NEOTROPICAL BIOLOGY AND CONSERVATION

Neotropical Biology and Conservation 21(3): 223–243 (2026)
DOI: 10.3897/neotropical.21.e187054

Research Article

The role of environmental heterogeneity in the diversity of the amphibian fauna of the Transmexican Volcanic Belt

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Abstract

Mexico's complex topography, variety of climates, geological history, and geographic position combine to produce heterogeneity in the amphibian fauna of biogeographic regions such as the Transmexican Volcanic Belt (TVB), a physiographic province with a semi-warm western region and a temperate eastern region. Richness, endemicity, and phylobetadiversity patterns of amphibian communities in the TVB were evaluated using different grid-cell sizes. A total of 143 species in 36 genera were studied. Species richness was higher in the eastern region than in the western region. Endemicity and phyloendemicity values were low, except in a few cells in the eastern region. The amphibian communities in the TVB comprise distinct assemblages, and biotic interactions are the primary drivers of community structure. Taxonomic and phylogenetic beta diversity indices were correlated with geographic distance, and differences in precipitation seasonality between the Last Glacial Maximum (LGM) and current conditions, as well as soil temperature, were the main factors explaining species turnover. The study results confirm that environmental heterogeneity promotes high levels of taxonomic and phylogenetic diversity among the Mexican amphibian fauna. These findings may be useful in future management and conservation efforts.

Key words: Conservation, habitat filtering, overdispersion, phylobetadiversity, phylogenetic diversity, soil temperature

OPEN ACCESS

Academic editor: Piter Boll
Received: 30 January 2026
Accepted: 21 June 2026
Published: 2 July 2026

ZooBank: https://zoobank.org/B58D19DC-D7A9-4978-9CCD-5FC8571D60F4

Citation: Gómora-Cercas J, Martínez-Méndez N, Díaz de la Vega-Pérez A, Mejía O (2026) The role of environmental heterogeneity in the diversity of the amphibian fauna of the Transmexican Volcanic Belt. Neotropical Biology and Conservation 21(3): 223–243. https://doi.org/10.3897/neotropical.21.e187054

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Introduction

Biodiversity is the product of several historical and ecological factors and is commonly quantified using taxonomic richness (e.g., species or other taxonomic ranks). However, it has been demonstrated that phylogenetic diversity (PD) can be a more informative alternative to taxonomic richness, as it provides a quantitative framework for comparing biodiversity among geographic areas and clades, allowing assessment of the degree of evolutionary history shared among those areas (Miller et al. 2018).

Among the proposed indices to assess the PD of a region, Faith's PD index (PD; Faith 1992) is one of the most widely used, although there are several other metrics, such as the phylogenetic diversity index (PDI; Tsirogiannis et al. 2012), net relatedness index (NRI; Webb et al. 2002), and nearest taxon index (NTI; Webb et al. 2002). These latter metrics also allow the evaluation of phylogenetic clustering or overdispersion of taxa (Webb et al. 2008; Sandel 2017), making it possible to identify the main processes that drive community assemblages (Graham and Fine 2008).

For example, under a phylogenetic niche conservatism scenario (Münkemüller et al. 2015), the species present in a community will be phylogenetically more closely related than would be expected by chance. This pattern is commonly attributed to habitat filtering as the main driver of community structure. If the species present in a community are less related than expected by chance, an overdispersion pattern driven by ecological interactions is revealed (Webb et al. 2002). Finally, the absence of phylogenetic structure suggests that the community is driven by neutral processes such as ecological drift (Heino 2011). However, it can also reflect scale-dependent processes or methodological flaws.

Beta (β) diversity encompasses a complex set of factors that reflect life history traits, such as reproductive strategies; ecological traits, such as vagility, niche breadth, resource use and biotic interactions; and physiographic features of the landscape, such as environmental anisotropy and geographic distance, that lead to a lack of connectivity and isolation (Rodríguez et al. 2019). Thus, β diversity studies can provide useful information about the ecological and evolutionary factors that maintain diversity (Legendre and De Cáceres 2013).

The study of β diversity can be partitioned into turnover and nestedness (Baselga 2010). Species turnover refers to the replacement of species between localities or regions due to limited dispersal and environmental conditions. In contrast, species nestedness arises when the set of species in a community is a subset of those in other regions. Nevertheless, traditional metrics based exclusively on the taxonomic facet treat species as evolutionarily independent units that are ecologically equivalent (Swenson et al. 2012). Therefore, a new approach has emerged based on the study of phylobetadiversity, which estimates the phylogenetic distance between communities in a way that allows local processes, such as biotic interactions and environmental filtering, to be related to regional processes, such as speciation and trait evolution (Graham and Fine 2008).

Improving knowledge of the causes of diversity in highly heterogeneous regions such as Mexico is a high-priority task for conservation efforts (Calderón-Patrón et al. 2016). The megadiversity of Mexico results from the combination of moderate α diversity (local) and high β diversity (between sites). Areas of high species richness and high endemism do not overlap (Koleff and Soberón 2008). β diversity is high in central and southern Mexico and varies with spatial scale, being higher at large, coarse scales (Rodríguez et al. 2019). In addition, worldwide, in taxa with low vagility, such as amphibians, the turnover component of β diversity is higher than nestedness (Baselga et al. 2012). Nevertheless, despite being well characterized as a descriptive factor, the topographic, ecological, and historical drivers of such differences have not been well explored.

The diversity of amphibians in the Transmexican Volcanic Belt (TVB) is a product of its complex geological history, its variety of climates, and its position as a transition zone between the Nearctic and Neotropical regions (Pérez-Roblero et al. 2019). The TVB is located between ca. 19°N and 21°N, with a west-

to-east orientation from Cabo Corrientes in Nayarit to Sierra de Chinconquiaco in Veracruz (Gámez et al. 2012). The TVB is 900 km long, with an average width of 130 km and a mean elevation of 2,500 m a.s.l. This physiographic province was formed over the last 19 million years through four main volcanic episodes, with the western section being the oldest and the eastern section the youngest.

The asynchronous geological events that formed the province are reflected in a heterogeneous distribution of species richness and endemism (Gómez-Tuena et al. 2005; Koleff and Soberón 2008). Several subprovinces in the TVB have been recognized. The western subprovince is characterized by semi-warm and subhumid climates. The eastern subprovince is characterized by temperate subhumid to semicold subhumid climates. The vegetation ranges from tropical deciduous forests and xerophytic shrublands to oak and pine forests (Suárez-Mota et al. 2013; Morrone 2019).

