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ORIGINAL ARTICLE

Taxonomic and functional diversity of the amphibian and reptile communities of the state of Durango, Mexico

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Abstract
Taxonomic and functional diversity metrics have been used together to describe functional patterns through species richness in a given area or region. Many scientists have shown that these two metrics can be positively correlated; nevertheless, other studies have found the opposite. In either case, the usefulness of both metrics has helped to develop more reasoned conservation strategies in areas where biodiversity loss is occurring at an accelerated rate. In this study, we calculated metrics of both taxonomic and functional diversity in amphibian and reptile communities located in a variety of vegetation types (xeric scrub, pine forest, pine-oak forest, cloud forest, oak forest, and tropical dry forest) in the state of Durango. Using species richness (157 species: 36 amphibians and 121 reptiles) for the state of Durango, we found that the amphibian communities present in pine forest and pine-oak forest showed high values of taxonomic diversity (high Delta + values), meaning that the communities in these vegetation types are composed of a complex network of families and genera. The same result was true of reptiles present in oak forest, tropical dry forest, and xeric scrub. The communities formed by the snakes showed high values of functional richness, functional evenness, and functional dispersion in all vegetation types, as did the lizard communities present in xeric scrub. This indicates that the ecological functions of lizards and snakes (i.e., predators; pest controllers; links in the trophic chain) are an integral element of the functioning of these ecosystems. These results showed that vegetation types with greater taxonomic and functional diversity in amphibians and reptiles are sites that promote the sustainability of an ecosystem in particular ways, making them more suitable for conservation of these vertebrates. The information from this study can be useful in developing protection programs and implementing conservation strategies for several biological groups in particular areas of Durango and the Sierra Madre Occidental, helping to ensure the permanence of the remarkable biota of northern Mexico.

Keywords Species richness · Community · Vegetation types · Herpetofauna · Ecoregion · Biogeography

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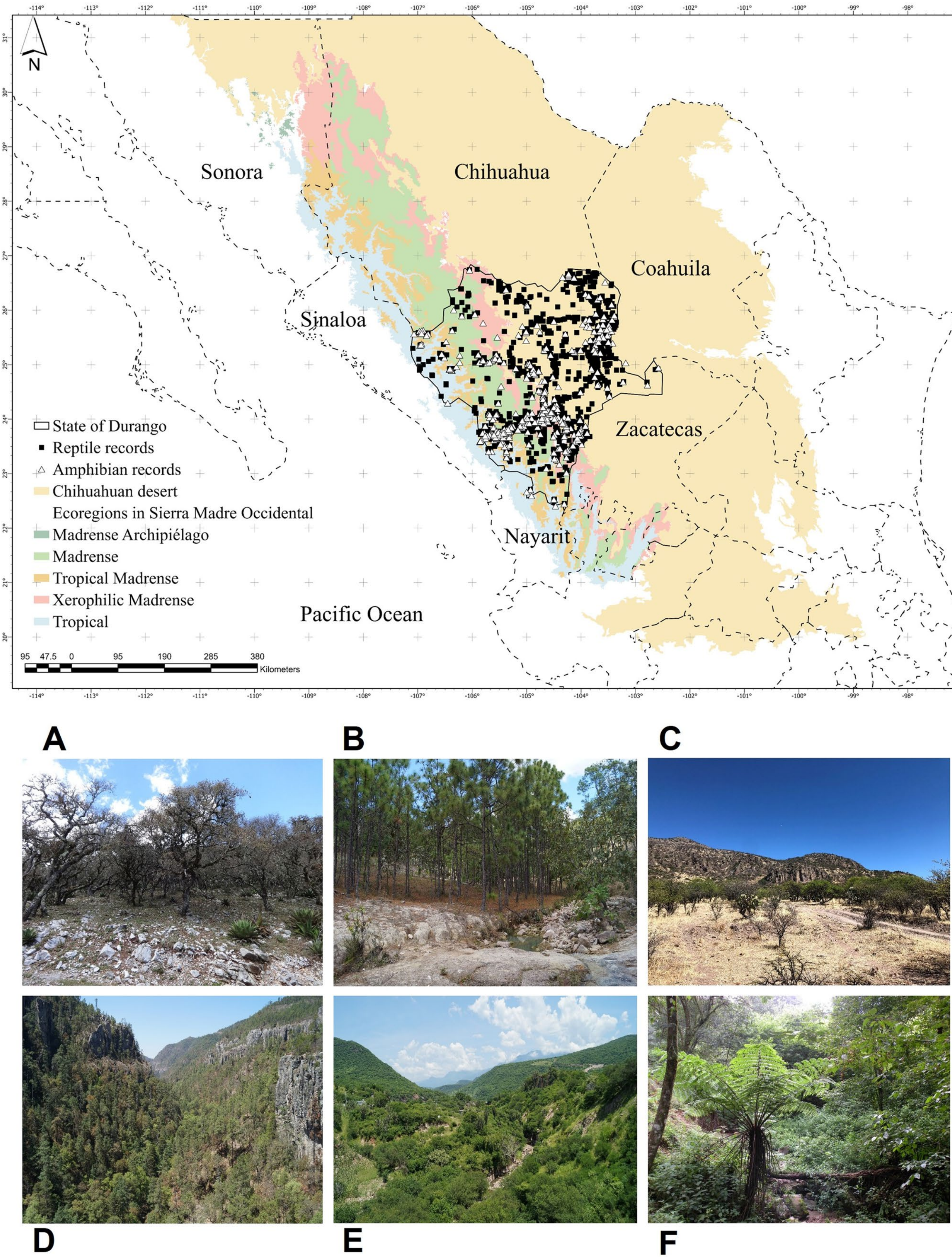
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◂**Fig. 1** Amphibian and reptile records and vegetation types used in this study. **A** Oak forest (dry season), Pablillo, in the municipality of Galeana, Nuevo León, at an elevation of 2580 m; **B** Oak-pine forest (dry season), El Duraznito, in the municipality of El Nayar, Nayarit, at an elevation of 2200 m; **C** Xeric scrub (dry season), Rancho El Bufalo, in the municipality of Canatál, Durango, at an elevation of 2025 m; **D** Pine forest (dry season), Salto del Agua Llovida, Durango, Durango, at an elevation of 1900 m; **E** Tropical dry forest (wet season), La Guerra, in the municipality of El Nayar, Nayarit, at an elevation of 465 m; **F** Cloud forest (wet season), Medio Monte, in the municipality of San Bartolo Tutotepec, Hidalgo, at an elevation of 1800 m. Photographs by Uriel Hernández-Salinas

Introduction

Geographic regions with a complex topography favor diversity, species richness, turnover of species among sites, and functionality of ecosystems (Chen et al., 2011). An example of a complex geographic area is Mexico, which has been subject to countless vicariance events that have resulted in the formation of barriers and corridors for upland and lowland species. Mexico is also the product of two great biogeographical regions (Neartic and Neotropical), which together give rise to the Trans-Mexican Volcanic Belt (Halffter, 1976; Halffter et al., 2008; Morrone, 2015), producing one of the most outstanding faunas in the world, including amphibians (431) and reptiles (989) (numbers updated to March 08, 2023; Ramírez-Bautista in press).

Due to the complex evolutionary and biogeographic history of the herpetofauna of Mexico, its analysis can be approached through numerous different metrics such as, phylogenetic, genetic, ecological, evolutionary, taxonomic, and functional metrics (Cruz-Elizalde et al., 2022). The relationship between these last two metrics (taxonomic and functional diversity) has been controversial, since taxonomic diversity and the functioning of ecosystems are not clear yet; however, the functional diversity approach can be used to explain this relationship (Cadotte et al., 2011; Cilleros et al., 2016; Larson et al., 2021).

At the end of the twentieth century, Clarke and Warwick (1998, 1999) and Warwick and Clarke (1995, 1998), introduced the concept of taxonomic diversity as an extension of species richness and diversity. They consider that a community with closely related species is less biodiverse in a phylogenetic sense than a community with low relatedness among species. Based on this concept, the average taxonomic index Delta + ($\Delta +$) and average taxonomic variation Lambda + ($\Lambda +$) were used to distinguish the degree of taxonomic relationship among plant and animal communities within the same ecosystem.

The concept of functional diversity was introduced by Faith (1996) and applied analytically by Petchey and Gaston (2002). According to Faith (1996), functional diversity is the key to understanding the relationship between the structure of communities and ecosystem function, considering first that the functional traits of species (type of diet, reproduction, behavior) are the most important characteristics determining the proper functioning of ecosystems (Violle et al., 2007). In addition, several studies have pointed out that the association between taxonomic and functional diversity is not always significant or predictable, because functional diversity components such as evenness and dispersion are independent of the number of species in the community (Jarzyna & Jetz, 2018; Mason et al., 2005; Morelli et al., 2018; Mouchet et al., 2010; Villéger et al., 2008).

