Journal of Biogeography (*J. Biogeogr.*) (2017) **44**, 2145–2160

ORIGINAL ARTICLE

Biogeographical transitions in the Sierra Madre Oriental, Mexico, shown by chorological and evolutionary biogeographical affinities of passerine birds (Aves: Passeriformes)

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ABSTRACT

Aim To locate areas of biogeographical transitions within the Sierra Madre Oriental (SMO), Mexican transition zone.

Location Eastern Mexico (18° to 27° N – 90° to 96° W) and the Americas.

Methods We deconstructed passerine fauna into biogeographical affinities to map their integration in the studied area. We defined and quantified two features of biogeographical affinity based on raw distributional range concordance (chorological affinity), and on ancestral state reconstruction of published phylogenies (evolutionary biogeographical affinity). Then, we divided the SMO into 500 m elevation intervals and 1.2° latitudinal belts. Point records of resident passerine birds were used to compute species turnover and to map the dominance and heterogeneity of biogeographical affinities along the gradient.

Results Considering the gradient of biogeographical affinities, we identified the sharpest transition at elevations of *c.* 1500 m from the southern evergreen cloud forests to the canyons of the middle Pánuco basin (*c.* 22° of latitude) and then turning eastwards, following the Pánuco river through the semi-deciduous lowland forest to the river mouth in the Gulf of Mexico.

Main conclusions Our analysis allowed us to map a gradual pattern of variation based on a quantitative definition of biogeographical affinities. This approach is particularly useful for the analysis of rather small areas where a regional biota cannot be partitioned concomitantly with regionalization procedures. Our findings support previous suggestion of a middle elevation zone of mixture between Neotropical and Nearctic biotas, as shown by their chorotypes and cenocrons, and highlight the Pánuco river as a biogeographical boundary dividing northern and southern assemblages based on bird distributions in north-eastern Mexico.

Keywords

Cenocrons, chorotypes, distributional patterns, elevational gradient, Mexican transition zone, mountain biogeography, species distribution, transition zone

INTRODUCTION

One of the most challenging tasks for biogeographers has been to delimit the boundaries between biogeographical regions. This is complicated because different taxa exhibit varied degrees of juxtaposition in geographical space. Thus, discordant lines drawn on maps to indicate location of biogeographical boundaries have been proposed by different authors between the same biogeographical regions.

All world biogeographical schemes have recognized the division between the Nearctic and Neotropical regions and the boundary between them has been repeatedly located in Mexico. Sclater (1858) and Wallace (1876) included the

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doi:10.1111/jbi.13015

plateau of central Mexico as the southern limit of the Nearctic region. Darlington (1957) summarized the transition of vertebrate faunas as the overlap of faunal elements in a broad area including Mexico and Central America. In a more detailed analysis, Halffter (1987) defined the Mexican transition zone as the complex area where the Neotropical and Nearctic faunas overlap, from south-western United States to the Nicaraguan lowlands. Halffter (1987) also noted an elevational zonation among different 'distributional patterns' (equivalent to cenocrons: animal or plant groups, which disperse into a given area between definite limits of geological time; see Morrone, 2014a) based on insects: Mesoamerican taxa were the most frequent at lower altitudes (< 2000 m), Nearctic and Palaeoamerican taxa dominated between 2000 and 3000 m, and Nearctic taxa were found almost exclusively above 3000 m. Studies of elevation gradients in Mexico have focused mainly on ecological patterns, such as species richness, abundance, life-forms and conservation priorities rather than on the role of elevation in structuring the transition zone (e.g. Navarro-Sigüenza, 1992; Sánchez-Cordero, 2001; Sánchez-González & López-Mata, 2005; Contreras-Lozano *et al.*, 2011; but see Lobo & Halffter, 2000). On the other hand, most studies focusing on the Mexican transition zone have been bidimensional (latitude-longitude), dividing the studied area in grid cells or drawing generalized tracks; the elevational occurrence of taxa on the mountain slopes has not been a major focus (e.g. Ortega & Arita, 1998; Morrone & Márquez, 2001; Escalante *et al.*, 2004; Ríos-Muñoz & Navarro-Sigüenza, 2012; Kobelkowsky-Vidrio *et al.*, 2014). In this study, we analyse the elevation gradient of passerine fauna in a mountain range of the Mexican transition zone (Morrone, 2014b).

Biogeographical transitions appear when two different set of taxa that share a similar geographical distribution come into contact in an area where physical features, environmental conditions and ecological factors allow mixture, but also constrain their distribution further into one another (Ferro & Morrone, 2014). As transition zones involve a passage between two biogeographical units, which in turn are defined by species distributions, a fundamental aspect to be analysed is the biogeographical affinities of the taxa occurring in the study area. Although widely used, biogeographical affinity is a poorly defined term. Depending on the context, it could refer to the coincidence of distributions with a predefined geographical location (e.g. latitude, tropical or temperate; Beare *et al.*, 2004), a biogeographical region (e.g. Nearctic affinity; Schils & Coppejans, 2003), an ecological association to biome or landscape (e.g. forest or savanna affinity; Bruzul & Hadly, 2007), or to the area where the evolutionary diversification of a lineage has occurred (Harison & Grace, 2007). We use herein two different approaches to analyse biogeographical affinities: chorotypes and cenocrons. Chorotypes are based on the concordance of geographical distribution areas among species, corresponding herein to chorological affinity; whereas cenocrons are based on geography and timing of clade diversification, corresponding herein to evolutionary biogeographical affinity (see revision of concepts in Morrone, 2014a).

In the present study, we used passerines as attributes for characterization of the area around the Sierra Madre Oriental (SMO) (biological geography). However, as biogeographical affinities are properties of species (geographical biology), the deconstruction of passerine fauna was based on species attributes: their geographical distributions. Furthermore, we defined two categories of biogeographical affinities, chorotypes and cenocrons, based on different biogeographical features. The chorological affinity refers to the geographical distributional range congruence of taxa, geographical alliances or affinities among taxa, without reference to any predefined geographical area. The evolutionary biogeographical affinity involves the geographical context in which a clade has diversified, thus implying a pre-defined area (Neotropical/Nearctic in this case) where taxon distributions are compared and assigned a category (elements *sensu* Passalacqua, 2015). The evolutionary biogeographical affinity also included an explicit historical component inferred thorough ancestral state reconstruction in taxon phylogenies. The distinction of subsets within a biota has been present since the dawn of biogeographical analyses, particularly those grouped according to their geographical distribution and those according to their region of origin and time when they became integrated into a given biota (see reviews in Morrone, 2014a; and Passalacqua, 2015). Although implicit in several interpretations of the biogeographical composition of a biota, different terms have been applied to similar concepts and vice versa, leading to confusion. In this study, we defined clearly biogeographical affinities, distinguishing these two subsets within the passerine fauna.

To define quantitatively the chorological affinities of different species, we applied the protocol developed by Olivero *et al.* (2011) to detect chorotypes as fuzzy sets. For cenocrons, we employed the phylogenetic relationships and evolutionary history of Passeriformes. This taxon appears as a monophyletic group in all recent phylogenies (e.g. Prum *et al.*, 2015), and a Gondwanic origin has been suggested for the taxon as a whole (Moyle *et al.*, 2016), with a basal split between suboscines (suborder Tyranni) in Western Gondwanaland, and oscines (suborden Passeri) in Eastern Gondwanaland (Ericson *et al.*, 2002). The latter dispersed into the Northern Hemisphere, whereas the former diversified mainly in South America during the Cenozoic isolation of the continent (Barker *et al.*, 2004). In the Americas, this basal split is still noticeable: New World suboscines correspond to lineages mainly restricted to the Neotropical region while oscines are dominant in North America.

Here, we aim to draw at a fine spatial resolution the biogeographical transitions within the SMO by quantifying changes in the frequencies of passerine chorotypes and cenocrons across the latitudinal and altitudinal gradient. The

SMO constitutes one of the five mountain systems of the Mexican transition zone (Morrone, 2014b), and has lower levels of bird endemism than the other systems, facilitating the analysis of regional passerine fauna. If the legacy of such a deep biogeographical transition in the Mexican mountains is preserved by passerine distributions, we expect to recover a relationship between groups of species with a given biogeographical affinity to certain elevations along the altitudinal gradient. Following Halffter's (1987) analysis on the entomofauna of the Mexican transition zone, we predict mainly Nearctic chorotypes and cenocrons on the mountaintops, whereas lowlands should be Neotropical with a mixture somewhere at mid elevations.

