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Ecological niche differentiation among Aztec fruit-eating bat subspecies (Chiroptera: Phyllostomidae) in Mesoamerica

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Artibeus aztecus is a Mesoamerican montane bat with three currently recognized, allopatric subspecies. No study has evaluated the phylogenetic status of the subspecies. However, through an analysis of its ecological niche and its geographic distribution, here we analyze whether there is differentiation of the climatic requirements for each subspecies, assessing whether niche evolution is a potential factor in subspecies differentiation. We assayed ecological niche models for each subspecies, analyzed the response curves for the most important climatic variables of each model, and generated the potential distribution model for each subspecies. We assayed a background similarity test between the subspecies to determine how similar their niches were. We found differences in climatic requirements for the three allopatric subspecies and the most important variables and their response curves. Potential distribution models concur with Mesoamerican highlands and highlight the lowlands of the isthmus of Tehuantepec and the Nicaraguan depression as possible geographic barriers. Differences found between ecological niches for each subspecies contrast with previous findings for the species and other phyllostomid bats. Niche conservatism may have caused geographic isolation in the past, and differences in environmental requirements may have appeared later. Molecular and morphological analyses are necessary to clarify the taxonomic status of these populations and the evolutionary processes involved in their diversification.

Artibeus aztecus es un murciélago montano mesoamericano, cuyas tres poblaciones alopátricas son reconocidas como subespecies. Sin embargo, no hay estudios filogenéticos que permitan aclarar su situación taxonómica, por lo que, a través del análisis de su nicho ecológico y distribución geográfica, se analizó si existe diferenciación en los requerimientos climáticos para cada subespecie, evaluando si la evolución del nicho es un factor potencial en la diferenciación de las subespecies. Se llevaron a cabo modelos de nicho ecológico para cada subespecie, se analizaron las curvas de respuesta de las variables más importantes y, se generó el modelo de distribución potencial para cada subespecie. Adicionalmente se realizaron pruebas de similitud de *background* entre las tres subespecies para determinar qué tan similares son sus nichos. Se encontraron diferencias en los requerimientos climáticos entre las tres subespecies, así como en las variables más importantes y sus curvas de respuesta. Los modelos de distribución potencial coinciden con las tierras altas de Mesoamérica y destacan las zonas bajas del istmo de Tehuantepec y la depresión de Nicaragua como posibles barreras geográficas. Las diferencias encontradas en los nichos ecológicos de las subespecies contrastan con los hallazgos previos para la especie y otros murciélagos filostómidos. Conservadurismo de nicho ecológico pudo provocar aislamiento geográfico en el pasado y las diferencias en los requerimientos climáticos pudieron aparecer después. Son necesarios análisis moleculares y morfológicos que permitan conocer de manera más amplia los patrones evolutivos involucrados en la diversificación de la especie.

Keywords: Geographic barriers; Mesoamerica; neotropical bats; niche divergence; ecological speciation.

Introduction

Artibeus aztecus is a medium-sized phyllostomid bat that inhabits the highlands of Mesoamerica. The three allopatric populations of this taxon are recognized as subspecies (Davis 1969): *Artibeus aztecus aztecus*, found from Sinaloa and Nuevo León to Oaxaca in México; *Artibeus aztecus minor*, located from Chiapas, México, to Honduras; and *Artibeus aztecus major,* found from Costa Rica and Panama.

The subspecies *A. a. aztecus* was typical in evergreen forests at relatively high elevations in the mountains bordering the Mexican Plateau, as low as 1000 m in cloud forest and as high as 2,400 m in the pine-fir forest, it has been recorded in pine-oak forest, coniferous forest, *Abies* forest, cloud montane forest, agricultural areas (López-González and García-Mendoza 2006; Segura-Trujillo and Navarro-Pérez 2010; Briones-Salas *et al.* 2019; Cerón-Hernández *et al.* 2022); In Veracruz (México) it is considered vulnerable because it inhabits forest fragments but can use riparian vegetation as corridors to cross grasslands (Cerón-Hernández *et al.* 2022). In the case of *A. a. minor*, it has been reported in coniferous forest, montane cloud forest, grasslands, areas with secondary vegetation, agricultural landscapes and in human settlements (Davis 1969; Kraker-Castañeda *et al.* 2017; Lorenzo *et al.* 2017; Medina-Van Berkum *et al.* 2020). *Artibeus a. major* is the only subspecies whose distributional pattern was not associated with conifers, but with "cloud forest" atmospheric conditions (Davis 1969); there are records of the subspecies in tropical premontane rainforest and tropical lower montane rainforest (Zamora-Mejías and Rodríguez-Herrera 2017; Pineda-Lizano and Chaverri 2022).

