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NICHO ECOLÓGICO Y AISLAMIENTO GEOGRÁFICO DE LAS SUBESPECIES DEL MURCIÉLAGO MESOAMERICANO *ARTIBEUS AZTECUS* (CHIROPTERA: PHYLLOSTOMIDAE)

TESIS

(**POR ARTÍCULO CIENTÍFICO**)

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

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Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
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THE BEGINNING OF ONE THING
CAN BE THE REST OF EVERYTHING

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RESUMEN

Artibeus aztecus es un murciélago montano mesoamericano, cuyas tres poblaciones alopátricas son reconocidas como subespecies. Sin embargo, no hay estudios suficientes 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. Adicionalmente, se evaluó si el conservadurismo de nicho ecológico está influyendo en sus procesos de especiación, para aclarar su situación taxonómica. Se realizaron 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 una. Adicionalmente se realizaron pruebas de similitud de *background* entre las tres subespecies para determinar qué tan similares son sus nichos. Los modelos de distribución potencial coinciden con las tierras altas de Mesoamérica, destacando las zonas bajas del istmo de Tehuantepec y la depresión de Nicaragua como posibles barreras geográficas. Se encontraron diferencias en los requerimientos climáticos entre las tres subespecies, así como en las variables más importantes y sus curvas de respuesta. Las diferencias encontradas en los nichos ecológicos de las subespecies contrastan con los hallazgos previos de conservadurismo de nicho en la especie y los murciélagos en general. Es posible que un precedente conservadurismo de nicho ecológico, sumado a las barreras geográficas, haya promovido la divergencia de nicho que se presenta actualmente en las tres subespecies. Por lo cual, son necesarios análisis moleculares y morfológicos que permitan conocer de manera más amplia los patrones evolutivos de la especie, que también serán útiles para poder tomar una decisión taxonómica sobre las subespecies.

ABSTRACT

Artibeus aztecus is a Mesoamerican montane bat whose three allopatric populations are currently recognized as subspecies. Although there are not enough studies that allow us to clear its taxonomic status so, through an analysis of its ecological niche and its geographic distribution, we analyzed whether there is diversification of the climatic requirements for each subspecies, assessing whether niche conservatism is influencing its evolutive processes, to clear its taxonomic status. We performed ecological niche models for each subspecies, analyzed the response curves for most important climatic variables of each model, and generated the potential distribution model for each subspecies. Additionally, we carried out a background similarity test between the subspecies to determine how similar their niches are. Potential distribution models agree with Mesoamerican highlands, highlight the lowlands of the Isthmus of Tehuantepec and the Nicaraguan depression as possible geographic barriers. We found differences in climatic requirements for the three subspecies, as well as in the most important variables and their response curves. Differences found between ecological niches for each subspecies contrast with previous findings for the species and bats. It is possible that niche conservatism, added to geographic barriers, has promoted niche divergence in the three subspecies. Thus, molecular and morphological analyses are necessary to widely know the evolutionary patterns involved in the diversification of the species and to take a taxonomic decision about the subspecies.

INTRODUCCIÓN GENERAL

Mesoamérica es una de las áreas con mayor diversidad de ecosistemas y especies del mundo (León-Paniagua *et al*. 2007; Daza *et al*. 2010; Bryson *et al*. 2011b; González *et al*. 2011; Ruiz-Sánchez y Ornelas 2014). Abarca la porción de la región Neotropical situada entre México y Panamá (Cavers *et al*. 2003; Castoe *et al*. 2009a; Arbeláez-Cortés *et al*. 2010; Bryson *et al*. 2011a). Los principales eventos que han moldeado su alta biodiversidad se relacionan con la orogénesis y la historia de su dinámica climática, dichos fenómenos crearon nuevos hábitats, corredores, barreras y oportunidades ecológicas que promovieron la diferenciación genética y fenotípica en diferentes tiempos y escalas espaciales (McCormack *et al*. 2008; González *et al*. 2011; Gutiérrez-García y Vázquez-Domínguez 2012).

La historia geológica de Mesoamérica y los cambios climáticos del Cuaternario han configurado la biota mesoamericana, considerada una mezcla de especies entre las regiones Neártica y Neotropical (Smith y Klicka 2010; Ornelas *et al*. 2013) y el producto de múltiples eventos de diversificación *in situ* (León-Paniagua *et al*. 2007; Bryson *et al*. 2011a; Gutiérrez-García y Vázquez-Domínguez 2012; Parra-Olea *et al*. 2012). Además, estos factores son causas importantes del gran número de especies y taxones endémicos que presenta la zona, identificada como un *hotspot* de biodiversidad del mundo (Myers *et al*. 2000; Mittermeier *et al*. 2011), tal como sucede para las especies de murciélagos del Nuevo Mundo (Ortega y Arita 1998). La región Mesoamericana, por lo tanto, ofrece un valioso campo de estudio para investigar los procesos ecológicos y evolutivos que originan y mantienen la biodiversidad (Becerra y Venable 2008; Gutiérrez-García y Vázquez-Domínguez 2012). Dentro de esta región, destaca el subgénero *Dermanura* (Phyllostomidae: Stenodermatinae), el cual comprende principalmente de los murciélagos pequeños del género Artibeus (Owen 1987, 1991). Se distribuye desde el centro de México hasta Bolivia y el sur de Brasil y consta de alrededor de doce especies (Hoofer *et al*. 2008; Solari *et al*. 2009).

El murciélago frugívoro azteca, *Artibeus aztecus* Andersen, 1906, es un murciélago filostómido mediano, con una longitud corporal total de 59 a 75 mm y un antebrazo de 41 a 49 mm de largo, siendo la especie más grande del subgénero *Dermanura* (Solari *et al*. 2019). Su coloración dorsal varía de color café oscuro a café claro (López Ortega y Ayala 2005). El rostro es corto y la hoja nasal está bien desarrollada. No tiene cola y su uropatagio es estrecho y cubierto con pelo. Su fórmula dental es i 2/2, c 1/1, p 2/2, m 2/2 (x2) (Solari *et al*. 2019).

Se distribuye en tres áreas geográficamente aisladas de Mesoamérica: la primera incluye las áreas montañosas que rodean el Altiplano mexicano y atraviesan las montañas del Faja Volcánica Transmexicana hasta la Sierra Madre del Sur en Oaxaca, México; la segunda área cubre las regiones montañosas desde Chiapas hasta Honduras (Núcleo Centroamericano), y la tercera cubre las montañas de Costa Rica y el oeste de Panamá (Davis 1969; Solari *et al*. 2019; Fig. 1). Este murciélago habita principalmente en bosques de pino, pino-encino y bosques nublados, aunque también se ha encontrado en plantaciones de plátano y mango, así como en ecosistemas más secos como la selva baja cercana a bosques de coníferas y el valle de Comayagua, a elevaciones entre 600 a 3300 m, pero más comúnmente arriba de los 1000 m (López Ortega y Ayala 2005; Solari *et al*. 2019). Se ha reportado que puede alimentarse de plantas de los géneros *Ficus* y *Cupressus*, así como de las especies *Prunus serotine* y *Carataegus mexicana* (Solari *et al*. 2019).

Artibeus aztecus fue descrita por Andersen (1906), siendo diferenciada por tener un mayor tamaño que *Artibeus toltecus*. Un estudio filogenético de la familia Stenodermatinae, sugirió que el grupo que incluía a esta especie debería ser denominado *Dermanura*, siendo llamada *Dermanura azteca* (Owen 1987). En estudios posteriores, su estado taxonómico ha sido objeto de controversias (López Ortega y Ayala 2005; Hoofer *et al*. 2008; Redondo *et al*. 2008; Solari *et al*. 2009). Actualmente, tras una revisión de caracteres moleculares, la especie fue reasignada como *Artibeus aztecus* (Baker *et al*. 2016)

Sus tres poblaciones alopátricas son reconocidas como subespecies, a partir de una comparación de tamaño y color, aunque también se ha asumido que hay aislamiento reproductivo (Davis 1969): *Artibeus aztecus aztecus*, encontrada desde Sinaloa y Nuevo León a Oaxaca, en México, su pelaje es de color café pálido a madera; *Artibeus aztecus minor*, localizada desde Chiapas, México, a Honduras, es la subespecie más pequeña y con una coloración más negruzca que *A. a. aztecus*; y *Artibeus aztecus major*, localizada en Costa Rica y Panamá, es la subespecie de mayor tamaño y con el pelaje más oscuro, de color negro intenso, y la única cuyo patrón de distribución no está asociado a coníferas (Davis 1969; Webster y Jones 1982).

