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Research Article

History, climate, and competition shape ecological specialization in the Emberizoidea radiation

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Ecological specialization shapes biodiversity patterns, yet the relative importance of historical, climatic, and biotic drivers of specialization remains debated. We investigated how time since colonization (TSC), climatic stability (decomposed in temperature and precipitation stability), and competition influence ecological specialization across diet, foraging behavior, and habitat dimensions in Emberizoidea bird assemblages globally and across three bioregions (Nearctic, Neotropics, Palearctic). Using phylogenetic data, species distributions, and trait databases, we quantified specialization with the Gini Index and modeled its predictors using spatial autoregressive models. Globally, diet and habitat specialization increased with TSC and competition, while foraging specialization decreased with the same predictors. Regional patterns diverged markedly: in the Nearctic, competition increased foraging specialization, and climatic stability decreased diet and habitat specialization; in the Neotropics, TSC and temperature stability promoted diet specialization, competition enhanced habitat specialization but decreased diet and foraging specialization, while all three factors reduced foraging specialization; in the Palearctic, competition and temperature stability increased diet specialization, while TSC promoted habitat but decreased diet and foraging specialization. These contrasting patterns reveal that ecological specialization emerges from contingent interactions between evolutionary history, climatic stability, and biotic factors rather than universal rules, with different specialization axes responding distinctly to the same drivers across biogeographic contexts.

Keywords: biogeography, climatic stability, competition, macroecology, time since colonization

Introduction

Ecological specialization is a widely recognized concept in ecology (Devictor et al. 2010). It refers to the degree to which a species is restricted in the range of ecological resources or conditions it can exploit (Futuyma and Moreno 1988, Devictor et al.

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2010). Specialization allows species to exploit particular environmental conditions efficiently, developing unique traits and adaptations that enhance their survival and reproductive success within their specialized niche (Levins 1968). Therefore, comprehending how patterns and processes shape ecological specialization at large spatial and temporal scales can help us understand the role of the environment in the niche delimitation of species, thus providing valuable insights for various fields, such as ecology, biodiversity, and conservation (Colles et al. 2009).

Researchers consider ecological specialization a syndrome-like alteration of several traits to exploit specific resources effectively (Devictor et al. 2010, Morelli et al. 2021). Consequently, the degree of specialization can differ across multiple niche dimensions (Benedetti and Morelli 2024). For example, a species could be specialized in a particular feeding strategy while being a generalist regarding diet itself (Morelli et al. 2019, Benedetti et al. 2022). Thus, measures of ecological specialization are best considered multidimensional (Devictor et al. 2008, Luck et al. 2013), utilizing data about multiple species traits such as behavior, habitat, or diet (Devictor et al. 2010). This multidimensional approach permits the identification of different mechanisms shaping specialization patterns, and allows us to infer the determinants of how the aforementioned traits evolved (García-Andrade et al. 2023).

Factors such as how long species have occupied a particular geographical area or their time since colonization (TSC), climate stability, and the level of interspecific competition species have experienced have been identified as key influences on ecological specialization (Dobzhansky 1950, Jocque et al. 2010). In particular, theoretical models have shown that high specialization within populations can arise from high levels of competition, either through resource depletion or interference among individuals (Jones and Post 2016, Halloway and Brown 2021). However, despite the widely acknowledged significance of ecological specialization in environmental and evolutionary processes, the relative importance of the possible underlying drivers in the development of ecological specialization continues to be debated (Jocque et al. 2010, Belmaker et al. 2012).

TSC is thought to play a critical role in shaping ecological specialization (Lynch 1987). Over longer periods of evolutionary time, natural selection can fine-tune species' traits, allowing them to adapt to specific resources and abiotic conditions (Haag and Ebert 2004, Jablonski et al. 2006). This process leads to the evolution of highly specialized species, each occupying a distinct niche (Cracraft 1985). Importantly, this specialization is more likely to occur because species tend to remain within their ancestral biomes, a phenomenon known as phylogenetic biome conservatism where, rather than shifting to entirely new biomes, species often exhibit biome stasis, staying in environments similar to their ancestors (Crisp et al. 2009). This retention of ancestral biomes provides a lasting context for specialization to develop over time, as species adapt to the specific conditions of their long-established ecosystems (Wiens and Donoghue 2004, Crisp et al. 2009).

Concordantly, ecologists have suggested that climatic stability is one the main promoters of ecological specialization (Jocque et al. 2010). The link between climatic stability and ecological specialization is reinforced by a positive feedback loop, where specialized species confined to narrow niches are less able to adapt to new conditions, leading to further increased specialization within climatically stable areas (Elena and Sanjuán 2003). Moreover, rapid environmental changes driven by climatic instability could lead to extinction or increased migration (Svenning et al. 2015), resulting in strong selection towards high dispersal abilities (Gandon and Michalakis 1999). Such selective pressures cause homogenization of the gene pool, preventing the genetic divergence between populations, and the continuous adaptation to local resources, while actively selecting for generalist species with broader niches (Case and Taper 2000, Elena and Lenski 2003, Jocque et al. 2010).

Competition is also argued to play a significant role in shaping ecological specialization among species (Dobzhansky 1950). As resources become limited, coexisting species must compete for access (Tilman 1987). This competition can drive the evolution of specialized traits that would allow species to utilize specific resources more effectively, partitioning species niches and thereby reducing competition and promoting speciation (MacArthur 1969). Over time, this process can lead to distinct ecological niches and specialized adaptations among different species (Belmaker et al. 2012). For example, studies have shown that different finch species on the Galápagos Islands have adapted to utilize distinct dietary resources, leading to niche segregation (Villegas et al. 2021). Similarly, in Neotropical bird assemblages, rapid specialization occurred following colonization, filling the eco-morphospace (Imfeld and Barker 2022). This specialization was driven by interspecific competition and a predator–prey arms race between arthropods and insectivorous birds (Sherry et al. 2020), ultimately reducing competition by allowing species to occupy distinct ecological niches (Imfeld and Barker 2022).