Artibeus aztecus is a frugivorous bat. Fruit-eating bats in *Artibeus* are considered important in seed dispersal (Saldaña-Vázquez 2019), which is essential for forest regeneration and maintenance of plant genetic diversity and composition (Wang and Smith 2022), thereby being crucial to forest conservation and management (Jordano *et al.* 2011). In central México *A. aztecus* eats wild figs (*Ficus* sp.), capuli cherries (*Prunus serotine*), cypress (*Cupressus* sp), and Mexican hawthorn (*Crataegus Mexicana*; Solari *et al.* 2019).

Previously, Davis (1969) treated the three populations as subspecies, having observed only subtle differences in color and some cranial, mandibular, forearm, and phalanx measurements. He also assumed no interbreeding among the three populations. *Artibeus a. major* is the largest of the three subspecies, and *A. a. minor* is the smallest, while *A. a. aztecus* is the least dark subspecies. Later, a study that tested the degree to which the potential distribution of one taxon predicted the geographic distribution of its putative sister taxon and vice versa, using the chi-squared statistic to evaluate statistical significance. The study found that the subspecies *A. a. aztecus* and *A. a. minor* have similar ecological niches (Peterson *et al.* 1999). These conclusions were confirmed with the reanalysis of the data using chi-square test statistic and background similairity test using both *I* and *D* metrics (Warren *et al.* 2008).

As in other groups of vertebrates (Fitzpatrick and Turelli 2006; Zink 2012; Heinicke *et al.* 2017), including bats (Roberts 2006; Datzmann *et al.* 2010; Monteiro and Nogueira 2011; Morales-Martínez *et al.* 2021), geographic isolation is likely driving the diversification process between the central and northern subspecies of the *A. aztecus* distribution. Long-term geographic isolation of populations could lead to the accumulation of genetic or phenotypic differences through neutral or selective processes (Baker and Bradley 2006). If distinct ecological conditions are present in each region, they may stimulate the divergence process (Turelli *et al.* 2001; Kozak and Wiens 2006).

The study of the environmental requirements of species and the possible differences between them can be a useful tool in evaluating the taxonomic status of populations (Buermann *et al.* 2008; Lentz *et al.* 2008; Tocchio *et al.* 2015; Guevara and Sánchez-Cordero 2018). Ecological niche-based modeling (ENM) is a tool that permits the exploration of geographic and ecological processes by relating species occurrence records with environmental data (Kozak and Wiens 2006; Phillips *et al.* 2006; Kozak *et al.* 2008). ENM may help make taxonomic decisions by making niche comparisons between populations or species or by identifying regions that could isolate them (Rissler and Apodaca 2007; Martínez-Gordillo *et al.* 2010; Arribas *et al.* 2013; Aguilar 2019; Hending 2021).

Here we evaluate the similarities -or differences- between the climatic requirements of the three subspecies of *A. aztecus*, using background similarity tests (as in Warren *et al.* 2008; but we used a higher number of specimens for each subspecies) and comparing its potential geographic distributions to better understand the ecological resemblance of the subspecies and clarify the taxonomic status of this bat across Mesoamerica. Based on previous studies, we hypothesize that niche conservatism has caused the isolation of *A. aztecus* populations and possible morphological divergence.

