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Comparison of Amphibians and Reptiles in Neighboring Biogeographic Provinces to the Sierra Madre Oriental Biogeographic Province of Mexico

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Abstract.—**As part of the Transition Zone in Mexico, the Sierra Madre Oriental (SMO) is an important biologically diverse region. To better understand the herpetofauna of the SMO, we compiled a list of amphibians and reptiles along with their conservation status. We also compared its herpetofauna to that of neighboring provinces. The SMO is home to 382 native species of amphibians and reptiles, representing 40 families (14 amphibians and 26 reptiles) and 120 genera (35 amphibians and 85 reptiles). Fifty-one of the 382 native species (18 amphibians and 33 reptiles) are endemic to the SMO. Cluster analyses for both amphibians and reptiles identified the herpetofauna of the Transvolcanic Belt as the most similar to that of the SMO. Seventy-four species, 50 amphibians and 24 reptiles, are listed as Vulnerable, Endangered, or Critically Endangered in the International Union for Conservation of Nature (IUCN) Red List, 56 (16 amphibians and 40 reptiles) are categorized as threatened (A) or in danger of extinction (P) by the Secretaría del Medio Ambiente y Recursos Naturales of Mexico (SEMARNAT), and 147 (60 amphibians and 87 reptiles) are categorized as high risk by the Environmental Vulnerability Score (EVS). Most species listed in a conservation concern category by the IUCN face habitat destruction due to conversion to agricultural land or urbanization, especially in cloud forests. Our study highlights that the SMO is a key region of herpetological diversity in Mexico, underscoring its significant role in regional conservation priorities. Our findings suggest that conservation efforts across Mexico should focus on physiographic similarities between regions, rather than just geographic proximity, to better address the needs of herpetofauna and their habitats.**

Key Words.—endemic species; hábitat destruction; herpetofauna; preservation; protection; similarities.

Resumen.—**Como parte de la Zona de Transición de México, la Sierra Madre Oriental (SMO) es una provincia con gran diversidad biológica. Compilamos una lista de anfibios y reptiles de la SMO y su estado de conservación, comparándola con las provincias vecinas. La SMO alberga 382 especies nativas de anfibios y reptiles, que representan 40 familias (14 anfibios y 26 reptiles) y 120 géneros (35 anfibios y 85 reptiles). Cincuenta y una de estas 382 especies (18 anfibios y 33 reptiles) son endémicas a la SMO. La herpetofauna de la Franja Transvolcánica es la más similar a la de la SMO. Setenta y cuatro especies, 50 anfibios y 24 reptiles, están catalogadas como Vulnerables, En Peligro o En Peligro Crítico en la Lista Roja de la Unión Internacional para la Conservación de la Naturaleza (UICN), 56 (16 anfibios y 40 reptiles) están clasificadas en una categoría de riesgo por la Secretaría del Medio Ambiente y Recursos Naturales de México (SEMARNAT), y 147 (60 anfibios y 87 reptiles) están categorizadas como de alto riesgo por el Índice de Vulnerabilidad Ambiental (EVS). La mayoría de las especies catalogadas en una categoría de preocupación para la conservación por la UICN enfrentan la destrucción del hábitat debido a la conversión a tierras agrícolas o la urbanización, especialmente en bosques nubosos. Nuestro estudio destaca que la SMO es una región clave de diversidad herpetológica en México, lo que subraya su importante papel en las prioridades regionales de conservación. Nuestros hallazgos sugieren que los esfuerzos de conservación en todo México deben centrarse en similitudes fisiográficas entre regiones, no solo en proximidad geográfica, para abordar mejor las necesidades de la herpetofauna y sus hábitats.**

Palabras Clave.—destrucción del hábitat; especies endémicas; herpetofauna; preservación; protección; similitudes.

Introduction

The Sierra Madre Oriental (SMO) biogeographic province is a long mountain range that runs northwest to southeast and divides northeastern Mexico and contains a central region of valleys and hills. The SMO lies in the northern limit of the Neotropical region and the southern limit of the Nearctic region (Morrone 2019). It is therefore one of the five biogeographic provinces in the Transition Zone of Mexico proposed by Morrone et al. (2017) and Morrone (2019). Because of its topography, the SMO presents a variety of environments and conditions resulting in a rich biodiversity (Salinas-Rodríguez 2018); however, our knowledge of the diversity and conservation status of the flora and fauna of the SMO is still incomplete.

The environmental conditions of the SMO allow the cultivation of a variety of agricultural crops, which has resulted in a growing human population (Salinas-Rodríguez 2018). The increasing human population has driven an increase in land converted to agriculture and livestock production, resulting in deforestation, replacement of original vegetation with introduced grasses, and contamination of soils and aquatic habitats with agricultural pollutants, as well as urbanization, mining, illegal logging of forests, and increased industrialization resulting in serious threats to the biodiversity of the region (e.g., Calderón et al. 2019; Mayani-Paras et al. 2019; Ochoa-Ochoa et al. 2021). This has led to substantial loss of native habitats across the SMO (Suárez-Mota et al. 2017).

Given its location in the Transition Zone and its environmental degradation, the SMO is of conservation interest for amphibians and reptiles. To fully understand the importance of the SMO to the diversity and conservation of amphibians and reptiles in Mexico, however, the herpetofauna and its conservation status needs to be enumerated. It is also important to place its diversity in the context of its neighboring provinces. Such an understanding allows for an examination of the contribution of the SMO to the Mexican herpetofauna and highlights it potential role in the conservation of the amphibians and reptiles of megadiverse Mexico.

Here we summarize the amphibian and reptile species of the SMO biogeographic province and their conservation status and similarity with its neighboring biogeographic provinces. For amphibians and reptiles, species lists are available for all of the states that form the SMO (Table 1). We used this information to build a comprehensive list of the species of these two classes of vertebrates from the SMO.

Materials and Methods

Study site.—The biogeographic province of the SMO is located in the northeast of Mexico, and runs from the center of Nuevo León to join the Transvolcanic Belt in the states of Puebla and Veracruz. The SMO has a rugged topography and is a relatively continuous mountain range interrupted by extensive valleys in Nuevo León resulting in a series of relatively small Sierras that extend to the west through of a set of transverse mountain ranges running through southwestern Coahuila and entering the Chihuahuan Desert (Fig. 1). It includes parts of the states of Coahuila, Nuevo León, San Luis Potosí, Tamaulipas, Guanajuato, Querétaro, Hidalgo, Veracruz, and Puebla (modified from Morrone 2019). To the northeast and east, the SMO is bordered by the Tamaulipas province (border length = 625 km)

Table 1. Mexican states comprising the Sierra Madre Oriental and the corresponding sources listing the species inhabiting the Sierra Madre Oriental regions of each state.

