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Reopening the case of the enigmatic record hitherto referred to as the Mayan shrew, *Cryptotis mayensis* (Mammalia, Soricidae)

Lázaro Guevara[1,*], Reinhard E. Matadamas[2,3], Stephanye Mata-González[1,3], Paola Zeferino[1], and Joaquín Arroyo-Cabrales[4]

[1]Colección Nacional de Mamíferos, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70-153, CP 04510 Mexico City, Mexico. E-mail: matags_bio@ciencias.unam.mx (SMG); E-mail: paola-zeferino@ciencias.unam.mx (PZ)
[2]Museo de Zoología Alfonso L. Herrera, Facultad de Ciencias, Universidad Nacional Autónoma de México, Apartado Postal 70-153, CP 04510 Mexico City, Mexico. reinhardmata@ciencias.unam.mx (REM).
[3]Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México.
[4]Instituto Nacional de Antropología e Historia, Subdirección de laboratorio y Apoyo Académico, Laboratorio de Arqueozoología "M. en C. Ticul Álvarez Solórzano", Moneda Núm. 16, Col. Centro, 06060 Ciudad de México, México. E-mail: arromatu@hotmail.com (JAC)
[*]Corresponding author: llg@ib.unam.mx

The Mayan small-eared shrew, *Cryptotis mayensis*, is endemic to the Yucatán Peninsula, with records from México, Belize, and Guatemala. For half a century, skull fragments from dozens of individuals found in pellets of the barn owl (*Tyto furcata*) in Guerrero, Mexico, previously identified as the Mayan shrew, have intrigued taxonomists and biogeographers. A previous robust analysis of current and fossil *C. mayensis* dentary samples, including those from Guerrero, showed a high morphometric similarity between them. Given that these owl pellet remains are located 1,000 km from the known distribution of *C. mayensis* in the Yucatán Peninsula, this has raised the hypothesis that they are not an isolated population of *C. mayensis* but rather an as-yet-undescribed species. By integrating new specimens of *C. mayensis* from the Yucatán Península and Guerrero, as well as *Cryptotis lacandonensis*, the sister species of *C. mayensis*, we reanalyzed the morphological attributes. In addition, we used paleodistribution estimates to investigate the possible isolation of the records previously referred to as *C. mayensis* in Guerrero, Mexico. Multivariate analyses of morphological data from the cranium and dentary revealed high similarity in size among the three samples analyzed, especially between *C. mayensis sensu stricto* and *Cryptotis* from Guerrero. Paleodistribution models suggest that the population of Guerrero has remained in long-term isolation from the populations of the Yucatan Peninsula due to a very large area with unsuitable conditions for the connectivity of the shrew population during the last glacial-interglacial cycle. It is possible that the Guerrero population is an independent lineage, despite its morphological similarity to *C. mayensis sensu stricto*; however, genetic evidence to confirm this is essential.

Keywords: Eulipotyphla, morphometrics, Neotropics, niche modelling, taxonomy

La musaraña maya de orejas cortas, *Cryptotis mayensis*, es endémica de la Península de Yucatán, con registros en México, Belice y Guatemala. Durante medio siglo, fragmentos de cráneo de docenas de individuos, encontrados en egagrópilas de lechuza común (*Tyto furcata*) en Guerrero, México, que anteriormente se identificaron como la musaraña maya, han intrigado a taxónomos y biogeógrafos. Un exhaustivo análisis previo de muestras dentales actuales y fósiles de *C. mayensis*, incluidas las de Guerrero, mostró una alta similitud morfométrica entre ellas. Dado que estos restos de egagrópilas se encuentran a 1000 km de la distribución conocida de *C. mayensis* en la Península de Yucatán, esto ha planteado la hipótesis de que no se trata de una población aislada de *C. mayensis*, sino de una especie aún no descrita. Al integrar nuevos especímenes de *C. mayensis* de la Península de Yucatán y de Guerrero, así como de *C. lacandonensis*, especie hermana de *C. mayensis*, reanalizamos los atributos morfológicos. Además, utilizamos estimaciones de paleodistribución para investigar el posible aislamiento de los registros previamente atribuidos a *C. mayensis* en Guerrero, México. Los análisis multivariados de datos morfológicos del cráneo y del dentario revelaron una alta similitud en tamaño entre las tres muestras analizadas, especialmente entre *C. mayensis sensu stricto* y *Cryptotis* de Guerrero. Los modelos de paleodistribución sugieren que la población de Guerrero ha permanecido aislada durante largo tiempo de las poblaciones de la Península de Yucatán debido a una extensa área con condiciones desfavorables para la conectividad poblacional durante el último ciclo glacial-interglacial. Es posible que la población de Guerrero sea un linaje independiente, a pesar de su similitud morfológica con *C. mayensis sensu stricto*; sin embargo, es indispensable contar con evidencia genética que lo confirme.

Palabras clave: Eulipotyphla, modelado de nicho, morfometría, Neotrópico, taxonomía

Shrews of the genus *Cryptotis* are small mammals found from southern Canada to northern South America. So far this century, the number of species within this genus has doubled due to intensive taxonomic research, making it the third most diverse genus among the 29 genera of shrews, with 55 species (Mammal Diversity Database 2025). Advances in taxonomic studies have refined previous proposals regarding the evolutionary relationships among several species and established species groups within the genus that may represent monophyletic groups (Guevara and Cervantes 2014; He *et al.* 2015; 2021). One such group is the *Cryptotis nigrescens* group, which includes eight species found from southern Mexico to northern Colombia (Woodman and Timm 2023): *C. mayensis*, *C. merriami*, *C.*