The effect of potentially important factors driving ecological specialization can vary across biogeographical regions due to various factors (Smith et al. 2018). Differences in environmental conditions can create distinct selective pressures, shaping ecological specialization in unique ways across regions (Chase and Myers 2011). Additionally, geographical variation in the availability of resources, the presence of competitors, and the intensity of predation can influence the evolution of specialized ecological strategies (Belmaker and Jetz 2015). Historical factors, such as past geological events and species dispersal patterns, further contribute to the observed differences in ecological specialization between biogeographical areas (Smith et al. 2020).

Here, we explore a subset of likely important factors influencing specialization, focusing on climatic stability (decomposed in temperature and precipitation stability), TSC, and competition by using the Emberizoidea superfamily as a model group. These small to medium-sized birds (approximately 832 species; Barker et al. 2015) have motivated significant ecological and evolutionary inquiries, from Darwin's finches to MacArthur's wood warblers. The Emberizoidea superfamily is considered to be around 18 million years old and is found in nearly all of the New World and parts of the Old World, showcasing a broad spectrum of ecological, behavioral, and morphological variation (Lowther 1975, Holmes 1990, Forshaw and Kirshner 1991, Curson 1994). There have been indications that this group's diversification and functional evolution are much more rapid than expected by simple birth–death processes (Imfeld and Barker 2022). This rapid evolution suggests that ecological specialization has played a vital role in shaping its diversity, by driving morphological and ecological divergence (Schoener 1965, Abrahamczyk et al. 2014, Dehling et al. 2016). Therefore, our study aims to illuminate the importance of a set of possible factors influencing specialization in members of the Emberizoidea, which have demonstrated an exceptional ability to exploit ecological opportunities and capitalize on various dietary and habitat niches.

In this study, we investigated how TSC, climatic stability, and competition influence ecological specialization in bird assemblages of the Emberizoidea clade, both globally and across major bioregions. We quantified three facets of ecological specialization (diet, foraging behavior, and habitat) at the assemblage level. TSC was estimated using the maximum branch length (MBL) of the oldest species in each assemblage, climatic stability was quantified for both long-term variability in temperature and precipitation since the Pliocene, and competition was inferred from the phylogenetic structure of assemblages (net relatedness index, NRI). Together, these analyses allow us to evaluate the relative roles of historical, environmental, and biotic factors in shaping specialization patterns within Emberizoidea. We hypothesize that TSC, climatic stability, and competition would each positively influence specialization, but that their effects would differ across bioregions and among specialization axes (Table 1).

Material and methods

Phylogenetic and assemblage data

To perform our analyses, we used the maximum clade credibility tree of a calibrated species-level phylogeny for Emberizoidea (Barker et al. 2015). This phylogeny represents the relationships of approximately 95% of the clade's extant species (Barker et al. 2015). Breeding season distributions for the species of the Emberizoidea clade were compiled using the Bird Life International species' range maps (BirdLife International and Handbook of the Birds of the World 2024). Based on these distributions, we constructed species assemblages in equal-area grids of 1° × 1°. The final dataset, including phylogenetic, geographical, and trait data, comprised 589 species (≈ 73% of total Emberizoidea species). To test the possibility that different factors affect specialization distinctively in a given geography, we separated the species pool into three bioregions according to Olson's realms: the Nearctic, Neotropic, and Palearctic (Olson et al. 2001). The Afrotropic was omitted as it had an overall low species richness per assemblage (at most three species). We analyzed specialization across these biogeographic regions because they encompass broad-scale evolutionary, ecological, and historical contexts that have shaped species' assemblage structure (Holt et al. 2013).

Avian specialization

We derived three types of ecological specialization for the Emberizoidea superfamily: diet, foraging, and habitat. We used the trait database EltonTraits 1.0 (Wilman et al. 2014) to extract diet and foraging specialization. EltonTraits is a global species-level compilation that contains the key attributes for 9993 extant bird species, including the diet and foraging behavior proportions for the Emberizoidea superfamily. Specifically, the diet data in EltonTraits are provided as percentage estimates of different food categories (e.g. invertebrates, vertebrates, plants, and other resources) consumed by each species. Similarly, foraging behavior data are supplied as percentage estimates of different foraging strategies (e.g. ground foraging, aerial foraging, or arboreal foraging) employed by each species. We used these percentage values to calculate diet and foraging specialization indices, reflecting the degree of niche breadth or reliance on specific resources or behaviors. Furthermore, we discarded categories not present in any of the Emberizoidea species. For habitat specialization, we extracted the proportional use of ecoregions where the species are present during their breeding season using the BirdLife International species' range maps 2024 and Olson's Ecoregions of the World (Olson et al. 2001, Belmaker et al.

Table 1. Summary of the hypotheses tested for the determinants of ecological specialization. Each hypothesis outlines the proposed mechanism, the predictor variable used to capture it, and the expected direction of the effect on specialization. TSC, time since colonization; NRI, net relatedness index.

Hypothesis	Mechanism	Predictor variable	Expected effect on specialization
Climatic stability modulates specialization (H1)	Stable climates allows specialism to develop while fluctuating climates select for generalist strategies to cope with variability in resource availability	Temperature stability; precipitation stability	Positive (greater stability = more specialization)
Longer TSC promotes specialization (H2)	Longer regional persistence allows for niche partitioning and evolutionary adaptation to local conditions	TSC	Positive (older assemblages = more specialization)
High competition promotes specialization (H3)	Coexisting species partition ecological space to minimize competition, favoring niche differentiation	Phylogenetic clustering (NRI)	Positive (more related species = stronger competition = more specialization)

2012). This approach allowed us to comprehensively assess ecological specialization across multiple dimensions for the Emberizoidea superfamily. The degree of specialization in diet, foraging behavior, and habitat was estimated using the Gini index of inequality (Gini 1921), recently adopted for ecological research (Morelli et al. 2019). This index is based on the Gini coefficient of statistical dispersal, ranging from 0 to 1. Values of 0 represent perfect equality, while values of 1 represent maximum inequality. The Gini coefficient is estimated with the following formula:

$$G = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}\left|x_i - x_j\right|}{2n^2\left(\tilde{x}\right)}, \qquad (1)$$

where $\tilde{x}$ is the mean value of proportions of diet/foraging behavior/habitat categories used by the species, n is the total number of categories, and $|x_i - x_j|$ is the absolute difference in proportional use between categories i and j. In the context of avian specialization, values closer to 0 indicate a more equal use of the resources, thus indicating generalism. Values closer to 1 indicate specialization on a single resource. Finally, we calculated specialization for each assemblage as the average of each particular Gini index by species richness (Supporting information).

