Niche conservatism and convergence in birds of three cenocrons in the Mexican Transition Zone

Viridiana Lizardo [Equal first author, 1, 2], Erick García Trejo [1], Juan J Morrone [Corresp. Equal first author, 1]

[1] Evolutionary Biology, Universidad Nacional Autónoma de México, Mexico City, CdMx, México

[2] Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Mexico City, CdMx, México

Corresponding Author: Juan J Morrone
Email address: juanmorrone2001@yahoo.com.mx

Background. The niche conservatism hypothesis postulates that species' distributions are constrained by physiological and phylogenetic factors, resulting in the creation of richness hotspots and the presence of older lineages in the ancestral climatic conditions. Conversely, niche convergence occurs when species successfully disperse to novel environments, diversifying and resulting in areas with high phylogenetic clustering and endemism, low diversity, and lower clade age. The Mexican Transition Zone exhibits both patterns as its biotic assembly resulted from successive dispersal events of different biotic elements called cenocrons. Our study proposes that biogeographic transitionality in the area is a product of niche conservatism in the Nearctic and Typical Neotropical cenocrons and niche convergence in the Mountain Mesoamerican cenocron.

Methods. To test this, we split the avifauna into three species sets that represent cenocrons (set of taxa that share the same biogeographic history, which constitute an identifiable subset within a biota by their common biotic origin and evolutionary history). Then, we correlated richness, endemism, phylogenetic diversity, number of nodes, and crowning age with environmental and topographic variables. These correlations are then compared with the predictions of niche conservatism versus niche convergence. We also detected areas of higher species density in environmental space and interpret it as an environmentally transition zone where birds' niches converge.

Results. Our findings support the general theory behind the MTZ framework, as species followed the expected predictions on how their niches evolved. Nearctic and Typical Neotropical species behaved as predicted by niche conservatism, whereas Mountain Mesoamerican species and the total of species correlations indicate a case of niche convergence. We also detected that cenocron assemblages have distinct ecological and evolutionary characteristics on a macroecological scale, and that environmental conditions where the three cenocrons overlap are in the Mesoamerican region.

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5   Viridiana Lizardo[1,2], Erick García-Trejo[3], Juan J. Morrone[1]
6
7   [1] Museo de Zoología 'Alfonso L. Herrera', Departamento de Biología Evolutiva, Facultad de
8   Ciencias, Universidad Nacional Autónoma de México (UNAM), Mexico City, Mexico.
9   [2] Posgrado en Ciencias Biológicas, Unidad de Posgrado, Edificio A, 1er. Piso, Circuito de
10   Posgrados, Ciudad Universitaria, Universidad Nacional Autónoma de México (UNAM), Mexico
11   City, Mexico.
12   [3] Unidad de Informática para la Biodiversidad, Departamento de Biología Evolutiva, Facultad de
13   Ciencias, Universidad Nacional Autónoma de México (UNAM), Mexico City, Mexico.
14
15   Corresponding Author:
16   Juan J. Morrone[1]
17   Museo de Zoología 'Alfonso L. Herrera', Departamento de Biología Evolutiva, Facultad de
18   Ciencias, Universidad Nacional Autónoma de México (UNAM), Coyoacan, Mexico City, 04510,
19   México
20   Email address: morrone@ciencias.unam.mx
21

Abstract

22
23   **Background.** The niche conservatism hypothesis postulates that species' distributions are
24   constrained by physiological and phylogenetic factors, resulting in the creation of richness
25   hotspots and the presence of older lineages in the ancestral climatic conditions. Conversely,
26   niche convergence occurs when species successfully disperse to novel environments,
27   diversifying and resulting in areas with high phylogenetic clustering and endemism, low
28   diversity, and lower clade age. The Mexican Transition Zone exhibits both patterns as its biotic
29   assembly resulted from successive dispersal events of different biotic elements called cenocrons.
30   Our study proposes that biogeographic transitionality in the area is a product of niche
31   conservatism in the Nearctic and Typical Neotropical cenocrons and niche convergence in the
32   Mountain Mesoamerican cenocron.
33   **Methods.** To test this, we split the avifauna into three species sets that represent cenocrons (set
34   of taxa that share the same biogeographic history, which constitute an identifiable subset within a
35   biota by their common biotic origin and evolutionary history). Then, we correlated richness,
36   endemism, phylogenetic diversity, number of nodes, and crowning age with environmental and
37   topographic variables. These correlations are then compared with the predictions of niche
38   conservatism versus niche convergence. We also detected areas of higher species density in
39   environmental space and interpret it as an environmental transition zone where birds' niches
40   converge.

41 **Results.** Our findings support the general theory behind the MTZ framework, as species
42 followed the expected predictions on how their niches evolved. Nearctic and Typical Neotropical
43 species behaved as predicted by niche conservatism, whereas Mountain Mesoamerican species
44 and the total of species correlations indicate a case of niche convergence. We also detected that
45 cenocron assemblages have distinct ecological and evolutionary characteristics on a
46 macroecological scale, and that environmental conditions where the three cenocrons overlap are
47 in the Mesoamerican region.

48

Introduction

49
50 Diversity patterns emerge from the overlap of species distributions (Wiens, 2011), which are the
51 geographical representation of ecological niches. The characteristics of these diversity patterns
52 can change since niches can evolve (Holt, 2009) or be conserved over evolutionary time (Wiens
53 & Graham, 2005). According to the niche conservatism hypothesis, physiological constraints
54 prevent species from dispersing into contrasting environments (Wiens & Donoghue, 2004; Lobo,
55 2007). Therefore, it is expected to find richness hotspots, phylogenetically clustered species, and
56 older lineages in the ancestral climatic conditions (Qian & Ricklefs, 2016). Niche conservatism
57 is a widely described pattern for latitudinal gradients, for example, in mammals (Buckley *et al.*,
58 2010), birds (Hawkins *et al.*, 2006, 2007), insects (Löwenberg-Neto & Carvalho, 2020; Chazot *et
59 al.*, 2021), ferns (Hernández-Rojas *et al.*, 2021), and angiosperms (Qian & Sandel, 2017; Qian *et
60 al.*, 2018; Yue & Li, 2021). There is also evidence of the inverse pattern, known as niche
61 convergence (Qian & Ricklefs, 2016), that emerges from an early dispersal of multiple lineages
62 to novel environments followed by a diversification slowdown (Jablonski *et al.*, 2006; Qian &
63 Ricklefs, 2016), which causes the co-occurrence of lineages from different ages and backgrounds
64 in environmental conditions that differ from their ancestral niche. This pattern predicts that, as
65 the environmental conditions differ from the ancestral niche, average clade age increases
66 (Jablonski *et al.*, 2006; Qian *et al.*, 2018) and phylogenetic clustering decreases (Hawkins *et al.*,
67 2014; Qian & Ricklefs, 2016) due to the lack of niche conservatism (Qian & Ricklefs, 2016;
68 Qian *et al.*, 2019). Niche convergence has been described in plants (Cavender-Bares *et al.*, 2004;
69 Bryant *et al.*, 2008; Cavender-Bares *et al.*, 2011; Culmsee & Leuschner, 2013; González-Caro *et
70 al.*, 2014; Qian, 2014; Hagen *et al.*, 2021), vertebrates (Rolland *et al.*, 2014; Hagen *et al.*, 2021),
71 and Opiliones (Benavides *et al.*, 2021).
72 The Mexican Transition Zone (MTZ) offers an opportunity to study the interaction of both
73 processes in producing complex diversity patterns, as it is a region where lineages from Nearctic
74 and Neotropical origins coexist in an environmentally heterogeneous area. This area has a rich
75 endemic biota distributed in a clear elevational zonation that parallels the latitudinal gradient
76 (Espinosa-Organista *et al.*, 2008; Morrone, 2017), reflecting gradual temperature changes that
77 delimit the Nearctic from the Neotropics (Ficetola *et al.*, 2017). Its diversity gradients have been
78 shaped by temperature, latitude, and physiography (Ficetola *et al.*, 2017; Halffter, 2017; Halffter
79 & Morrone, 2017; Morrone, 2020). The MTZ was assembled by the successive dispersal events
80 of cenocrons, which are sets of taxa that dispersed from both North and South America (Halffter,