Hasta la fecha, son poco los estudios que han intentado contribuir al conocimiento de la variación intraespecífica y que soporten el estatus taxonómico de las subespecies (Davis 1969; Castañeda-Rico 2005). Un estudio morfológico realizado entre dos de las subespecies (*A. a. aztecus* y *A. a. minor*) en México, detectó dos agrupaciones fenéticas correspondientes a cada subespecie, siendo *A. a. aztecus* de mayor tamaño que *A. a. minor*. Por otro lado, también sugirió la necesidad de emprender estudios biogeográficos y ecológicos que permitieran analizar el efecto que las barreras geográficas, como el Istmo de Tehuantepec, han tenido sobre las subespecies, así como la inclusión de individuos de *A. a. major*, para evaluar el estatus taxonómico de toda la especie (Castañeda-Rico 2005).

Dado que el aislamiento geográfico entre las poblaciones puede restringir el flujo genético y estimular cambios en los nichos (Graham *et al*. 2004; Wiens y Graham 2005), los modelos de nicho ecológico y distribución geográfica pueden ser herramientas útiles para analizar la variación ecológica dentro de *A. aztecus*. Estas herramientas mencionadas permiten caracterizar los requerimientos ambientales de las especies e identificar áreas geográficas adecuadas para su distribución potencial, así como analizar si existe divergencia o conservadurismo del nicho entre poblaciones o especies (Warren *et al*. 2008; Anderson 2012).

Los usos potenciales de los modelos de nicho en problemas taxonómicos incluyen pruebas de divergencia en requerimientos ecológicos, para evaluar si las diferencias en preferencias ambientales entre poblaciones distribuidas de forma simpátrica, parapátrica o alopátrica pueden apoyar el estatus como especies diferentes (Guevara y Sánchez-Cordero 2018). En el caso de poblaciones distribuidas de forma alopátrica, los modelos de nicho pueden proveer evidencia de aislamiento geográfico si la región que separa entidades potencialmente independientes contiene áreas no idóneas que sirven como barreras geográficas (Wiens 2004; Raxworthy *et al*. 2007). Así, estos métodos pueden ser útiles para estudiar el papel de las barreras geográficas en los patrones de variación y, por consiguiente, proponer inferencias robustas al diagnosticar especies.

Por lo anterior, el objetivo de este trabajo es caracterizar los requerimientos ambientales de las tres subespecies de *Artibeus aztecus*, con la finalidad de analizar si existe diferenciación al interior de la especie y así poder contribuir a clarificar su estatus taxonómico. Utilizando modelos de nicho ecológico y distribución geográfica, así como pruebas de similitud de *background* para poner a prueba si los nichos ecológicos han sido conservados o han divergido entre las tres subespecies.

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

Diferenciación de nicho ecológico entre las subespecies de *Artibeus aztecus* (Chiroptera: Phyllostomidae) en Mesoamérica

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Abstract.

Introduction: Artibeus aztecus is a Mesoamerican montane bat whose three allopatric populations are currently recognized as subspecies. However, there is not any study that evaluates 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 conservatism is influencing its evolutive processes, to ascertain its taxonomic status.

Methods: 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.

Results: Potential distribution models agree with Mesoamerican highlands and highlight the lowlands of the Isthmus of Tehuantepec and the Nicaraguan depression as possible geographic barriers. We found differences in climatic requirements for the three allopatric subspecies and the most important variables and their response curves.

Discussion and conclusions: 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 widely know the evolutionary patterns involved in the diversification of the species and make a taxonomic decision about the populations.

Key words: geographic barriers; Mesoamerica; neotropical bats; niche divergence;

ecological speciation.

Resumen.

Introducción: 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 el conservadurismo de nicho ecológico está influyendo en sus procesos de especiación, para aclarar su situación taxonómica.

Métodos: 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.

Resultados: 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. Se encontraron diferencias en los requerimientos climáticos entre las tres subespecies, así como en las variables más importantes y sus curvas de respuesta.

Discusión y conclusiones: Las diferencias encontradas en los nichos ecológicos de las subespecies contrastan con los hallazgos previos para la especie y otros murciélagos filostómidos. Es posible que el conservadurismo de nicho ecológico, sumado a las barreras geográficas, haya promovido la divergencia de nicho que se presenta actualmente en las tres subespecies. Por lo cual, son necesarios análisis moleculares y morfológicos que permitan conocer de manera más amplia los patrones evolutivos involucrados en la diversificación de la especie, para poder tomar una decisión taxonómica sobre las poblaciones.

Palabras clave: barreras geográficas; divergencia de nicho; especiación ecológica; Mesoamérica; murciélagos neotropicales.

Introduction

Artibeus aztecus Andersen, 1906 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*, from Sinaloa and Nuevo León to Oaxaca in Mexico; *Artibeus aztecus minor*, from Chiapas, Mexico, to Honduras; and *Artibeus aztecus major*, from Costa Rica and Panama.

Previously, Davis (1969) treated the populations as subspecies because their differences were subtle, being observed in color and some cranial, mandibular, forearm, and phalanx measurements. He also assumed no interbreeding among the three populations, *A. 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, two studies based in chi-squared tests, found that the subspecies *A. a. aztecus* and *A. a. minor* have similar ecological niches (Peterson *et al*. 1999; Warren *et al*. 2008). A more recent morphometric study between two of the subspecies (*A. a. aztecus* and Mexican specimens from *A. a. minor*), confirmed the subspecies as two different phenetic units, being *A. a. aztecus* larger than *A. a. minor*, and suggested additional analyses that would allow their recognition as full species (Castañeda-Rico 2005).

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), we suspect that geographic isolation is likely driving the diversification process between the central and northern subspecies of the *A. aztecus* distribution. The long-term geographic isolation of populations could stimulate the accumulation of genetic or phenotypic differences through neutral or selective processes

(Baker and Bradley 2006). Additionally, the ecological conditions of each region, may reinforce speciation by changing the environmental similarities along the evolutionary time scale (Turelli *et al*. 2001; Kozak and Wiens 2006).

The study of the environmental requirements of the species and the possible differences between them can be, therefore, of great help in evaluating the taxonomic status of the species (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 combining 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).

Hence, here we evaluate the similarities -or differences- between the climatic requirements of the three subspecies of *A. aztecus* 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.

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, Mexico City, Mexico, MZFC-M), the Mammal Collection of CIDIIR Durango (Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Durango, Instituto Politécnico Nacional, Durango City, Mexico, 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*. 2019) 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. Records for the final database are shown in Appendix 1.

We are following the advice on the use of genus *Artibeus* rather than *Dermanura* as proposed by Baker *et al*. (2016) and Cirranello *et al*. (2016) (*contra* Burgin *et al*. 2018).

Environmental data

We used 15 bioclimatic variables (Table 1, Supplementary material; 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 linking between 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), whose algorithm suggests which variables to use for the modeling according to a correlation threshold. The threshold selected for this analysis was $r < 0.7$.

Ten of the original climate variables were highly correlated with other variables and were excluded from analysis. For the final analysis, there were used: annual mean temperature (bio01), mean diurnal range (bio02), isothermality (bio03), annual precipitation (bio12), and precipitation of the driest month (bio14).

