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Niche overlapping in *Hypopachus* (Anura: Microhylidae) and new record of *Hypopachus variolosus* in Central Mexico

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ABSTRACT

Introduction: Microhylidae is one of the most diverse anuran families. The *Hypopachus* genus comprises a group of relatively unknown fossorial frogs distributed from the United States to Panama. To date, their environmental requirements and niche overlap among species remain unstudied.

Objectives: To assess niche overlap among four Sheep Frog species, genus *Hypopachus*, and report a sighting of *Hypopachus variolosus* in the State of Mexico after 66 years with no records.

Methods: We conducted fieldwork in Tonicato, State of Mexico, Mexico. The vegetation consists of low deciduous forest under a semi-warm subhumid climate. We modeled the environmental occupation of *H. variolosus*, *H. ustus*, *H. barberi*, and *H. pictiventris* through a principal component analysis and kernel density estimation, calculated niche overlap using Schoener's D metric, and modeled the environmental suitability of each species using the maximum entropy algorithm.

Results: On 25 October 2024, we captured a male *H. variolosus* measuring 25.4 mm. A significant niche overlap was detected only between *H. variolosus* and *H. ustus*. Preference for low temperatures distinguishes *H. barberi* from the other species, while preference for high precipitation regimes sets *H. pictiventris* apart. *H. variolosus* has the broadest distribution range, occurring from Texas to Western Panama, followed by *H. ustus*, which ranges from the coasts of the Gulf of Mexico and the Pacific in Mexico to Nicaragua. *H. barberi* is distributed from the state of Chiapas, Mexico, to Northern Nicaragua. The most range-restricted species is *H. pictiventris*, found from Southeastern Nicaragua to Western Panama.

Conclusions: Our results suggest that meso- and microclimatic variables may play a key role in reducing competition among sympatric *Hypopachus* species. Additionally, the conditions of high temperatures and low rainfall that prevail in Mexico and Central America, favor the extensive distribution of *H. variolosus* and *H. ustus*.

Key words: environmental ordination; Sheep Frogs; species distribution model; State of Mexico; Tonicato.

RESUMEN

Solapamiento de nicho en *Hypopachus* (Anura: Microhylidae) y nuevo registro de *Hypopachus variolosus* en el Centro de México

Introducción: Microhylidae es una de las familias de anuros más diversas. El género *Hypopachus* comprende un grupo de ranas fosoriales relativamente desconocidas, distribuidas desde Estados Unidos hasta Panamá. Hasta la fecha, sus requerimientos ambientales y el grado de solapamiento de nicho entre especies no han sido estudiados.



Objetivos: Evaluar el solapamiento de nicho entre cuatro especies de ranas del género *Hypopachus* y reportar un avistamiento de *Hypopachus variolosus* en el Estado de México tras 66 años sin registros.

Métodos: Realizamos trabajo de campo en Tonatico, Estado de México. La vegetación del área corresponde a selva baja caducifolia y el clima es semicálido subhúmedo. Modelamos la ocupación ambiental de *H. variolosus*, *H. ustus*, *H. barberi* y *H. pictiventris* mediante análisis de componentes principales y estimación de densidad kernel, calculamos el solapamiento de nicho utilizando el índice D de Schoener y modelamos la distribución geográfica de cada especie mediante el algoritmo de máxima entropía.

Resultados: El 25 de octubre de 2024 capturamos un macho de *H. variolosus* con una longitud de 25.4 mm. Se detectó un solapamiento de nicho significativo únicamente entre *H. variolosus* y *H. ustus*. *Hypopachus barberi* se distingue de las demás especies por su preferencia por temperaturas bajas, mientras que *H. pictiventris* se caracteriza por habitar en zonas con altos niveles de precipitación. *Hypopachus variolosus* presenta el rango de distribución más amplio, desde Texas hasta el oeste de Panamá, seguido de *H. ustus*, que se extiende desde las costas del Golfo de México y el Pacífico hasta Nicaragua. *Hypopachus barberi* se distribuye desde el estado de Chiapas en México, hasta el norte de Nicaragua, mientras que *H. pictiventris* es la especie con el rango más restringido, habitando desde el sureste de Nicaragua hasta el oeste de Panamá.

Conclusiones: Nuestros resultados sugieren que las variables meso- y microclimáticas pueden desempeñar un papel clave en la reducción de la competencia entre especies simpátricas de *Hypopachus*. Además, las condiciones de altas temperaturas y baja precipitación predominantes en México y Centroamérica favorecen la amplia distribución de *H. variolosus* y *H. ustus*.

Palabras clave: ordenación ambiental; Ranas ovejeras; modelo de distribución de especies, Estado de México, Tonatico.

INTRODUCTION

Microhylidae is one of the most diverse and complex amphibian families, comprising up to 769 species in 58 genera (Frost, 2026). In the Americas, this family includes three subfamilies: Adelastinae (distributed in South America), Otophryinae (South America), and Gastrophryinae (from the United States of America to Argentina, De Sá et al., 2012; AmphibiaWeb, 2025). The subfamily Gastrophryinae includes 12 genera with 80 species, among them the genus *Hypopachus* (Kerferstein 1867), commonly known as Sheep Frogs. This genus consists of five species: *Hypopachus barberi* (Barber's Sheep Frog, Schmidt 1939), *Hypopachus pictiventris* (Nicaragua Narrowmouth Toad, Cope 1886), *Hypopachus ustus* (Two-spaded Narrowmouth Toad, Cope 1886), *Hypopachus variolosus* (Mexican Narrowmouthed Toad, Cope 1886), and the recently described *Hypopachus guancasco* (Firneno et al. 2020), commonly called the Lenca Sheep Frog (De Sá et al., 2012; Firneno et al., 2020; Frost, 2026).

Sheep Frogs are a relatively unknown group of small, fossorial anurans distributed

from Texas to Panama (Greenbaum et al., 2011; Frost, 2026). *Hypopachus* species exhibit globular bodies with mostly opaque dorsal coloration. Citing to Greenbaum et al. (2011) "their secretive habits and brief reproductive seasons contribute to their rarity in collections" limiting our knowledge of their natural history. One of the most studied aspects of *Hypopachus* is its evolutionary relationships within the genus and the Microhylidae family (Greenbaum et al., 2011; De Sá et al., 2012; Firneno et al., 2020). Phylogenetic analyses indicate that *H. ustus*, previously classified as *Gastrophryne usta*, represents the most basal lineage within *Hypopachus*, whereas *H. barberi* and the recently described *H. guancasco* form a more derived clade (Greenbaum et al., 2011; De Sá et al., 2012; Firneno et al., 2020).