81   1987; Halffter & Morrone, 2017; Morrone, 2020). Each cenocron represents an evolutionary

82   biotic unit with a distribution linked to current environmental conditions (Lobo, 2007), indicating

83   'ecological inertia' (Halffter & Morrone, 2017) or 'biogeographic memory' (Lobo, 1999), which

84   can be interpreted as a measure of niche conservatism.

85   Each of the cenocrons in the MTZ has a proposed age derived from its species distribution size,

86   niche width, phylogenetic affinities, and differential species richness between regions (Juárez-

87   Barrera *et al.*, 2020). These ideas (summarised in Table 1) offer testable hypotheses about the

88   evolutionary processes behind the area's diversity patterns. The Nearctic and Typical

89   Neotropical cenocrons have conserved niches due to their recent dispersal, as proposed by Wiens

90   and Donoghue (2004) as part of the niche conservatism hypothesis. On the other hand, the

91   Mountain Mesoamerican cenocron has a Neotropical origin but its maximum species richness is

92   distributed in mountain moist forests which are colder and wetter than the lowlands (their

93   suspected ancestral niche). These species also show high endemicity and speciation hotspots at

94   mountain tops result of *in situ* radiations (Halffter & Morrone, 2017; Hagen *et al.*, 2021) and

95   higher diversification rates due to the impossibility of dispersing back to the ancestral niche

96   (Arriaga-Jiménez *et al.*, 2020).

97   Although these patterns have been described in numerous works (listed in Morrone, 2020), their

98   relationship with niche evolution has never been tested. Therefore, our aim is to test whether

99   cenocrons are composed of clades pre-adapted to local conditions or of convergent assemblages

100   with evolutionarily independent lineages. We do so by comparing how the clade age,

101   phylogenetic diversity, and species richness correlate with environmental variables (Qian *et al.*,

102   2021). We propose that biogeographic transitionality is a product of niche conservatism in

103   Nearctic and Typical Neotropical cenocron's species, whereas endemicity is a product of niche

104   convergence caused by older dispersal from the Neotropics to colder environments in mountain

105   moist forests and *in situ* diversification of the Mountain Mesoamerican cenocron (Halffter &

106   Morrone, 2017; Hagen *et al.*, 2021). Therefore, we expect high and contrasting correlations of

107   Nearctic and Typical Neotropical species with environmental variables because they have

108   conserved niches. If the Mountain Mesoamerican niches are conserved, the correlations will be

109   comparable to the Typical Neotropical species, whereas if correlations are weak or like those of

110   Nearctic species, niches will be convergent. To evaluate this, we calculate the richness,

111   phylogenetic diversity, weighted endemism, number of nodes, and age of each cenocron and its

112   correlation with environmental and topographic variables.

113

Materials & Methods

115   *Study Area*

116   The MTZ includes the mountain regions of Mexico, Guatemala, Honduras, and El Salvador

117   (Halffter, 1987; Halffter & Morrone, 2017; Morrone, 2020; De Mendonça & Ebach, 2020). We

118   used a polygon of the MTZ (Fig. 1, left) that includes the Sierra Madre Occidental, Sierra Madre

119   Oriental, Transmexican Volcanic Belt, Sierra Madre del Sur, and Chiapas Highlands

120   biogeographic provinces (Morrone, 2020), and adjacent lowlands. In the mountain bird database,

121   Quintero & Jetz (2018) named this area as the Mexico and Sierra Madre de Chiapas mountain
122   ranges.
123   To describe the environmental space of this area, we performed a principal component analysis
124   to the climate layers from WorldClim 2.0 (Fick & Hijmans, 2017) with a resolution of 2.5 arc
125   min. The details of the analysis and results of the PCA are available in Appendix 1 in Supporting
126   Information. The first two components explain 80% of the environmental variation (56.8%,
127   23.2%, respectively, Table S02 in the supplementary material Appendix 1) and were used to
128   visualise the existing climate conditions in the MTZ (Fig. 1, right).
129

130   *Phylogenetic data*
131   We used Jetz et al.'s (2012) dated phylogeny with Hacket et al.'s (2008) backbone. The original
132   phylogeny includes all the 9,993 species described by the time of its publication (available at
133   https://birdtree.org/downloads). We used the last set of the stage two trees with the Hackett
134   backbone which includes 1,000 trees to incorporate phylogenetic uncertainty. We pruned the
135   phylogeny to keep only the selected species, listed in Appendix 2 and plotted in Fig. S1
136   Appendix 1 in Supporting Information. All the analyses were ran through the 1,000 trees set to
137   incorporate phylogenetic uncertainty.
138

