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Which global circulation model works best for my region? Concordance with genetic data for a Neotropical shrew

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Copious questions in global change biology require estimates of climatic suitability for species in the past or future, often via transfers of ecological niche models (ENMs) using outputs from global circulation models (GCMs). However, available GCMs differ markedly, affecting hindcasts and forecasts of species potential distributions. We propose using demographic inferences based on genetic data (indicative of either population-level continuous occupation or postglacial colonization) to test which GCM leads to a better match with reality for ENM hindcasting. We implement an intuitive worked example for four isolated focal populations of a montane shrew *Cryptotis mexicanus* in central-eastern Mexico, by comparing suitability maps at the Last Glacial Maximum (LGM) and today. We built an optimized Maxent niche model and transferred it to the LGM based on four GCMs (CCSM4, IPSL-CM5A-LR, MIROC-ESM, MPI-ESM-P), followed by phylogeographic analyses to test hypotheses of changes in distribution according to each GCM. CCSM4 and IPSL-CM5A-LR indicated an LGM suitability area for *C. mexicanus* mainly in the southern portion of its range, suggesting that extant focal populations to the north result from postglacial colonization. In contrast, MIROC-ESM and MPI-ESM-P indicated LGM suitability for three or all the populations, respectively. Genetic results for the four focal populations showed high genetic diversity and signals of constant population size. Because only the hindcast based on MPI-ESM-P generated the prediction of stable occupation for all four sites, we interpret that its estimate (a cold and wet LGM climate) best approximates reality for this system. Future studies can apply this framework using more extensive genetic or genomic data and finer temporal resolutions, also exploring differences in the assumptions and methodologies underlying the various GCMs.

Keywords: cloud forest, glaciations, paleodistribution, phylogeography, Quaternary

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Introduction

Understanding species distributions through time is one of the major areas of research for biodiversity and global change biology. These include both forecasts of future distributions and reconstructions of past ones. As a complement to consideration of land cover, dispersal barriers, and traits related to dispersal ability and population growth, researchers often employ a suite of techniques usually termed ecological niche modeling (ENM) or species distribution modeling to characterize a species' environmental associations and hence predict suitability across the study region (Soley-Guardia et al. 2019, Franklin 2023). Typically built with recent occurrence records and climatic data, such models can be applied to climatic scenarios in the past or future to estimate suitability – the species' potential distribution – at those times (Guevara et al. 2019, Guevara 2020).

Transfers of ENMs across time rely on data regarding climatic scenarios estimated by global circulation models (GCMs), which are mathematical representations of the physical processes regulating climate (Braconnot et al. 2012). For example, ENMs are often applied to GCM estimates for the Last Glacial Maximum (LGM), the most recent glacial episode of the Pleistocene, which is known to have significantly influenced the divergence, demography, and genetic variability of present-day populations and species (Clark et al. 2009, Wyatt et al. 2021). Despite the particularities of each glaciation that occurred during the Quaternary, the LGM can also serve as a proxy for the major distributional shifts expected during global cooling events (Paillard 2015). Considering the inherent uncertainties in estimates of past – and future – climates, various GCMs have been developed by different research groups, each using a particular set of initial states, equations and algorithms to simulate the climate. Given these differences, GCMs frequently exhibit notable variations in estimated climates (e.g. regarding cooling intensity and precipitation regimes) across the planet (Knutti 2008, Varela et al. 2015). Transferring ENMs onto the output of these different GCMs greatly impacts the reconstruction of cross-time potential distributions (Peterson et al. 2018, Guevara 2024). For example, when two GCMs vary markedly regarding precipitation and temperature, they can yield distinct divergent estimates of the species' past potential ranges (Guevara et al. 2019).

Despite high variation in estimated potential distributions based on different GCMs – and the great importance of ENM transfers to global change biology – little guidance exists for selecting GCMs (Varela et al. 2015, Guevara et al. 2018, Hausfather et al. 2022). Given this lack of established protocols, researchers employing niche models to reconstruct paleodistributions usually choose one a priori or make an ensemble of predictions based on using two or more (Collevatti et al. 2013, Gassert et al. 2013, Guevara et al. 2019). The difficulty in selecting GCMs for estimating hypothesized paleodistributions is exacerbated by the lack of knowledge about past climates in many regions of the world, particularly in tropical and subtropical areas. Indeed, palaeoecological data (primarily fossilized pollen samples from lake sediments) in these regions remain sparse and sometimes contradictory regarding whether past glacial times were characterized by intense cold accompanied by drought or abundant precipitation (Bush and Silman 2004, Ramírez-Barahona and Eguiarte 2013).

