RESEARCH

Open Access

Understanding the role of ecological divergence in the evolution of isolated populations in the *Arremonops rufivirgatus* species complex across Mesoamerica



Ronald A. Fernández-Gómez¹¹⁰, David A. Prieto-Torres²⁰, Adolfo G. Navarro-Sigüenza^{1,3}¹⁰ and Luis A. Sánchez-González^{1*}¹⁰

Abstract

Background The topographic complexity and wide range of environmental conditions of the Neotropical region have allowed the evolution of the most diverse avifauna in the world. Distributional patterns within this avian diversity mirror this complexity, and many species show allopatric distributions in environmentally continuous regions. Here, we used environmental variables and historical presence records to understand the evolution of the distribution of three isolated groups (Gulf, Pacific, and Yucatan Peninsula) of the Olive Sparrow (*Arremonops rufivirgatus*) species complex. We assessed the role of environmental factors underlying geographic distribution patterns in the complex based on ecological niche modeling and performed paleoclimatic reconstructions to assess distributional changes based on suitable areas during the Late Pleistocene.

Results Niche similarity was not rejected in the Pacific/Yucatan comparison, but the Gulf/Pacific and Gulf/ Yucatan comparisons showed niche differentiation. We found regions with low climatic suitability representing a biogeographic barrier for the Pacific and the Yucatan groups, but not for the Yucatan and the Gulf groups, suggesting that biotic factors, such as competition with ecologically similar species, may be involved in geographic isolation.

Conclusions Our results suggest that allopatric distributions in the three groups within the *A. rufivirgatus* complex probably evolved due to biotic interactions with ecologically similar species in the relatively environmentally continuous areas across the Gulf Slope, but to range contractions leading to isolation in the Yucatan and the Pacific groups.

Keywords Allopatry, Isolated distributions, Niche similarity, Neotropics, Paleodistribution, Songbird

*Correspondence: Luis A. Sánchez-González lasg@ciencias.unam.mx ¹Museo de Zoología, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City, Mexico



© The Author(s) 2025. **Open Access** This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creative.commons.org/licenses/by-nc-nd/4.0/.

Tlalnepantla, Mexico

Querétaro 76230, Mexico

²Laboratorio de Biodiversidad y Cambio Global (LABIOCG), Facultad de

³Unidad Multidisciplinaria de Docencia e Investigación, Facultad de

Estudios Superiores Iztacala, Universidad Nacional Autónoma de México,

Ciencias, Universidad Nacional Autónoma de México, Campus Juriquilla,

Background

The Neotropical region holds the most diverse avifauna in the world [1, 2]. Some of the factors driving this species' richness are related to topographic complexity and the geological history of the region (e.g [3]).,. These features have configured a complex range of environmental conditions in which species may differentiate due to macrohabitat preferences and climatic tolerances [4], but at the same time providing them with opportunities for dispersal and colonization [5].

Despite being the highest in the world, avian Neotropical diversity is likely underestimated (see [6]), especially due to the difficulties in establishing species limits and phylogenetic relationships, and, until recently, an almost exclusively qualitative-based assessment of environmental niche evolution and local adaptative responses [7]. Recent integrative studies, including new theoretical and quantitative tools for delimiting taxonomic units and niche evolution, have provided valuable information for a better understanding of the evolutionary patterns underlying biodiversity [8, 9].

Although geographic speciation is likely dominant in Neotropical birds [10, 11], the quantitative study of climatic niche evolution in geographical isolation and its relationship with species diversification under a niche modelling framework, has been relatively recently addressed [5, 12]. In closely-related species, niche conservatism may remain after geographic isolation [13, 14], since it is expected that isolated populations retain ancestral environmental conditions due to shared ancestry, therefore showing a limited fitness outside the ancestral niche [15, 16]. However, populations may shift to different ecological niches over time, resulting in adaptation to local ecological conditions [17–19]. This scenario implies both differences in niche characteristics due to environmental divergence among the accessible areas for each species, as well as the maintenance of isolated distributions due to unsuitable areas among populations (e.g [14, 20, 21]).

Species Distribution Models (SDMs) and Ecological Niche Models (ENMs) are essential tools in understanding how species are distributed across the geographic and environmental space, as well as in the role of the evolution of environmental niches in the speciation process [12, 20]. Modern approaches involving ENM include the quantifying of the environmental niche overlap between taxa, allowing us to understand the significance that ecological and geographical factors have in biotic diversification, as well as the assessment of biogeographic boundaries separating closely related taxa [22]. Recent research in Mesoamerican birds has shown the relationship between lineage divergence and ecological heterogeneity in different geographic settings. In montane birds of the Chestnut-capped Brushfinch (*Arremon* *brunneinucha*) complex, most lineages showed low climatic niche overlap, suggesting niche divergence in allopatric populations (e.g [20]), while in lowland birds, historical changes in the climatic conditions along the seasonally tropical dry forest in the Pacific slope led to the geographic restriction that probably promoted the adaptation and differentiation in different bird species (e.g [23, 24]).

The Olive Sparrow (Arremonops rufivirgatus; Passerifomes, Passerellidae), is a sedentary Neotropical bird with geographically isolated populations across the lowlands of Mesoamerica (Fig. 1). Based on subtle plumage variations and an allopatric distribution [25, 26], some taxonomic proposals group their populations in putative evolutionary lineages, recognizing two (rufivirgatus, superciliosus; [27, 28]) or three species with a disjunct distribution (rufivirgatus, from extreme SE Texas to the northern Isthmus of Tehuantepec in the Gulf slope; superciliosus, from Sinaloa in western Mexico to northwestern Costa Rica in the Pacific slope; and verticalis from the Yucatan Peninsula; [29–33]). More recently, the study of the acoustic divergence in the songs and behavioral responses also supported three groups, suggesting behavioral isolation [34]. Differentiation may be expected due to the widespread but allopatric distribution of this species complex, which covers several climates and habitats, implying that environmental variation may have played a role in the divergence and evolution of these groups.

Here, we assessed the significance of niche environmental variables in shaping the historical and current geographical distribution of three isolated groups within the *Arremonops rufivirgatus* complex through the development and analyses of SDMs. We also hypothesized ecological niche differentiation due to the geographic disruption of suitable environments among these groups. Finally, we discuss the implications of environmental drivers and geographic patterns as potential reinforcers of the divergence of isolated populations in this species complex.

