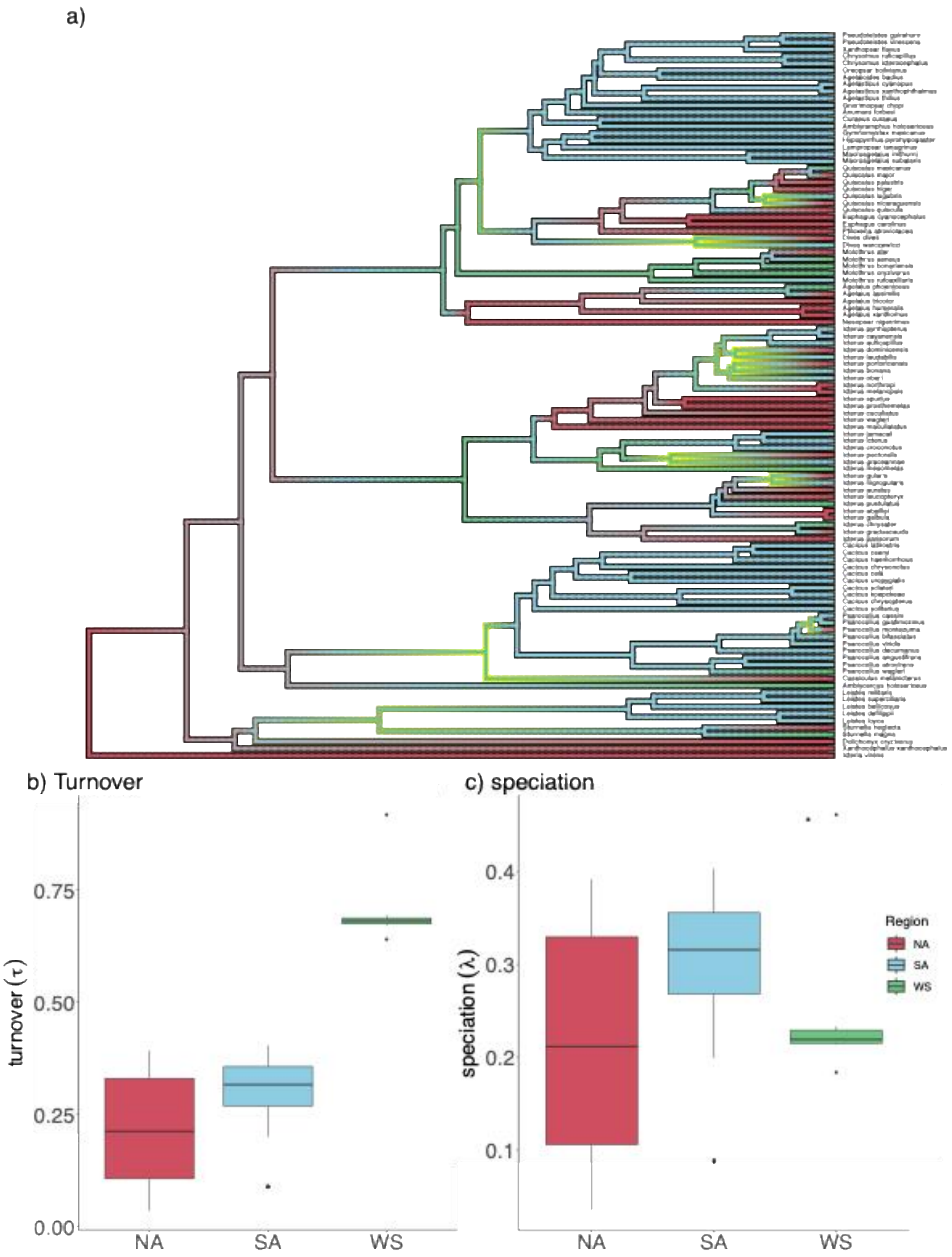
a)
b) Turnover
turnover (τ)
0.00
0.25
0.50
0.75
NA
SA
WS
c) speciation
speciation (λ)
0.1
0.2
0.3
0.4
NA
SA
WS
Region
NA
SA
WS

Figure 3: a) Marginal reconstruction of geographic states mapped onto the Icteridae phylogeny, with branch colors indicating the most probable geographic state at each node and tip: red = North America endemic, blue = South America endemic, green = widespread (present in both regions). Branch color intensity reflects the marginal probability of the most probable state, with more saturated colors indicating higher confidence. Yellow branch outlines indicate lineages with higher model-averaged speciation rates. b) Distribution of model-averaged turnover rates (τ) across tips grouped by geographic state (NA = North America endemic, SA = South America endemic, WS = widespread). c) Distribution of model-averaged speciation rates (λ) across tips grouped by geographic state.