Materials and methods

Occurrence data. We collected georeferenced occurrence records for the three populations from the Mammal Collection of the Zoology Museum, UNAM (Facultad de Ciencias – Universidad Nacional Autónoma de México, México City, México, MZFC-M), the Mammal Collection of CIDIIR Durango (Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Durango, Instituto Politécnico Nacional, Durango City, México, CRD), and from the databases of VertNet (downloaded on July 27, 2020) and of the Global Biodiversity Information Facility (GBIF, http://www.gbif.org; downloaded on April 30, 2021: https://doi.org/10.15468/dl.e2b69x), using the name "*Artibeus aztecus*" recorded from 1960 to the present (2020-2021). To reduce sampling bias, we spatially thinned our original data set using the *spThin* package (Aiello-Lammens *et al.* 2015) in R 4.0.3. While retaining the greatest number of localities possible, thinning ensured that the distance between all pairs of localities exceeded 10 km (Boria *et al.* 2014). Records for the final database are shown in Supplementary material 1. We follow Baker *et al.* (2016) and Cirranello *et al.* (2016) in using *Artibeus* rather than *Dermanura* (*contra* Burgin et al. 2018).

Environmental data. We used 15 bioclimatic variables (Supplementary material 2; Hijmans *et al.* 2005, www.worldclim.org) at ~5 km resolution, excluding the four layers that combine precipitation and temperature information into the same layer since they show odd spatial anomalies between neighboring pixels (Escobar *et al.* 2014), apparently as a consequence of their linked temperature and precipitation variables (Campbell *et al.* 2015). We extracted the climatic data using ArcMap (ArcGIS Desktop: Release 10.4).

We used a Pearson correlation test to detect and exclude highly correlated environmental variables. The analysis was performed in R with the library *ntbox* (Osorio-Olvera *et al.* 2020), which filters the variables that summarize the environmental information of the presences (occurrences) data according to a correlation threshold; this algorithm suggests which variables to use for the modeling part. The threshold selected for this analysis was $r < 0.7$.

Calibration area. The dispersal capacity of the species, M of the BAM diagram in distribution theory (Soberón and Nakamura 2009), is useful for choosing the calibration area in niche modeling analysis (Barve *et al.* 2011). Since the dispersal ability of *A. aztecus* is unknown, we used ArcMap

(ArcGIS Desktop: Release 10.4) to generate the calibration area for each subspecies, with a buffer distance of 1° (~111 km) around occurrences, as a similar distance has been observed in movements of *A. lituratus,* another species of the genus (Arnone *et al.* 2016).

Ecological niche modelling. We developed niche models for each of the three subspecies of *A. aztecus* using the maximum entropy method implemented in Maxent version 3.4.4 (Phillips *et al.* 2006). To select the models with the optimal settings for each subspecies, we built various models with all the possible combinations of linear, quadratic, and product features, with different percentages of training locations (25 % and 50 %) and different regularization multipliers (from 0.0 to 2.0 in 0.5 steps), analyzing 70 models for each subspecies. We used 10,000 randomly selected pixels within each generated calibration area as the background sample. All the models were generated and evaluated with the library *kuenm* (Cobos *et al.* 2019) in R.

We selected the final models based on two evaluation metrics. First, we used partial receiver-operating characteristic (ROC) approaches, as to avoid at least some of the failings of classical ROC approaches (Peterson *et al.* 2008). We used an acceptable omission error threshold of E = 5 and 100 replicate 50% bootstrap resamplings to establish whether the ROC AUC (area under the curve) ratio was above 1.0. Secondly, we used the 5 % training omission rate (OR05), which shows the proportion of test localities with suitability values lower than those excluding the 5 % of training locations with the lowest predicted suitability. Omission rates above the 10% expectation typically indicate model overfitting (Muscarella *et al.* 2014). The final models were bootstrapped 10 times and we analyzed the data obtained from the average model.

We analyzed and compared the response curves of the three variables with the highest percentage of contribution and permutation importance for each model. The potential distribution of each subspecies were projected to the Mesoamerican region and to generate binary maps, we chose the 10th percentile training presence threshold (Peterson *et al.* 2007, 2011). We performed these analyses in ArcMap (ArcGIS Desktop: Release 10.4).