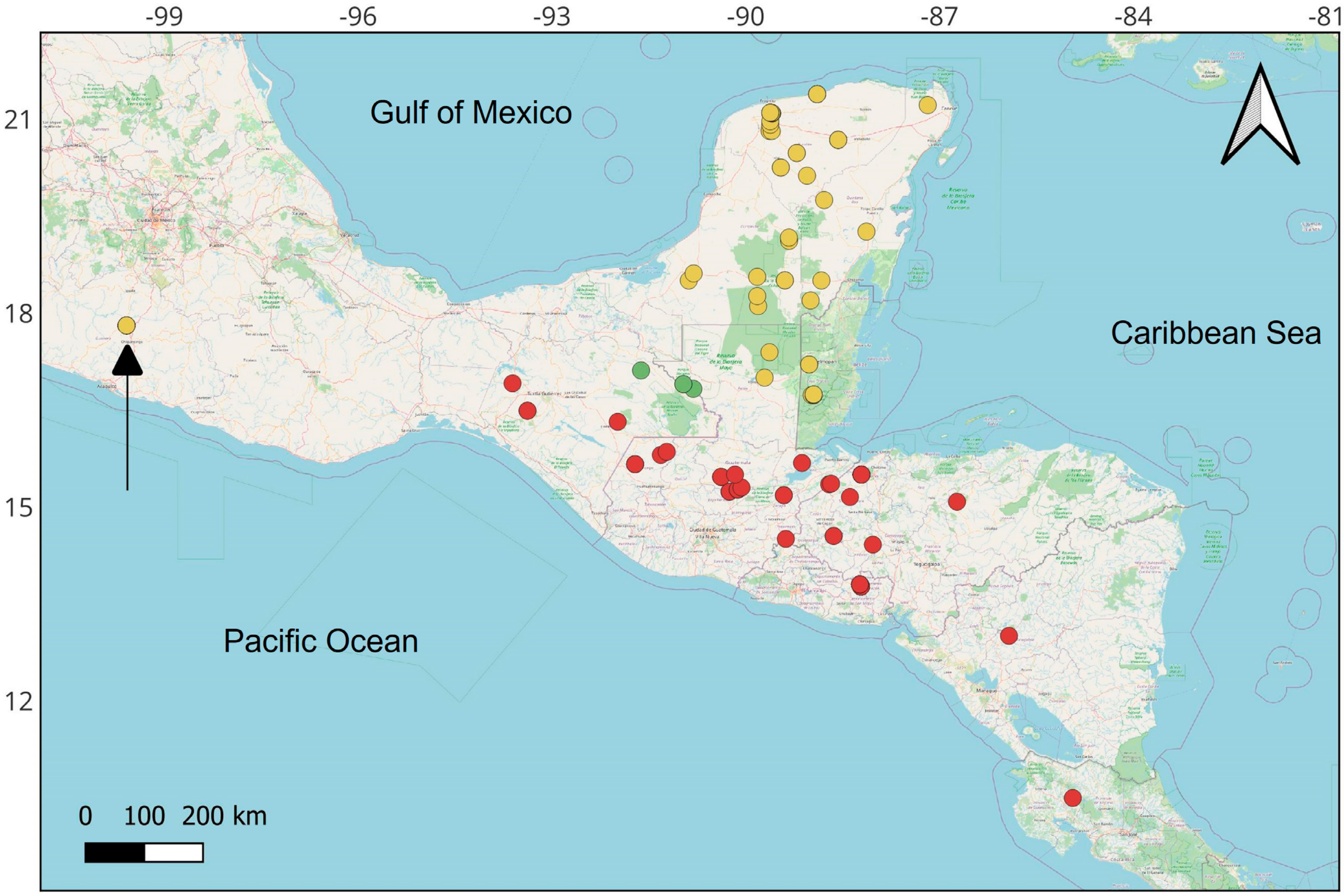

Figure 1. Occurrence records of small-eared shrews of the *Cryptotis nigrescens* group north of Mesoamerica (Guevara *et al.* 2015): Mayan shrew, *Cryptotis mayensis* (yellow dots); Lacandona shrew, *C. lacandonensis* (green dots), and Merriam's shrew, *C. merriami* (red dots). The arrow indicates the approximate location of owl pellet records obtained in 1969.

lacandonensis, *C. nigrescens*, *C. hondurensis*, *C. merus*, *C. brachyonyx*, and *C. colombianus*.

Within the *Cryptotis nigrescens* group, *C. mayensis* (the Mayan shrew) is the most boreal in distribution and endemic to the Yucatán Peninsula, with records from Mexico, Belize, and Guatemala (Lorenzo *et al.* 2019; Woodman 2019). *Cryptotis mayensis* was described based on one specimen "from a Maya ruin at Chichén Itzá, Yucatan", collected on February 5, 1901, by E. W. Nelson and E. A. Goldman (Merriam 1901; Woodman and Timm 1993), and its specific epithet "*mayensis*" refers to the predominant Mayan culture in the region (Carraway 2007; Guevara and Ramírez-Chaves 2025). It remained a little-known species until more specimens were collected decades later (Choate 1970). Nowadays, *C. mayensis* is distributed in lowland areas, usually at <100 m elevation, although a noteworthy record is from the Chiquibul Forest Reserve, Belize, at about 600 m elevation (Engilis *et al.* 2012). It inhabits lowland tropical forests, characterized by dry scrub, deciduous, and seasonally dry forests (Carraway 2007). *Cryptotis mayensis* has also been reported from Pleistocene fossils in the Loltún and Actun Spukil caves, Yucatán (Hatt 1953). The species most closely related to *C. mayensis* is *C. lacandonensis* (the Lacandona shrew), whose distribution is restricted to the Selva Maya on the border between Mexico and Guatemala, in humid tropical forests and seasonally flooded areas at elevations below 200 m (Guevara *et al.* 2014; Pérez *et al.* 2019).

For half a century, mandibles and incomplete skulls from almost 40 individuals found in pellets of the barn owl (*Tyto furcata;* previously *T. alba*) in Guerrero have intrigued taxonomists and biogeographers (López-Forment and Urbano 1977). The pellets were collected by William López-Forment in September 1969, within a stony and arid area surrounding the Cueva del Zopilote, located 13 km south of the Mezcala Bridge (Figure 1; Ramírez-Pulido and Sánchez-Hernández 1972). Based on the similarity of dental features and cranial and dental size, the preliminary assignment of the owl pellet was made to *C. mayensis* (Choate 1970; Woodman and Timm 1993). Their anatomical characteristics allowed these remains to be classified as belonging to the *C. nigrescens* group and not to the *C. goldmani* or *C. parvus* groups, which may also inhabit that region of Guerrero (Guevara *et al.* 2015). For example, the shape of the dentary, the location of the zygomatic plate, and the cusps on the lower and upper third molars are typical of what is observed in *C. mayensis* (Woodman and Timm 1993). Woodman (1995) analyzed current and fossil *C. mayensis* dentary samples, including those from Guerrero, to test the hypothesis that phenotypic changes may be a possible response to Quaternary climatic factors.