Study area

The dispersal capacity of the species is essential 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

Correlative ecological niche models use associations between environmental variables and occurrence sites to define suitable environmental conditions (Peterson *et al*. 2011). We developed niche models for the three subspecies of *A. aztecus* separately 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 using the features suggested by Maxent according to the number of localities of each subspecies, with different percentages of training locations (25% and 50%) and different regularization multipliers (from 0.0 to 2.0 in 0.5 steps), analyzing 10 models for each subspecies. We used 10,000 randomly selected pixels within the study area of each subspecies as the background sample.

We selected the final models based on two evaluation metrics. First, we inspected the value for the area under the receiver operating characteristic curve using randomly selected test localities (AUC_{test}). Values of AUC greater than 0.8 are considered good (Swets 1988; Araújo *et al*. 2005), indicating that the model will properly differentiate between presences and random background samples. Secondly, we used the 10% training omission rate (OR10), which shows the proportion of test localities with suitability values lower than those excluding the 10% of training locations with the lowest predicted suitability. Omission rates above the 10% expectation typically indicate model overfitting (Muscarella *et al*. 2014).

We analyzed and compared the response curves of the three variables with the highest percentage of contribution and permutation importance for each model. To generate binary maps, we chose the 10th percentile training presence threshold (Peterson *et al*. 2007, 2011).

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 habitat suitability 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). 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 (AUCtest: 0.767, OR10: 0.135); *A. a. minor*: linear and quadratic features, and regularization multiplier of 1.5 (AUCtest: 0.824, OR10: 0.053); and *A. a. major*: linear feature and regularization multiplier of 2 (AUCtest: 0.724, OR10: 0.5).

The three most important variables for the model of the subspecies *A. a. aztecus* were the annual mean temperature, the mean diurnal range of temperature, and the annual precipitation; for the model of *A. a. minor*, there were the annual mean temperature, the isothermality, and the precipitation of the driest month, and for the model of *A. a. major*, there were the annual mean temperature, the mean diurnal range of temperature, and the isothermality (Table 1).

Analyzing the response curves for the annual mean temperature, the only important variable in common for all subspecies, the highest values (> 0.8) of suitability for *A. a. aztecus* are found at annual mean temperatures between 7.5 °C and 17 °C, while for *A. a. minor* occurs at values lower than 19 °C, and for *A. a. major* at less at 20 °C (Figure 1, Supplementary material). For the mean diurnal range of temperature, in *A. a. aztecus* the highest suitability is found at values between 7 °C and 13 °C, while in *A. a. minor* it is found at values upper than 9.5 °C (Figure 1a, b; Supplementary material). For the isothermality, the highest suitability for *A. a. minor* (>0.7) was in values upper than 72 °C, while for *A. a. major* it was found in values upper than 80 °C (Figure 1b, c; Supplementary material). For the annual precipitation, the highest suitability for *A. a. aztecus* (>0.8) was found at values upper than 2000 mm (Figure 1a, Supplementary material). Finally, for the precipitation of the driest month, the highest suitability for *A. a. minor* was found in values below 40 mm (Figure 1b, Supplementary material).

All potential distribution models showed close correspondence to known distributions of each population, showing an association with the highlands of Mexico 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), followed by *A. a. minor* and *A. major* (*D* = 0.3, *I* = 0.62) and *A. a. aztecus* and *A. a. minor* (*D* = 0.405, *I* = 0.731). Observed Schoener's *D* and Hellinger's *I* values were significatively lower than those of the null distribution in all cases, which is particularly clear in the comparisons between *A. a. aztecus* and *A. a. major* (Figure 3b). 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).

Discussion and conclusions

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-eating bat reported by Davis (1969). He indicated that *A. a. aztecus* was considered typical in evergreen forests at relatively high elevations in the mountains bordering the Mexican Plateau, low at 1000 m in cloud forest and high at 2400 m in the pine-fir forest. In the case of *A. a. minor*, the conspicuous element of the habitat was conifer forest. *Artibeus a. major* is the only subspecies whose distributional pattern was not associated with conifers, suggesting that the distribution was correlated with "cloud forest" atmospheric conditions (Davis 1969). Is in the 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).

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, such as birds (Puebla-Olivares *et al*. 2008; Arbeláez-Cortés *et al*. 2010) and snakes (Castoe *et al*. 2009b). In bats, it is considered a significant barrier that limits the distribution of *Sturnira hondurensis*, separating it from its sister species *S. burtonlimi* (Torres-Morales 2019).

***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 phylogenetic niche conservatism in phyllostomid bats (Peixoto *et al*. 2017), suggesting their niche may have evolved under a strong evolutionary stasis (Stevens 2004, 2011).

However, 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, therefore, gene flow between adjacent populations (Gascon *et al*. 2000; Gehring *et al*. 2012). Lineages may thus exhibit niche divergence, for example, due to phylogenetic niche conservatism driving continued adaptation to local niches, leading populations to diverge over time away from the ancestral niche (Pyron *et al*. 2015). Then, niche differentiation may indicate that some lineages might have followed alternative evolutionary pathways (Martínez-Gordillo *et al*. 2010).

Here, we found signals of ecological niche differentiation among the three subspecies of Aztec fruit-eating bat (Tables 1, 2; Figures 2, 3). The three subspecies of *A. aztecus* present different climatic preferences that may indicate they are evolving independently. However, it is important to highlight that comparative analyses of ecological niches and geographic distributions are insufficient to set species limits. Still, they may offer some guidelines to explore speciation mechanisms (Tocchio *et al*. 2015) and thus determine the taxonomic status of the species. Therefore, further studies are necessary to learn about the evolutionary history of *A. aztecus* and clarify the taxonomic situation of the three subspecies. Certainly, 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 and (Warren *et al*. 2010). In this study, we defined it using the movement data of a congeneric species of *A. aztecus*, so the results must be carefully interpreted. More studies are necessary to know the dispersal capacity for each subspecies to probably make a better decision about the reference area for niche models and comparisons.

It is essential to clarify the phylogenetic relationships among the subspecies to understand better allopatric speciation and historical biogeography (Martínez-Gordillo *et al*. 2010). Studies that have analyzed the diversification of the genus *Artibeus* and the subgenus *Dermanura*, have included a few samples of at least two subspecies except *A. a. major* (Owen 1987; Hoofer *et al*. 2008; Redondo *et al*. 2008; Solari *et al*. 2009; Baker *et al*. 2016). Phylogeographic analyses have assessed the effect of lowlands (Isthmus of Tehuantepec and Nicaraguan Depression) and climatic fluctuations in the evolution patterns of montane species in Mesoamerica (León-Paniagua *et al*. 2007; Jiménez and Ornelas 2016; Hernández-Canchola 2018; Rodríguez-Gómez *et al*. 2021), so it can be helpful to know the genetic structure and evolution of the three subspecies. In addition, more morphological analyses are necessary to assess the phenotypic variation among the subspecies (e.g., Castañeda-Rico 2005). It is imperative to include specimens of the three subspecies to analyze the possible effect of environmental conditions on their morphology, as seen in other Mesoamerican montane species (Rodríguez-Gómez *et al*. 2013, 2021; Hernández-Canchola 2018).

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 is due to the interaction between former ecological niche conservatism and the emergence of geographic barriers, such as Isthmus of Tehuantepec and Nicaraguan Depression that promoted the subsequent ecological differentiation. Despite these environmental differences, we consider that subspecies pertaining to *Artibeus aztecus* should keep their current taxonomic awaiting further analyses that provide more evidence probably allowing us to recognize them as full species.