Background similarity test. We used background similarity tests to assess niche differentiation between *A. aztecus* subspecies (Warren *et al.* 2010). This test determines whether ENMs are more similar than expected by chance, based on the geographical regions where each subspecies reside. This type of analysis is particularly important when allopatric populations are being compared because some differences in niches may inevitably follow from the fact that distinct geographic regions rarely encompass identical distributions of environmental variables (Warren *et al.* 2010). We developed 100 replicate comparisons of each population's known occurrences against the background (points drawn from the accessible area) of the other (sample size matching those available for the "background" population). The background similarity tests were performed with the *ENMTools* package version 1.0.4 (Warren *et al.* 2021) in R.

We assess similarity in pairwise combinations of subspecies using two similarity measures: Schoener's *D* (1968) and Hellinger's *I*. These similarity measures are obtained by comparing the estimates of normalized probability calculated for each grid cell of a study area using a Maxent-generated ENM. Both indexes range from 0, when spaces predicted environmental tolerances do not overlap, to 1, when all grid cells are estimated to be equally suitable for both species. Niche similarity is inferred when the observed value falls above the distribution of expected values. In contrast, the difference is inferred when the observed value falls to the left of the distribution (Warren *et al.* 2010).

Results

We analyzed 151 confirmed *A. aztecus* occurrences: 104 for *A. a. aztecus*, 38 for *A. a. minor,* and 9 for *A. a. major* (Figure 1). Ten of the original climate variables were highly correlated with other variables and were excluded from analysis. For the final analysis, we used: annual mean temperature (bio01), mean diurnal range (bio02), isothermality (bio03), annual precipitation (bio12), and precipitation of the driest month (bio14). Final models with the optimal settings for each subspecies were as follow: *A. a. aztecus*: linear, quadratic, and product features, and regularization multiplier of 1 (Mean AUC ratio: 1.195, OR05: 0.096); *A. a. minor*: linear and quadratic features, and regularization multiplier of 0.5 (Mean AUC ratio: 1.426, OR05: 0.0); and *A. a. major*: linear, quadratic and product features and regularization multiplier of 1.5 (Mean AUC ratio: 1.687, OR05: 0.5).

The most important variable for the model of all the subspecies was the annual mean temperature, while the annual precipitation was the only variable that was not placed between the the three most important models for any model. The second and third variable for each model were: mean diurnal range and precipitation of the driest

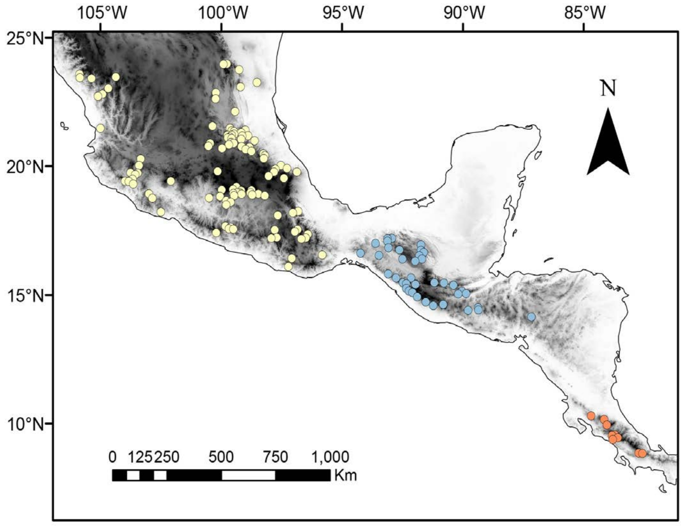

Figure 1. Occurrence records for the three subspecies of *Artibeus aztecus*: *Artibeus aztecus aztecus* (yellow), *Artibeus aztecus minor* (blue) and *Artibeus aztecus major* (light red).

month for *A. a. aztecus*, precipitation of the driest month and isothermality for *A. a. minor*, and isothermality and mean diurnal range for *A. a. major* (Table 1).

