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Broad geographic dispersal is not a diversification driver for Emberizoidea

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The movement of species to new geographical areas has been proposed to be crucial for speciation. As such, dispersal has been regarded as a likely explanation for the variation in species richness among clades. The Emberizoidea are a highly diverse Oscine bird clade native to the New World that has been characterized for their ubiquitous distribution both ecologically and geographically, making this group ideal to test how biogeographical dispersal could promote speciation. To do so, we relate dispersal rates with speciation rates of Emberizoidea families using a combination of bioregionalization analysis, ancestral area reconstruction and speciation rate estimation methods. We found that the Emberizoidea superfamily likely arose from a widespread ancestor distributed over the New World, with its range evolution being primarily driven by range contraction and the main cladogenetic events for the clade occurring within bioregions. Moreover, we demonstrate that dispersal rates between bioregions showed no relationship with speciation rates, suggesting that the movement to new geographical spaces is not a driver of speciation in this group. Instead, cladogenetic events within individual bioregions promoted by range stability prove to be an important driver for speciation at broad spatial scales for Emberizoidea families.

1. Introduction

Species richness varies across geographical space, evolutionary time and among lineages [1]. Indeed, different regions have different numbers of species, these numbers have changed through time and some lineages are more species-rich than others. Understanding the causes driving such variation has been of interest to biologists for decades [2]. Ultimately, this spatial, temporal and phylogenetic variation in species richness is the result of differences in the net diversification rates—the balance between speciation and extinction—biogeographical dispersal between regions, and differential age of clades when these have the same diversification rate (i.e. same rate of speciation and extinction [3–5]). In addition to these fundamental processes, species richness variation can also result from dispersal of lineages to different regions, adding more species to new regions via range expansion or reducing the species richness from the source regions via range contraction [6,7].

Differential diversification among lineages has been suggested to result from the effect of facing different environments, often following dispersal events to novel geographical areas, allowing posterior adaptation to new environmental conditions [8–10]. Thus, speciation could be triggered by such dispersal events, where populations become geographically isolated from one another and might experience divergence facilitated by the availability of novel ecological opportunities [11] or neutral drift [12]. This suggests a close relationship between dispersal and speciation, where the arrival of species to novel areas is crucial for promoting lineage diversification [4,13]. In fact, it has been proposed that the majority of speciation events might occur shortly after the establishment of a lineage in new environments following dispersal events, mainly owing to high ecological opportunity [14]. Such ecological opportunity can result from either a lack of competitors or, more likely, the existence of novel resources/ecological spaces not exploited/occupied by already established competitor species [10], reducing competition and providing high resource availability, which facilitates rapid speciation and specialization [15]. Moreover, dispersal events can relieve species from diverse stressors such as parasites and competitors [16], and expose them to contrasting landscapes and topography within which they can diversify [17]. Thus, it is assumed that lineage dispersal would have a considerable impact on their diversification [18]. Alternatively, speciation rates could increase following ecological release within a region and without the need of dispersal events to new regions. In this case, ecological release could be achieved by novel uses of an already developed adaptation [11] or by the development of key adaptations [19] as a result of ecological specializations, derived from either continuous adaptation to stable regions [20] or competition diffusion [21]. Moreover, restricted dispersal could also lead to hybridization, which has been suggested to allow species to rapidly explore new adaptive landscapes, inducing bursts of speciation [22].

Given that variation in dispersal events of lineages may naturally influence their speciation rates [8,23], the movement of organisms and their successful establishment across geographical boundaries would be an important incentive for their diversification [24]. Large geographical areas are usually delimited by such geographical boundaries, within which lineage composition reflects the historical processes that have moulded biodiversity's distribution, defining the so-called bioregions [25]. Consequently, biogeographical regionalization has often used both ecological and historical relationships of extant species for its construction [26–28]. In recent years, the increasing availability of molecular phylogenies has paved the way for using phylogenetic information when creating bioregions (i.e. phylogenetic bioregionalization [29]). These methods can help reveal biodiversity's spatial and evolutionary structure [30,31], by identifying phylogenetically distinct biogeographical units resulting from the evolutionary processes (speciation, extinction, dispersal and niche conservatism) that determine the formation of species assemblages [29].

Both restricted dispersal and high dispersal to new bioregions have been proposed as drivers of speciation within clades by promoting local specialization and adaptation to novel ecological opportunities, respectively [32]. However, there has been more support for the possibility that range expansions resulting from high dispersal abilities are the main driver of diversification over large areas [24]. This support arose from an increasing number of studies proposing that colonization has been the main cause of diversification for continental and insular landmasses [23,24,33–37]. Evidence suggests that if lineages differed in their dispersal and colonization opportunities of different bioregions, these differences would be reflected in their speciation rates and geographical extension [18,38,39], explaining the dissimilarity in species richness within clades [24].

Birds vary widely in their capacity to disperse to and colonize new geographical spaces [40]. Some species can perform long uninterrupted seasonal displacements over broad areas, whereas others are incapable of traversing forest gaps or even small water bodies, which consequently affects their propensity for dispersing to new geographical areas [24,32,41]. Considering that the frequency and speed at which bird lineages spread to new regions could significantly influence their diversification, the varying dispersal abilities among species could lead to distinct opportunities for dispersal events [32,42,43]. Therefore, these differences in dispersal could explain the distinct diversification patterns and resulting species richness differences among bird lineages.

Here, we evaluated the influence of lineage dispersal between different biogeographical regions on the speciation patterns of the Emberizoidea superfamily. Our main hypothesis was that differences in dispersal events and resulting colonization of new regions among emberizoid lineages would explain their distinct speciation rates and resulting species richness patterns. Specifically, we were interested in whether lineages that successfully moved into new biogeographical regions experienced higher rates of speciation than those confined to their ancestral regions and if other factors, such as range evolution, have influenced the current diversity patterns within this superfamily. By investigating this relationship, we aimed to uncover whether dispersal had played a crucial role in driving the speciation processes of these birds.