He found a high degree of morphometric similarity between the modern samples from Yucatán and Guerrero, which differ slightly from the fossil samples. Given that these remains from owl pellets are located about 1,000 km from the known distribution of *C. mayensis* in the Yucatán Peninsula, this has raised the hypothesis that they are not from an isolated population of *C. mayensis*, but rather from an as-yet-undescribed species (Woodman and Timm 1993; Monroy-Gamboa 2021). The reason for this remarkable geographic isolation has been intuitively attributed to Quaternary environmental changes that have eliminated suitable habitat for this group of shrews between Guerrero and the Yucatán Peninsula, leaving a small population in Guerrero completely isolated (Choate 1970; Woodman and Timm 1993).

To our knowledge, no additional samples or complete specimens of these shrews have been obtained in Guerrero so far, and conducting fieldwork is currently unfeasible due to the high and growing insecurity in that region of the country (Carpio-Domínguez 2021), which has hindered the resolution of the enigma of *C. mayensis* records in Guerrero. In addition, genetic data remain limited for Neotropical *Cryptotis*, which complicates progress in resolving complex taxonomic questions. Over the last two decades, our team and collaborators have consulted with several natural history museums to refine databases for the genus *Cryptotis*, thereby obtaining high-quality morphological and geographic data (Guevara *et al.* 2024). This raises the possibility of reopening old taxonomic and biogeographical questions and addressing them with consideration of new evidence.

Hence, by integrating morphological and distributional analyses, we aim to reexamine the origin of the records referred to as *Cryptotis mayensis* in Guerrero, Mexico, in a more in-depth manner. To do so, (1) we collected more morphological information on populations of interest to assess morphological variation, and (2) we modeled the environmental requirements for *C. mayensis* in the Yucatán Peninsula to estimate its distributional pattern across the Late Quaternary. We predict that including more data will reveal significant differences between samples from the Yucatán Peninsula and Guerrero, suggesting long-term geographic isolation and divergence at a specific level.

Materials and methods

Specimens examined. All specimens examined in the present study are housed in the following collections: Colección Nacional de Mamíferos, Instituto de Biología, Universidad Nacional Autónoma de México, México City (CNMA); Colección Zoológica Regional Mammalia, Instituto de Historia Natural y Ecología (CZRMA); Colección Mastozoológica, El Colegio de la Frontera Sur, San Cristóbal de las Casas (ECO-SC-M); The University of Kansas Natural History Museum, Lawrence (KU); Museo de Zoología "Alfonso L. Herrera", Facultad de Ciencias, Universidad Nacional Autónoma de México, México City (MZFC), Colección de Mamíferos de la Universidad, Autónoma de Yucatán, Mérida (UADY), the National Museum of Natural History, Smithsonian Institution, Washington (USNM), and Colección de Mamíferos, Universidad Veracruzana, Xalapa (UV).

We examined 25 *Cryptotis mayensis sensu stricto* specimens from the Yucatan Peninsula (CNMA 23796-23801; ECO-SC-M 2354-2356, 2358; KU 91463, 143892; UADY 833-840; USNM 170862, 108087, 173000; UV 3535, 3758), 37 skull remains recovered from the owl pellets in Guerrero (CNMA 11031-11043, 12666-12688, 12690), and two specimens of its sister species, *C. lacandonensis* (MZFC 7107, 7168) to gain a better understanding of the possible morphological variation within this clade. It is important to highlight that the material available for *C. lacandonensis* and *C. merriami* in Mexico is extremely scarce (Lorenzo *et al.* 2019; Guevara *et al.* 2024).

Morphometric analyses. Given the fragmentary nature of owl pellets and the difficulty of recovering complete material from all individuals, we performed separate morphometric analyses of the skull and mandibles. We obtained measurements of 20 skulls from the Yucatan Peninsula, 34 from Guerrero, and two from *C. lacandonensis*. For mandibles, we measured 20 right dentaries from the Yucatan Peninsula, seven right dentaries from Guerrero, and two right dentaries from *C. lacandonensis*.

We recorded four measurements of the cranium and five of the mandible (Figure 2) using a Mitutoyo electronic caliper, 500-171-20 model, at 0.1 mm precision under a stereomicroscope: interorbital breadth (IO), breadth of palate across second molars (M2B), breadth of zygomatic plate (ZP); length of molariform toothrow (MTR), height of coronoid process (HCP), the height of articular condyle (HAC), height of coronoid valley (HCV), lower toothrow length (TRD), distance from the upper border of the articular condyle to the posterior edge of the m3 (LAM). Tabular univariate statistics include mean ± SD and total range for each variable (Table 1).

To characterize and evaluate overall size variation across all specimens, we performed principal component analyses (PCA). To explore the cohesion of known species and samples from Guerrero and identify variables that distinguish them, we used discriminant function analyses (DFA). We performed multivariate analyses on correlation matrices of log10-transformed variables for the cranium and mandible separately, using Statistica software (StatSoft Inc. 2005).

Potential distribution over time. To investigate the possible long-term geographic isolation of *Cryptotis* from Guerrero, we modeled the climatic niche of *C. mayensis sensu stricto*. Based on the hypothesis of niche conservatism, we assume that the environmental requirements of the samples from Guerrero are similar to those of *C. mayensis s.s.*, which will allow us to predict its distribution and, therefore, understand the possible dynamics in distribution during the last glacial-interglacial cycle. Hence, we estimated the potential distribution of *C. mayensis s.s.* through time, using the