Materials and methods

Defining the units of analysis

Given that the geographic distribution of the Olive Sparrow spans three major lowland Mesoamerican regions with contemporary ecological and geographical continuity [26, 33], we used these areas for our ecological analyses. This criterion is further supported and congruent with behavioral isolation [34] and taxonomical proposals recognizing three groups [29]. Thus, in this study, we considered three isolated geographic groups within the Olive Sparrow complex: the Gulf group (including *rufivirgatus, ridgwayi* and *crassirostris*), the Pacific group (including *superciliosus, sumichrasti, sinaloae* and



Fig. 1 Occurrence records for three studied groups within *Arremonops rufivirgatus* complex used to perform the Ecological Niche Models (ENMs). Colored dots represent each group, purple = *rufivirgatus* (Gulf), red = *superciliosus* (Pacific), light orange = *verticalis* (Yucatan). Two biomes are shown on the map, representing the Tropical Dry Forests (orange) and the Tropical Moist Forests (green)

chiapensis), and the Yucatan group (including *verticalis* and *rhyptothorax*).

Occurrence data gathering

We compiled a database of all available records of A. rufivirgatus in (1) the 'Atlas of Distribution of Mexican Birds' [35, 36]; (2) The Global Biodiversity Information Facility (GBIF, 2023; available in: http://www.gbif.org); (3) obser vational occurrences in eBIRD (The Cornell Lab of Ornithology-The Audubon Society, ebird.org); and (4) sound records from private and public acoustic libraries, such as Macaulay Library, Cornell Laboratory (http://macaulayli brary.org), Biblioteca de Sonidos de Aves del Museo de Zoología 'Alfonso L. Herrera' (Facultad de Ciencias, Universidad Nacional Autónoma de México), Banco de Sonidos de las Aves de México BSAM (Instituto de Ecología, A.C., México), Xeno-Canto (Xeno-canto Foundation, http://xeno-canto.org), and Sounds of Nature SONAT private collection (A. Celis-Murillo). We complemented all this information with records from our field surveys carried out in México from 2016 to 2020 [34, 37] and 2022 to 2023. In total, we obtained 129,212 occurrence records.

We performed a data cleaning procedure on all compiled records through manual inspections and software tools. We used *OpenRefine* (http://openrefine.org) for cleaning and transforming databases from different sources, which allowed us to fix inconsistencies and merge and match similar values. We also validated the information corresponding to date records and georeferencing accuracy. For this latter, we visualized the congruence of coordinates with the geography using QGIS v.3.28 [38]. We used the *Species Matching* tool (https:// www.gbif.org) for taxonomic validation, normalization, and correction of the binomial nomenclature and synonymies based on the GBIF Backbone Taxonomy.

We verified the correspondence between the historical range and the species distribution models using the Mesoamerican birds' digital maps set [39], as well as in the species distribution maps of the birds of the world [40]. For records in citizen science platforms (e.g., eBird), we retained only those supported with photographic, video, or audio evidence. We removed ambiguous information related to the locality and records with problematic or inaccurate species' occurrence. We also followed the BirdLife International species datasheet [41] to remove those records beyond the known upper elevation limits of each group, as well as those records without information on climatic data.

We further performed spatial and environmental data cleaning using climatic and elevation layers (see Environmental data). We retained occurrence records within the timeframe covered by the climatic variables and evaluated the climatic suitability to include records from 1979 to 2013 (see Environmental data). Additionally, for locality records from 2014 to 2022, we performed an outlier exclusion procedure in the environmental space outside of the interquartile range of three environmental variables, representing the annual average values of temperature and humidity (annual mean temperature [bio 01], annual precipitation [bio 12]), and precipitation seasonality [bio 15] for occurrences from 2014 to 2022 [42]. This procedure allowed us to both reduce the sampling bias and improve data quality [43]. These steps are important to identify problematic or imprecise species' occurrences with incorrect climatic values because the choice of a climatic baseline and the reduction of sampling biases influence model performance [44, 45].

Finally, we used "*spThin*" [46] for R [47] to correct for spatial biases due to the high density of occurrences in some areas (see [13]). For this step, we estimated the most appropriate distance among the presence records and the nearest neighbor to retain only those records separated by at least 1 km, which also corresponds to the spatial resolution of environmental layers used in the analyses. After these steps, we obtained a total of 5,491 occurrence records for the three groups, which are divided as follows: Gulf group = 3,543; Pacific group = 1,151; and Yucatan group = 797. All geographic coordinates were transformed to decimal degrees based on the WGS84 datum.

Defining the accessible area (M)

The concept of the area 'M' (defined as the historical region accessible to dispersal or colonization by the species over some relevant time interval [13, 48]) is considered as an important step in ecological niche modeling, since it supports the outcome of calibration, evaluation, and comparison of models [49]. Therefore, we defined M according to the BAM (biotic and abiotic environmental conditions, and movement) diagram [13, 48]. To do this, we delimited M area for each modeled group by the overlapping of occurrence records with biogeographic regions and terrestrial ecoregions [50]. We assumed that the M area may be reached by dispersal from existing populations, thus probably representing the species' tolerance

limits and, therefore, the historical and ecological barriers to dispersal. Based on previous studies with marked individuals reporting limited movements and high natal philopatry in *A. rufivirgatus* [33, 34, 51], we draw a buffer of 13 km around the area M of each group to account for potential dispersal events (Fig. 2).

Environmental data

We used bioclimatic and vegetation variables to characterize the environmental niches for each group. We downloaded 19 bioclimatic variables from CHELSA v.1.2 [52] with a spatial resolution of 30 arc sec ($\approx 1 \text{ km}^2$) describing temperature and precipitation, seasonality, and other limiting environmental factors in a period ranging from 1979 to 2013. Additionally, for the ecological niche comparison in the present, we used a total of four vegetation variables related to habitat heterogeneity based on the textural features of the Enhanced Vegetation Index (EVI), acquired by the Moderate Resolution Imaging Spectroradiometer (NASA-MODIS/Terra; available at http://earthenv.org). The EVI metrics obtained were: (1) coefficient of variation, which measures the normalized dispersion; (2) standard deviation, which measures the dispersion; and (3) dissimilarity, which measures the difference between adjacent pixels. We also used a layer of percent tree cover (PTC) representing the density of trees on the ground (available at https://globalmaps.gith ub.io/ptc.html). Finally, to avoid collinearity biases due to the inclusion of redundant environmental variables, we selected and retained 16 variables (Table 1) based on the Variance Inflation Factor (VIF < 10), as implemented in 'usdm' [53] for R.