Because intraspecific patterns of genetic diversity reflect the demographic history of populations, they represent a potential data domain to inform GCM selection. For instance, high levels of intra-specific genetic diversity (e.g. high numbers of mitochondrial haplotypes or high diversity in microsatellite loci) can signal high past population sizes, which could be associated with climate stability over time (Carnaval et al. 2009). In contrast, low diversity is often associated with decreases in population size or genetic bottlenecks (Lande 1988, Beheregaray et al. 2003, Li and Durbin 2011). Examples include Pleistocene refugia, where many different species endured the glacial periods of the Quaternary and each maintained high population sizes if the suitable area was large enough, typically preserving high levels of genetic diversity in those populations. Additionally, post-glacial expansion out of refugia could lead to low genetic diversity in current populations farther away from the area inhabited during the glaciation (Petit et al. 2003, Galbreath 2011). Coalescent methods provide a complementary approach to trace ancestral lineages and estimate likely ancestral origins (Excoffier et al. 2009), and thus infer historical population structure and range expansion, which can serve as benchmarks for improving GCM selection. Indeed, the combination of ENM and phylogeography has contributed to a greater understanding of the historical demography of species, their patterns of genetic variation, and the abiotic conditions where their populations diversified (Alvarado-Serrano and Knowles 2014, Luna-Aranguré and Vázquez-Domínguez 2020, 2021). Abiotic variables are essential in phylogeography, given their influence on processes such as isolation, divergence, and speciation, and are also the backbone of ecological niche modeling (Kozak et al. 2008). We propose further development of this longstanding integration of ENM and phylogeography, harnessing genetic data to promote a holistic consideration of different data streams and analyses (Franklin 2023).

Here, we aim to help fill the void regarding GCM selection by proposing a framework for analyzing the genetic signals in a modern species to glimpse back into the past, with the goal of identifying which GCMs provide the most reasonable reconstructions of past conditions in a specific geographical region. By applying a niche model to present conditions as well as reconstructions of climate at the LGM, it is possible to hypothesize changes in the species' distribution under various respective GCMs. Specifically, by comparing maps of present suitable conditions with those for past climates (under each of the GCMs), researchers can make explicit predictions regarding distributional changes and demographic history for different populations across the species' current range (Alvarado-Serrano and Knowles 2014, Worth et al. 2014, Cabanne et al. 2016, Luna-Aranguré and

Vázquez-Domínguez 2020, 2021). These predictions will depend on the GCM used (Guevara et al. 2018, Guevara 2024). Then, phylogeographic analyses of genetic data can be used to test which paleodistributional hypothesis led to demographic predictions that most closely align with the genetic evidence, consequently supporting which GCM would be most realistic for a given region.

As an implementation of this framework, we assess signals of genetic diversity and demographic changes in response to climatic shifts during the last glacial–interglacial transition in the Mexican small-eared shrew *Cryptotis mexicanu* (Soricidae), a small mammal highly associated with cloud forest in the northernmost Neotropics (Guevara et al. 2018). Cloud forest species are an excellent system to illustrate this framework since even minimal changes in temperature and precipitation can affect their geographic distribution. We start with an optimized niche model, estimating the species' potential distribution in the present and during the LGM according to four GCMs. Then, based on the distributional changes from each of the hypothesized paleodistributions to the present, we establish two general predictions regarding the expected genetic/demographic signals across different portions of the species' current distribution according to each past climatic scenario: 1) areas of continuous suitability over time and hence predicted constant population size and high genetic diversity; 2) areas of postglacial colonization, where a reduction in past population size and current genetic variability is predicted. Finally, we test these predictions based on phylogeographic analyses with data from the mitochondrial cytochrome b gene (Fig. 1). Whereas the potential exists for generating massive amounts of genomic data and conducting advanced computational techniques for analyzing them, this simple worked analysis serves as an intuitive example for understanding the fundamental logic and workflow of the proposed framework.

Material and methods

Optimized niche model

We used georeferenced records of the Mexican small-eared shrew, *C. mexicanus*, confirmed through morphological analysis and used in previous studies (Guevara et al. 2018, Pinilla-Buitrago 2023, Vilchis-Conde et al. 2023). These localities constitute a variety of sites representative of the range of environmental conditions that the species inhabits (Guevara et al. 2018, Pinilla-Buitrago 2023). To reduce the effects of spatial sampling bias, which can negatively impact model performance, we performed a spatial thinning of 5 km around records using the 'spThin' ver. 0.2.0 package (Aiello-Lammens et al. 2015) in R ver. 4.3.2 (www.r-project.org). The thinning procedure reduced the original database from 64 to 41 unique localities (Supporting information). We generated a 0.5 decimal degree buffer around the occurrence localities after thinning to delineate the study area and build niche models. This study area includes environments that likely have been accessible to this cloud forest species given its dispersal limitations and the configuration of barriers (Anderson and Raza 2010, Barve et al. 2011).

As predictors, we used four bioclimatic variables based on 30-arcsec monthly precipitation and temperature data from CHELSA ver. 2.1 (Karger et al. 2017). Based on previous studies on the importance of various bioclimatic variables on the distribution of *C. mexicanus*, these four variables capture extreme climatic conditions and are the most ecologically informative (Guevara et al. 2018, Pinilla-Buitrago 2023): the maximum temperature of the warmest month (BIO05), the minimum temperature of the coldest month (BIO06), precipitation of wettest month (BIO13), and precipitation of driest month (BIO14). This set of four variables was used for model calibration based on current conditions and then transferred to past climatic reconstructions.