We focused on the Emberizoidea clade given its high species richness, being the second most species-rich bird clade native to the New World (*ca* 832 species [44]) after the suboscine radiation of the tyrannids, wide distribution, as well as varied dispersal abilities among its lineages, which have been the subject of previous phylogenetic and biogeographical studies for the whole clade and particular taxonomic families [44–46]. The Emberizoides are hypothesized to have originated in North America, after the dispersal of the clade's ancestor from Asia through the Beringia land-bridge [44,47]. Some emberizoid lineages returned to the Old World, where they established in Eurasia and Africa. In contrast, the most diverse South American lineages were likely derived from gradual range expansions from North America [44], suggesting multiple colonization events and distinct dispersal opportunities among lineages (families) within the emberizoid clade. This speciose clade has a global distribution, and its species occur over varied environments and geographical settings [44,48–51], making the Emberizoidea an excellent clade to test the effects of biogeographical dispersal on speciation.

2. Methods

(a) Phylogenetic and geographical data

We obtained geographical distributions of emberizoid species from the BirdLife International range maps [52], comprising 705 out of the 835 recognized species according to the Clements checklist [53]. Range maps for 130 species were not available given lack of data or protected data for endangered species. We acquired phylogenetic relationships of 795 species of the Emberizoidea superfamily from the maximum credibility clade (MCC) phylogeny of Barker *et al*. [44], pruned to match those species with distribution maps, resulting in a total of 705 (84.4%) species with both phylogenetic and geographical information.

(b) Biogeographical regionalization

To delimit the biogeographical regions for Emberizoidea, we applied a phylogenetic regionalization. This method allows identifying evolutionarily distinct biogeographical regions by considering the evolutionary relationships of species among assemblages [29]. These regions can later be used to reconstruct the biogeographical history of a clade across them, mainly because the current occupation of such regions can result from different histories dictated by evolutionary processes (e.g. cladogenetic and anagenetic events of dispersal and range evolution) that are not directly evaluated when delimiting such regions [29] but require additional methods to reconstruct such biogeographical history (see §2c). To conduct the regionalization, we first transformed the distribution maps into a 1° × 1° presence–absence matrix, using the species' breeding ranges. Then, we used Simpson's phylogenetic index of dissimilarity ($p\beta_{\mathrm{sim}}$) to calculate phylogenetic turnover between assemblages [54]. The $p\beta_{\mathrm{sim}}$ metric quantifies the phylogenetic turnover of shared branch lengths within assemblages and is commonly used in biogeographical regionalization given its independence from species richness variation [25,29]. We assessed several clustering algorithms to choose the best algorithm describing the phylobeta distance matrix, evaluated using the cophenetic correlation coefficient [29,55]. The algorithms tested included complete linkage, unweighted pair-group method using averages (UPGMA), unweighted pair-group method using centroids (UPGMC), weighted pair-group method using averages (WPGMA), weighted pair-group method using centroids (WPGMC), Ward's minimum variance, and divisive hierarchical method of divisive analysis (DIANA). We used the 'elbow' method [56] to determine the optimal number of clusters (k) that allows the best depiction of the observed phylogenetic matrix [29,57]. Although the selection of clusters has appeared to be mostly arbitrary [58], the 'elbow' method allows a more objective selection by providing the optimal point given the variance of the phylogenetic distance matrix explained by k [29]. This optimal point is achieved when the explained variance does not significantly increase with additional number of clusters [56]. Finally, we computed a non-metric multidimensional scaling (NMDS) using the phylogenetic distance among grid-cells calculated with the optimal clustering algorithm (UPGMA) and the chosen k-value to assemble distinct biogeographical regions for the Emberizoidea superfamily, resulting in geographically cohesive units of phylogenetically distinct assemblages maximizing the contribution of *in situ* speciation relative to dispersal [24,29]. These phylogenetically informed biogeographical regions consistently corresponded to other bioregions for different clades and areas, effectively capturing and uncovering evolutionary information from biogeographical regions used previously—such as Wallace's [54] and others [24,59]. The workflow to construct such biogeographical regions was achieved using the 'phyloregion' package [57] for the computational language R v. 3.6.3 [60].

(c) Ancestral area reconstruction and transition rates

We used the previously delimited biogeographical regionalization to evaluate distinct models of ancestral area reconstruction employing the BioGeoBEARS R package [61]. The evaluated models were Bayesian approximations of those most commonly used for ancestral reconstruction representing different biogeographical histories (DEC, DIVA and BAYAREA [61,62]; electronic supplementary material, figure S4.6). We also included a parameter that allows founder event speciation in these models (represented as +J on the models). This resulted in six alternative models: DEC, DEC+J, DIVA, DIVA+J, BAYAREA and BAYAREA+J. After calculating the log-likelihood scores of the models, we used the Akaike information criteria (AICs) to select the best-fitting one. Afterwards, we determined the probabilities of the regional states for the phylogeny [61,62]. While it has been proposed that model selection in BioGeoBEARS might be subject to bias with the inclusion of the +J parameter [63], its inclusion for comparison with pure anagenetic dispersal models remains supported [64], and has been employed to investigate the role of dispersal in macroevolutionary dynamics (see electronic supplementary material figure S4.8; table S4.9) [65]. Furthermore, given that Emberizoidea species have high dispersal abilities, especially the species that diverged earlier from the clade, such as the members of Calcariidae and Rhodinocichlidae [66], we opted to run all models unconstrained (i.e. without including a distance-dependent parameter).

