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# Climatic niche differentiation and paleodistribution of the longtail alpine garter snake complex *Thamnophis scalaris* (Squamata: Colubridae): holocene refugia in the Mexican highlands

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## Abstract

Mexico's topographic and environmental heterogeneity, in combination with environmental fluctuations of the Neogene-Quaternary, has uniquely influenced the evolutionary history and distribution patterns of the region's flora and fauna, sometimes causing closely related species to exhibit distinct climatic niches. Our study aimed to characterize the climatic niches of *Thamnophis scalaris* and *Thamnophis scaliger*, as well as evaluate the impact of the Pleistocene-Holocene transition on their paleodistributions. We generated 357 models per species, each with three sets of distinct combinations of climatic variables, based on 108 occurrence records for *T. scalaris* and 62 for *T. scaliger*. We evaluated the niche overlap, equivalency, and similarity between both species and transferred the present-day models to eight distinct historical periods, with the goal of encompassing the distinctive climatic variation of the Pleistocene-Holocene (P-H) transition. Both species showed significant differences in their respective climatic regimes and did not display climatic niche conservatism (the tendency of species to retain ancestral ecological characteristics), despite their previously reported ecological, morphological, and biogeographic similarities. Likewise, they seem to have responded similarly to the environmental changes in the P-H, with both paleodistributions experiencing expansion phases during glacial periods and contraction phases during interglacial periods. Possible areas of refugia that remained climatically stable and viable for both species throughout this period were identified. These refugia could potentially harbor a greater genetic diversity with respect to regions that recently acquired suitable conditions for the establishment of these populations. As such, this work offers a methodological procedure that may be used as an early inference for identifying specific regions of interest in phylogeographic studies and conservation planning.

## Highlights

- Comparative studies that provide insight into the climatic niche tendencies of temperate species can reveal important information regarding common responses to past and future environmental changes in montane ecosystems.
- The environmental and topographic heterogeneity of the Mexican highlands harbor environmental gradients that can be extreme enough to favor the divergence of closely related lineages.
- The climatic segregation of *Thamnophis scalaris* and *T. scaliger* allows their coexistence despite their morphological and ecological similarities.
- Cold-adapted species likely were able to subsist in highland climatic refugia during the interglacial periods.
- Regions that have maintained climatic suitability for montane species throughout glacial/interglacial periods could be relevant areas for the conservation of their intraspecific diversity.

**Keywords:** Climatic segregation, ecological niche modeling, Natricinae, Neogene-Quaternary, niche divergence, Pleistocene-Holocene transition, species distribution models, Trans-Mexican Volcanic Belt

## Introduction

Climate is considered one of the most relevant and impactful factors affecting the evolutionary histories of species, directly influencing biogeographic, ecological, and genetic patterns. These patterns can arise as a consequence of environmental transitions along a gradient or due to climatic changes occurring on a geological scale (Lomolino et al. 2010, McCormack et al. 2010, Martínez-Freiría et al. 2017). In particular, the drastic climatic fluctuations throughout the Neogene-Quaternary (N-Q) impacted biota around the world in different ways and intensities, resulting, for example, in rapid changes in species distribution, divergence processes, and extinction events (Hewitt 1996, 2004). Accordingly, these events left a particular pattern that has been studied through approaches such as the Pleistocene Refugia (PR) hypothesis, via different lines of evidence such as genomic data, the fossil record, and species distribution modeling (Haffer 1969, Dynesius and Jansson 2000, Mestre et al. 2022).

The PR hypothesis states that, during the past glacial periods, the increase in ice caps across the northern and southern hemispheres caused an overall temperature decrease and consequently, the reduction of some species distribution areas with populations persisting in lowland allopatric refugia (Haffer 1969, Husemann et al. 2014). The subsequent ice cap retreat during interglacial periods provided favourable conditions that facilitated the spread and interconnection of previously isolated populations (Halffter 1987, Salvi et al. 2014, Valdivia-Carrillo et al. 2017). However, contrary to the aforementioned, some cold-adapted montane species, such as *Crotalus intermedius* Troschel, 1865 (Bryson Jr et al. 2011a), *Cryptotis mexicana* (Coues 1877) (Guevara 2020), and *Nelsonia neotomodon* Merriam, 1897 (León-Tapia 2021), could have responded according to the Sky-Island dynamic (S-Id) (Mastretta-Yanes et al. 2015), experiencing an expansion in their distributional ranges via dispersion into adjacent mountain ranges through lowland corridors during the glacial periods, followed by retreat to highland allopatric refugia during the interglacial periods.

The effect of both scenarios (i.e., PR and S-Id) could have been even more drastic in geographically heterogeneous areas (e.g., Mexican highlands), uniquely modifying the distributional ranges and genetic diversity of many species (Mastretta-Yanes et al. 2015). Environmental gradients along elevations can be extreme enough to promote diversification processes across relatively short geographic distances, through the tendency to preserve ecological characteristics in ancestor-descendant sequences (i.e., Niche Conservatism (NC), Pyron and Burbrink 2009b, Gutiérrez-Ortega et al. 2020) or by adaptations to new environments (i.e., Niche Divergence (ND), Pyron and Burbrink 2009a). These processes stemming from elevational heterogeneity have been postulated as one of the main biodiversity drivers in Mexican montane ecosystems (Bryson Jr et al. 2011b, Gutiérrez-Ortega et al. 2020, Moreno-Contreras et al. 2020). Despite this, the effect

of N-Q climatic oscillations on Mexican montane species and their possible ecological-evolutionary (e.g., NC and ND), and biogeographical (e.g., PR and S-Id) consequences are largely unexplored, with the exception of a few studies on birds (McCormack et al. 2010, Moreno-Contreras et al. 2020), mammals (León-Tapia 2021), reptiles (Cisneros-Bernal et al. 2022), and plants (Gutiérrez-Ortega et al. 2020).