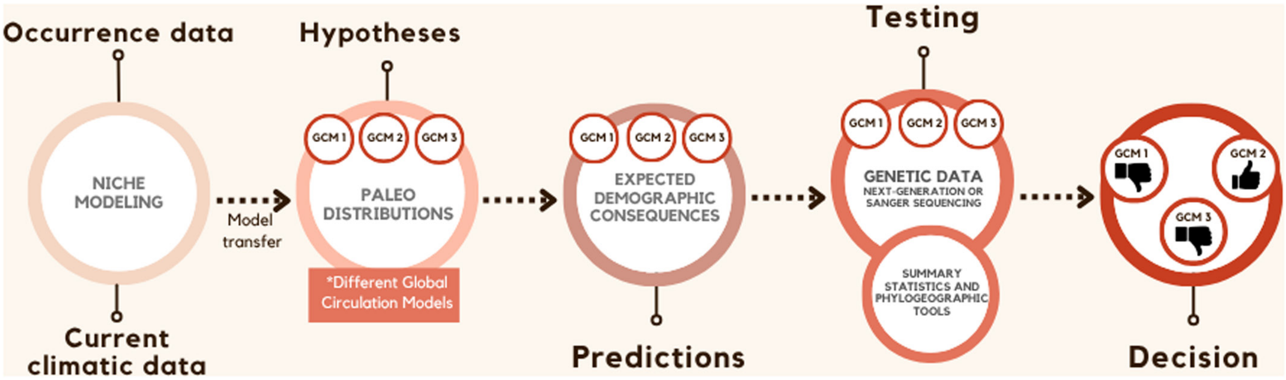

Figure 1. Illustration of the proposed framework for deciding which general circulation model (GCM) is most realistic in the past in a given study region. The workflow uses niche modeling and then includes the generation of distributional hypotheses for a species in the present and in the past based on different general circulation models (GCMs). Next, it makes demographic predictions based on each hypothesis and performs phylogeographical testing to decide which GCM is most realistic in the past (for the given study system). In this hypothetical example, the genetic evidence supports the paleodistributional hypothesis generated with the GCM 2. GCM 1 and GCM 3 would be considered less realistic for this study area.

We used the maximum entropy method in Maxent ver. 3.4.3 to model a species' climatic associations and estimate its potential distribution (Phillips et al. 2017). To ensure a complete representation of the species' occupied environments, we included in the background region all pixels within the delimited study area. To assess a variety of model settings and later select those approximating optimal levels of complexity, we built models with different combinations of feature classes (Linear; Linear and Quadratic; Hinge; Linear, Quadratic, and Hinge; Linear, Quadratic, Hinge and Product) and regularization multipliers (0.5–5.0 with 0.5 step intervals) using 'ENMeval' ver. 2.0.4 (Kass et al. 2021), applying a spatial block approach to cross-validation to yield model performance statistics. These combinations of feature classes and regularization multipliers yielded 50 candidate models.

We used sequential criteria to select the optimal settings for building the final model. First, we retained the models with the lowest delta AICc (within four units). Then, out of those models retained we inspected the number of parameters in the model and two validation statistics based on threshold-dependent (omission rate, specifically OR10, using a threshold set by the 10% training omission rate) and threshold-independent (AUC for testing points, or AUCval) measures that helped to gauge performance in terms of overfitting and discrimination, respectively (Gerstner et al. 2018). We examined these and selected as optimal the model with the fewest parameters (non-zero weights to given features), then the lowest overfitting (low omission rate), and finally the highest discriminatory capacity (high AUC) (Supporting information).

Current and past potential distribution hypotheses

In addition to visualizing the optimal niche model in the present, we also transferred it to the Last Glacial Maximum based on four alternative GCMs: the Community Climate System Model (CCSM4; Collins et al. 2006), Institut Pierre-Simon Laplace (IPSL-CM5A-LR; Dufresne et al. 2013); the Model for Interdisciplinary Research on Climate (MIROC-ESM; Ohgaito et al. 2020), and the Max-Planck-Institute für Meteorologie model (MPI-ESM-P; Giorgetta et al. 2013). We projected the model to the same extent as the calibration area. To identify any major differences for each bioclimatic variable among the conditions estimated by the four GCMs, we extracted past climatic values for each pixel within the study area and used descriptive statistics to examine differences among them (Supporting information).

To extrapolate into non-analog conditions, we inspected the upper and lower tails of individual response curves of each variable and the truncation points. This allowed us to decide whether to use clamping (default in Maxent) or unconstrained extrapolation (Guevara et al. 2018, Kass et al. 2021). To identify uncertainty due to model extrapolation, we obtained areas where non-analog conditions occurred compared with the present, using the multivariate environmental similarity surface (MESS; Elith et al. 2010, Supporting information).