Analyzing the response curves for the annual mean temperature, the only important variable in common for the three subspecies, the highest values (> 0.6) of suitability for *A. a. aztecus* are between 14 °C and 20 °C, while for *A. a. minor* they are bewteen 14 and 20 °C, and for *A. a. major* at less at 18 °C (Supplementary material 3). For the mean diurnal range of temperature, in *A. a. aztecus* the highest suitability is between 8 °C and 14.5 °C, while in *A. a. major* it is above 6.5 °C (Supplementary material 3a, c). For the isothermality, the highest suitability for *A. a. minor* was above 70, while for *A. a. major* it was above 76 (Supplementary material 3b, c). For the precipitation of the driest month, the highest suitability for *A. a. aztecus* was found at values over 30 mm and for *A. a. minor* at values between 20 mm and 100 mm (Supplementary material 3a, b).

All potential distribution models showed close correspondence to known distributions of the three populations, showing an association with the highlands of México and Central America (Figure 2). We found relatively wide distributions for the three subspecies, so each model predicted potential distribution areas corresponding with the distribution of the other subspecies. For the three models, the montane regions were separated by less-suitable lowland areas (≤ 500 m), representing potential barriers to the dispersal of each subspecies (*e. g.*, the Isthmus of Tehuantepec and the Nicaraguan Depression).

Pairwise comparisons indicated that *A. a. aztecus* and *A. a. major* have the lowest niche overlap (*D* = 0.246, *I* = 0.485) and *A. a. aztecus* and *A. a. minor* have the highest niche similarity (*D* = 0.405, *I* = 0.731). Observed Schoener's *D* and Hellinger's *I* values were significantly low compared to the null distribution in all cases (Figure 3). Comparisons involving *A. a. minor* showed *D* and *I* values closer to those from the left tail of the null distributions, but significantly different than expected (Figure 3a, c). In sum, background similarity tests indicated that the ecological niche models of the three subspecies were more different than expected by chance (Table 2).

Table 1. Percentage of contribution and permutation importance of climatic variables used in MaxEnt model for each subspecies of *Artibeus aztecus*.

Subspecies	Variable	Percentage of contribution	Permutation importance
A. a. aztecus	Annual mean temperature	55.5	52
	Mean diurnal range	36.8	37.7
	Precipitation of driest month	2.7	3.3
	Isothermality	2.7	0.8
	Annual precipitation	2.3	6.2
A. a. minor	Annual mean temperature	75.8	46.3
	Precipitation of driest month	10.9	13.3
	Isothermality	9.1	25
	Annual precipitation	2.9	13.7
	Mean diurnal range	1.3	1.6
A. a. major	Annual mean temperature	91.4	87.5
	Isothermality	5.7	5
	Mean diurnal range	2.1	6.8
	Annual precipitation	0.8	0.7
	Precipitation of driest month	0	0