State	Sources
Coahuila	Lemos-Espinal and Smith (2008), Lemos-Espinal and Smith (2016); Lazcano et al. (2019).
Hidalgo	Lemos-Espinal and Smith (2015), Lemos-Espinal and Dixon (2016), Ramírez-Bautista et al. (2020).
Guanajuato	Leyte-Manrique et al. (2022).
Nuevo León	Lemos-Espinal et al. (2016); Nevárez-de los Reyes et al. (2016), Lemos-Espinal et al. (2018a).
San Luis Potosí	Lemos-Espinal and Dixon (2013); Lemos-Espinal et al. (2018b).
Querétaro	Dixon and Lemos-Espinal (2010), Cruz-Elizalde et al. (2019, 2022).
Puebla	Woolrich-Piña et al. (2017).
Tamaulipas	Farr (2015), Terán-Juárez et al. (2016).
Veracruz	Torres-Hernández et al. (2021).

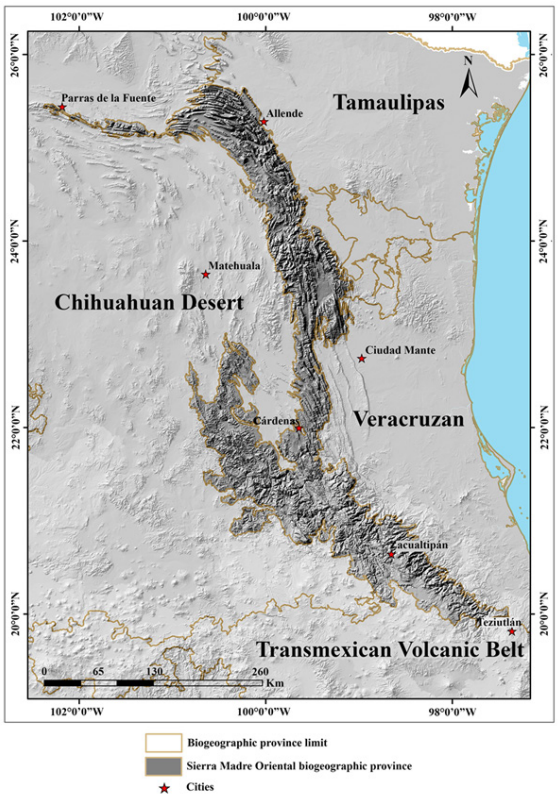

Figure 1. Topographic map of the Sierra Madre Oriental biogeographic province of Mexico (from Advanced Spaceborne Thermal Emission & Reflection Radiometer Global Digital Elevation Model Version 2 [ASTER GDEM2] 2011).

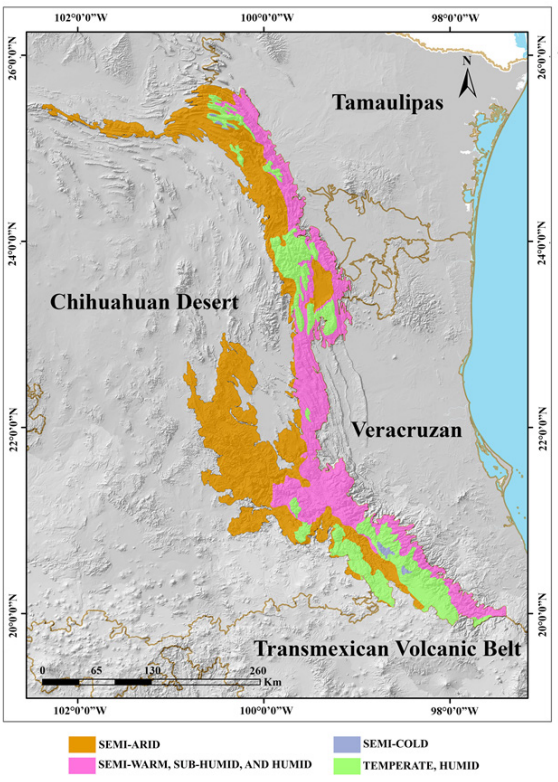

Figure 2. Climate map of the Sierra Madre Oriental biogeographic province of Mexico (from García 1998).

to the southeast by the Veracruzan province (border length = 1,271 km), to the south by the Transvolcanic Belt (border length = 307 km), and to the west by the Chihuahuan Desert (border length = 3,397 km). The SMO is divided into two subprovinces, the Austro-Oriental, which corresponds to the northern part of the province, north of the Moctezuma River and includes the Sierra in San Luis Potosí, Coahuila, Nuevo León, and Tamaulipas, and the Hidalguense, which corresponds to the southern part of the province, south of the Moctezuma River and includes the Sierra in Hidalgo, Guanajuato, Querétaro, and Veracruz. The climate of the SMO is highly variable, ranging from semi-arid to alpine and subalpine (Suárez-Mota et al. 2017; Salinas-Rodríguez 2018; Fig. 2). The vegetation of the SMO is also varied, including xerophytic scrub, coniferous forests dominated by the genera *Abies, Pinus*, and *Quercus*, mesophilic mountain forest (Rzedowski 1996; Fig. 3).

Data sources and analytical methods.—Using the available literature, we collected species lists for amphibians and reptiles for all of the Mexican states included in the Sierra Madre Oriental biogeographic province (Coahuila, Guanajuato, Hidalgo, Nuevo León, Puebla, Querétaro, San Luis Potosí, Tamaulipas, and Veracruz) that we updated using additional literature (see Appendix 1). We follow Frost (https://amphibiansoftheworld.amnh.org/index.php.) and AmphibiaWeb (https://amphibiaweb.org.) for amphibian names and Uetz et al. (http://www.reptile-database.org.) for reptile names. We use the definition of the Sierra Madre Oriental biogeographic province provided by Morrone (2005, 2006, 2019), and Morrone et al. (2017). In addition, we recorded the conservation status and population trends of each species based on the Red List of the International Union for Conservation of Nature (IUCN 2024), Secretaría del Medio Ambiente y Recursos Naturales of Mexico (SEMARNAT 2019), and Environmental Vulnerability Scores from Wilson et al. (2013a,b).

We used Hierarchical Clustering Analyses based on Jaccard's Similarity Coefficients for Binary Data as the distance metric with single linkages methods (nearest neighbor) to generate clusters of the SMO and neighboring biogeographic provinces (Transvolcanic Belt, Veracruzan, Tamaulipas, and Chihuahuan Desert) based on their amphibians

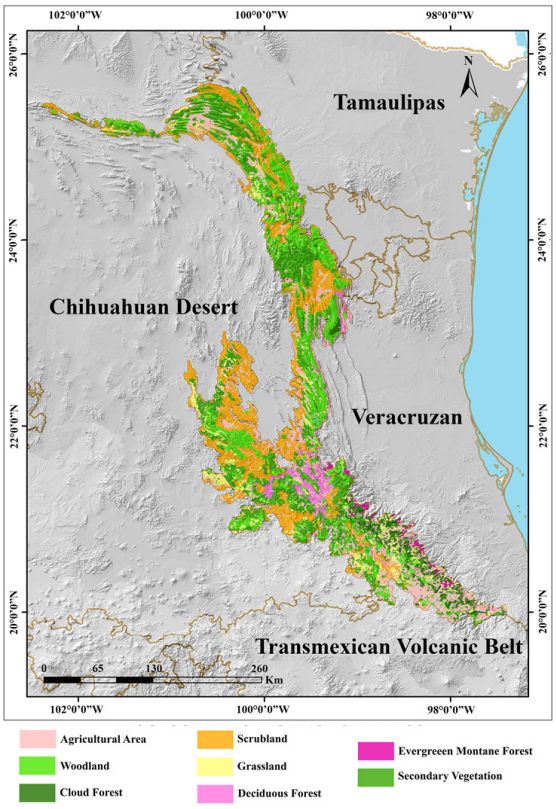

Figure 3. Vegetation map of the Sierra Madre Oriental biogeographic province of Mexico (from Instituto Nacional de Estadística y Geografía 2016).