To map the suitable areas across the study area, we divided the continuous predictions into binary ones (suitable versus unsuitable) using two thresholding rules for comparison of results: the minimum training presence threshold of Maxent (MTP; or lowest presence threshold sensu Pearson et al. 2007), and the 10th percentile training presence (10P). Suitability values above the thresholds were preserved in the original continuous format (logistic transformation). For comparison, we also included a map based on the ensemble of the four GCMs. The ensemble was made by summing the binary maps with minimum training presence thresholds and retaining the areas where at least two of the four predictions coincided. We quantify spatial overlap between resulting maps using a pairwise Schoener's *D* metric in the 'terra' package (Hijmans 2025). This metric varies from 0 (no overlap) to 1 (full overlap) (Warren et al. 2008).

Genetic predictions and testing

As focal populations for analysis, we focused on four geographically isolated sites ('sky islands') adjacent to the Sierra Madre Oriental. This allowed us to test discrete predictions of population-level genetic/demographic signals as hypothesized via the suitability maps obtained using each respective GCM and a map of their ensembling. The four focal populations correspond to: 1) El Cielo, 2) Sierra de Otontepec, 3) Los Mármoles, and 4) Sierra Norte de Puebla (Fig. 2). The demographic predictions for each of the four populations were established by overlaying the current binary potential distribution map and each of the respective reconstructed potential paleodistributions. When a given current focal population also had suitable conditions at the LGM, we inferred that the site would have been continuously occupied (stable population over time); in contrast, when the LGM retrojection for a population did not indicate suitable conditions, we conjectured that the current population would be the result of post-glacial colonization. For genetic testing, we used cytochrome b sequences. Some of these were previously obtained: for El Cielo (5 sequences), Sierra de Otontepec (6), and Sierra Norte de Puebla (7). Additionally, we generated 13 sequences for Los Mármoles (Supporting information). DNA extraction, amplification, and sequencing details follow Guevara and Cervantes (2014) and Mayen-Zaragoza et al. (2019).

We assessed population genetics via several approaches. We calculated the number of haplotypes (H), as well as haplotype (h) and nucleotide ($\boldsymbol{\sigma}$) diversity, to describe intraspecific genetic diversity for each of the four focal populations. We also estimated Fu's Fs (Fu 1997) and Tajima's *D* (Tajima 1989) indices in DnaSP ver. 6 (Rozas et al. 2017) to evaluate whether data departed from a neutral model of evolution due to factors such as a population bottleneck or sudden expansion (Cabanne et al. 2016, Luna-Aranguré and Vázquez-Domínguez 2020, Rico et al. 2023). We assessed genealogical relationships among haplotypes by constructing a median-joining (MJ) network in 'POPart' ver. 1.7 (Leigh and Bryant 2015). Additionally, we implemented a Bayesian phylogeographic and ecological clustering analysis (BPEC) with 'BPEC' ver. 1.3.1 (Manolopoulou et al. 2020) to obtain

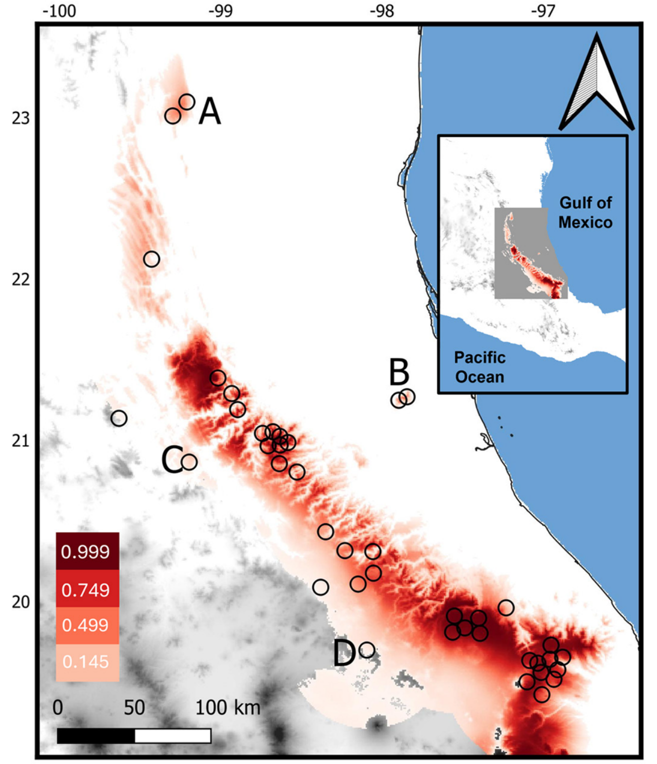

Figure 2. Present potential distribution of the Mexican small-eared shrew, *Cryptotis mexicanus*, in central-eastern México. The map shows increasingly warmer colors of pink and red for higher suitability above the minimum training presence threshold of an optimized ecological niche model, with areas of lower prediction transparent (showing topography in white-to-gray). The four 'sky islands' for the focal populations analyzed are: (A) El Cielo, (B) Sierra de Otontepec, (C) Los Mármoles, and (D) Sierra Norte de Puebla. Hollow circles denote documented localities for the species.

measures of uncertainties for haplotype relationships and identify likely ancestral haplotypes to help infer the histories of the current samples. Following preliminary short runs, the final BPEC analysis was done using four maximum migrations, the minimum parsimony relaxation value (zero), and two runs with 20 million steps in MCMC, with 10 000 posterior samples saved.