Previously published studies have examined the drivers of β diversity in the Mexican amphibian fauna, but not in the TVB. For example, Calderón-Patrón et al. (2016) analyzed the turnover rate of terrestrial vertebrates in six ecoregions of Hidalgo and found that vegetation type was a key factor. Rodríguez et al. (2019) found that β diversity was related to precipitation heterogeneity. Calderón-Patrón et al. (2024) studied patterns of β diversity among Oaxaca physiographic provinces and found that high rates of species turnover were associated with climate and soil moisture.

Given that amphibians are small ectothermic organisms that are highly dependent on environmental humidity, the following expectations were formulated:

(a) A higher proportion of Anura occurs in the western region, which is characterized by semi-warm and subhumid climates, and a higher proportion of Caudata occurs in the eastern region, which is characterized by temperate to semicold subhumid climates, reflecting different life history traits and adaptive strategies (Niehaus et al. 2006; Carroll and Carroll 2025; Hallmann and Griebeler 2020).
(b) Grid cells with high species richness do not coincide with those exhibiting high endemism levels.
(c) Communities show significant phylogenetic clustering, consistent with habitat filtering.
(d) β diversity of the amphibian fauna of the TVB is dominated by the turnover component, with geographic distance and bioclimatic variables being the main drivers.

Material and methods

The study area was the TVB, as defined by CONABIO (2025). A list of Mexican amphibian species was obtained from Ramírez-Bautista et al. (2023), and all historical collection records available in GBIF were downloaded using the dismo R package (Hijmans et al. 2017). The collection records were clipped to the TVB shapefile in QGIS (QGIS Development Team 2024), and a series of quality filters was applied to filter these records (Jin and Yang 2020). Finally, scientific names were updated and validated following the Amphibian Species of the World portal (Frost 2025).

For the phylogenetic analysis, data on 1,000 species trees occurring in the TVB were downloaded from the supertree established by Jetz and Pyron

(2018), available at VertLife (https://vertlife.org/data). Thus, a maximum clade credibility tree was obtained using TreeAnnotator (Drummond and Rambaut 2007) and converted to an ultrametric tree using the ape package 5.8 (Paradis and Schliep 2019). All analyses were performed in R (R Core Team 2023) and QGIS (QGIS Development Team 2024). The complete code and input files used are available at Figshare (https://doi.org/10.6084/m9.figshare.32411361).

The geographic space of the TVB was split using square grid cells of different sizes to incorporate geographic scale, landscape heterogeneity, and life history traits (García 2006; Hengl 2006). Grid-cell size ranged from a fine resolution (0.125° × 0.125°), which accounts for the limited dispersal and relatively small home range of amphibians, to a coarse macroecological resolution widely used in macroecology (1° × 1°), in increasing intervals of 0.125° (Liao et al. 2025), using the raster package 3.6-20 (Hijmans 2015).

A presence–absence matrix was built with the fossil package 0.4.0 (Vavrek 2011). Species richness by cell was estimated using the sqldf package 0.4-11 (Grothendieck 2017). The percentages of Anura and Caudata species in each grid cell were then estimated as the proportion of each group × 100. Weighted endemism (EI) (Crisp et al. 2001) and phylogenetic endemism (PE) (Rosauer et al. 2009) by cell were estimated using the phyloregion package 1.0.6 (Daru et al. 2020).

Phylogenetic community structure indices, PD, PDI, and the standardized effect size (SES) of phylogenetic diversity to eliminate the positive association between species richness and phylogenetic diversity, were estimated using the PhyloMeasures package 2.1 (Tsirogiannis and Sandel 2016). Meanwhile, NRI and NTI were estimated using the standardized mpd.query and mntd.query functions over 1,000 permutations in the PhyloMeasures package 2.1 (Tsirogiannis and Sandel 2016).

Taxonomic dissimilarity (βccT) (Clarke and Warwick 2001) was estimated with the function taxondive in vegan 2.6-4 (Oksanen 2024). Taxonomic and phylogenetic beta diversities (βSOR) were decomposed into their components of turnover (βSIM) and nestedness (βNES) (Baselga et al. 2018) using the functions beta.pair and phylo.beta.pair in the betapart 1.6 R package (Baselga and Orme 2012) and were classified as low, medium, or high (Mourelle and Ezcurra 1997).

To determine which variables could explain β-diversity patterns of the amphibian fauna of the TVB, a series of predictor variables from previous studies was used. The predictor variables were classified into three categories: contemporary bioclimatic, historical bioclimatic, and landscape variables.

Eight bioclimatic variables, BIO2 (mean diurnal range), BIO3 (isothermality), BIO6 (min temperature of coldest month), BIO12 (annual precipitation), BIO14 (precipitation of driest month), BIO15 (precipitation seasonality), BIO18 (precipitation of warmest quarter), and BIO19 (precipitation of coldest quarter) that describe trends and variation in temperature and precipitation (da Silva et al. 2014), were retrieved from CHELSA (Karger et al. 2017).

Differences in four bioclimatic variables related to physiological constraints of amphibians that could limit their dispersal were evaluated: BIO4D (temperature seasonality), BIO6D (min temperature of the coldest month), BIO15D (precipitation seasonality), and BIO17D (precipitation of the driest quarter). These variables were estimated as the difference between current conditions and the Last Glacial Maximum (LGM; 21,000 years ago) using CHELSA.

Finally, seven landscape variables, geographic distance, slope, evapotranspiration rate, aridity index, NDVI (normalized difference vegetation index), soil

temperature, and soil moisture, were included as predictor variables (Cushman 2006; Lion et al. 2019; Rodríguez et al. 2019; Hong et al. 2025). Geographic distances were estimated using the haversine distance between grid-cell centroids in the geosphere R package 1.6-8 (Hijmans 2026). Slopes were estimated from a digital elevation model with the raster terrain analysis tool in QGIS.

Potential evapotranspiration and aridity indices were downloaded from the Global Aridity Index and Potential Evapotranspiration (ET_0) Database, version 3.1 (Zomer et al. 2022). Finally, NDVI, as well as soil temperature and moisture, were generated in Google Earth Engine (GEE) using ad hoc scripts in the JavaScript API (Gorelick et al. 2017).