139   *Species selection*
140   We selected species listed in the MTZ mountain ranges (Mexico and Sierra Madre de Chiapas
141   mountain ranges, Quintero & Jetz 2018) whose distribution is certain and have native
142   distribution (breeding season and resident) according to the Handbook of the Birds of the World
143   (BirdLife International and Handbook of the Birds of the World, 2020). A total of 10 orders, 47
144   families, 326 genera and 808 species were selected (see the Supplementary Material Appendix
145   2). Most of these species are distributed in the MTZ and Mesoamerica (286 species) or have
146   more than 80% of their distribution in the MTZ (246 species). To assure that only monophyletic
147   groups are analysed, we identified the sister species or clades of each of the species distributed in
148   the study area by finding the parental node and its descendants in all the trees. Some species
149   were removed from the tree in advance to do analyses faster, based on their biology, natural
150   history and known distribution. We removed the species of the aquatic bird orders (Suliformes,
151   Phaethontiformes, Procellariiformes, Charadriiformes, Anseriformes, Podicipediformes,
152   Gaviiformes, Ciconiiformes, Pelecaniformes, Gruiformes, and Eurypygiformes), migratory
153   families (Parulidae, Hirundinidae, and Motacillidae), widespread families (Accipitridae,
154   Cathartidae, Columbidae, Falconidae, Tytonidae and Strigidae), and families not distributed in
155   the Americas (Alaudidae, Certhiidae, Otididae, and Prunellidae). This was done using Jetz et
156   al.'s (2012) dated phylogeny with Hacket et al. (2008), all the analyses were repeated through the
157   1,000 trees included in the set to incorporate phylogenetic uncertainty. We prunned the
158   phylogeny to keep only the selected species, listed in Appendix 2 and plotted in Fig. S1
159   Appendix 1 in Supporting Information.
160

161 *Cenocron assignment*
162 The original concept of cenocron was based on the differential richness of clades as a proxy of
163 the ancestral area (Juárez-Barrera *et al.*, 2020). So, we used Morrone's (2014) regionalization for
164 the Americas, and the ecoregions' realms for the rest of the world, then recoded these areas as
165 the northern hemisphere (Nearctic, Palearctic, or Saharo-Arabian), the southern hemisphere
166 (Afrotropics or Neotropics), or Mesoamerican (Mexican Transition Zone and Mesoamerican
167 dominion). To indicate shared evolutionary history, we used the family classification and we
168 assigned each family to a cenocron using these rules: 1) Nearctic if the family has >80% of its
169 species distributed in the Northern hemisphere or if it has more species in the Northern
170 hemisphere than in the Southern hemisphere or Mesoamerica, and phylogenetically related
171 species are Nearctic; 2) Mountain Mesoamerican if a family has more species in Mesoamerica
172 than in the Southern and Northern Hemispheres, and if phylogenetically related species are
173 Neotropical; and 3) Typical Neotropical if a family has >80% of its species distributed in South
174 America and phylogenetically related species are Neotropical (Fig. 2). A detailed description and
175 code of this section are included in the Appendix 1 in Supporting Information.
176
177 *Species distribution models*
178 Occurrence data for years 1950 to 2020 were obtained from the Birds' Database compiled by
179 CONABIO (2021) and GBIF. The occurrence query in GBIF included native occurrence data
180 from specimens and observations, marked as without spatial issues, with less than 10 km of
181 uncertainty and a coordinate precision >0.01. Since the data set was too large, it was split into
182 several data sets that can be found on GBIF.org (2021a-h). We used 'CoordinateCleaner' (Zizka
183 *et al.*, 2019) to remove duplicated records, records at sea, and near geographic centroids. We also
184 omitted records outside the Bird Life breeding distribution maps. Species with more than 5,000
185 records were downsampled to this number, we thinned the data to ensure >5km of distance
186 between records (Aiello-Lammens *et al.*, 2015). Finally, we split the data into training (75%) and
187 testing (25%) for the model construction and validation.
188 As ecological and historical conditions shape species distributions, we had to include both
189 factors to build species distribution models. As ecological factors, we used the climate layers
190 from WorldClim 2.0 (Fick & Hijmans, 2017) and ENVIREM (Title & Bemmels, 2018) with a
191 resolution of 2.5 arc min. We selected variables of high biological importance with a low
192 Variance Inflation Factor (VIF, available in the '*usdm*' package by Naimi *et al*., 2014) to avoid
193 multicollinearity. This analysis calculates the severity of multicollinearity in an ordinary least
194 squares regression analysis of environmental variables in the extent of the MTZ mountain
195 systems (Fig. 1, left). The selected variables fall into three categories: (1) topographic: elevation,
196 slope, and topographic roughness index, the elevation data from WorldClim were used to create
197 the slope and Terrain Ruggedness Index; (2) moisture: Thornthwaite's aridity index, climatic
198 moisture index, and annual precipitation; and (3) temperature: maximum temperature of the
199 coldest month, minimum temperature of the coldest month, maximum temperature of the
200 warmest month, minimum temperature of the warmest month.

201   To include historical factors, the climate layers were cropped to include only those areas that
202   have been accessible to the species over a relevant time (Soberón & Nakamura, 2009). We
203   obtained this area, known as the accessible area or M (Barve *et al.*, 2011), by masking the raster
204   environmental data with the breeding occurrence records and the biogeographic provinces of the
205   Nearctic region (Escalante *et al.*, 2021) and the Neotropical region (Morrone *et al.*, 2022).
206   To model the potential distributional area for each bird species, we used the *MaxEnt* algorithm
207   version 3.4.4 (Phillips *et al.*, 2006) using the SDMTune package in R (Vignali *et al.*, 2020). We
208   applied a Maximum test sensitivity plus specificity threshold (Liu *et al.*, 2005) for obtaining the
209   binary maps. The models were evaluated using area under the Curve (AUC) and True Skill
210   Statistics (TSS). A detailed description and code of this section is included in Appendix 1 of the
211   Supporting Information.
212
213   *Assemblage Measures*
214   We used the distribution models to calculate raster data of alpha diversity (species richness), age
215   (Mya), number of nodes, phylogenetic diversity (PD), and weighted endemism. Alpha diversity
216   was obtained as the sum of the binary distribution maps of each species. Age is the mean branch
217   length value of all the species found per cell, and number of nodes is the number of nodes from
218   tip to root of all the species found per cell. We made a community matrix from 50 thousand
219   randomly selected points and cell of 2.5 arc min to create a community matrix for the calculation
220   of phylogenetic diversity and weighted endemism. Phylogenetic diversity was calculated with
221   correction for changes in species richness using the *tip shuffle* model (Laffan & Crisp, 2003).
222   Weigted endemism is species richness inversely weighted by species ranges. Both indices were
223   obtained using the package 'phyloregion' (Daru *et al.*, 2020).
224
225   *Cenocron assemblage's response to environmental variables*
226   To compare whether these assemblage measures are different between cenocrons, we used a one-
227   way ANOVA with a Tukey's HSD post hoc test. Then, we evaluated whether the assemblage
228   measures are correlated with the environmental variables used to model the species distribution
229   (elevation, slope, topographic roughness index, Thornthwaite's aridity index, climatic moisture
230   index, annual precipitation, maximum temperature of the coldest month, minimum temperature
231   of the coldest month, maximum temperature of the warmest month, minimum temperature of the
232   warmest month). To do so, we applied a Pearson correlation test and compared the coefficient
233   values between cenocrons to detect whether their assemblage responds to environmental
234   variables and the direction of this response (positive vs. negative), and all tests with $p < 0.05$
235   were accepted as significative. All the analyses were conducted using the R Statistical language
236   (version 4.1.0; R Core Team, 2021).
237
238   *Diversity in environmental and geographic space*
239   We evaluated the overlap of species richness in both geographic and environmental space. In the
240   geographic space, this was done as the sum of the predicted distribution models by cenocron. In