Despite well-established phylogenetic and taxonomic frameworks, the ecology of *Hypopachus* species remains largely understudied. *Hypopachus variolosus* and *H. ustus* are among the better-known species within the genus. For *H. variolosus*, recent studies have reported new localities (Tres Mariás Islands, Nayarit, Mexico, Chaculá, Huehuetenango, Guatemala, Parque Walter Thilo Deininger, La

Libertad, El Salvador) (De la Torre et al., 2010; Ruballo-Marroquín & Morán-Hidalgo, 2013; Eisermann, 2017), arboreal foraging behavior (Meléndez-Cumí & Nahuat-Cervera, 2023), and the first documented case of ectromelia in the species (Díaz-García & Reyes-Servín, 2023). *Hypopachus ustus* was recently recorded after four decades without sightings in the state of Sinaloa, Mexico (Castro-Bastidas et al., 2023), and its habitat suitability was described for the first time in Guerrero, Mexico. (González-Fernández et al., 2022). Additionally, at local and landscape scales, the occurrence and activity of *H. ustus* have been associated with warmer conditions and reduced precipitation and negatively affected by increasing urbanization and landscape modification (Luna-Gómez et al., 2017; Ramírez-Arce et al., 2022). In contrast, *H. barberi*, *H. guancasco*, and *H. pictiventris* remain scarcely studied. *Hypopachus barberi* has not been the focus of recent research beyond its phylogenetic relationships, *H. guancasco* has only been mentioned in its original description (Firreno et al., 2020), and *H. pictiventris* has been studied in terms of vocalization analysis and skin microbiota composition (Abarca et al., 2018; Twining & Cossel, 2021). Except for *H. ustus*, no detailed studies have examined the ecological relationships of these species with their environment.

The ecological niche is commonly defined as the set of environmental conditions under which a species can maintain viable populations, conceptualized as an n-dimensional hypervolume of ecological requirements (Hutchinson, 1957). Within this framework, the fundamental niche represents the full range of abiotic conditions suitable for species persistence, whereas the realized niche reflects the portion effectively occupied in nature after constraints imposed by biotic interactions and dispersal limitations (Soberón & Peterson, 2005; Peterson et al., 2011). Ecological niche modeling uses species occurrence data and environmental predictors to characterize this realized climatic niche in environmental space and to project it geographically as areas of environmental suitability (Soberón & Peterson, 2005; Peterson et al.,

2011). By linking environmental conditions to species distributions, this approach provides a quantitative framework to examine ecological differentiation, geographic distribution limits, and the degree of niche overlap among related taxa (Elith & Leathwick, 2009; Peterson et al., 2011). Niche overlap refers to the degree to which species occupy similar regions of environmental space, and it is widely used to infer ecological similarity, potential competition, and mechanisms of coexistence or environmental differentiation among taxa (Schoener, 1968; Warren et al., 2008; Broennimann et al., 2012).

Understanding niche overlap, geographic overlap, and environmental preferences in *Hypopachus* species is crucial to address the limited ecological information available for most species in the genus, particularly regarding their environmental requirements and distribution patterns. These aspects provide valuable insights into habitat use, potential interspecific competition, and ecological requirements (Franklin, 2012; Broennimann et al., 2012), which are especially valuable for species with low detectability and limited ecological information, such as many fossorial amphibians (Baumgardt et al., 2021). Additionally, documenting species occurrences is fundamental for assessing conservation priorities, particularly for species with scarce historical records (Raxworthy et al., 2003; Guisan et al., 2013). In this context, the objectives of this study were to (i) model the geographic projection of environmental suitability for four species of the genus *Hypopachus* (*H. variolosus*, *H. ustus*, *H. barberi*, and *H. pictiventris*), (ii) identify the main climatic factors associated with their environmental preferences, and (iii) quantify the degree of niche overlap among species in environmental space and its geographic expression. Given the broad geographic ranges and partially overlapping distributions reported for some species (Greenbaum et al., 2011), we hypothesized that *Hypopachus* species would show partial niche overlap, but also environmental differentiation along key climatic gradients, particularly temperature and precipitation, reflecting distinct ecological requirements. Furthermore, we



document a new occurrence of *H. variolosus* in the State of Mexico after 66 years without confirmed records, providing updated distributional information that contributes to refining the environmental context and conservation relevance of this species.

MATERIALS AND METHODS

Occurrence data and environmental predictors: To model the environmental suitability and assess the niche overlap of four species of the genus *Hypopachus*: *H. variolosus*, *H. ustus*, *H. barberi*, and *H. pictiventris* (excluding *H. guancasco* due to the insufficient number of available occurrence records), we employed the Wallace R-based interface (Kass et al., 2023), which integrates various packages for ecological niche modeling and environmental space characterization. Occurrence data were retrieved from the Global Biodiversity Information Facility (GBIF.org, 2026) using the spocc (Owens et al., 2024) package, setting a maximum query of 1 000 occurrence records per species. After removing duplicate records and those without uncertainty values, occurrence data were further curated to minimize potential taxonomic and geographic errors. Records were cross-checked against the current taxonomy and known geographic distributions of each species based on Greenbaum et al. (2011) and Firreno et al. (2020). Occurrences located outside the documented distribution ranges or in regions where species presence is considered unlikely were carefully reviewed and excluded when necessary. No temporal filtering was applied, since historical records can provide valuable information for characterizing species climatic niches when geographic accuracy is verified. Final dataset sizes were: 512 entries for *H. variolosus*, 143 for *H. ustus*, 43 for *H. barberi*, and 30 for *H. pictiventris*. Bioclimatic variables were obtained from WorldClim version 2 (Fick & Hijmans, 2017) at a resolution of 2.5 arc-minutes through the raster (Hijmans, 2025) and geodata (Hijmans et al., 2025) packages in R. These variables include temperature descriptors (e.g., annual mean temperature, thermal

extremes, and variability) and precipitation descriptors (e.g., annual precipitation, seasonality, and extreme conditions). The selected variables (Bio1, Bio2, Bio3, Bio5, Bio6, Bio7, Bio8, Bio9, Bio12, Bio14, Bio15, and Bio19) were chosen based on a preliminary correlation analysis conducted in Google Earth Engine (see supplementary SMT 1), aiming to reduce multicollinearity among predictors, considering a threshold value of $|r| < 0.8$, while retaining those with known ecological relevance for amphibian distribution. Although Bio6 showed high correlation with BIO1 and BIO7, it was retained due to its ecological relevance as a proxy for minimum thermal tolerance. Spatial thinning of occurrence points was conducted using the spThin (Aiello-Lammens et al., 2015) package to assess potential sampling bias and spatial over-representation. A minimum distance of 1 km between occurrence records was applied as an exploratory filtering criterion, no records were removed during this process, indicating an absence of clustered occurrences at this spatial scale. The study region was delineated to encompass the known distribution range of the genus, including Southern United States, Mexico, Central America, and Panama. Within this extent, 1 000 background points were randomly sampled per species to represent the environmental background for model calibration.