Geographic spatial projection from ecological niche modeling

We obtained potential distribution models for each group using a maximum entropy algorithm, as implemented in MaxEnt v.3.4.4 [54], which calculates the most probable distributional range of a taxon based on the occurrence (presence-only data) and the environmental variables of the accessibility area. We followed a calibration protocol to configure a set of parameters to access model complexity, and evaluated and selected the best model based on the omission rate range using 'kuenm' v.1.1.9 [55] for R. We defined the following arguments for calibration: 15 regularization multipliers (0.2, 0.4, 0.6, 0.8, 1, 1.2, 1.4, 1.6, 1.8, 2, 2.5, 3, 3.5, 4, 5) and feature classes (l=linear, q = quadratic, p = product, t = threshold, and h = hinge) in the basic combination ("l", "lq", "lqp", "lqpt", "lqpt"). This configuration generated 75 candidate models per group, which were evaluated via the partial receiver operating characteristic (partial-ROC; [56]) by analyzing the proportion of 10 bootstrap replicates with the area under the curve (AUC-ratio). We selected all statistically significant



Fig. 2 Representation of the geographical and environmental space in the Olive Sparrow species complex. Maps show pairwise comparison and overlapping area (diagonal line patterns) between each group's estimated distributions. A transparent colored polygon represents the accessible area (M) of each group. Plots along the diagonal (**A**, **E**, **I**) represent occurrence density in the environmental space for each group, with the color gradient indicating the suitability of environmental conditions. The shared area (M) is represented by a continuous line in each map (the dashed line represents 50% of the available environment)

models meeting the omission rate criteria (less than 5%) and with the least complexity based on the Akaike information criterion corrected for small sample sizes (AICc).

We then created presence/absence maps (continuous probability from 0 to 1; [54]) from the logistic values of the suitability maps, using the minimum training presence (MTP) as the threshold value [57]. To test the environmental equivalence among groups, we used binary maps for inter-prediction (degree of geographical matching) of the different group models. We expected that if the environmental niche is similar among species, models should forecast similar potential distribution ranges despite barriers to dispersal (see [7]). Later, for each group, we described the environmental profiles that defined the potential areas and calculated the ranges for each of the variables considered in sites where models predicted areas currently suitable [58]. Then, we extracted the values of the environmental variables for each group and performed a Discriminant Function Analysis (DFA) using the '*MASS*' package in R [59] to assess the conditions defining how suitability areas differ among groups.

Niche overlap in the ecological space

To test niche similarity/differentiation among the three groups in the Olive Sparrow complex, we performed a Principal Component Analysis (PCA) using the retained environmental variables shared among the three groups and analyzed their ecological overlapping using PCAenv, an ordination technique quantifying niche overlap calibrated on the entire environmental space occupied by the studied taxa [60]. We then calculated pairwise niche overlap values using Schoener's *D* index [61], which measures the similarity of suitable habitats for a pair of models by assessing the overlap along the principal component scores discriminating differences between the

Table 1 Environmental variables retained and used to perform ENMs in each group of the *Arremonops rufivirgatus* complex. For each group, we show the variance inflation factor (VIF value). Shared variables among the three groups in bold

Variable	Description	VIF		Shared variables		
		Gulf	Pacific	Yucatan	_	
bio_01	mean annual air temperature	6.126			1	
bio_02	mean diurnal air temperature range	5.718			1	
bio_03	isothermality	9.448	3.139	6.347	3	
bio_04	temperature seasonality		7.185		1	
bio_05	mean daily maximum air temperature of the warmest month		6.542	9.467	2	
bio_08	mean daily mean air temperature of the wettest quarter	4.252	6.563	8.805	3	
bio_09	mean daily mean air temperature of the driest quarter	6.031		1.765	2	
bio_11	mean daily mean air temperature of the coldest quarter			2.569	1	
bio_13	precipitation amount of the wettest month		7.174	2.992	2	
bio_14	precipitation amount of the driest month	3.932	7.336	3.867	3	
bio_15	precipitation seasonality	9.823	9.469		2	
bio_18	mean monthly precipitation amount of the warmest quarter	4.466	3.886	3.389	3	
bio_19	mean monthly precipitation amount of the warmest quarter	3.295	5.623		2	
evi_cv	coefficient of variation of Enhanced Vegetation Index	4.940	8.600	6.381	3	
evi_dis	dissimilarity of the Enhanced Vegetation Index	4.591	8.842	6.228	3	
tree_ptc	percent of tree cover	1.625	1.081	1.226	3	
Retained variables		12	12	11	7	

environmental space occupied by the studied taxa. The index ranges from 0 to 1 and is interpreted as follows: 0–0.2, no or very limited overlap; 0.2–0.4, low overlap; 0.4-0.6, moderate overlap; 0.6-0.8, high overlap; and 0.8-1.0, very high overlap [62]. As in the A. rufivirgatus groups, species showing fragmented distributions may have different accessible environments that may reflect a different environmental distribution unrelated to their ecological preferences [12]. Therefore, we performed a similarity test to correct for the effects of differential suites of environments available for each group on the niche differentiation [17]. We then tested the null hypothesis of niche similarity compared to background environments. From this perspective, niche similarity is accepted if the observed D values are significantly greater than expected from 1,000 pseudoreplicated data sets, allowing random shifts [17, 60].

Ecological barriers and paleodistributions

To test whether species' range limits are bounded by abrupt environmental conditions that may act as ecological barriers, we performed the ribbon range-breaking test, as implemented in ENMTools [63], which allowed us to explore whether the ranges of two taxa are divided by unsuitable habitats representing an environmental transition within the drawn limits [22]. We generated 100 pseudo-replicates of the ribbon for this analysis through the combined range of each pairwise group comparison. We kept constant the width of the ribbon (about 70 km), estimated using QGIS v.3.28 ([38]) based on the width of the continuity and overlapping area predicted in the distribution models among each paired comparison in the three Olive Sparrow groups. We located the first ribbon at the Isthmus of Tehuantepec (Pacific/Gulf comparison) and a second ribbon at the base of the Yucatan peninsula (Gulf/Yucatan and Gulf/Pacific comparisons) (Fig. S1). We calculated Schoener's *D* and Warren's *I* (a measure to quantify the dissimilarity between two probability distributions based on the Hellinger distance) values from the pseudo-replicates to generate null distributions for comparison with empirical values. In the ribbon range-breaking test, ENMs were generated for each set of occurrences on each side of the line and the ribbon using a maximum entropy algorithm.