The *Thamnophis scalaris* Cope, 1861 complex is composed of two natricine colubrid species endemic to the highlands of south-central Mexico (Rossman et al. 1996). *Thamnophis scalaris* has a present-day disjunct distribution across most of the mountains of the Trans-Mexican Volcanic Belt (TMVB), the southern Mexican Plateau (MP), and the Sierra Madre Oriental (SMOr), found in elevations from 2100 to 4270 masl (Rossman et al. 1996). The other species of the complex, *T. scaliger* (Jan, 1863), has a disjunct distribution limited to the central TMVB and the southern MP, within a narrow elevational range from 2280 to 2570 masl (Rossman et al. 1996). Both species exhibit several similarities in their morphology (Rossman et al. 1996, Rossman and Gongora 1997), their behavior, being diurnal with peak activity in the rainy season (Rossman et al. 1996), and their ecology, being closely associated with temperate mesohabitats, such as subalpine grasslands (e.g., *Festuca toluensis* Kunth) surrounded by *Pinus* forests (Rossman et al. 1996, Rossman and Gongora 1997).

With this context, the *Thamnophis scalaris* species complex is an ideal model to perform a comparative study that explores the climatic tendencies of cold-adapted species and their possible reaction and consequences to the environmental changes of the Pleistocene-Holocene (P-H) transition. These results will improve our understanding of the species diversity that exists in Mexico's mountain ecosystems and help estimate their response to future environmental changes.

We hypothesized that: 1) despite their morphological and ecological similarities, differential habitat selection, through the segregation of climate niche (i.e., low climate niche overlap), would allow *Thamnophis scalaris* and *T. scaliger* to cohabit along the south-central Mexican highlands; and 2) in response to the climate oscillations during the Pleistocene-Holocene transition, *T. scalaris* and *T. scaliger* would experience a drastic reduction in their ranges, consistent with S-Id, forming allopatric refugia in the south-central Mexican highlands.

We aimed to characterize the climatic niches of *T. scalaris* and *T. scaliger* in order to: 1) assess the existence of climatic niche conservatism or divergence; 2) estimate the impact of the climatic oscillations of the P-H transition on their paleodistributions; and 3) identify areas that may have remained suitable and climatically stable for both species across the P-H transition. The results ultimately could be used as an early inference in phylogeographic or conservation planning studies to identify specific regions that may be housing greater genetic diversity.

## Materials and Methods

### Collection of occurrence data

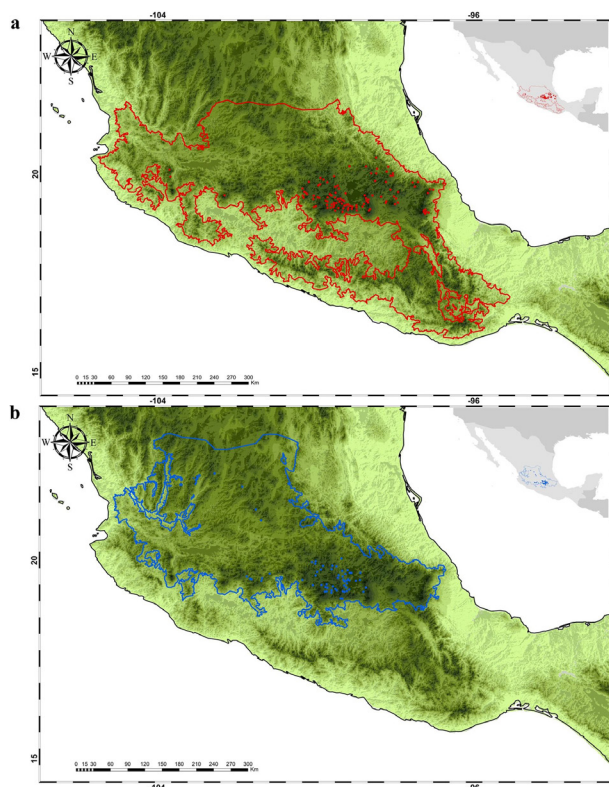
We first downloaded all occurrence records of *Thamnophis scalaris* and *T. scaliger* available on GBIF (GBIF 2021a, b), VertNet (VertNet 2021a, b), IDigBio (IDigBio 2021a, b), INaturalist (INaturalist 2021a, b) and EncicloVida (EncicloVida 2021a, b). We also obtained occurrence records from deposited specimens in the Museo de Zoología at the Facultad de Ciencias, Universidad Nacional Autónoma de México. This preliminary dataset consisted of 926 records for *T. scalaris* and 334 records for *T. scaliger*. Next, we eliminated all records that were duplicates, incomplete, showed high spatial correlation ( $<5 \text{ km}^2$ ), fell outside the known distribution for each species, had a different temporality to the range of bioclimatic variables (i.e., 1979–2013, Karger et al. 2017), or had atypical environmental values based on our biological knowledge of *T. scalaris* and *T. scaliger* (e.g., occurrence records with values outside the altitudinal range reported for both species) (Rossman et al. 1996).

### Accessible area

The geographic accessibility area, or “M” according to the BAM diagram (see Soberón and Peterson 2005), is characterized as the region that is accessible to the species without barriers to their dispersion (Soberón and Nakamura 2009). In order to train the *Thamnophis scalaris* and *T. scaliger* climatic niche models, we defined an “M” for each species based on three criteria: 1) having a geographic shape similar to the known area of distribution, assuming the distribution range is the result of the adaptation and dispersion capacity of the species (Zunino and Zullini, 2003), as well as factors related to their physiological limitations (Root, 1988) and biotic interactions (Wiszniewski et al. 2013); 2) considering the shape and extent of the biogeographic provinces proposed by Escalante et al. (2021) and their associated terrestrial ecosystems proposed by Olson et al. (2001); and 3) including a margin of approximately 10 km radius around the presence records to account for possible dispersion of individuals (Gregory and Stewart 1975, Shonfield and Koskin 2019) (Fig. 1). This framework aimed to delimit accessibility areas using both biological and geographic evidence that effectively restricts the set of climatic conditions used, which is critical to the development of the models and subsequent analyses (Barve et al. 2011, Peterson 2011).

### Environmental data, model calibration, and model construction

To quantify the climatic niches of *T. scalaris* and *T. scaliger*, we obtained bioclimatic data from CHELSA v1.2b (Karger et al. 2017). This data set includes a set of 19 variables spanning distinct aspects of precipitation and temperature from 1979 and 2013 at a resolution of 2.5 arc min. ( $\sim 5 \text{ km}^2$  per pixel) (see Supplementary Table S1 for the description of each bioclimatic variable).