Vegetation was quantified using NDVI derived from multispectral satellite imagery processed in GEE for the period 1990–2024 using surface reflectance imagery from Landsat 5, Landsat 7, Landsat 8, and Landsat 9 Collection 2 Level-2 products. Images were filtered to the study area and masked to remove clouds and cloud shadows using QA_PIXEL quality bands. Surface reflectance values were scaled according to Collection 2 recommendations. NDVI was calculated for each image as:

$$NDVI = NIR - Red/NIR + Red,$$

NDVI layers were clipped to the study area and exported as GeoTIFF files at 30-arc-second spatial resolution (~1 km).

Hourly ERA5-Land soil temperature data were extracted from 1 January 2001 to 31 December 2020 using the variable soil_temperature_level_2 (7–28 cm). Multi-year mean layers were computed for each depth. Surface soil moisture was estimated by integrating satellite observations from the SMAP SPL3SMP_E/005 mission and reanalysis data from ERA5-Land. Daily SMAP soil moisture data (~0–5 cm) and hourly ERA5-Land volumetric_soil_water_layer_1 data (0–7 cm) were extracted from April 2015 to December 2023. Values outside the physically plausible range of 0–0.6 $m^3\ m^{-3}$ (Rasheed et al. 2022) were masked before analysis. Multi-year means were calculated, and missing SMAP values were filled using ERA5-Land estimates to generate a continuous surface soil moisture layer. Both soil temperature and soil moisture rasters were clipped to the TVB, reprojected to geographic coordinates (EPSG:4326), resampled to a 30-arc-second (~1 km) resolution, and exported as GeoTIFF files.

The raster files obtained were used to estimate the least-cost distances between geographic centroids in the topoDistance package 1.0.2 (Wang 2020). To reduce the number of variables and collinearity in each of the three datasets, a variance inflation factor was estimated using the vifcor function in the usdm package 2.1.7 (Naimi et al. 2014). Finally, the resulting matrices were analyzed using hierarchical partitioning multiple regression, as implemented in the hier.part package 1.0-6 (Nally and Walsh 2004), using the all.regs function, selecting the model with the highest likelihood, and evaluating the significance of the explanatory variables in the model with the rand.hp function over 1,000 permutations.

Finally, to assess whether the results were congruent with previous conservation proposals, the shapefile of Mexico's Priority Terrestrial Conservation Areas (PCTCA; Arriaga-Cabrera et al. 2000) was downloaded, clipped to the TVB polygon, and intersected with the different estimator polygons recovered in this study.

Results

A total of 32,038 of the 39,711 downloaded collection records for 144 species were retained after quality filtering. The order Anura included 92 species in 27 genera, the order Caudata 50 species in eight genera, and the order Gymnophiona two species in one genus. Fine-resolution grid-cell sizes (0.125°–0.375°) resulted in many empty cells or cells with only a single species, whereas coarser resolutions (0.625°–1°) poorly reflected the heterogeneity of the TVB. Therefore, results are presented only for the 0.5° grid-cell size. The remaining results are available upon request.

Species richness in the eastern region ranged from 24 to 38 species. The western region showed lower species richness, with values ranging from one to 16 species per cell (Fig. 1A). Phylogenetic diversity (PD) ranged widely (PD = 309–2,558), with high values in both subregions (Fig. 1B). Nevertheless, when PD was standardized (SES), most cells showed lower PD than expected by chance, with seven cells located in the western region showing higher values (Fig. 2A). The order Anura predominated in the western region, with values ranging from 86.3% to 100%. The values in the eastern region were lower (40%–72.1%). The