Results

Climate during the LGM

The four GCMs displayed notable differences in the estimated climate during the LGM in the study region (Supporting information). CCSM4 and IPSL-CM5A-LR suggested that during the cold months, the minimum temperature was lower than that calculated by MIROC-ESM and MPI-ESM-P, with differences as great as 10°C (e.g. between IPSL-CM5A-LR and MPI-ESM-P). In contrast, the four GCMs led to more similar predictions for the warmest month, except for MIROC-ESM, which did not show as much drop in temperature. IPSL-CM5A-LR indicated notably high precipitation during the rainy season, relative to the other three reconstructions. In contrast, MPI-ESM-P was the only one that did not suggest extreme aridity during dry months.

Optimal niche model and potential distributions across time

We selected one of the 50 candidate models as optimal (Linear and Quadratic, 1.0; AICc = 421.015; delta AICc = 3.281). Extrapolations of response curves from that model to non-analogous conditions were more ecologically realistic when using the unconstrained approach for most tails of the predictor variables. However, for the BIO13 variable, we applied clamping at the upper tail to prevent the species' response from continuing to increase beyond the point of truncation. Because the differences between results for the two thresholds were minimal, we discuss those for MTP since it is more intuitive and ensures that all occurrence records fall within the areas indicated as suitable. Detailed information about all the model results is available in the Supporting information.

Spatial predictions based on the selected model indicated a medium-to-high current suitability associated with montane habitats, concordant with natural history information for the species. Lowlands and the highest-elevation forests lacked suitable conditions, as did drier highland regions. The current potential distribution is more naturally fragmented in the northern extensions of the Sierra Madre Oriental, with two of the four 'sky islands' appearing as disjunct from the main body of the Sierra even at this low threshold (Fig. 2).

The predicted geographic patterns of suitability for the LGM differed across GCMs, with variation in both how much of the study area was indicated as suitable and in the spatial patterns of suitability. A consistent pattern of all reconstructions was a potential paleodistribution farther to the south than today. The CCSM4 and IPSL-CM5A-LR scenarios showed the strongest past contractions toward the south, although they differed notably. Whereas CCSM4 indicated high suitability towards the coastal mountains and low plains of the Gulf of Mexico, IPSL-CM5A-LR did so in the interior to the south of the high volcanoes of Central Mexico (Fig. 3). In contrast, MIROC-ESM and MPI-ESM-P showed broader potential paleodistributions, although only the latter suggested suitable conditions in the northernmost portions of the study area. In quantitative terms, the estimates based on MPI-ESM-P and MIROC-ESM resulted in the greatest overlap (*D* = 0.811), while CCSM4 showed the least similarity with the rest of the three scenarios (versus IPSL-CM5A-LR, *D* = 0.466; versus MIROC-ESM, *D* = 0.474; versus MPI-ESM-P, *D* = 0.446). The ensemble map showed greatest similarity to the MIROC-ESM prediction (Supporting information).

The MESS maps also differed substantially among GCMs (Supporting information). They indicated non-analog conditions at the LGM in the southern section of the species' current distribution according to MIROC-ESM and IPSL-CM5A-LR. In contrast, CCSM4 and MPI-ESM-P showed only extremely small areas with non-analog conditions,