Finally, to identify the historical range extent and stability areas of each group, we performed a paleoclimatic reconstruction of the distribution of suitable areas during the Late Pleistocene climatic fluctuations using the same methodological approach as for the ENM (see above). We used the environmental variables from CHELSA v.1.2 [52] with a spatial resolution of 2.5 min ($\sim 5 \text{ km}^2$) to perform the niche models at the present. We projected models to suitable climatic conditions during the Mid-Holocene (Mid-Hol, 6000 Ya) and to the Late Pleistocene climate fluctuations, including the Last Glacial Maximum (LGM; 21,000 Ya) and the Last Interglacial (LIG, \sim 120,000–140,000 Ya). Since vegetation variables are not available in paleo-temporal scales, we used the retained climatic variables shared among the three groups (bio 03, bio 08, bio 14, bio 18), which we downloaded from PALEOCLIM (Paleclim.org [64]), with a spatial resolution of 2.5 min (~5 km). We created presence/absence maps (from the logistic values of the suitability maps) using the minimum 10-percentile training

|--|

Group	Regularization multipliers	feature	Mean AUC ratio	Omission rate 5%	AICc	W AICc	Parameters		
A) Models v	A) Models with climate-vegetation variables for current								
Gulf	0.6	lqpth	1.594	0.049	65975.163	0.519	189		
Pacific	0.2	lqp	1.607	0.048	20126.355	1	57		
Yucatan	0.2	lq	1.567	0.041	13435.672	1	13		
B) Models with climate variables for paleodistribution									
Gulf	0.0.2	lqp	1.41	0.034	52016.95	1	12		
Pacific	0.6	lqp	1.487	0.048	16519.97	1	10		
Yucatan	0.2	lq	1.452	0.062	10292.42	1	8		

presence as the threshold value. To assess the stability and reliability of the transference of the models to the past, we performed an extrapolation risk analysis via the Mobility-Oriented Party (MOP) test as implemented in "NicheToolbox" [65]. This procedure allowed us to identify regions where environmental conditions in past climates deviated significantly from those in the calibration period, thus flagging areas where model predictions may be less reliable [66]. We performed the analyses considering random sampling of 25% for each area M.

Results

Present geographical distributions

We selected a set of significant environmental variables for model building for each group (Table 1). Overall, selected final models were used to perform 10 replicates, which showed significant partial ROC test values (>1.5, Table 2A).

Based on the MTP threshold and our binary maps, the largest geographic range was estimated for the Gulf group, which covers the lowlands of the Gulf of Mexico and is limited by the elevations of the Sierra Madre Oriental; a clear bottleneck is shown in the northeastern slope of the Trans-Mexican Volcanic Belt in central Veracruz. According to our geographic model, currently non-occupied but suitable areas were highlighted at the northern and central Isthmus of Tehuantepec, as well as in the southern Yucatan peninsula (Fig. 2A, B). The potential distribution estimated for the Pacific group runs almost continuously from northwestern Mexico (southern Sinaloa), where the predicted distribution is limited by the highlands of the Sierra Madre Occidental and Sierra Madre del Sur, across the Pacific slope to the lowlands of Costa Rica. There is a distributional gap likely due to the humid lowlands of southeastern Mexico (Soconusco) and southern Guatemala (Fig. 2C, D). The smallest potential distribution range was estimated for the Yucatan group, which covers the Yucatan peninsula and small and isolated areas in the central Chiapas depression (Fig. 2E, F).

We calculated the geographical distribution overlap as an indirect estimation of the ecological niche overlap. In general, we found that predicted distributions showed **Table 3** Confusion matrix for prediction of Arremonops groupsbased on the environmental ranges of shared environmentalvariables

Prediction/Reference	Gulf	Pacific	Yucatan
Gulf	642,783	62,597	22,965
	(88.25%)	(8.59%)	(3.15%)
Pacific	73,171	699,041	47,371
	(8.93%)	(85.29%)	(5.78%)
Yucatan	68,904	43,541	119,053
	(29.76%)	(18.81%)	(51.43%)

a limited (<17%) geographical matching among groups (Table S1). The three groups showed a potentially suitable geographical distribution overlap in the southern Yucatan Peninsula; suitable areas for two of the groups were in the central Isthmus of Tehuantepec and central Veracruz and northern Oaxaca (Fig. 2). We found the highest geographic overlap between the Gulf and the Yucatan groups (17%, Fig. 2E), in contrast, the smallest overlapping area was between Pacific and Yucatan (3%, Fig. 2D).

Additionally, only seven of the environmental variables retained based on the VIF criteria were shared by all three species groups. These are related to variation in the ranges of temperature, precipitation, and vegetation (Table 1). The DFA showed high accuracy in the classification of the different *Arremonops* groups, suggesting that conditions defining the suitability areas among groups differ (0.821, 95% CI=0.820,0.821, Kappa=0.7, P < 0.001; Table 3, S2, Fig. S2).

Niche overlap in the ecological space

The PCA analysis indicated that the two first principal components explain 54.72% of the environmental variation (Fig. S3). The first principal component (PC1) explained a 31.61% of the total variation and was strongly associated with the habitat structure (percent of tree cover [tree_ptc]) and the relation of annual and daily temperature oscillations (isothermality [bio_03]), while the second principal component (PC2) explained a 23.11% of the total variation and was strongly associated with the canopy structure and its variation (coefficient of variation of Enhanced Vegetation Index [evi_cv] and dissimilarity of the Enhanced Vegetation Index [evi_dis]). Our results indicated no or very limited ecological niche overlap (Schoener's D < 0.2, Table S3) for each paired comparison among geographic groups. According to the background tests in the Gulf/Pacific and Gulf/ Yucatan comparisons, results indicated a low niche similarity, suggesting that the ecological niche in each group is not more similar than random expectations in

Similarity - Gulf (occ) vs. Pacific (bkg)

Similarity - Gulf (occ) vs. Peninsula (bkg)



Similarity - Pacific (occ) vs. Peninsula (bkg)



both directions. Such results allowed us to reject niche similarity among these groups. However, we could not reject niche similarity in the Pacific/Yucatan comparison (Fig. 3).





Similarity - Peninsula (occ) vs. Gulf (bkg)



Similarity - Peninsula (occ) vs. Gulf (bkg)



Fig. 3 Results of the background niche similarity test for each paired comparison among groups, measured by Schoener's D. Histograms correspond to the expected distribution based on the randomization of the data. A vertical red line with a diamond represents niche overlap values compared to a null distribution of background divergence

Table 4 Schoener's D values and significance of ribbon range-breaking test

Pairwise group comparison		Ribbon range-breaking							
G1	G2	G1 vs. G2	Р	G1 vs. Ribbon	Р	G2 vs. Ribbon	Р	Outside vs. Ribbon	Р
Gulf	Pacific	0.207	0.050*	0.307	0.198	0.429	0.089	0.446	0.465
Gulf	Yucatan	0.196	0.139	0.272	0.396	0.348	0.287	0.366	0.327
Pacific	Yucatan	0.137	0.010*	0.256	0.436	0.400	0.436	0.472	0.149



Fig. 4 Results from the ribbon range-breaking test between pairwise groups. Vertical bar plots show values of Schoener's *D* in flanking regions. Significance is shown as ns = non-significant and *=P < 0.05. Vertical density plots indicate the distribution of Warren's *I* values from 100 unique pseudo-replicates calculated between the flanking regions and the ribbon

Biogeographic boundaries and paleodistributions

Schoener's *D* values from the ribbon range-breaking test suggest a region with unsuitable environmental conditions separating the Pacific group from the Yucatan and the Gulf groups (P < 0.05; Table 4; Fig. 4), but not among the Gulf and Yucatan groups (P = 0.139). Additionally, the environmental conditions of the ribbon in the flanking regions are no more different from one another

than expected by chance for all the paired comparisons (P < 0.05, Table 4; Fig. 4).