To determine the dispersal and historical colonization of the taxonomic families of Emberizoidea, we conducted a stochastic biogeographical mapping (SBM) of 1000 replicates using the selected ancestral reconstruction model. Using the SBMs, we identified the nodes having well supported biogeographical shifts (dispersal events), taking into consideration only those that appeared in more than 75% of the stochastic mappings and did not belong to transitions at the tips. In addition, transition events (i.e. the number of transitions within and among ancestral areas of the clade, TEs). These TEs were estimated by obtaining the mean number of events per family of Emberizoidea for the 1000 SBM replicates. The main events calculated were anagenetic dispersal (dispersal TE) and range contraction (range contraction TE).

(d) Diversification dynamics

We estimated the Emberizoid variation in speciation rates for each family of Emberizoidea using Bayesian Analysis of Macroevolutionary Mixtures (BAMM) v. 2.5 [5]. BAMM uses an algorithm to explore different diversification models with varying rates of speciation and extinction known as 'reverse jump Markov chain Monte Carlo' (RJMCMC). Using the RJMCMC, BAMM generates a posterior distribution of tip-level (species) speciation and extinction rates that are continuous throughout the phylogeny, allowing the identification of potential evolutionary rate shift scenarios (defined as a clade that shares rates of speciation and extinction that fluctuates from the posterior distribution). These rate shift scenarios are sampled in the proportion of posterior probability of shifts obtained through RJMCMC, and have been found in some cases to be extremely sensitive to the prior expected shifts [67]. We tested the sensitivity of our data to different values of the prior expected number of changes (1, 5, 10 and 50), finding that the posterior probability of shifts was highly consistent regardless of the prior. We used the BAMMtools R package [68] to estimate the priors for lambda (λ) and mu (μ) before executing the RJMCMC for a total of 10 000 000 generations on the Barker *et al*. [44] pruned MCC Emberizoidea tree, considering a sampling fraction of 0.84. Following the chain convergence confirmation, we removed the first 10% of samples as burn-in. We determined the most probable rate shifts through sampling by determining the rate shift configurations that were recovered in >25% of the samples. Afterwards, we calculated the mean speciation rate for the samples with the most probable rate shifts as identified by BAMM.

We chose BAMM as our speciation rate estimator because it considers speciation rate variation within clades unlike other estimators such as the Method of Moments (see electronic supplementary material table S3.6) [69]. BAMM also allows the detection of rate shifts over time which can be linked to possible dispersal events. Recently, there has been a concern about the identifiability of diversification parameters using molecular phylogenies [70], where multiple combinations of speciation and extinction rates over time can result in the same observed diversification pattern. However, BAMM is still a viable approach because it relaxes the assumption that all lineages share the same evolutionary rates at a given time and allows for lineage-dependent rates. While Louca & Pennell [70] are concerned with estimating exact, identifiable values of diversification rate parameters, BAMM's goal is often to determine whether one lineage is diversifying faster than another. While it can still be affected by the identifiability issues of the exact rate parameters estimation, its use is still valuable to compare speciation rates among lineages within a larger clade, making it an appropriate approximation for our study [71,72].

Finally, we used the previously calculated mean speciation rates to define an average speciation rate for each emberizoid family. Speciation rates summarized at a higher taxonomic level, such as families, can inform our understanding of evolutionary patterns and processes shaping different lineages, and in our case, this approach allowed us to draw comparisons with other studies addressing diversification dynamics at the same taxonomical level [45,59,73], while also allowing exploring of the influence of factors such as historical dispersal and range dynamics on the speciation patterns of such lineages.

(e) Dispersal as driver for speciation

To test if dispersal events were related to the speciation dynamics of Emberizoidea, we compared the lineages that presented well supported dispersal events to a different bioregion with contemporary lineages that did not. To do so, first we used the nodes that presented well supported dispersal events according to the SBMs. Then, for each of these 'focal' nodes, we excluded its descendant and parent nodes and identified other nodes with similarly dated divergence times using an interval of 1.863 million years (average time for cladogenesis in Emberizoidea) and that did not present well supported dispersal. For each of these nodes, including the focal one, we obtained its average speciation rate as follows: the immediate branch length after the cladogenetic events (nodes) was drawn proportional to its marginal speciation rate and this branch length was averaged across the posterior distribution of BAMM estimates. Finally, we compared the average speciation rate of each focal node with the distribution of speciation rate values from the similarly aged nodes using a one-tailed test.

Lastly, we performed two phylogenetic generalized least squares (PGLS) models using families as our units to test the relationship between dispersal and range contraction events with the speciation rates among these monophyletic lineages. Since these lineages (families) are phylogenetically related, using PGLS models allowed us to explicitly consider the phylogenetic non-independence among observations (here families) and avoid type 1 errors. In the first model, we examined the influence of dispersal (dispersal transition rate; dTr) on speciation rates. In the second model, we explored the effect of local extinction or range contraction (range contraction transition rate; eTr) on speciation rates. In both PGLS models, we controlled for phylogenetic nonindependence among families using a pruned version of the Barker *et al*. [44] MCC containing only one representative of each family. We estimated rates for both events: dispersal transition rate (dTr) and range contraction transition rate (eTr) were estimated using the TEs spanning from the most common ancestor and divided by the total number of evolutionary events of each Emberizoidea family. In this case, the dispersal transition rate (dTr) could be interpreted as the number of times any lineage in each family had a dispersal movement across bioregions (e.g. transitions from region A to B) according to the stochastic mappings. Likewise, the range contraction transition rate (eTr) could be interpreted as the number of times any lineage in each family was extirpated from a bioregion because of local extinction (e.g. the transition from region AB to B).