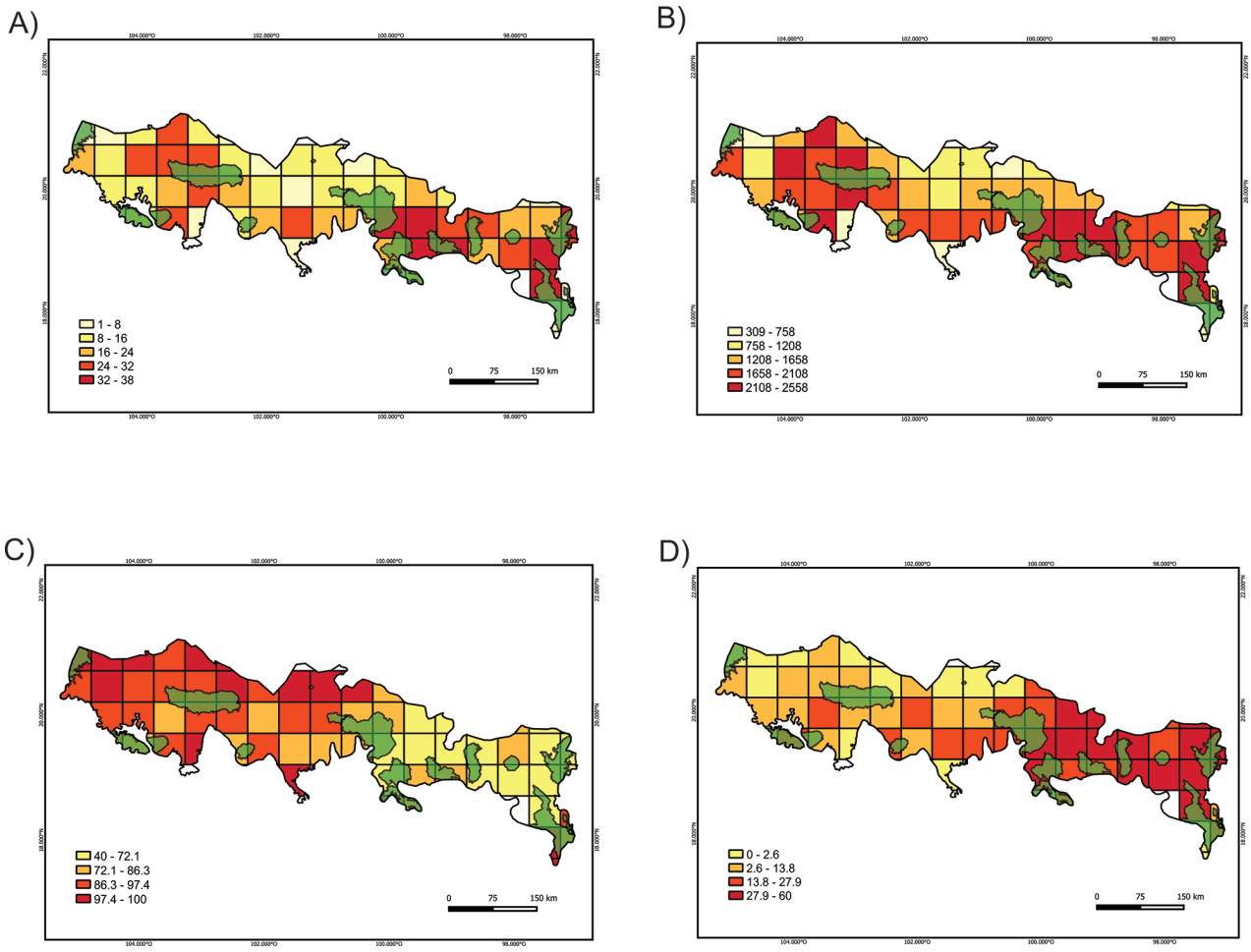

Figure 1. Alpha diversity patterns of the amphibian fauna of the Transmexican Volcanic Belt in grid cells of 0.5°. **A.** Species richness (SR); **B.** Phylogenetic diversity (PD); **C.** % of total species in the cell included in the order Anura; **D.** % of total species in the cell included in the order Caudata. Values were calculated individually for each cell. Priority Terrestrial Conservation Areas (PCTCA) are highlighted in green.

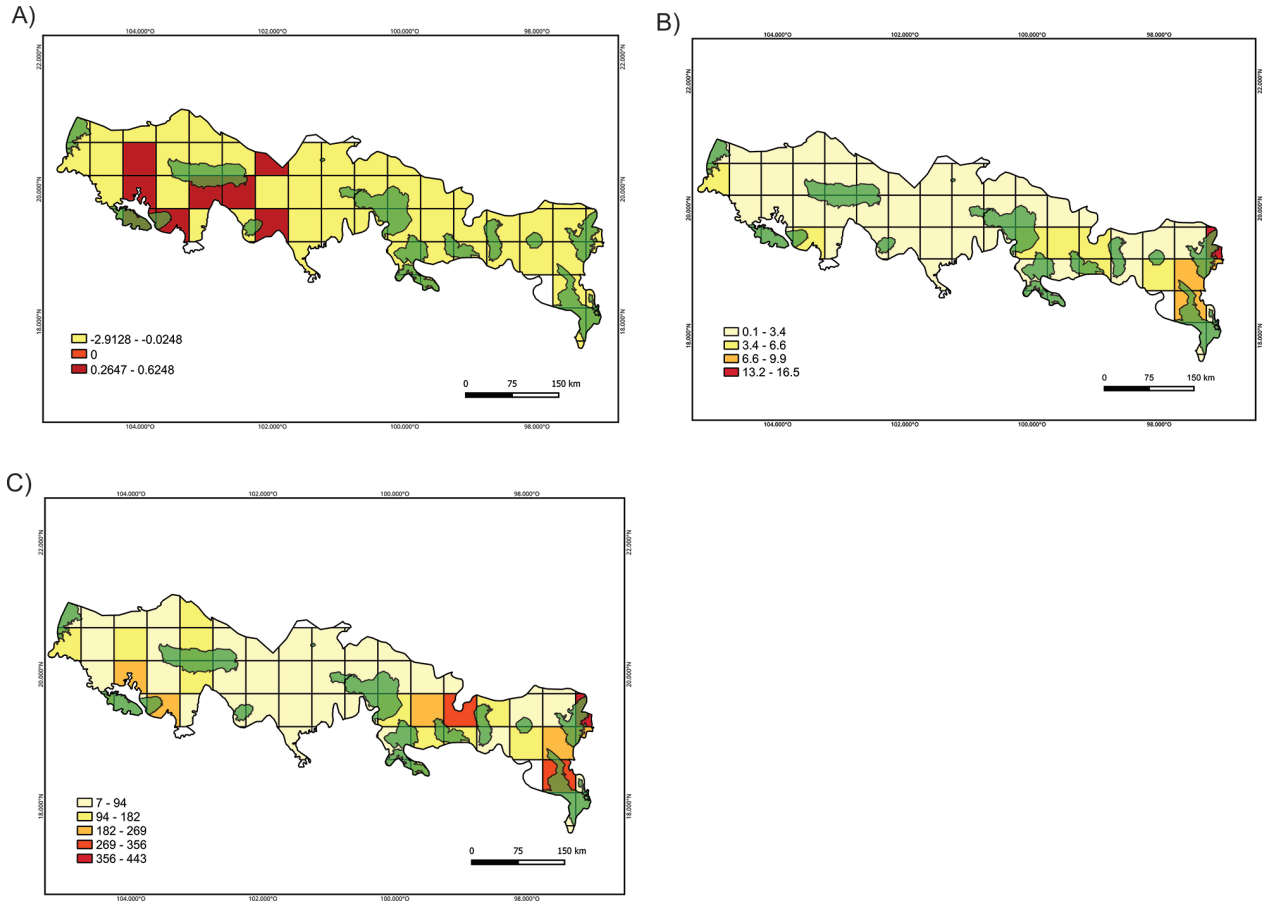

Figure 2. Endemicity patterns of the amphibian fauna of the Transmexican Volcanic Belt in grid cells of 0.5°. **A.** Standardized phylogenetic diversity (SES); **B.** Endemicity index (EI); **C.** Phylogenetic endemism index (PE). Values were calculated individually for each cell. Priority Terrestrial Conservation Areas (PCTCA) are highlighted in green.

order Caudata was more abundant in the eastern region (13.8%–60%; Fig. 1C) and almost absent in the western region (0%–13.8%; Fig. 1D).

Values of the endemism index (EI) were low in most of the TVB, especially in the western region (EI = 0.1–6.6). Only a single cell in the eastern region had a high EI value (EI = 13.22–16.5) (Fig. 2B). A similar pattern was observed for the phylogenetic endemism index (PE). Most cells had low values (PE = 7–94), especially in the western region. Most high phylogenetic endemism values applied to cells in the eastern region (PE = 269–443) (Fig. 2C).

The phylogenetic diversity index (PDI) values indicate that overdispersion is the main factor shaping the phylogenetic community structure of the amphibian fauna in the TVB (Fig. 3A). In the NTI index, negative values were concentrated mainly in the eastern region, whereas in the western region, a few cells had positive values, suggesting habitat filtering (Fig. 3B). Lastly, in the NRI index, negative values were concentrated in the western region (NRI = −5.2 to −1.7) and positive values in the eastern region (NRI = 0.1–1.8) (Fig. 3C).