Environmental suitability modeling:

The environmental suitability models were calibrated using the maximum entropy algorithm (Phillips et al., 2006) implemented in the maxnet package (Phillips, 2021) through ENMeval (Muscarella et al., 2014). A spatial partitioning scheme with four spatial blocks ($K = 4$) was applied to partition the occurrence data into training and testing subsets, following a block cross-validation strategy to account for spatial autocorrelation. Regularization multipliers between 1 and 2 were tested with a step value of 1, and linear, quadratic, hinge, and product feature classes (LQHP) were used to allow flexible model responses. Clamping was enabled to prevent extrapolation to

environmental conditions outside the observed range, and parallelization was disabled to ensure consistent reproducibility. The models were evaluated employing the area under the curve metric. Finally, binary presence-absence maps were generated by applying the 10th percentile training presence threshold, which excludes the lowest 10 % of occurrence suitability values to account for potential errors in occurrence data while producing conservative estimates of the environmental suitability model.

Environmental space characterization and niche overlap: To evaluate niche overlap between species, we employed a series of procedures based on ordination methods and kernel density estimation, implemented in the R packages *ade4* (Thioulouse et al., 2018), *ecospat* (Di Cola et al., 2017), and *ks* (Duong, 2007). Principal Component Analysis (PCA) was conducted using the *dudi.pca* function from the *ade4* package including only the selected bioclimatic variables after depuration. The analysis was based on a correlation matrix, with the arguments *center* and *scale* both set to *TRUE*, ensuring that all environmental predictors received equal weight regardless of their units or scales (Legendre & Legendre, 2012). This approach yields a standardized environmental space where distances between occurrence points approximate Mahalanobis distances, providing a more ecologically relevant measure of dissimilarity (Legendre & Legendre, 2012; Broennimann et al., 2012). To estimate the density of occurrences in the environmental space, we employed the kernel density estimation method detailed by Broennimann et al. (2012) and implemented in the *ecospat.grid.clim.dyn* function of the *ecospat* package (Di Cola et al., 2017). The environmental space was represented by a 100×100 grid generated from the first two PCA axes, where the *x* and *y* axes correspond to PC1 and PC2, respectively. For each grid cell, the density of occurrences and background points was estimated using the *kde* function from the *ks* package (Duong, 2007), providing a smoothed representation of species utilization across environmental gradients.

To evaluate differences in climatic conditions among species, the values of the selected bioclimatic variables were extracted for all occurrence records. The distribution of each variable across species was explored using box-and-whisker plots to visualize central tendency, dispersion, and potential outliers. Because sample sizes differed among species and the distribution of several variables departed from normality, differences in bioclimatic conditions among species were evaluated using non-parametric tests. For each variable, a Kruskal–Wallis test was performed to assess overall differences among species. When significant differences were detected, pairwise comparisons were conducted using Wilcoxon rank-sum tests with Benjamini–Hochberg correction to account for multiple testing. These analyses and graphical visualizations were performed in R.

Niche overlap was quantified using Schoener's *D* implemented through the *ecospat.niche.overlap* function in the *ecospat* package (Di Cola et al., 2017). Schoener's *D* (Schoener, 1968) is calculated as:

$$D = 1 - 0.5 \sum_{i=1}^n |PX_{it} - PY_{it}|$$

where PX_{it} and PY_{it} represent the proportions of occurrences in the environmental category for species *X* and *Y*, respectively. This metric ranges from 0 (no overlap) to 1 (complete overlap).

Additionally, binary overlap indices (*BinOv*, $\text{BinOv1} \geq 2$, and $\text{BinOv2} < 1$) were calculated using the *ecospat.niche.dyn.index* function. These indices were originally developed to study niche changes in biological invasions (Guisan et al., 2014). *BinOv* estimates the proportion of environmental space shared by two species, whereas the directional indices $\text{BinOv1} \geq 2$ and $\text{BinOv2} < 1$ quantify the degree of niche inclusion between species. These metrics allow evaluation of overall niche similarity as well as asymmetric overlap and differences in niche breadth (Guisan et al., 2014). To assess whether the observed niche overlap was greater than expected by chance, we conducted a niche

similarity test following the method proposed by Warren et al. (2008). This test randomly shifts both species' niches around the background extent and recalculates the overlap indices for each permutation. The observed overlap is then compared to the distribution of simulated overlaps, with significance determined by a one-tailed test ($p < 0.05$). If the observed overlap exceeds 95 % of the simulated values, the test indicates that the two species share more similar niches than expected by random chance.

Field record documentation: We conducted fieldwork in the Niltze Ecological Park, located in the Tonatico municipality, State of Mexico, Mexico (Fig. 1A), to sample amphibian species and document the diversity in the area. After the sampling period, we took standardized photographs of everyone from three different planes (frontal, dorsal, and lateral) later used for the identification of organisms. All the individuals collected were released in

the exact place where they were sighted. Niltze Ecological Park is in the Southern region of the State of Mexico and is characterized by extensive areas of low deciduous forest under a semi-warm subhumid climate. The park is considered a well-conserved zone surrounded by natural areas and a rural population patch from Tonatico. However, the municipality's growth is increasingly directed toward this area. The occurrence of *H. variolosus* detected during this survey was incorporated into the study to update its known distribution and to provide an independent field record within the environmental context identified by the species environmental suitability model.