All paleodistribution model projections showed high performance (ROC partial > 1.4, Table 2B), indicating that models are significantly better than expected by chance. High environmental suitability areas for the three groups in the Olive Sparrow complex showed changes in size and location in comparison to the present (Fig. 5). Thus,



Fig. 5 Presence-absence maps for the three Olive Sparrow groups based on ecological niche models projected onto the geographic areas for the Gulf group (violet), Pacific group (red), and Yucatan group (orange). Maps depict suitable historical distribution areas for climate niches across the Present, the Holocene, and Last Glacial Maximum (LGM) and Last Interglacial (LIG) periods of the late Pleistocene. For the Present, maps show the distribution within the accessible area. Darker colors depict regions of historical climatic stability in a pairwise comparison with the Present. Smaller areas for Yucatan group in LGM are pointed with arrows

for the Gulf group, LIG indicated widespread suitability across the central and southern Gulf slope from extreme southern USA and northwestern Mexico to Panama. Climatic changes produced range contractions during the LGM, with suitable areas mostly restricted to the Gulf Slope and the northern Isthmus of Tehuantepec, across the Pacific slope and the northeastern Yucatan peninsula. Later, in the Mid-Holocene, the geographic range expanded towards the northern Gulf slope, most of which has been maintained up to the present.

For the Pacific group, LIG showed suitable environments isolated in three main regions throughout the Pacific slope: (1) from northern Sinaloa to eastern Guerrero in Mexico, (2) the southern Isthmus of Tehuantepec in southeastern Mexico, and (3) from southern Guatemala to western Nicaragua. This widespread distribution severely contracted to highly isolated habitat patches across the Pacific slope and the southern Yucatan peninsula. Most of these isolated patches disappeared during the Mid-Holocene, and suitable environmental conditions were restricted to northern Mexico and contracted even to smaller regions across the Pacific slope. Suitable areas in the present resemble the distribution during the LIG, suggesting recolonization from these small patches. For the Yucatan group, LIG showed isolated suitable areas in Mesoamerica, which severely contracted in the LGM, maintaining small and isolated regions in the base of the Yucatan peninsula, southern Central America (probably in the Volcanic Arc in El Salvador), and in the Pacific slope (southern Sinaloa). However, suitable environmental conditions in the Mid-Holocene recovered in the Yucatan Peninsula, from which this taxon expanded to most of the areas in the present. In general, according to environmental suitability maps, the historically suitable areas for all three groups appear as mainly allopatric, except in some parts of the Yucatan Peninsula in different time intervals (Fig. 5).

Finally, our MOP analysis showed high congruence in the climatic conditions among past and present ENM models but showed some regions with non-analogous climatic conditions for all groups during the LIG (e.g. northern Central America and the southwestern Mexico; Fig. S4).

Discussion

Species' distributional patterns and their environmental tolerances allow the understanding of the role of ecological factors in speciation and niche evolution [67]. In

polytypic taxa, using lower taxonomic rank categories to estimate potential distributions and ecological niche similarities (or differences) has been recommended as a more accurate approach [7]. This approach allowed us to find niche divergence in the three groups analyzed within the Olive Sparrow complex, suggesting that Grinnellian niches are not conserved, awarding ecological differentiation among groups.

The niche conservatism hypothesis predicts that the distribution of closely-related species is limited by contrasting environments due to physiological constraints [68, 69]. This pattern may be expected as closely related taxa share ancestral environmental suitability (see [13, 70]). Nevertheless, our similarity tests indicated that there are niches with low environmental similarity for most of our pairwise comparisons. Although we found low similarity in the ecological niches of the Pacific and the Yucatan groups, we cannot reject the niche conservatism hypothesis [12, 60]. Niche conservatism has been found in other birds with similar allopatric distributional patterns in seasonally dry tropical forests in the Yucatan peninsula and the Mesoamerican Pacific slope, suggesting that currently disjunct geographic distribution may be due to range contraction [14]. However, the Yucatan group inhabits a wider range of environmental conditions, covering both dry and moist forests in the Yucatan peninsula, suggesting that the occupation of some habitats in the region may be due to ecological release, probably promoted by niche differentiation and further expansion [71]. Thus, whether the lack of significant niche similarity between the Yucatan and the Pacific groups may be due to a widespread ecological distribution or to historical range contraction remains to be tested.

Overall, the geographic distribution for the three groups in the Olive Sparrow species complex mirrors emergent evolutionary patterns of the Mesoamerican lowland forests related to the historical climate changes that may have promoted the evolution of different lineages in these biomes (e.g [14, 23, 72, 73]).,. Despite the fragmented distribution and differences in environmental conditions, the projection of the niche models on each other's geographic distribution showed some overlapping areas, as in the northern Isthmus of Tehuantepec (Gulf/ Pacific; Fig. 2) and the southern Yucatan peninsula (Gulf/ Pacific, Gulf/Yucatan, Pacific/Yucatan; Fig. 2). The current absence of occurrence records in these areas may be associated either with historical isolation among populations due to environmental barriers (see below), or to the role that biotic interactions may have in maintaining and reinforcing geographic isolation and divergence among groups.

The niche divergence found between the Gulf and the Yucatan groups suggests local adaptation and tolerance to

different environments despite the apparent geographic continuity of the lowlands. Similar scenarios have been proposed in codistributed bird taxa, such as the Buffbellied hummingbird Amazilia yucatanensis [74], and the White-tipped Dove Leptotila verreauxi [24], which showed concordant phylogeographic breaks in the southern Gulf of Mexico slope, separating populations between northern (Gulf slope) and southern (Yucatan peninsula) groups with non-equivalent niches. Our tests on biogeographic boundaries revealed environmental differences between most groups due to the potential presence of unsuitable areas in the southern Yucatan peninsula and the Isthmus of Tehuantepec. This latter region seems to act as a barrier for the Pacific population due to environmental differences found in the comparisons between the Gulf/Pacific and Pacific/Yucatan groups, which may limit dispersal in these populations. However, the area in the southern Yucatan Peninsula apparently does not represent a barrier of unsuitable climatic conditions for the Gulf and Yucatan groups. Additionally, the barrier did not show differences with the involved taxa on both sides in all comparisons, suggesting that probably biotic factors have maintained the isolation in these groups. A similar scenario has been reported in three *Leptotila* lineages in Mesoamerica, in which the environmental differences among lineages and the presence of a potential unsuitable region in the Isthmus of Tehuantepec have likely promoted secondary contact [24]. Our results may also indicate that other factors such as biological interactions with closely related taxa with similar niche requirements, may have a significant role in maintaining differentiation and isolation in the geographically isolated Olive Sparrow populations.