and reptiles separately. We visually identified clusters by examining the resulting cluster tree and grouping biogeographic provinces based on shared nodes. We also used the species lists to calculate pair-wise Jaccard distances between the SMO and its four neighboring biogeographic provinces for amphibians and reptiles, separately. In addition, we estimated four geospatial variables using the map of biotic provinces of Mexico by Morrone et al. (2017) on a Lambert Conformal Conic projection in Datum WGS84 in ArcGIS 10.8.1 (Esri, Redlands, California, USA): (1) shared border length between pairs of provinces using the Polygon Neighbors Tool; (2) the straight-line distance between centroids of pairs of provinces using the Feature to Point Tool and Point Distance; (3) the area of each province using the Calculate Geometry Tool; and (4) the perimeter of each province using the Calculate Geometry Tool. We also used this software to determine the latitudinal and longitudinal limits of each province using the layer properties option. We used non-parametric Spearman's ρ tests to examine correlations of Jaccard distance estimates for amphibians and reptiles between pairs of biogeographic provinces and shared border length and distance between their centroids. We performed cluster analyses using Systat 13.2 (Systat Software Inc., San Jose, California, USA) and all other statistical analyses using JMP 16.2 (SAS Institute, Cary, North Carolina, USA). We used an α-value of 0.05 for analyses.

Results

Species richness.—The SMO hosts 382 native species of amphibians and reptiles, 123 amphibians and 259 reptiles. These species belong to 40 families, which include 14 amphibian families (11 anurans and three caudates) and 26 reptile families (one crocodile, 14 lizards, eight snakes, and three turtles), and 120 genera (35 amphibians and 85 reptiles). Compared to the total number of families and species present in Mexico, these numbers are relatively large, with the SMO being home to 72.7% (40/55) of the families, 77.4% (120/155) of the genera, and 27.3% (382/1,399) of the amphibian and reptile species found in Mexico. For amphibians, the SMO is home to 87.5% (14/16) of the families, 63.6% (35/55) of the genera, and 28.3% (123/435) of the species that inhabit Mexico. For reptiles, the SMO is home to 66.7% (26/39) of the families, 54.8% (85/155) of the genera, and 26.9% (259/964) of the species. Of the 382 native species, 51 (18 amphibians and 33 reptiles) are endemic to the SMO. Seven species have been introduced to the SMO: the Cuban Flat-headed Frog (*Eleutherodactylus planirostris*) from the West Indies; the Common Bullfrog (*Rana catesbeiana*) that occurs naturally in northeastern Mexico; and three lizards and one snake from the Mediterranean, Asia, Africa, Middle East, or Oceania, the Stump-toed Gecko (*Gehyra mutilata*), the Common House Gecko (*Hemidactylus frenatus*), the Mediterranean House Gecko (*Hemidactylus turcicus*), and the Brahminy Blindsnake (*Indotyphlops braminus*). Also, the Spiny Softshell Turtle (*Apalone spinifera*) is naturally found in northern Mexico, but its distribution also extends into southeastern Canada, throughout much of the eastern U.S., and across northern and northeastern Mexico.

General distribution.—For seven of the 14 amphibian families that inhabit the SMO, ≥ 50% of their species are endemic to Mexico. Eighty-four (68.3%) of the 123 native amphibian species that inhabit the SMO are endemic to Mexico, 18 (14.6%) of them to the SMO (Supplementary

Information Table S1). Most of the remaining 66 endemic species have a distribution that is limited to eastern Mexico, 63 of them are shared with the Transvolcanic Belt and 22 of these 63 species are shared only between the SMO and the Transvolcanic Belt (Supplementary Information Table S2). Another 18 are shared between the SMO, the Transvolcanic Belt and another biogeographic province. Another eight species are shared among four provinces including the SMO and the Transvolcanic Belt. Another six occupy five provinces including the SMO and the Transvolcanic Belt, five inhabit six biogeographic provinces including the SMO and the Transvolcanic Belt, and three species occupy seven biogeographic provinces including the SMO and the Transvolcanic Belt: Pine Toad (*Incilius occidentalis*), Mountain Treefrog (*Dryophytes eximius*), and Small-ear Hyla (*Rheohyla miotympanum*). Only one of the 84 species (Wiegmann's Toad, *Incilius marmoreus*) endemic to Mexico inhabits eight biogeographic provinces including the Sierra Madre Oriental and the Transvolcanic Belt. The only three species endemic to Mexico that are not endemic to the SMO and that do not inhabit the Transvolcanic Belt, are Puebla Treefrog (*Sarcohyla charadricola*) and Dwarf Splayfoot Salamander (*Chiropterotriton dimidiatus*) that have been recorded in the SMO and the Chihuahuan Desert, and Schmidt's Pigmy Salamander (*Thorius schmidti*) that inhabits both the SMO and the Sierra Madre del Sur. Twenty-two of the species endemic to Mexico that inhabit the SMO are shared with the Veracruzan province, 21 with the Chihuahuan Desert, 21 with the Sierra Madre Occidental, 12 with the Balsas Basin, eight with the Sierra Madre Occidental, six with the Chiapas Highlands, four with the Pacific Lowlands, and one with Tamaulipas (Supplementary Information Table S2).

The distribution of the native reptile species of the SMO is similar to that of amphibians. Twelve (46.2%) of the 26 families of reptiles in the SMO have ≥ 50% of their species endemic to Mexico. Of 259 native species, 148 (57.1%) are endemic to Mexico, and 33 (12.7%) are endemic to the SMO (Supplementary Information Tables S1 and S3). Another 24 species endemic to Mexico are shared between the SMO and another biogeographic province of Mexico: seven with the Chihuahuan Desert; seven with the Veracruzan; five with the Transvolcanic Belt; four with the Sierra Madre del Sur; and one with Tamaulipas (*Plestiodon dicei* [Dice's Short-nosed Skink]). Twenty-six of the reptile species endemic to Mexico occur in the SMO and two other biogeographic provinces; 29 are shared between the SMO and three other biogeographic provinces; 15 occur in the SMO and four other biogeographic provinces; seven inhabit the SMO and five other biogeographic provinces; seven in the SMO and six other biogeographic provinces; and four in the SMO and seven other biogeographic provinces; and three occur in the SMO and the eight other biogeographic provinces (Supplementary Information Table S3).