241   the environmental space, the species was obtained as the overlap of species distribution models
242   in the PCA described above. Furthermore, we evaluated the overlap of species in environmental
243   space to detect the environmental conditions in which species from three cenocrons converge,
244   called the environmental transition zone, and then projected it into geographic space to propose a
245   transition zone where the niches converged.
246

Results

248   The three cenocrons had a statistically significant differences in all measures ($p < 0.001$) and the
249   effect of the grouping in all response variables was statistically significant ($p < .001$). The effect
250   size was medium on age (F(2, 275377) = 9045.87, p < .001; Eta2 = 0.06, 95% CI [0.07, 1.00]),
251   mean number of nodes (F(2, 277014) = 16871.00, p < .001; Eta2 = 0.11, 95% CI [0.12, 1.00]),
252   species richness (F(2, 288741) = 10887.15, p < .001; Eta2 = 0.07, 95% CI [0.08, 1.00]), and
253   weighted endemism (F(2, 275413) = 18211.31, p < .001; Eta2 = 0.12, 95% CI [0.13, 1.00]),
254   while the effect size on PD is large (F(2, 275128) = 55903.64, p < .001; Eta2 = 0.29, 95% CI
255   [0.31, 1.00]). Effect sizes were labelled according to Makowski *et al.* (2020).
256   The species of the Typical Neotropical cenocron have higher species richness, endemism, and
257   PD than the others (Fig. 3). In the species of the Nearctic cenocron, although it has a medium
258   crown age and number of nodes, the distribution leans towards lower values. Additionally, this
259   cenocron has more derived species than the other two cenocrons, with lower richness, PD, and
260   endemism. The species of the Mountain Mesoamerican cenocron have a narrower but more
261   uniform distribution in all measures.
262   All correlations were significant ($p < 0.01$, Fig. 4), except for temperature values of the coldest
263   mountain month, and the correlation of all the species with the minimum temperature of the
264   coldest month. Nearctic and Typical Neotropical cenocrons' measures are more correlated to
265   environment than the values of the Mountain Mesoamerican cenocron and the total of the
266   analysed species (Fig. 4). The Nearctic cenocron measures have the highest coefficient values
267   and are positively correlated with higher latitudes and negatively correlated with annual
268   precipitation and temperature, while the Typical Neotropical cenocron measures are the opposite.
269   The topographic variables are more correlated with the Mesoamerican cenocron measures than
270   with the other two cenocrons. The Mountain Mesoamerican cenocron's coefficients are low but
271   have the same direction than those of the Nearctic. Slope and ruggedness are only correlated with
272   the mountain Mesoamerican. Despite predictions, the Mountain Mesoamerican cenocron is not
273   correlated with any humidity variable.
274   Geographic richness patterns show the expected overlap in mountain regions (Fig. 5a-d). The
275   Typical Neotropical cenocron (Fig. 5e) follows the general pattern in the lowlands of both the
276   Pacific and the Gulf of Mexico (Fig. 5d). Nearctic species have a distinct distribution that
277   follows the Sierra Madre Occidental all the way up to Canada (Fig. 5b). Mountain Mesoamerican
278   species are restricted to mountain regions (Fig. 5a), which act as a barrier between the Nearctic
279   and Neotropical regions. The environmental distribution of the Typical Neotropical species
280   shows higher species density in quadrant than the total species pattern, but still has the same

281 approximate distribution. Nearctic species (Fig. 5b) are restricted to the quadrant of high
282 temperature variability, seasonality, and warmer summer (see Fig. 1). Mountain Mesoamerican
283 species (Fig. 5e) share the same environmental space than Typical Neotropical species.
284 The geographic representation of the environmental overlap of the three cenocrons is found in
285 the Mexican and Central American mountain regions, including the highlands and lowlands
286 facing the oceans (Fig. 6). The northern limit gradually disappears between the Sierra Madre
287 Occidental and the Arizona Mountain Forests. The southern limit matches with the Páramo
288 region in Colombia.
289

Discussion

291 We found that both niche conservatism and convergence occur in the MTZ when the species are
292 separated into cenocrons. Our method of assigning species to a cenocron statistically significant
293 differences between the groups, not only in terms of their average age, endemism, and richness,
294 but also in how these measures change along the environmental gradients. The age, richness, and
295 phylogenetic diversity of the Nearctic and Typical Neotropical cenocrons decrease as they move
296 away from their ancestral niche as predicted by niche conservatism. The Nearctic cenocron is
297 correlated with high latitudes, low annual precipitation, and cold environment, while the Typical
298 Neotropical cenocron exhibits the opposite pattern. Contrastingly, the Mountain Mesoamerican
299 cenocron and the total of species have low correlations with environmental variables, which
300 indicates that niche convergence is shaping these diversity patterns (Qian & Ricklefs, 2016).
301 This result is consistent with the predictions for the cenocrons (Table 1) in which recent dispersal
302 results in niches that are conserved towards the ancestral environment (temperate for Nearctic
303 and warm for Typical Neotropical). Even without accounting for the cenocron splitting, the
304 correlations found for the total species suggests that the MTZ is a region of niche convergence.
305 Relative niche conservatism has been reported in the MTZ, where conservatism was found at the
306 species level but not at the family level, indicating that vicariance drives speciation and then
307 ecological differences evolve (Peterson *et al.*, 1999). This is consistent with the recent dispersal
308 of the Typical Neotropical and Nearctic cenocrons into the MTZ and the more ancient dispersal
309 of the Mountain Mesoamerican cenocron. Niches will always be conserved to some extent
310 (Wiens & Graham, 2005), but not among all taxa, environmental variables or timescales (Stigall,
311 2014). Examples of both niche conservatism and niche evolution exist in the literature, as
312 reviewed by Wiens and Graham (2005), Pearman *et al.* (2008) and references cited above.
313 Attempting to explain the complexity of how diversity distributes solely based on one of these
314 patterns is an oversimplification, especially in a complex area as a transition zone. So, we focus
315 our discussion on the finding of niche evolution and the possible processes behind it. We test
316 several hypotheses on the assembly of MTZ biota, using niche evolution as a synthetic
317 conceptual framework and the cenocron framework as a temporal scale.
318