The taxonomic diversity of animal communities present in various vegetation types or ecosystems of Mexico is high, and each community has functional features determined by its evolutionary history in its area of distribution, origin (Nearctic or Neotropical), ecological interactions, and use of resources (microhabitat and food), which together are the result of the evolutionary process that species have undergone within their habitats over time (Ricklefs & Miller, 1999). Amphibians and reptiles are one of the richest groups in Mexico; with almost 70% of them regarded as country endemic, and consequently representing very particular functional characteristics. For example, in the case of amphibians, their life cycles take place in both aquatic and terrestrial environments, which provide different functional features (oxygenation of water bodies, insect predators; Zug et al., 2001) according to their stage of development. Reptiles, particularly some groups of snakes and lizards, contribute to the environment with functional features in their diet (e.g., specialists or generalists; Pianka, 1966), show both modes of reproduction in the same families (viviparous and oviparous; e.g., Phrynosomatidae, Colubridae; Klauber, 1982; Tinkle et al., 1970), and exhibit different foraging tactics (sit-and-wait, widely-foraging; Pianka, 1966), and diverse reproductive cycles (seasonal, annual, continuous, among others; Tinkle et al., 1970; Calderon-Mandujano 2011; Sánchez, 2011). However, functional and taxonomic analyses on these groups have been practically null (Berriozabal-Islas et al., 2017; Cruz-Elizalde et al., 2022; Peña-Joya et al., 2020). The communities of amphibians and reptiles of the state of Durango represent suitable study models for taxonomic and functional analysis, since the herpetofauna of this state is among the richest in northern Mexico, distributed along four ecoregions (arid and semiarid, quebradas, sierra, and valleys; González-Elizondo et al., 2007, 2012; Fig. 1), and three biogeographic provinces (Sierra Madre Occidental, Chihuahuan Desert, and Mexican Plateau; Espinosa-Organista et al., 2008; Morrone, 2001). These facts confer a high probability of occurrence of different assemblages of species, and therefore different functional traits (e.g., ecological, morphological, and behavioral characteristics) in each community, which makes it worthy of being explored under an evolutionary scenario for the many biological groups.

Although Durango is one of the largest states in Mexico, and with one of the best known herpetofaunas in this country (Lemos-Espinal et al. 2019), currently there is no study that has jointly evaluated taxonomic and functional diversity of the communities of amphibians and reptiles for the state. Therefore, the objective of this study is to determine the direction of associations between taxonomic and functional diversity (species richness and evenness) across amphibian and reptile communities present in different vegetation types in the state of Durango.

Methods

Study site

The state of Durango is located in north-central Mexico, represented mostly by the Sierra Madre Occidental, and to a lesser extent by the Chihuahuan Desert, and the Mexican Plateau (INEGI, 2012; Fig. 1). The surface area encompasses 123,181 km^2, making it the fourth largest state in the country, covering 6.3% of the total area of Mexico (Gonzalez-Elizondo et al. 2012; INEGI, 2012). The state is bordered by Chihuahua to the north, Coahuila and Zacatecas to the east, Nayarit to the south, and Sinaloa to the west (Fig. 1). The range of elevation within the state goes from 130 to 3,000 m above sea level (m.a.s.l; González-Elizondo et al., 2007; INEGI, 2012). According to Rzedowski (1978), Durango has 12 vegetation types; however, for this study, amphibian and reptile communities present in only six vegetation types were analyzed [cloud forest (CF), pine-oak forest (POF), pine forest (PF), oak forest (OF), xeric scrub (XS), and tropical dry forest (TDF; Fig. 1 and Online Appendix)]. Each species of amphibian and reptile was assigned to one or more communities according to the vegetation types in which they are distributed in the state (see Online Appendix); this was performed by projecting the species records on the vegetation and elevation layers for the state of Durango (Fig. 1; INEGI, 2012).

Data gathering

We generated a list of amphibian and reptile species for the state of Durango from field work, literature (Smith & Taylor, 1945, 1948, 1950; Duellman, 2001; Campbell & Lamar, 2004; Gadsden et al., 2006; Valdez Lares et al., 2013; Lemos-Espinal et al. 2019), and records obtained from scientific collections; National Amphibian and Reptile Collection (CNAR), the Herpetological Collection of the Museum of Zoology "Alfonso L. Herrera" (MZFC-UNAM), the Universidad Nacional Autónoma de Mexico, and the Collection of Amphibians and Reptiles of CIIDIR Unidad Durango-Instituto Politécnico Nacional (total records = 2691 amphibians, and 7889 reptiles). We based the taxonomic classification of the species on the works of Wilson et al. (2013a, 2013b), and updated species scientific names up to February 2023, based on Frost (2023) for amphibians and Uetz et al. (2023) for reptiles. In addition, we assessed recent taxonomic changes in both groups to update the identification of species as much as possible (Duellman et al., 2016; Meza-Lázaro & Nieto-Montes de Oca, 2015; Nieto-Montes de Oca et al., 2017; Rovito et al., 2015; Ruane et al., 2014; Wilson et al., 2013a, 2013b).

Data analysis

Hotspot and sample coverage

Considering the abundances (geographic records) of the study groups (amphibians, reptiles, and herpetofauna), we performed a hotspot analysis with the Getis-Ord Gi* statistic (Getis & Ord, 1992); this tool calculates the distance of each record with the total area (123,181 km; González-Elizondo et al., 2012) and applies the z-score to represent those areas, a high z-value represents areas considered Hotspots; lower z-values represent Coldspots (Getis & Ord, 1992). With the same records, we spatially measured the sample coverage, for which we made a buffer area of 1.5 km^2 for each record and using the tool "calculate geometry" present in the phyton console of the ArcGis Pro 3.0.3, we measured the buffer areas and compared with the total area of the state of Durango. Finally, we generated a species-accumulation curve using the sample coverage index proposed by Hsieh et al. (2016), which employs a routine of 100 random resamples on the abundances of each group, considering the principles of rarefaction, observation, and extrapolation available in the iNEXT program (Hsieh et al., 2016).

Taxonomic diversity

First, we numerically describe the richness of species for the vegetation types used in this study (CF, POF, PF, OF, XS, and TDF), and then estimate the taxonomic diversity, considered as a measure of distance of the phylogenetic relationship among the species present in one or several vegetation types. This type of diversity is part of a phylogenetic or Linnean classification that shows phylogenetic relationship among species, depicting the hierarchical levels such as class, order, family, and genus (Clarke & Warwick, 1998). Because amphibians and reptiles have divergent phylogenetic histories, the two groups were analyzed separately in this study. We calculated the average taxonomic distinctness (Delta = $\Delta+$) and the variation in taxonomic distinctness (Lambda = $\Lambda+$; Clarke & Warwick, 1998) to determine the taxonomic diversity of amphibian and reptile communities present in the types of vegetation of the state of Durango considered in this study. This method assumes that a community has a close phylogenetic relationship among species. The formulas for taxonomic diversity and variation are as follows: $\Delta+=[2\Sigma\Sigma i<j\ \omega_{ij}]/[S\ (S-1)]$ and $\Lambda+=[2\Sigma\Sigma\ i<j\ (\omega_{ij}-\Delta+)2]/[S\ (S-1)]$; where ω_{ij} is the taxonomic distance between each pair of species groups i and j, and S is the total number of observed species in the sample (Warwick & Clarke, 1995). A high value of $\Delta+$ reflects low taxonomic relationship among species. $\Lambda+$ is a measure of non-evenness in community structure in each vegetation type. A high value of $\Lambda+$ indicates under or overrepresentation of the species in the samples. To detect differences in taxonomic distinctiveness of each vegetation type, species were analyzed under the null model of randomization (Clarke & Warwick, 1998). This model uses the values of mean and variance of the species number with a confidence interval of 95% obtained by 1,000 random samplings (Clarke & Warwick, 1998). For these analyses, the amphibian and reptile classifications were based on Wilson et al. (2013a, 2013b), in both cases considering five taxonomic categories (species, genus, family, order, and class). The taxonomic diversity analysis was carried out with PRIMER 5 program for Windows (Clarke & Gorley, 2001).