RESULTS

Environmental suitability modeling:

Based on binary geographic projections of environmental suitability derived using the 10th percentile training presence threshold, The areas of environmental suitability of *Hypopachus*

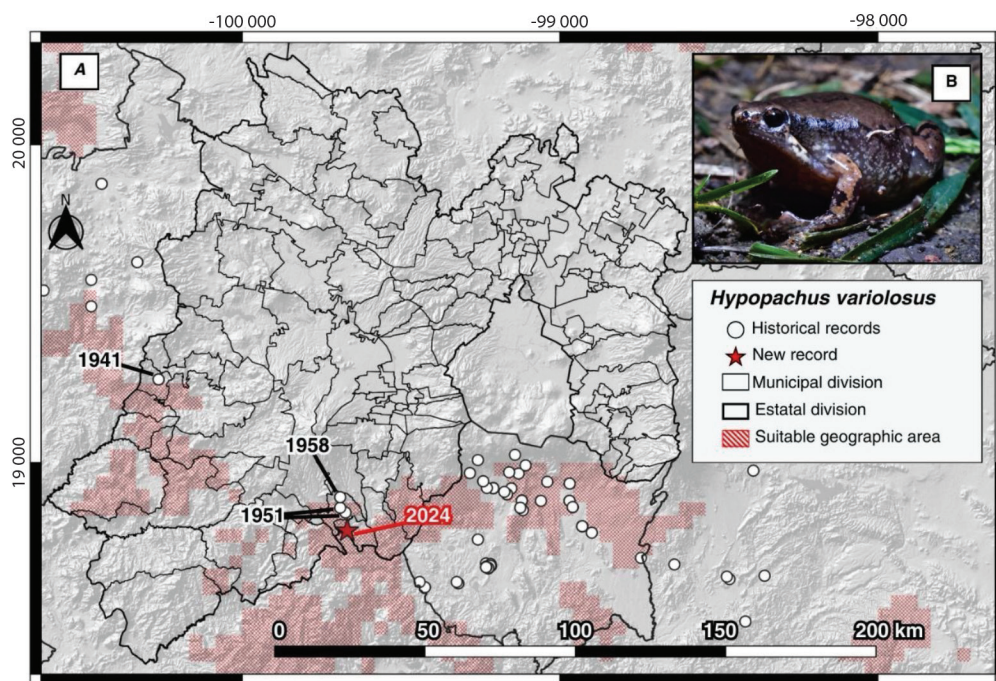


Fig. 1. A. Historical records of *Hypopachus variolosus* in the State of Mexico, the suitable geographic area for the species and the new 2024 record in Tonatico. B. Photograph of a male *H. variolosus* in Niltze Ecological Park, Tonatico, State of Mexico.

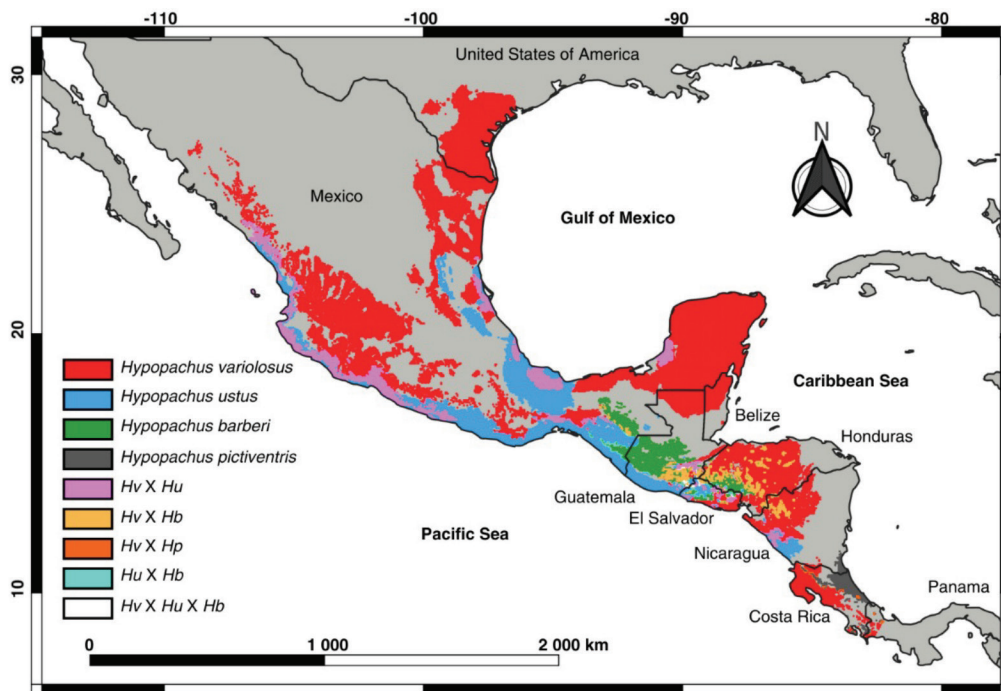


Fig. 2. Geographic projection of environmental suitability of the four *Hypopachus* species across their entire range, highlighting areas of distribution overlap. Hv = *H. variolosus*, Hu = *H. ustus*, Hb = *H. barberi*, and Hp = *H. pictiventris*.

variolosus extends from Southern Texas in the United States to Western Panama, encompassing Mexico (Sierra Madre Occidental, Sierra Madre Oriental, Sierra Madre del Sur, Trans-Mexican Volcanic Belt, Yucatán Peninsula, and most of the Pacific and Gulf of Mexico coasts), Guatemala (Northern Petén, Northeastern, and Southeastern regions), Belize (mainly Corozal and Orange Walk, with scattered distribution in Stann Creek), El Salvador (across most of the country), Honduras (except the Northwestern region), Nicaragua (excluding most of the Atlantic lowlands), and Costa Rica (primarily in the Pacific lowlands). *Hypopachus ustus* ranges from Mexico to Nicaragua, occupying the coastal lowlands of all intervening Central American countries, except Belize. Its environmental suitability in Honduras is restricted to the Western Valle de Sula and Lempa regions, while its distribution in Nicaragua appears isolated from the rest of its range. *Hypopachus*

barberi occurs from Southern Mexico (limited to the state of Chiapas) to Northwestern Nicaragua, passing through Guatemala, Honduras, and El Salvador, largely avoiding the range of *H. ustus*. Finally, *Hypopachus pictiventris* is distributed from Southeastern Nicaragua to Western Panama, occupying most of the Caribbean lowlands of Costa Rica while avoiding the Northern Pacific lowlands of the country (Fig. 2). The AUC values of the environmental suitability models indicate high reliability across all models: *H. variolosus* = 0.89, *H. ustus* = 0.94, *H. barberi* = 0.98, and *H. pictiventris* = 0.99.

Environmental space characterization and niche overlap: The first two PCA axes explained 71.41 % of the total variance in environmental conditions (PC1 = 47.86 %, PC2 = 23.54 %). PC1 was mainly associated with temperature level and seasonal moisture, showing high positive loadings for annual mean

temperature (Bio01), minimum temperature of the coldest month (Bio06), mean temperature of the driest quarter (Bio09), and annual precipitation (Bio12), and negative loadings for temperature variability, including mean diurnal range (Bio02) and annual temperature range (Bio07). PC2 was primarily related to heat intensity and thermal stability, with strong positive contributions from maximum temperature of the warmest month (Bio05) and mean temperature of the wettest quarter (Bio08), and negative contributions from isothermality (Bio03). These gradients indicate that temperature-related variables differentiate the environmental space occupied by *H. variolosus* and *H. ustus*, whereas variation in thermal stability and seasonal heat conditions distinguishes *H. barberi*. Precipitation-related variables, particularly annual and seasonal precipitation, separate *H. pictiventris* from the remaining species (Fig. 3).