3. Results

(a) Biogeographical regionalization of Emberizoidea

The best clustering algorithm representing the phylogenetic turnover among assemblages was UPGMA (electronic supplementary material, table S1.1). The optimal number of clusters (*k*) was 8, based on its convergence and low levels of stress (0.008) suggesting well supported clusters (electronic supplementary material, table S1.2). The NMDS ordination, therefore, defined eight global regions of the Emberizoides (electronic supplementary material, figure S1.1). The New World was divided into four distinct regions: North America (B), middle-America (F), eastern South America (G) and western South America (H). The Old World was divided in three distinct regions: Eurasia (C), South Asia (D) and Africa (E). In contrast, the Arctic (A) region occurred in both the New and the Old Worlds (figure 1*a*).

(b) Ancestral area reconstruction

The results of the different models for ancestral area reconstruction using the eight bioregions showed that the BAYAREA+J model received both the lowest AIC score and the highest likelihood ratio (table 1). This model assumes that cladogenetic events are explained by the result of within-region speciation and range evolution as an anagenetic event via dispersal or range contraction (see electronic supplementary material, figure S2.2; S2.3; S2.4). Based on this selected model, we found that Emberizoidea exhibited two main biogeographical histories: (i) widespread common ancestors in the New World for the whole clade and most families, where range contraction produced by local extinction drove range evolution, and (ii) an early jump dispersal from the New World to the Old World in the crown of Emberizidae, with an ancestral area for this family comprising Eurasia, South Asia and Africa (region CDE).

The most recent common ancestor of the Emberizoidea is suggested by the BAYAREA+J model to have inhabited a wide area ranging from the Arctic and North America to south Patagonia, comprising the whole of the New World bioregions (ABFGH), where range contraction produced by local extinction seems to have driven speciation (figure 1*b*). A similar pattern of a widespread ancestor was observed for most emberizoid families, although covering a slightly smaller area than the ancestor of the superfamily. Within the New World clades, the model results indicate that Rhodinocichlidae originated in an area comprising current North America, middle-America, and eastern South America (region BFG). Calcariidae likely originated in an area comprising the Arctic and North America regions (region AB). The clades Cardinalidae, Thraupidae, Passerellidae, Parulidae and Icteridae appear to have originated in the area comprising most of the New World except the Arctics (region BFGH). The clades Phaenicophilidae, Spindalidae and Icteriidae wereare associated with origins in the areas comprising North America and middle-America (region BF). The clade Zeledoniidae likely originated in middle-America and eastern South America (region FG). Nesospingidae, Teretistridae and Calyptophilidae originated entirely from middle-America (F). Finally, the Mitrospingidae ancestral area is likely the eastern South American region (G; table 2). Notably, excluding the only Old World lineage (Emberizidae) from the regionalization and ancestral area reconstruction did not alter the results, as the reconstructed areas for all clades (superfamily and the other families) remained consistent (see electronic supplementary material, figure S4.7; table S4.8).

Using the stochastic mappings (SBMs), we found seven well supported dispersal events for the Emberizoidea superfamily (figure 2*a*). The most frequently recovered dispersal event belonged to the Emberizidae family crown (node Z), with a movement from the New World (ABFGH) to the Old World (CDE). The other six well supported dispersal events belong to: the *Setophaga striata*, *Setophaga pensylvanica*, *Setophaga petechia* common ancestor (node T), which showed a dispersal event and range expansion from North and middle-America (BF) to the Arctics (ABF); the common ancestor of *Setophaga delicata, Setophaga subita* (node U), which is suggested to have dispersed from middle-America (F) to eastern South America (G); the common ancestor of *Tangara florida*, *Tangara icterocepahala* (node V), with a dispersal event and range expansion from South America (GH) to middle-America (FGH); the common ancestor of *Tangara gyrola* and *Tangara lavinia* (node W), with a dispersal event and range expansion from South America (GH) to middle-America (FGH); the common ancestor of *Diglossa baritula* and *Diglossa plumbea* (node X), with a dispersal event and range expansion from South America (GH) to middle-America (FG); and the common ancestor of *Sporophila hypoxantha*, *Sporophila palustris* and *Sporophila ruficollis* (node Y), with a dispersal event and range expansion from eastern South America (G) to western South America (GH).

Results from the SBMs also showed that all emberizoid families had low dispersal transition rates (dTr; electronic supplementary material, table S2.3). As expected from the BAYAREA models which penalize range expansion in favour of range inheritance, all dispersal events were anagenetic, occurring along the branches of the lineages rather than through splitting (cladogenetic) events. Among these families, the highest dTr was shown by the oldest families of Emberizoidea: Calcariidae and Rhodinocichlidae. The lowest dTr values were shown by Thraupidae and Phaenicophilidae, most likely owing to their relatively stable ranges. Thraupidae remained constrained to South America, whereas Phaenicophilidae remained in middle-America.

The range contraction transition rate (eTr) was generally high among the Emberizoidea families (electronic supplementary material, table S2.4). Given range inheritance being prioritized by the BAYAREA+J model, small ancestral areas can only be possible by range reduction due to local extinction. Accordingly, the high eTr present in most low diversity (less than four species) families (Spindalidae, Nesospingidae, Zeledoniidae, Teretistridae, Mitrospingidae and Rhodinocichlidae) can be explained by their restricted ancestral areas. The remaining monospecific family Icteriidae did not present a high eTr, perhaps owing to its more extensive ancestral area (middle-America and North America). The species-rich Thraupidae family had the lowest eTr, providing further evidence of this family's range stability.