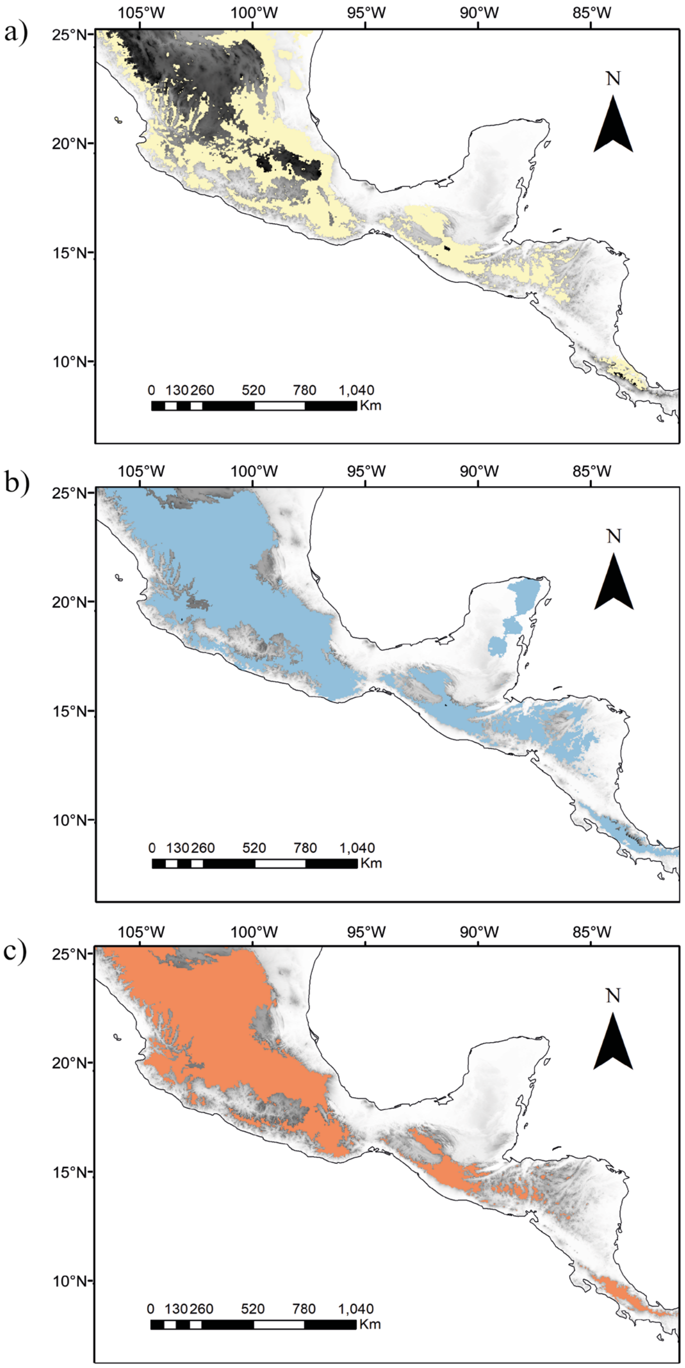

Figure 2. Maxent predicted potential distribution for (a) *Artibeus a. aztecus,* (b) *A. a. minor*, and (c) *A. a. major*.

Discussion

Potential distributions and geographical barriers. The niche models and potential distribution maps seem to support the findings of the habitat preference of the Aztec fruit-