According to our results, ecological differentiation has maintained the allopatric distribution in the Olive Sparrow species complex. Based on phylogenetic analyses in New World Sparrows [75, 76], the Arremonops northern clade (A. rufivirgatus and A. chloronotus) diverged relatively recently (~3.03 Ma) in comparison to the clade in southern Central and South America (A. conirostris and A. tocuyensis). These results suggest that the northern Arremonops clade colonized new regions during the Late Pliocene and Pleistocene climate cycles. Late Pleistocene climatic suitability indicates that the distribution of the Gulf group has expanded and maintained since the Mid-Holocene to northeastern Mexico and Texas. The vanishing suitable areas detected in southern México (mainly in the Yucatan Peninsula) and northern Central America may be due to biological interactions involving a potential competitive exclusion with A. chloronotus and A. conirostris a local scale. The dynamic biotic history between these taxa and their related environmental preferences may sustain differentiation over time, thereby delaying and limiting opportunities for colonization,

similar to findings in other species [77]. The high fragmentation detected in suitable areas across the Pacific slope since the LIG suggests that the Pacific group should be evaluated in more detail, as some populations in this group, which includes four apparently isolated subspecies, may be restricted by ecological barriers, the competitive interactions, or geographic isolation as has been found in similarly codistributed bird taxa [21, 23, 73, 78, 79].

Subsequent climatic changes and stable climatic areas during the LGM may have promoted opportunities for allopatric diverge in isolation, as in other bird lineages (e.g. [78].; Columbidae: *Leptotila verreauxi* [24], Picidae: *Melanerpes santacruzi* [80]; Tyrannidae: *Attila spadiceus* [81]; Cuculidae: *Piaya cayana* [23]; Corvidae: *Calocitta* [21]. A detailed reconstruction of the historic paleoclimatic distribution in the Olive Sparrow and the *Arremonops* genus with support of multidisciplinary approaches using molecular, genetic, and morphological analysis is needed to understand the historical and ecological process associated with historical climatic stability that may support these divergence patterns.

Supplementary Information

The online version contains supplementary material available at https://doi.or g/10.1186/s12862-025-02373-z.

Supplementary Material 1

Acknowledgements

The first author extends his gratitude to the Universidad Nacional Autónoma de México (Dirección General de Asuntos del Personal Académico, DGAPA-UNAM, México) for the Postdoctoral scholarship supporting this research. We thank Alejandro Gordillo-Martínez for his assistance and support during the study of specimens from the ornithology and bird sound collections at the Museo de Zoología 'Alfonso L. Herrera'. R.A.F-G. Thanks to Reinhard Matadamas, Luis Enrique Sánchez, Bill Chan, Orlando Espinosa, and Erick Corro for their comments and support during the analysis. Aldo Echeverria and Gerardo Linares greatly supported fieldwork at the Yucatan Peninsula. We sincerely thank Dr. Bryan T. Smith, Andrzej Falniowski, Vidhi Sarin and two anonymous reviewers for comments and suggestions that greatly improved our manuscript.

Author contributions

RAF-G and LAS-G conceived and designed this research. RAF-G compiled and collected the data and performed the analyses. RAF-G and LAS-G wrote the manuscript. LAS-G supervised the study. DAP-T supported the design of the methodology and validated the analyses. AGN-S reviewed and edited the manuscript. All authors reviewed and edited the manuscript. All authors read and approved the final manuscript.

Funding

This research was supported by a postdoctoral fellowship granted to RAF-G. by the Dirección General de Asuntos del Personal Académico of the Universidad Nacional Autónoma de México (DGAPA-UNAM), the Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (DGAPA-UNAM; PAPIIT IN-214521 to LAS-G), the support of the National System of Researchers of Mexico (SNII-CONAHCYT), and the Developing Nation Grant provided by the Animal Behavior Society.

Data availability

The datasets supporting the conclusions of this article are available in the GitHub repository: https://github.com/ronaldehido/Olive-Sparrow_ENM.

Declarations

Ethics approval and consent to participate

Our research was carried out under ethical guidelines and approved permits by the Dirección General de Vida Silvestre de México (SEMARNAT; Permits: SGPA/DGVS/01319/16; SGPA/DGVS/ 00853/17; SGPA/DGVS/002783/18; SGPA/ DGVS/003508/18, SPARN/DGVS/01058/22). Sound files from Xeno-Canto are Open Access. Access to the Macaulay Library, Banco de Sonidos de las Aves de México and Biblioteca de Sonidos de Aves del Museo de Zoología, was by direct email request to the curators (M. Medler, F. González, A. Gordillo), and records from SONAT were by email request to the owner (T. Celis).

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

Clinical trial

Not applicable.

Received: 25 October 2024 / Accepted: 7 April 2025 Published online: 16 April 2025

References

- Smith BT, McCormack JE, Cuervo AM, Hickerson MJ, Aleixo A, Cadena CD, et al. The drivers of tropical speciation. Nature. 2014;515:406–9.
- Harvey MG, Bravo GA, Claramunt S, Cuervo AM, Derryberry GE, Battilana J, et al. The evolution of a tropical biodiversity hotspot. Sci (80-). 2020;370:1343–8.
- Cadena CD, Klicka J, Ricklefs RE. Evolutionary differentiation in the Neotropical montane region: molecular phylogenetics and phylogeography of *Buarremon* brush-finches (Aves, Emberizidae). Mol Phylogenet Evol. 2007;44:993–1016.
- Graham CH, Ron SR, Santos JC, Schneider CJ, Moritz C. Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. Evol (NY). 2004;58:1781–93.
- Title PO, Burns KJ. Rates of Climatic niche evolution are correlated with species richness in a large and ecologically diverse radiation of songbirds. Ecol Lett. 2015;18:433–40.
- Freeman BG, Pennell MW. The latitudinal taxonomy gradient. Trends Ecol Evol. 2021;36:778–86.
- Mota-Vargas C, Rojas-Soto OR. Taxonomy and ecological niche modeling: implications for the conservation of wood partridges (genus *Dendrortyx*). J Nat Conserv. 2016;29:1–13.
- Sharma S, Winner K, Mäkinen J, Jetz W. Measuring the evolution of n-dimensional environmental niches. Ecography (Cop). 2025;2025:273–86.
- Winker K. An overview of speciation and species limits in birds. Ornithology. 2021;138:1–27.
- 10. Price TD. Speciation in birds. Greenwood village. CO.: Roberts & Compary; 2008.
- 11. Brumfield RT. Perspectives in ornithology: inferring the origins of lowland Neotropical birds. Auk. 2012;129:367–76.
- McCormack JE, Zellmer AJ, Knowles LL. Does niche divergence accompany allopatric divergence in *Aphelocoma* Jays as predicted under ecological speciation? Insights from tests with niche models. Evol (N Y). 2010;64:1231–44.
- Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, et al. Ecological niches and geographic distributions. Princeton University Press; 2011.
- 14. Chan PT, Arroyo-Cabrales J, Prieto-Torres DA, Sánchez-González LA. The role of ecological niche conservatism in the evolution of bird distributional patterns in Mesoamerican seasonally dry forests. J Biogeogr. 2024.
- Wiens JJ, Graham CH. Niche conservatism: integrating evolution, ecology, and conservation biology. Annu Rev Ecol Evol Syst. 2005;36:519–39.
- 16. Wiens JJ. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. Evol (N Y). 2004;58:193.