(c) Diversification dynamics

The BAMM posterior samples showed four potential speciation shifts in more than 25% of the samples. These most probable shifts occurred as an increase of speciation rates in the crown of Icteridae, Icteriidae and Parulidae; in the passerellid genus *Atlapetes*; and in *Sporophila* and *Geospiza* within Thraupidae (figure 2*a*). The superfamily showed an overall decrease in its speciation over time (figure 2*b*), with a mean speciation rate of $\lambda = 0.22$ species per million years. The families with the highest mean speciation rates were Icteriidae ($\lambda = 0.271$), Icteridae ($\lambda = 0.265$) and Parulidae ($\lambda = 0.264$), given by the speciation shift at the node of the common ancestor of these families, which showed an accelerated rate. In contrast, Phaenicophilidae ($\lambda = 0.108$), Emberizidae and Cardinalidae families showed the lowest mean speciation rates ($\lambda = 0.107$; table 2; electronic supplementary material table S3.5).

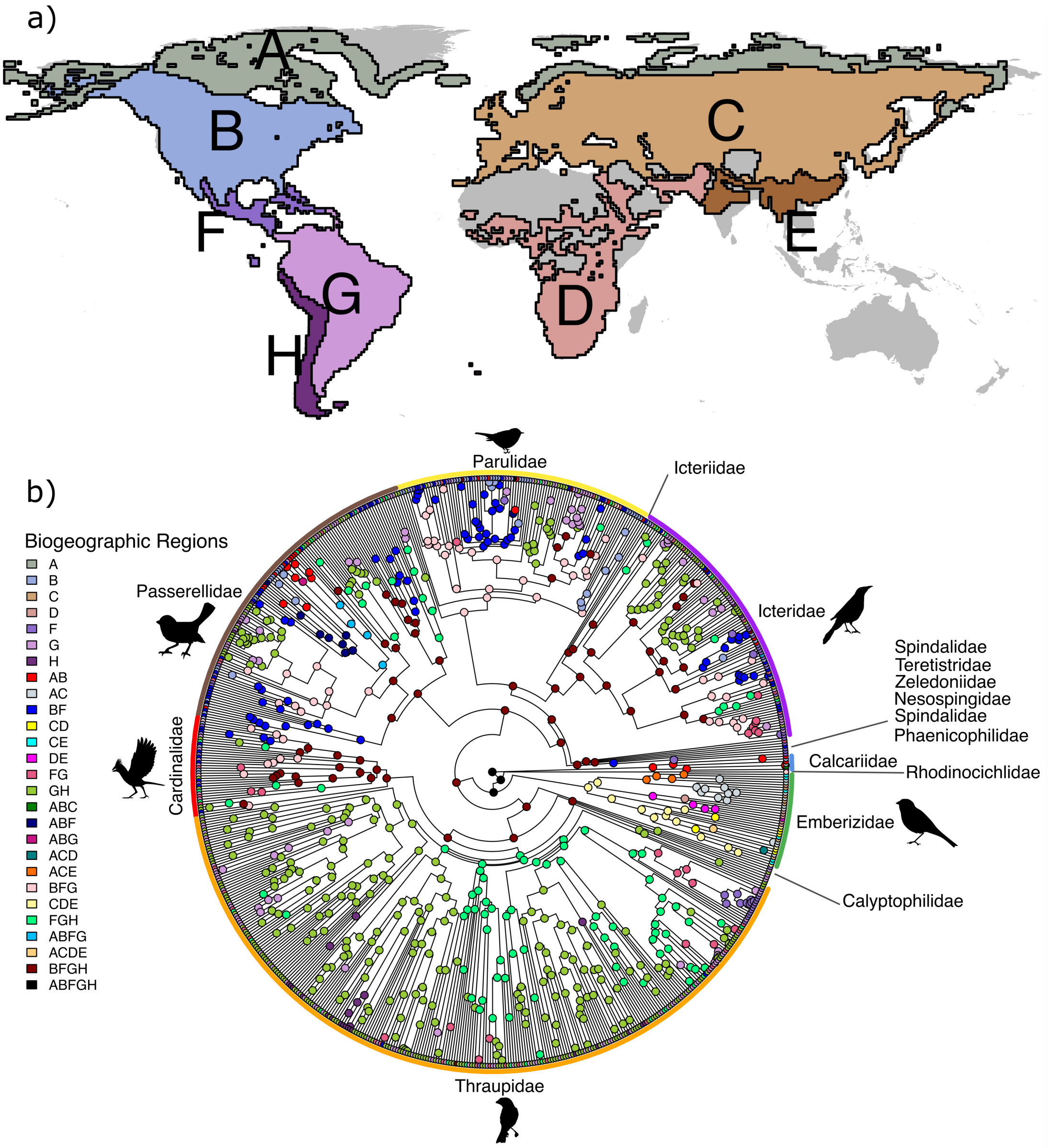

Figure 1. (a) Emberizoid bioregionalization according to the phylogenetic distance clusters provided by non-metric multidimensional scaling (NMDS). A, Arctic; B, North America; C, Eurasia; D, Africa; E, South Asia; F, middle-America; G, eastern South America; H, western South America. (b) Most probable global ancestral state estimates under unconstrained BAYAREA+J model (dispersal = 0.0022, extinction = 0.087, *j* = 0.004, log-likelihood (LnL) = −1698) on the Emberizoidea superfamily. Colours with single letters correspond to bioregions from (*a*), while colours with multiple letters represent a region resulting rom the combination of the said bioregions (e.g. AB represents a region formed by the Arctic and North America).

Table 1. BioGeoBEARS model selection; LnL = log-likelihood; *n* = number of parameters; *d* = dispersion; *e* = extinction, *j* = jump dispersal.

model	LnL	*n*	*d*	*e*	*j*	AIC	AIC_wt
DEC	−2198	2	0.01	0.01	0	4399	2.80×10^{-217}
DEC+J	−2085	3	0.019	1.00×10^{-12}	0.0003	4179	1.00×10^{-168}
DIVALIKE	−2224	3	0.022	1.00×10^{-12}	0.0019	4453	5.30×10^{-229}
DIVALIKE+J	−2224	3	0.022	1.00×10^{-12}	0.0019	4453	5.30×10^{-229}
BAYAREALIKE	−1702	2	0.0022	0.089	0	3408	0.063
BAYAREALIKE+J[a]	−1698	3	0.0022	0.087	0.0004	3402	0.98

[a] Best model according to LnL and Akaike information criterion.