Functional diversity

Functional diversity analyses were done by functional group; in other words, one analysis was done specifically for amphibians (anurans and salamanders) and another for turtles, lizards, and snakes present in each type of vegetation. This is because each functional group has particular life histories and functional traits (McGill et al., 2006; Mlambo, 2014; Weiher et al., 2011). For these analyses, seven functional traits were included, five categorical (foraging type, diet, habit, activity, and reproductive mode) and two numerical (average value of the biomass [mass] and snout–vent length [SVL]). In general, these variables are correlated in both groups (see Online Appendix; Casanoves et al., 2011; Laliberté & Legendre, 2010). These functional traits came from two sources of information: 1) field work, and 2) natural history of each species (Campbell & Lamar, 2004; Duellman, 2001; Lemos-Espinal & Smith, 2007; Murphy & Méndez de la Cruz, 2010; Vitt & Caldwell, 2014).

To obtain a general value of functional diversity from the selected functional traits, it was necessary to evaluate functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis; Mason et al., 2007; Villéger et al., 2008). FRic measures the volume of functional space occupied by the community, its values are represented as the difference between the lowest and highest value of the analysis (Mason et al., 2005). FEve measures the regularity of the distribution of the abundance of species of a community in functional space; the values of FEve range from 0 to 1, being 1 when all species are equally represented and 0 when the presence of species in the community is unequal (Villéger et al., 2008). FDis measures the average distance of each species to the centroid formed by those species that are the most abundant in the community. This measure is larger when the functional characteristics of the species are more numerous, indicating a greater differentiation of the ecosystem (Laliberté & Legendre, 2010). A high value of FDis indicates that organisms are more adapted to the ecosystem, which implies greater resistance when invasive species arrive (Laliberté & Legendre, 2010). For the functional diversity analysis, Gower's distance measurement was used due to the inclusion of both continuous and categorical data (Online Appendix). Functional diversity indices were calculated using the Functional Diversity package in R (Laliberté & Legendre, 2010; R Core Team 2022).

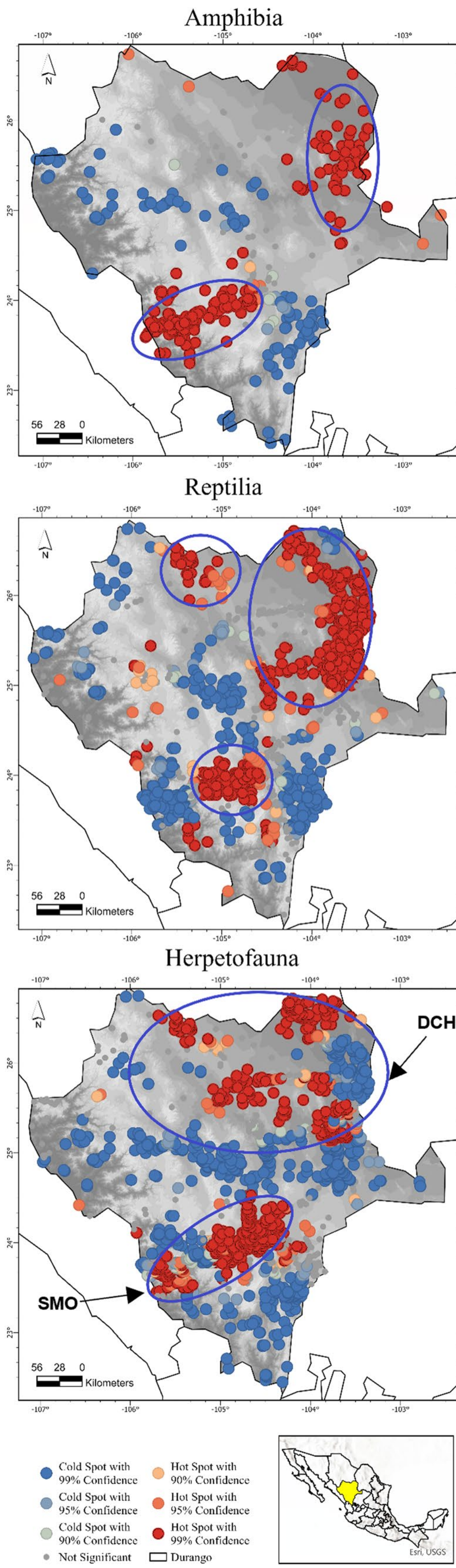
Results

Species richness, hotspot, and sample coverage

We found records for 157 species of amphibians and reptiles from Durango, represented by 4 orders, and 31 families (see Online Appendix). Of these species, 36 (23%) are amphibians and 121 (77%) reptiles. Forty-five percent (72 species) of the state's herpetofauna is Mexican endemic (see Online Appendix). The community present in xeric shrub included the highest number of species (102 total; 19 amphibians [19%] and 83 reptiles [81%]; see Online Appendix). The community with the second highest species richness was found in the pine-oak forest (47 total: 12 amphibians [25%] and 35 reptiles [75%]). The tropical dry forest contains a community comprised of 41 species (13 amphibians [32%] and 28 reptiles [68%]). Thirty- two species are recorded in pine forest (9 amphibians [28%] and 23 reptiles [72%]); oak forest has 18 species (5 amphibians [28%] and 13 reptiles [72%]), and cloud forest contained only two species, a toad (*Incilius occidentalis*) and a lizard (*Gerrhonotus infernalis*; see Online Appendix).

The hotspot analysis identified areas with high species richness. For example, in both groups (amphibians and reptiles) two important areas can be observed, the first is located in the northeastern region, and the second in the southeastern region of Durango (Fig. 2); a third area of species richness can be observed in the northern region of Durango, mainly in reptiles (Fig. 2). When amphibians and reptiles (herpetofauna) are represented together, it is possible to observe two large areas of richness or hotspot, one located in the northern region and the other in the southeastern region of Durango (Fig. 2). Both areas constitute sites with faunas typical of the Sierra Madre Occidental and Chihuahuan Desert, distributed in large areas

Fig. 2 Hotspots for amphibians and reptiles in the state of Durango ▸ Mexico. Map generated from the Getis Ord and Moran index. Red circles represent species-rich areas, which also represent sites with high sampling effort. *SMO* Sierra Madre Occidental, *DCH* Chihuahuan Desert



of temperate forests and xeric scrub at elevations ranging from 1500 to 2400 m.a.s.l (Figs. 1 and 2).

On the other hand, the sample coverage analysis recognized that amphibians represent only 2.11% (2608.4 km^2) of the sampled coverage in the state, while reptiles represent 6.7% (8253.7 km^2) of the sampled area. When both groups (herpetofauna) are combined, the sampled coverage in the state of Durango increases to 8.8% (10,862.1 km^2). A species-accumulation curve applied to the abundance data for each group (amphibians, reptiles, and herpetofauna), showed an exponential growth (species accumulation), followed by an asymptotic phase (Fig. 3), which is equivalent to stating that the herpetofaunal inventory for the state of Durango has a high percentage of completeness (Fig. 3).

Taxonomic diversity

For amphibians, pine forest and pine-oak forest were the vegetation types with the highest values of taxonomic diversity (Delta+; Figs. 4 A, B and 5). This means that the amphibian communities present in these vegetation types have high taxonomic levels (i.e., species in a community are represented by multiple genera and families), while their high value of taxonomic variation (Lambda+) is related to over or underrepresentation of some taxonomic groups (Fig. 4A, B). Although xeric scrub presented the highest number of species (19), it showed a medium Delta+value; the same occurred for oak forest and tropical dry forest (Fig. 4A). For taxonomic variation (Lambda+), the vegetation types cloud forest, oak forest, and xeric scrub were within the confidence intervals, below but close to the average. Taxonomic variation in the tropical dry forest was marginally above the confidence intervals, showing a low taxonomic representativeness of genera and families in this analysis (Figs. 4B and 5).

In the case of reptiles, the communities present in the xeric scrub presented the highest values of taxonomic diversity (Delta+; Figs. 4C and 5), and the communities present in tropical dry forest, oak forest, pine forest, and oak-pine forest presented medium values (Fig. 4C). This indicates that the communities that inhabit xerophytic ecosystems, as well as temperate and tropical ecosystems, have high and medium taxonomic complexity, respectively. Cloud forest had below-average Delta+and Lambda+values, indicating lower taxonomic diversity (Figs. 4D and 5).