- Warren DL, Glor RE, Turelli M. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evol (N Y). 2008;62:2868–83.
- Broennimann O, Treier UA, Müller-Schärer H, Thuiller W, Peterson AT, Guisan A. Evidence of Climatic niche shift during biological invasion. Ecol Lett. 2007;10:701–9.
- 19. Lenormand T. From local adaptation to specialization: specialization and reinforcement. Int J Ecol. 2012;2012:1–11.
- Moreno-Contreras I, Sánchez-González LA, Arizmendi M, del Prieto-Torres C, Navarro-Sigüenza DA. Climatic niche evolution in the *Arremon Brunneinucha* complex (Aves: Passerellidae) in a Mesoamerican landscape. Evol Biol. 2020;47:123–32.
- Sánchez-González LA, Castillo-Chora VJ, Arbeláez-Cortés E, Navarro-Sigüenza AG. Diversification and secondary contact in the magpie-jays (*Calocitta*) throughout the Pacific lowlands of Mesoamerica. J Zool Syst Evol Res. 2021;59:2371–86.
- Glor RE, Warren D. Testing ecological explanations for biogeographic boundaries. Evol (N Y). 2011;65:673–83.
- Sánchez-González LA, Cayetano H, Prieto-Torres DA, Rojas-Soto OR, Navarro-Sigüenza AG. The role of ecological and geographical drivers of lineage diversification in the squirrel cuckoo *Piaya Cayana* in Mexico: a mitochondrial DNA perspective. J Ornithol. 2023;164:37–53.
- Espinosa-Chávez OJ, Navarro-Sigüenza AG, Rodríguez-Correa H, Sánchez-González LA. Highly divergent sympatric lineages of Leptotila verreauxi (Aves: Columbidae) suggest a secondary contact area in the isthmus of Tehuantepec, Mexico. Avian Res. 2024;15(January):100160.
- 25. Parkes KC. Variation in the Olive sparrow in the Yucatan Peninsula. Auk. 1974;86:293–5.
- 26. Howell SNG, Webb S. A guide to the birds of Mexico and Northern central America. Oxford, UK: Oxford University Press; 1995.
- 27. Clements JF, Schulenberg TS, Iliff MJ, Fredericks TA, Gerbracht JA, Lepage D et al. The eBird/Clements checklist of birds of the world: v2022. 2022.
- 28. Gill F, Donsker D, Rasmussen P. IOC World Bird List (v13.1). 2023.
- 29. Navarro-Sigüenza AG, Peterson AT. An alternative species taxonomy of the birds of Mexico. Biota Neotrop. 2004;4:1–32.
- Rising J. Olive sparrow (Arremonops rufivirgatus). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E, editors. Handbook of the birds of the world. Barcelona: Lynx Edicions; 2011.
- 31. Dickinson EC, Christidis L. The Howard & Moore complete checklist of the birds of the world. 4th edition. Eastbourne, UK.: Aves Press; 2014.
- 32. del Hoyo J. All the birds of the world. Barcelona: Lynx Edicions; 2020.
- Brush T. Olive sparrow (Arremonops rufivirgatus), version 2.0. In: Rodewald PG, editor. Birds of the world. Ithaca, NY, USA.: Cornell Lab of Ornithology; 2023.
- Fernández-Gómez RA, Morales-Mávil JE, Sosa-López JR. Geographic variation and divergence of songs in the Olive sparrow species complex. J F Ornithol. 2020;91:77–91.
- Navarro S, AG, Townsend Peterson A, Gordillo-Martínez A. A Mexican case study on a centralised database from world natural history museums. Data Sci J. 2002;1:45–53.
- Navarro-Sigüenza AG, Townsend Peterson A, Gordillo-Martínez A. Museums working together: the atlas of the birds of Mexico. Bull Br Ornithol Club. 2003;123A:207–25.
- Fernández-Gómez RA, Morales-Mávil JE, Hernández-Salazar LT, Sosa-López JR. Asymmetric behavioural responses to divergent vocal signals in allopatric Neotropical sparrows. Anim Behav. 2021;174:41–50.
- 38. QGIS.org. QGIS Geographic Information System. 2024.
- Navarro-Sigüenza AG, Gordillo-Martínez A, Townsend Peterson A, Ríos-Muñoz CA, Gutiérrez-Arellano CR, Méndez-Aranda D, et al. Mapas de Distribución de Las Aves terrestres Nativas de Mesoamérica. Ciudad de México; 2018.
- 40. BirdLife, International. Handbook of the Birds of the World. Bird species distribution maps of the world. 2019.
- BirdLife International. Arremonops rufivirgatus. The IUCN Red List of Threatened Species 2021:eT22721392A138547833. 2021. https://www.iucnredlist.or g/species/22721392/138547833. Accessed 2 Sep 2023.
- Prieto-Torres DA. Práctica 28. Adquisición y biocuración de Datos distribucionales. In: Escalante T, García-Trejo EA, Morrone JJ, editors. Biogeografía práctica. Ciudad de México: Universidad Nacional Autónoma de México, Facultad de Ciencias; 2024. pp. 105–7.
- Robertson MP, Visser V, Hui C, Biogeo. An R package for assessing and improving data quality of occurrence record datasets. Ecography (Cop). 2016;39:394–401.