MATERIALS AND METHODS

Study area

The study area corresponds to the SMO, a mountain range located in north-eastern Mexico (Fig. 1a). It runs parallel to the Gulf of Mexico (Atlantic Ocean) for approximately 800 km, from the U.S. border (26° S) to 19° S, where it comes into contact with the Trans-Mexican Volcanic Belt. The higher elevations surpass 4500 m, acting as barriers for the humidity from the Atlantic Ocean and produce abundant precipitations on the eastern slope, which supports the northernmost extension of the Neotropical humid montane forests (Brown & Kappelle, 2001). Conversely, in the inner slope, the effect of rain shadow produces xeric conditions in the Mexican Plateau. To enhance the representation of different species, we defined our study area as a 150 km buffer around de borders of the SMO province (defined by Morrone, 2014b), thus including part of the adjacent Mexican Plateau and Veracruzan biogeographical provinces (Fig. 1a), which belong to the Nearctic and Neotropical regions, respectively.

Data set

On a digital map of the defined buffer, we selected point records of 15,330 specimens housed in museum collections (see Appendix S1 in Supporting Information) of resident passerine birds species in 1517 localities compiled by Navarro *et al.* (2003) (Fig. 1b). Of the 276 resident species, 264 had available shape files of the whole geographical distribution range in Nature Serve (Ridgely *et al.*, 2003). We constructed a species presence–absence matrix of 1° square grid cells (5501 cells) by cutting a merged template of all bird species distributional ranges from the American continent map to exclude unnecessary zero values of unoccupied areas. This matrix was used to search for congruent distributional patterns among all species range. The coarse 1° square grid cell analysis allowed to detect continental significant coincident distributional patterns, but no pattern was recovered for the narrow range species inhabiting Mesoamerica. Thus, we performed a second analysis on a 0.5° grid presence–absences matrix (3693 cells), repeating the same procedure but excluding those species previously assigned to a chorotype in the 1° size analysis.

To identify cenocrons, we used literature sources. Diversification events during the history of the continent for the suborder and family level were based on published results (Ericson *et al.*, 2002; Barker *et al.*, 2004, 2015; Burns *et al.*, 2014). For lower taxonomical categories and more recent historical time, we compiled and optimized published phylogenies listed in Appendix S2. For local analysis in the SMO, we divided the whole mountain range into eight elevation classes of 500 m each, from sea level to above 4000 m, and seven equal belts of 1.2° latitude. Distributions of species along elevation were reconstructed based on georeferenced localities and extracted from a digital elevation model at 30 m resolution. We listed species distributional records

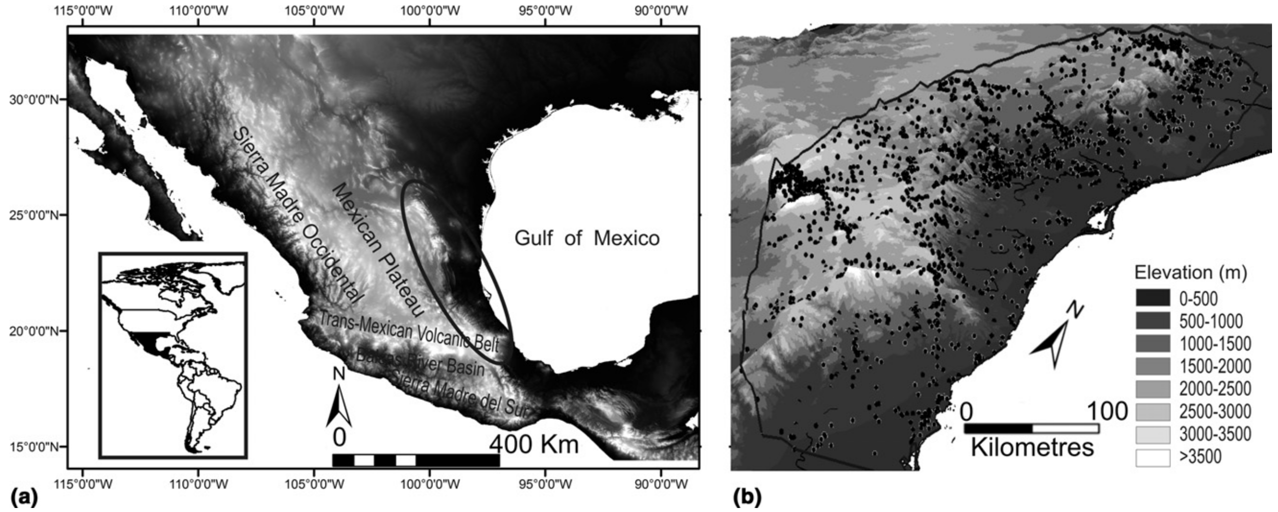

Figure 1 Study area. (a) Location of the Sierra Madre Oriental (ellipse) in Mexico and main physiographical features of the country. (b) Detail of the studied area showing the elevation gradient and the sampling localities.

within each elevation and latitudinal belt to map the variation of biogeographical affinities across the study area.

Analyses

Definition of chorotypes

We used a technique for detection of chorotypes as fuzzy sets, implemented in 'RMACOQUI'package for R (Olivero *et al.*, 2011). This method is based on a quantitative classification of distributional areas. First, similarities between the geographical distributions of each pair of species are calculated using the Baroni-Urbani & Buser's (1976) index. The index has a table of critical values which is used to perform exact randomization tests comparing the observed similarity values with all possible outcomes to detect significant similarities. Then, a dendrogram built with the agglomerative unweighted pair-group method using arithmetic averages is examined to identify branches that exhibit significant positive within-branch shared distributions and significantly disjunct from adjoining branches. An index of internal homogeneity and distinctness (IH, ranging from −1 to +1) is derived considering pairwise comparisons of the proportion of significant similarity and significant dissimilarity in every branch. A given branch of the dendrogram is considered a chorotype if IH = 1 or positive, higher than subsequent nested clusters and statistically significant. Significance is evaluated comparing the frequency of significant similarities within a tested cluster and the most similar branch of the dendrogram by means of a G-test of independence. Finally, a series of fuzzy logic parameters is computed based on the average of similarities between each species distribution and all the distributions in a chorotype. The computation of fuzzy logic parameters allows us to evaluate the degree of membership of any particular distribution to every chorotype, the overlap between chorotypes and the degree to which a chorotype is included into another chorotype (see Olivero *et al.*, 2011).

Definition of cenocrons

The term cenocron was coined by Reig (1962) to denote the geographical situation and relative timing where a given taxonomic group was incorporated into a biota (e.g. the flora and fauna of a region; Stejneger, 1901) prior to *in situ* diversification. Cenocrons are thus linked to centres of evolutionary diversification at a continental scale, where a major portion of the evolutionary diversification of a taxon has occurred, but not necessarily the initial one, which is denoted by the term ancestry ('*abolengo*') following Reig (1962). We use the concept to designate the evolutionary biogeographical affinities of lineages, and named them according to their minimum age considering the earliest time of implantation in the continent, despite the fact that several modern families have diversified more recently. Oscines arrived to North America presumably via Beringia with a subsequent rapid diversification (Barker *et al.*, 2004, 2015). While suboscines remained restricted to South America until the emergence of the Panama Isthmus in the Plio-Pleistocene, oscines invaded and radiated in South America at least twice, first during the late Miocene and then by the time of the closure of the Panama Isthmus (Burns *et al.*, 2014; Barker *et al.*, 2015). To detect trans-American diversification events during the Plio-Pleistocene Great American Biotic Interchange (GABI), which occurred mainly at the generic or specific level, we optimized published phylogenies, coding the distribution of every species in the phylogenies as a binary character (South or North America) based on the location of the species distribution range. We considered North America from Alaska to the Panama Isthmus, including the Greater Antilles; and South America from the Panama Isthmus to Tierra del Fuego, including the Lesser Antilles. We then optimized the distributions on the phylogenies using Fitch parsimony to identify trans-American diversification events. When a trans-American diversification event was identified for a given species group or genus, it was included in the Plio-Pleistocene cenocron, the most recent one, and the evolutionary biogeographical affinity assigned according to the basal node assignation.