**Figure 1.** Occurrence records and accessibility areas for *Thamnophis scalaris* (a) and *T. scaliger* (b).

We trimmed the 19 bioclimatic variables to the shape of the “M” for each species. Next, we created 3 sets of variables. We selected Set 1 to capture the extreme conditions of the study area, considering the same variables for both species: Bio1, Bio5, Bio6, Bio12, Bio13, and Bio14. Set 2 was selected according to the Variance Inflation Factor (VIF) to identify those variables that present collinearity problems (i.e.,  $VIF > 10$ ) (Montgomery and Peck, 1992, Naimi et al. 2014), considering the same variables for both species: Bio1, Bio4, Bio12, Bio14, and Bio15. Set 3 was chosen based on the biological knowledge of each species (Rossman et al. 1996), using the variables Bio1, Bio4, Bio11, Bio12, Bio15, Bio16, and Bio17 for *T. scalaris*, and Bio1, Bio4, Bio7, Bio11, Bio12, Bio15, Bio16, and Bio17 for *T. scaliger*.

Using the kuenm package (Cobos et al. 2019b), we generated 357 calibrated models per species, using 17 combinations of regularization multipliers (0.1 to 1 in 0.1 increments, followed by 2, 3, 4, 5, 6, 8, 10) and every possible combination of linear, quadratic, and product classes in Maxent 3.4.1 to determine the optimal configuration that minimizes overfitting model (Phillips et al. 2004). We based model selection on three criteria: 1) statistical significance of the lowest values of partial receiver operating characteristics ( $pROC$ ); 2) the predictive power denoted by low omission rates ( $OR$ )  $< 5\%$  (Cobos et al., 2019); 3) lowest values of Akaike Information Criterion corrected for small sample sizes ( $AICc$ ) (Lobo et al. 2008, Peterson et al. 2008, Cobos et al. 2019b).

We constructed the final model based on the best set of previously mentioned parameters, using 75% of the data to generate the model and 25% to evaluate it, with 10 bootstrap replicates (Phillips et al. 2004, Cobos et al. 2019b). We binarized every model output using the 10<sup>th</sup> percentile for the minimum training presence to classify the prediction (0 = inadequate; 1 = adequate), excluding 10% of the lowest aforementioned values because they may be representing erroneous records in the dataset. (Pearson et al. 2007).

### Niche overlap, equivalency, and similarity

We evaluated the existence of environmental similarities associated with the occurrence data of each species with a student's t-test with *p* values adjusted by Holm-Bonferroni, using the bioclimatic variables from Set 1. In order to determine the existence of ecological niche overlap between *T. scalaris* and *T. scaliger*, we calculated the density of occurrences and environmental factors under the PCA-env approach as proposed by Broennimann et al. (2012) using Schoener's *D* index (Schoener 1968) in the ecospat package (Di Cola et al. 2017). After this, we performed a niche equivalence test, due to both species share quite similar environmental conditions (Rossman et al. 2016), and this test may confirm if the occupied climatic niches of both species were equivalent and mutually predictable across their distribution (Warren et al. 2008). This test was determined by comparing the real niche overlap values (*D*) to a null distribution of 1000 pseudo-replicates overlap values. The non-equivalence of ecological niches was determined if the niche overlap value of *T. scalaris* and *T. scaliger* was significantly lower than the overlap values from the null distribution ( $p < 0.05$ ) (Warren et al., 2008).

To assess the potential climatic niche similarities in both species, we conducted a niche similarity test using *rand.type = 1* and "greater" arguments in the ecospat package (Di Cola et al. 2017), which effectively tests for the presence of NC (i.e., the overlap of both species' niches is more similar than expected by chance). This is accepted when the observed overlap (Schoener's *D*) is significantly different ( $p < 0.05$ ) with respect to the overlap values of the niche obtained through the pseudo-replicates (Warren et al. 2008, Broennimann et al. 2012). Given that the niche similarity test is unidirectional, we conducted two tests: 1) *T. scalaris* vs. *T. scaliger*; and 2) *T. scaliger* vs. *T. scalaris*. This test was repeated 1000 times to be sure that the null hypothesis could be rejected with a high level of confidence (Warren et al. 2008, Broennimann et al. 2012). To facilitate the interpretation of the results, we followed the metric proposed by Rödder and Engler (2011): null or very limited overlap (0–0.2), low overlap (0.2–0.4), moderate overlap (0.4–0.6), high overlap (0.6–0.8), and very high overlap (0.8–1.0).

Additionally, we compared the climatic niches of *T. scalaris* and *T. scaliger* through a minimum-volume ellipsoid model to test the null hypothesis that the two ellipsoids adjusted to the real observations overlapped at least as much as the random data ellipsoid using the ellipsem package (Cobos et al. 2019a). We generated

1000 pseudo-replicates to compare with the real niche overlap value. In this context, we rejected the null hypothesis if the real niche overlap value was significantly different ( $p < 0.05$ ) with respect to the overlap values obtained from the pseudo-replicates. We calculated the overlap value, known as Jaccard's Index (*J*), as the proportion of total points contained within the intersection of the two ellipsoids (*A* and *B*);  $J = A \cap B / A \cup B$ . Ranging between  $J = 0$  (no overlap) and  $J = 1$  (complete overlap) (Mammola 2019).

### Model Transferring

We transferred the final model for each species to eight distinct historical time frames that encompass the climatic variation of the P-H transition: the late Pleistocene, including the Interglacial Period (130 ka) (Otto-Bliesner et al. 2006), the Last Glacial Maximum (20 ka) (Karger et al. 2017), the Heinrich H1 Event (17.0–14.7 ka), Bølling-Allerød (14.7–12.9 ka), and the Younger Dryas (12.9–11.7 ka) (Fordham et al. 2017); and the Holocene, partitioned into the early (11.7–8.3 ka), middle (8.3–4.2 ka), and late Holocene (4.2–0.3 ka) (Fordham et al. 2017). Transferring models entails the need for extrapolation, due to the possible existence of non-analogous climatic conditions (i.e., extreme temperature values than those present in the calibration area). According to Anderson (2013), we allow the model to estimate the response value to the truncation point (i.e., extrapolation by clamping) based on response curves obtained for each species (Supplementary Figure S1, S2), making constant the response outside of the range of the training area (Phillips et al. 2006, Cobos et al. 2019b).