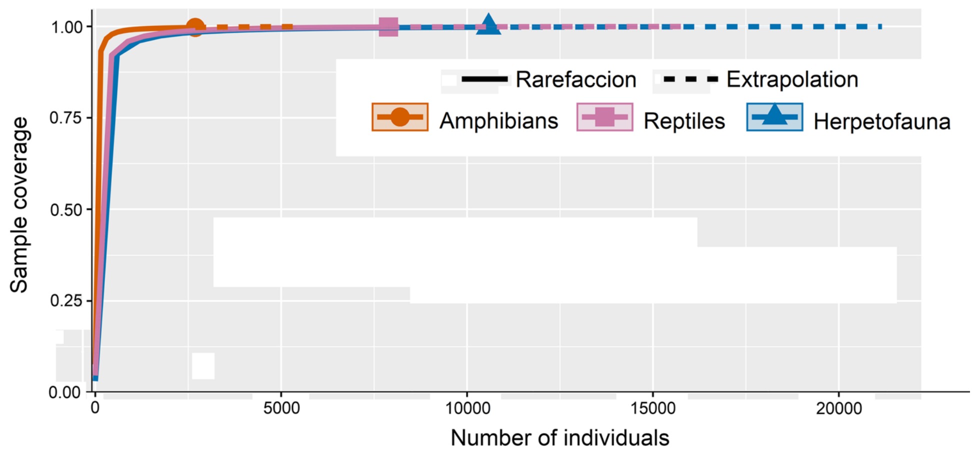


Fig. 3 Accumulation curve for the amphibians, reptiles and herpetofauna of the state of Durango, Mexico. The inventory of each group shows a high completeness. The lines (orange, pink and blue) represent the accumulation of species for each group analyzed

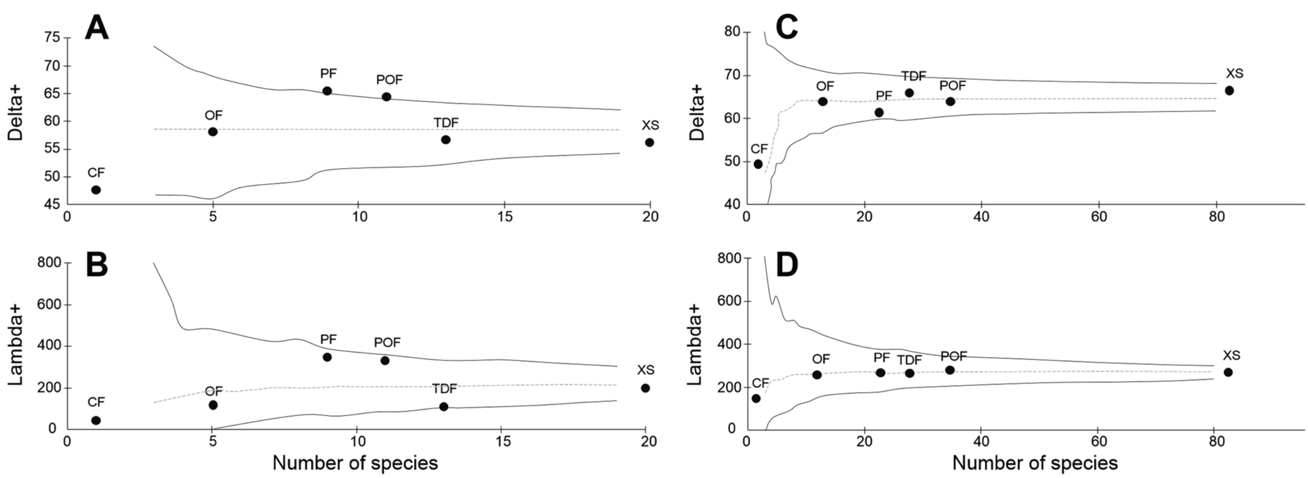


Fig. 4 Average taxonomic diversity (Delta +) and variation of taxonomic diversity (Lambda +) for analyzed amphibian communities (**A**, **B**) and reptile communities (**C**, **D**) in different types of vegetation and ecoregions of the state Durango. Pine-oak forest = POF, pine forest = PF, oak forest = OF, cloud forest = CF, xeric scrub = XS, tropical dry forest = TDF. The curved lines represent the 95% confidence interval, and the dotted line the average value generated by the model

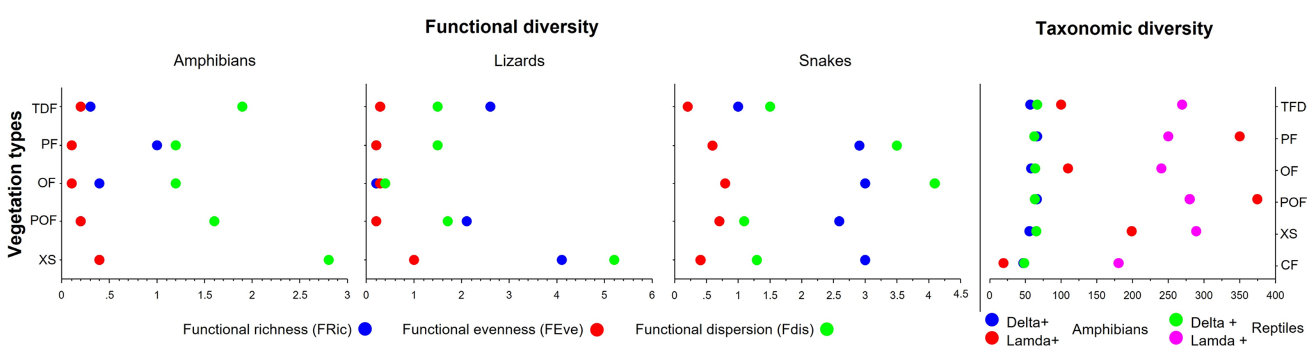


Fig. 5 Functional and taxonomic metric values for the amphibians and reptiles of the state of Durango. The information in this figure is complementary to Table 1

Species traits and functional diversity

Most amphibian species reported for the state of Durango have an insect-based diet (see Online Appendix), but the toad *Rhinella horribilis* has an omnivorous diet. The frog *Lithobates catesbeianus* is recorded as a species with an insectivorous and carnivorous diet, and three salamander species of the genus *Ambystoma* are considered to be insectivores and herbivores (Online Appendix). In terms of habit, 24 species of amphibians have terrestrial and aquatic habits, nine species are exclusively terrestrial; one frog (*L. montezumae*) is aquatic and another (*Agalychnis dacnicolor*) arboreal. Twenty-one species have nocturnal and twilight activity, and seven species show activity throughout the day (diurnal/night/twilight; Online Appendix).

Four turtle species are omnivorous, terrestrial, and aquatic, and have diurnal and twilight activity; only *Gopherus flavomarginatus* is herbivorous and terrestrial. Of the total number of lizards, 52 species have an insect-based diet and are terrestrial and saxicolous; 15 species are arboreal. Thirty-nine species of lizards have diurnal activity, and the rest are nocturnal (Online Appendix). In the case of snakes, which is the largest functional group of the herpetofauna in the state of Durango, all species of this group have a carnivorous diet and live in terrestrial habitats; a minority (two species) live in trees. Fifty-one species are diurnal, and more than half of the total are nocturnal and twilight active (Online Appendix).

In terms of functional diversity, snakes showed the highest values of richness and functional evenness in all types of vegetation; lizards showed the highest values of the three parameters of functional diversity only for xeric scrub (Table 1 and Fig. 5). In the analysis of functional diversity for amphibians, relatively high values of functional dispersion were observed for pine forest. The amphibians present in xeric scrub showed high values of functional dispersion (Table 1 and Fig. 5). Turtles had high values of functional dispersion and low values of richness and functional evenness for xeric scrub; results for this group (turtles) were reported only for xeric scrub due to their null representation in the rest of the vegetation types (Table 1 and Fig. 5).

Table 1 Functional diversity values of amphibian and reptile communities present in different vegetation types in the state of Durango

Vegetation types	Amphibians	Lizards	Snakes	Turtles
Functional richness				
Xeric scrub	0.4 (19)	4.1 (39)	3.0 (39)	0.5 (5)
Pine-oak forest	0.2 (12)	2.1 (10)	2.6 (24)	
Tropical dry forest	0.3 (13)	2.6 (14)	1.0 (14)	
Pine forest	1.0 (9)	0.2 (5)	2.9 (18)	
Oak forest	0.4 (5)	0.2 (5)	3.0 (8)	
Functional evenness				
Xeric scrub	0.4	1	0.4	0.6
Pine-oak forest	0.2	0.2	0.7	
Tropical dry forest	0.2	0.3	0.2	
Pine forest	0.1	0.2	0.6	
Oak forest	0.1	0.3	0.8	
Functional dispersion				
Xeric scrub	2.8	5.2	1.3	3
Pine-oak forest	1.6	1.7	1.1	
Tropical dry forest	1.9	1.5	1.5	
Pine forest	1.2	1.5	3.5	
Oak forest	1.2	0.4	4.1	

The numbers in parentheses represent the species richness of the respective community

Discussion

Species richness

Environmental heterogeneity and the complex topography of Mexico are recognized as the main factors that generate variations in the distribution, richness, and evolutionary history of the species within different biological groups (Rodríguez et al., 2003). The environmental heterogeneity and rugged topography of Mexico promote diverse regions and biogeographic provinces that contain a species composition of both amphibians and reptiles (Ochoa-Ochoa et al., 2014) with a remarkable degree of endemism (Flores-Villela et al., 2010; Ochoa-Ochoa et al., 2014).