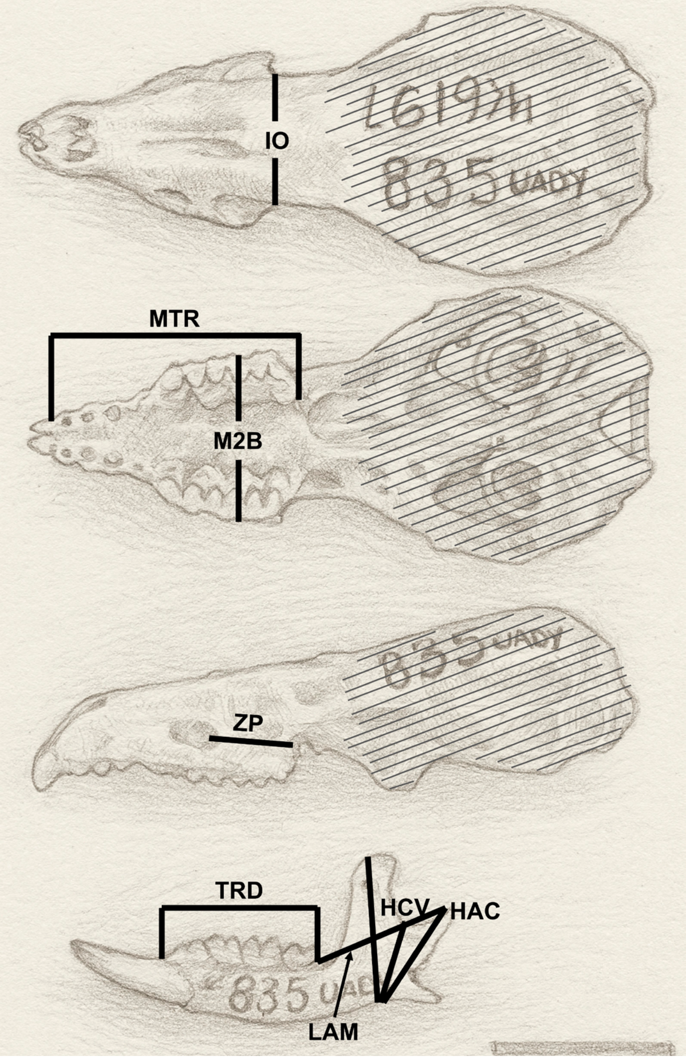

Figure 2. AI-generated image from scientific photographs of a *Cryptotis mayensis* specimen to illustrate the nine qualitative characters measured in the skull and mandible. The lines represent the region of the skull that is generally destroyed or severely damaged in specimens from the owl pellets collected in Guerrero. Scale bar: 5 mm.

Table 1. Cranial and mandibular measurements of three samples of small-eared shrews (Mammalia, *Cryptotis*) from the *Cryptotis nigrescens* group. Statistics are mean ± SD and range, and the number of samples examined by variable.

	***C. mayensis* s.s.**	**Guerrero**	***C. lacandonensis***
IO	4.51 ± 0.19	4.42 ± 0.19	4.75 ± 0.01
	4.88 - 4.22	4.77 - 4.14	4.76 - 4.74
	n = 20	n = 27	n = 2
ZP	2.33 ± 0.23	2.35 ± 0.14	2.53 ± 0.23
	2.67 – 1.68	2.60 – 2.05	2.69 – 2.36
	n = 23	n = 28	n = 2
MTR	4.90 ± 0.16	4.99 ± 0.14	5.28 ± 0.07
	5.17 – 4.57	5.30 – 4.45	5.33 – 5.23
	n = 23	n = 25	n = 2
M2B	5.11 ± 0.22	5.21 ± 0.14	5.21 ± 0.14
	5.63 - 4.49	5.50 – 5.02	5.50 – 5.02
	n = 23	n = 21	n = 2
HCP	5.19 ± 0.26	5.34 ± 0.23	5.43 ± 0.11
	5.54 - 4.7	5.83 – 5.18	5.50 – 5.35
	n = 22	n = 7	n = 2
HAC	3.73 ± 0.18	3.73 ± 0.15	3.61 ± 0.09
	4.07 – 3.4	3.94 – 3.53	3.67 – 3.54
	n = 22	n = 7	n = 2
HCV	2.82 ± 0.19	2.86 ± 0.14	2.75 ± 0.07
	3.13 – 2.3	3.03 – 2.59	2.80 – 2.70
	n = 22	n = 7	n = 2
LAM	4.77 ± 0.21	4.69 ± 0.29	5.00 ± 0.01
	5.08 - 4.24	4.97 – 5.54	5.00 – 4.99
	n = 22	n = 7	n = 2
TRD	5.37 ± 0.19	5.36 ± 0.27	5.73 ± 0.16
	5.68 – 5.02	5.54 - 4.9	5.84 – 5.62
	n = 22	n = 5	n = 2

present conditions, the Mid-Holocene, and the Last Glacial Maximum (LGM), as climatic extremes during the Quaternary. Ecological niche models (ENMs) and cross-time projections were optimized using the 'kuenm' package (Cobos *et al.* 2019) and the Maxent modeling algorithm (Phillips *et al.* 2017) in R software version 4.4.2 (R Core Team, 2025).

Our initial database was obtained from Guevara *et al*. (2024), which contains 118 unique localities and represents the most up-to-date and refined database available for *C. mayensis*. To reduce bias introduced by field sampling strategies, we spatially filtered the full set of species occurrence records using the spThin package (Aiello-Lammens *et al.* 2015). We retained only records that were at least 5 km apart, resulting in a final data set of 22 unique locations for calibrating and evaluating niche models. For further analysis, we spatially partitioned our data (i.e, checkerboard) into 70% for model calibration and 30% for model evaluation.

As environmental predictors, we initially selected 19 bioclimatic variables from the WorldClim v2.1 portal (Fick and Hijmans 2017). These variables describe various aspects of temperature and precipitation and were downloaded at a 30-second resolution for the period from 1970 to 2000. All bioclimatic layers were downloaded from the terra package using WorldClim version 2.1 climate data for the period 1970-2000 at a 30-second resolution. Then, we computed Pearson's correlation coefficient for each pairwise comparison to assess whether the variables are highly correlated and to decide which, if any, should be removed. Thus, we retained the variables BIO4 (temperature seasonality (standard deviation ×100)), BIO6 (minimum temperature of coldest month), BIO11 (mean temperature of coldest quarter), and BIO16 (precipitation of wettest quarter) because they showed lower correlations with the other variables in the calibration area ($r \leq 0.8$).

For model calibration, we delimited an area by combining ecoregions (Dinerstein *et al.* 2017) and biogeographic provinces (Morrone 2014) that encompass our unique locations, excluding areas unlikely to be accessible to the species given their dispersal abilities (Barve *et al.* 2011). To obtain a high representation of the environments available in the study area, we randomly sampled ~195,000 pixels within the delimited area (50% of the total area; Guevara *et al.* 2018). To identify model settings approximating optimal levels of complexity, we constructed niche models with a wide variety of combinations of feature classes (Linear; Linear and Quadratic; Linear, Quadratic, and Product; Linear, Quadratic, Product, and Threshold; Linear, Quadratic, Product, Threshold, and Hinge) and regularization multipliers (0.4 – 6 at 0.25 intervals). This process yielded 115 unique FC-RM combinations. To select the optimal settings for building a final Maxent model, we examined the omission rate (OR5) at a 5% training omission rate threshold and the area under the curve (AUC) for testing points. These two metrics help evaluate performance with respect to overfitting and discrimination, respectively.