We performed an analysis of Mobility Oriented Parity metric (MOP) in order to avoid an incorrect interpretation of the transferred areas using the kuenm package (Cobos et al. 2019b). Positive values indicate the existence of analogous climates between the two comparisons, while negative values indicate the presence of non-analogous conditions (Owens et al. 2013).

We estimated the impact of the Pleistocene-Holocene transition on *T. scalaris* and *T. scaliger* distribution range, calculating the proportion of change in the current distribution model compared with each of the of P-H transition temporalities, by quantifying the loss or gain of pixels with a value of 1 (i.e., presence) on each previously binarized map.

We performed all analyses in R v. 4.1.3 (R Core Team 2022). R-scripts generated in our study are available from the first author upon request.

## Results

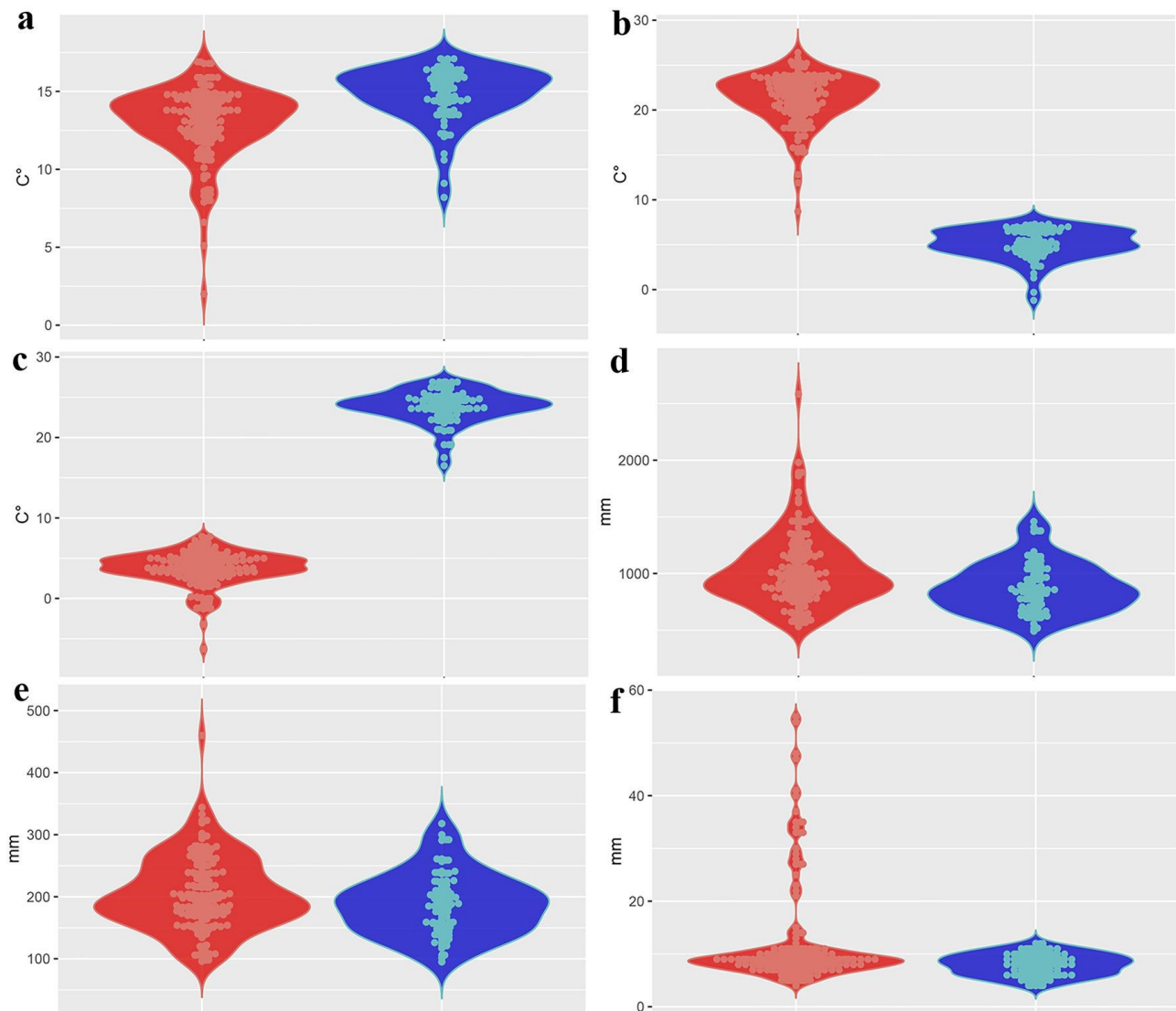
### Environmental data

Cleaning the original dataset based on the above criteria left us with a total of 108 occurrence records for *T. scalaris* and 62 for *T. scaliger* to be used in the subsequent analyses (Fig. 1). Of the 357 models generated for *T. scalaris*, three complied with the statistical criteria previously described. The best model obtained an *RM* = 0.4, *feature classes* = 1, *pROC* = 0, *OR* = 0.037, *AICc* = 1.913 and was constructed from Set

1, whose contribution percentages per environmental variable were as follows: Annual Mean Temperature (71.1%), Min Temperature of Coldest Month (9.4%), Max Temperature of Warmest Month (8.5%), Precipitation of Wettest Month (2.5%), Annual Precipitation (2%), and Precipitation of Driest Month (0.6%). Of the 357 models generated for *T. scaliger*, five models complied with the statistical criteria, of which the best model obtained an  $RM = 0.6$ ,  $feature\ classes = q$ ,  $pROC = 0$ ,  $OR = 0$ ,  $AICc = 1.837$ , and was constructed from Set 1, whose contribution percentages for each environmental variable were: Max Temperature of Warmest Month (71.1%), Precipitation of Driest Month (14.5%), Min Temperature of Coldest Month (7.1%), Annual Precipitation (4.8%), Precipitation of Wettest Month (1.9%), and Annual Mean Temperature (1.5%). All tests showed statistically significant values, indicating that

the generated models for each species were sufficiently robust to continue with the remaining analyses.