319 *Cenocron Assignation*

320 Our method is the first one to classify species applying simple rules. Previous studies assigned
321 groups to cenocrons based on expert knowledge for the MTZ (Halffter's original works), used
322 multivariate analyses using ecological traits for Iberian dung beetles (Lobo, 2007), or manually
323 linked distribution and phylogenetic data for Patagonian fauna (Roig-Juñent *et al.*, 2018).
324 However, our study stands out as the first to test cenocron assemblages for distinct ecological
325 (richness, endemism, and PD) and evolutionary (age and number of nodes) characteristics on a
326 macroecological scale. Yet, the classification method still needs to be improved by using strict
327 phylogenetic data and important geological events (e.g., uplift of barriers) or diversification
328 rates.
329
330 *Conserved Niches*
331 Niche conservatism predicts higher species richness within environments occupied by species'
332 ancestors (Wiens & Donoghue, 2004), lower age and PD within environments that differ from it
333 (Qian & Ricklefs, 2016). The Nearctic and Typical Neotropical cenocrons follow this pattern.
334 This is explained by the time since species-rich regions have been colonized for a long time and
335 have accumulated richness (Fine, 2015; Pyron *et al.*, 2015; Machac, 2020). These cenocrons
336 were the last cenocrons to disperse into the MTZ (Miocene-Pliocene, and Pliocene-Pleistocene,
337 respectively, O'Dea *et al.*, 2016; Morrone, 2020). Therefore, there has not been enough
338 opportunity for the species to shift niches. Before that, South America was an island continent,
339 which resulted in a large diversification and high levels of endemism (Ricklefs, 2002) and a high
340 specialization to tropical environments. After the Panamanian Bridge lifted and allowed the
341 dispersal of the Typical Neotropical cenocron into the MTZ, birds dispersed as described for the
342 well-understood mammalian interchange (Smith & Klicka, 2010) and their dispersal was also
343 asymmetric. Unlike the northern taxa, the avian families in the Neotropics remain almost entirely
344 restricted to that region (Smith & Klicka, 2010; Smith *et al.*, 2012). For instance, Furnariidae
345 represent the largest continental radiation of vertebrates endemic to the Neotropics (Villalobos *et*
346 *al*, 2020).
347 Dispersal from north to south has been more frequent. This is not only because the MTZ had a
348 continuous connection with North America throughout its history (Smith & Klicka, 2010), but
349 also because its mountains are higher when coming from the Neotropics (Janzen, 1967).
350 Therefore, mountain passes are physiological, not topographic, barriers to dispersal (Ghalambor
351 *et al.*, 2006) and act as a such only when there is little or no climatic overlap between the
352 lowlands and the mountains. In temperate zones, the warm season in high elevation can be
353 equivalent to the cold season in the lowlands, which allows species to track the preferred niche
354 seasonally and promoting niche conservatism. This does not happen in the tropics where there is
355 not much seasonal variation in temperature. This hypothesis is linked to the suggestion that
356 seasonal migration promoted colonization of the tropics from the north, which is the mechanism
357 that Emberizoidea seem to have followed to colonize the tropics from the north temperate region
358 and is consistent with niche conservatism (Winger *et al.*, 2014). As a result, tropical mountains

359   can be generally structured into distinct thermal zones, with relatively little thermal overlap
360   between low and high elevation sites across seasons (Muñoz & Bodensteiner, 2019).
361
362   *Convergent niches*
363   The Mountain Mesoamerican cenocron does not follow the pattern expected when niches are
364   conserved, since it does not correlate with the environmental variables. The species of the
365   Mountain Mesoamerican cenocron are distributed at the lower and more variable temperature
366   extremes of the Typical Neotropical cenocron's distribution (quadrant IV in the environmental
367   space), suggesting that the Mountain Mesoamerican cenocron represents a subset of the Typical
368   Neotropical cenocron in multivariate space.
369   The Mountain Mesoamerican cenocron, representing the oldest dispersal in our analysis, has
370   been subject to a lot of climatic fluctuations and landscape shifts. Its species dispersed from
371   South America to Central America in the Oligocene and diversified in the mountains and
372   dispersed into Mexico during the Pliocene (Rocha-Méndez *et al.*, 2019; Morrone, 2020). This
373   dispersal took place during Earth's most recent period of sustained global warmth (Dekens *et al.*,
374   2007), characterized by warmer temperatures at high-latitudes and reduced temperature
375   differences between the Equator and the poles (Fedorov *et al.*, 2013). At that time, mountains
376   where the Mountain Mesoamerican cenocron dispersed were covered by warm-tempered forests
377   (Mastretta-Yanes *et al.*, 2015). additionaly, there was a highland corridor connecting the
378   mountains of Central America and Mexico through the Isthmus of Tehuantepec (Mastretta-
379   Yanes *et al.*, 2015), which played a role in the geographical setting of the Mountain
380   Mesoamerican cenocron's dispersal (Halffter *et al.*, 1995; Halffter & Morrone, 2017; Rocha-
381   Méndez *et al.*, 2019; Morrone, 2020). The Mountain Mesoamerican cenocron spread northwards
382   from Panama across Central America lowlands, and its lineages started to diverge during the
383   Pliocene at 5.8 Ma (Rocha-Méndez *et al.*, 2019). Subsequently, a period of intense ice age cycles
384   began (Dekens *et al.*, 2007). In response to these cycles, according to the niche conservatism
385   hypothesis, the main response is dispersal (Lobo, 2007; Donoghue, 2008). However, when it is
386   not possible to disperse back, adaptation to novel climatic niches promotes speciation and/or
387   impedes extinction (Cooney *et al.*, 2016).
388   The fragmentation of the once continuous cloud forest due to Pleistocene climatic fluctuations
389   (Luna Vega *et al.*, 1999), the partial loss of the connection along the Isthmus of Tehuantepec
390   (Mastretta-Yanes *et al.*, 2015), and the lift of high stratovolcanoes in the Transmexican Volcanic
391   Belt (Ferrari *et al.*, 2012) promoted semi-permeable barriers to dispersal (Rocha-Méndez *et al.*,
392   2019). These events fragmented the cloud forest into areas of high endemism (Luna Vega *et al.*,
393   1999) and great genetic diversity (Rocha-Méndez *et al.*, 2019). A vicariant model of the
394   Mountain Mesoamerican forests and sky island dynamics explains patterns (Luna Vega *et al.*,
395   1999; Sánchez-González *et al.*, 2008; Fjeldså *et al.*, 2012; Sosa & Loera, 2017) and the
396   intraspecific genetic structure (Rocha-Méndez *et al.*, 2019). Furthermore, the current diversity
397   gradients are related with climate (Sosa & Loera, 2017). This agrees with Peterson (1999), who
398   noticed the importance of separating geographical and environmental space and adding a