Variation of species richness and species turnover

To describe the elevational and latitudinal pattern of species replacement, we used the β_{sim} turnover index, which focuses on compositional differences rather than differences in number of species between assemblages; thus, specifically depicting species replacement rather than richness gradients (Koleff *et al.*, 2003). We calculated this index for pairwise comparisons between elevational and latitudinal intervals along the gradient using formulas in Koleff *et al.* (2003). Variation in species richness was determined by counting the total number of species within each elevation belt of 500 m. For every latitudinal band of equal elevation, distributions were considered continuous; similarly, altitudinal distributions were considered continuous between lower and higher records within latitudinal segments. Latitudinal and altitudinal trends were depicted using linear or polynomial regression (quadratic, cubic); the best model was selected applying the small sample second-order bias correction of Akaike information criterion AICc, implemented in AICcmodavg package for R (Burnham & Anderson, 2004). We applied an arcsine square root transformation to normalize data distribution.

Mapping variation in biogeographical affinities

To distinguish gradients of biogeographical affinities across the studied area, we counted the number of species belonging to a given chorotype and cenocron relative to the total number of species in each belt. To find patterns of variation between chorotypes at the local scale, we tested for pairwise correlations between chorotype frequencies across the studied area (Ríos-Muñoz & Navarro-Sigüenza, 2012). Then, to assess if there was an association between local variation and global similarity of chorotypes, we calculated the fuzzy overlap values, which are a measure of similarity between two chorotypes in their whole geographical extent (Olivero *et al.*, 2011); and we tested the correlation between fuzzy overlap values and the correlation coefficients previously obtained from local variation in the frequencies for chorotype pairs. We expected a positive correlation between both indices if geographical range similarities are preserved at a local scale.

To find the places of maximum mixture, we used the relative frequency of chorotypes and cenocrons to calculate the Simpson index of diversity (H_{sim}) (Simpson, 1949). This index measures the degree of concentration, thus higher values of H_{sim} indicate more concentration (homogeneity) and lower values indicate more diversity (heterogeneity). To map the most heterogeneous expanses in the SMO, the values of the Simpson index (H_{sim}) in every group of localities were ranked in ascending order and grouped using Jenks' natural breaks algorithm. This algorithm divides localities maximizing the differences between values by setting the boundaries where there are relatively big differences in the index values, creating group of localities with similar scores. We then used contour lines around localities of similar values to create a map of heterogeneity isoclines, highlighting gradual changes in dominance and hotspots of heterogeneity in biogeographical affinities.

RESULTS

Chorotypes: Significant congruent geographical range distributional patterns

We obtained 11 chorotypes including 245 species, representing 93% of the 264 analysed and 89% of all the species recorded in the studied area (see Appendix S2). For the 1° latitude-longitude grid-cells analysis, we obtained three chorotypes (Fig. 2). Chorotype 1 (C1) included 24 species distributed in the Nearctic region. Chorotype 2 (C2) comprised 31 species from western North America. Chorotype 3 (C3) included 45 species distributed mainly in the Neotropical region. Values of internal homogeneity and significance for all chorotypes are reported in Table 1.

The remaining species included in the smaller grain analysis (0.5° square grids) resulted in eight distributional patterns (Fig. 3). Chorotype 4 (C4) included five species from the central coastal plains of the Gulf of Mexico, corresponding to the Tamaulipas biogeographical province. Chorotype 5 (C5) included 61 species restricted to the Mexican highlands of the Sierras Madres, Trans-Mexican Volcanic Belt, and some of them reaching Chiapas and the Central American highlands south to the Nicaraguan lowlands. Chorotype 6 (C6) included eight species distributed in the same highlands described previously but extending southwards to South America as a narrow strip through the eastern slopes of the Andes mountain forest, far south to the Tropic of Capricorn. Chorotype 7 (C7) included three species ranging from the Central American lowlands to the Caribbean coast of northern South America. Chorotype 8 (C8) is also comprised of three species mainly distributed in the Atlantic coast of Central America, the Pacific coast of South America, the eastern slopes of the Northern Andes and the Guiana Shield. Chorotype 9 (C9) is composed by 12 species that occupy the SMO, Sierra Madre del Sur and Chiapas Highlands. Chorotype 10 (C10) includes 23 species from the lowlands of eastern Central America and the Pacific coast of South America reaching the Guayaquil Gulf in Ecuador. Chorotype 11 (C11) included 30 species which occupy the Pacific and Atlantic coastal lowlands of Mexico and Central America.

Cenocrons: Location and timing of clade diversification

Of the 276 species present in the study area 271 were assigned to cenocrons defined for the American continent (Fig. 4, see Appendix S2). The basal split between oscines (suborder Passeri) and suboscines (suborder Tyranni) was the starting point to define the cenocrons. New World suboscines, isolated in South America during the Cenozoic, began their diversification in South America *c.* 40 Ma (Ericson *et al.*, 2002). We named this as Eocene cenocron of Neotropical diversification and Gondwanic ancestry (Fig. 4b). Oscines constituted the basal North American stem, which dispersed from Eurasia into the New World through Beringia around 30 Ma (Barker *et al.*, 2004). We named this Oligocene cenocron of Holarctic diversification and Gondwanic ancestry (Fig. 4a). The family Thraupidae was recently found to be an almost entirely endemic Neotropical taxon, now including several genera previously assigned to Emberizidae, that reached South America around the mid Miocene (Burns *et al.*, 2014). It constitutes a different cenocron, the Miocene cenocron of Neotropical diversification and Holarctic ancestry (Fig. 4c). Finally, the Plio-Pleistocene cenocron (Fig. 4d), linked to the GABI, involved the ingression of typical Neotropical taxa (suboscines and Thraupidae) to North America and vice versa. Several species groups or genera belonging to northern families, however, have diversified successfully throughout South America and re-entered into North America. These diversification events were identified as Plio-Peistocene cenocron of Neotropical diversification and Nearctic ancestry.

Latitudinal and altitudinal variation in species turnover and species richness

Turnover rates showed an abrupt maximum at low latitudes (19.2°) remaining rather constant northwards for all elevation belts (Fig. 5a). Regression analysis of latitudinal turnover combining all the elevation belts was significant for the linear model selected by AIC values (Table 2). The results of individual analyses for each elevation belt showed a curvilinear trend for the lowest elevation (500 m), with a peak at *c.* 22° of latitude (Table 2). The trend gradually turns into a linear model for higher elevations always with the highest