Most cells (69%) exhibited high values of taxonomic dissimilarity, especially in the eastern region (Fig. 3D). The values of the taxonomic and phylogenetic beta diversity indices ranged from medium to high for βSOR and βSIM and were low for βNES (Fig. 4A–F). The taxonomic βSOR values (Fig. 4A) were in the medium range. The phylogenetic βSOR values were high, particularly in the western region (Fig. 4D). The βSIM values were in the medium range overall,

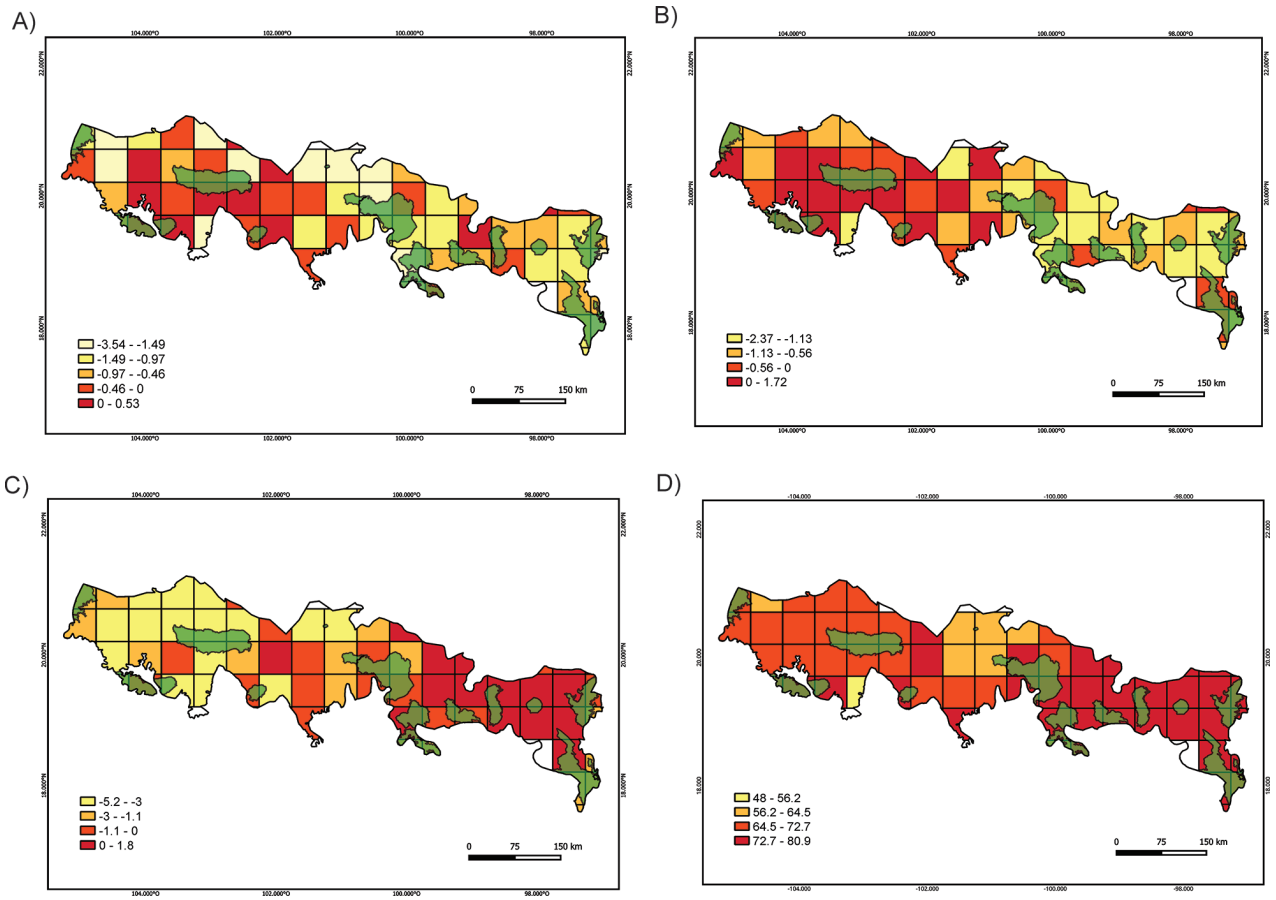

Figure 3. Phylogenetic community structure and taxonomic dissimilarity of the amphibian fauna of the Transmexican Volcanic Belt in grid cells of 0.5°. **A.** Phylogenetic diversity index (PDI); **B.** Nearest taxon index (NTI); **C.** Nearest relatedness index (NRI); **D.** Taxonomic dissimilarity (βccT). Values were calculated individually for each cell. Priority Terrestrial Conservation Areas (PCTCA) are highlighted in green.

with high values of the phylogenetic estimator concentrated in the western region and low βNES throughout the TVB.

Of the initial set of 19 explanatory variables, only eight that did not show collinearity were maintained: geographic distance, BIO6, BIO14, BIO4D, BIO15D, BIO17D, slope, and soil temperature. All variables were statistically significant ($p < 0.05$) after 1,000 randomizations. The amount of variance explained by the models ranged from 5.9% for both taxonomic (βNES) and phylogenetic (phyloβNES) nestedness to 25.4% for taxonomic βSOR (Table 1). The variables with the greatest contribution to the model were BIO15D for taxonomic βSOR (16.8%), BIO14 for phylogenetic βSOR (23.2%), soil temperature for the turnover component (βSIM) of both facets (15.7%), and BIO17D for the nestedness component of both facets (27.1%) (Fig. 5).

The degree of correspondence among cells exhibiting high values of richness, phylodiversity, endemism, β diversity estimators, and the PCTCA varied markedly among the descriptors (Figs 1–4). Cells with high values of species richness (SR ≥ 38) concentrated in the eastern region showed overlap with PCTCA polygons (Fig. 1A). For PD (PD ≥ 2,108), all but two cells in the western region showed overlap with PCTCA polygons (Fig. 1B), whereas for SES, three of the cells that showed higher values of PD than expected by chance were not included in a PCTCA (Fig. 2A).