Time since colonization

We used MBL to approximate the time since colonization (TSC). This approach provides insights into colonization time because it represents the earliest period when the assemblage began to form. The presence of the oldest species in the assemblage, based on phylogenetic divergence, indicates that suitable ecological conditions existed at least as far back as their origin or arrival, offering a minimum estimate for colonization. MBL has been reported to be highly correlated to the age of first colonization of an assemblage according to ancestral range reconstructions (García-Andrade et al. 2023). Each MBL was calculated by extracting the branch length from the Emberizoidea phylogeny corresponding to the earliest diverging species within each assemblage (Supporting information). This measurement reflects the age, in millions of years, of the oldest species present in the assemblage. By identifying the earliest phylogenetic divergence, MBL serves as a proxy for the timing of colonization, marking the earliest point at which the assemblage could have begun to form. The presence of these early-diverging species suggests that suitable ecological conditions existed at least since their origin or arrival, providing a conservative, minimum estimate for colonization (Pinto-Ledezma et al. 2019).

Birds are highly vagile organisms capable of long-distance dispersal, but their strong philopatry (tendency to return to breeding areas) and relatively limited propensity for biome shifts (Claramunt 2021) enhance the reliability of MBL as a proxy for colonization history. For Emberizoidea in particular, evidence suggests broad dispersal abilities have not erased the signal of long-term persistence within regions (Arango et al. 2025a). This assumption follows from the observed phylogenetic signal in species' geographic ranges (Crisp et al. 2009, Cardillo 2015), which implies that current distributions often reflect ancestral positions. Nonetheless, we acknowledge that the MBL approach assumes range conservatism (that early colonizing lineages have persisted in situ) and this assumption can be criticized, as it may be violated by major historical range shifts (Diamond 2018). With these caveats, MBL provides a conservative and standardized temporal framework for comparing colonization history across assemblages.

Competition

Competition was measured from the phylogenetic structure of each assemblage, quantified with the NRI. The NRI measures the standardized effect sizes of the observed mean phylogenetic distance between species pairs in a given assemblage relative to that of random assemblages from a species pool (Webb 2000). NRI is defined as follows:

$$\mathrm{NRI} = -1\frac{MPD_o - MPD_r}{S_{MPD_r}}, \qquad (2)$$

where MPD_o is the observed pairwise distance of all species within an assemblage, $MPDr$ is the mean pairwise distance of random assemblages, and S_{MPD_r} is the standard deviation of MPD_r. Significantly positive NRI values (> 1.96) indicate phylogenetic clustering of species and likely high competition (i.e. species present in a given assemblage are more closely related than expected by chance on average, thus sharing several niche aspects). Significantly negative NRI values (< −1.96) indicate phylogenetic overdispersion of species (i.e. species present in a given assemblage are more distantly related than expected by chance on average, thus being present by either competitive exclusion or environmental filtering; Webb 2000). To calculate the MPD_r, we used a null model that randomizes taxon labels on the phylogeny for the species included in the sampling pool but maintains the species richness of the given assemblages (Kissling et al. 2012). We calculated the NRI 1) globally (Supporting information) and 2) by using each bioregion's species pool. We used the NRI as a proxy for potential competition intensity, assuming that closely related species are more likely to share phylogenetically conserved traits relevant to their ecology and thus overlap in niche dimensions (Belmaker et al. 2012).

While we acknowledge that niche-based metrics such as trophic guild can also be informative, we argue that phylogenetic relatedness provides a broader representation of competition beyond trophic overlap, as many ecologically relevant traits in birds (and particularly Emberizoidea) tend to be phylogenetically conserved (Belmaker et al. 2012, Conway and Olsen 2019, Vinciguerra and Burns 2021). This makes NRI a useful proxy that also accounts for unmeasured traits, potentially offering a more accurate approximation of competitive interactions. In this framework, NRI reflects the outcome of proximity in an assemblage (i.e. the degree of phylogenetic clustering within assemblages) rather than inferring specific assembly mechanisms as originally proposed by Webb (2000).

Climatic stability

Climatic stability was calculated by averaging the inverse mean annual temperature (MAT) and mean annual precipitation (MAP) instability between different time periods between the Pliocene (ca 3.3 Million years ago, Mya) to the present, using the PaleoClim database (Brown et al. 2018). The PaleoClim database contains the climatic information for the Pleistocene (from the late Holocene to the Pleistocene ca 787 ka; Otto-Bliesner et al. 2006, Fordham et al. 2017, Brown et al. 2018), the mid-Pliocene (3.205 Mya; Hill 2015), and the Pliocene (ca 3.3 Mya; Dolan et al. 2015). Temperature and precipitation stability were calculated using the following formula, where values of 0 denote perfect stability:

$$C_S = -1\left(\frac{\sum_{i=2}^{n}\left|c_i - c_{i-1}\right|}{n}\right), \tag{3}$$

here c_i is the climatic variable at time period i and n the total number of time periods. Under this framework, higher values (or values close to 0) indicate lower changes over time (more stability), whereas lower values indicate larger changes (less stability). All climatic variables were obtained at a native resolution of 2.5 arc-minutes and aggregated to a 1° grid by averaging, to match the spatial resolution of the assemblage data (Supporting information).