The remaining 111 species of reptiles found in the SMO are not endemic to Mexico and can be divided into three groups. The first group consists of 38 species shared between the U.S. and Mexico, of which most (35) are also found in the Chihuahuan Desert, but three species do not occur in the Chihuahuan Desert: the Tamaulipan Hooknose Snake (*Ficimia streckeri*), which is also found in Tamaulipas and Veracruzan provinces, the Thornscrub Vine Snake (*Oxybelis microphthalmos*) found in nine biogeographic provinces, and the Western Twin Spotted Rattlesnake (*Crotalus pricei*) also found in the Sierra Madre Occidental. The second group includes 61 species that range into Central or South America, all of them also occur in the Chiapas Highlands, and all but Middle American Gopher Snake (*Pituophis lineaticollis*), also inhabit the Veracruzan. In addition, some of these 61 species also occur in the Transvolcanic Belt (46), Sierra Madre del Sur (43), Yucatan Peninsula (41), the Pacific Lowlands (27), Tamaulipas (9), Chihuahuan Desert (5), and Sierra Madre Occidental (1). Interestingly, the Balsas Basis is home to only 16 of these 61 species, even though it is closer to the SMO than several of the other provinces that share a larger number of species with the SMO (e.g., Sierra Madre del Sur, Chiapas Highlands, and Pacific Lowlands), which may be due to the Balsas Basin having a lower overall species richness than the other three provinces, housing only 207 species compared to 517 for the Sierra Madre del Sur, 353 for the Chiapas Highlands, and 326 for the Pacific Lowlands (Lemos-Espinal and Smith 2024). The Balsas Basin, however, shares around the same percentage of species with the SMO (7.7%, 16/207) as the Sierra Madre de Sur 8.3% (43/517) and the Pacific Lowland 8.3% (27/326). The third group consists of 12 widespread species found from the U.S. to Central or South America, with all of these species also occurring in the Veracruzan and Chiapas Highlands provinces, and all but one, the Eastern Racer (*Coluber constrictor*) are also found in the Transvolcanic Belt, nine inhabit the Chihuahuan

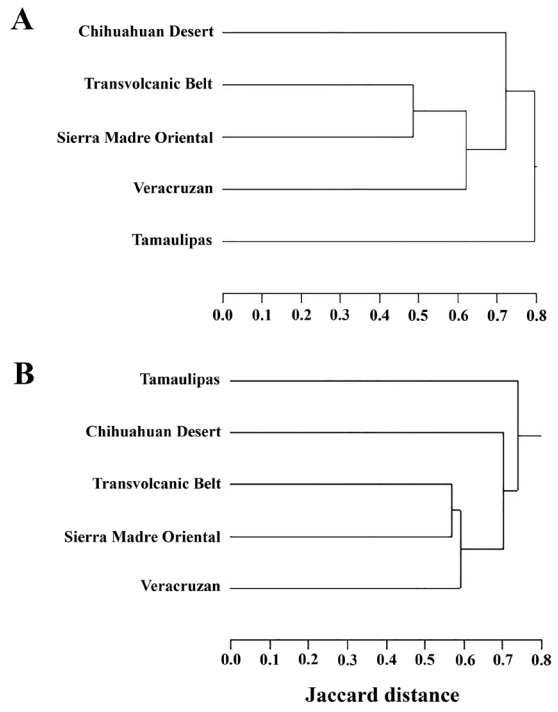

Figure 4. Cluster trees for (A) amphibians and (B) reptiles of the Sierra Madre Oriental, Mexico, and its neighboring biogeographic provinces.

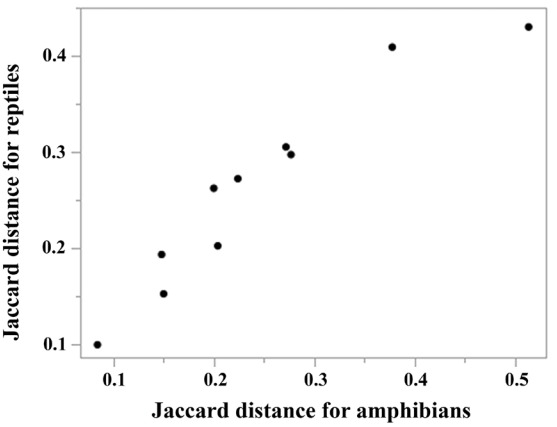

Figure 5. The correlation between the Jaccard distance of amphibians and reptiles across the Sierra Madre Oriental and its neighboring biogeographic provinces in Mexico.

Desert, nine occur in Tamaulipas, eight in the Pacific Lowlands, seven in the Sierra Madre del Sur, seven in the Yucatan Peninsula, six in the Balsas Basin, six in the Sierra Madre Occidental, and four in the Sonoran Desert.

Comparison with neighboring provinces.—The SMO shares a high number of species of amphibians and reptiles with many of its neighboring provinces (Appendix Table 1). This is particularly true for the anurans. The high percentages of shared anuran species between neighboring provinces and the SMO are likely due to these provinces falling within the humid tropics of eastern Mexico. This is supported by the lower proportion of shared species between the SMO and the Nearctic provinces, the Chihuahuan Desert and Tamaulipas. The SMO shares the most species of salamanders with the Transvolcanic Belt but shares many fewer species with the Veracruzan, Chihuahuan Desert, and Tamaulipas. Salamander species, especially from the family Plethodontidae, are almost exclusively found in eastern and southeastern Mexico, as can be seen by the high numbers of endemic species of the transitional provinces: SMO, Transvolcanic Belt, and Sierra Madre del Sur. More than half (74) of the Plethodontid species (141) that inhabit Mexico are endemic to one of these three biogeographic provinces (Lemos-Espinal and Smith 2024). The number of reptile species shared between the SMO and its neighboring provinces is similar to that of amphibians, with the highest overlap with the Transvolcanic Belt and Veracruzan, whereas overlaps with the Chihuahuan Desert and Tamaulipas are lower but still higher than for amphibians (Appendix Table 1).

The cluster analysis for amphibians identified the Transvolcanic Belt as the province most closely associated with the SMO (Fig. 4). The Veracruzan province is then clustered with the pairing of the SMO and the Transvolcanic Belt. Following this, the Chihuahuan Desert followed by Tamaulipas join the cluster tree. The cluster tree for reptiles follows generally a similar pattern (Fig. 4).