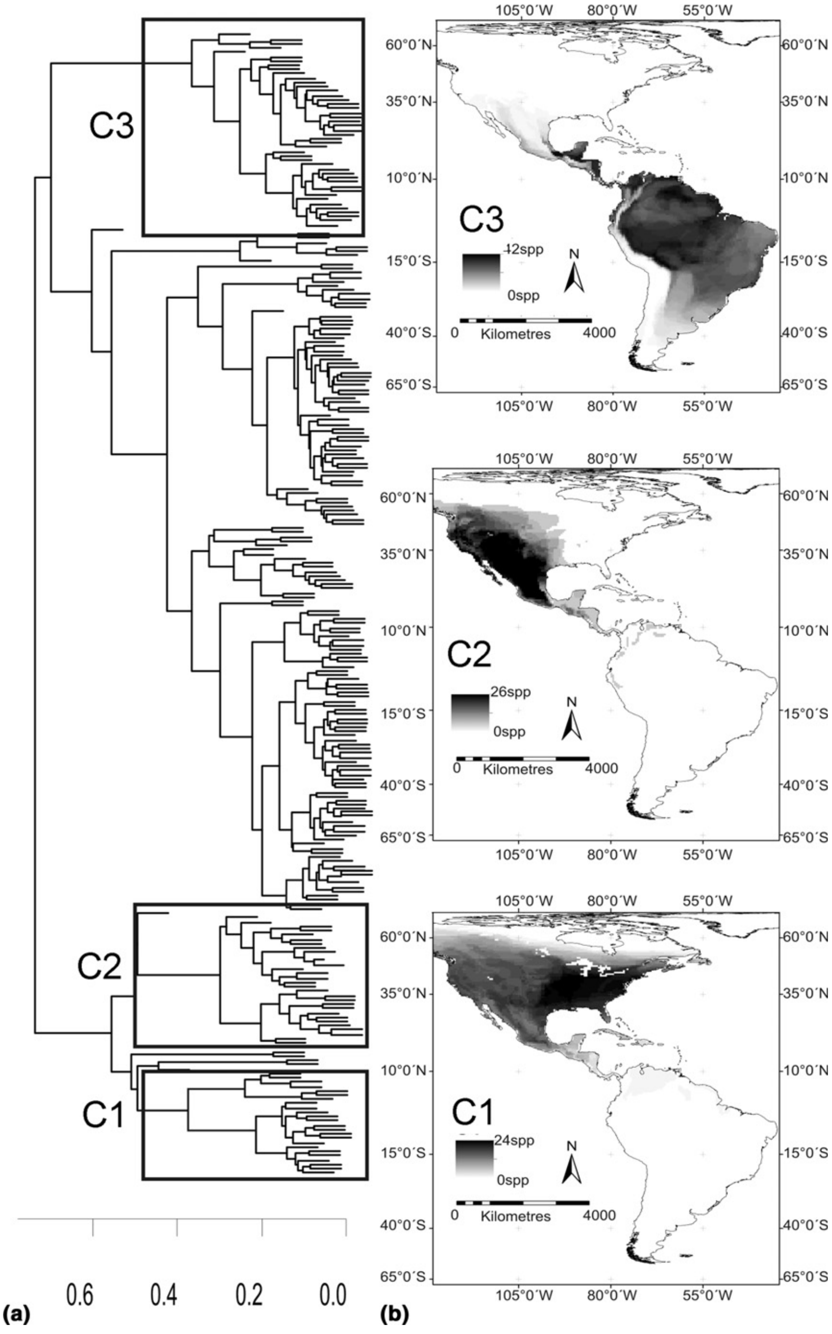

Figure 2 Result of whole distributional ranges analysis of passerine birds present in the Sierra Madre Oriental obtained for the 1 × 1° grid cell. (a) Clusters of significant coincident distributional ranges are indicated by rectangles and coded as C1, C2, C3. (b) Sum of species' geographical distributions belonging to each chorotypical cluster.

turnover values at the lowest (19.2°) latitude, but most models were not significant.

Elevation trends in turnover showed a peak at 1500 m (Fig. 5b). Significant trends were found for curved models of second- and third-order polynomials. The AIC value was slightly lower for the non-significant linear model than the quadratic one (Table 3). For individual latitudinal belts, three out of seven latitudinal belts reached the highest values at 1500 m, two at 2500 m, one at 2000 m and one 3000 m. According to AIC values, the best models were curved, either quadratic or cubic, although not significant (Table 3).

Species richness decreased with latitude (Fig. 5c) but peaked at mid elevation, around 1500–2000 m (Fig. 5d). Latitudinally, AIC values were slightly lower for the quadratic model (Table 4) but were 'U' shaped, not hump shaped. For the three lowest altitudinal belts (500, 1000 and 1500 m), the selected model was linear and significant. For the upper elevation belts of the gradient, the trend was of higher order although not significant. Altitudinally, a significant second-

Table 1 Results of coincident geographical range distributional analysis for the resident passerine birds present in the Sierra Madre Oriental using two grid sizes. IH are values of internal homogeneity, *G* is the value of the *G*-test of independence and *P* is the significance.

Grain size	Chorotype	IH	*G*	*P*	Entropy
1° × 1°	C1	0.337	50,286	< 0.001	0.305
1° × 1°	C2	0.491	55,961	< 0.001	0.431
1° × 1°	C3	0.868	3,752,291	< 0.001	0.334
0.5° × 0.5°	C4	0.368	6545	= 0.011	0.281
0.5° × 0.5°	C5	0.469	85,515	< 0.001	0.434
0.5° × 0.5°	C6	0.837	36,576	< 0.001	0.422
0.5° × 0.5°	C7	0.851	4527	= 0.033	0.318
0.5° × 0.5°	C8	0.851	4527	= 0.033	0.219
0.5° × 0.5°	C9	0.369	69,638	< 0.001	0.491
0.5° × 0.5°	C10	0.314	186,093	< 0.001	0.358
0.5° × 0.5°	C11	0.311	58,199	< 0.001	0.5

order model was selected according to AIC values (Table 5). For individual latitudinal belts also a significant curved model was selected, either a second or third order, except for the 24–25.2° interval (Table 6).

Local variation in biogeographical affinities

The frequency of each chorotype in the studied area is shown in Appendix S3. Three chorotypes were more frequent at high elevations (C1, C2 and C5). The two chorotypes occupying a major part of North America (C1 and C2), dominant in the northern highlands, were positive and significantly correlated with each other (Table 6). These chorotypes were in turn negatively and significantly correlated with C3, chorotype coincident with the Neotropical region. Additionally, C1 and C2 were negatively and significantly correlated with chorotypes distributed from the

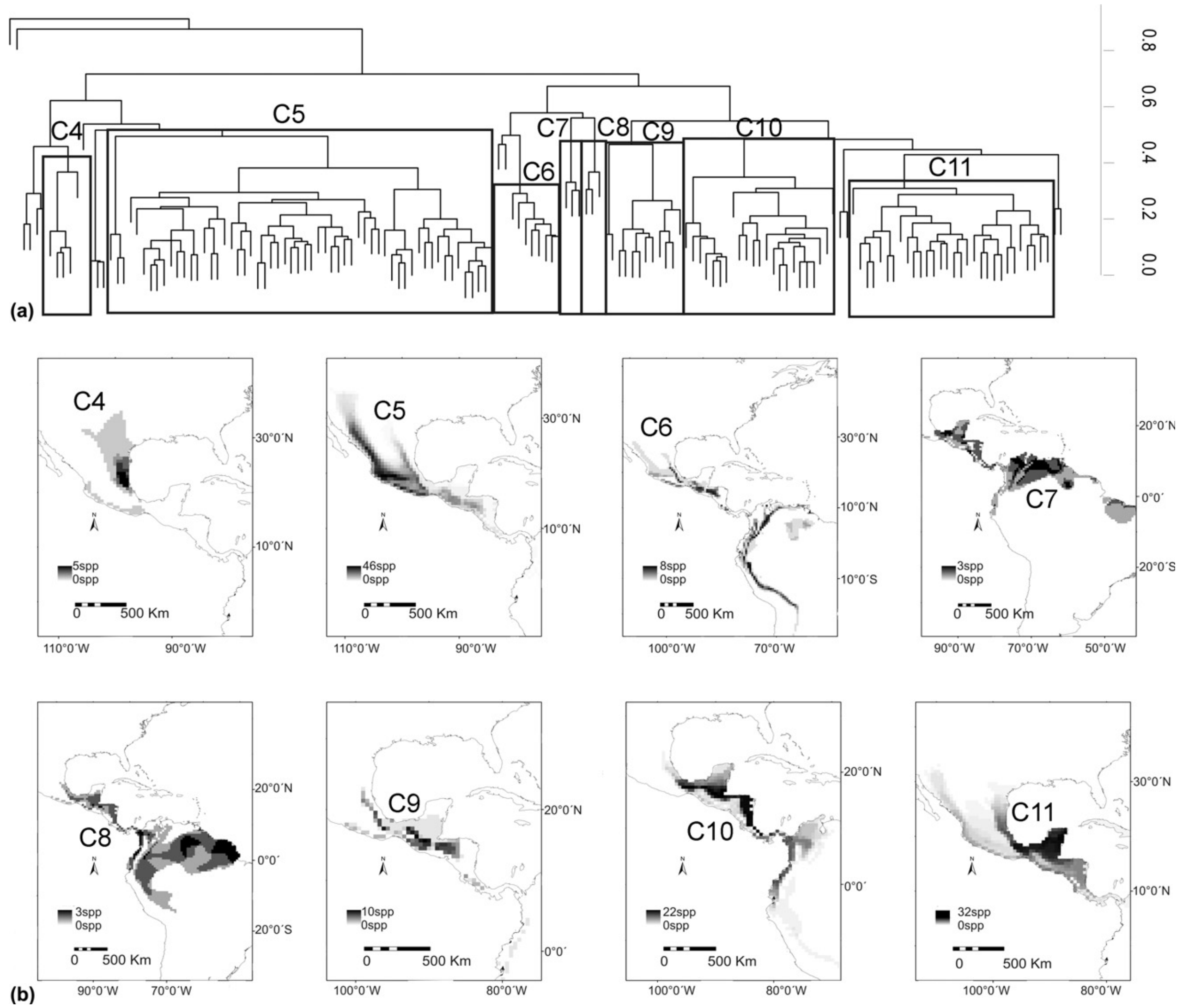

Figure 3 Result of significant coincident distributional ranges of passerine birds present in the Sierra Madre Oriental obtained for the 0.5 × 0.5° analysis. (a) Clusters of significant coincident distributional ranges are indicated by rectangles coded as C4, C5, C6, C7, C8, C9, C10 C11. (b) Sum of species' geographical distributions belonging to each chorotypical cluster.