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Figures

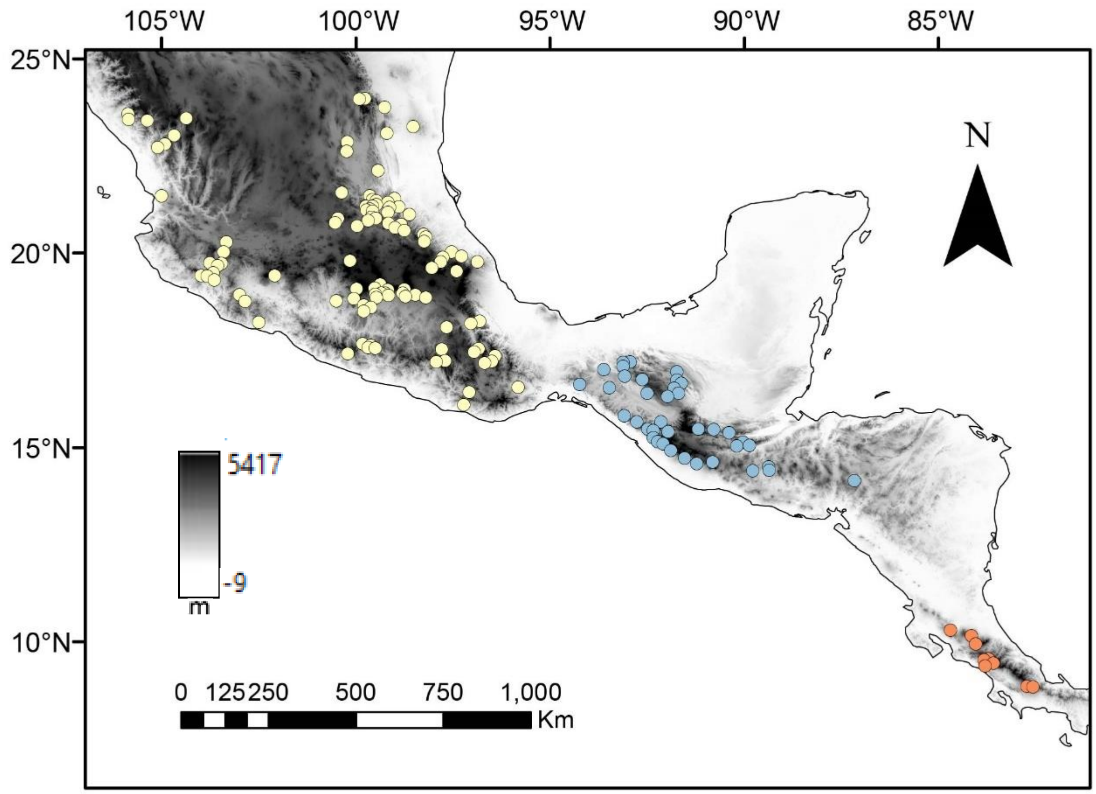

Figure 1. Localities of the three subspecies of *Artibeus aztecus* analyzed in this work: *Artibeus aztecus aztecus* (yellow), *Artibeus aztecus minor* (blue) and *Artibeus aztecus major* (red).

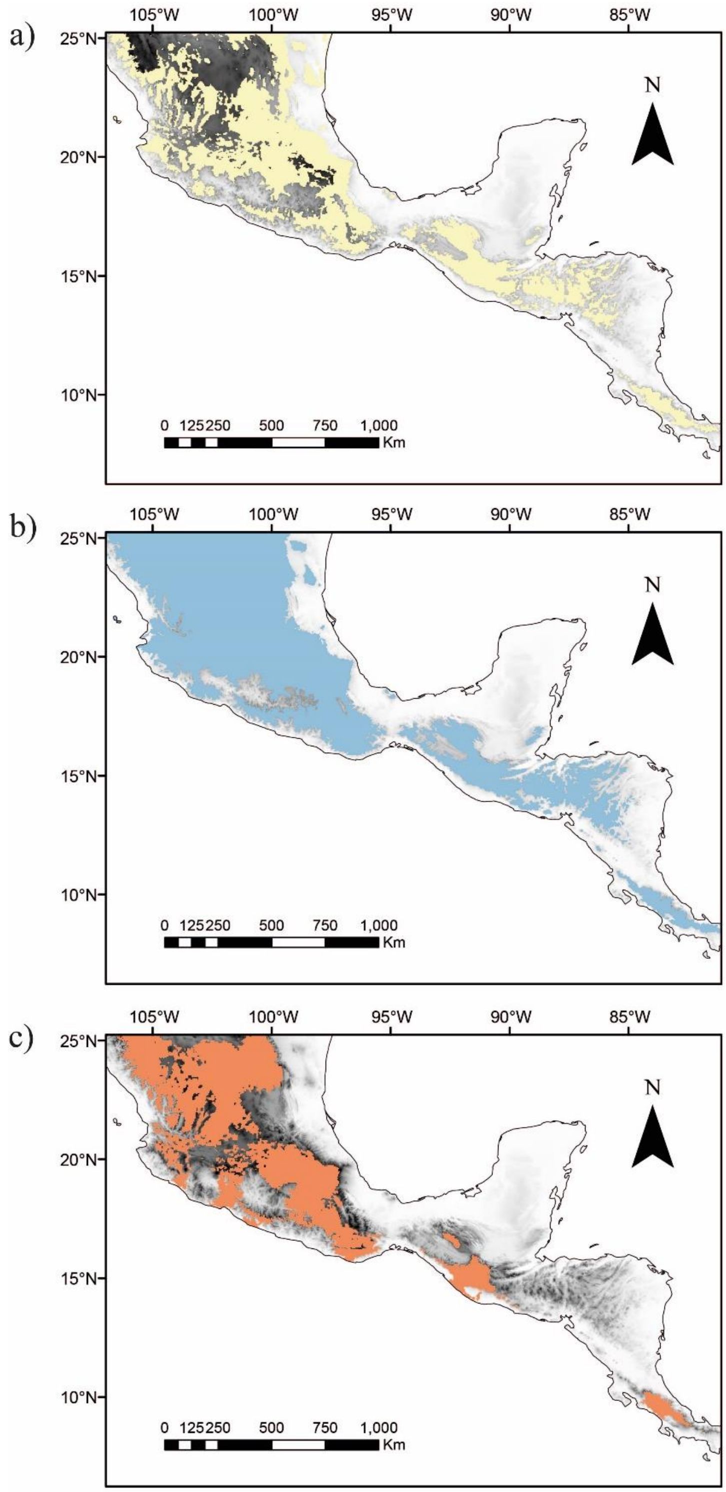

Figure 2. Maxent predicted potential distribution for (a) *Artibeus a. aztecus,* (b) *A. a. minor,* and (c) *A. a. major*.