Jaccard distances between provinces of amphibians and reptiles were significantly positively correlated (n = 10, Spearman's $\rho = 0.964$, $P < 0.001$; Fig. 5). Amphibian Jaccard distances were not correlated with the length of the shared border between biogeographic provinces (n = 10, Spearman's $\rho = 0.334$, $P = 0.345$) or with the distance between centroids (n = 10, Spearman's $\rho = -0.333$, $P = 0.347$). Reptile Jaccard distances were not correlated with the length of the shared border between biogeographic provinces (n = 10, Spearman's $\rho = 0.316$, $P = 0.374$). Reptile Jaccard distances were also not correlated with the distance between centroids (n = 10, Spearman's $\rho = -0.527$, $P = 0.117$). The number of amphibians and reptiles was not correlated with the territorial area of the biogeographic provinces (both amphibians and reptiles: n = 5, Spearman's $\rho = -0.600$, $P = 0.285$), or the longitude (both amphibians and reptiles: n = 5,

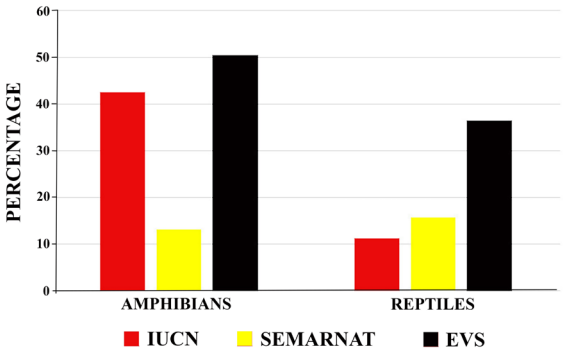

Figure 6. Percentage of amphibian and reptile species with conservation concern status categorized as Threatened (red bar) by the International Union for Conservation of Nature (2024), in danger of extinction (yellow bar) by the Mexican government (Secretaría del Medio Ambiente y Recursos Naturales of Mexico 2019), or deemed to have a high environmental vulnerability score (black bar) by Wilson et al. (2013a,b) for the Sierra Madre Oriental biogeographic province of Mexico.

Spearman's ρ = 0.300, *P* = 0.624) and latitude of the centroid (both amphibians and reptiles: n = 5, -0.700, *P* = 0.188).

Conservation status.—Seventy-four (21.9% = 74/337 assessed) of the 382 native species of amphibians and reptiles that inhabit the SMO are included in a threatened categories of the IUCN Red List, 56 (14.7% = 56/382 assessed) are classified under the risk categories of Threatened (A) or In Danger of Extinction (P) by SEMARNAT, and 148 (40.8% = 147/360 assessed) are considered high risk by the EVS (Fig. 6, Appendix Table 2). Fifty amphibians, equivalent to 41.3% (50/121 assessed), are included in the IUCN Red List, 13 as Vulnerable, 20 Endangered, and 17 Critically Endangered. Most of these species have a decreasing population trend, and all of them, except *Notophthalmus meridionalis* (Texas Triton), are endemic to Mexico, and 11 are endemic to the SMO. All of these species are experiencing the rapid loss of their habitats, which are being urbanized and transformed for agricultural use (IUCN 2024). In addition, some species are threatened by the amphibian chytrid fungus, *Batrachochytrium dendrobatidis*, and others are negatively impacted by the introduction of non-native predators and competitors, such as bullfrogs, sport fish, and crayfish (IUCN 2024). Sixteen amphibian species (13.0% = 16/123) are categorized as threatened (A) or in danger of extinction (P) by SEMARNAT; and 60 species are considered of high risk by EVS (50.4% = 60/119; Appendix Table 2). For reptiles, 11.1% (24/216 assessed) are included in some category of conservation concern in the IUCN Red List, 15.4% (40/259 assessed) are categorized as threatened (A) or in danger of extinction (P) by SEMARNAT, and 36.1% (87/241 assessed) are considered high risk by the EVS (Fig. 6). Sixteen of the 24 species listed in a category of conservation concern by the IUCN are categorized as high risk by the EVS, and only five of them are listed in the risk category of Threatened (A) by SEMARNAT (Fig. 6, Appendix Table 2).

Discussion

The SMO represents a critical area for amphibian and reptile biodiversity in Mexico. Its high species richness and the number of endemic species highlight the ecological and biogeographic significance of this biogeographic province (see also Johnson et al. 2017; Montiel-Canales et al. 2019; Montiel Canales and Goyenechea Mayer Goyenechea 2022). The distribution patterns observed in the SMO reveal key insights into the historical biogeography, conservation challenges, and the complex interplay of environmental factors influencing species diversity.

The relatively restricted distribution of most amphibian and reptile species from the SMO (i.e., endemics at a regional or national level) indicates the importance of the SMO in hosting several unique species of amphibians and reptiles, likely due to the complex environment of the SMO leading to the evolution of the richness of endemic species in eastern Mexico. The presence of 123 amphibian species and 259 reptile species underscores the evolutionary and ecological processes shaping this region. The isolation of mountain ranges, like the SMO, and historical climate changes have led to high levels of speciation (Halffter and Morrone 2017; Morrone et al. 2017; Morrone 2019; Wollenberg Valero et al. 2019). The complex topography and climatic gradients of the Sierra Madre Oriental contribute to this phenomenon by creating diverse microhabitats that facilitate niche differentiation and speciation (Salinas-Rodríguez 2018).

Comparison with neighboring provinces.—The comparison between the SMO and neighboring biogeographic provinces reveal interesting patterns of species sharing. The higher percentages of shared species of reptiles of the SMO and the Chihuahuan Desert and Tamaulipas compared to amphibians is probably due to the greater mobility of reptiles and their independence from humid places. Furthermore, the northwestern projection of the SMO that enters the Chihuahuan Desert in southern Coahuila,

Table 2. Surface area (SA; km²) of the Sierra Madre Oriental, Mexico, and its four neighboring biogeographic provinces; length of the border (Length; km) between the Sierra Madre Oriental and each neighboring province; distance (km) from the centroid of the Sierra Madre Oriental to each neighboring province; number of species shared between the Sierra Madre Oriental and each neighboring province (No. species); and total number of species (Total No.) in the Sierra Madre Oriental and each of the four neighboring provinces.

Province	SA (km²)	Length (km)	Distance (km)	No. species	Total No.
Sierra Madre Oriental	51,897	--	--	--	382
Transvolcanic Belt	82,839	307	314.4	251	427
Veracruzan	191,451	1,271	520.8	204	340
Chihuahuan Desert	578,001	3,397	582.1	144	262
Tamaulipan	106,829	625	430.3	74	116

facilitates the presence of a large number of species of reptiles characteristic of the Chihuahuan Desert in the SMO. These percentages also reflect the fact that the SMO is a Transition province, which is home to a combination of Neotropical species, mainly present in the Veracruzan province, and Nearctic species, mainly present in the Chihuahuan Desert and Tamaulipas. Likewise, the high percentages of species shared between the SMO and the Transvolcanic Belt are because they are both transition provinces with extensive mountain ranges (Morrone et al. 2017; Morrone 2019). This pattern of the SMO being a transition province is also seen within the states in which the SMO occurs. For example, within Querétaro, the herpetofauna of the SMO regions of the state share the most species with the Central Plateau (Cruz-Elizalde et al. 2022). In Hidalgo, the SMO regions of the state shared the most species with the Gulf Coast Lowlands (Ramírez-Bautista et al. 2020). In Puebla, the SMO clusters with the Transvolcanic Belt and the Gulf Coast Lowlands (Woolrich-Piña et al. 2017).

Geographic proximity.—Our results suggest that the geographical characteristics, such as shared borders and distances between centroids, do not influence the number of species shared between the SMO and neighboring provinces but are a result of the physiographic similarity of the provinces (Table 2; see also Lemos-Espinal and Smith 2023 for a similar result looking at the similarity of the herpetofaunas of Mexican states). Although the SMO and the Transvolcanic Belt share only 307 km of border, are very close to each other (314.4 km separation), and are characterized by high mountains with great climatic and vegetative variability, so they host similar types of flora and fauna, especially around their contact zone. On the other hand, the Chihuahuan Desert, which has a 3,397 km long border with the SMO and is the closest (263.5 km between centroids; Table 2) shares fewer species, likely due to differences in their physiography. Thus, the similarity of provinces in terms of their herpetofauna more likely reflects the similarity of their habitats rather than simple geography or proximity. Therefore, conservation approaches should focus more on physiography than proximity to develop regional policies, regulations, and management plans.