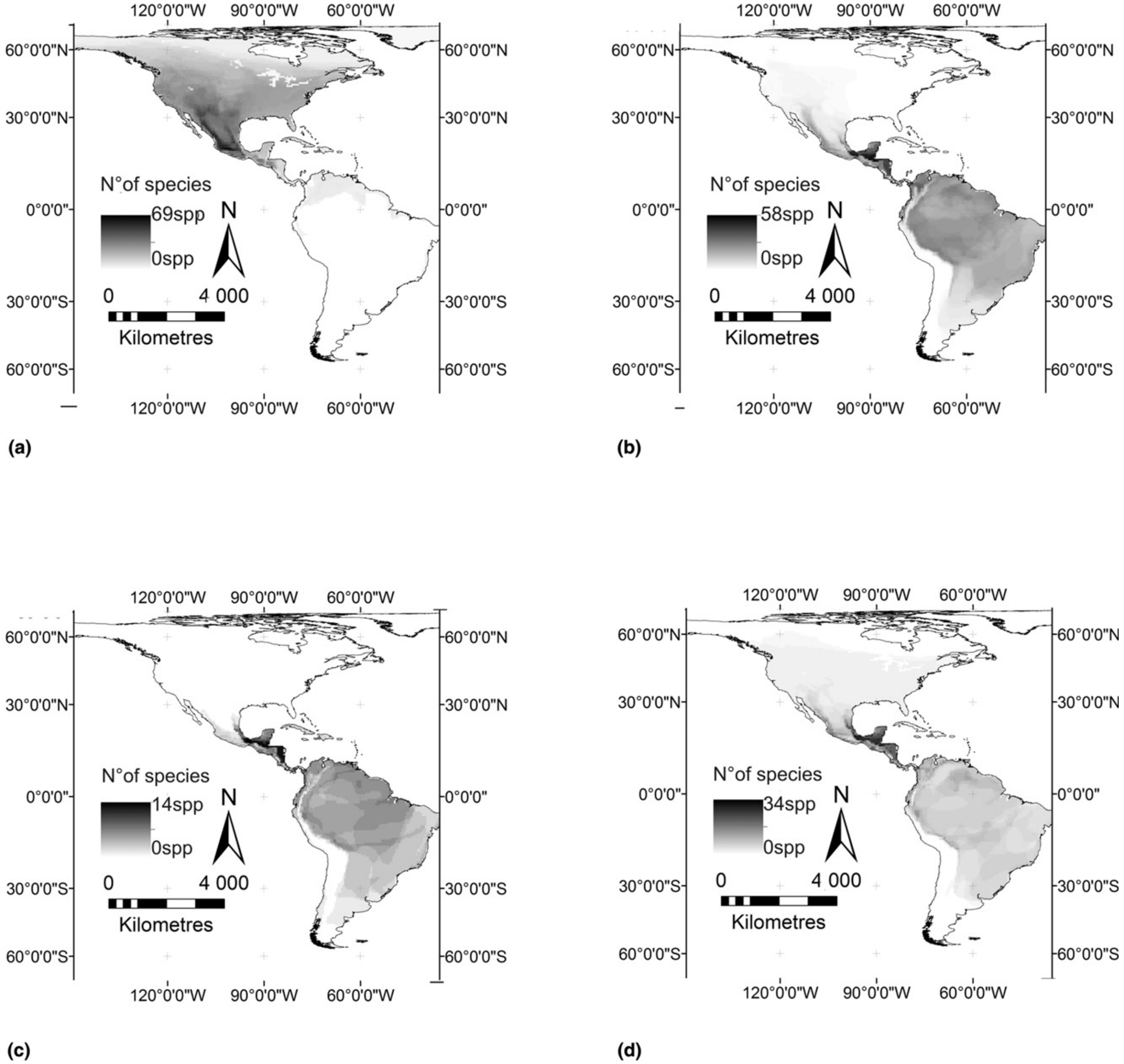

Figure 4 Cenocrons for the passerine birds of the Sierra Madre Oriental in the American continent used to identify evolutionary affinity. Nearctic affinity: (a) Oligocene North American cenocron of Holarctic diversification and Gondwanic ancestry. Neotropical affinity: (b) Eocene South American cenocron of Neotropical diversification and Gondwanic ancestry. (c) Miocene cenocron of Neotropical diversification and Holarctic ancestry. (d) Plio-Pleistocene cenocron of Neotropical diversification and Nearctic ancestry.

studied area southwards through Central and South America distributed C5–C11 (see Table 6). The Mesoamerican montane chorotype C5 dominant in the southern highlands, was negatively and significantly correlated with C1, C3 and C4 but positively correlated with C6 and C9, these latter containing species distributed in the mountain systems of Central America and the tropical eastern Andes. Five chorotypes (C3, C4, C7, C10 and C11) were more frequent at low elevations. Chorotype C3 dominated the southern lowlands and was significantly correlated with six chorotypes (C6–C11), all distributed through Central and South America (see Fig. 3). Chorotype C4 (central Gulf of Mexico) peaked at the northern lowland and was only significantly positively correlated with chorotype C11 (Mesoamerican coast) but negatively with C5. Chorotypes C7, C10 and C11 were positively correlated to each other and with C8 (Table 6). Finally, three chorotypes (C6, C8 and C9) peaked at mid elevations. While chorotype C6 peaked at 2000 m in the northern studied area, C8 peaked at 2000 m in the southern studied area and C9 all along the latitudinal gradient. These chorotypes, however, were positively and significantly correlated with each other, as well as with several chorotypes distributed in through Central and South America, but negatively correlated with North American chorotypes (see Table 6). The

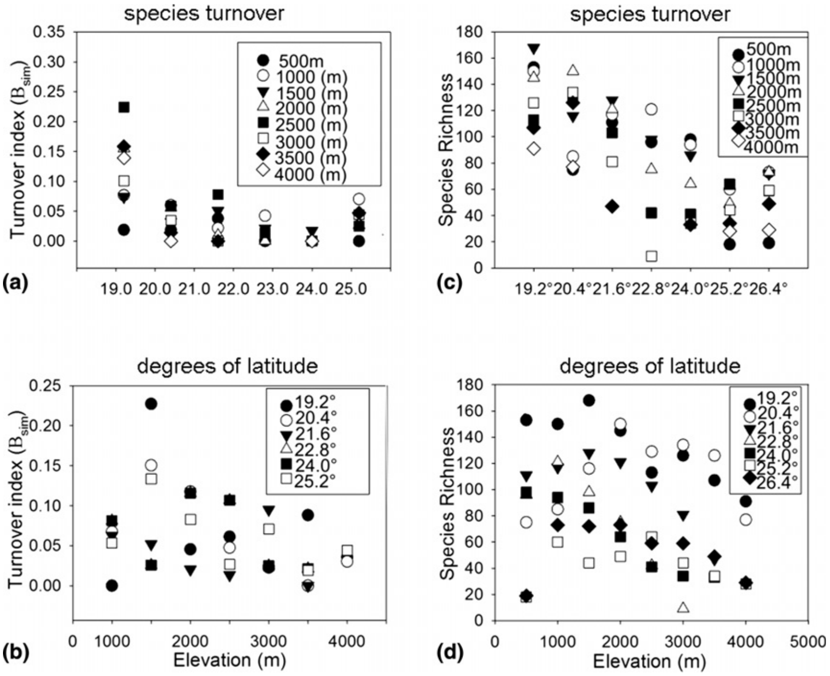

Figure 5 Result of local analysis of passerine bird species turnover and species richness in the elevation and latitudinal gradient of the Sierra Madre Oriental. (a) Species turnover against latitude. (b) Species turnover against elevation. (c) Species richness against latitude. (d) Species richness against elevation.

Table 2 Results of polynomial regression analyses of resident passerine bird species turnover against latitude for every elevation interval in the Sierra Madre Oriental.