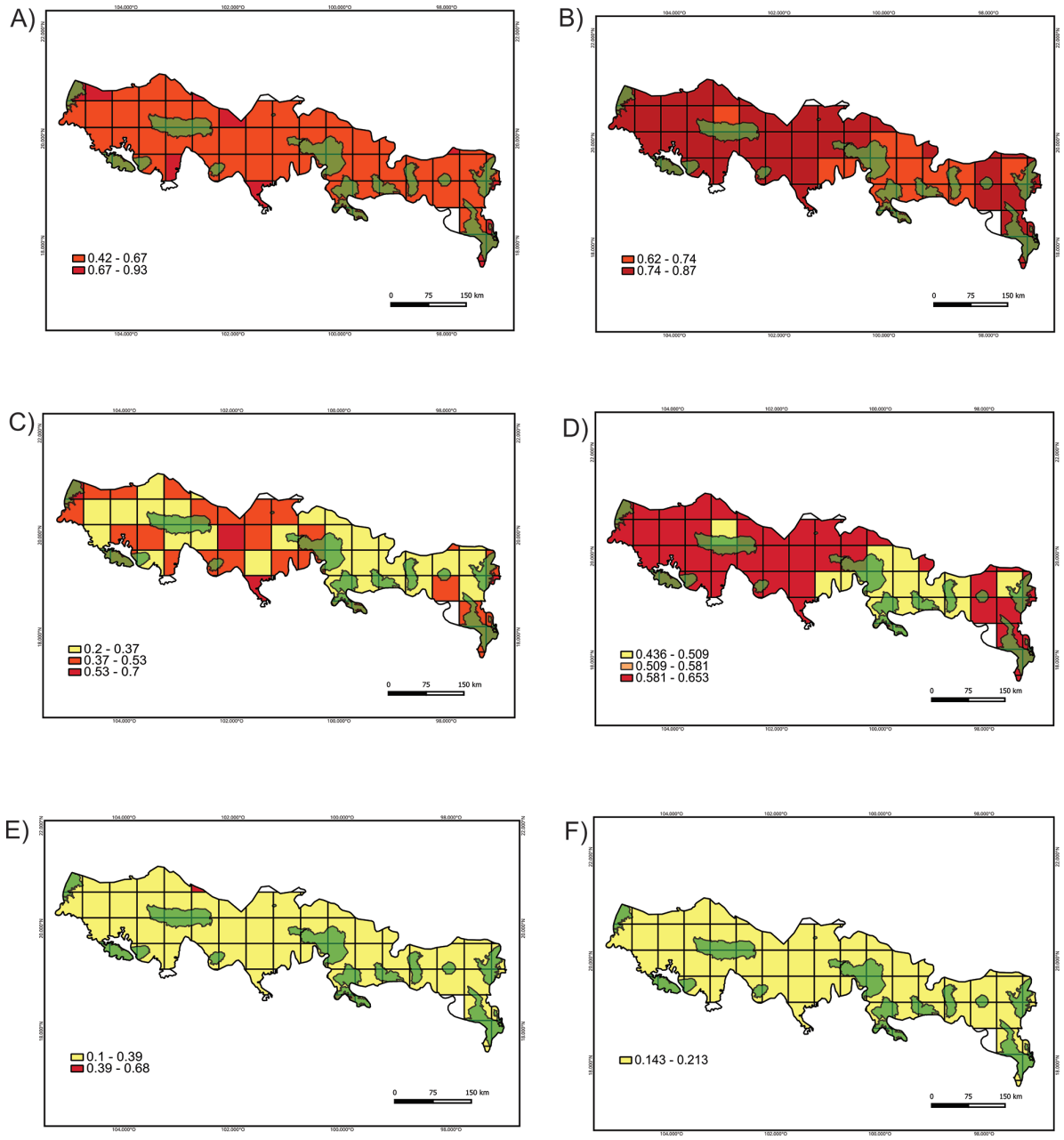

Figure 4. β diversity patterns of the amphibian fauna of the Transmexican Volcanic Belt in grid cells of 0.5°. **A.** Taxonomic βSOR; **B.** Phylogenetic phyloβSOR; **C.** Taxonomic turnover (βSIM); **D.** Phylogenetic turnover (phyloβSIM); **E.** Taxonomic nestedness (βNES); **F.** Phylogenetic nestedness (phyloβNES). Values were estimated as the average of each focal cell and its neighboring cells within a radius of 0.5°, following the procedure described by Neto (2015). Priority Terrestrial Conservation Areas (PCTCA) are highlighted in green.

A similar pattern was observed for endemism and phylogenetic endemism (Fig. 2B, C). However, one cell with high phylogenetic endemism in the eastern region was only marginally included within a PCTCA polygon (Fig. 2C). In contrast, dissimilarity metrics indicated low overlap. For taxonomic dissimilarity (Fig. 3D), three cells in the western region fell outside the polygons, and most of the surface of the eastern region, characterized by high levels of dissimilarity, showed limited coverage by PCTCA polygons. For the β diversity descriptors, most PCTCA polygons encompassed areas with the lowest levels of taxonomic and phylogenetic β diversity and turnover (Fig. 4A–D).