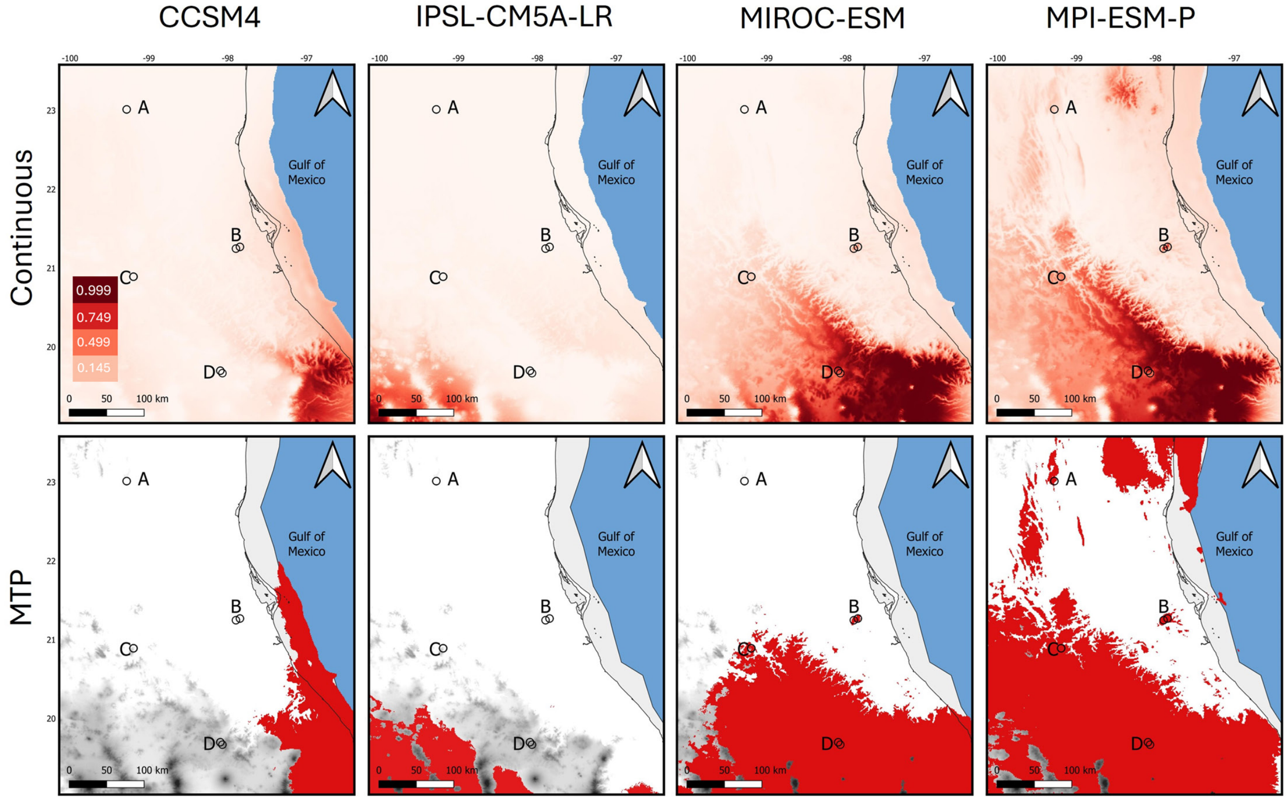

Figure 3. Last Glacial Maximum potential paleodistributions of the Mexican small-eared shrew, *Cryptotis mexicanus*, in central-eastern México. The potential distributions are shown according to the transfer of the optimized ecological niche model based on each of the four general circulation models (see text for abbreviations). For continuous maps (top row), redder colors indicate higher suitability. Binary maps (bottom row) are based on the minimum training presence (MTP) threshold. The hollow circles depict the four focal populations (on 'sky-islands') studied for genetic testing: (A) El Cielo, (B) Sierra de Otontepec, (C) Los Mármoles, and (D) Sierra Norte de Puebla.

indicating less pronounced differences between the present and the LGM.

Generating and testing predictions

The four GCMs and their ensembling led to vastly different predictions regarding population history (and expected genetic consequences) for the four focal sites (Table 1, first five rows). Because the transfers of the niche model to LGM climatic conditions based on both CCSM4 and IPSL-CM5A-LR showed a far-southern refugium of the potential distribution of *C. mexicanus*, they suggested that all four current focal populations result from postglacial colonization. On the contrary, MPI-ESM-P indicated long-term persistence of suitable conditions for all four populations (although

Table 1. Genetic predictions, inferred history of ancient localities, results, and interpretations for each of the four focal populations ('sky-islands') of the Mexican small-eared shrew, *Cryptotis mexicanus*, studied in central-eastern México. Predictions of population history (and genetic consequences in parentheses) were made according to the integration of current potential distributions and paleodistributions: 1) stable area occupied since the Last Glacial Maximum (high genetic diversity and signal of constant population size), and 2) post-glacial colonization (low genetic diversity and signal of past population size reduction). The predictions are given for each of the four global circulation models and their ensemble (using the minimum training presence threshold; see Fig. 2).

Global circulation model	El Cielo (A)	Sierra de Otontepec (B)	Los Mármoles (C)	Sierra Norte de Puebla (D)
CCSM4	post-glacial colonization	post-glacial colonization	post-glacial colonization	post-glacial colonization
IPSL-CM5A-LR	post-glacial colonization	post-glacial colonization	post-glacial colonization	post-glacial colonization
MIROC-ESM	post-glacial colonization	stable area	stable area	stable area
MPI-ESM-P	stable area	stable area	stable area	stable area
Ensemble	post-glacial colonization	stable area	stable area	stable area
Haplotype diversity	1.000	0.654	0.733	1.000
Nucleotide diversity	0.005	0.002	0.002	0.007
Tajima's *D*	−0.978	1.648	1.063	−1.157
Fu's *Fs*	−1.223	0.758	1.995	−2.309
Genetic diversity interpretation	stable, larger population	stable population	stable population	stable, larger population

with a notable contraction in the geographic extent and suitability level at the LGM for population A), overall signaling a constant population size for each of them. MIROC-ESM showed a paleodistribution similar to that of MPI-ESM-PP in the southern and central portions of the study region but differed farther north (with a much smaller area indicated as suitable). Thus, the MIROC-ESM paleodistribution predicted long-term persistence for populations C, D and B in the southern and central portions of the species' range (with a marked reduction in area for population B), and post-glacial expansion for population A in the north (Table 1). The ensemble model led to the same prediction as MIROC-ESM.