The student's t-test found significant differences in variables associated with temperature: Bio 1 ( $t = -5.5956$ ,  $df = 153.68$ ,  $p = 0.0001$ ), Bio 5 ( $t = 45.401$ ,  $df = 169.46$ ,  $p = 0.0001$ ), Bio 6 ( $t = -58.581$ ,  $df = 129.21$ ,  $p = 0.0001$ ), and precipitation: Bio 12 ( $t = 3.6925$ ,  $df = 164.94$ ,  $p = 0.0003$ ), Bio 13 ( $t = 2.0102$ ,  $df = 146.59$ ,  $p = 0.0462$ ), Bio 14 ( $t = 5.0095$ ,  $df = 123.57$ ,  $p = 0.0001$ ) (Fig. 2). According to the PCA analysis, the first two principal components (PC) were statistically significant, representing 48.46% and 38% of the variation, respectively. These two components were used to represent the climatic niches of *T. scalaris* and *T. scaliger* in a bidimensional gradient. PC1 was comprised of variables associated with temperature, while PC2, on the other hand, was made up of variables associated with precipitation (Fig. 3a). Even though



**Figure 2.** Violin plots of the selected bioclimatic variables, from values extracted for occurrence records of *Thamnophis scalaris* (red) and *T. scaliger* (blue). Annual Mean Temperature (a), Max Temperature of Warmest Month (b), Min Temperature of Coldest Month (c), Annual Precipitation (d), Precipitation of Wettest Month (e), and Precipitation of Driest Month (f).

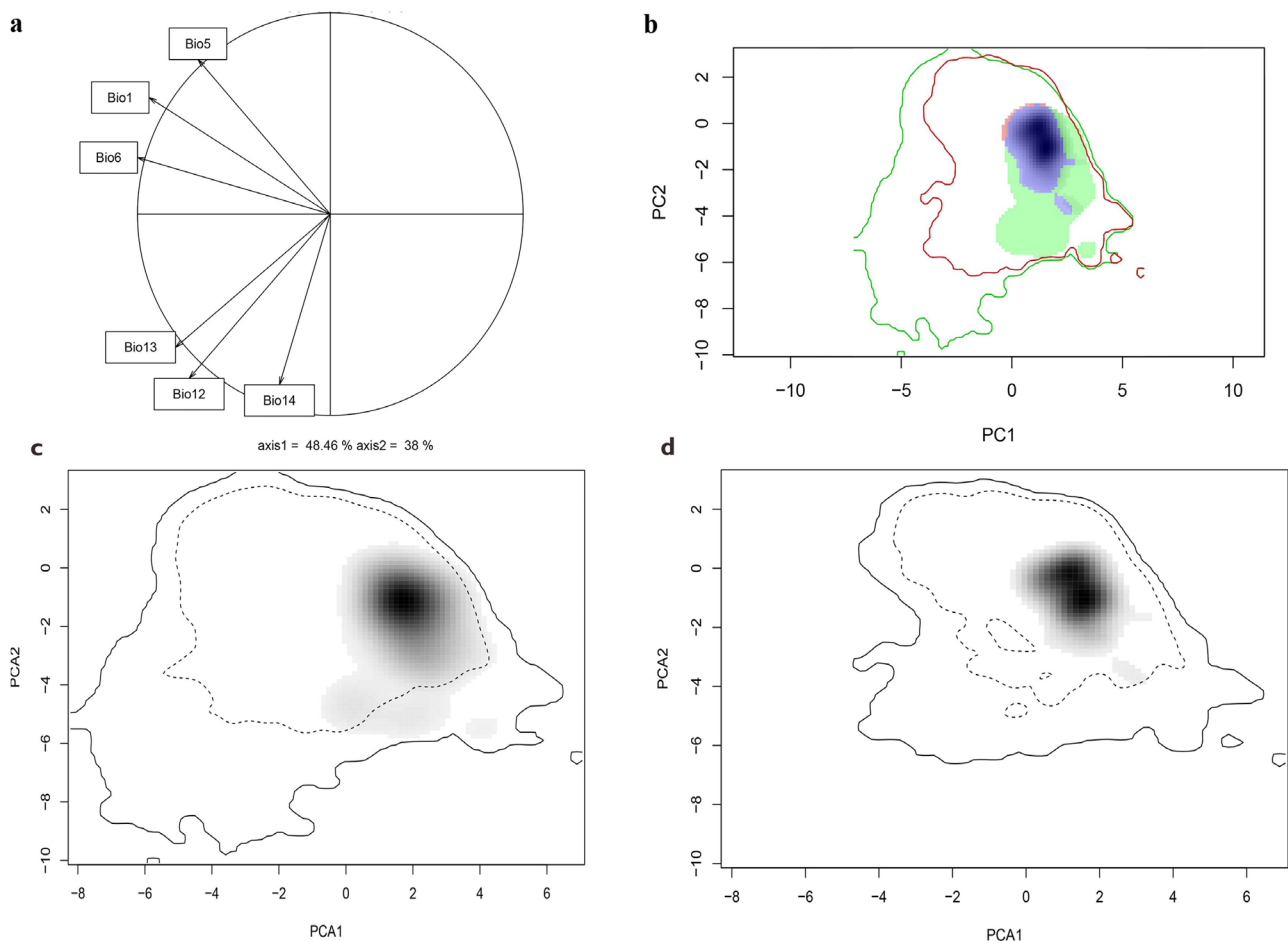
both species occupied a small fraction of the available environmental space, *T. scalaris* showed a wider climatic niche with respect to *T. scaliger* based on the first and second PCs (Fig. 3; Supplementary Figure S6).

The MOP comparison between the calibration area and the nine previous scenarios revealed different magnitudes of areas of strict extrapolation, the same ones that were omitted from the geographic projection of the potential areas of distributions of each species in every period previously mentioned (Supplementary Figure S7, S8).

### Niche overlap, equivalency, and similarity

According to the observed values of Schoener's  $D$  ( $D = 0.14$ ), *T. scalaris* and *T. scaliger* present a null or very limited overlap of climatic niche space

(Fig. 3b). Furthermore, the equivalency test ( $p < 0.05$ ) indicated that the climatic niches of both species are not equivalent amongst themselves. The results obtained from the similarity test indicate that the climatic niches are not more similar than expected by chance in both directions ( $p > 0.05$ ), causing us to reject the hypothesis of climatic niche conservatism (NC) (Supplementary Figure S5). The overlap analyses based on ellipsoids indicated little overlap of climatic niche between *T. scalaris* and *T. scaliger*. ( $J = 0.11$ ). Based on the significance values of the null models with respect to the niche overlap values ( $p < 0.05$ ), we reject the null hypothesis, and consider the climatic niches of the two species to be different (Supplementary Figure S6b).