399   temporal scale when evaluating niche conservatism. Overall, the *in situ* endemic radiations
400   associated with mountain uplifts and climatic fluctuations (Hagen *et al.*, 2021) used to explain
401   the vicariant pattern in the Mountain Mesoamerican cenocron, along with our results are
402   consistent with a niche convergence diversification model.
403
404   *Environmental Transition Zone*
405   The Mexican Transition Zone provinces overlap with temperate and tropical conditions (Fig. 1),
406   which, according to the environmental overlap hypothesis (Janzen, 1967), make these mountains
407   a semi-permeable barrier. This agrees with the definition of a transition zone as partial barriers or
408   filters that restrict differentially the distribution of each biotic component (Ferro & Morrone,
409   2014). The area found in our results corresponds to the MTZ (Morrone, 2020), but goes beyond
410   the Nicaraguan Depression. This region represents the distributional boundary for many bird taxa
411   (Sánchez-Ramos *et al.*, 2018), and is considered the southern limit of the MTZ (Halffter &
412   Morrone, 2017) The simpler explanation to this could be the greater dispersal abilities of birds.
413   Nevertheless, the environmental overlap model suggests that the MTZ has a larger overlap with
414   the Neotropics. Thus, it makes it easier for populations to disperse upwards in the mountains or
415   northwards.
416

Conclusions

418   Our analysis of bird data supports the general theory behind the MTZ framework. The cenocrons
419   follow the expected predictions on niche evolvution. Cenocrons that recently dispersed (Nearctic
420   and Typical Neotropical) show niche conservatism since they are correlated to the measured
421   environmental variables. Contrastingly, the Mesoamerican mountains are an area of niche
422   convergence for they show little to no correlation with the environmental variables. The total
423   vifauna in the MTZ also follows a pattern of niche convergence, which is also as expected in a
424   biogeographical transition zone. The diversity patterns in complex biogeographic areas like the
425   MTZ are shaped by time-dependent processes that affect species differently. Therefore, it is
426   important to incorporate a historical perspective to ecological studies to better understand these
427   patterns.
428   While niche conservatism may drive speciation in some clades, it does not explain overall
429   patterns of diversification (Cooney *et al.,* 2016). Recently dispersed cenocrons (Nearctic and
430   Typical Neotropical) tracked the most favourable conditions along the latitudinal and
431   environmental gradient, which allowed them to retain their ancestral niche. In contrast, the
432   Mountain Mesoamerican cenocron has encountered multiple environmental changes in a
433   heterogeneous topography. As a result, each isolated population of these species had a different
434   closest analogue of the ancestral niche (Pyron *et al.,* 2015) leading to geographical convergence
435   of lineages from different ancestral niches in these mountains. Our takeaway message is that
436   complex biogeographic patterns result from intricate evolutionary processes. To unravel this
437   complexity, it is crucial to incorporate a time-scale perspective, since niche conservatism is scale
438   dependent (Losos, 2008). Incorporating the historical context by dividing the analysis into

439 cenocrons is an effective way to do so, allowing to add historical context to the ecological
440 analyses, which is fundamental to understand niche evolution.
441

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448

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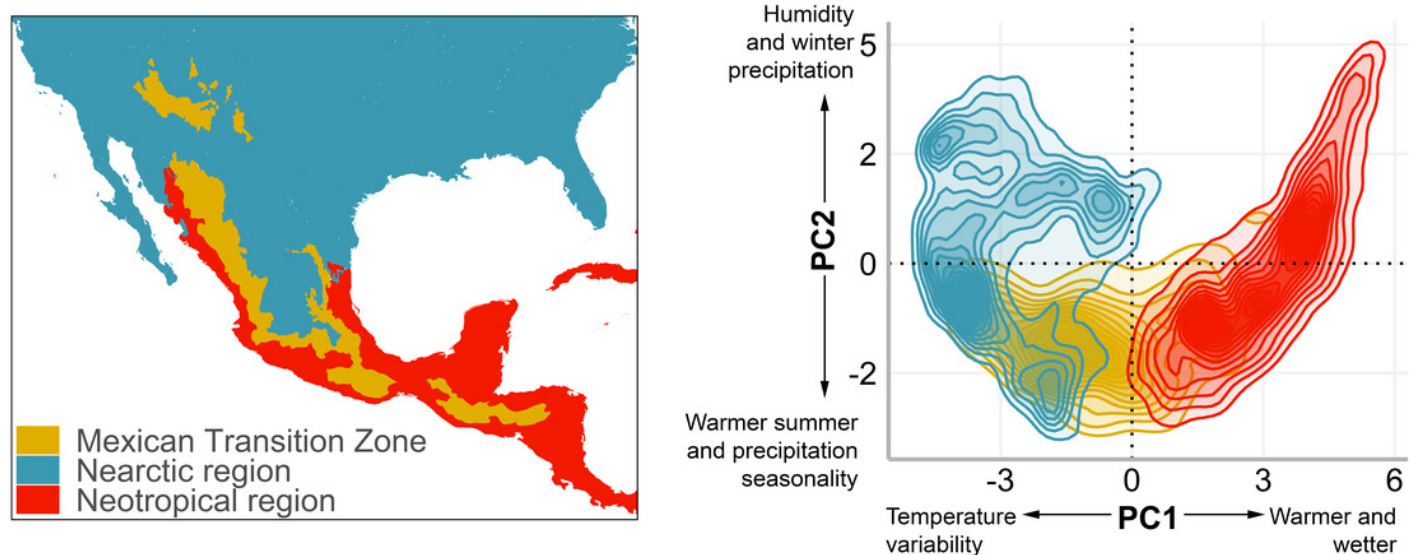595 35:89–126. DOI: 10.1071/SB22002.