Regarding genetic diversity and population-demographic patterns, all four focal populations showed high diversity. We identified 18 haplotypes distributed among the four populations, with no haplotypes shared across sites. El Cielo (population A) harbored five unique haplotypes, Sierra de Otontepec (B) and Los Mármoles (C) each contained three haplotypes, and Sierra Norte de Puebla (D) exhibited the highest haplotype count with seven unique haplotypes. Although the number of haplotypes per population varied, all sites showed patterns consistent with high genetic diversity and strong population structure (Fig. 4). Nucleotide diversity was also high, especially in two of the populations, namely the northernmost (El Cielo) and southernmost (Sierra Norte de Puebla), which had the highest values of haplotype diversity (both $h = 1.0$) as well as higher nucleotide diversity ($\boldsymbol{\sigma} = 0.005$ and 0.006, respectively) compared with Sierra de Otontepec ($h = 0.73$; $\boldsymbol{\sigma} = 0.002$) and Los Mármoles ($h = 0.065$; $\boldsymbol{\sigma} = 0.002$). None of the values for Fu's *Fs* and Tajima's *D* indices were statistically significant for any of the populations. Thus, high genetic diversity and non-significant demographic indices agree with a signal of constant population size. Both the median-joining haplotype network and the BPEC results revealed four clusters (each matching one of the populations analyzed), with no haplotypes shared among populations, numerous unique (terminal) ones, and no ancestral haplotype sampled (Fig. 4A, B, C). None of the four populations showed the classical 'star-shaped' haplotype network characteristic of a recently expanded population (one common haplotype surrounded by uncommon ones closely related to it; Bandelt et al. 1999). Instead, each comprised a network of haplotypes of similar frequencies, related but separated from each other by one or more mutations. Although not sampled or likely extinct, the ancestral haplotype was inferred to have the closest genealogical connection to the current haplotype found in the Sierra Norte de Puebla, suggesting that the most ancient haplotype would be from this population.

Discussion

Estimating potential paleodistributions, especially during the LGM, has allowed researchers to propose distributional shifts occurring during the most recent glacial–interglacial cycle, which are helpful for a better understanding of the

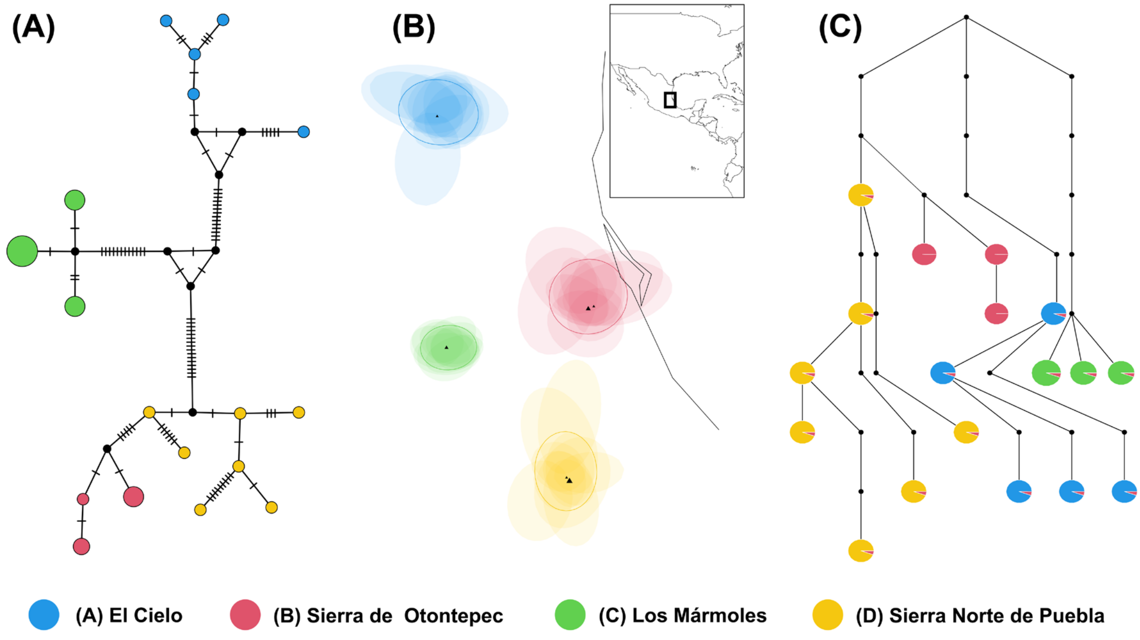

Figure 4. Phylogeographic analyses among populations of the Mexican small-eared shrew, *Cryptotis mexicanus*, using cytochrome b sequences based on four focal populations (on 'sky islands'; blue, green, red, and yellow) in central-eastern Mexico. (A) Median-joining haplotype network. The circle size is proportional to the observed haplotype frequency, black points are missing haplotypes, and the dashed lines denote mutational steps between haplotypes. (B) Map of results from the Bayesian phylogeographic and ecological clustering (BPEC) analysis, showing the geographic distribution of the haplotypes, contour plots denoting the localities (black triangles) assigned to each of the four phylogeographic clusters identified, and transparent contour plots indicating uncertainty for each cluster. (C) Clustered tree plot from the BPEC showing the genealogical relationships among unique haplotypes, where black points are the missing haplotypes (not sampled or extinct), and the pie chart shows posterior probabilities per cluster for the sampled haplotypes.

factors and processes generating current distributional patterns (Carnaval et al. 2009, Collevatti et al. 2013). Faced with such an opportunity, the generation of paleodistributions has been warmly and prolifically received in systematics, phylogeography, population genetics and landscape genetics (Alvarado-Serrano and Knowles 2014, Luna-Aranguré and Vázquez-Domínguez 2020, 2024, Franklin 2023). The current results emphasize first that important variations among reconstructed paleodistributions due to the use of different GCMs can be overlooked in the whirlwind of current and upcoming studies, and second that the field should stop to consider the need to determine which GCM might be the most realistic in specific study areas. Not doing so could lead to results so unrealistic (or with such great bounds of uncertainty) that they cannot be used for biological inferences or practical applications (Araújo et al. 2019).