These patterns are consistent with the climatic conditions at species occurrence points in which the distribution of bioclimatic conditions

differed significantly among species for all the studied variables according to the Kruskal–Wallis test (see SMT 2). Pairwise comparisons revealed that *H. pictiventris* differed significantly from the remaining species across most precipitation-related variables, reflecting its restriction to warm and humid environments. In contrast, climatic differences between *H. variolosus* and *H. ustus* were generally smaller, consistent with their partial niche overlap (see SMT 3). The distribution of bioclimatic values at occurrence points provides an empirical representation of species-specific environmental responses, allowing identification of the climatic conditions most strongly associated with each species without relying solely on model-derived response curves. *Hypopachus ustus* ($\bar{X} = 25.36\text{ }^{\circ}\text{C}$) occurs in warmer annual mean temperatures than *H. variolosus* ($\bar{X} = 23.23\text{ }^{\circ}\text{C}$), but similar to *H. pictiventris* ($\bar{X} = 25.57\text{ }^{\circ}\text{C}$). Conversely, *H. barberi* inhabits its cooler environments ($\bar{X} = 18.49\text{ }^{\circ}\text{C}$). The mean diurnal temperature range is highest in *H. variolosus* ($\bar{X} = 12.40\text{ }^{\circ}\text{C}$) compared to the

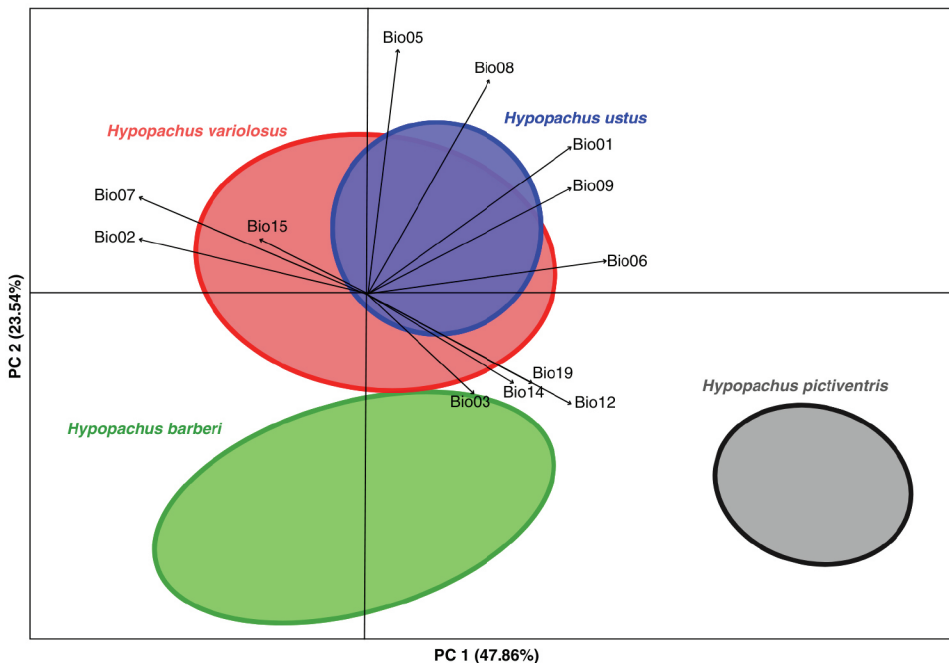


Fig. 3. Principal component analysis and scree plot illustrating the environmental ordination and overlap between the four *Hypopachus* species studied.

other species (*H. ustus* $\bar{X}$ = 11.74 °C, *H. barberi* $\bar{X}$ = 11.37 °C, *H. pictiventris* $\bar{X}$ = 8.14 °C). Isothermality is greatest in *H. pictiventris* ($\bar{X}$ = 76.10 %) and lowest in *H. variolosus* ($\bar{X}$ = 59.22 %), with intermediate values in *H. ustus* ($\bar{X}$ = 67.94 %) and *H. barberi* ($\bar{X}$ = 70.50 %). The maximum temperature of the warmest month is similar between *H. variolosus* and *H. ustus* ($\bar{X}$ = 33.86 °C and $\bar{X}$ = 33.76 °C respectively), followed by *H. pictiventris* ($\bar{X}$ = 31.20 °C) and last, *H. barberi* ($\bar{X}$ = 26.55 °C). A similar pattern is observed in the minimum temperature of the coldest month which is highest for *H. pictiventris* ($\bar{X}$ = 20.50 °C), lower for *H. barberi* ($\bar{X}$ = 10.39 °C) and *H. variolosus* ($\bar{X}$ = 11.83 °C), and with intermediate values in *H. ustus* ($\bar{X}$ = 16.33 °C). The annual temperature range is widest in *H. variolosus* ($\bar{X}$ = 22.02 °C), while *H. pictiventris* supports the narrowest range ($\bar{X}$ = 10.69 °C), consistent with its preference for more stable warm environments. *H. ustus* ($\bar{X}$ = 17.43 °C) and *H. barberi* ($\bar{X}$ = 16.15 °C) occupy intermediate ranges. During the wettest quarter, *H. variolosus* ($\bar{X}$ = 25.50 °C), *H. ustus* ($\bar{X}$ = 26.47 °C), and *H. pictiventris* ($\bar{X}$ = 25.52 °C) experience similar temperatures, whereas *H. barberi* prefers colder temperatures ($\bar{X}$ = 19.18 °C). In the driest quarter, *H. pictiventris* ($\bar{X}$ = 26.19 °C) tolerates the highest temperatures, followed by *H. ustus* ($\bar{X}$ = 24.20 °C), *H. variolosus* ($\bar{X}$ = 20.73 °C), and *H. barberi* ($\bar{X}$ = 17.69 °C). *Hypopachus pictiventris* requires higher annual precipitation volumes ($\bar{X}$ = 3511 mm) than the other species (*H. variolosus* $\bar{X}$ = 1060 mm, *H. ustus* $\bar{X}$ = 1538 mm, *H. barberi* $\bar{X}$ = 1727 mm). This pattern is mirrored in the precipitation of the driest month (*H. pictiventris* $\bar{X}$ = 109 mm, *H. barberi* $\bar{X}$ = 25 mm, *H. variolosus* $\bar{X}$ = 20 mm, *H. ustus* $\bar{X}$ = 12 mm). Regarding precipitation seasonality (coefficient of variation), *H. ustus* exhibits the highest variation ($\bar{X}$ = 97.59 %), followed by *H. barberi* ($\bar{X}$ = 82.70 %) and *H. variolosus* ($\bar{X}$ = 68.97 %), while *H. pictiventris* supports only low precipitation variability ($\bar{X}$ = 38.57 %). Finally, during the coldest month, *H. pictiventris* receives the highest precipitation volumes ($\bar{X}$ = 1014 mm) compared to the other

species (*H. variolosus* $\bar{X}$ = 139 mm, *H. ustus* $\bar{X}$ = 86 mm, *H. barberi* $\bar{X}$ = 144 mm; Fig. 4).