To date, the herpetofauna of Durango represents 11% of the Mexican herpetofauna (431 amphibians and 989 reptiles, numbers updated to March 08, 2023; Ramírez-Bautista in press). The amphibian richness of Durango (36 species; Lemos-Espinal et al. 2019), has increased by 12.9% over that reported by Parra-Olea et al. (2014; 27 species), and as for reptiles (121 species; Lemos-Espinal et al. 2019), it has increased by 9.3% over that reported by Flores-Villela and García-Vázquez (2014; 97 species). Likewise, the total number of species for Durango is higher than that reported for other states in northern Mexico, such as Baja California (119 species; Lemos-Espinal, 2015), Nuevo León (139 species: Nevárez-de-los-Reyes et al. 2016), Coahuila (143 species; Lazcano et al., 2019), and Zacatecas (78 species; Flores-Villela & García-Vázquez, 2014; Parra-Olea et al., 2014). However, this species richness is similar to that of other states of northern and central Mexico but lower than that of Chiapas (330 species; Johnson et al., 2015), Veracruz (359 species; Torres-Hernández et al., 2021) and Oaxaca (480 species; Mata-Silva et al., 2021). The three latter states are the richest Mexican entities in the number of amphibians and reptiles. The species richness of Durango is equivalent to 36% of the species present in northern

Mexico (379 species; Lavín-Murcio & Lazcano, 2010), an area that includes the Chihuahuan Desert, Sinaloa, Sierra Madre Occidental, Sierra Madre Oriental, and Tamaulipas, reflecting a remarkable richness of species of temperate and xerophilous ecosystems of the northern portion of Mexico. This pattern has been previously described by Flores-Villela et al. (2010) and Lavín-Murcio and Lazcano (2010), who pointed out that in arid and temperate ecosystems such as in mountainous regions covered by pine forest, oak forest, and pine-oak forest of the northern region of Mexico, there is a significant amount of biodiversity from western North America, as well as a high level of endemism that is not comparable to any other region.

The 157 herpetofaunal species of Durango represent a high completeness of the inventory, as supported by our species-accumulation curve (Fig. 3). This result may seem contradictory if we consider that our sampling area represents only 8.8% of the total area for the state. This may be justified by the fact that the number of records and species used for this study represent a "sample" of the total richness and diversity of the herpetofauna of Durango. This sample is composed of records covering the main vegetation types and ecoregions of the state, and although they may seem few (records: 2691 amphibians, and 7889 reptiles), they are distributed throughout the entire state. Our accumulation curve can predict the completeness of an inventory; however, it is far from demonstrating that we have recorded 100% of the species (Moreno & Halffter, 2000; Jimenez-Valverde and Hortal 2003). In Durango there are areas of difficult access and consequently have not been sampled for decades. For instance, the San Pedro Mezquital River Basin, Jesus Maria River Basin, Nazas River Basin, Cañón de Fernández, and large areas of pine-oak forest in the northern portion of the state have not been explored thoroughly; therefore, we suspect that these areas likely hold species that so far have not been included in our inventory.

We observed a large number of endemic species in the xerophytic and temperate ecosystems of the state of Durango (see Online Appendix); this richness of endemisms for the state is found in the Madrense region of pines and oaks, the Madrense xerophytic region of the Sierra Madre Occidental and in the xerophytic scrub of the Chihuahuan Desert (Fig. 1). These regions coincide with the hotspots zones (SMO, DCH) indicated in our Fig. 2, considered to be areas of interest in terms of endemism due to the contact zone created among the three biogeographic provinces, the Sierra Madre Occidental, Chihuahuan Desert, and Mexican Plateau (Arriaga et al., 1997; Van Devender et al., 2005; González-Elizondo et al. 2012; Rodríguez-Gutiérrez 2022). This pattern of higher number of endemics in xerophytic and temperate ecosystems of the Sierra Madre Occidental and Chihuahuan Desert has been observed in other groups; for example, in pines (González-Elizondo et al., 2012), agaves (González-Elizondo et al. 2009), bats (López-González, 2003; López-González et al., 2014), and turtles (Morafka, 1982), an additional reason as to why these ecosystems should be considered important for conservation. However, it should be noted that the hotspots (SMO and DCH) shown in Fig. 2 represent the most explored areas in Durango, as they historically have been popular collecting sites for both Mexican and foreign herpetologists for many years (e.g., Durango-Mazatlán region, the Laguna region and Mapimí Biosphere Reserve, the latter between Durango and Coahuila; McCranie & Wilson, 1987, 1990; Webb, 1984), due to their easy access and also are regarded as safer than those found in the northern and western regions of Durango (Fig. 2). In fact, these regions (northern and western Durango) together with the southern portion of the state of Chihuahua and eastern Sinaloa represent a megaregion called "El Triangulo Dorado," considered a dangerous zone because of frequent illegal activities (e.g., drug processing and clandestine logging). It has been pointed out that this megaregion can be considered a biodiversity hotspot because there are large areas of temperate and tropical forests that have not been explored for more than a century. In addition to illegal activities, this region also experiences strong local conflicts among indigenous groups with respect to land boundaries, subsequently making field work in this region quite challenging (Bye, 1995; CONABIO 2017; Secretaría de Marina 2020; UNODC 2020).

Taxonomic and functional diversity

To date, it has been noted that taxonomic diversity outcomes may or may not be positively correlated with some components of functional diversity, such as functional richness (FRic; Morelli et al., 2018). The pine forest amphibian community presented high values of taxonomic diversity and functional richness, together with a lower value of evenness and a moderate value of dispersion (Figs. 4 and 5). This result suggests that the functional characteristics of the amphibian community in this type of vegetation (pine forest) do not extend to all available niches, assuming that competition for niche resources is not particularly high, since there are still niches available for other species of amphibians or for other groups of vertebrates. Ochoa-Ochoa et al. (2019) also found that functional diversity for a wide number of amphibian communities was positively correlated with species richness. The authors noted that in some cases this association may vary according to latitude. On the other hand, the amphibian communities present in the pine-oak forest, pine forest, and tropical dry forest presented medium values of functional diversity, despite being well represented taxonomically (Figs. 4 and 5). This result confirms that a high value of taxonomic diversity is not always associated with a high value of diversity in functional terms and suggests that there are similarities among the species of a community in terms of ecological roles and functions. A similar pattern was shown by Morelli et al. (2018) in their study of taxonomic and functional diversity in an assemblage of birds in disturbed and conserved environments of central Italy.

The reptile communities present in the xeric scrub also had high values of taxonomic and functional diversity (Figs. 4 and 5). This result suggests that this group of vertebrates may be well adapted to the arid conditions of this environment, as has been observed in other reptile communities from deserts (Chiacchio et al., 2020). At the taxonomic group level, the lizard community of the xeric scrub presented a higher value of functional diversity than the snakes, despite the fact that both communities contain the same number of species (39 species). According to Cadotte et al. (2011), taxonomic diversity may vary among communities for two reasons; because of differences in species richness, or because of functional differences among species. Therefore, these results may be due to the fact that the functional characteristics of lizard species are less redundant or more informative than those found in snakes, which is confirmed by the high values of evenness and functional dispersion shown by lizards. This in turn indicates that the lizards that inhabit xeric scrub have a greater dispersion of functions, as they can use a greater number of habitat types and have broader diets than snakes (see Online Appendix). This result is consistent with that observed by Cooke et al. (2019) when they analyzed the functional diversity of birds and mammals across several ecoregions worldwide. They found that birds and mammals do not contribute equally to functional richness and dispersal, because birds have a higher functional dispersion, being a more species-rich, gregarious, and migratory group.

The snakes present in pine-oak forest, pine forest, and oak forest are, however, a taxonomically rich group with high values of functional richness (Figs. 4 and 5). This result can be viewed from a functionally redundant perspective, because snakes are a group formed mostly by rare species with a functional contribution that is not very perceptible but important. Poos et al. (2009) stated that the presence of functional groups with many redundant species, such as snakes, gives the ecosystem resilience to disturbance events, resulting in a group that is most important for the conservation and functioning of these ecosystems.