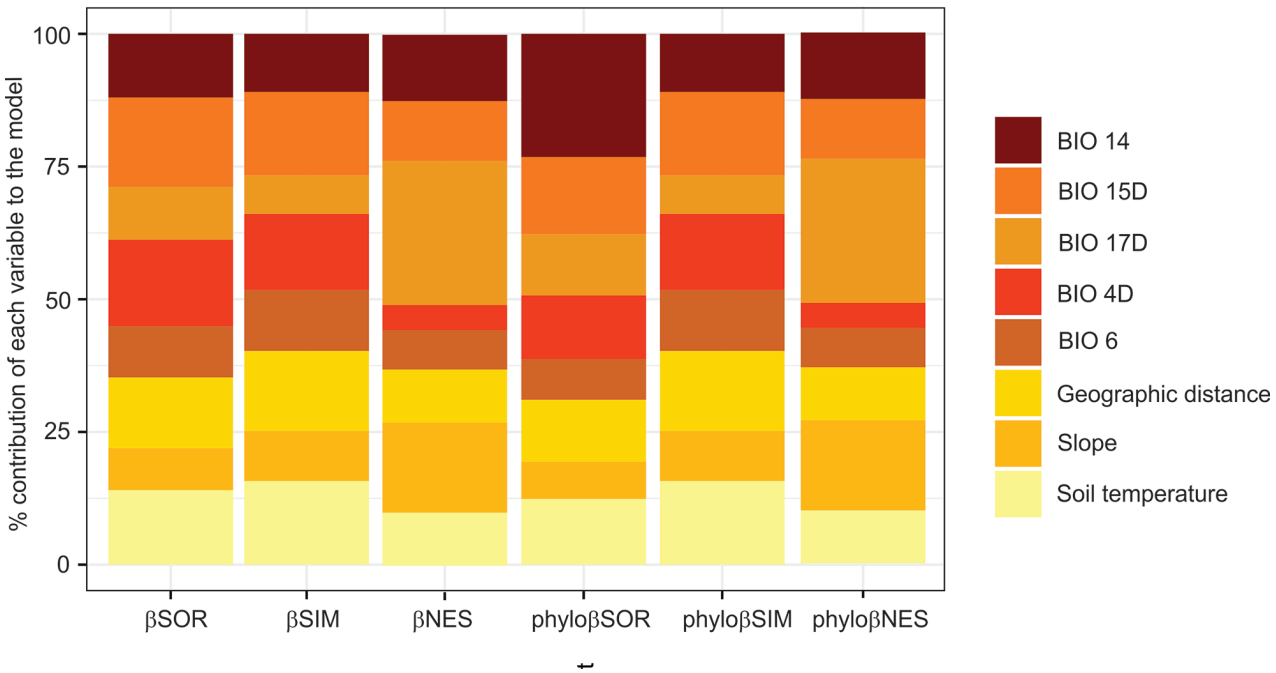

Figure 5. Relative contribution of contemporary climate, historical climate and landscape variables for the taxonomic and phylogenetic beta diversity components of the amphibian fauna of the Transmexican Volcanic Belt.

Table 1. R^2 values obtained by regression analysis implemented in hier.part, relating current bioclimatic, historical bioclimatic, and landscape variables to the different facets and components of β diversity of the amphibian fauna of the Transmexican Volcanic Belt.

	βSOR	βSIM	βNES	phylo βSOR	phylo βSIM	phylo βnes
R^2	0.254	|0.216	0.059	0.237	0.198	0.059

Discussion

Species diversity

The amphibian species richness pattern showed a heterogeneous distribution within the TVB, with lower values in the western region and higher values in the eastern region. Several alternative scenarios could explain this pattern. Topographic and climatic complexity have been suggested as promoters of local diversity in amphibians (Soares and Brito 2007; Calderón-Patrón et al. 2016; Kypraios-Skrekas et al. 2024), favoring the diversification and origin of microendemic species, especially in the eastern region of the TVB, which is characterized by the occurrence of many salamander species (Figs 1A, 2A, B).

An alternative explanation for the observed patterns may involve the influence of Pleistocene refugia, in which mountain systems served as transient environments that facilitated the fragmentation and isolation of species distributional ranges. This process may have been particularly important for amphibians, which are characterized by relatively low rates of climatic niche evolution (Baselga et al. 2012; Bonetti and Wiens 2014). Such evolutionary constraints likely limited environmental tracking during past climatic fluctuations, promoting persistence within climatically stable refugia and subsequent *in situ*

differentiation (Wiens 2004). These dynamics are consistent with the maintenance of lineages exhibiting independent evolutionary trajectories (Stein et al. 2014; Rahbek et al. 2019), a pattern further supported by the negative NRI and NTI indices obtained in the analyses (Fig. 3B, C).

It has been suggested that climatic niche breadth is influenced by environmental prevalence, that is, the geographic availability of particular climatic regimes throughout the evolutionary history of lineages (Pie et al. 2021). In ectothermic taxa, environmental prevalence has been identified as a strong predictor of species richness (Meyer and Pie 2018), suggesting that amphibian diversity in the TVB may reflect local adaptation to prevailing climatic conditions. For instance, the eastern region is dominated by temperate and subhumid forests, where species adapted to high precipitation are more likely to occur (Parra-Olea et al. 2014; Calderón-Patrón et al. 2024). In contrast, vegetation in the western region ranges from tropical deciduous forests to temperate forests, where dominant species belonging to families such as Hylidae, Craugastoridae, and Bufonidae exhibit adaptive strategies, including reproduction in temporary ponds or direct development (Lescano et al. 2015; Serrano 2016; Osnaya-Becerril et al. 2022; Barbosa-Fontana et al. 2023).

Factors that determine community structure

Taxonomic distinctiveness was positively correlated with species richness in the TVB. It has been suggested that geographic areas with high species richness are composed of species with restricted distributions, thereby increasing taxonomic distinctiveness (Koleff and Soberón 2008). However, this could also occur in highly variable environments, where the patchy distribution of elements such as vegetation can lead to an insular distribution due to different physiographic and climatic features (Olson et al. 2001). Four of the seven first-level ecoregions present in Mexico occur in the TVB, namely semiarid highlands, tropical dry forests, tropical wet forests, and temperate forests (Olson et al. 2001). These heterogeneous landscapes promote ecological conditions that favor species isolation and assemblages composed of species with different ecological roles. The results showed high turnover rates and low nestedness, as observed in amphibians in other mountain areas (Rodríguez et al. 2019; Cruz-Elizalde et al. 2022) or areas with complex topographies (Calderón-Patrón et al. 2024). This finding supports the notion that β-diversity nestedness is associated with physiological constraints, whereas species turnover is associated with speciation (Baselga et al. 2012).

The TVB is characterized by rugged topography, which promotes sharp gradients in elevation, temperature, and precipitation. It also creates geographic barriers to dispersal, especially for taxa such as amphibians, which have low vagility and high philopatry (Fonte et al. 2019). Despite the low variance explained by the model, the results of this study were similar to those found in analyses of tadpoles in several Brazilian biomes. In those studies, the explained variance for beta diversity was approximately 23% at the subcontinental scale. They also showed that spatial environmental gradients mainly drive beta diversity through dispersal limitation. These variables are more important than simple geographic distance (Garey et al. 2023).

In previous studies, precipitation seasonality (BIO15) has been associated with beta diversity in amphibians because highly variable precipitation can be reflected in more microhabitats, favoring species replacement through an environmental gradient, particularly in environments with temporary ponds (Martin and Ferrer 2015; Rodríguez et al. 2019). The findings support the previous assertions, as differences in precipitation seasonality between the LGM and current conditions represented the variable with the highest contribution to taxonomic βSOR (Fig. 5).

The role of historical climate perturbations has rarely been explored in amphibians. However, taxonomic and phylogenetic turnover is high in regions with stable climatic conditions. These stable conditions promote specialization and reduce extinction rates. At the same time, contemporary variables act as filters, precluding dispersal from stable to unstable regions. Thus, amphibian fauna turnover is mediated by historical constraints at a broad scale and by local conditions at a local scale (da Silva et al. 2014).

Despite the relationships found between predictor variables and various beta diversity estimators, the amount of variance explained was low. In particular, nestedness is highly dependent on several factors, such as the size of grid cells, the extent of the geographical region, and the resolution of data collection. This could be explained by several hypotheses, including selective colonization and extinction, habitat nestedness, and disturbances (Shi et al. 2024).