Regarding ecological niche overlap, the occurrence density grids of the four species demonstrate that *H. variolosus* and *H. ustus* exhibit higher occurrence densities under environmental conditions associated with the positive region of axis 2, while *H. barberi* and *H. pictiventris* predominantly occupy environmental conditions embedded in the negative region of axis 2 and the negative and positive regions of axis 1, respectively (Fig. 5A). These patterns indicate differential occupation of the environmental space among species, except for *H. variolosus* and *H. ustus*. This result is supported by the Schoener's D metric, which was higher between these species ($D = 0.35$) compared to the other species pairs ($D < 0.1$; Fig. 5A). Binary overlap indices provided additional information on the structure and directionality of the shared environmental space among species (Fig. 5A). For the pair *H. variolosus*–*H. ustus*, the results indicated a clearly asymmetric pattern, with a larger proportion of the niche of *H. ustus* contained within the broader environmental space occupied by *H. variolosus*. In comparisons involving *H. barberi*, overlap values were generally low in terms of Schoener's D, yet the binary indices suggest partial niche inclusion with other species. In contrast, species pairs involving *H. pictiventris* showed the weakest overlap structure, characterized by minimal niche inclusion and near absence of shared environmental space with the remaining species, particularly in comparison with *H. barberi* and *H. ustus* (Fig. 5A). Likewise, the niche similarity test revealed that only the niche overlap between *H. variolosus* and *H. ustus* was more similar than expected by random (Fig. 5B). Despite this, niche overlap exists among some species pairs, except between *H. ustus* and *H. pictiventris*, and between *H. barberi* and *H. pictiventris* (Fig. 5A).

Field record documentation: On 25 October 2024, we captured a frog at coordinates 18.78594, -99.66955 (WGS84), within the Niltze Ecological Park (Fig. 1A). The specimen

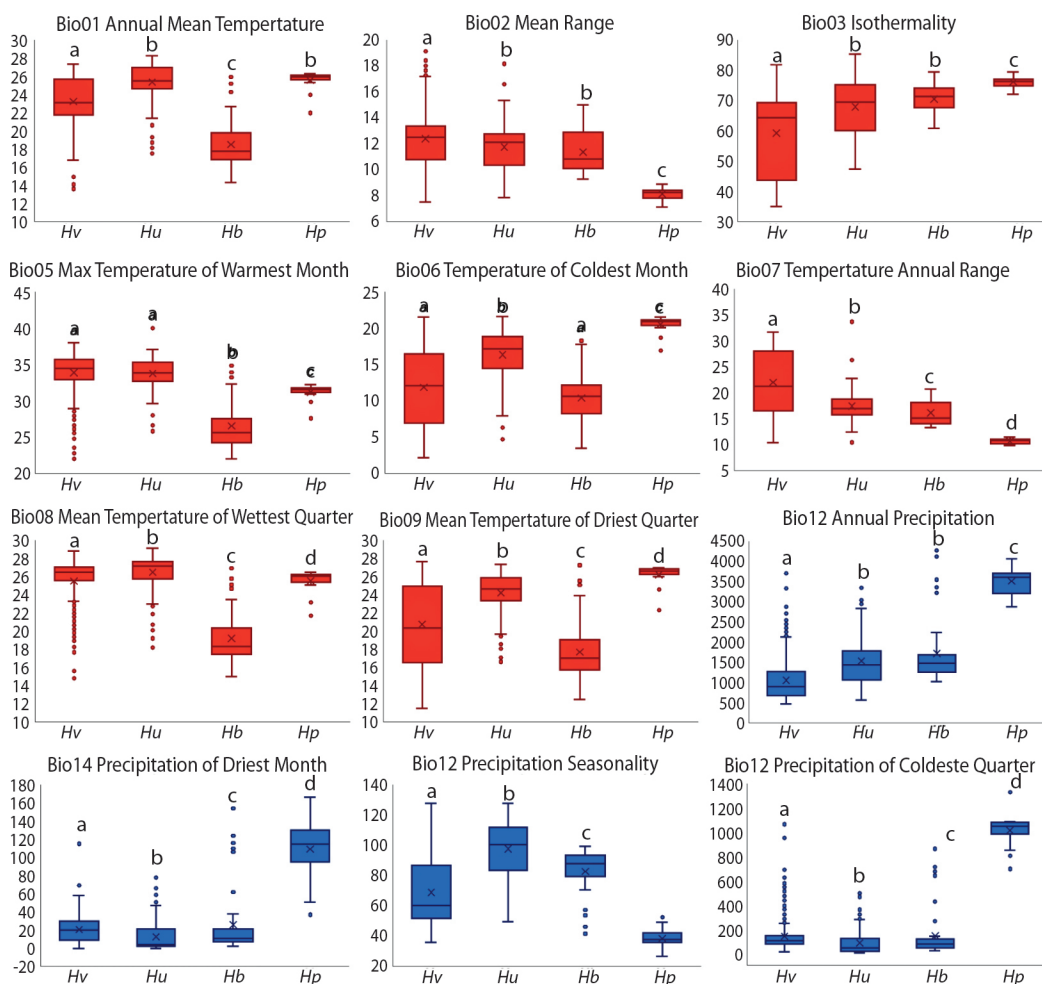


Fig. 4. Box-and-whisker plots show the environmental conditions occupied by each *Hypopachus* species. Hv = *H. variolosus*, Hu = *H. ustus*, Hb = *H. barberi*, and Hp = *H. pictiventris*. Red colors represent temperature related variables; blue colors represent precipitation related variables.

measured 25.4 mm and was sexed as a male based on the presence of a nuptial pad, dermal spines on the toes, and size (Nelson, 1974).