The values of functional evenness present in lizards of the xeric scrub and in snakes of the pine-oak forest, pine forest, and oak forest (Figs. 4 and 5) showed a pattern consistent with the values of functional richness. This shows that the reptile species (lizards and snakes) present in these types of vegetation are represented more equitably than the rest of the functional groups (turtles and amphibians) are, thus favoring the stability and resilience of the ecosystems they occupy.

In this study, the highest values of functional dispersion were for amphibians and lizards of the xeric scrub and for the snakes of the pine forest and oak forest. According to Cooke et al. (2019) and Legras et al. (2020), high values of functional dispersion demonstrate a high degree of niche differentiation, which is equivalent to the communities having high resistance when they receive invasive species because there is a greater number of occupied niches. These communities are therefore the best candidates for targeted conservation strategies. In this regard, Farias and Jaksic (2009) found high values of functional dispersion across multiple years in an ensemble of predators located in a national reserve in northern Chile. These authors described that the low availability of resources affected the functional dispersion values through the behavior (functional characteristics) of the predators. They pointed out that in productive years, a greater number of functional species are integrated into the community, exerting high predation pressure on the ecosystem, increasing functional richness and dispersion, and thus decreasing functional evenness. Functional dispersal is, therefore, a way to observe changes in community structure at different times and scales, so it is advisable to include information on the most dominant and rare species in an analysis of taxonomic and functional diversity to obtain clearer results on how the functional roles of species disperse in their ecosystems.

Conclusions

According to our species-accumulation curve, the 157 species (36 amphibians and 121 reptiles, of which 72 species are endemic) present in Durango, embody a high percentage of completeness of the inventory. However, we are aware of large information gaps in areas that have not been sampled in the state; therefore, we consider that there are species missing from our inventory. On the other hand, we located two areas of high species richness or hotspots for the herpetofauna of the state of Durango (see Fig. 2). These hotspots are located in contact areas between biogeographic provinces (SMO and DCH) considered areas of high biodiversity, and coincide with intense sampling areas, such as the Durango-Mazatlán region (south-central Durango), the Laguna region, and the Mapimí Biosphere Reserve (both between Durango and Coahuila). Presumably, our hotspots can be considered as areas of scientific interest, but this statement remains to be confirmed with other biological groups. On the other hand, the amphibian community in the PF and the reptiles in the XS presented high values of taxonomic and functional diversity, while the amphibian communities present in the POF, OF and TDF presented medium values of functional diversity, despite being the best taxonomically represented communities. This confirms the fact that a high value of taxonomic diversity does not always correlate positively with high values of functional diversity, suggesting that the species likely are under recent processes of adaptation to their environments, maintaining the possibility that niches are available. We are confident that the amount of ecological information will provide a reliable and accurate picture of the herpetofauna of Durango, and support the establishment of future conservation strategies in areas where biodiversity is being lost at an alarming rate.

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Availability of data and materials Online Appendix, list of species of amphibians and reptiles and functional characteristics.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

Arriaga, L., Aguilar, C., Espinosa-Organista, D., & Jiménez, R. (1997). Regionalización ecológica y biogeográfica de México. Taller de la Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico City, Mexico.

Berriozabal-Islas, C., Badillo-Saldaña, L. M., Ramírez-Bautista, A., & Moreno, C. E. (2017). Effects of habitat disturbance on lizard functional diversity in a tropical dry forest of the Pacific coast of Mexico. *Tropical Conservation Science, 10*, 1–11. https://doi.org/10.1177/1940082917704972

Bye, R. (1995). Prominence of the Sierra Madre Occidental in the biological diversity of Mexico. In: DeBano, L. F., Folliott, P. F., Ortega Rubio, A., Gottfried, G. J., Hamre, R. H., & Edminster, C. B. (eds), Biodiversity and Management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico. United States Department of Agriculture Forest Service, General Technical Report RM (pp. 19–27).

Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology, 48*, 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Calderón-Mandujano, R. R. (2011). Estrategia para el manejo de anfibios sujetos a uso en México. In: Sánchez, O., Zamorano, P., Peters, E., & Moya, H. (eds), Temas sobre conservación de vertebrados silvestres en México. Secretaría de Medio Ambiente y Recursos Naturales, Instituto Nacional de Ecología, Ciudad de México (pp. 71–82).

Campbell, J. A., & Lamar, W. W. (2004). *The Venomous reptiles of the Western Hemisphere* (Vol. 2). Comstock/Cornell University Press.

Casanoves, F., Pla, L., Di Rienzo, J. A., & Díaz, S. (2011). F Diversity: A software package for the integrated analysis of functional diversity. *Methods in Ecology and Evolution, 2*, 233–237. https://doi.org/10.1111/j.2041-210X.2010.00082.x

Chen, S., Jiang, G., Zhang, J., Li, Y., & Qian, H. (2011). Species turnover of amphibians and reptiles in eastern China: Disentangling the relative effects of geographic distance and environmental difference. *Ecological Research, 26*, 949–956. https://doi.org/10.1007/s11284-011-0850-3

Chiacchio, M., Grimm-Seyfarth, A., Henle, K., & Mihoub, J. B. (2020) Water availability as a major climatic driver of taxonomic and functional diversity in a desert reptile community. *Ecosphere 11*(7), e03190. https://doi.org/10.1002/ecs2.3190

Cilleros, K., Allard, L., Grenouillet, G., & Brosse, S. (2016). Taxonomic and functional diversity patterns reveal different processes shaping European and Amazonian stream fish assemblages. *Journal of Biogeography, 43*, 1832–1843. https://doi.org/10.1111/jbi.12839

Clarke, K. R., & Warwick, R. M. (1999). The taxonomic distinctness measure of biodiversity: Weighting of step lengths between hierarchical levels. *Marine Ecology Progress Series, 184*, 21–29.

Clarke, K. R., & Gorley, R. N. (2001). PRIMERv5: User Manual/Tutorial. PRIMER-E, Plymouth, UK.

Clarke, K. R., & Warwick, R. M. (1998). A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology, 35*, 523–531. https://doi.org/10.1046/j.1365-2664.1998.3540523.x

CONABIO, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. (2017). La biodiversidad de Durango. Estudio de Estado. Mexico, Ciudad de México.

Cooke, R. S. C., Bates, A. E., & Eigenbrod, F. (2019). Global trade-offs of functional redundancy and functional dispersion for birds and mammals. *Global Ecology and Biogeography, 28*, 484–495. https://doi.org/10.1111/geb.12869

Cruz-Elizalde, R., Ochoa-Ochoa, L. M., Flores-Villela, O. A., & Velasco, J. A. (2022). Taxonomic distinctiveness and phylogenetic variability of amphibians and reptiles in the cloud forest of Mexico. *Community Ecology, 23*, 87–102. https://doi.org/10.1007/s42974-022-00075-w

Duellman, W. E. (2001). The Hylid Frogs of Middle America. Contributions to Herpetology, Volume 18, Society for the Study of Amphibians and Reptiles, Ithaca, New York, United States.

Duellman, W. E., Marion, A. B., & Hedges, S. B. (2016). Phylogenetics, classification, and biogeography of the treefrogs (Amphibia: Anura: Arboranae). *Zootaxa 4104*, 1–109. https://doi.org/10.11646/zootaxa.4104.1.1

Espinosa-Organista, D., Ocegueda-Cruz, S., Aguilar-Zúñiga, C., Flores-Villela, O., & Llorente-Bousquets, J. (2008). El conocimiento biogeográfico de las especies y su regionalización natural. Conocimiento actual de la biodiversidad. In J. Soberón, G. Halffter, & J. Llorente-Bousquets (eds), *Capital natural de México* (Vol. I, pp. 33–65). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. México.

Faith, D. P. (1996). Conservation priorities and phylogenetic pattern. *Conservation Biology, 10*, 1286–1289.

Farias, A. A., & Jaksic, F. M. (2009). Hierarchical determinants of the functional richness, evenness and divergence of a vertebrate predator assemblage. *Oikos, 118*, 591–603. https://doi.org/10.1111/j.1600-0706.2008.16859.x

Flores-Villela, O., Canseco-Márquez, L., Ochoa-Ochoa, L. M. (2010). Geographic distribution and conservation of the Mexican central highlands herpetofauna. In: Wilson, L. D., Townsend, J. H., & Johnson, J. D. (eds), *Conservation of the Mesoamerican Amphibians and Reptiles*. Eagle Mountain Publisher, L.C. Eagle Mountain, Utah, USA (pp. 302–321).