Statistical analyses

To evaluate potential collinearity among predictors, we performed a variance inflation factor (VIF) analysis, which quantifies how much the variance of a model coefficient is inflated due to collinearity with other predictors, with lower values indicating less correlation among predictors. All predictors had VIF values < 3 (Supporting information), indicating that collinearity was not high enough to bias model estimates (Zuur et al. 2010). To describe the effects of TSC, climate stability, and competition on specialization, we applied simultaneous autoregressive models (SARs). SARs are linear regression models that correct the potential spatial autocorrelation of the data (Kissling et al. 2007). Spatial autocorrelation was assessed using a covariance matrix to correct for the model residuals in cases of spatial dependence. The covariance matrix in the SAR models was defined based on a spatial weights matrix, which was constructed using a distance-based neighborhood criterion (e.g. inverse distance weighting or k-nearest neighbors) to account for the spatial relationships among assemblages. We tested the effects of the explanatory variables (TSC, climatic stability, and competition) in multiple combined models (Supporting information) to evaluate their joint influence on the different facets of specialization, such as diet, foraging behavior, and habitat (Eq. 1) as response variables., rather than testing them separately. To account for model selection uncertainty, we compared alternative spatial autoregressive (SAR) models using Akaike's information criterion (AIC). For each model set, we calculated ΔAIC and model weights, and then averaged parameter estimates across all models with $\Delta\text{AIC} < 2$ (Burnham and Anderson 2002) (Supporting information). SARs account for patterns in the response variables that are related to the assemblages' locations but not necessarily predicted by the explanatory variables, thus avoiding Type 1 errors (Kissling and Carl 2008). All spatial data were processed using the 'sf', 'terra', and 'raster' packages for the R statistical programming (www.r-project.org) and all statistical analyses were performed using the 'spedp' package (Bivand and Piras 2015) for R (www.r-project.org).

Results

At a global scale, the ecological specialization of Emberizoid assemblages was generally high, with habitat specialization having the highest average Gini index ($\tilde{x} = 0.817$; SD = 0.059; median = 0.821; range = 0.671–0.937). Diet specialization had an average Gini index of 0.781 (SD = 0.02; median = 0.777; range = 0.666–0.888), while foraging specialization had an average Gini index of 0.719 (SD = 0.045; median = 0.716; range = 0.6–0.833).

Globally, diet specialization was positively associated with both competition and TSC, indicating that assemblages with greater phylogenetic clustering and longer evolutionary histories tended to harbor species with narrower dietary niches (Supporting information). Foraging specialization showed a contrasting pattern: while TSC and competition were again the strongest predictors, their effects were negative, suggesting that older and more clustered assemblages included species with broader foraging strategies (Supporting information). Habitat specialization largely mirrored the pattern of diet specialization, showing positive associations with both competition and TSC. Assemblages characterized by long persistence and high relatedness therefore tended to contain species with narrower habitat requirements (Supporting information; Fig. 1).

Patterns varied across regions. Regional analyses revealed divergent patterns. In the Nearctic, diet specialization was negatively related to competition, TSC, and temperature stability (Supporting information). Foraging specialization was positively associated with competition but negatively with TSC (Supporting information). Habitat specialization showed a weak positive relationship with precipitation stability but negative associations with both temperature stability and competition (Supporting information; Fig. 2).

In the Neotropics, diet specialization increased with both temperature stability and TSC but declined with competition (Supporting information). Foraging specialization was negatively associated with competition and TSC, and in a lesser degree with precipitation stability (Supporting information). Habitat specialization in the Neotropics, by contrast, increased with competition and, to a lesser degree, with precipitation stability (Supporting information; Fig. 3).

In the Palearctic, diet specialization was positively associated with both competition and temperature stability but