- Roubicek AJ, VanDerWal J, Beaumont LJ, Pitman AJ, Wilson P, Hughes L. Does the choice of climate baseline matter in ecological niche modelling? Ecol Modell. 2010;221:2280–6.
- Boria RA, Olson LE, Goodman SM, Anderson RP. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecol Modell. 2014;275:73–7.
- Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP. SpThin: an R package for Spatial thinning of species occurrence records for use in ecological niche models. Ecography (Cop). 2015;38:541–5.
- 47. R Core Team. R: a lenguage and environment for statistical computin. 2023.
- Soberón J, Peterson AT. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodivers Inf. 2005;2:1–10.
- Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A, Maher SP, Peterson AT, et al. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol Modell. 2011;222:1810–9.
- Rojas-Soto O, Forero-Rodríguez JS, Galindo-Cruz A, Mota-Vargas C, Parra-Henao KD, Peña-Peniche A et al. Calibration areas in ecological niche and species distribution modelling: unravelling approaches and concepts. J Biogeogr 2024; May 2023:1–13.
- Brush T, Olive, Sparrow. Arremonops rufivirgatus. In: Brush T, editor. Nesting birds of a tropical frontier: the lower Rio Grande Valley of Texas. Texas: Texas A&M University; 2005.
- Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, et al. Climatologies at high resolution for the Earth's land surface areas. Sci Data. 2017;4:170122.
- Naimi B. Usdm: uncertainly analysis for species distribution models. R Package. 2015.
- 54. Phillips SJ, Anderson RP, Schapire RE. Maximum entropy modeling of species geographic distributions. Ecol Modell. 2006;190:231–59.
- Cobos ME, Townsend Peterson A, Barve N, Osorio-Olvera L, Kuenm. An R package for detailed development of ecological niche models using maxent. PeerJ. 2019;2019:1–15.
- Peterson AT, Papeş M, Soberón J. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecol Modell. 2008;213:63–72.
- 57. Liu C, White M, Newell G. Selecting thresholds for the prediction of species occurrence with presence-only data. J Biogeogr. 2013;40:778–89.
- Widholzer RL, Prieto-Torres DA. Novel data on the distribution patterns and ecological differentiation of four species of treefrogs (Hylidae: *Boana*) in southeastern South America. North West J Zool. 2022;18:168–78.
- Venables W, Ripley B. Modern applied statistics with S. Fourth Edi. New York: Springer; 2002.
- Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, et al. Measuring ecological niche overlap from occurrence and Spatial environmental data. Glob Ecol Biogeogr. 2012;21:481–97.
- 61. Schoener TW. The Anolis lizards of bimini: resource partitioning in a complex fauna. Ecology. 1968;49:704–26.
- 62. Rödder D, Engler JO. Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks. Glob Ecol Biogeogr. 2011;20:915–27.
- 63. Warren DL, Glor RE, Turelli M, ENMTools. A toolbox for comparative studies of environmental niche models. Ecography (Cop). 2010;33:607–11.
- Brown JL, Hill DJ, Dolan AM, Carnaval AC, Haywood AM. PaleoClim, high Spatial resolution paleoclimate surfaces for global land areas. Sci Data. 2018;5:180254.
- Osorio-Olvera L, Lira-Noriega A, Soberón J, Peterson AT, Falconi M, Contreras-Díaz RG, et al. Ntbox: an R package with graphical user interface for modelling and evaluating multidimensional ecological niches. Methods Ecol Evol. 2020;11:1199–206.
- Owens HL, Campbell LP, Dornak LL, Saupe EE, Barve N, Soberón J, et al. Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. Ecol Modell. 2013;263:10–8.
- Smith GW, Rodríguez-Sánchez F, Wang H-H, Warren D. Niche Estimation above and below the species level. Trends Ecol Evol. 2019;34:260–73.
- Wiens JJ, Donoghue MJ. Historical biogeography, ecology and species richness. Trends Ecol Evol. 2004;19:639–44.
- Khaliq I, Fritz SA, Prinzinger R, Pfenninger M, Böhning-Gaese K, Hof C. Global variation in thermal physiology of birds and mammals: evidence for phylogenetic niche conservatism only in the tropics. J Biogeogr. 2015;42:2187–96.
- Peterson AT, Soberón J, Sánchez-Cordero V. Conservatism of ecological niches in evolutionary time. Sci (80-). 1999;285:1265–7.
- Herrmann NC, Stroud JT, Losos JB. The evolution of 'ecological release' into the 21st century. Trends Ecol Evol. 2021;36:206–15.

- Arango A, Villalobos F, Prieto-Torres DA, Guevara R. The phylogenetic diversity and structure of the seasonally dry forests in the neotropics. J Biogeogr. 2021;48:176–86.
- Castillo-Chora VDJ, Sánchez-González LA, Mastretta-Yanes A, Prieto-Torres DA, Navarro-Siguënza AG. Insights into the importance of areas of Climatic stability in the evolution and maintenance of avian diversity in the Mesoamerican dry forests. Biol J Linn Soc. 2021;132:741–58.
- Vásquez-Aguilar AA, Macswiney GMC, Rodríguez-Gómez F, Ornelas JF. Mitochondrial, morphological and environmental data partially support current subspecies designation in *Amazilia yucatanensis* hummingbirds. Biol J Linn Soc. 2023;138:413–36.
- Klicka J, Keith Barker F, Burns KJ, Lanyon SM, Lovette IJ, Chaves JA, et al. A comprehensive multilocus assessment of sparrow (Aves: Passerellidae) relationships. Mol Phylogenet Evol. 2014;77:177–82.
- Barker K, Burns KJ, Klicka J, Lanyon SM, Lovette IJ. New insights into new world biogeography: an integrated view from the phylogeny of Blackbirds, Cardinals, sparrows, tanagers, warblers, and allies. Auk. 2015;132:333–48.
- 77. Anderson RP. When and how should biotic interactions be considered in models of species niches and distributions? J Biogeogr. 2017;44:8–17.
- Barber BR, Klicka J. Two pulses of diversification across the isthmus of Tehuantepec in a montane Mexican bird fauna. Proc R Soc B Biol Sci. 2010;277:2675–81.

- Ornelas JF, Sosa V, Soltis DE, Daza JM, González C, Soltis PS et al. Comparative phylogeographic analyses illustrate the complex evolutionary history of threatened cloud forests of Northern Mesoamerica. PLoS ONE. 2013;8.
- Llanes-Quevedo A, Mastretta-Yanes A, Sánchez-González LA, Castillo-Chora VJ, Navarro-Sigüenza AG. The tangled evolutionary history of a long-debated Mesoamerican taxon: the Velazquez woodpecker (*Melanerpes santacruzi*, Aves: Picidae). Mol Phylogenet Evol. 2022;170 February.
- Mendonça P, Dias C, Aleixo A, Carneiro LS, Araripe J, Rêgo PS. do. Diversification across the Isthmus of Tehuantepec explains the phylogeographic arrangement of the widespread bright-rumped Attila (*Attila spadiceus*; Tyrannidae) and reveals the existence of two major lineages. J Ornithol. 2022;163:327–32.

Publisher's note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.