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Figure 1

The Mexican Transition Zone (Morrone, 2020) and mountain ranges considered from the Quintero & Jetz's (2018) database. Geographic location (left) and environmental space (right) of the Mexican Transition Zone, the Nearctic, and the Neotropics.
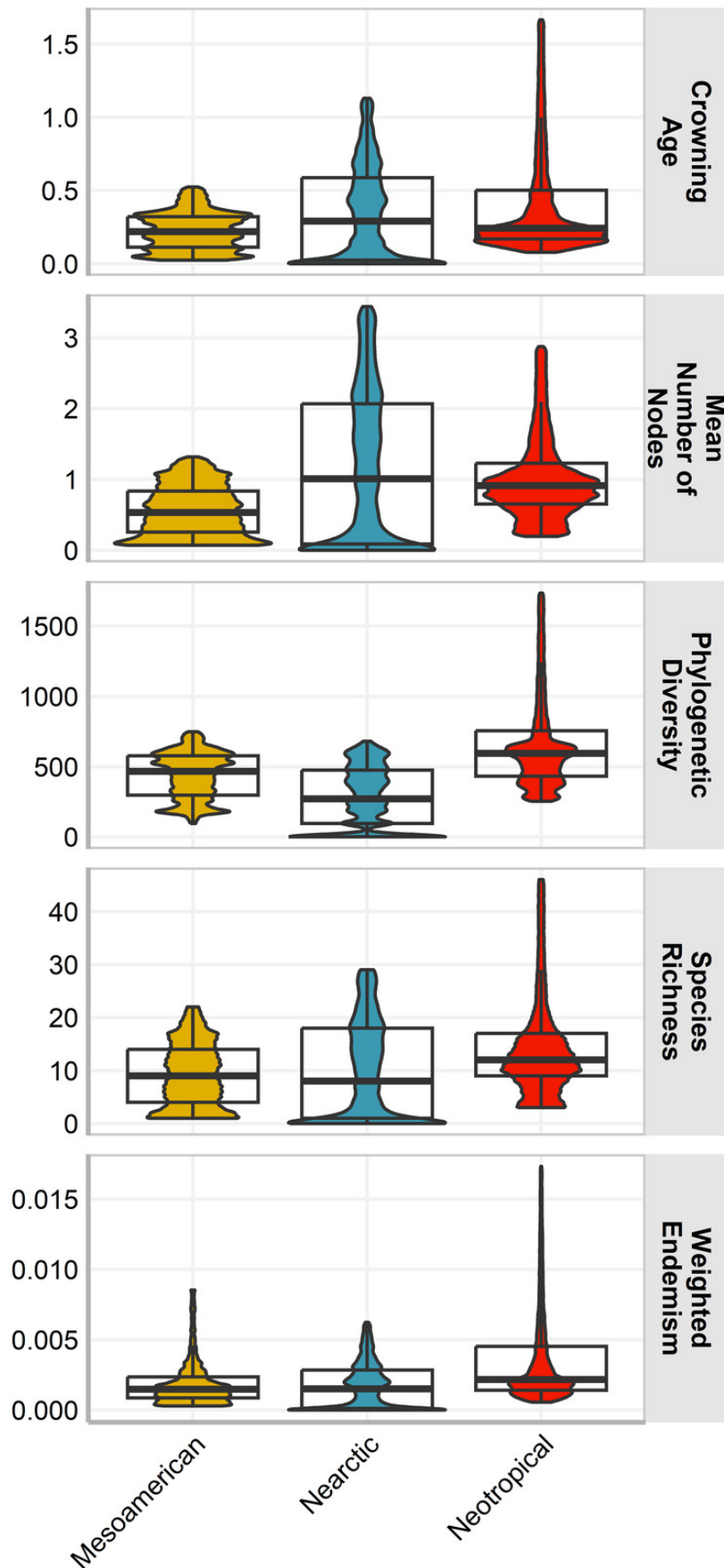
Figure 2

Cenocron membership of bird families in the Mexican Transition Zone, based on the number of species distributed in larger biogeographic regions and phylogenetic relationships.

Percentage of Species

Order	Family	Nearctic: Palearctic	Nearctic: Nearctic	Nearctic: Mesoamerican	Nearctic: Neotropical	Nearctic: Old World Tropics	Mesoamerican: Palearctic	Mesoamerican: Nearctic	Mesoamerican: Mesoamerican	Mesoamerican: Neotropical	Neotropical: Nearctic	Neotropical: Mesoamerican	Neotropical: Neotropical
Apodiformes	Apodidae										33%	33%	33%
	Trochilidae							9%	56%	35%			
Caprimulgiformes	Nyctibiidae											33%	67%
	Caprimulgidae							36%	36%	29%			
Coraciiformes	Alcedinidae										17%		83%
	Momotidae								62%	38%			
Cuculiformes	Cuculidae										24%	24%	53%
Galliformes	Odontophoridae							22%	67%	11%			
	Cracidae								78%	22%			
	Phasianidae	33%	44%	11%		11%							
Passeriformes	Tyrannidae										22%	32%	47%
	Thraupidae											41%	59%
	Thamnophilidae											4%	96%
	Polioptilidae										33%	33%	33%
	Icteridae										24%	18%	58%
	Furnariidae											25%	75%
	Formicariidae											20%	80%
	Dendrocolaptidae											27%	73%
	Cotingidae											24%	76%
	Coerebidae												100%
	Cardinalidae										21%	38%	41%
	Bombycillidae										33%	33%	33%
	Vireonidae							41%	45%	14%			
	Turdidae							39%	57%	4%			
	Troglodytidae							25%	50%	25%			
	Pipridae								75%	25%			
	Peucedramidae								100%				
	Corvidae						3%	29%	47%	21%			
	Sturnidae	100%											
	Sittidae		100%										
	Remizidae		100%										
	Reguliidae	33%	67%										
	Passeridae	100%											
	Paridae		78%	22%									
	Mimidae		67%	25%	8%								
	Laniidae		100%										
	Fringillidae	25%	42%	25%		8%							
	Emberizidae		45%	41%	14%								
	Cinclidae		100%										
	Aegithalidae		100%										
Piciformes	Ramphastidae											50%	50%
	Galbulidae												100%
	Bucconidae												100%
	Picidae	3%	44%	38%	16%								
Psittaciformes	Psittacidae								62%	38%			
Tinamiformes	Tinamidae											50%	50%
Trogoniformes	Trogonidae											47%	53%