We transferred the final model onto the present, Mid-Holocene, and LGM climatic conditions to estimate potential distributions over the last interglacial–glacial cycle across Central America (i.e., from Mexico to Panama). We used unconstrained extrapolation for model projection, disabling the default 'clamping' option in Maxent (Guevara *et al.* 2018). To consider the variability in past climatic reconstructions (Guevara *et al.* 2019), we used three different General Circulation Models (GCMs): the Community Climate System Model (CCSM4), the Model for Interdisciplinary Research on Climate (MIROC-ESM), and the Max-Planck-Institute für Meteorologie (MPI). We downloaded past bioclimatic layers from the WorldClim database at a resolution of 2.5 arc-min. To identify uncertainty due to model extrapolation, we created a Multivariate Environmental Similarity Surface (MESS) map, which helps detect areas where non-analog conditions occur.

Finally, to display the final maps for the present and the paleoclimatic scenarios, we classified the continuous model output into suitable and unsuitable conditions using the 10th percentile training presence threshold. This threshold excludes the lowest 10% of suitability scores from locations where the species is known to occur (Merow *et al.* 2013). We retained the suitability values in the original continuous format above this threshold to show the suitability gradient, and we also converted the original model output into a binary prediction of suitable-unsuitable areas. Using binary maps (0 = unsuitable; 1 = suitable), we summed the present and past potential distribution maps (for each of the three GCMs) to identify regions that have remained climatically suitable for *C. mayensis*.

Results

Considering the fragmentary origin of the owl pellet remains from Guerrero and the limitations this entails, they are very similar to *Cryptotis mayensis sensu stricto*. The zygomatic plate is quite broad (ZP = 2.35 ± 0.14 mm); the anterior border of the zygomatic plate runs from the parastyle-mesostyle valley to the mesostyle of M1, and the posterior border runs from the metastyle of M2 to the middle of M3. The mandible is moderately long (LAM = 4.69 ± 0.29 mm), and the coronoid process of the mandible is high (HCP = 5.34 ± 0.23 mm); the anterior border of the mandible joins the horizontal ramus at approximately a right angle.

Principal component analysis. For the analysis of the skulls, the principal components 1 and 2 explained 78.6% of the variation in the data (PC 1 = 60.6% and PC 2 = 18.0%) and were primarily correlated with the length of molariform toothrow (MTR) and the breadth of zygomatic plate (ZP), respectively. In the plot of 1st PCs from the PCA, the specimens of Lacandona shrew tended to plot among the largest in the sample (Figure 3a). Regarding the analysis of the dentary, the principal components 1 and 2 explained 70.6% of the variation in the data (PC 1 = 55.6% and PC 2 = 15.0%) and were primarily correlated with the height of articular condyle (HAC) and distance from the upper border of the articular condyle to the posterior edge of the m3 (LAM), respectively. A plot of the 1st PCs from the PCA highlights again the difference in size of *C. lacandonensis* with respect to *C. mayensis sensu stricto* and the samples from Guerrero, which tend to show a very similar pattern of variation in size (Figure 3). In general, the PCA analyses indicate that the specimens of *C. mayensis sensu stricto* and *Cryptotis* from Guerrero exhibit a similar pattern of morphometric variation and differ from *C. lacandonensis*.

Discriminant function analysis. For the analysis of the crania, the 1st function accounts for over 80.7% of the explained variance (Table 2), which is weighted most heavily by the length of molariform toothrow (MTR), contrasted with the interorbital breadth (IO). A plot of the two canonical axes failed to show a clear separation of the samples in multivariate space. The DFA based on the four cranial variables did not efficiently discriminate the Guerrero specimens from the other species (Wilks' Lambda = 0.652; F8,66 = 1.9626; P < 0.0651). In addition, the DFA of the four cranial variables produced moderate to null correct classification rates of 75%, 53%, and 0% for *C. mayensis sensu stricto* (n = 20), *Cryptotis* from Guerrero (n = 17), and *C. lacandonensis* (n = 2), respectively, demonstrating the high morphometric similarity between the samples. In general, the length of molariform toothrow (MTR) is the measure that most helps distinguish samples, but only between the Lacandona shrew from the other two groups.

Table 2. Standardized coefficients of canonical variables based on four and five log-transformed cranial and mandibular variables, respectively, of three samples of small-eared shrews (Mammalia, *Cryptotis*) from the *Cryptotis nigrescens* group.

	Cranial			**Mandibular**	
	Root 1	**Root 2**		**Root 1**	**Root 2**
IO	-0.324328	-1.03949	**HCP**	0.527026	-0.675966
PZ	-0.368533	-0.43909	**HAC**	0.531030	0.912683
MTR	0.959846	0.05730	**HCV**	0.559793	-0.500879
M2B	0.530850	0.51862	**LAM**	-0.776315	0.529173
-	-	-	**TRD**	-0.948245	-0.673339
Eigenval	0.399078	0.09528		1.000187	0.180837
Explained variance (%)	80.7%	19.2%		84.7%	15.3%