Further research is needed to evaluate the effects of other variables, such as landscape connectivity (Cushman 2006; Lion et al. 2019; Rodríguez et al. 2019) and geomorphology. The latter may serve as a significant driver, suggesting that historical factors could outweigh contemporary climate variables in determining beta diversity. This is particularly relevant because barriers can restrict species dispersal between regions (Luiz et al. 2016), especially in the TVB, which has a highly complex geological and hydrological history (López et al. 2026).

Altitudinal range could limit amphibian dispersal and greatly affect species replacement and nestedness due to weaker competitive exclusion and stronger habitat filtering (Wang et al. 2022). Although a digital elevation model was included in the estimation of the least-cost pathways, it is possible that the complexity of the topography of the TVB was not fully captured. Therefore, further studies that split the collection records by altitudinal ranges and include water ponds and another set of variables that better describe the complexity of the landscape would be necessary to disentangle the drivers of the beta diversity patterns of the amphibian fauna in this region.

Finally, although functional diversity was not evaluated directly, the results of this study could serve as a proxy for characterizing it, given the expectation that cells with high values of alpha and beta phylogenetic diversity will, in most cases, exhibit different functional traits. Thus, high values of phylobetadiversity turnover could suggest functional turnover and a high number of strategies (Ochoa-Ochoa et al. 2019).

The high dissimilarity among cells observed herein suggests that each cell harbors unique lineages that are important for conserving phylogenetic diversity. This poses a key challenge to preserving the evolutionary history of these species assemblages (Mourelle and Ezcurra 1997; Qian et al. 2021). To address this challenge, a clear alternative is to prioritize cells with higher values of phylogenetic endemism, as this approach captures highly

divergent assemblages made up of species with restricted distributions (Paúl et al. 2023). These areas present an opportunity to focus protection and conservation efforts on ecosystems and amphibian communities.

Challenges for conservation of the TVB amphibian fauna

There is no clear consensus on the criteria for establishing biological conservation areas. In practice, natural protected areas are often designed according to non-biological criteria, including aesthetic value or their location in little-impacted areas (Juárez-Ramírez et al. 2025). For example, the priority conservation areas proposed by CONABIO were defined based on a combination of biological and socioeconomic criteria (Arriaga-Cabrera et al. 2000), including widely used hotspot indicators such as species richness, endemism, and the presence of threatened and charismatic species (Caldecott et al. 1996; Orme et al. 2005; Lamoreux et al. 2006; Leroux and Schmiegelow 2007; Meuser et al. 2009). Nevertheless, this proposal omits other important facets, such as phylodiversity and β diversity.

Phylogenetic diversity has emerged as a descriptor for conservation planning because it incorporates both species richness and rarity (Winter et al. 2013). In addition, it highlights so-called feature diversity, i.e., the diversity of traits within a community that enables species to respond to environmental change and enhances their potential utilitarian value (Cardillo 2023). Nonetheless, the functional role of feature diversity in an ecosystem is not adequately assessed by phylogenetic diversity. Closely related species would be expected to show niche overlap and, consequently, contribute less to the uniqueness of ecosystem functions than more distantly related species. Under this assumption, grid cells with negative values for both NRI and NTI could be considered conservation priorities. Nevertheless, this approach may be biased by phylogenetic uncertainty and underestimation of PD resulting from incomplete or uneven clade sampling (Cardillo 2023). In contrast, β diversity increases gamma diversity, leading to the selection of the complete regional species pool. Thus, turnover suggests that conservation efforts should prioritize protecting multiple sites to preserve regional diversity, whereas high nestedness indicates that conservation strategies should focus on species-rich areas (Socolar et al. 2016; Pérez-Rocha et al. 2023).

A recent study evaluating the aforementioned facets of diversity revealed that 90% of Mexico's mammal species are distributed within protected areas and that most of the remaining species belong to taxa with low dispersal abilities, such as rodents (Aguilar-Tomasini et al. 2021). The results reflect the pronounced topographic and climatic heterogeneity of the TVB, which gives rise to amphibian assemblages with little to no spatial congruence among the four biodiversity facets examined herein: species richness, endemism, phylogenetic diversity, and beta diversity. In particular, when turnover dominates the component of beta diversity, two main scenarios related to biological conservation arise. The first is that, if habitat filtering dominates, it is better to preserve the highest number of areas, regardless of their species richness; preserving the regional pool with a few grid cells is difficult. Conversely, if overdispersion dominates, it is better to preserve a high number of heterogeneous areas regardless of their richness because

phylogenetic diversity can only be preserved by including the wide range of ecological requirements of species (Escoriza and Ruhí 2014).

This lack of congruence is particularly concerning for a taxonomic group that is highly sensitive to anthropogenic disturbances, especially within the TVB (Camarena-Hernández et al. 2024), and that includes many species currently classified under a risk category by the IUCN (49% of species in Anura and 70% of species in Caudata). Many of these species also have extremely restricted geographic distributions and specialized microhabitat requirements (Frías-Alvarez et al. 2010). Consequently, more detailed analyses, including assessments of potential shifts under future climate change scenarios, are necessary to redefine the boundaries of priority conservation areas in Mexico to protect most of the diversity of the TVB amphibian fauna.

Conclusion

Species richness, endemism, and phylogenetic endemism of the amphibian fauna in the TVB are higher in the eastern region, which is characterized by temperate, subhumid climates and harbors greater caudate diversity. Most community assemblages are structured by phylogenetic overdispersion, with habitat filtering explaining only a small proportion of the variation in grid cells. The TVB exhibits high levels of both taxonomic and phylogenetic beta diversity, coupled with low nestedness. Geographic distance and soil temperature emerged as the main drivers shaping amphibian diversity patterns. Finally, most facets of biodiversity showed limited spatial overlap with the current priority conservation areas established under Mexican legislation, highlighting the complexity of conserving this biologically vulnerable group.

Acknowledgements

This work is part of the first author's Master's thesis. The authors also acknowledge Irene Goyenechea, Rocío Demartín, Liliana Saboyá, and the associate editor Piter Boll for their useful comments, which helped improve the manuscript.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
No AI tools were used in the preparation of this manuscript.

Funding

JGC acknowledges SECIHTI for the student grant received.

Author contributions

Conceptualization: OM, NMM. Data curation: JGC, ADVP. Formal analysis: JGC, OM. Investigation: NMM. Methodology: JGC, NMM. Project administration: OM. Supervision: ADVP, OM, NMM. Writing – original draft: JGC. Writing – review and editing: OM, NMM, ADVP.

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Data availability

All of the data that support the findings of this study are available in the main text.