Figure 3

Box plot of the assemblage characteristics of the three cenocrons found in the Mexican Transition Zone. The letters indicate the groups found in a Tukey HSD test result of a one way ANOVA.
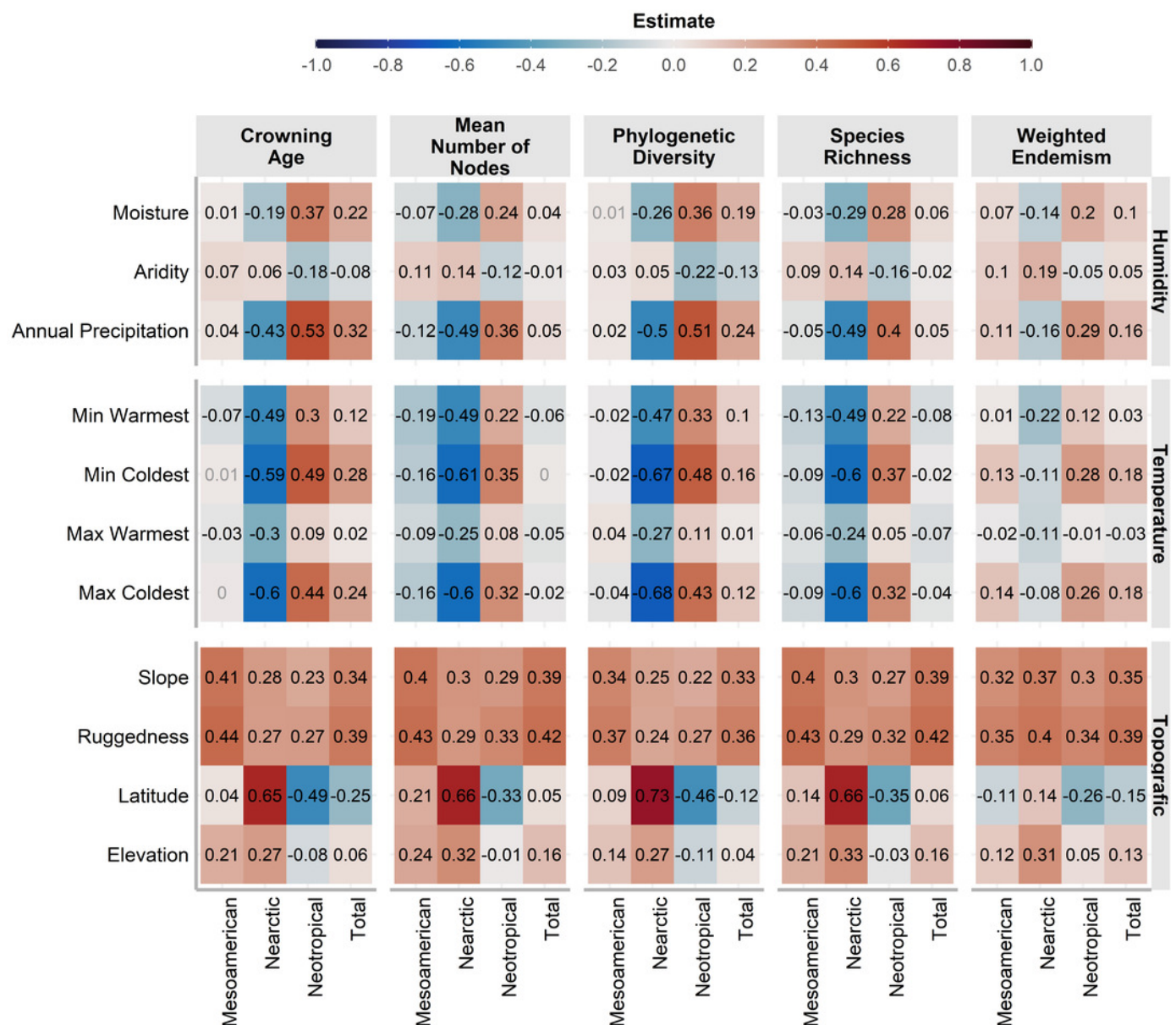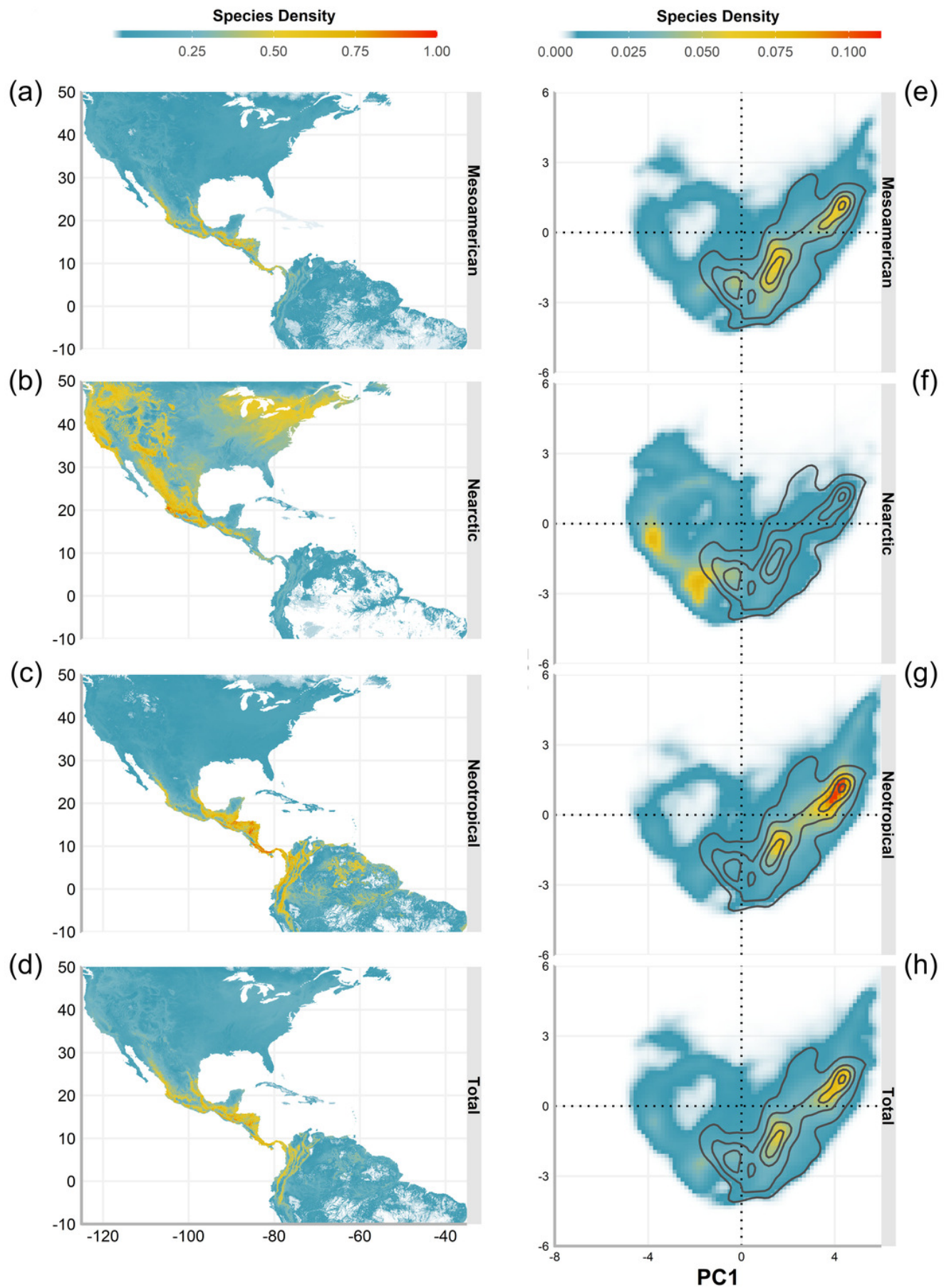
Figure 4

Pearson correlation test estimates between environmental variables and assemblage characteristics of the birds belonging to the three cenocrons. Numbers in light grey indicate nonsignificant correlations (*p*>0.5).

Figure 5

Geographic (a-d) and environmental (e-h) distribution of bird species density (number of species on a single pixel / number of species in the cenocron) of the Mexican Transition Zone cenocrons.

Figure 6

Geographic representation of the environmental overlap (grey) between the three cenocrons of the Mexican Transition Zone, compared to the areas (yellow) that correspond to the Mexican Transition Zone (sensu Morrone, 2020).