**Figure 3.** Visualization and quantification of the climatic niches of *Thamnophis scalaris* and *T. scaliger*. (a) Correlation plot for the principal component analysis (PCA) indicating the contribution of the six bioclimatic variables: Mean Annual Temperature (Bio1), Max Temperature of Warmest Month (Bio5), Min Temperature of Coldest Month (Bio6), Annual Precipitation (Bio12), Precipitation of Wettest Month (Bio13), and Precipitation of Driest Month (Bio14). (b) Available environmental space of *T. scalaris* (green solid line) and *T. scaliger* (red solid line) in a bidimensional space, based on the principal component analysis. The green and red shadings represent the occurrence density of each species, and the blue shaded area represents the niche overlap. Individual climatic niche space of *Thamnophis scalaris* (c) and *T. scaliger* (d). The solid and dashed lines represent 100% and 50% of the available environmental space, respectively. Shaded areas represent the density of each species occurrences (high density in black).

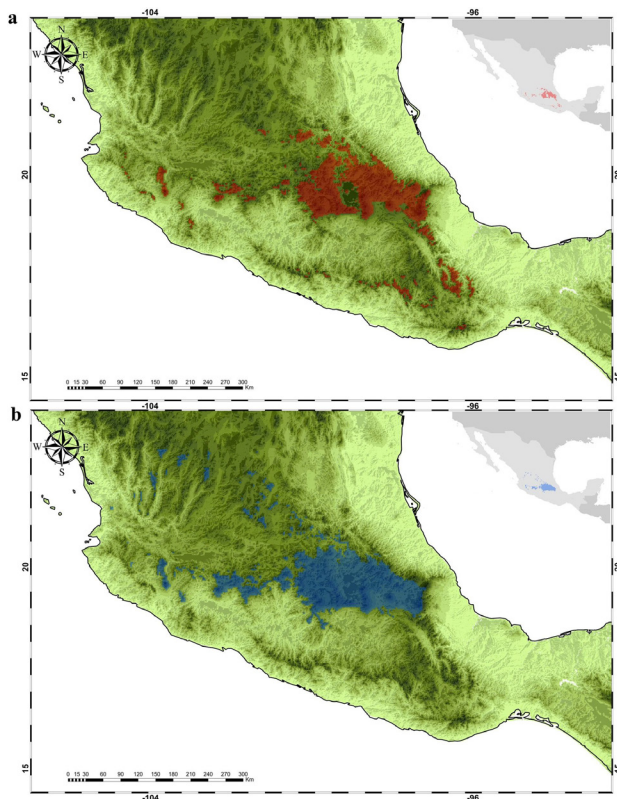
## Current potential distribution

### *Thamnophis scalaris*

The current potential distribution of *T. scalaris* shows a disjunct pattern, restricted to the high elevational regions within the TMVB, the southern SMO, and the northern SMS (Fig. 4a). Specifically, four main zones of climatic suitability across these three mountain ranges were recovered. The largest of these is concentrated in the eastern TMVB and southern SMO, forming a continuum between the states of Queretaro, Hidalgo, Veracruz, Puebla, Tlaxcala, Ciudad de Mexico, Morelos, and Estado de Mexico. The other three zones of climatic suitability for this species were found in the western of TMVB (Jalisco and Michoacan states) and in the southeast (Oaxaca state). These last three areas are separated from each other by lowland zones (<2000 m) dominated by grasslands, scrublands, and oak forests (Rzedowski and Huerta, 1994, Espinosa et al. 2008) that are environmentally uninhabitable for this species due to their warmer, drier climates (Fig. 4a).

### *Thamnophis scaliger*

The current potential distribution of *T. scaliger* shows a disjunct pattern restricted to the high elevations of the TMVB and in the southern MP that is comprised of three principal zones of climatic suitability (Fig. 4b). The first is located in the central TMVB,



**Figure 4.** Current potential distribution based on climate suitability of *Thamnophis scalaris* (a) and *Thamnophis scaliger* (b).

forming a continuum between the states of Queretaro, Hidalgo, Puebla, Tlaxcala, Ciudad de Mexico, Morelos, and Estado de Mexico. The second zone is located in the western TMVB in Michoacan, while the third is made up of small, isolated regions situated in the southern MP, in the states of Aguascalientes, Guanajuato, and Jalisco. Even though this third province comprises several mountainous regions that provide adequate climatic conditions for the persistence of its populations, the lowlands (<2000 m), with warmer and drier climates dominated by xeric vegetation (Rzedowski & Huerta, 1994; Espinosa et al. 2008), possibly represent a barrier that impedes the connectivity of the populations from the TMVB (Fig. 4b).

## Paleodistribution

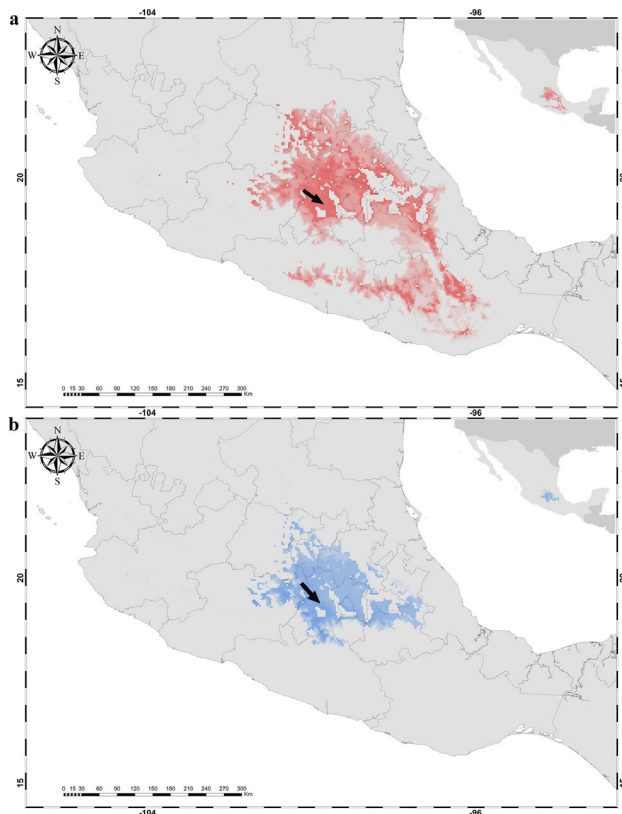
Except for the Late Holocene, our models showed that the climatically favorable areas for *T. scalaris* have been decreased drastically in size throughout the P-H transition compared to the extension obtained for current models: Late Holocene (19%), Mid Holocene (-15%), Early Holocene (-45%), Younger Dryas (-64%), Bølling-Allerød (-90%), Heinrich Stadial (-76%), Last Glacial Maximum (-87%), and Last Interglacial (-44%) (Supplementary Figure S3). A similar pattern is observed for *T. scaliger*: Late Holocene (-45%), Mid Holocene (-53%), Early Holocene (74%), Younger Dryas (48%), Bølling-Allerød (-77%), Heinrich Stadial (-62%), Last Glacial Maximum (-81%), and Last Interglacial (96%) (Supplementary Figure S4).