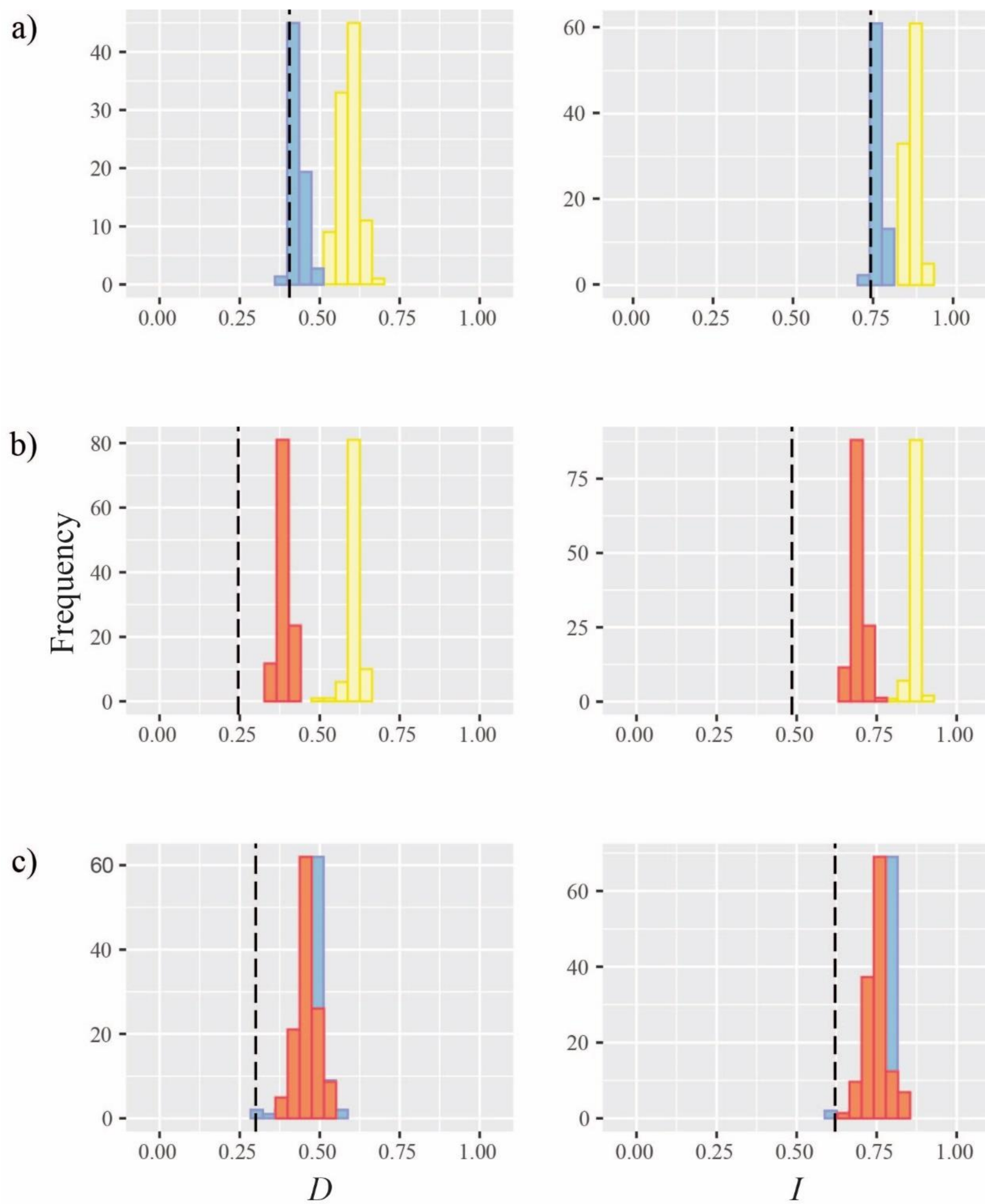

Figure 3. Niche overlap values for Schoener's *D* (left) and Hellinger's *I* (right) compared to a null distribution: (a) *Artibeus a. aztecus* (yellow) vs. *A. a. minor* (blue), (b) *A. a. aztecus* vs. *A. A. major* (red), (c) *A. a. minor* vs. *A. a. major.*

Tables

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	bio01	68.8	67.8
	bio02	30.5	26.9
	bio12	0.4	4.5
	bio03	0.2	0
	bio14	0.1	0.8
A. a. minor	bio01	97.4	95.6
	bio14	2.2	4.4
	bio03	0.4	0
	bio12	0	0
	bio02	0	0
A. a. major	bio01	59.5	43.6
	bio03	25.7	25.1
	bio02	14.8	31.3
	bio12	0	0
	bio14	0	0

Table 2. Results of the background similarity test among the three subspecies of *Artibeus aztecus*. Observed Schoener's *D* and Hellinger's *I* values, and p-values are shown.

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

Appendix 1. Geographic records of *Artibeus aztecus*

Subspecies	Longitude	Latitude	Institution	Catalog number	Country	State/Province	Locality
Artibeus aztecus aztecus	-99.76897775	23.97030461	KUM	98427	México	Nuevo León	Zaragoza
Artibeus aztecus aztecus	-99.912712	23.96176	TTU	57046	México	Nuevo León	1 km S Ejido San Josecito, Cueva San Josecito
Artibeus aztecus aztecus	-99.257167	23.749883	TCWC	29154	México	Tamaulipas	12 mi W Encino, Rancho del Cielo
Artibeus aztecus aztecus	-105.868167	23.5875	MZFC-M	15607	México	Sinaloa	El Palmito "La Chara Pinta"
Artibeus aztecus aztecus	-104.367	23.465167	CRD	CRD4756	México	Durango	Costado del Balneario 'La Joya'
Artibeus aztecus aztecus	-105.8514909	23.43623738	KUM	94950	México	Sinaloa	Santa Lucía
Artibeus aztecus aztecus	-105.37	23.408333	MSU	MR.4774	México	Durango	Pueblo Nuevo
Artibeus aztecus aztecus	-98.524444	23.251389	CNMA	34198	México	Tamaulipas	El Encino
Artibeus aztecus aztecus	-99.200833	23.088056	CNMA	34798	México	Tamaulipas	Cueva de la Salamandra, 6.55 km NW Gómez Farías
Artibeus aztecus aztecus	-104.6785655	23.03183642	CRD	CRD8495	México	Durango	Las Ramadas
Artibeus aztecus aztecus	-100.216392	22.859167	ENCB	30738	México	San Luis Potosí	6.5 Km W Presa de Guadalupe
Artibeus aztecus aztecus	-104.921916	22.807644	UAZ	UAZ 02515	México	Nayarit	Rancho del Bajio del Monte, 2 km NE of Tomates, ca. 5 km W of Rio Cihuacora
Artibeus aztecus aztecus	-105.095833	22.7125	UAZ	UAZ 09985	México	Nayarit	El Maguey, eastward from Huajicori, ca. 6400 ft.
Artibeus aztecus aztecus	-100.231675	22.621939	USNM	556318	México	San Luis Potosí	Cueva de la Joya De La Puente, 14 mi S (carr.), San Francisco
Artibeus aztecus aztecus	-99.427778	22.125833	MZFC-M	7501	México	San Luis Potosí	San Nicolás de los Montes
Artibeus aztecus aztecus	-100.361063	21.5627	ENCB	42965	México	Guanajuato	6.8 km N, 8.7 km E Mesas de Jesús
Artibeus aztecus aztecus	-105.005833	21.475	MZFC-M	5677	México	Nayarit	El Cuarenteño, 3 km NNE
Artibeus aztecus aztecus	-99.646667	21.467333	TCWC	26220	México	Querétaro	Conca, 2. mi NW
Artibeus aztecus aztecus	-99.00010743	21.39719533	UAMI	8946	México	San Luis Potosí	Las Pozas, 3 Km N Xilitla
Artibeus aztecus aztecus	-99.571146	21.369056	TCWC	26217	México	Querétaro	2 mi SSE Conca, Hacienda X-Conca
Artibeus aztecus aztecus	-99.4725	21.344167	CNMA	20057	México	Querétaro	14 km N Río Jalpan
Artibeus aztecus aztecus	-99.174722	21.298333	ENCB	16579	México	Querétaro	9.1 km N, 33 km E Jalpan
Artibeus aztecus aztecus	-99.472572	21.24427	TTU	46739	México	Querétaro	3 km N Jalpan
Artibeus aztecus aztecus	-99.737957	21.208383	TCWC	58046	México	Querétaro	Río Blanco
Artibeus aztecus aztecus	-99.568889	21.199167	MZFC-M	1043	México	Querétaro	Ahuacatlán, 2.8 SW
Artibeus aztecus aztecus	-98.888333	21.183889	MZFC-M	7615	México	Hidalgo	El Sótano, 1 km E del Cerro Jarros
Artibeus aztecus aztecus	-99.12611	21.1775	MZFC-M	7205	México	Querétaro	Santa Inés, 2 km W
Artibeus aztecus aztecus	-99.645278	21.136667	MZFC-M	1048	México	Querétaro	Puerto de Tejamanil
Artibeus aztecus aztecus	-99.73333	21.1	MZFC-M	1067	México	Querétaro	Camargo
Artibeus aztecus aztecus	-99.566667	21.083333	MZFC-M	1040	México	Querétaro	Pinal de Amoles, 3.5 km SE
Artibeus aztecus aztecus	-99.176944	21.053194	MZFC-M	7452	México	Hidalgo	3 km SE Laguna Seca
Artibeus aztecus aztecus	-98.626667	20.987222	CNMA	40926	México	Hidalgo	5.3 km E Tlanchinol
Artibeus aztecus aztecus	-99.603333	20.921	TCWC	39147	México	Querétaro	San Joaquín, 2 mi W by road
Artibeus aztecus aztecus	-99.491944	20.897222	ENCB	14217	México	Querétaro	2 km S, 8 km E San Joaquin
Artibeus aztecus aztecus	-100.459124	20.892695	TCWC	28611	México	Querétaro	20 km NW (by road) San Joaquin
Artibeus aztecus aztecus	-99.681924	20.836098	TCWC	39146	México	Querétaro	9.5 mi W Maconi, Rancho Agua Fria
Artibeus aztecus aztecus	-100.531961	20.786916	TCWC	25767	México	Querétaro	2.4 mi W El Madrono, 5200 ft