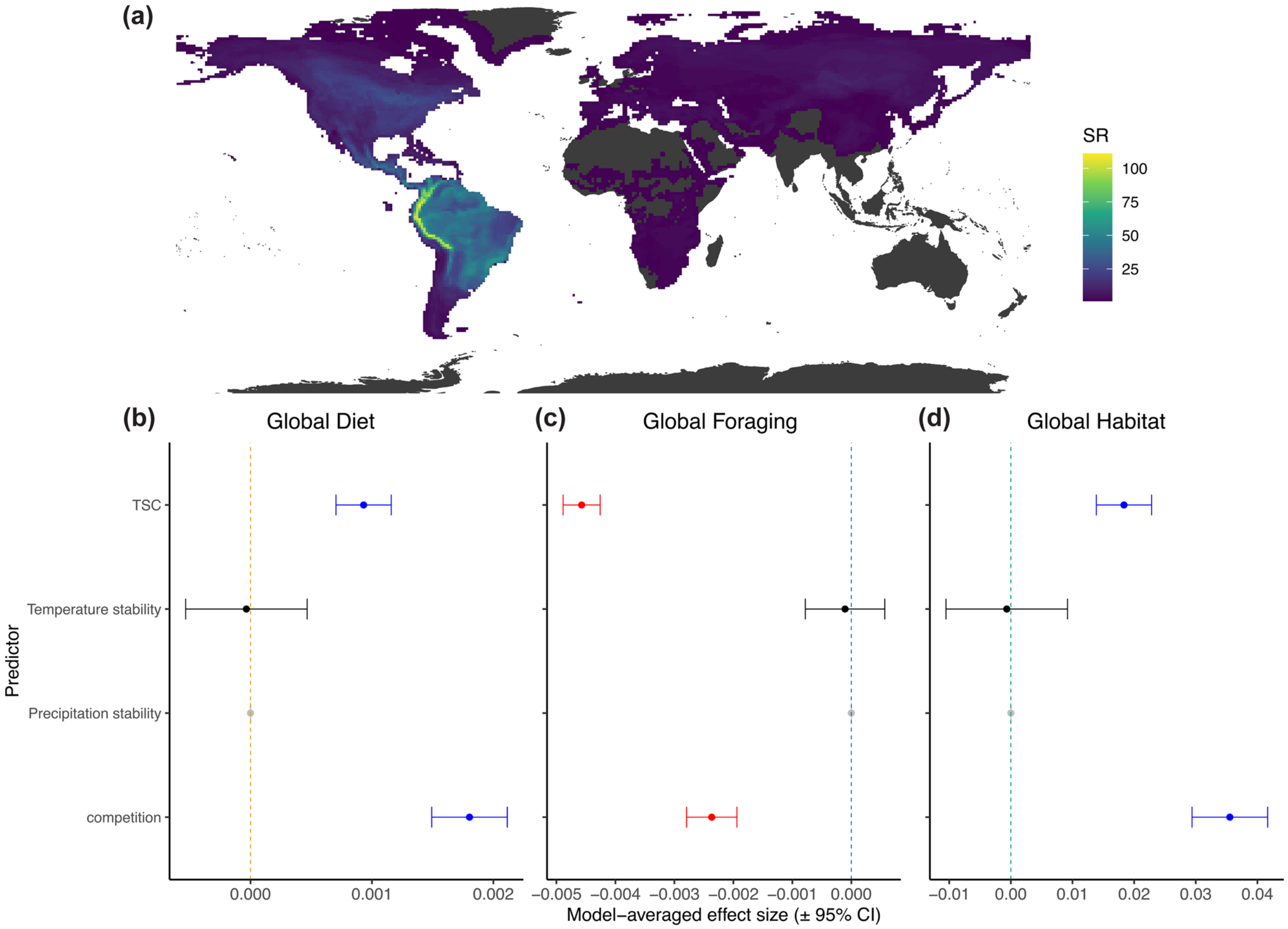

Figure 1. Global patterns of species richness and predictors of ecological specialization. (a) Map of global species richness (SR) of Emberizoidea. Model-averaged effect sizes (± 95% CI) of climatic stability, competition, and evolutionary history on three dimensions of specialization: diet (b), foraging behavior (c), and habitat (d). Positive (blue) effect sizes indicate higher specialization with increasing predictor values; negative (red) effect sizes indicate lower specialization with increasing predictor values. Black are non-significant effect sizes (Supporting information).

negatively with TSC (Supporting information). Foraging specialization again showed a negative relationship with TSC (Supporting information). Habitat specialization, however, increased with both TSC and temperature stability (Supporting information; Fig. 4), indicating that older and historically stable environments favored stronger habitat specialization.

Discussion

Our analyses reveal that ecological specialization in Emberizoidea assemblages is shaped by a complex interplay of evolutionary history, climatic stability, and competition, with the strength and direction of effects varying across the different types of specialization and biogeographical regions. At the global scale, assemblages with longer evolutionary histories and higher competition exhibited greater dietary and habitat specialization, consistent with H2 (longer persistence promotes specialization) and H3 (competition promotes specialization; Table 1). Over long timescales, lineages may accumulate adaptations to local resources, and niche overlap among closely related species may drive partitioning of diet and habitat (Haag and Ebert 2004, Jablonski et al. 2006). In contrast, foraging specialization decreased with both predictors, contrary to expectations, suggesting that older, more clustered assemblages may instead favor behavioral flexibility in foraging. One possible explanation is that behavioral plasticity allows coexistence when diet and habitat are already finely partitioned, reducing the risk of competitive exclusion (Pianka 1974, Vander Meiden et al. 2024). This divergence underscores the importance of treating specialization as a multidimensional phenomenon rather than as a unidimensional trait (Devictor et al. 2010, Morelli et al. 2019).

Regional patterns diverged markedly from global expectations, reflecting differences in environmental history and biogeography. In the Nearctic, diet specialization declined with temperature stability, competition, and TSC, contradicting