We identified a possible climatic refugia for *T. scalaris* and *T. scaliger* in the central region of the TMVB, in present-day southern Hidalgo state and north-central Estado de Mexico. Our models indicate that these regions have remained climatically stable and suitable for both species throughout the P-H transition (Fig. 5).

## Discussion

Using ecological niche modeling (ENM), species climatic tendencies can be quantified and contrasted to estimate the effects of distinct environmental factors on species' evolutionary histories (McCormack et al. 2010, Pyron et al. 2015, Moreno-Contreras et al. 2020). This methodology has received growing attention due to its fluid integration with evolutionary biology and biogeography (Wooten and Gibbs 2012, Burbrink et al. 2021). Comparative studies that provide insight into the climatic niche tendencies of montane species can reveal patterns of common responses to past environmental changes, resulting in an improved understanding of the mechanisms linked to the origin and persistence of diversity in mountain landscapes (Mastretta-Yanes et al. 2018, León-Tapia 2021, Cisneros-Bernal et al. 2022). Our results expand on the ecological, biogeographical, and evolutionary knowledge regarding the *Thamnophis scalaris* species complex. Furthermore, we explain how these two closely related species in morphology and ecology (Rossman et al. 1996, Rossman and Gongora 1997, Manjarrez et al. 2007, Reguera et al. 2011) can coexist





**Figure 5.** Geographic projection of the areas that have remained climatically suitable for *Thamnophis scalaris* (a) and *Thamnophis scaliger* (b) throughout the Pleistocene-Holocene transition. The black arrows indicate the areas corresponding to the Toluca valley and the Lerma River basin.

in a particular region, specifically through habitat selection (see below).

The climatic niche suitability for *T. scalaris* reflects a greater extension in the west-central TMVB, specifically in areas closely associated with high-altitude stratovolcanoes such as the Nevado de Toluca, the Sierra de Ajusco-Chichinautzin, Popocatepetl, Iztaccíhuatl, La Malinche, and the Citlaltépetl. *Thamnophis scaliger*, on the other hand, presents a distribution geographically restricted to the lower-elevation mountainous regions, including the plains of the Toluca Valley, the Mexico Valley, and the Puebla-Tlaxcala Valley. Interestingly, *T. scaliger* has not been recorded from this latter region, possibly due to the existence of physical and/or climatic barriers such as the Popocatepetl and Iztaccíhuatl volcanoes, with highlands to the north (>2700 masl) and lowlands to the south (<2000 masl). This is concordant with the altitudinal range reported for this species (Rossman et al. 1996), and likely is a relevant factor limiting the species' dispersion towards the eastern part of the TMVB.

Despite the potential distributions and climatic niches of both species being modeled based on the same set of variables (see above), a lack of similarity exhibited in their climatic niches indicates that each species is taking advantage of different forms or intensities of the environmental conditions present in

their areas of distribution, including the central portion of the TMVB, where both coexist (Rossman et al. 1996). This is relevant given that sympatry is considered to be contingent on morphological or trophic diversity that allows the coexistence of two similar species (Pigot and Tobias 2013), something apparently absent in *T. scalaris* and *T. scaliger* (Rossman and Gongora 1997). Therefore, based on our findings and *in situ* observations, both species could be reducing competition by segregating their climatic niches, possibly being separated by an altitudinal gradient (Arlettaz 1999). In this sense, each species could have acquired its particular climatic niche identity independent of their ancestral conditions, exhibiting a similar pattern as seen in other vertebrates such as *Nelsonia* (León-Tapia 2021), *Aphelocoma* (McCormack et al. 2010), and *Arremon* (Moreno-Contreras et al. 2020). This seems to be a common response in montane species to the topographic and environmental heterogeneity of regions such as the TMVB, as detailed below.

Hallas et al. (2022) proposed that the common ancestor between *T. scalaris* and *T. scaliger* diverged in the early Pliocene by dispersal events. This is consistent with the absence of niche conservatism (NC) registered between both species, where niche divergence (ND) would favor dispersal along the heterogeneous landscape of the TMVB and ultimately, the adaptation to distinct environmental conditions (Burbrink and Pyron 2010). According to Pyron et al. (2015) and Burbrink and Pyron (2010), if populations have experienced drastic ecological changes causing ancestral niche conditions to no longer be available, natural selection could favor speciation through the divergence of ecological niches. Therefore, the climatic ND within a species complex could be considered an additional line of evidence for taxonomic diversification. This is congruent with reported genetic and biogeographic information (Hallas et al. 2022), providing a more solid hypothesis of the independence of evolutionary lineages from an ecological perspective, as reported by Rissler and Apodaca (2007).

The impact that climatic changes of the Neogene-Quaternary had on distributions of different taxa has been backed up by both fossil and molecular evidence (Hewitt 1996, 2004, López-García et al. 2010, Lowe and Walker 2014). Our models add an ecological perspective that agree with both lines of evidence, indicating that the low temperatures prevalent throughout the Pleistocene caused the geographic range expansion of *T. scalaris* and *T. scaliger* through the lowlands of south-central Mexico. This is also supported by fossil evidence for *T. scalaris* (~14 ka) (Álvarez and Huerta 1975) (Supplementary Figure S1f) and other co-distributed mountain species in the TMVB such as *Crotalus triseriatus* (Wagler, 1830), *Storeria sp.*, and *Barisia sp.* (Cruz et al. 2021). In all these cases, fossil material has been recovered from lowlands (~2300 masl), which are currently not environmentally suitable for any of the aforementioned species. At the same time, highlands (>3000 masl) of volcanoes such as the Nevado de Toluca, Popocatepetl, Iztaccíhuatl, La Malinche, and Citlaltépetl, which are currently inhabited

by *T. scalaris* and *T. scaliger*, were climatically unsuitable for both species during the LGM due to the expansion of volcanic glaciers, which caused the mountainous vegetation of which both species are associated to descend below their present-day altitudes, facilitating the snakes' dispersion through intermontane corridors (D'Antoni 1993, McDonald 1993, Mastretta-Yanes et al. 2015) (Supplementary Figure S1, S2).