Artibeus aztecus aztecus	-99.157776	20.771111	ENCB	17582	México	Hidalgo	0.4 Km N, 0.6 Km W Nicolás Flores
Artibeus aztecus aztecus	-98.83583	20.736668	ENCB	9766	México	Hidalgo	3 Km N Hualula
Artibeus aztecus aztecus	-99.97	20.698333	TCWC	28611	México	Querétaro	San JoaquÍn, 20 km NW by road
Artibeus aztecus aztecus	-98.984167	20.655556	MZFC-M	5840	México	Hidalgo	Tolantongo
Artibeus aztecus aztecus	-98.748886	20.581944	ENCB	30496	México	Hidalgo	2 km SE Metztitlán
Artibeus aztecus aztecus	-98.254165	20.486389	ENCB	18034	México	Hidalgo	2 Km N, 2 Km W San Bartolo Tutoltepec
Artibeus aztecus aztecus	-98.201389	20.408333	MZFC-M	6527	México	Hidalgo	San Bartolo Tutotepec
Artibeus aztecus aztecus	-98.246944	20.306389	MZFC-M	9039	México	Hidalgo	Tenango de Doria, El Cirio
Artibeus aztecus aztecus	-103.334793	20.290358	TTU	38042	México	Jalisco	10 mi W Chapala
Artibeus aztecus aztecus	-103.400001	20.03389	ENCB	34431	México	Jalisco	San Sebastián, 1.5 km E
Artibeus aztecus aztecus	-97.52923462	20.02976195	UAMI	1291	México	Puebla	Rancho Las Margaritas
Artibeus aztecus aztecus	-97.2747832	19.9217117	UAMI	13312	México	Veracruz	7 Km SW Tlapacoyan
Artibeus aztecus aztecus	-97.7584467	19.887803	MZFC-M	13272	México	Puebla	Tetela de Ocampo, Xochititan
Artibeus aztecus aztecus	-100.151389	19.800833	CNMA	19682	México	Michoacán	2 km W El Oro
Artibeus aztecus aztecus	-97.814639	19.78225	MZFC-M	13057	México	Puebla	Tetela de Ocampo, Cerro las Espejeras, Boca de Mina
Artibeus aztecus aztecus	-96.86292	19.77025	MZFC-M	11242	México	Veracruz	Misantla, Villa Nuevo
Artibeus aztecus aztecus	-103.750033	19.7465578	KUM	120431	México	Jalisco	Venustiano Carranza, 2 km E of
Artibeus aztecus aztecus	-103.4625	19.7318829	KU	31869	México	Jalisco	Ciudad Guzmán, 2 Mi N of
Artibeus aztecus aztecus	-103.554	19.6731	UMMZ	113685	México	Jalisco	N Slope Nevado de Colima
Artibeus aztecus aztecus	-98.03924535	19.61811248	UAMI	3766	México	Tlaxcala	1.5 Km E El Convento
Artibeus aztecus aztecus	-97.4134	19.53117	MZFC-M	13243	México	Puebla	Cerro Miqueco, campamento provisional
Artibeus aztecus aztecus	-103.672855	19.487819	OMNH	27397	México	Colima	2 km NE La Yerbabuena
Artibeus aztecus aztecus	-102.093611	19.427972	CM-UMSNH	3212	México	Michoacán	Parque Nacional Barranca del Cupatitzio
Artibeus aztecus aztecus	-103.980278	19.417778	CNMA	41620	México	Colima	2 km NW Ranchitos
Artibeus aztecus aztecus	-103.828515	19.407568	OMNH	6177	México	Colima	14 km NE Pueblo Nuevo
Artibeus aztecus aztecus	-103.640759	19.305679	OMNH	31725	México	Colima	El Cobano
Artibeus aztecus aztecus	-99.378333	19.193611	CNMA	7151	México	México	Barranca de los Ídolos, 32 km SW México, D.F.
Artibeus aztecus aztecus	-99.508331	19.103056	ENCB	22704	México	México	7.5 km E Tenango de Arista
Artibeus aztecus aztecus	-99.981392	19.078056	ENCB	26062	México	México	3.5 km N, 6 km E Temascaltepec
Artibeus aztecus aztecus	-98.749443	19.064167	ENCB	8720	México	México	3 Km E Popo park
Artibeus aztecus aztecus	-99.17093621	19.05757926	UAMI	11812	México	Morelos	2 Km E Tres Marías
Artibeus aztecus aztecus	-99.245278	18.974444	CNMA	15200	México	Morelos	Universidad de Morelos
Artibeus aztecus aztecus	-99.34889	18.96944	MZFC-M	5561	México	México	Carr. Ocuilan-Cuernavaca, 2 km al SE del km 11
Artibeus aztecus aztecus	-98.793611	18.966111	CNMA	19678	México	México	8 km S Ozumba
Artibeus aztecus aztecus	-99.504448	18.948055	ENCB	35302	México	México	1 km W Malinalco
Artibeus aztecus aztecus	-98.463302	18.933001	ENCB	28524	México	Puebla	Atlixco; 4 km NW
Artibeus aztecus aztecus	-103	18.927778	MZFC-M	4304	México	Michoacán	El Resumidero
Artibeus aztecus aztecus	-99.159164	18.918333	ENCB	11602	México	Morelos	Cuernavaca; 7.5 km E
Artibeus aztecus aztecus	-98.729164	18.891666	ENCB	21042	México	Morelos	Tetela del Volcán
Artibeus aztecus aztecus	-98.19452349	18.85786966	UAMI	9659	México	Puebla	5 Km S, 5 Km E Tecola
Artibeus aztecus aztecus	-99.464996	18.856667	ENCB	35313	México	México	1 km N San Pedro Chichicasco
Artibeus aztecus aztecus	-100.04528	18.826944	ENCB	21586	México	México	3 km S, 8 km W Sultepec