(d) Dispersal as driver for speciation

We found that none of the nodes that presented well supported dispersal events had higher speciation rates than other nodes with similar divergence dates and that did not present dispersal events (electronic supplementary material, figure S5.9). Moreover, most observed speciation rates of dispersed lineages were consistently lower than the mean speciation rate of the

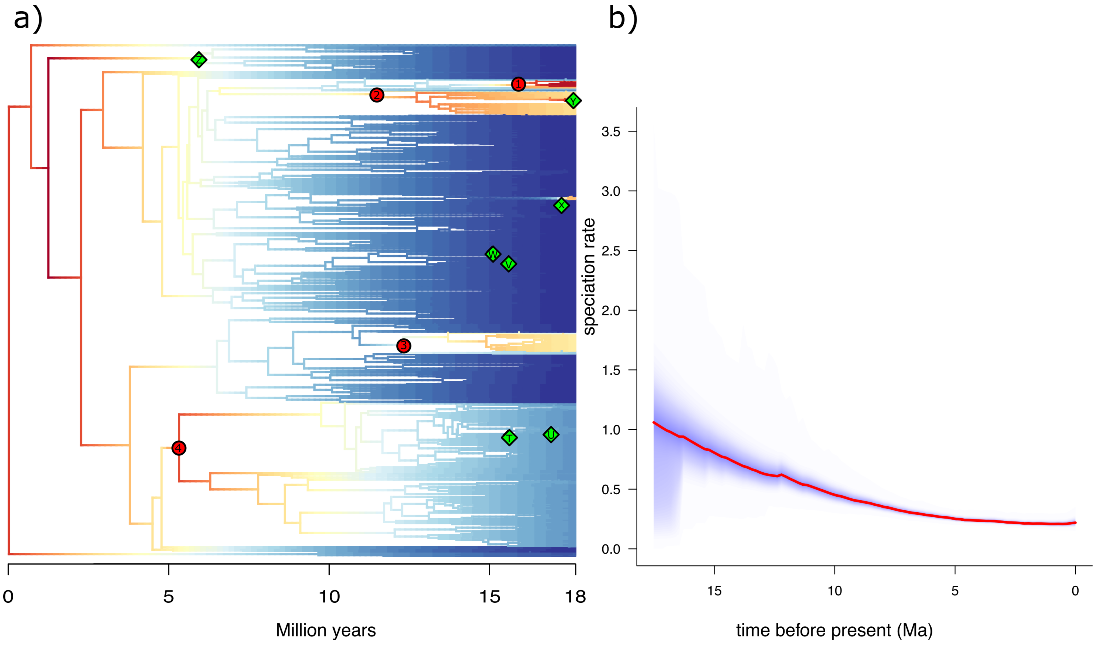

Figure 2. (a) Speciation rates of the maximum credibility clade Emberizoidea tree. Warmer colours indicate accelerated rates, whereas colder colours represent decelerated rates. Red circles represent the most probable speciation rate shifts ($f > 0.25$); speciation rate shifts of (1) *Geospiza*, (2) *Sporophila*, (3) *Atlapetes* and (4) Icteridae–Parulidae crown. Green diamonds represent focal nodes that showed consistent dispersal in the SBMs, with their respective letters. (b) Speciation over time of the Emberizoidea clade, showing a constant decrease in speciation. Speciation rate is indicated as the number of speciation events per million years.

Table 2. Most probable ancestral areas, the marginal probability of the said areas, the crown age and average speciation rate (mean λ) for the Emberizoidea clades.

clade	most probable ancestral area	probability	approx. crown age (Ma)	mean λ
Emberizoidea	ABFGH	0.543	17.51	0.22091
Rhodinocichlidae	BFG	1	16.83	0.2058978
Calyptophilidae	F	1	14.16	0.12749132
Thraupidae	BFGH	0.853	13.37	0.21949153
Mitrospingidae	G	1	12.43	0.1115978
Teretistridae	F	1	11.89	0.11411857
Zeledoniidae	FG	1	11.89	0.11327628
Spindalidae	BF	1	11.37	0.11025294
Nesospingidae	F	1	11.37	0.11026345
Icteriidae	BF	1	11.29	0.27120057
Cardinalidae	BFGH	0.962	11.2	0.10742496
Passerellidae	BFGH	0.956	11.1	0.23205014
Phaenicophilidae	BF	0.195	10.27	0.10838138
Emberizidae	CDE	0.37	10	0.10747028
Icteridae	BFGH	0.989	9.8	0.26560809
Calcariidae	AB	0.72	7.94	0.16174875
Parulidae	BFGH	0.808	7.85	0.2649963

lineages without dispersal (electronic supplementary material, table S5.10). According to the BAYAREA+J model, the PGLS indicate that the association between dispersal rates (dTr) and speciation rates was not significant ($R^2 = 0.0$, $p = 0.636$, $\lambda = 0$; figure 3*a*). However, the PGLS where eTr predicted speciation showed a significant negative relationship ($R^2 = 0.339$, $p < 0.05$, $\lambda = 1$; figure 3*b*; electronic supplementary material table S3.7)—suggesting that range stability might be a potential driver for speciation and thus diversification in Emberizoidea.