The individual was initially identified by EARV as *Hypopachus variolosus* Cope, 1866, based on its geographical distribution and morphological traits, including a small head, globose body, and size. This identification was later validated by Dr. Víctor H. Jiménez-Arcos from the *Laboratorio de Herpetología, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México*, based on the dorsal

coloration pattern (which is more diffused in *H. variolosus* compared to *H. ustus*, where the pattern forms a well-defined “Christmas tree” shape) and the size relationship between the metatarsal tubercles and foot length (*H. ustus* has proportionally larger metatarsal tubercles than *H. variolosus*). The individual, now confirmed as *H. variolosus* (Fig. 1B), was found on a soccer field, less than one meter from a cement structure forming the floor of a grocery and food store. Although the site appears disturbed, it is located approximately 15 m from

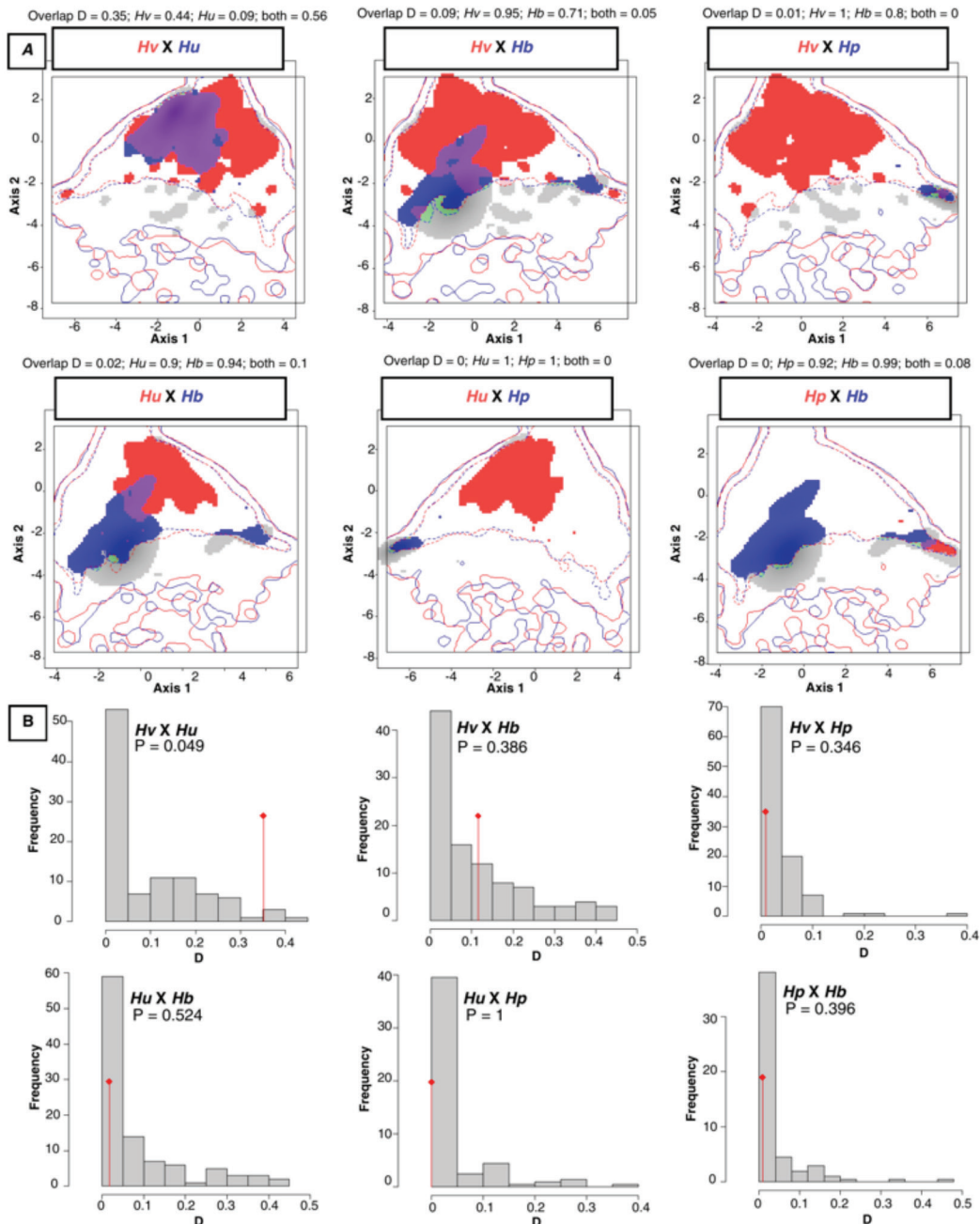


Fig. 5. A. Niche overlap between the studied *Hypopachus* species based on the occurrence density grid. Red represents the environmental space occupied by species 1, blue represents that of species 2, and purple indicates areas where both species overlap. Shaded areas outside the darkest colors represent the available environmental background, with darker tones corresponding to the 50 % highest occurrence density for each species. The values above each niche overlap graph correspond to Schoener's D metric and the binary overlap indices (BinOv, proportion of shared environmental space; BinOv1>2 and BinOv2<1, directional niche inclusion between species). **B.** Similarity test results: the red line represents the observed overlap, and if it exceeds 95 % of the simulated overlaps ($p < 0.05$), the two species are considered more similar than expected by chance. *Hv* = *Hypopachus variolosus*, *Hu* = *H. ustus*, *Hb* = *H. barberi*, and *Hp* = *H. pictiventris*.



a body of water with good quality (Ph: 7, hardness: 250 ppm, negative to coliforms, hydrogen sulfide: 0 ppm, lead: 0.5 ppb, cooper: 0 ppm, mercury: 0 ppm, total chlorine: 0 ppm, nitrate: 0 ppm, nitrite: 0 ppm, fluoride: 4 ppm), embedded within a well-preserved deciduous lowland forest. The new occurrence of *H. variolosus* in the Niltze Ecological Park was environmentally consistent with the climatic conditions observed across the species' distribution. Bioclimatic values at this locality fell within the observed range for most predictors and were consistently contained within the 5-95 % percentile interval of occurrence records (see SMT 4). Furthermore, the locality was located within the area of environmental suitability predicted by the species distribution model (Fig. 1A), supporting the climatic representativeness of this record within the environmental suitability of the species.