Artibeus aztecus aztecus	-100.501099	18.777399	ENCB	43545	México	Guerrero	El Guayabal, 8 km W Bejucos
Artibeus aztecus aztecus	-102.848077	18.765488	UMMZ	110526	México	Michoacán	7.5 Mi by Road E Dos Aguas
Artibeus aztecus aztecus	-99.79556	18.6525	MZFC-M	4233	México	México	Mamatla
Artibeus aztecus aztecus	-99.606667	18.606944	MZFC-M	4216	México	Guerrero	Parque Estatal 'El Huizteco'
Artibeus aztecus aztecus	-99.79556	18.50639	MZFC-M	4220	México	Guerrero	Ixcateopan
Artibeus aztecus aztecus	-96.813889	18.255556	CNMA	38655	México	Oaxaca	Rancho Nuevo
Artibeus aztecus aztecus	-102.503333	18.226389	MZFC-M	10182	México	Michoacán	Plan de Armas
Artibeus aztecus aztecus	-97.033889	18.1975	CNMA	38663	México	Puebla	5 km NW Puerto de la Soledad
Artibeus aztecus aztecus	-97.661389	18.093889	ENCB	40394	México	Oaxaca	2 km SW San Juan Nochixtlán
Artibeus aztecus aztecus	-99.82528	17.66333	MZFC-M	222	México	Guerrero	Filo de los Caballos, 3 km NE, El Puerto
Artibeus aztecus aztecus	-99.608333	17.630833	MZFC-M	6192	México	Guerrero	Jalapa
Artibeus aztecus aztecus	-99.68556	17.56611	MZFC-M	1359	México	Guerrero	Omiltemi
Artibeus aztecus aztecus	-99.50083333	17.55138889	MVZ	34904	México	Guerrero	Chilpancingo
Artibeus aztecus aztecus	-96.84667	17.54667	MZFC-M	6535	México	Guerrero	Zoquiapam, Boca de los Ríos
Artibeus aztecus aztecus	-97.78333	17.52167	MZFC-M	8686	México	Oaxaca	San Martín Caballero
Artibeus aztecus aztecus	-96.955556	17.460833	MZFC-M	6536	México	Oaxaca	Cieneguilla
Artibeus aztecus aztecus	-100.203611	17.42	MZFC-M	6799	México	Guerrero	Nueva Delhi
Artibeus aztecus aztecus	-96.423611	17.356389	OAXMA	1356	México	Oaxaca	El Arco, 5.5 km NE Ixtlán de Juárez
Artibeus aztecus aztecus	-97.70472	17.23722	MAM	16355	México	Oaxaca	Hwy 125, km 123 Putla-Tlaxiaco
Artibeus aztecus aztecus	-96.506111	17.222778	MCNB	319	México	Oaxaca	Oaxaca, 18.5 Km N, 2.25 Km E
Artibeus aztecus aztecus	-97.929167	17.207778	CNMA	39153	México	Oaxaca	20 km N Putla Villa de Guerrero
Artibeus aztecus aztecus	-96.683056	17.172222	OAXMA	20	México	Oaxaca	18.5 km N, 2.25 km W, Oaxaca
Artibeus aztecus aztecus	-95.826944	16.547222	CNMA	39419	México	Oaxaca	10 km SW San Sebastián Jilotepec
Artibeus aztecus aztecus	-97.082222	16.424722	CNMA	8479	México	Oaxaca	36.5 km N San Gabriel Mixtepec
Artibeus aztecus aztecus	-97.21948782	16.09328445	CASMAM	14983	México	Oaxaca	9 miles west San Gabriel Mixtepec
Artibeus aztecus major	-84.69973932	10.30111148	MR	MR.32350	Costa Rica	Puntarenas	Hotel Flor-Mar Super Soda, Monteverde
Artibeus aztecus major	-84.15	10.167	LSUMZ	14736	Costa Rica	Heredia	Varablanca
Artibeus aztecus major	-84.05	9.95	LSUMZ	12881	Costa Rica	San José	San Gerardo
Artibeus aztecus major	-83.717	9.567	LSUMZ	14732	Costa Rica	Cartago	Villa Mills, La Georgina
Artibeus aztecus major	-83.835	9.5330556	MNCR	MNCR-M1351	Costa Rica	San José	Finca La Montaña Fría, Zapotal, Providencia
Artibeus aztecus major	-83.589	9.45	LSUMZ	12880	Costa Rica	San José	Fila la Maquina, ca. 3 km E Canaan
Artibeus aztecus major	-83.8063888	9.3861111	MNCR	MNCR-M1230	Costa Rica	San José	San Gerardo
Artibeus aztecus major	-82.73333	8.86667	UMMZ	116673	Panamá	Chiriqui	Río Chiriqui Viejo
Artibeus aztecus major	-82.5666667	8.85	ROM	44327	Panamá	Chiriqui	Cerro Punta
Artibeus aztecus minor	-92.942222	17.200278	CNMA	25451	México	Chiapas	Rincón, 4 mi NW Pueblo Nuevo Solistahuacan
Artibeus aztecus minor	-93.117778	17.184167	MZ-UNICACH	692	México	Chiapas	Cerro La Ventana, 6 Km al N - 4.5 Km al E
Artibeus aztecus minor	-93.125	17.086389	MZ-UNICACH	1114	México	Chiapas	El Molino, 2.6 Km al N - 2 Km al E Coapilla
Artibeus aztecus minor	-93.616667	17	CNMA	30409	México	Chiapas	Selva El Ocote
Artibeus aztecus minor	-91.734828	16.953423	TCWC	37388	México	Chiapas	12 km N Berriozabal
Artibeus aztecus minor	-93.075	16.834722	ZOOMAT	52	México	Chiapas	Parque Nacional Cañón del Sumidero
Artibeus aztecus minor	-92.633333	16.75	ECO-SC-M	701	México	Chiapas	Reserva Ecológica Moxviquil, 2.5 Km al NE de San Cristóbal de Las Casas, por Periférico Norte

Artibeus aztecus minor	-91.736944	16.736667	UAZ	9606	México	Chiapas	Finca Patichuiz, 53 Km al NE de Las Margaritas
Artibeus aztecus minor	-91.62491728	16.65716035	LACM	19195	México	Chiapas	Las Margaritas, 33 mi NE (approx); Finca Patachuiz
Artibeus aztecus minor	-94.23747907	16.61881663	CASMAM	14684	México	Oaxaca	The Big Valley, Cerro Baul, about 22 km by air NW Rizo de Oro
Artibeus aztecus minor	-93.478056	16.541389	CNMA	30409	México	Chiapas	Selva del Ocote
Artibeus aztecus minor	-91.803333	16.526389	UAZ	9476	México	Chiapas	La Soledad, 25.7 Km al NE de Las Margaritas
Artibeus aztecus minor	-91.7	16.4	UAZ	UAZ 9476	México	Chiapas	La Soledad, approx. 16 mi. northeastward from Las Margaritas, ca. 3600 ft.
Artibeus aztecus minor	-92.501092	16.390517	ECO-SC-M	3994	México	Chiapas	Río Blanco
Artibeus aztecus minor	-91.981389	16.315278	MVZ	167472	México	Chiapas	Las Margaritas
Artibeus aztecus minor	-93.093333	15.823056	CZRMA	1731	México	Chiapas	Rancho Buena Vista III, Rancho El Cebú
Artibeus aztecus minor	-92.141389	15.658333	MZ-UNICACH	1152	México	Chiapas	Frontera Comalapa
Artibeus aztecus minor	-92.766944	15.656389	CNMA	20846	México	Chiapas	Reserva de la Biósfera El Triunfo, 7 km SSE
Artibeus aztecus minor	-92.487222	15.483889	CZRMA	1900	México	Chiapas	Ejido Letrero, Barrio Villa Morelos
Artibeus aztecus minor	-91.18	15.48	LACM	53658	Guatemala	Huehuetenan go	Quezaltenango, 231 km N (by road); Barillas
Artibeus aztecus minor	-90.78811	15.46208	MVZ	226950	Guatemala	El Quiche	Chimel Grande, 12.6 km N, 9.0 km E Uspatan
Artibeus aztecus minor	-92.337964	15.432442	ECO-SC-M	2422	México	Chiapas	Cerro Mozotal. La Gravera 6.7 Km SW Porvenir
Artibeus aztecus minor	-91.9625	15.4053	USAC	1539	Guatemala	Huehuetenan go	Sosí Chiquito, aldea
Artibeus aztecus minor	-90.4	15.383	LSUMZ	14746	Guatemala	Alta Verapaz	San Cristobal Verapaz
Artibeus aztecus minor	-92.345	15.248333	CZRMA	2023	México	Chiapas	Ejido Libertad Calera
Artibeus aztecus minor	-92.228611	15.1575	CZRMA	1998	México	Chiapas	Ejido Toquian Chiquito
Artibeus aztecus minor	-90.03488	15.14378	MVZ	184698	Guatemala	Baja Verapaz	3 km S, 7 km E of Chilasco, (Finca Miranda)
Artibeus aztecus minor	-92.09561	15.09414	MZFC-M	10017	México	Chiapas	Volcán Tacaná, poblado Chiquihuites
Artibeus aztecus minor	-89.866667	15.05	ROM	78571	Guatemala		13 km NW of Usumatlan, Sierra De Las Minas
Artibeus aztecus minor	-90.193387	15.043613	TCWC	17519	Guatemala	Baja Verapaz	1 km SE San Jeronimo, 1000 m
Artibeus aztecus minor	-91.885528	14.92375	ECO-SC-M	2886	Guatemala		Finca El Vergel. Aldea Feria. San Rafael Pie de la Cuesta
Artibeus aztecus minor	-91.5317	14.7261	USAC	1246	Guatemala	Quetzaltenan go	Quetzaltenango, Parque Regional Municipal, zona de influencia; Santa María de Jesús
Artibeus aztecus minor	-90.819444	14.632021	TCWC	14391	Guatemala	Chimaltenan go	2 mi S Chimaltenango, 5700 ft
Artibeus aztecus minor	-91.2289	14.5908	USAC	439	Guatemala	Sololá	Atitlán, Área de Usos Múltiples; Mirador
Artibeus aztecus minor	-89.3797	14.5083	USAC	4346	Guatemala	Chiquimula	Reserva de Biosfera La Fraternidad
Artibeus aztecus minor	-89.367	14.417	ROM	101364	El Salvador	Santa Ana	Parque Nacional Montecristo, Bosque Nebuloso
Artibeus aztecus minor	-89.77953	14.40923	MVZ	228227	Guatemala	Jutiapa	Parque Nacional Volcán Suchitán, ca. 4.8 km S & 4.0 km W Santa Catarina Mita
Artibeus aztecus minor	-87.169676	14.145003	TCWC	48998	Honduras	Francisco Morazán	El Hatillo, 6 mi NE Tegucigalpa, on road to La Tigra