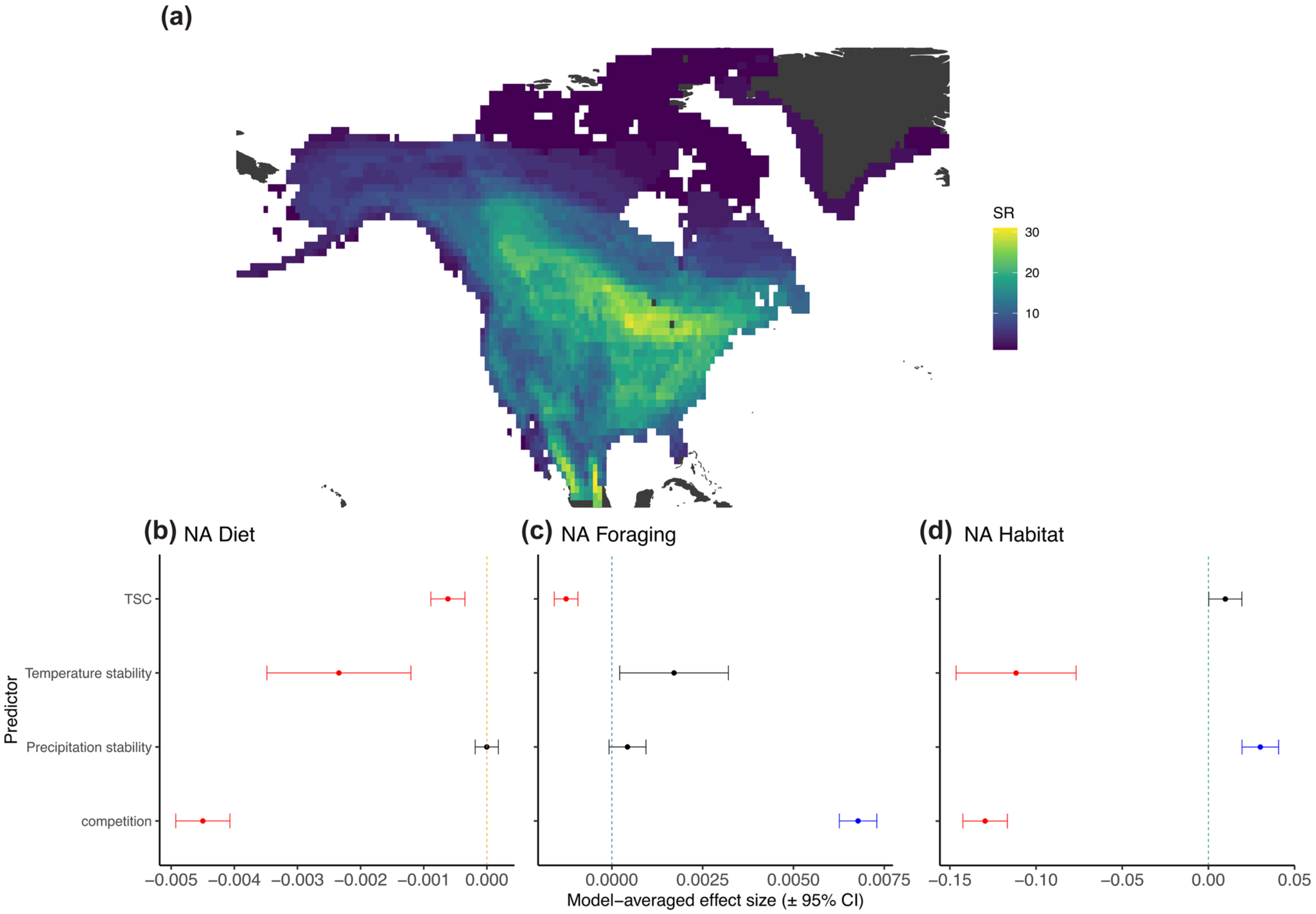

Figure 2. Nearctic patterns of species richness and predictors of ecological specialization. (a) Map of Nearctic species richness (SR) of Emberizoidea. Model-averaged effect sizes (± 95% CI) of climatic stability, competition, and evolutionary history on three dimensions of specialization: diet (b), foraging behavior (c), and habitat (d). Positive (blue) effect sizes indicate higher specialization with increasing predictor values; negative (red) effect sizes indicate lower specialization with increasing predictor values. Black are non-significant effect sizes (Supporting information).

H1, H2, and H3. This pattern suggests that in more stable environments with longer evolutionary persistence and higher competition, species may have evolved broader dietary niches. Over time, niche saturation and high species packing can favor trophic generalism, where behavioral shifts in the frequency and mode of resource use allow overlapping dietary niches to persist under competitive conditions (Dehling et al. 2022).

Competition increased foraging specialization, indicating that species may alleviate dietary overlap by diversifying their foraging behaviors, a pattern consistent with MacArthur's classic observations of parulid warblers in the Nearctic (MacArthur 1958). This suggests that, for Emberizoidea, behavioral differentiation in foraging may act as a mechanism to defuse competition while maintaining broad dietary niches.

Habitat specialization was negatively related to temperature stability and competition, while positively related to precipitation stability, which may reflect the strong philopatry and migratory behavior of Nearctic Emberizoidea (Claramunt 2021). As climates fluctuated, species tracked suitable habitats, reinforcing narrow habitat associations despite variable conditions (Bruderer and Salewski 2008, Winger et al. 2014). However, fluctuating precipitation could disrupt vegetation structure and resource distributions, favoring generalist habitat use (Chen et al. 2020). Together with the negative effect of temperature stability, these results imply that different climatic dimensions act on habitat specialization in distinct ways: while rainfall predictability fosters narrow habitat associations, temperature variability could be reinforced by migratory behavior and philopatry.

In the Neotropics, diet specialization increased with both temperature stability and TSC, consistent with H1 and H2. Stable tropical climates likely provide consistent resource bases over long periods of time that facilitate specialization (Cracraft 1985, Jablonski et al. 2006, Crisp et al. 2009). Yet, competition reduced diet specialization, contrary to H3. This pattern parallels that observed in the Nearctic, where in species-rich assemblages, strong and persistent competition may not promote fine niche partitioning but instead favor trophic flexibility, broadening resource use to mitigate