Flores-Villela, O., & García-Vázquez, U. O. (2014). Biodiversidad de Reptiles en México. *Rev Mex Biodivers, S85*(Supplement), S467–S475. https://doi.org/10.7550/rmb.43236

Frost, D. R. (2023). Amphibian species of the world: An online reference. Version 6.0. http://research.amnh.org/herpetology/amphibia/index.html. American Museum of Natural History, New York, USA. Accessed February 2023.

Gadsden, H., Estrada-Rodríguez, J. L., & Leyva-Pacheco, S. V. (2006). Checklist of amphibians and reptiles of the Comarca Lagunera in Durango-Coahuila, Mexico. *Bulletin of the Chicago Herpetological Society, 41*, 2–9.

Getis, A., & Ord, J. J. (1992). The analysis of spatial association by use of distance statistics. *Geographical Analysis, 24*(3), 189–206. https://doi.org/10.1111/j.1538-4632.1992.tb00261.x

González-Elizondo, M. S., González Elizondo, M., & Márquez Linares, M. A. (2007). Vegetación y ecorregiones de Durango. Plaza y Valdés Editores-Instituto Politécnico Nacional. México, City.

González-Elizondo, M., Galván Villanueva, R., López Enríquez, I. L., Reséndiz Rojas, L., & González Elizondo, M. S. (2009). Agaves, magueyes, lechuguillas y noas del Estado de Durango y sus alrededores. CIIDIR Unidad Durango Instituto Politécnico Nacional. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. Mexico, City.

González-Elizondo, M. S., González-Elizondo, M., Tena-Flores, J. A., Ruacho-González, L., & López-Enríquez, I. L. (2012). Vegetación de la Sierra Madre Occidental, México: una síntesis. *Acta Bot Mex, 100*, 351–403. https://doi.org/10.21829/abm100.2012.40

Halffter, G. (1976). Distribución de los insectos en la Zona de Transición Mexicana: Relaciones con la entomofauna de Norteamérica. *Folia Hentomologica Mex, 35*, 1–64.

Halffter, G., Llorente-Bousquets, J., & Morrone, J. J. (2008). La perspectiva biogeográfica histórica. Conocimiento actual de la biodiversidadIn J. Soberón, G. Halffter, & J. Llorente-Bousquets (Eds.), *Capital Natural de México* (Vol. I, pp. 67–86). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. México.

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution, 7*(12), 1451–1456. https://doi.org/10.1111/2041-210X.12613

INEGI. (2012). Guía para la interpretación de cartografía, uso del suelo y vegetación escala 1:250 000, serie IV. Aguascalientes, México: Instituto Nacional de Estadística y Geografía.

Jarzyna, M. A., & Jetz, W. (2018). Taxonomic and functional diversity change is scale dependent. *Nature Communications, 9*, 2565.

Jiménez-Valverde, A., & Hortal, J. (2003). Las curvas de acumulación de especies y la necesidad de evaluar la calidad de los inventarios biológicos. *Rev Bér Aracnol, 8*, 151–161.

Johnson, J. D., Mata-Silva, V., García-Padilla, E., & Wilson, L. D. (2015). The herpetofauna of Chiapas, Mexico: Composition, distribution, and conservation. *Mesoamerican Herpetology, 2*, 272–329.

Klauber, L. M. (1982). *Rattlesnakes, their habits, life histories, and influence on mankind*. University of California Press.

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology, 91*, 299–305. https://doi.org/10.1890/08-2244.1

Larson, E. I., Poff, N. L., Funk, W. C., Harrington, R. A., Ondratieff, B. C., Morton, S. G., & Flecker, A. S. (2021). A unifying framework for analyzing temporal changes in functional and taxonomic diversity along disturbance gradients. *Ecology, 102*, e03503. https://doi.org/10.1002/ecy.3503

Lavín-Murcio, P. A., & Lazcano, D. (2010). Geographic distribution and conservation of the herpetofauna of northern México. In: Wilson, L. D., Townsend, J. H., & Johnson, J. D. (eds), *Conservation of the Mesoamerican Amphibians and Reptiles*, Eagle Mountain Publisher, L.C. Eagle Mountain, Utah, USA (pp. 274–301).

Lazcano, D., Nevárez-de-los-Reyes, M., García-Padilla, E., Johnson, J. D., Mata-Silva, V., DeSantis, D. L., & Wilson, L. D. (2019). The herpetofauna of Coahuila, Mexico: Composition, distribution, and conservation status. *Amphibian & Reptile Conservation, 13*, 31–9.

Legras, G., Loiseau, N., Gaertner, J. C., Poggiale, J. C., & Gaertner-Mazouni, N. (2020). Assessing functional diversity: The influence of the number of the functional traits. *TAG Theoretical and Applied Genetics, 13*, 117–126. https://doi.org/10.1007/s12080-019-00433-x

Lemos Espinal, J. A., Smith, G. R., & Valdez Lares, R. (2019). *Amphibians and Reptiles of Durango*. ECO Herpetological Publishing and Distribition, Louisville, Kentucky. USA.

Lemos-Espinal, J. A., & Smith, H. M. (2007). Anfibios y reptiles del estado de Chihuahua, México. Universidad Nacional Autónoma de México y Comisión para el Conocimiento y Uso de la Biodiversidad.

Lemos-Espinal, J. A. (2015). *Amphibians and Reptiles of the US-Mexico Border States/Anfibios y reptiles de los Estados de la Frontera México-Estados Unidos*. Texas A&M University Press.

López-González, C. (2003). Murciélagos (Chiroptera) del estado de Durango, México: Composición, distribución y estado de conservación. *Vertebr Mex, 13*, 15–23.

López-González, C., Lozano, A., García-Mendoza, D. F., & Villanueva-Hernández, A. I. (2014). Mammals of the San Pedro-Mezquital River Basin, Durango-Nayarit, Mexico. *Check List, 10*, 1277–1289. https://doi.org/10.15560/10.6.1277

Mason, N. W. H., Lanoiselée, C., Mouillot, D., Irz, P., & Argillier, C. (2007). Functional characters combined with null models reveal inconsistency in mechanisms of species turnover in lacustrine fish communities. *Oecologia, 2007*, 441–452.

Mason, N. W. H., Mouillot, D., Lee, W. G., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos, 111*, 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

Mata-Silva, V., García-Padilla, E., Rocha, A., DeSantis, D. L., Johnson, J. D., Ramírez-Bautista, A., & Wilson, L. D. (2021). A reexamination of the herpetofauna of Oaxaca, Mexico: Composition update, physiographic distribution, and conservation commentary. *Zootaxa, 4996*, 201–252. https://doi.org/10.11646/zootaxa.4996.2.1

McCranie, J. R., & Wilson, L. D. (1987). The Biogeography of the Herpetofauna of the Pine-Oak Woodlands of the Sierra Madre Occidental of Mexico. *Contrib Biol Geol, 72*, 1–31.

McCranie, J. R., & Wilson, L. D. (1990). Annotated bibliography to the herpetofauna of the pine-oak woodlands of the Sierra Madre Occidental. *Mexico. Smithson Herpetol Inf Serv, 84*, 2–16. https://doi.org/10.5479/si.23317515.84.1

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol Evol, 21*, 178–185. https://doi.org/10.1016/j.tree.2006.02.002

Meza-Lázaro, R. N., & Nieto-Montes De Oca, A. (2015). Long forsaken species diversity in the Middle American lizard *Holcosus undulatus* (Teiidae): Species Diversity in *Holcosus undulatus*. *Zoological Journal of the Linnean Society, 175*, 189–210. https://doi.org/10.1111/zoj.12264

Mlambo, M. C. (2014). Not all traits are "functional": Insights from taxonomy and biodiversity-ecosystem functioning research. *Biodiver Conserv, 23*, 781–790. https://doi.org/10.1007/s10531-014-0618-5

Morafka, D. (1982). The status and distribution of the Bolsón tortoise (*Gopherus flavomarginatus*). In: Bury, B. E. (ed.), *North American tortoises: conservation and ecology*, United States Department of the Interior, Fish and Wildlife Service, Washington D. C (pp. 71–94).

Morelli, F., Benedetti, Y., Perna, P., & Santolini, R. (2018). Associations among taxonomic diversity, functional diversity and evolutionary distinctiveness vary among environments. *Ecological Indicators, 88*, 8–16. https://doi.org/10.1016/j.ecolind.2018.01.022

Moreno, C. E., & Halffter, G. (2000). Assessing the completeness of bat biodiversity inventories using species accumulation curves. *Journal of Applied Ecology, 37*, 149–158.