Conservation concerns and recommendations.—At the state level, the SMO is often the region with the highest conservation priority ranking of all physiographic regions (e.g., Hidalgo: Ramírez-Bautista et al. 2020; Puebla: Woolrich-Piña et al. 2017; Querétaro: Cruz-Elizalde et al. 2022). The SMO is subject to strong anthropogenic pressures, such as wood extraction, agriculture, livestock, and expansion of human settlements, such that much of the native vegetation has been transformed into some type of anthropogenic cover, causing the loss of its natural habitats (Reyes-Hernández et al. 2009; Castro-Navarro et al. 2017; Sahagún-Sánchez and Reyes-Hernández 2018; see also Cruz-Elizalde et al. 2022; Leyte-Manrique et al. 2022). This is the main conservation threat faced by amphibians and reptiles in the SMO, which due to the physiographic conditions in the SMO can lead to the total loss of the limited area where these species are found (Zola-Rodríguez et al. 2024), with resulting loss of species (e.g., Berriozabal-Islas et al. 2018). The mountain cloud forest that represents < 1% of the land area of Mexico houses a high biological diversity (Rzedowski 1996) and appears to be particularly important for amphibians (Becerra-Soria et al. 2022). In the SMO, this particular habitat is located mainly in southern San Luis Potosí, northeastern Querétaro, eastern Hidalgo, and northeastern Puebla, and it experiences substantial anthropogenic effects, partly because of the unsustainable use of its resources (Ochoa-Ochoa et al. 2017, 2021; Lara-Tufiño et al. 2019).

For example, in the Xilitla region, large tracts of mountain cloud forest have been cut down to establish coffee, mandarin, and orange plantations, and the calcareous rocks that predominate in the region are frequently extracted for construction projects (pers. obs.). These forests face similar problems in other parts of the SMO where species characteristic of these habitats, such as the Banded Arboreal Alligator Lizard (*Abronia taeniata*), Knob-scaled Lizard (*Xenosaurus grandis*), Newman's Knob-scaled Lizard (*X. newmanorum*), Flathead Knob-scaled Lizard (*X. platyceps*), Marcella's Graceful Brown Snake (*Rhadinaea marcellae*), Sumichrast's Garter Snake (*Thamnophis sumichrastri*), and Slender-horned Pitviper (*Ophryacus undulatus*) face habitat destruction (pers. obs.), which will likely continue unless protection is extended and enforced in these areas. The transformation of cloud forests, which are crucial habitats for many endemic species in the SMO, exemplifies the severe impact of human activities (Ochoa-Ochoa et al. 2017, 2021). The rapid loss of these forests not only reduces habitat availability but also affects the ecological functions and microclimates necessary for the survival of numerous species (Ochoa-Ochoa et al. 2017, 2021) and is likely to accelerate with climate change (Rojas-Soto et al. 2012; Ponce-Reyes et al. 2013; Jiménez-García and Peterson 2019).

Pollution, particularly of aquatic systems, poses an additional threat, primarily to amphibians (Calderón et al. 2019; Ramírez-Bautista et al. 2020; Cruz-Elizalde et al. 2022; Zola-Rodríguez et al. 2024). Stream pollution can disrupt reproductive cycles and decrease habitat quality, exacerbating the decline of amphibian populations (Boone et al. 2007). These threats are compounded by the introduction of non-native species (Boone et al. 2007; Calderón et al. 2019).

In Mexico the laws protecting habitats and species are often poorly enforced, resulting in virtually no real environmental protection, especially with respect to excessive extraction of resources without due consideration of environmental impacts, causing the extirpation of populations of wildlife unique to this province (e.g., Sanjurjo-Rivera et al. 2021; Díaz-Osorio et al. 2022). In addition, several species in the IUCN Red List are Data Deficient or have not been evaluated. Likewise, species lists in risk categories, such as those in the NOM-059 generated by SEMARNAT, quickly become outdated because they are rarely updated (see also Lorenzo and González-Ruiz 2018). Most of the known species in Mexico are not listed (NL) in the NOM-059, because the current version was drawn up in 2010 and slightly modified in 2019. Therefore, it does not take into account a large number of species, nor the most recent scientific names of the species that have been described or modified since 2010 (e.g., see Appendix 1 for the numerous sources that have made recent changes to the herpetofauna lists for just the SMO). Thus, a number of species with NL status are not species that do not necessarily merit protection but are simply species that were described or whose names were modified after 2010. In addition, Quintero et al. (2014) found that many of the species of Mexican amphibians that were considered Data Deficient by the IUCN Red List were declining, emphasizing the need to obtain more data on species currently lacking proper conservation assessments. Similarly, in a global assessment, Isa et al. (2024) found that amphibians that had been previously assessed as Data Deficient by the IUCN Red List were more likely to be subsequently assessed as Vulnerable, Endangered, or Critically Endangered than in other categories. It is highly recommended that these lists be updated regularly through appropriate consultation with experts from each taxonomic group, and that environmental protection programs be carried out with the local participation of the human population and non-governmental organizations. These organizations should develop long-term sustainable conservation programs that are free of government intervention and do not change every time the federal government changes.

Conservation efforts should also consider the ecological characteristics of the habitats of the SMO. Protecting areas with high species richness and endemism, particularly cloud forests and riparian zones, will be crucial (Ochoa-Ochoa et al. 2017, 2021). Involving local communities and non-governmental organizations in conservation planning can enhance the effectiveness and sustainability of these efforts, as has been suggested for other regions and ecosystems in Mexico (e.g., Sanjurjo-Rivera et al. 2021; Najera-Medell et al. 2024).

Conclusion.—Our results suggest that the SMO is an important center of amphibian and reptile diversity in Mexico. In addition to its high species richness, the SMO shows high levels of endemism. Overall, our findings suggest that conservation efforts should focus on physiographic similarities rather than simple geographic proximity. Understanding the types of habitats and environmental conditions that

support species richness can help take decisions on conservation policies, regulations, and management plans for the region. The role of the SMO in hosting unique species can be understood through its geological history and tectonic activity. The SMO has been shaped by geological processes such as mountain building, volcanic activity, and plate tectonics, which have created a variety of habitats and isolated ecological niches. These historical processes contribute to the evolutionary history of the species found there, leading to high levels of endemism. In summary, the biodiversity of the SMO reflects a complex interplay of historical, ecological, and biogeographical factors. Understanding these dynamics and their consequences is crucial for developing effective conservation strategies that address both the specific needs of the unique species of the region and the broader environmental challenges they face.

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Appendices

Appendix 1. List of the literature sources used to create the species lists of amphibians and reptiles of the Sierra Madre Oriental, Mexico, used in this publication.