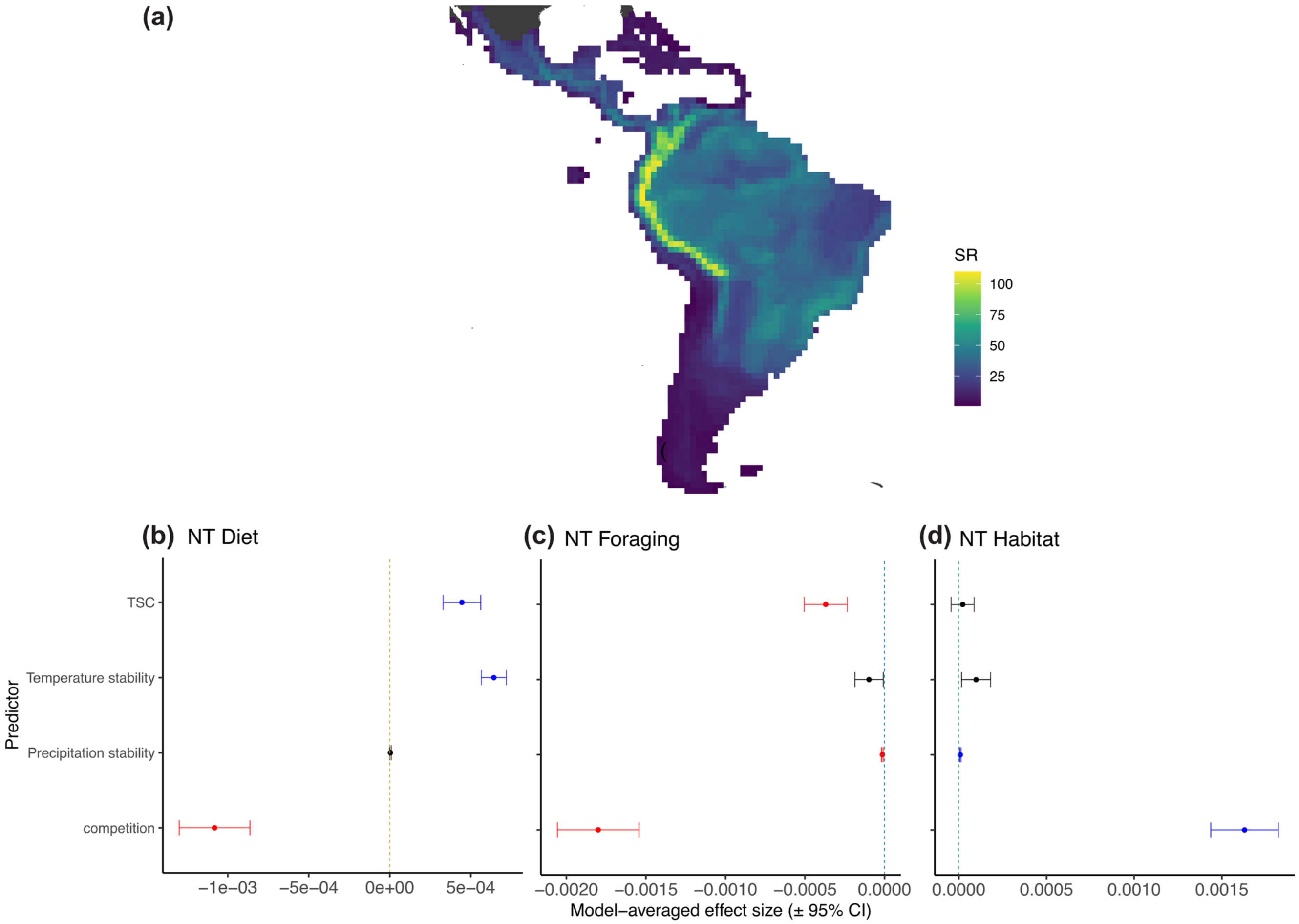

Figure 3. Neotropical patterns of species richness and predictors of ecological specialization. (a) Map of Neotropical species richness (SR) of Emberizoidea. Model-averaged effect sizes (± 95% CI) of climatic stability, competition, and evolutionary history on three dimensions of specialization: diet (b), foraging behavior (c), and habitat (d). Positive (blue) effect sizes indicate higher specialization with increasing predictor values; negative (red) effect sizes indicate lower specialization with increasing predictor values. Black are non-significant effect sizes (Supporting information).

overlap (Dehling et al. 2022) or reduce vulnerability to scarcity (Kent et al. 2022).

Foraging specialization, by contrast, decreased with TSC, competition, and, to a lesser extent, with precipitation stability, contradicting H1, H2, and H3. One explanation is that over long timescales, niche saturation and high species packing in tropical assemblages favor behavioral flexibility in foraging rather than strict specialization, allowing coexistence when diet and habitat are already tightly partitioned (Pianka 1974). Reduced foraging behavior specialization under competition further suggests that behavioral plasticity minimizes direct overlap among species, particularly where intraspecific competition is stronger than interspecific competition (Araújo et al. 2011, Sherry et al. 2020). These results suggest that while competition selects for broader diets and more flexible behaviors, over time species partition their dietary niches but keep foraging behavior flexibility. The weak negative effect of precipitation stability further implies that predictable rainfall regimes do not constrain foraging strategies as they do diet, and that fluctuating rainfall may instead favor opportunistic foragers capable of exploiting transient resources (Liu et al. 2020).

Habitat specialization was positively associated with competition and in a lesser way precipitation stability, consistent with H1 and H3, suggesting that high competition and stable precipitation regimes might promote adaptation to specific physionomies, consistent with evidence that certain Neotropical oscines adapted to distinct open habitats and forest strata, such as savannas and dry forests (Wiley 1991). As such, stable rainfall regimes may sustain predictable resource diversity (Esquivel-Muelbert et al. 2017, Liu et al. 2020) and physiognomy preservation (Arango et al. 2021), allowing Emberizoidea to evolve narrower strategies closely related to habitat selection (Ravigné et al. 2009), while unstable rainfall might select for generalists (Jocque et al. 2010).

The Palearctic showed a different combination of influencing factors. Diet specialization was promoted by