		Altitudinal belts						
Model	Combined	500 m	1000 m	1500 m	2000 m	2500 m	3000 m	3500 m
Linear	AIC = 109.93	AIC = 24.75	AIC = 20.78	AIC = 18.92	AIC = 19.02	AIC = 21.27	AIC = 16.16	AIC = 14.09
	R^2 = 0.30	R^2 = 0.40	R^2 = 0.35	R^2 = 0.27	R^2 = 0.76	R^2 = 0.86	R^2 = 0.18	R^2 = 0.38
	P = 0.00005	P = 0.17	P = 0.20	P = 0.28	P = 0.02	P = 0.007	P = 0.39	P = 0.18
Quadratic	AIC = 119.16	AIC = 19.75	AIC = 28.35	AIC = 17.35	AIC = 36.94	AIC = 23.89	AIC = 24.02	AIC = 30.11
	R^2 = 0.45	R^2 = 0.81	R^2 = 0.86	R^2 = 0.32	R^2 = 0.99	R^2 = 0.93	R^2 = 0.84	R^2 = 0.96
	P = 0.000002	P = 0.07	P = 0.04	P = 0.55	P = 0.0007	P = 0.01	P = 0.06	P = 0.005
Cubic	AIC = 117.21	AIC = 29.71	AIC = 26.56	AIC = 31.71	AIC = 37.94	AIC = 26.42	AIC = 28.29	AIC = 37.35
	R^2 = 0.35	R^2 = 0.89	R^2 = 0.87	R^2 = 095	R^2 = 0.99	R^2 = 0.97	R^2 = 94	R^2 = 0.99
	P = 0.000001	P = 0.26	P = 0.18	P = 0.06	P = 0.007	P = 0.04	P = 0.81	P = 0.009

Table 3 Results of polynomial regression analyses of resident passerine bird species turnover against elevation for the seven latitudinal bands in the Sierra Madre Oriental.

		Latitudinal belts						
Model	Combined	18.0°–19.2°	19.2°–20.4°	20.4°–21.6°	21.6°–22.8°	22.8°–24.0°	24.0°–25.2°	25.2°–26.4°
Linear	AIC = 110.48	AIC = 23.03	AIC = 26.03	AIC = 16.53	AIC = 18.54	AIC = 21.29	AIC = 11.69	AIC = 17.79
	R^2 = 0.07	R^2 = 0.28	R^2 = 0.14	R^2 = 0.14	R^2 = 0.08	R^2 = 0.523	R^2 = 0.039	R^2 = 0.058
	P = 0.06	P = 0.21	P = 0.452	P = 0.45	P = 0.58	P = 0.065	P = 0.66	P = 0.60
Quadratic	AIC = 111.05	AIC = 21.11	AIC = 26.56	AIC = 16.36	AIC = 16.55	AIC = 19.46	AIC = 9.88	AIC = 19.62
	R^2 = 0.14	R^2 = 0.29	R^2 = 0.38	R^2 = 0.3705	R^2 = 0.082	R^2 = 0.53	R^2 = 0.065	R^2 = 0.454
	P = 0.04	P = 0.49	P = 0.37	P = 0.4995	P = 0.879	P = 0.21	P = 0.874	P = 0.29
Cubic	AIC = 115.13	AIC = 22.12	AIC = 25.37	AIC = 14.71	AIC = 16.91	AIC = 32.21	AIC = 9.48	AIC = 28.90
	R^2 = 0.24	R^2 = 0.54	R^2 = 0.45	R^2 = 0.40	R^2 = 0.38	R^2 = 0.94	R^2 = 0.25	R^2 = 0.891
	P = 0.008	P = 0.47	P = 0.56	P = 0.73	P = 0.76	P = 0.02	P = 0.79	P = 0.05

Table 4 Results of polynomial regression analyses of resident passerine bird species richness against latitude for every elevational belt in the Sierra Madre Oriental.

Model/Altitude	Combined	Individual belts							
		500	1000	1500	2000	2500	3000	3500	4000
Linear	AIC = 495.07	AIC = 71.05	AIC = 67.06	AIC = 64.47	AIC = 65.736	AIC = 68.72	AIC = 73.83	AIC = 60.51	AIC = 29.16
	R^2 = 0.55	R^2 = 0.69	R^2 = 0.56	R^2 = 0.82	R^2 = 0.79	R^2 = 0.58	R^2 = 0.49	R^2 = 0.61	R^2 = 0.97
	P = 0.000	P = 0.02	P = 0.05069	P = 0.004	P = 0.007	P = 0.04	P = 0.07	P = 0.06	P = 0.01
Quadratic	AIC = 495.52	AIC = 72.61	AIC = 69.06	AIC = 65.00	AIC = 65.08	AIC = 68.69	AIC = 70.51	AIC = 59.68	AIC = 25.85
	R^2 = 0.576	R^2 = 0.71	R^2 = 0.56	R^2 = 0.85	R^2 = 0.8594	R^2 = 0.68	R^2 = 0.76	R^2 = 0.75	R^2 = 0.9936
	P = 0.000	P = 0.08	P = 0.18	P = 0.02	P = 0.01977	P = 0.09704	P = 0.05546	P = 0.1181	P = 0.08
Cubic	AIC = 495.54	AIC = 73.36	AIC = 70.66	AIC = 66.73	AIC = 53.09	AIC = 67.44	AIC = 70.37	AIC = 60.35	
	R^2 = 0.588	R^2 = 0.75	R^2 = 0.59	R^2 = 0.86	R^2 = 0.98	R^2 = 0.80	R^2 = 0.82	R^2 = 0.8071	
	P = 0000	P = 0.18	P = 0.38	P = 0.72	P = 0.004	P = 0.13	P = 0.11	P = 0.2749	

correlation coefficient between pairs of chorotype frequencies at the local scale was significantly correlated with the fuzzy overlap values (i.e. similarity between chorotypes) obtained by R-MACOQUI for the 0.5° analysis (R = 5.42 P = 0.002).

The frequency of species with Nearctic or Neotropical evolutionary biogeographical affinities is shown in Appendix S3. Species with Nearctic evolutionary biogeographical affinities clearly dominated in the north-western highlands (70% on average above 1500 m); on the contrary, species of Neotropical evolutionary biogeographical affinities peaked in the southern half of the studied area.

Mapping zones of maximum biogeographical affinities mixture

Simpson's index of diversity situated the maximum mixture of both biogeographical affinities at mid elevation, between 1500–2500 m, on the eastern slopes of the southern SMO. The chorotype mixture peaked at 1500 m in two hotspots of chorological heterogeneity: one in the middle Moctezuma river basin, at 1500 m altitude, and the other on the eastern slopes of the Trans-Mexican Volcanic Belt, in the southernmost part of the studied area, also at 1500 m (shaded areas in Fig. 6a). Both hotspots of chorological heterogeneity were connected by a narrow strip of localities at 1500 m (solid line in Fig. 6a). Then, the gradient of chorological heterogeneity splits; one group of localities continues northwards on the western slopes of the SMO, following the Verde river at *c.* 1000 m, and the other group of localities was situated in the coastal lowlands around the Pánuco river (dashed line in Fig. 6a). The following group of localities in the heterogeneity gradient include the lowlands north of the Pánuco river to near 24° and the lowlands in the southernmost studied area (dotted line in Fig. 6a). Finally, the last mapped group of localities were situated in the highlands of the southern studied area, including parts of the central Mexican Plateau, valleys of the Trans-Mexican Volcanic Belt, and on the lower eastern slopes (1000 m) of the northern SMO.

The most heterogeneous expanses considering the evolutionary biogeographical affinities were also located at mid elevations (1500–2000 m) in the central and southern parts of the SMO. The following most heterogeneous areas in evolutionary biogeographical affinities were the lowlands around the Pánuco river and part of the eastern slopes and foothills (1000–1500 m) of the northern SMO (solid line in Fig. 6b). The next groups of localities in the heterogeneity gradient included all the eastern slope and foothills of the northern SMO, the lowlands between *c.* 21° and 24° and highlands of the southern SMO, particularly valleys of the Trans-Mexican Volcanic Belt (dashed line in Fig. 6b). The last group of localities in the evolutionary biogeographical gradient of mixture encompass all the eastern slopes and lowlands of the studied area and the highlands of the southern studied area, the valleys of the Trans-Mexican Volcanic Belt and parts of the Mexican plateau (dotted line in Fig. 6b).

Table 5 Results of polynomial regression analyses of resident passerine bird species richness against elevation for every latitudinal belt in the Sierra Madre Oriental.