5. Discussion

This study challenges the previous hypothesis that the Emberizoidea superfamily originated in North America and subsequently dispersed to other regions, leading to its diversification [44]. Contrary to our hypothesis and earlier research, our

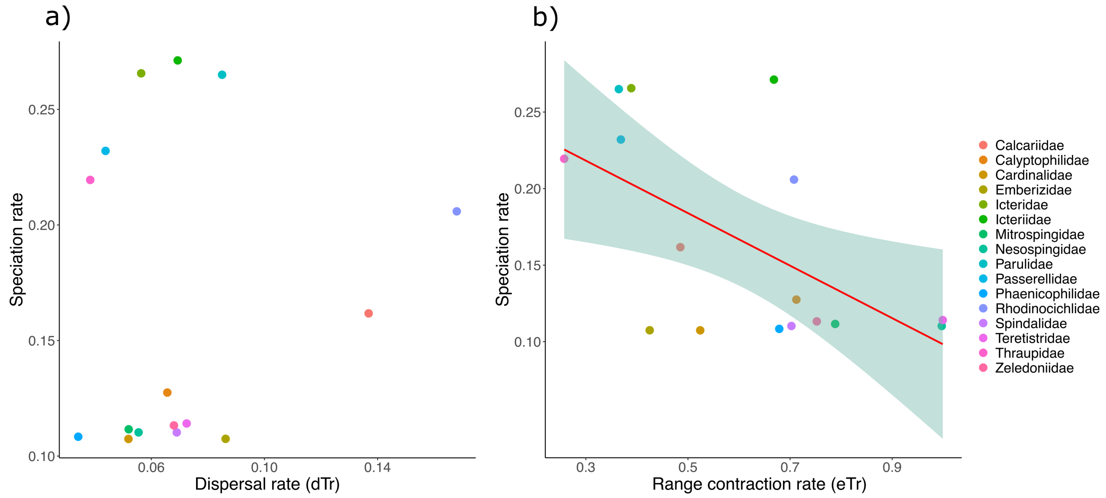

Figure 3. BAMM mean speciation rate for each family of Emberizoidea plotted against (*a*) dispersal transition rate (dTr), where there is no relationship ($R^2 = 0$, $p = 0.49$, $\lambda = 0$), and (*b*) range contraction rate (eTr), where there is a significative negative relationship between range contraction transition and speciation rates ($R^2 = 0.319$, $p < 0.05$, $\lambda = 1$).

findings suggest that the current diversity of this superfamily resulted from range contraction and *in situ* speciation within distinct biogeographical regions instead of dispersal events between regions. Additionally, we observed an initial rapid speciation at the crown of the clade followed by a slowdown over time, a pattern often perceived as density-dependent diversification (electronic supplementary material figure S3.5) [73,74]. Certain clades, however, exhibited accelerated speciation, probably owing to the exploitation of new ecological opportunities within their bioregions. Overall, speciation within the Emberizoidea superfamily seems to be decoupled from dispersal events, with stable environments allowing continuous diversification within occupied biogeographical regions and available ecological spaces.

Our research provides significant insights into the speciation of the Emberizoidea superfamily. Contrary to previous assumptions, we found that dispersal events between bioregions did not significantly influence the speciation rates of the clade and that, overall, important dispersal events between regions might have been scarce. Our selected ancestral area reconstruction model (BAYAREA+J) assumes no range evolution at cladogenetic events [62], implying that two daughter lineages would inherit the same range as their ancestor. Accordingly, within-region speciation is the suggested explanation for cladogenetic events under this model. Moreover, range evolution in this model is explained by range contraction through local extinction events [61,62] As such, the current distributional patterns of Emberizoidea and its composing lineages (families) are better explained by *in situ* speciation and gradual range reductions due to local extinction within different bioregions. Although ancestral state reconstruction is known to become less accurate with increasing evolutionary time, displaying higher error at deeper nodes [75,76], the model comparison approach has demonstrated that best-fit models are more likely to estimate ancestral ranges more accurately [61] while informing us about the importance of different macroevolutionary dynamics underlying diversity patterns, such as dispersal and range contraction in our case [64]. Nevertheless, results from ancestral area reconstructions as applied here should be taken with caution as they rely solely on extant lineages without considering fossil ones that actually went extinct, which may hinder the reliability of such an approach given the dynamic history of environments and lineages. Approaches that explicitly consider true extinction by incorporating fossil evidence have only very recently been proposed [77]. Unfortunately, such evidence is mostly scarce for birds and for Emberizoidea in particular, whose scant fossil record corresponds to currently identified genera and occupied regions (e.g. genus *Emberizide* in Eurasia [78]), thus hindering their use in these new approaches but also suggesting that their inclusion would not substantially change our conclusions based on extant taxa.

Despite our selected reconstruction model favouring range inheritance and contraction as processes of range evolution, it also identified well supported dispersal events. Notably, it confirmed the jump dispersal of the Emberizidae family most recent common ancestor from the New World to Eurasia, likely via the Bering passage, aligning with previous findings by Cai *et al*. [59]. This dispersal event has been considered the primary driver of rapid speciation of this family within Eurasia, characterizing this lineage's evolution as a geographical radiation [59]. However, our results did not show the expected increase in the speciation rate for this family typically associated with radiations of any type [11]. Moreover, the evidence supporting rapid speciation following the dispersal to Eurasia, such as an apparent early burst and a density-dependent pattern, appears to precede the divergence of Emberizidae. This pattern might instead date back to the divergence of Emberizoidea from Fringillidae or even earlier. Accordingly, density-dependent diversification has been proposed for other emberizoid families besides Emberizidae [59] that have no reported dispersal events at their crown, such as Parulidae [73] and Thraupidae [79], backing the general trend for the whole Emberizoidea clade.