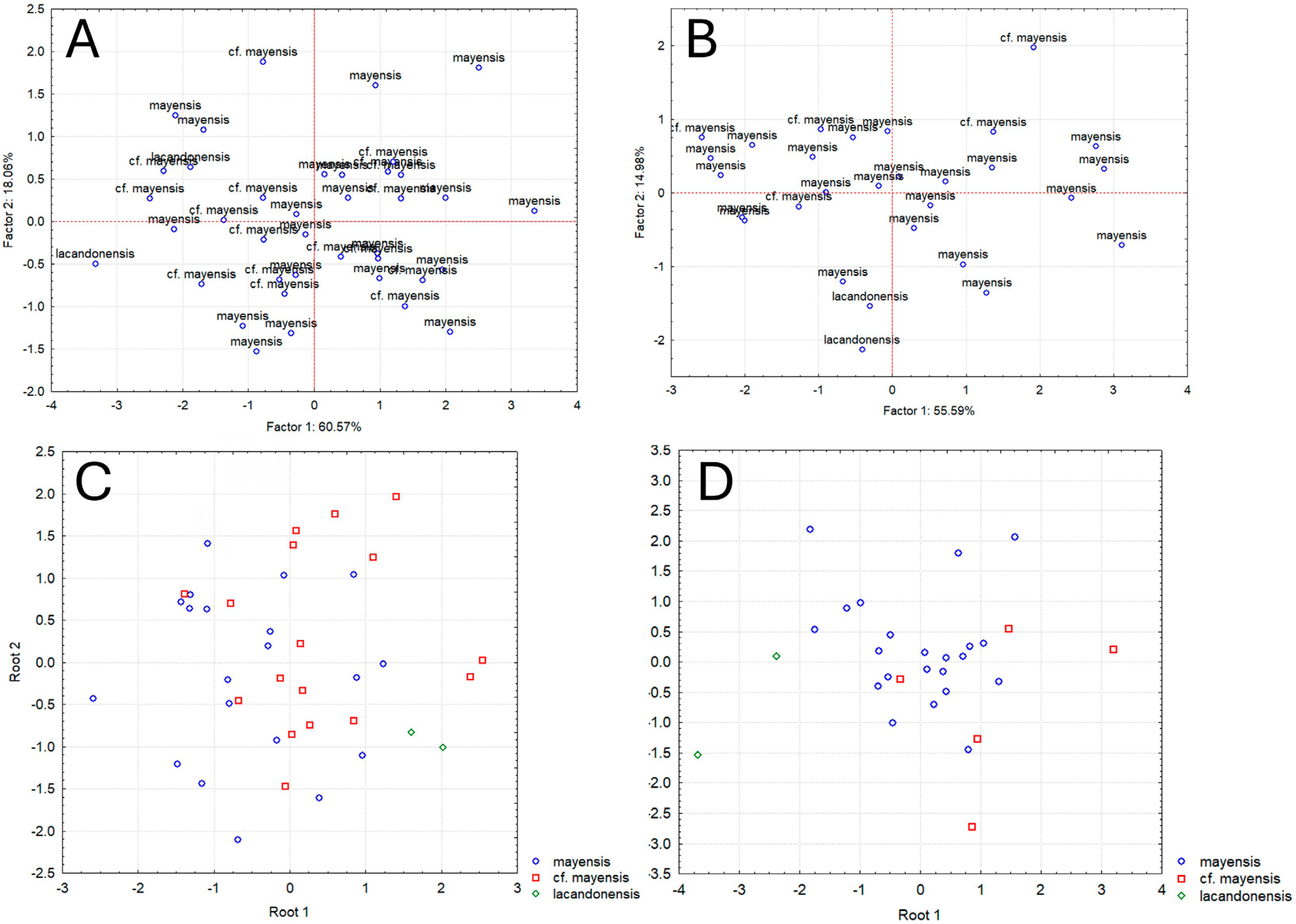

Figure 3. Plot of scores on first two axes from principal components (PCA) and discriminant function (DFA) analyses of the cranium and mandibles of specimens from *Cryptotis mayensis* s.s., *C. lacandonensis,* and samples from Guerrero, México. A, PCA for cranium; B, PCA for mandibles; C, DFA for cranium; D, DFA for mandibles.

On the other hand, for the analysis of the mandibles, the 1st function accounts for over 85% of the explained variance (Table 2), which is weighted most heavily by the lower toothrow length (TRD), contrasted with the height of the articular condyle (HAC). A plot of the two canonical axes shows that the specimens of the Lacandona shrew are slightly separated on the first axis due to their larger size. In contrast, the second axis does not allow a clear separation between the three samples (Figure 3d). The DFA based on the five variables showed better performance than the one based only on the skull for distinguishing the a priori groups (Wilks' Lambda = 0.423; F10,44 = 2.3621, P < 0.0246). In addition, the DFA produced correct classification rates of 100%, 40%, and 50% for *C. mayensis sensu stricto* (n = 22), *Cryptotis* from Guerrero (n = 5), and *C. lacandonensis* (n = 2), respectively, suggesting that this structure may have a greater contribution to distinguishing between taxa. In general, lower tooth length (TRD) in isolation is the measure that most helps distinguish samples, but again, only between the Lacandona shrew and the other two taxa (*C. lacandonensis*: 5.73 ± 0.16 mm*; C. mayensis s.s.*: 5.37 ± 0.19 mm; Guerrero: 5.36 ± 0.27 mm).

In sum, considering the small sample size of *C. lacandonensis*, multivariate analyses of the cranium and dentary indicate high similarity in size across the three samples analyzed, especially between *C. mayensis sensu stricto* and *Cryptotis* from Guerrero. *Cryptotis lacandonensis* is distinguishable from the other two by its larger size, which can be more easily detected by measuring both the upper and lower tooth rows (Table 1).

Biogeographic analyses. Of the 115 niche models generated for *C. mayensis sensu stricto*, four stood out for their better performance based on significance, omission rate, and AICc. Although these four models did not show significant differences, we present the output of the model that performed slightly better. This model was implemented using the following feature classes and regularization multiplier: Linear and Quadratic, with a value of 1.2 (AUC: 0.829; mean AUC ratio: 1.8392; omission rate at 5%: <0%). Of the four variables used to build the final model, precipitation of the wettest quarter (BIO 16) was the most important, indicating a steep decline in climatic suitability when precipitation exceeds 400 mm. Accordingly, the model suggests a current potential distribution that is closely linked to the distribution of warm-humid and warm-dry forests of the Yucatan Peninsula and the Pacific slope, including the area surrounding the Cueva del Zopilote, Guerrero, where the owl pellets were collected. Between the estimated suitable conditions for *C. mayensis s.s.* on the Yucatan Peninsula and those towards the Pacific slope, there are more than 500 km of areas with unsuitable habitat for this shrew, where more humid and temperate climates predominate across several mountain ranges (Figure 4).