		Individual belts						
Model/Latitude	Combined	18.0°–19.2°	19.2°–20,4°	20.4°–21.6°	21.6°–22.8°	22.8°–24.0°	24.0°–25.2°	25.2°–26.4°
Linear	AIC = 6533.4 $R^2 = 0.079$ $P = 0.04$	AIC = 67.7 $R^2 = 0.78$ $P = 0.003$	AIC = 680.77 $R^2 = 0.06$ $P = 0.5$	AIC = 664.79 $R^2 = 0.62$ $P = 0.03$	AIC = 656.60 $R^2 = 0.81$ $P = 0.01$	AIC = 652.19 $R^2 = 0.93$ $P = 0.0003$	AIC = 671.50 $R^2 = 0.007$ $P = 0.8$	AIC = 675.86 $R^2 = 0.02$ $P = 0.7$
Quadratic	AIC = 533.47 $R^2 = 0.11$ $P = 0.05$	AIC = 67.5 $R^2 = 0.8377$ $P = 0.01$	AIC = 68.18 $R^2 = 0.84$ $P = 0.008$	AIC = 39.88 $R^2 = 0.99$ $P = 0.00006$	AIC = 48.9 $R^2 = 0.96$ $P = 0.007$	AIC = 54.09 $R^2 = 0.93$ $P = 0.003$	AIC = 66.13 $R^2 = 0.60$ $P = 0.09$	AIC = 67.54 $R^2 = 0.73$ $P = 0.03$
Cubic	AIC = 534.11 $R^2 = 0.13$ $P = 0.06$	AIC = 68.35 $R^2 = 0.86$ $P = 0.03$	AIC = 67.53 $R^2 = 0.8918$ $P = 0.02$	AIC = 41.61 $R^2 = 0.99$ $P = 0.001$	AIC = 42.23 $R^2 = 0.99$ $P = 0.01$	AIC = 40.12 $R^2 = 0.99$ $P = 0.0008$	AIC = 66.96 $R^2 = 0.65$ $P = 0.19$	AIC = 64.10 $R^2 = 0.86$ $P = 0.03$

DISCUSSION

In this analysis, we quantified the strength and breadth of a continental transition zone at a local scale using the conceptual framework outlined by Ferro & Morrone (2014). This approach suggests the deconstruction of the biota into its chorological categories and then quantifies the integration of these subsets across a given area. We defined two categories: chorotypes and cenocrons. Chorotypes refer to biogeographical affinities on a single temporal plane (chorological affinity), whereas cenocrons have an explicit temporal dimension, the historical component printed in taxa phylogenies (evolutionary biogeographical affinity). The relationship between historical and ecological processes in shaping species distributions has long been debated with neither a general consensus nor a protocol to jointly evaluate influences of each process. The assumption that congruence among the geographical distribution of different taxa is a product of a common history of differentiation caused by isolation is widely accepted among evolutionary biogeographers. Chorotypes, however, have been interpreted as either assemblages of species with certain ecological requirements within a given biogeographical area or as groups of species assumed to share a common biogeographical history and originated in the same area (Morrone, 2014a). Evaluating whether historical versus environmental factors are determinant of chorotype composition is beyond the aim of this study. Olivero *et al.* (2011) interpreted the degree of fuzziness of a chorotype, measured by the entropy value (Table 1), as a sign of historical influence on species distributions. The less fuzziness (low entropy) would indicate a stronger role of history in chorotype configuration, presumably via hard geographical barrier; while the more fuzziness (high entropy) indicates blurred geographical limits as a consequence of different dispersal patterns driven by idiosyncratic responses to ecological factors. According to our analysis of cenocrons, chorotypes C1, C2 and C4 are almost completely composed by species with Nearctic evolutionary affinity (C1: 92%; C2: 90% and C4: 100%); and chorotypes C3, C6, C10, C11 species composition are almost entirely of Neotropical affinity (C3: 100%; C6: 100%; C10: 97% and C11: 92%). On the contrary, chorotype C5 (65% of Nearctic and 35% of Neotropical affinity) and C9 (50% each) are conspicuously even regarding their species' evolutionary biogeographical affinity. Both chorotypes encompass mountain systems widely recognized as belonging to the Mexican transition zone (Morrone, 2014b). Thus, these chorotypes can be considered transitional regarding the evolutionary biogeographical affinities of their species. Even when these chorotypes have high entropy values (second and third ranked), the highest value was for C11, almost entirely composed by species of Neotropical affinity (Table 1, see Appendix S2). A plausible explanation are the Pleistocene climatic cycles of cooling and warming that occurred during the emergence of the Panama land bridge, providing sequential dispersal routes for Nearctic and Andean species in glacial periods and for Neotropical rain forest species during interglacial periods (Barrantes, 2008; Smith *et al.*, 2012). In Mesoamerican mountain areas, altitudinal migration of life zones might have allowed the persistence of recently established populations and isolation led to speciation resulting in endemic taxa with similar distributional ranges but different evolutionary biogeographical affinities. In the lowlands, however, climatic oscillations would produce expansion and retraction of seasonally deciduous dry forest and rain forest during arid and wet periods respectively, probably resulting in high fuzziness of chorotype composed mainly by species of Neotropical biogeographical affinities. Phylogeographical analyses may be useful to test the relationship between chorotype fuzziness and historical stability.

At a local scale, according to the turnover index values, the major break in passerine bird composition is coincident with the Trans-Mexican Volcanic Belt. This mountain range is one of the most prominent of the Mexican territory, having the most important variation in relief and the highest summits of the country. It has been found to represent the limit between the northern and southern biotas in a cladistic biogeographical analysis (Marshall & Liebherr, 2000) and

Table 6 Result of Spearman rank correlation analysis on the local (within the Sierra Madre Oriental) variation in the frequency of passerine bird chorotypes (above diagonal). Values of fuzzy overlap, interpreted as similarity between different passerine birds chorotypes, for analysis of comparable grid size analysis (below diagonal).

	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11
C1		$R = 0.288$ $P = 0.03$	$R = -0.333$ $P = 0.01$	$R = 0.241$ $P = 0.07$	$R = -0.371$ $P = 0.005$	$R = -0.639$ $P = 0.00$	$R = -0.259$ $P = 0.05$	$R = -0.384$ $P = 0.004$	$R = -0.5$ $P = 0.000$	$R = -0.365$ $P = 0.006$	$R = -0.142$ $P = 0.30$
C2	0.601		$R = -0.78$ $P = 0.000$	$R = -0.267$ $P = 0.051$	$R = -0.116$ $P = 0.40$	$R = -0.601$ $P = 0.0002$	$R = -0.329$ $P = 0.01$	$R = -0.537$ $P = 0.000$	$R = -0.616$ $P = 0.000$	$R = -0.502$ $P = 0.000$	$R = -0.678$ $P = 0.000$
C3	0.382	0.37		$R = 0.233$ $P = 0.09$	$R = -0.394$ $P = 0.003$	$R = 0.484$ $P = 0.000$	$R = -0.454$ $P = 0.000$	$R = -0.699$ $P = 0.000$	$R = -0.469$ $P = 0.00$	$R = -0.68$ $P = 0.000$	$R = -0.831$ $P = 0.000$
C4					$R = -0.326$ $P = 0.01$	$R = -0.069$ $P = 0.62$	$R = -0.131$ $P = 0.34$	$R = -0.154$ $P = 0.26$	$R = -0.0498$ $P = 0.72$	$R = -0.19$ $P = 0.16$	$R = -0.369$ $P = 0.006$
C5				0.458		$R = -0.303$ $P = 0.025$	$R = -0.18$ $P = 0.19$	$R = -0.252$ $P = 0.06$	$R = -0.283$ $P = 0.03$	$R = -0.261$ $P = 0.05$	$R = -0.2$ $P = 0.000$
C6				0.406	0.476		$R = 0.212$ $P = 0.12$	$R = 0.442$ $P = 0.000$	$R = 0.75$ $P = 0.000$	$R = 0.352$ $P = 0.009$	$R = 0.2$ $P = 0.14$
C7				0.328	0.348	0.649		$R = 0.576$ $P = 0.000$	$R = 0.201$ $P = 0.14$	$R = 0.787$ $P = 0.000$	$R = 0.295$ $P = 0.03$
C8				0.259	0.272	0.537	0.676		$R = 0.423$ $P = 0.001$	$R = 0.821$ $P = 0.000$	$R = 0.543$ $P = 0.00$
C9				0.445	0.561	0.594	0.484	0.36		$R = 0.33$ $P = 0.014$	$R = 0.161$ $P = 0.24$
C10				0.359	0.384	0.595	0.641	0.466	0.61		$R = 0.496$ $P = 0.0001$
C11										0.64	