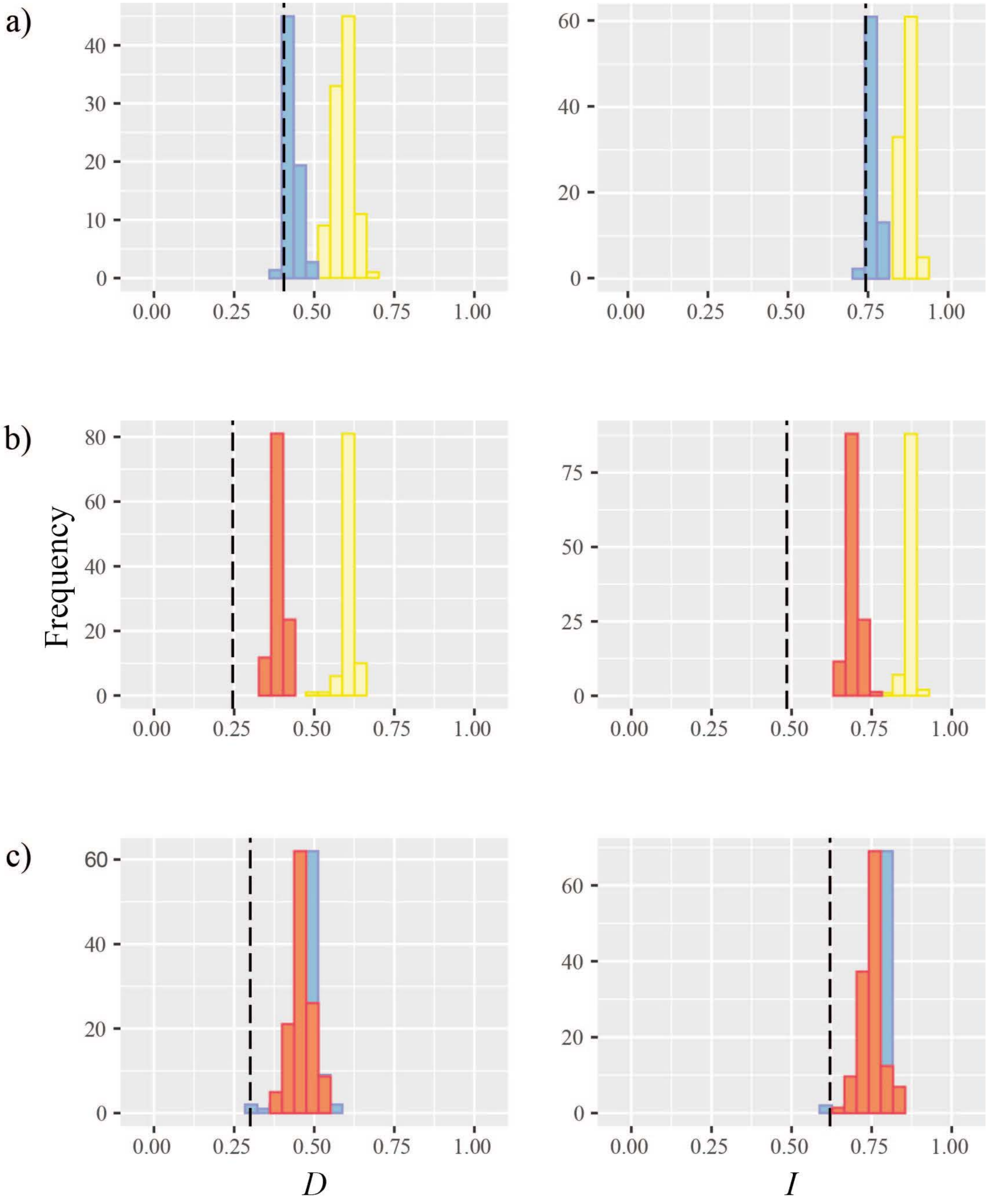

Figure 3. Niche overlap values for Schoener's *D* and Hellinger's *I* compared to a null distribution: (a) *Artibeus a. aztecus* (yellow) vs. *A. a. minor* (blue), (b) *A. a. aztecus* vs. *A. A. major* (red), (c) *A. a. minor* vs. *A. a. major*.

eating bat populations reported previously. Mesoamerican highlands, where the models indicate the potential distribution for each subspecies, include a complex assemblage of montane ecosystems containing high biodiversity and endemism (Parra-Olea *et al.* 2012; Bryson *et al.* 2018; Blair *et al.* 2019). Less-suitable areas, such as the Isthmus of Tehuantepec and the Nicaraguan Depression, may act as current geographic barriers to dispersal, limiting contact between the populations, as proposed previously for the subspecies *A. a. aztecus* and *A. a. minor* (Davis 1969; Peterson *et al.* 1999).

Isthmus of Tehuantepec has been proposed as a biogeographic barrier associated with allopatric speciation in a broad range of taxa (Sullivan *et al.* 2000; León-Paniagua *et al.* 2007; Castoe *et al.* 2009; Daza *et al.* 2010; Rodríguez-Gómez *et al.* 2013, 2021) and, climatically, has been considered a barrier for dispersal of oak species, and by separating tropical ecosystems from those with more substantial Nearctic influence (Rodríguez-Correa *et al.* 2015). The climatic effect of this barrier on the subspecies *A. a. aztecus* and *A. a. minor* contrasts with the similar niches found between two haplogroups of the Honduran yellow-shouldered bat *Sturnira hondurensis*, another Mesoamerican highland bat (Hernández-Canchola 2018).

On the other hand, the Nicaraguan Depression has been considered a major feature determining genetic and biogeographic patterns (Gutiérrez-García and Vázquez-Domínguez 2013). The evolutionary impact of this barrier is reflected in genetic differentiation between sister taxa of vertebrates, including birds (Puebla-Olivares *et al.* 2008; Arbeláez-Cortés *et al.* 2010) and snakes (Castoe *et al.* 2009). Our findings about the separation between *A. a. minor* and *A. a major* are similar to the conclusions of Torres-Morales (2019), who considered Nicaraguan Depression as a significant barrier that limits the distribution of *Sturnira hondurensis*, separating it from its sister species *S. burtonlimi*.