When the model was transferred to Mid-Holocene and LGM conditions, the predictions showed an apparent reduction in suitable areas across the three GCMs, with the reduction even more pronounced during the LGM (Figure 4). During the Mid-Holocene, approximately 6,000 years ago, suitable conditions for *C. mayensis* appear to have persisted across much of the Yucatan Peninsula; however, this is less extensive if we consider only the continental crust at the surface or currently exposed. On the Pacific slope, conditions may have occurred in a more restricted area and farther from the area surrounding Cueva del Zopilote. During the LGM, around 20,000 years ago, suitable conditions for *C. mayensis* declined considerably on the Yucatán Peninsula and the Pacific coast, although less drastically in the latter region. As in the Mid-Holocene, favorable climatic conditions for *Cryptotis mayensis* may have been restricted to a smaller area, farther from Cueva del Zopilote.

The MESS analysis indicates that the climatic conditions of the various paleoclimatic scenarios closely resemble those of the calibration area, particularly in the Yucatan Peninsula and along the Pacific slope. This similarity in climatic conditions is consistent across the three analyzed Global Climate Models (GCMs), with positive values observed in these regions. In contrast, areas indicating non-analogous climatic conditions are primarily located in northern Mexico. Specific scenarios, such as the MIROC model during the mid-Holocene, also reveal regions with non-analogous climates that seem to correspond with mountainous areas in Chiapas and central Mexico. However, these areas of high uncertainty do not impact the predicted distribution of *C. mayensis*. Overall, the MESS analysis reinforces our model projections, showing that climatic conditions in the Pacific region remained within the range used to train the model.

In sum, none of the three-time-slice analyses support the hypothesis of a corridor of suitable conditions for the connectivity of shrew populations with requirements similar to those of *C. mayensis* during the last glacial-interglacial cycle or in analogous climatic phases.

Discussion

Owl pellets and an old biogeographical dilemma. We are still in the discovery stage on the diversity and distribution of Neotropical shrews (Woodman 2019; Guevara *et al.* 2024). For example, the environmental requirements and geographical distribution of most species remain poorly delimited and contain much information gaps due to the difficulty of collecting specimens in the field and the lack of more taxonomists specializing in this group. Pellet analyses have been a beneficial source for complementing these knowledge gaps, as they can provide records of rare or difficult-to-collect species (Avenant 2005; Biedma *et al.* 2019). However, due to the fragmentary nature of the specimens and the difficulty in unequivocally assigning the geographical origin of individuals consumed by raptors, the taxonomic identification of samples can be a significant challenge.

The claim that pellets recovered in Cueva del Zopilote, Guerrero, come from the Barn owl, *Tyto furcata*, was based on the identification by the renowned ornithologist Allan R. Phillips, who conducted numerous expeditions in Mexico (López-Forment and Urbano 1977). This bird of prey is very common in both natural and altered ecosystems, feeding on small mammals, including shrews (Biedma *et al.* 2019). The area surrounding the Cueva del Zopilote was described by the original collector as stony and arid, with plant species of the genera *Bursera*, *Ceiba*, *Cephalocereus, Erythrina*, *Ficus*, and *Ipomoea*. In addition to this species of shrews, records of common mammal species on the Pacific slope were also found, including *Heteromys irroratus*, *Osgoodomys banderanus*, *Tlacuatzin canescens*, *Megasorex gigas*, *Spilogale pygmaea*, and several bat species (Ramírez-Pulido and Sánchez-Hernández 1972; López-Forment and Urbano 1977). Interestingly, the record of two skulls of the climbing rat, *Ototylomys phyllotis*, is noteworthy, as its species' distribution ranges from the Yucatan Peninsula to Central America (Lawlor 1982; Espinosa-Martínez *et al.* 2017). The fact that at least these two terrestrial mammal species exhibit the same remarkable disjunct geographic distribution pattern further calls for clarifying the taxonomic status of the Guerrero individuals with additional sources of evidence and analytical methods.

New answers and new questions. The taxonomic uncertainty about the identity of the specimens from Guerrero has been addressed on several occasions using morphological comparisons with both current and Pleistocene samples of *Cryptotis mayensis s.s.* from the Yucatan Peninsula (Choate 1970; Woodman and Timm 1993; Woodman 1995). These analyses did not reveal significant and sufficient differences to distinguish a different species, so the Guerrero samples continue to be referred to as *C. mayensis* (Monroy-Gamboa 2021). Our new analysis, which includes a larger number of samples than previous studies, including *C. lacandonensis*, the sister species of *C. mayensis*, also did not allow a clear qualitative and quantitative distinction. However, we found that the Guerrero samples are morphologically more like *C. mayensis s.s.* than *C. lacandonensis*, a species found in wetter conditions at the base of the Yucatán Peninsula (Guevara *et al.* 2014). We cannot rule out that, if complete skulls and skeletons become available in the future, it may be possible to find differences that allow for discrimination, as has been the case when analyzing other structures such as the humeri or claws in shrews of this genus (Woodman and Morgan 2005; Woodman and Gaffney 2014). Future field studies, including proper methods for sampling shrews such as pitfall traps (Lorenzo *et al.* 2019), and increased sampling in the area