In regions where palynological data are still scarce, like the biodiversity-rich Neotropics, genetic data can be particularly instrumental in deciding which GCM climate scenario best matches reality (Guevara 2024). In the current example, we employ cytochrome b, a commonly used molecular marker that is relatively easy to sequence in labs throughout the biodiverse 'Global South', and is available for a relatively high number of vertebrate populations and species globally, making it particularly useful for these kinds of questions (Fonseca et al. 2023). Therefore, the framework we have outlined could be applied to this and other regions using the same or similar markers for other taxonomic groups (e.g. COI for insects, chloroplast coding regions for plants; Fig. 1). Additionally, using high-throughput sequencing data, which includes more complete phylogenetic information, offers rich data for testing paleodistributions. Such an approach would ultimately enable researchers to more thoroughly understand, with less uncertainty, what the past climate may have been like. More sophisticated analysis strategies can be used with such data. For example, coalescent simulations over a broad range of parameter sets derived from the alternative paleodistributional hypotheses can help identify more likely scenarios in quantitative terms (Prates et al. 2016, Mitka et al. 2023). Finally, in addition to the genetic data available, future studies can also take advantage of finer temporal resolutions, for example, the reconstructions using several timesteps between the past period and today (Krapp et al. 2021, Barreto et al. 2023, Karger et al. 2023). Such analyses could investigate the impact of more minor, yet likely significant, Quaternary climatic changes such as the mid-Holocene.

How and to what extent using some GCMs to estimate paleodistributions – in any given region or worldwide – leads to erroneous or limited inferences still must be evaluated. In the present example, we used four paleoclimatic scenarios that vary substantially between them (Varela et al. 2015). Due to GCM availability, researchers traditionally have had limited options for exploring the climate experienced during the LGM. Until a few years ago, for example, CCSM4 and MIROC-ESM were the most used GCMs since they were easily accessible in WorldClim, a database of high spatial resolution global climate estimates (Fick and Hijmans 2017). For the northern Neotropics, these two GCMs show notable discrepancies, especially in terms of precipitation, which leads to clear differences in reconstructed potential paleodistributions in various species (Ramírez-Barahona and Eguiarte 2014, Ornelas et al. 2019). CCSM4 has also often been used alone to estimate paleodistributions without a clear justification (Guevara 2024). In this study, the CCSM4-based paleoreconstruction for the species is far from matching what the genetic signal of *C. mexicanus* suggests; on the contrary, less-used climate scenarios appear more realistic (e.g. especially MPI-ESM-P). It is noteworthy that here, CCSM4 was the GCM that showed the greatest qualitative and quantitative differences with respect to the other climate scenarios evaluated (values of Schoener's *D*). The genetic concordance with the MPI-based paleodistribution suggests that, for this region, neither temperature nor precipitation was so drastically lower than today (e.g. during the coldest and driest months, respectively), in contrast to the outputs of other GCMs (Supporting information). Such climatic interpretations are relevant to copious issues related to species distributions, such as seasonality, phenology, biotic interactions, and other broader scientific questions related to the history of human colonization or plant domestication.

Other critical methodological issues also bear consideration in research reconstructing paleodistributions. Future studies should also consider the degree of environmental extrapolation required under each of the GCMs and take the respective potential distributions with corresponding caution (Guevara et al. 2019). For example, in this study, IPSL showed greater extrapolation-associated uncertainty in the southern part of the species' distribution. Ensemble or consensus maps are sometimes preferred by averaging or combining all estimated potential distributions based on two or more GCMs (Diniz-Filho et al. 2015, Sobral-Souza et al. 2015). This may help identify regions of agreement or lower uncertainty arising from different estimates—and should reflect the central tendency of alternative GCMs (Elith et al. 2010, Zhu et al. 2021). However, mixing diverse climate scenarios (some notably contrasting) dilutes the signal of the better models and can hinder understanding of the effects of climate change on biodiversity; therefore, protocols for identifying the best or most realistic ones and considering them either individually or in concert hold promise for identifying the most realistic scenarios (Hausfather et al. 2022, Paz et al. 2024). The framework outlined and illustrated here can play an important role in doing so, particularly for studies including reconstructed past distributions, leading to a better understanding of the effects of climate change on biodiversity.

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Data availability statement

There are no additional data for this paper

Supporting information

The Supporting information associated with this article is available with the online version.

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