Speciation, and species limits. There is a debate about how conserved the niches between closely related lineages are (Wiens and Graham 2005). Some previous studies have suggested the presence of phylogenetic niche conservatism in phyllostomid bats (Peterson *et al.* 1999; Stevens 2006, 2011; Warren *et al.* 2008), indicating that closely related species share the same climatic preferences. Alternatively, other authors have not found strong support for niche conservatism in phyllostomid bats (Peixoto *et al.* 2017), suggesting their niche may have evolved either under strong selection or randomly (Diniz-Filho *et al.* 2010).

However, former phylogenetic niche conservatism may promote ecological speciation. It can occur in areas with high geographic and ecological variations. In such regions, any geographic distance also results in environmental distance, promoting niche divergence. The combined topographic variation and ecological distance reduce dispersal and gene flow between adjacent populations (Gascon *et al.* 2000; Gehring *et al.* 2012). Lineages may thus adapt to local niches, leading populations to diverge from the ancestral niche (Pyron *et al.* 2015).

Table 2. Results of the background similarity pairwise comparisons among the three subspecies of *Artibeus aztecus*. Observed Schoener's *D* and Hellinger's *I* values and p-values (p-val) are shown.

Test	D	p - val	I	p - val
Artibeus a. aztecus vs *A. a. minor* background	0.405	0.01	0.731	0.01
Artibeus a. aztecus vs *A. a. major* background	0.246	0.01	0.485	0.01
Artibeus a. minor vs *A. a. aztecus* background	0.405	0.04	0.731	0.03
Artibeus a. minor vs *A. a. major* background	0.300	0.03	0.620	0.03
Artibeus a. major vs *A. aztecus* background	0.246	0.01	0.485	0.01
Artibeus a. major vs *A. a. minor* background	0.300	0.01	0.620	0.01

Here, we found signals of ecological niche differentiation among the three subspecies of Aztec fruit-eating bat (Tables 1 and 2, Figures 2 and 3). The three subspecies of *A. aztecus* present different climatic preferences that may indicate they are evolving independently. Therefore, further studies are necessary to learn about the evolutionary history of *A. aztecus* and clarify the taxonomic situation of the three subspecies. Certaintly, it is crucial to consider that the outcome and the interpretation of the similarity tests may be sensitive to the definition of the calibration area and environmental background (Warren *et al.* 2010), still, they may offer some guidelines to explore speciation mechanisms (Tocchio *et al.* 2015) and thus determine the taxonomic status of the species. In this study, we defined it using the movement data of a congeneric species of *A. aztecus*, so the results must be carefully interpreted. Further details on the dispersal capacity for each subspecies might improve reference area estimation for niche models.

It is essential to clarify the phylogenetic relationships among the subspecies to better understand their biogeographic history (Martínez-Gordillo *et al.* 2010). Studies that analyzed the diversification of *Artibeus* and the subgenus *Dermanura*, have included a few samples of at least two subspecies, but not *A. a. major* (Owen 1987; Hoofer *et al.* 2008; Redondo *et al.* 2008; Solari *et al.* 2009; Baker *et al.* 2016). Solari *et al.* (2009) recovered two clades of *A. aztecus*, represented by samples of *A. a. aztecus* and *A. a. minor*, with a genetic divergence of 3.6 % between them, a value that falls in the range necessary for species recognition suggested by Baker and Bradley (2006), so it is crucial to analyze the genetic divergence between the species using a larger number of samples that includes the three subspecies. In addition, morphological analyses that include all subspecies are necessary to assess phenotypic variation and its potential correlation with environmental conditions. A relationship between environmental conditions and morphology has been documented in other Mesoamerican montane species (Rodríguez-Gómez *et al.* 2013, 2021; Hernández-Canchola 2018).

In sum, our results offer a first look at the ecological variation of *Artibeus aztecus* and an additional view on understanding the processes that have shaped the diversification of montane bats in Mesoamerica. Climatic divergence among the three subspecies probably are due to the interaction between former ecological niche conservatism and the emergence of geographic barriers, such as the Isthmus of Tehuantepec and the Nicaraguan Depression that promoted the subsequent ecological differentation.

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