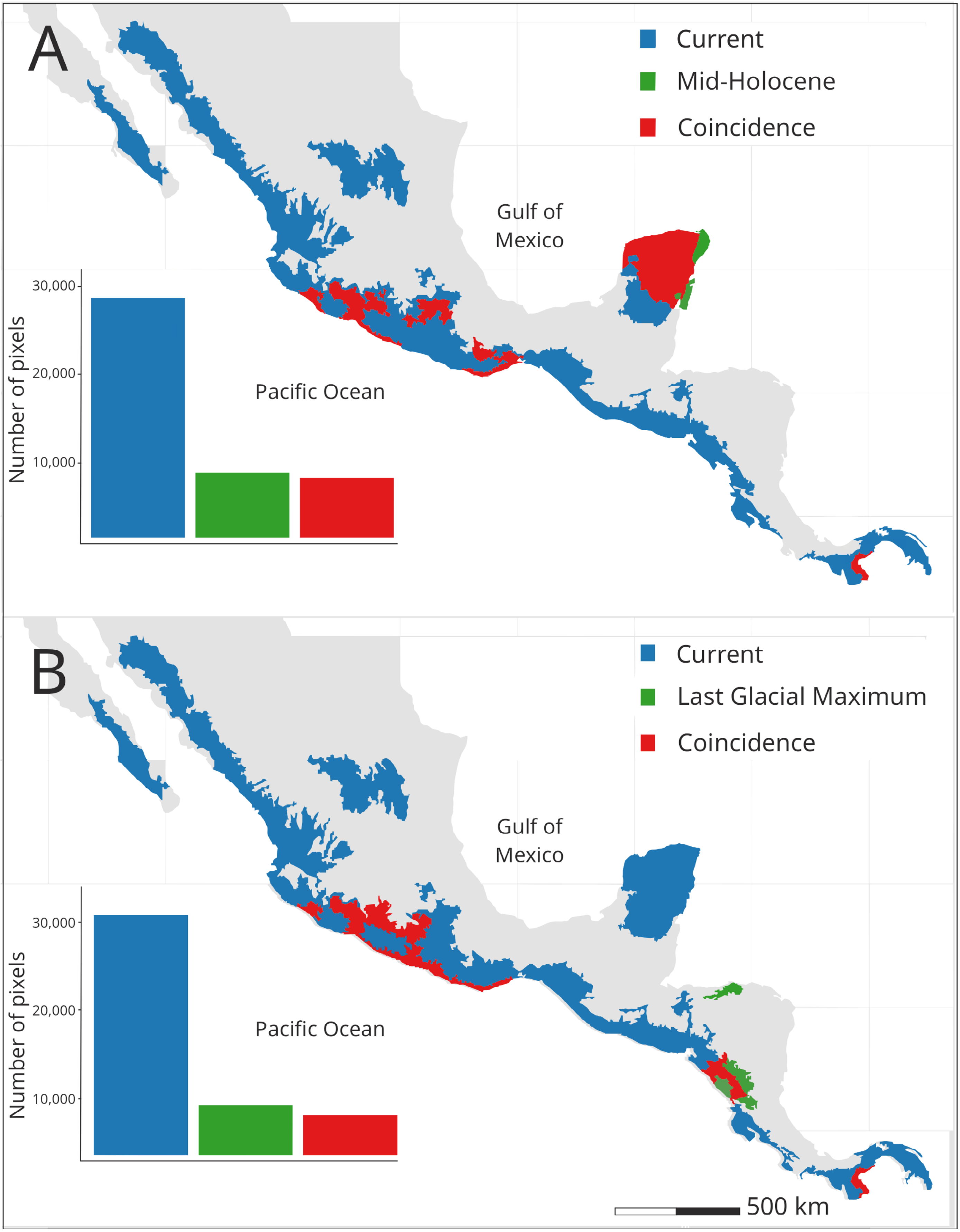

Figure 4. Potential distribution of the Mayan shrew, *Cryptotis mayensis*, estimated for the present, the Mid-Holocene, and the Last Glacial Maximum using ecological niche models. The estimation of Mid-Holocene (A), and Last Glacial Maximum (B) is based on the consensus of three general circulation models, CCSM4, MIROC-ESM, and MPI-ESM-P. The colors on the map indicate the three temporal scenarios considered: Present (blue), mid-Holocene or Last Glacial Maximum (green), and overlap zones between them (red). The bar chart shows the number of pixels estimated to contain suitable conditions for *C. mayensis* in each period.

near Cueva del Zopilote Cave, could be highly beneficial to searching for complete specimens of this shrew; however, as we mentioned earlier, the current public safety situation in this country could complicate this urgent action.

In any case, morphological differences are not the only source of evidence for recognizing differentiated lineages at a specific level in mammals (Baker and Bradley 2006; Bonilla-Sánchez *et al.* 2024). In recent years, improvements in sequencing technologies have made it possible to obtain genomic-scale data from old museum specimens by extracting DNA, including bones (Guimaraes *et al.* 2016). Therefore, the next step is to conduct a destructive analysis of the samples to extract DNA and analyze it in a phylogenetic context. Meanwhile, other methodological approaches can help solve the current puzzle. In this case, it is well recognized that correlative ecological niche modeling can help identify possible geographic barriers and isolated populations, thereby leading to the discovery of heretofore unknown populations or species (Raxworthy *et al.* 2003; Peterson *et al.* 2011).

With paleodistribution estimates, niche models allow inference of the possible long-term isolation in which populations have been maintained, assisting in decision-making on taxonomic status (Guevara *et al.* 2019). In the case of Neotropics, the Late Quaternary is a crucial period for understanding the current diversity of shrews (Barnosky 2005). The constant climatic fluctuations that have occurred over the last thousands of years have altered geographic distributions, causing expansion-contraction and fragmentation-connectivity events across populations (Choate 1970; Woodman and Timm 1999; Woodman 2005; Guevara and Sánchez-Cordero 2018). Some shrew populations may have remained isolated due to the complex topography of the region; consequently, long-term isolation could have promoted lineage divergence (Guevara and Sánchez-Cordero 2018).

Diversification within the *Cryptotis nigrescens* group may have been accentuated by Pleistocene climatic changes (Ceballos *et al.* 2010). Based on the hypotheses derived from the paleodistributions, we suggest that differentiation may have begun before or at the onset of the Quaternary. Still, glacial-interglacial cycles could have helped reinforce differentiation among taxa within the *C. nigrescens* group, which needs to be tested as environmental reconstructions in the region progress further (León-Carreño *et al.* 2025).

In summary, based on the morphological and biogeographic analyses presented here, along with previously published morphological studies (Choate 1970; Woodman 1995), it is possible that the Guerrero population is an independent lineage; however, genetic evidence to support this hypothesis is essential. The absence of records for any species from the *Cryptotis nigrescens* group on the Pacific slope, combined with a relatively high number of records for shrews from other groups or genera (Guevara *et al.* 2015; 2024), suggests that this lineage may have a very restricted distribution or even be extinct.

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Declaration of Artificial Intelligence use

ChatGPT Plus was used to generate Figure 2, with a scientific photograph of a museum specimen as input. Grammarly Pro, an AI writing assistant, was used to review the spelling and structure of English.

Author contributions

Lazaro Guevara: Conceptualization (lead); Data curation (supporting); Formal analysis (lead); Writing – review and editing (lead). Reinhard E. Matadamas: Data curation (lead); Formal analysis (lead); Writing – review and editing (supporting). Stephanye Mata-González: Formal analysis (lead); Writing – review and editing (supporting). Paola Zeferino: Conceptualization (supporting); Data curation (supporting); Joaquín Arroyo-Cabrales: Conceptualization (supporting); Writing – review and editing (supporting).

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