Arenas-Moreno et al. (2021); Badillo-Saldaña et al. (2018); Baeza-Tarin et al. (2018); Bryson et al. (2021); Burbrink and Guiher (2014); Campbell et al. (2018); Campillo-García et al. (2021); Carbajal-Márquez et al. (2020); Caviedes-Solis and Nieto-Montes de Oca (2018); Cox et al. (2018); Cruz-Elizalde et al. (2019); De la Torres-Loranca et al. (2020); Dixon and Lemos-Espinal (2010); Everson et al. (2021); Farr (2015); Fernández-Badillo et al. (2020); Grünwald et al. (2018); Guajardo Welsh et al. (2020); Hansen et al. (2016); Lazcano et al. (2019); Lemos-Espinal and Dixon (2013, 2016); Lemos-Espinal and Smith (2015, 2016, 2023); Lemos-Espinal et al. (2016, 2018a,b); Leyte-Manrique et al. (2022); Nevárez de los Reyes et al. (2016, 2019a,b); Palacios-Aguilar and Flores-Villela (2020); Ramírez-Bautista et al. (2020); Rautsaw et al. (2018); Schätti et al. (2020); Smith and Lemos-Espinal (2022); Sosa-Tovar et al. (2019); Tepos-Ramírez et al. (2021); Terán-Juárez et al. (2016); Torres-Hernández et al. (2021); Valencia-Herverth et al. (2020); Woolrich-Piña et al. (2017)

Appendix Table 1. Summary of the number of species shared between the Sierra Madre Oriental, Mexico, and its neighboring biogeographic provinces (excluding introduced species). The percentage of species shared between the Sierra Madre Oriental and each neighboring province is given in parentheses. Total refers to the number of species found in the Sierra Madre Oriental and its four neighboring provinces (i.e., the regional species pool), with the number in parentheses representing the percentage of the regional species pool found in the Sierra Madre Oriental. A dash (–) indicates that either the Sierra Madre Oriental or the neighboring province has no species in the taxonomic group, or that no species of that particular taxon are shared between the provinces. Abbreviations for the Biogeographic Provinces are: SMO (Sierra Madre Oriental), TVB (Transvolcanic Belt), Ver (Veracruzan), CD (Chihuahuan Desert), and Tam (Tamaulipas).

Taxa	SMO	TVB	Ver	CD	Tam	Total
Amphibia	123	93 (77)	59 (48)	38 (30.9)	19 (15.4)	230 (53.5)
Anura	76	62 (82.9)	52 (68.4)	30 (39.5)	18 (23.7)	142 (53.5)
Bufonidae	11	8 (72.7)	8 (72.7)	8 (72.7)	5 (45.5)	17 (64.7)
Centrolenidae	1	1 (100)	1 (100)	--	--	1 (100)
Craugastoridae	11	9 (81.8)	8 (72.7)	1 (9.1)	1 (9.1)	21 (52.4)
Eleutherodactylidae	10	8 (88.9)	6 (60)	2 (22.2)	2 (20)	22 (45.5)
Hylidae	26	23 (88.5)	15 (57.7)	9 (34.6)	3 (11.5)	47 (55.3)
Leptodactylidae	2	2 (100)	2 (100)	2 (100)	1 (50)	3 (66.7)
Microhylidae	4	2 (50)	4 (100)	2 (50)	2 (50)	4 (100)
Phyllomedusidae	1	1 (100)	1 (100)	--	--	3 (33.3)
Ranidae	7	6 (85.7)	4 (57.1)	4 (57.1)	1 (14.3)	20 (35)
Rhinophrynidae	1	--	1 (100)	--	1 (100)	1 (100)
Scaphiopodidae	2	2 (100)	2 (100)	2 (100)	2 (100)	3 (66.7)
Caudata	47	31 (66)	7 (14.9)	8 (17)	1 (2.1)	85 (55.3)
Ambystomatidae	1	1 (100)	--	1 (100)	--	15 (6.7)
Plethodontidae	45	30 (68.2)	6 (13.3)	7 (15.9)	--	67 (67.2)
Salamandridae	1	--	1 (100)	--	1 (100)	1 (100)
Sirenidae	--	--	--	--	--	2 (0)
Gymnophiona	--	--	--	--	--	3 (0)
Dermophiidae	--	--	--	--	--	3 (0)
Reptilia	259	158 (61)	145 (56)	106 (40.9)	55 (21.2)	530 (48.9)
Crocodylia	1	--	--	--	--	2 (50)
Crocodylidae	1	--	1 (100)	--	1 (100)	2 (50)
Squamata	250	153 (61.2)	137 (54.8)	103 (41.2)	50 (20)	493 (50.7)
Lacertilia	104	58 (55.8)	49 (47.1)	41 (39.4)	19 (18.3)	231 (45)
Anguidae	14	8 (57.1)	4 (28.6)	7 (53.8)	--	22 (63.6)
Anolidae	10	8 (80)	7 (70)	--	1 (10)	22 (45.5)
Corytophanidae	3	2 (66.7)	3 (100)	--	--	5 (60)
Crotaphytidae	1	--	--	1 (100)	1 (100)	4 (25)
Dibamidae	1	1 (100)	1 (100)	1 (100)	--	1 (100)
Diploglossidae	2	2 (100)	1 (50)	--	--	4 (50)
Eublepharidae	1	1 (100)	1 (100)	--	--	3 (33.3)
Helodermatidae	--	--	--	--	--	1 (0)
Iguanidae	2	2 (100)	2 (100)	--	2 (100)	5 (40)
Phrynosomatidae	34	18 (52.9)	9 (26.5)	22 (64.7)	10 (29.4)	85 (40)
Phyllodactylidae	--	--	--	--	--	4 (0)

Appendix Table 1, continued

Taxa	SMO	TVB	Ver	CD	Tam	Total
Scincidae	14	7 (50)	9 (64.3)	5 (35.7)	3 (21.4)	23 (60.9)
Sphaerodactylidae	1	1 (100)	1 (100)	--	--	3 (33.3)
Teiidae	5	4 (80)	3 (60)	4 (80)	2 (40)	26 (19.2)
Xantusidae	9	3 (33.3)	7 (77.8)	1 (11.1)	--	14 (64.3)
Xenosauridae	7	1 (14.3)	1 (14.3)	--	--	9 (77.7)
Serpentes	146	95 (66.7)	88 (60.3)	62 (42.5)	31 (21.2)	262 (55.7)
Boidae	1	1 (100)	1 (100)	--	1 (100)	2 (50)
Colubridae	48	29 (60.4)	36 (75)	27 (56.3)	15 (31.3)	89 (53.9)
Dipsadidae	49	32 (65.3)	30 (61.2)	13 (26.5)	4 (8.2)	83 (59)
Elapidae	4	3 (75)	3 (75)	1 (25)	1 (25)	10 (40)
Leptotyphlopidae	6	2 (33.3)	4 (66.6)	2 (33.3)	1 (16.7)	11 (54.5)
Loxocemidae	--	--	--	--	--	1 (0)
Natricidae	18	14 (77.8)	7 (38.9)	11 (61.1)	4 (42.2)	24 (75)
Typhlopidae	1	1 (100)	1 (100)	--	--	1 (100)
Viperidae	19	13 (68.4)	6 (31.6)	8 (42.1)	5 (26.3)	41 (46.3)
Testudines	8	5 (62.5)	7 (87.5)	3 (37.5)	5 (62.5)	35 (22.9)
Cheloniidae	--	--	--	--	--	4 (0)
Chelydridae	--	--	--	--	--	1 (0)
Dermatemydidae	--	--	--	--	--	1 (0)
Dermochelyidae	--	--	--	--	--	1 (0)
Emydidae	2	1 (50)	2 (100)	--	2 (100)	11 (18.2)
Geoemydidae	--	--	--	--	--	3 (0)
Kinosternidae	5	4 (80)	4 (80)	2 (40)	2 (40)	11 (45.5)
Testudinidae	1	--	1 (100)	1 (100)	1 (100)	2 (50)
Trionychidae	--	--	--	--	--	1 (0)
Total	382	251 (65.7)	204 (53.4)	144 (37.7)	74 (19.4)	760 (50.3)