Supplementary material

Table 1. Variables considered in the study

Included	Excluded
Annual mean temperature	Mean temperature of wettest quarter
Mean diurnal range	Mean temperature of direst quarter
Isothermality	Precipitation of warmest quarter
Temperature seasonality	Precipitation of coldest quarter
Maximum temperature of warmest month	
Minimum temperature of coldest month	
Temperature annual range	
Mean temperature of warmest quarter	
Mean temperature of coldest quarter	
Annual precipitation	
Precipitation of wettest month	
Precipitation of driest month	
Precipitation seasonality	
Precipitation of wettest quarter	
Precipitation of driest quarter	

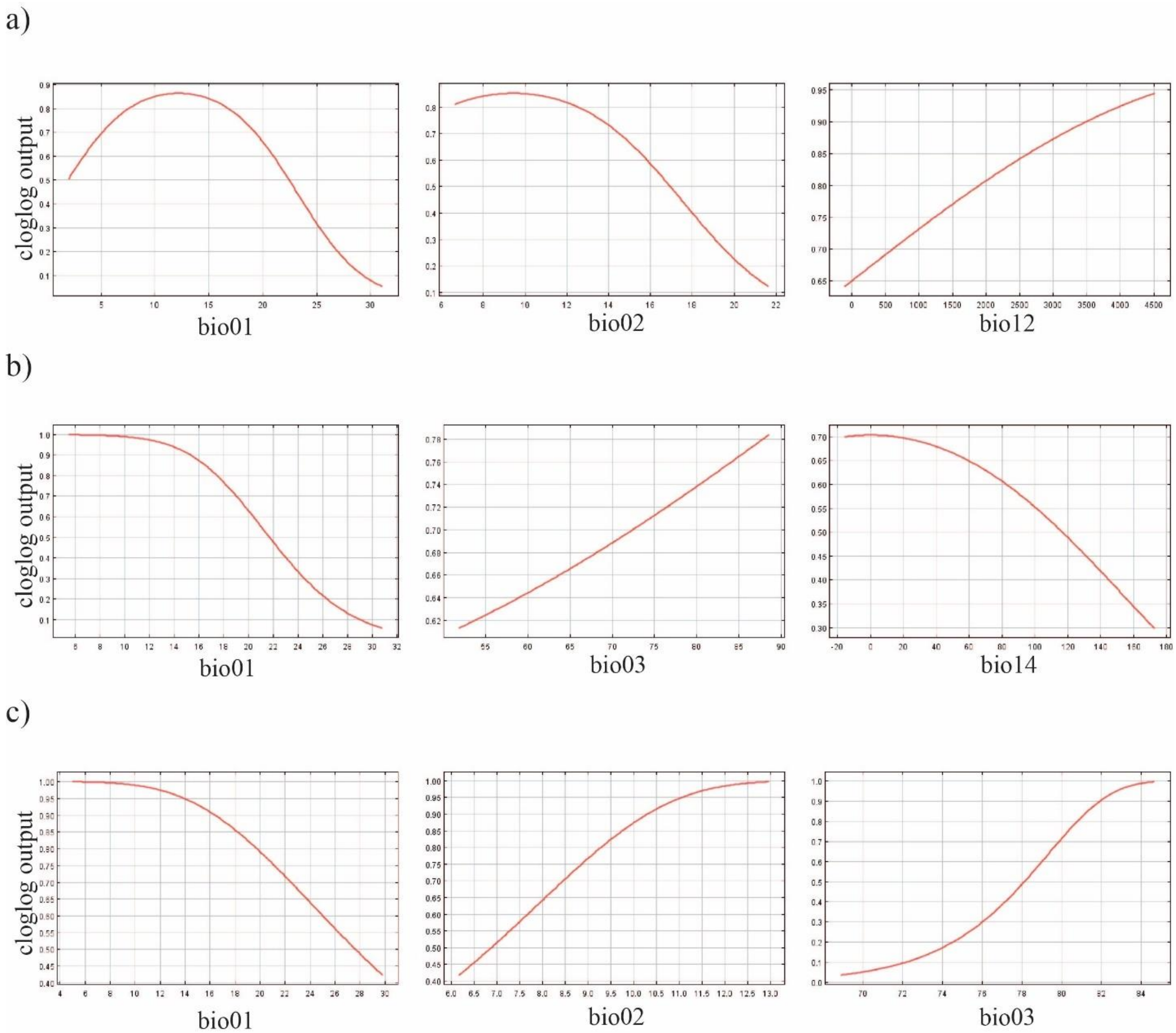

Figure 1. Response curves generated by Maxent for the three most important climatic variables of (a) *Artibeus aztecus aztecus* model, (b) *A. aztecus minor* model, and (c) *A. a. major* model.

DISCUSIÓN Y CONCLUSIÓN GENERAL

En este trabajo se analizaron y compararon los requerimientos climáticos y la distribución geográfica potencial de las tres subespecies de *Artibeus aztecus*, distribuidas en zonas montañosas de Mesoamérica. Se detectaron diferencias entre los taxones analizados, lo que sugiere diferenciación del nicho ecológico.
Si bien los modelos de distribución potencial parecen reflejar el precedente conservadurismo de nicho ecológico, se encontraron áreas no idóneas que parecen contribuir al aislamiento y divergencia del nicho en las subespecies. En concreto, es probable que las tierras bajas como el Istmo de Tehuantepec y la Depresión de Nicaragua estén actuando como barreras geográficas que promueven la evolución de las subespecies, como linajes independientes.
Para poner a prueba esta hipótesis, serán necesarios estudios moleculares y morfológicos que permitan conocer los patrones evolutivos de cada taxón y poder tomar la decisión taxonómica más adecuada sobre ellos.

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