Our findings support the idea that not all successful establishments in new regions lead to bursts in speciation [80]. While evolutionary radiations can indeed be the outcome of natural selection that derives from the occupation of new habitats and the use of new resources provided by a novel geographical area and environmental conditions after colonization [9,33], our research shows that accelerations in speciation rates without requiring the occupation of new geographical regions can also lead to radiations. These can be triggered by various factors, such as the exploitation of novel ecological opportunities by means of extinction of a predator/competitor, the evolution of a key innovation, novel uses of an already developed trait [79], or ecomorphological divergence [11,81]. This could be the case for the clades that presented speciation rate accelerations but not discernible dispersal events between bioregions.

For example, the speciation rate acceleration occurring at the crown of Icteriidae and Parulidae around 12.25 Ma coincides with the progressive global cooling during the middle to late Miocene (*ca* 14–9 Ma), which enabled the widespread distribution of C4 grasses in North America [82]. This ecosystem turnover likely produced novel ecological opportunities that the Icteridae and Parulidae clades could have exploited. This interpretation aligns with Rabosky & Lovette's [73] findings for the Parulidae family, which suggest that this clade underwent adaptive radiation driven by ecological opportunity on a continental scale within North America.

Moreover, the speciation rate shift in the *Atlapetes* genus has been related to the novel ecological opportunities provided by the later glacial cycles (*ca* 3.8–3 Ma) which modified montane forests, especially in the Andes [12,83]. Finally, the Thraupidae family presents two speciation rate accelerations that concur with those found by Burns *et al*. [45]. The first acceleration is present at the *Geospiza* genus, including some of Darwin's finches. The diversification of *Geospiza* is widely accepted to be the result of adaptive radiation in the Galapagos through ecological differentiation [84]. The second speciation rate acceleration present in Thraupidae is at the *Sporophila* genus. It has been suggested that the diversification of *Sporophila* is the result of the intrinsic evolvability of lineages composed of primarily finch-billed forms, which tend to diverge owing to various ecological factors, such as selection for efficient use of seeds of different sizes [45,85].

While important concerns have been raised about the estimation of macroevolutionary dynamics derived from BAMM, particularly when phylogenies are small or moderately sized (fewer than 100 tips and up to 1000 tips [86]), it is crucial to note that BAMM can still be used to compare rates between lineages of a clade, for example to determine if one lineage is diversifying faster than another [71]. In addition, potential biases of BAMM on the identification of diversity decline [86] do not necessarily apply to density-dependent diversification, which implies equal rates of speciation and extinction, thus zero net diversification, but not negative diversification [5]. Even if we were subject to such biases of BAMM, our observed pattern of speciation rate deceleration (and thus potential density-dependent diversification) would remain valid since the biases relate to under- (or over-)estimation of speciation rates at each time interval along the clade's history, which in our case would not affect the overall decelerating trend.

The dispersal rate of Emberizoidea families, calculated by dTr for each family, was not related to their speciation rates. This finding at the family level adds further evidence that dispersal of lineages between bioregions had no significant effect on Emberizoidea speciation rates, and therefore did not play a significant role in shaping the diversity of this clade. However, the rate of range contraction, calculated by the eTr, showed a significant negative relationship with the speciation rates of Emberizoidea families. Such a relationship posits the idea that range stability, or lack of range evolution, could be a possible a driver for speciation. Range stability might be linked to environmental stability, as rapid environmental changes could lead to extinction or increased migration, resulting in range contraction or range expansion, respectively [87,88]. This highlights the importance of environmental stability in establishing, diversifying and maintaining lineages while promoting specialization [89]. Indeed, Thraupidae, the family with the highest range stability in our results, was shown to have rapidly filled an ecomorphospace by increasing specialization and diffusing competition through the occupation of ecological spaces not filled by suboscine clades [21].

In sum, our findings advocate that ecological opportunity, habitat specialization and interspecific relationships within cohesive bioregions could have driven speciation in Emberizoidea, rather than dispersal events between regions. One possible explanation is an ecologically driven speciation, where feeding and behavioural specialization allow species to diverge within the same region. For example, neotropical bird sister taxa differ more significantly in ecological traits such as food competition, foraging habits and song when co-existing with closely related species [90]. Recent studies have shown that Emberizoidea may have a more rapid functional evolution than expected, fostering diversification in the clade [91]. Indeed, beak specialization in Thraupidae, Icteridae and Passerellidae directly correlates with speciation rates, regardless of range shape and size at continental scales [92]. Studies in Thraupidae also indicate that coexistence in the Neotropics, interspecific interactions, and predator–prey arms race between insectivores and arthropods drive evolutionary feeding specializations [21]. At the same time, sexual selection is thought to be a critical process for speciation [93], which, in the case of Parulidae, seems to be intimately associated with plumage and song divergence for closely related species [94]. Similarly, studies suggest that sexual selection through plumage and song evolution likely drives evolution in clades like Icteridae and Passerellidae [95,96]. These ecologically driven mechanisms could better explain within-region speciation for Emberizoidea than dispersal-mediated speciation. However, further formal analyses should be made to confirm such speculations.

6. Conclusion

Although we hypothesized that dispersal events were the main drivers for Emberizoidea speciation dynamics, our results showed that dispersal between bioregions was not as important for speciation in Emberizoidea as processes occurring within these bioregions such as range stability. Other processes that could have influenced speciation within bioregions of Emberizoidea may include trophic/habitat specialization, sexual selection through plumage and song evolution, diffusing competition, filling of ecomorphological spaces and behavioural divergences, all of which deserve formal evaluation for the whole clade.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The data that support the findings of this study are openly available in Figshare at [97].

Supplementary material is available online [98].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. A.A.: conceptualization, data curation, formal analysis, investigation, methodology, writing—original draft, writing—review and editing; J.P.-L.: methodology, supervision, writing—original draft, writing—review and editing; O.R.-S.: methodology, supervision, validation, writing—original draft, writing—review and editing; F.V.: conceptualization, investigation, methodology, resources, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed herein.

Conflict of interest declaration. We declare we have no competing interests.

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