Appendix Table 2. Summary of native species present in the Sierra Madre Oriental biogeographic province of Mexico by family, order or suborder, and class. Status summary indicates the number of species found in each IUCN conservation status in the order DD, LC, VU, NT, EN, CR (see Supplementary Information Table S1 for abbreviations; in some cases, species have not been assigned a status by the IUCN and therefore these may not add up to the total number of species in a taxon). Mean EVS (± standard error [SE]) is the mean Environmental Vulnerability Score ± 1 SE; scores ≥ 14 are considered high vulnerability (Wilson et al. 2013a,b), and risk category in Mexico according to SEMARNAT (2019) in the order NL, Pr, A, P (see Supplementary Information Table S1 for abbreviations).

			IUCN		SEMARNAT
Taxa	Genera	Species	DD, LC, NT, VU, EN, CR	Mean EVS ± SE	NL, Pr, A, P
Class Amphibia					
Order Anura	26	76	2,57,2,5,5,5	10.9 ± 0.46	49,17,8,2
Bufonidae	3	11	0,10,0,0,1,0	8.9 ± 1.10	9,2,0,0
Centrolenidae	1	1	0,1,0,0,0,0	10	1,0,0,0
Craugastoridae	1	11	1,8,0,0,2,0	13.3 ± 0.97	8,3,0,0
Eleutherodactylidae	1	10	1,9,0,0,0,0	14.6 ± 0.94	7,3,0,0
Hylidae	13	26	0,14,2,4,2,4	10.8 ± 0.74	16,3,7,0
Leptodactylidae	1	2	0,2,0,0,0,0	5.5 ± 0.50	2,0,0,0
Microhylidae	2	4	0,4,0,0,0,0	7.0 ± 1.08	1,3,0,0
Phyllomedusidae	1	1	0,1,0,0,0,0	13	1,0,0,0
Ranidae	1	7	0,5,0,1,0,1	11.9 ± 1.07	2,2,1,2
Rhinophrynidae	1	1	0,1,0,0,0,0	8	0,1,0,0
Scaphiopodidae	1	2	0,2,0,0,0,0	4.5 ± 1.50	2,0,0,0
Order Caudata	9	47	0,9,1,8,15,12	15.9 ± 0.35	20,21,5,1
Ambystomatidae	1	1	0,1,0,0,0,0	10	0,1,0,0
Plethodontidae	7	45	0,8,1,8,14,12	16.1 ± 0.32	20,20,5,0
Salamandridae	1	1	0,0,0,0,1,0	12	0,0,0,1
Subtotal	35	123	2,66,3,13,20,17	12.7 ± 0.39	69,38,13,3
Class Reptilia					
Order Crocodylia	1	1	0,1,0,0,0,0	13	0,1,0,0
Crocodylidae	1	1	0,1,0,0,0,0	13	0,1,0,0
Order Squamata	79	246	18,166,2,11,13,0	11.9 ± 0.21	148,64,37,1
Suborder Lacertilia	25	104	6,63,2,7,6,0	12.6 ± 0.29	62,28,13,1
Anguidae	4	14	2,5,0,1,2,0	14.3 ± 0.88	6,5,2,1
Anolidae	1	10	1,6,1,1,0,0	11.4 ± 1.10	6,3,1,0
Corytophanidae	3	3	0,3,0,0,0,0	9.3 ± 1.85	2,1,0,0
Crotaphytidae	1	1	0,1,0,0,0,0	13	0,0,1,0
Dibamidae	1	1	0,1,0,0,0,0	10	0,0,1,0
Diploglossidae	1	2	0,2,0,0,0,0	14	1,1,0,0
Eublepharidae	1	1	0,1,0,0,0,0	9	0,0,1,0
Iguanidae	2	2	0,2,0,0,0,0	12	0,2,0,0
Phrynosomatidae	3	34	1,23,1,2,2,0	13.1 ± 0.46	27,3,4,0
Scincidae	3	14	0,10,0,0,0,0	11.4 ± 0.43	9,4,1,0
Sphaerodactylidae	1	1	0,1,0,0,0,0	12	0,1,0,0
Teiidae	2	5	0,4,0,0,0,0	11.4 ± 0.81	4,1,0,0
Xantusidae	1	9	2,3,0,2,0,0	12.6 ± 1.04	3,4,2,0
Xenosauridae	1	7	0,1,0,1,2,0	14.7 ± 1.23	4,3,0,0

Appendix Table 2, continued

Taxa	Genera	Species	IUCN DD, LC, NT, VU, EN, CR	Mean EVS ± SE	SEMARNAT NL, Pr, A, P
Suborder Serpentes	54	146	12,103,0,4,7,0	11.4 ± 0.28	86,36,24,0
Boidae	1	1	0,1,0,0,0,0	10	1,0,0,0
Colubridae	21	48	1,41,0,0,2,0	10.6 ± 0.45	36,4,8,0
Dipsadidae	18	49	9,30,0,1,3,0	10.9 ± 0.47	28,21,0,0
Elapidae	1	4	1,3,0,0,0,0	12.5 ± 1.70	1,3,0,0
Leptotyphlopidae	2	6	0,2,0,0,0,0	10.3 ± 2.14	6,0,0,0
Natricidae	3	18	0,13,0,2,2,0	12.3 ± 0.79	6,0,12,0
Typhlopidae	1	1	0,1,0,0,0,0	11	1,0,0,0
Viperidae	7	19	1,12,0,1,0,0	14.1 ± 0.65	7,8,4,0
Order Testudines	5	8	0,3,2,0,0,0	13.6 ± 1.21	2,4,2,0
Emydidae	2	2	0,0,0,0,0,0	16.0 ± 3.00	2,0,0,0
Kinosternidae	2	5	0,2,2,0,0,0	11.8 ± 0.91	0,4,1,0
Testudinidae	1	1	0,1,0,0,0,0	18	0,0,1,0
Subtotal	85	259	18,170,4,11,13,0	12.0 ± 0.20	150,69,39,1
Total	120	382	20,236,7,24,33,17	12.2 ± 0.19	219,107,52,4