DISCUSSION

Both the geographic projections of environmental suitability and occurrence density grid indicate differences in environmental breadth among species. *Hypopachus variolosus* occupies the widest range of environmental conditions, followed by *H. barberi* and *H. ustus*, whereas *H. pictiventris* is restricted to warm and humid environments in Nicaragua, Costa Rica, and Panama. Despite its relatively constrained environmental space in the PCA, *H. ustus* exhibits a broad geographic distribution, suggesting that it occupies extensive lowland areas characterized by similar climatic conditions rather than a wide range of environmental gradients. This pattern is consistent with the high temperatures and relatively homogeneous climatic conditions along the Pacific and Gulf coastal regions of Mexico and Central America, among the warmest areas in Mesoamerica (Karmalkar et al., 2011), which are consistent with the climatic conditions identified as suitable for *H. ustus*.

Interestingly, the only significant niche overlap observed occurs between *H. variolosus* and *H. ustus*, despite their phylogenetic

distance. *Hypopachus ustus* represents a basal lineage within the genus, closely related to *H. pictiventris*, while *H. variolosus* forms a clade with *H. barberi* and the recently described *H. guancasco* (Firneno et al., 2020). This pattern suggests that heat tolerance and low precipitation requirements represent ancestral climatic traits within *Hypopachus*, whereas the ability of *H. barberi* to tolerate lower temperatures and the dependence of *H. pictiventris* on high precipitation reflect ecological divergence and climatic specialization (see phylogeny in Firneno et al., 2020). Together, these results are consistent with niche dynamics in which some environmental tolerances are conserved over evolutionary time (niche conservatism), while others shift or contract in response to environmental gradients, leading to lineage-specific ecological differentiation and, in some cases, increased climatic specialization (Peterson et al., 1999; Wiens & Graham, 2005; Pearman et al., 2008). Similar patterns of phylogenetically structured climatic niches have been reported in other amphibians, including niche conservatism constraining elevational distributions in Plethodontidae salamanders and ecological divergence along climatic gradients among closely related species of Dendrobatidae (Kozak & Wiens, 2010; Graham et al., 2004). The convergence of *H. variolosus*, *H. ustus*, and *H. barberi* within the Sierra Madre de Chiapas in Guatemala, Honduras, and El Salvador suggests that this mountain range may have acted as a regional diversification corridor. Phylogeographic evidence indicates that diversification within *Hypopachus* occurred during the late Miocene and Pliocene and is strongly associated with geographic structuring across Mesoamerica, consistent with historical isolation and environmental heterogeneity promoting lineage differentiation (Greenbaum et al., 2011). Mountain systems such as the Sierra Madre de Chiapas likely provided climatic gradients and dispersal barriers that facilitated ecological divergence, a pattern also documented for other tropical amphibians (Hua and Wiens, 2010).

The limited niche overlap among *Hypopachus* species in terms of environmental variables

indicates differentiation in their macroclimatic niches across their geographic ranges. Because our analyses were based on macroclimatic variables, the mechanisms underlying coexistence at local scales remain uncertain. Nevertheless, when species overlap geographically, similarities in key ecological and behavioral traits, such as the use of temporary ponds for reproduction during the rainy season (Reyes-Velasco, 2024; International Union for Conservation of Nature [IUCN], 2025; Universidad Francisco Marroquín, n.d.), similar call durations and frequencies (except for *H. ustus*; Twinning & Cossel, 2021), and comparable use of leaf litter and underground refuges (Twinning & Cossel, 2021; Reyes-Velasco, 2024; IUCN 2025), suggest that factors operating at finer ecological scales may influence local coexistence.

However, crucial aspects of the ecology of these species remain unexplored. For instance, dietary partitioning could play a key role in maintaining sympatry, yet only the diet of *H. variolosus* has been documented, consisting primarily of ants and termites (Mulaik & Sollberger, 1938), while the diets of the other species remain unknown. Other factors, such as differences in activity patterns or vegetation preferences, could further contribute to resource partitioning. Although broad-scale climatic variables provide a useful framework for explaining general distribution patterns, they are not the sole determinants of species occurrence or coexistence. Local ecological factors, such as microhabitat availability, vegetation structure, and resource use, may further influence species distributions. Overall, our knowledge of Mexican microhylids remains limited, and further research is necessary to fully understand the ecological interactions and distribution patterns of these species.

In 1941, two individuals of *Hypopachus variolosus* were collected from Ixtapan del Oro, 82 km from our 2024 record in Tonatico. These specimens were deposited in the collection of the Escuela Nacional de Ciencias Biológicas (ENCB) at the Instituto Politécnico Nacional, under catalogue numbers 2 905 and 2 906. Later, in 1951, two additional larval individuals

were collected from Ixtapan de la Sal, located six and eight km from our record, and were deposited in the American Museum of Natural History (AMNH) under catalogue numbers A-55217 and A-55218. The last known record of *H. variolosus* in the State of Mexico dates to 1958, also from Ixtapan de la Sal, corresponding to a specimen stored in the University of Michigan Museum of Zoology (UMMZ) under catalogue number 118902. Our 2024 record represents the first formal occurrence of this species in the State of Mexico after 66 years and the first record for the species in the Tonatico municipality. This finding highlights the importance of systematic surveys in historically under-sampled regions and contributes to filling distribution gaps for amphibians in central Mexico. Furthermore, the detection of *H. variolosus* in a peri-urban setting underscores its ability to persist in moderate modified environments. This finding is consistent with its broad geographic distribution and indicates a relatively wide environmental tolerance. Although the park is relatively well preserved, it is embedded within a landscape undergoing increasing land-use pressure associated with urban expansion. Small, protected areas like the Niltze Ecological Park, embedded within fragmented landscapes, can serve as important refuges for amphibians, particularly in regions where urbanization and agricultural expansion threaten natural ecosystems (Cushman, 2006; Hamer & McDonnell, 2008).

To our knowledge, this study is the first to describe the environmental conditions utilized by the four *Hypopachus* species together, providing a complete assessment of their environmental suitability maps, and quantify their niche overlap. As fossorial amphibians, these species are often understudied, making our results a valuable contribution to identifying the climatic conditions associated with their occurrence. By defining their environmental requirements and niche breadth, ecological niche models provide a baseline for inferring how changes in climate or habitat availability may affect the extent and location of suitable areas, thereby supporting assessments of species



vulnerability or persistence under environmental change. Despite this progress, critical aspects of their ecology remain unknown, including dietary specialization, microhabitat preferences, and interspecific interactions. Future studies integrating ecological, behavioral, and physiological data will be essential to fully understand the factors shaping their distribution and coexistence, ultimately improving conservation strategies for this poorly known group.

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See supplementary material
a34v74n1-Suppl 1

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