As with other montane taxa such as *Crotalus intermedius* (Bryson Jr et al. 2011a), *Crotalus ravus* Cope, 1865 (Cisneros-Bernal et al. 2022), and *Vipera seoanei* Lataste, 1879 (Martínez-Freiria et al. 2015), the impact of the P-H transition on the distribution range of *T. scalaris* and *T. scaliger* is consistent with the S-Id (Mastretta-Yanes et al. 2015). This also explains the present-day disjunct distribution observed in the longtail alpine garter snake species complex, with shows apparently isolated populations in the highlands in the northern and eastern TMVB. However, it is important to note that, despite the similar response to the P-H transition by *T. scalaris* and *T. scaliger*, the latter taxon seems to have experienced more drastic changes in its paleodistribution, which could be related to a more limited climate tolerance (Fig. S3), as suggested by its narrower altitudinal range (Rossman et al. 1996). This would be a critical factor to consider in relation to conservation planning.

According to our models, the zones that maintained climatic suitability for *T. scalaris* and *T. scaliger* are situated in the Toluca Valley and the basin of the Lerma River. Here, both species were able to find favorable conditions within their physiological limits to persist through the P-H transition. These temperate alluvial plains are dominated by pine forest and subalpine grasslands (Rzedowski and Huerta 1978, Espinosa et al. 2008) and have been recognized for their high herpetofaunal diversity (Aguilar et al. 2009). This could be indicative of a common response to the P-H transition among Nearctic amphibians and reptiles, given their restricted thermal tolerances (Figs. 2,3). Different populations could possess genetic footprints associated with the historic changes previously mentioned and the orography of the TMVB (Hewitt 1996, Mastretta-Yanes et al. 2015). By remaining climatically suitable and stable throughout the P-H transition, these regions may be housing a greater genetic diversity than zones that recently acquired adequate conditions for the establishment of these populations (e.g., Popocatepetl and Iztaccíhuatl) (Tribsch and Schönswetter 2003, Hewitt 2004, Mastretta-Yanes et al. 2018, Smith et al. 2022).

Future phylogeographic studies in the *Thamnophis scalaris* complex will help determine if the regions identified herein as possible Holocene refugia possess elevated levels of genetic diversity in comparison to non-refugia regions. Such has been reported in other cold-adapted species, such as *Anourosorex squamipes* Milne-Edwards, 1872 (He et al. 2016). If true, the management of conservation-aimed strategies would greatly benefit from knowing whether the areas currently established as ecological reserves also constitute historical climatically suitable regions for

cold-adapted species, and furthermore if these regions will remain suitable in future climatic scenarios. This is especially concerning considering that González-Fernández et al. (2018) report a drastic decrease in the climatically suitable areas of *T. scalaris* and *T. scaliger* by 2050 under a scenario of moderate to medium climate change. On top of this, the TMVB is the most populated region of the country, and its ecosystems currently face serious threats from human activities (Luna-Vega et al. 2007).

## Conclusions

Evidence suggests that montane species such as *Thamnophis scalaris* and *T. scaliger* have experienced a particular response in their potential distributions throughout the Pleistocene-Holocene transition. Specifically, these responses correspond with the S-Id, which predict an increase in climatically suitable areas during glacial cycles and a reduction and fragmentation of such areas during interglacial cycles. Regions that have maintained climatic suitability for these species throughout this period may be hosting greater genetic diversity than areas recently acquiring adequate conditions for population subsistence. These findings, in addition to providing an early inference for future phylogeographic studies, may also be valuable for management strategies aimed at the conservation of montane species, given the particular susceptibilities of each species under a future climate change scenario.

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## Author Contributions

LFHL and OFV initiated and designed the project. LFHL collected original data, performed analyses, and wrote the manuscript with help from OAFV and JAV. OAFV and JAV advised the theory and methodology.

## Data Accessibility Statement

All original data are available from the corresponding author.

## Supplemental Material

The following materials are available as part of the online article at <https://escholarship.org/uc/fb>  
**Table S1.** Set of 19 bioclimatic variables used to model the climatic niches of *Thamnophis scalaris* and *T. scaliger*.

**Figure S1.** Response curves of six environmental predictors of Set 1, used in the climatic niche model for *Thamnophis scalaris* among the replicated runs.

**Figure S2.** Response curves of six environmental predictors of Set 1, used in the climatic niche model for *Thamnophis scaliger* replicated runs.

**Figure S3.** Geographic projections of ecological niche modeling analyses of *Thamnophis scalaris* throughout the Pleistocene–Holocene transition fossil record for *T. scalaris*.

**Figure S4.** Geographic projections of ecological niche modeling analyses of *Thamnophis scaliger* throughout the Pleistocene–Holocene transition.

**Figure S5.** Background similarity tests based on 1000 pseudo-replicates generated and the observed value of real overlap (red line) between *T. scalaris* and *T. scaliger*, considering both reciprocal directions, *T. scalaris* vs *T. scaliger* (a) and *T. scaliger* vs *T. scalaris* (b).

**Figure S6.** Climatic niche breadth shown as minimum-volume ellipsoid niche estimations for Set 1 variables for *T. scalaris* (red) and *T. scaliger* (blue) (a) approach between *T. scalaris* and *T. scaliger* (b).

**Figure S7.** Mobility Oriented Parity (MOP) metric of nine scenarios projected for *T. scalaris* throughout Pleistocene–Holocene transition risk areas (red).

**Figure S8.** Mobility Oriented Parity (MOP) metric of nine scenarios projected for *T. scaliger* throughout the Pleistocene–Holocene transition risk areas (red).

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