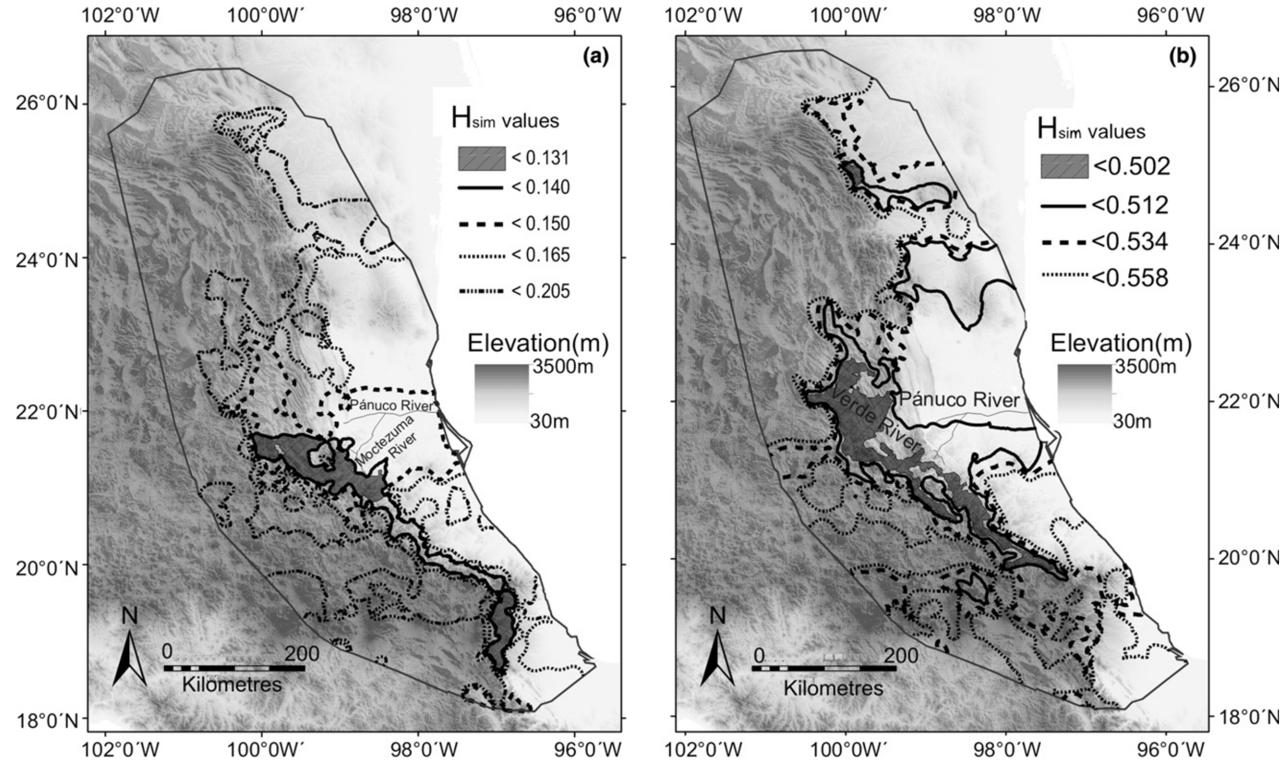

Figure 6 Contour map of biogeographical affinities mixture for passerine birds in the Sierra Madre Oriental obtained by Simpson index (H_{sim}) of diversity applied to the frequency of chorological affinity (a) and evolutionary biogeographical affinity (b).

also nodes were found in a track analysis (Escalante *et al.*, 2004). Our results indicate that this range constitutes an apparent barrier for several Neotropical birds, as shown by the frequency of both chorotypes and cenocrons in the studied area. This analysis should be extended southwards to evaluate if it is actually the major faunal break or if discontinuities in bird distributions are stronger in other areas, such as the Isthmus of Tehuantepec, proposed for insects (Halffter, 1987; Morrone & Márquez, 2001). The elevation pattern of species turnover in the SMO reflects at least a lowland and a highland assemblage, with their limit at about 1500 m. This provides evidence supporting the prediction of a mid elevation transitional zone based on the hypothesis derived from Halffter's classical insect biogeographical analysis. Furthermore, this can be corroborated by the partition of taxa according to their biogeographical affinities and the analysis of their variation and integration across the studied area (Ferro, 2013). Some chorotypes showed contrasting patterns of variation across the studied area while other showed similar patterns as measured by correlation coefficients. A striking result of the correlation in local variation of chorotypes is the negative significant correlation between North American chorotypes and those from Central and South America, but overall positively within them (Table 6). Moreover, there is a roughly overall positive correlation between chorotype similarity (measured by the fuzzy overlap) and chorotype variation within the studied area, indicating that global chorotypes tend to be preserved at a local scale. The local variation in the frequency of cenocrons also showed contrasting patterns. Species of Nearctic affinity peaked in the western highlands and northern lowlands opposed to species of Neotropical evolutionary affinity which peaked in the southern lowlands. This empirical finding corroborates the prediction that taxa assigned to distinct cenocrons should exhibit different gradients of variation across a biogeographical transition zone (Ferro & Morrone, 2014). The heterogeneity of cenocrons in a geographical location indicates the strength of a biogeographical transition zone in its most restrictive sense. The maximum mixture of cenocrones and chorotypes occur at mid elevation (1500–2000 m) and is stronger in the southern half of the studied area, paralleling results of species turnover measurements, but with an explicit biogeographical significance for each species. Thus, the three approaches here used to detect biogeographical transitions point out to similar locations within the studied area.

Considering gradual changes of biogeographical affinity mixture gradient, we can draw the sharpest biogeographical transition in the SMO from the southern evergreen cloud forests of the 'Carso Huasteco' to the canyons of the middle Pánuco basin and then turning eastwards, downslope following the Pánuco river through the semi-deciduous lowland forest to the river mouth in the Gulf of Mexico. This interruption corresponds to the mountain decrease in elevation from 4000 m to 2500 m (*c.* 22°); thus, topography together with increasing latitude is likely to generate discontinuities in ecological conditions, particularly humidity decline as suggested by vegetal communities. The Pánuco river basin has been identified as the northern limit for several plant species (Luna *et al.*, 2000) and proposed as the natural limit between the Austral Oriental and Hidalgo sub-provinces of the SMO province (Morrone, 2014b). Espinosa-Pérez & Huidobro-Campos (2005) also suggested that north-eastern Mexico is biogeographically distinct from the south-eastern Gulf coast for freshwater fishes. Similar differentiations have been reported for deciduous tropical forest trees (Cué-Bär *et al.*, 2006) and birds (Ríos-Muñoz & Navarro-Sigüenza, 2012). Here, we highlight the Pánuco river basin as a biogeographical boundary dividing northern and southern assemblages based on bird distributions in north-eastern Mexico.

Acknowledging that biogeographical transition zones involve areas of taxon juxtaposition rather than hard lines, we investigated gradients of species' biogeographical affinities to locate the sharpest biogeographical transition at a fine scale in the latitudinal and elevation gradient of the SMO. A major strength of this approach is the quantitative definition of biogeographical affinities based on two biogeographical features of species to map their integration as a gradual pattern. This approach is particularly useful for the analysis of rather small areas where regional faunas or floras cannot be defined concomitantly, but it may be also useful for continental analyses.

ACKNOWLEDGEMENTS

To José Carlos Guerrero and Jesús Olivero for their help computing chorotypes and to Alejandro Gordillo for coordinating data georeferencing. Also, to Pilar Benites and Sara Bertelli for providing literature and suggestions. I.F. thanks the support of the Universidad Nacional Autónoma de México (UNAM) through the postdoctoral fellowship programme 'Programa de Becas Posdoctorales en la UNAM', from the Dirección General de Asuntos del Personal Académico (DGAPA). We thank curators and collection managers of the biological collections mentioned in the Appendix S1 of supplementary material, for granting access to the data under their care. We appreciate valuable suggestions by three anonymous reviewers to the original manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Scientific collections that provided specimen data.

Appendix S2 Species list, the chorotype and cenocron to which they belong and source reference.

Appendix S3 Local variation in the frequency of chorotypes and cenocrons within the Sierra Madre Oriental.

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Editor: Fumin Lei