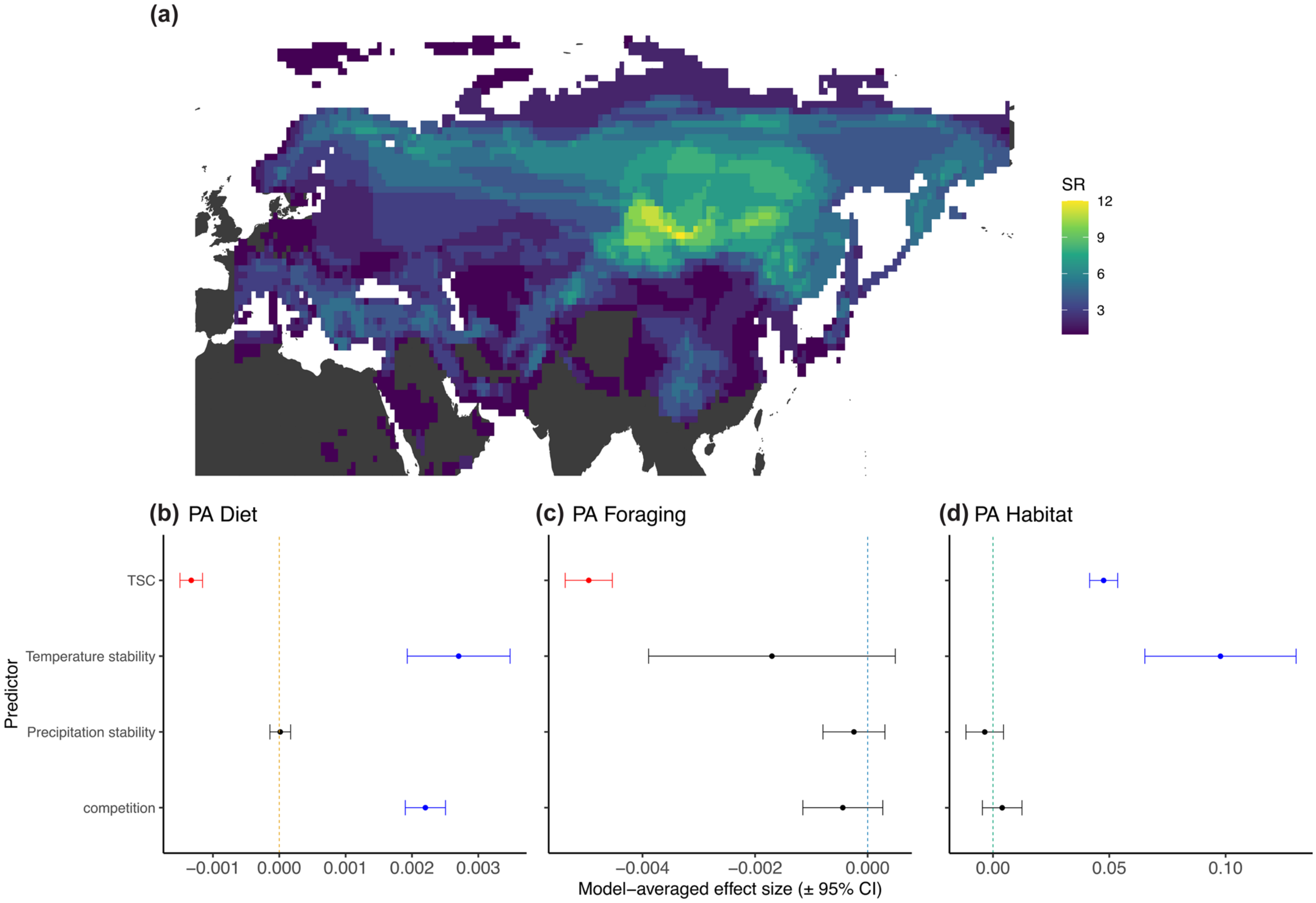

Figure 4. Palearctic patterns of species richness and predictors of ecological specialization. (a) Map of Palearctic species richness (SR) of Emberizoidea. Model-averaged effect sizes (± 95% CI) of climatic stability, competition, and evolutionary history on three dimensions of specialization: diet (b), foraging behavior (c), and habitat (d). Positive (blue) effect sizes indicate higher specialization with increasing predictor values; negative (red) effect sizes indicate lower specialization with increasing predictor values. Black are non-significant effect sizes (Supporting information).

competition and temperature stability, supporting H1 and H3, but was negatively associated with TSC, contradicting H2. Foraging specialization also declined with TSC, in contradiction with H2. One possible explanation is that early colonizers of what is now eastern Asia during the Miocene diversified into a wide array of diets and behaviors (Gavrilets and Vose 2005, Price 2008), while later expansions westwards were carried by already specialized species (Cai et al. 2021). Habitat specialization, however, increased with both TSC and climatic stability, consistent with the view that persistence in historically buffered environments promotes filtering into narrower ecological spaces (Cracraft 1985, Lynch 1987, Elena and Sanjuán 2003). This suggests that while dietary and foraging niches may reflect historical colonization dynamics, habitat niches respond more directly to stability over time.

Taken together, these results highlight that no single global factor can account for ecological specialization across all contexts. While H2 and H3 received broad support at the global scale, both were frequently contradicted in regional analyses, particularly in the Nearctic and Palearctic. H1 showed partial support, with climatic stability enhancing specialization in the tropics and Palearctic but exerting the opposite effect in the Nearctic. These contingencies illustrate that the ecological and historical backdrop of each region mediates how time, climate, and competition shape assemblages. They also emphasize that specialization along one dimension does not necessarily share influencing factors along another specialization dimension: Emberizoidea assemblages may evolve narrow diets and habitats but maintain broad foraging repertoires, or vice versa.

Despite these insights, several limitations should be acknowledged. Our use of phylogenetic structure as a proxy for competition provides a broad-scale perspective but cannot fully capture direct ecological interactions such as resource overlap or behavioral interference. Nevertheless its use allows us to account for niche overlap in ecologically relevant unmeasured traits (Belmaker et al. 2012). Similarly, while the Gini index allowed us to compare diet, foraging, and habitat axes, treating these dimensions separately may underestimate the multidimensional nature of ecological niches and the relationship of each specialization axis with each other. As with any correlative approach, causality cannot be firmly established, and although our predictors did not show problematic collinearity, other unmeasured traits (e.g. predation, mutualisms, land-use history, landscape heterogeneity) may also contribute to ecological specialization.

The proxy for colonization time (MBL) assumes persistence and range conservatism, which may not always hold, and our focus on breeding ranges excludes potential pressures during migration or wintering (Winger et al. 2019). However, the strong phylogenetic signal in Emberizoidea ranges (Arango et al. 2025a) indicates that the current distribution of these species is shaped by long-term ecological constraints and evolutionary history (Belmaker et al. 2012, Kennedy et al. 2017), making them more informative for understanding patterns of specialization.

Finally, the use of broad niche measures likely underestimates fine-scale ecological specialization, and our predictors represent only a subset of potential mechanisms shaping ecological specialization. Nevertheless our approach provides a conservative basis for testing specialization patterns (Belmaker et al. 2012, Morelli et al. 2019). Together, these caveats suggest that while our framework captures broad-scale patterns, future work integrating finer-scale ecological data, additional predictors, and multiple trait axes will be essential to refine our understanding of the factors driving ecological specialization.

In conclusion, the ecological diversity of Emberizoidea reflects both global rules and regional contingencies. Temperature and precipitation stability promote specialization in predictable environments, but instability can favor generalists. TSC fosters habitat specialization but has mixed effects on foraging and diet depending on regional disturbance history. Competition promotes specialization in some contexts but selects for generalism in others. Thus, we show that ecological specialization emerges not from a single global rule but from the contingent interaction of history, environment, and biotic interactions.

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Author contributions

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). **Marcell K. Peters**: Methodology (equal); Supervision (equal); Validation (equal); Writing – review and editing (equal). **Chaitanya S. Gokhale**: Funding acquisition (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Figshare Repository: https://doi.org/10.6084/m9.figshare.28741205.v1 (Arango et al. 2025b).

Supporting information

The Supporting information associated with this article is available with the online version.

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