Morrone, J. J. (2001). Biogeografía de América Latina y el Caribe. Manuales y Tesis Sociedad Entomológica Aragonesa, No. 3, Zaragoza, España.

Morrone, J. J. (2015). Halffter's Mexican transition zone (1962–2014), cenocrons and evolutionary biogeography. *Journal of Zoological Systemetics and Evoloutionary Research, 53*, 249–257. https://doi.org/10.1111/jzs.12098

Mouchet, M. A., Villéger, S., Mason, N. W. H., & Mouillot, D. (2010). Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology, 24*, 867–876.

Murphy, R. W., & Méndez de la Cruz, F. R. (2010). The herpetofauna of Baja California and its associated islands: A conservation assessment and priorities. In: Wilson, L. D., Townsend, J. H., & Johnson, J. D. (eds), *Conservation of the Mesoamerican amphibians and reptiles*. Eagle Mountain Publisher, L.C. Eagle Mountain, Utah, USA (pp. 238–273).

Nevárez-de-los-Reyes, M., Lazcano, D., García-Padilla, E., Mata-Silva, V., Johnson, J. D., & Wilson, L. D. (2016). The herpetofauna of Nuevo León, Mexico: Composition, distribution, and conservation. *Mesoamerican Herpetology, 3*(3), 558–638.

Nieto-Montes de Oca, A., Barley, A. J., Meza-Lázaro, R. N., García-Vázquez, U. O., Zamora-Abrego, J. G., Thomson, R. C., & Leaché, A. D. (2017). Phylogenomics and species delimitation in the knob-scaled lizards of the genus *Xenosaurus* (Squamata: Xenosauridae) using ddRADseq data reveal a substantial underestimation of diversity. *Molecular Phylogenetics and Evolution, 106*, 241–253. https://doi.org/10.1016/j.ympev.2016.09.001

Ochoa-Ochoa, L., Campbell, J. A., & Flores-Villela, J. A. (2014). Patterns of richness and endemism of the Mexican herpetofauna, a matter of spatial scale? *Biological Journal of the Linnean Society, 111*, 305–316. https://doi.org/10.1111/bij.12201

Ochoa-Ochoa, L. M., Mejía-Domínguez, N. R., Velasco, J. A., Marske, K. A., & Rahbek, C. (2019). Amphibian functional diversity is related to high annual precipitation and low precipitation seasonality in the New World. *Global Ecology and Biogeography, 28*, 1219–1229. https://doi.org/10.1111/jbi.13948

Parra-Olea, G., Flores-Villela, O., & Mendoza-Almeralla, C. (2014). Biodiversidad de anfibios en México. *Rev Mex Biodivers, S85*(Supplement), S460–S466. https://doi.org/10.7550/rmb.32027

Peña-Joya, K. E., Capul-Magaña, F. G., Rodríguez-Zaragoza, F. A., Moreno, C. E., & Tellez-López, J. (2020). Spatio-temporal discrepancies in lizard species and functional diversity. *Community Ecology, 21*, 1–12. https://doi.org/10.1007/s42974-020-00005-8

Petchey, O. L., & Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters, 5*, 402–411. https://doi.org/10.1046/j.1461-0248.2002.00339.x

Pianka, E. R. (1966). Convexity, desert lizards, and spatial heterogeneity. *Ecology, 47*, 1055–1059.

Poos, M. S., Walker, S. C., & Jackson, D. A. (2009). Functional-diversity indices can be driven by methodological choices and species richness. *Ecology, 90*, 341–347. https://doi.org/10.1890/08-1638.1

R Development Core Team. (2022). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org. Accessed 18 April 2022.

Ramírez-Bautista, A., Torres-Hernández, L. A., Cruz-Elizalde, R., Berriozabal-Islas, C., Hernández-Salinas, U., Wilson, L. D., Johnson, J. D., Porras, L. W., Balderas-Valdivia, C. J., Gonzáles-Hernández, A. X. S., & Mata-Silva, V. An updated list of the Mexican herpetofauna: with a summary of historical and contemporary studies. *Zookeys* (**in press**).

Ricklefs, R. E., & Miller, G. L. (1999). *Ecology* (4th ed.). Freeman.

Rodríguez, P., Soberón, J., & Arita, H. (2003). El componente de la diversidad beta de los mamíferos de México. *Acta Zool Mex (nueva Serie), 89*, 241–259.

Rodríguez-Gutiérrez, M. F. (2022). Analisis panbiogeografico de los Saurios de la Sierra Madre Occidental. Dissertation. CIIDIR Unidad Durango, Instituto Politécnico Nacional.

Rovito, S., Vásquez-Almazán, C. R., Papenfuss, T. J., Parra-Olea, G., & Wake, D. (2015). Biogeography and evolution of Central American cloud forest salamanders (Caudata: Plethodontidae: *Cryptotriton*), with the description of a new species. *Zoological Journal of the Linnean Society, 175*, 150–166. https://doi.org/10.1111/zoj.12268

Ruane, S., Bryson, R. W., Pyron, R. A., & Burbrink, F. T. (2014). Coalescent species delimitation in milksnakes (genus *Lampropeltis*) and impacts on phylogenetic comparative analyses. *Systematic Biology, 63*, 231–325. https://doi.org/10.1093/sysbio/syt099

Rzedowski, J. (1978). Vegetación de México. Editorial Limusa. Mexico City.

Sánchez, O. (2011). Evaluación y monitoreo de poblaciones silvestres de reptiles. In: Sánchez, O., Zamorano, P., Peters, E., & Moya, H. (eds) Temas sobre conservación de vertebrados silvestres en México. Secretaría de Medio Ambiente y Recursos Naturales, Instituto Nacional de Ecología, Ciudad de México (pp. 83–120).

Secretaria de Marina. (2020). Las Fuerzas Armadas Mexicanas participan en el monitoreo de cultivos ilícitos para combatir el delito de siembra de amapola en nuestro país. Available: https://www.gob.mx/semar [Accssed: 18 August 2022].

Smith, H. M., & Taylor, E. H. (1945). An annotated checklist and key to the snakes of Mexico. *Bulletin of the United States National Museum, 187*, 1–239. https://doi.org/10.5479/si.03629236.187.1

Smith, H. M., & Taylor, E. H. (1948). An annotated checklist and key to the Amphibia of Mexico. *Bulletin of the United States National Museum, 194*, 1–118. https://doi.org/10.5479/si.03629236.194

Smith, H. M., & Taylor, E. H. (1950). An annotated checklist and key to the reptiles of Mexico exclusive of the snakes. *Bulletin of the United States National Museum, 199*, 1–253. https://doi.org/10.5479/si.03629236.199

Tinkle, D. W., Wilbur, H. M., & Tilley, S. G. (1970). Evolutionary strategies in lizard reproduction. *Evolution, 24*, 55–74.

Torres-Hernández, L. A., Ramírez-Bautista, A., Cruz-Elizalde, R., Hernández-Salinas, U., Berriozabal-Islas, C., DeSantis, D. L., & Wilson, L. D. (2021). The herpetofauna of Veracruz, Mexico: Composition, distribution, and conservation status. *Amphibian and Reptile Conservation, 15*, 72–155.

Uetz, P., Freed, P., & Hošek, J., eds. (2023). The reptile database. Available: http://www.reptile-database.org. February 2023.

UNODC, Oficina de las Naciones Unidas contra la Droga y el Delito. (2020). Monitoreo de cultivos de amapola 2017–2018 (MEXK54, 2020). Gobierno de México. https://www.unodc.org/unodc/en/crop-monitoring/index.html. Accessed 29 May 2022.

Valdez Lares, R., Muñiz Martínez, R., Gadsden, H., Aguirre León, G., Castañeda Gaytán, G., & González Trápaga, R. (2013). Checklist of amphibians and reptiles of the state of Durango, México. *Check List, 9*, 714–724. https://doi.org/10.15560/9.4.714

Van Devender, T. R., Reeder, J. R., Reeder, C. G., & Reina, A. L. (2005). Distribution and diversity of grasses in the Yécora region of the Sierra Madre Occidental of eastern Sonora, Mexico. In J. L. E. Cartron, G. Ceballos, & R. S. Felger (Eds.), *Biodiversity, ecosystems, and conservation in Northern Mexico* (pp. 107–121). Oxford University Press.

Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology, 89*, 2290–2301. https://doi.org/10.1890/07-1206.1

Violle, C., Marie-Laure, N., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional. *Oikos, 116*, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Vitt, L. J., & Caldwell, J. P. (2014). *Herpetology, an introductory biology of amphibians and reptiles*. Utah: Elsevier.

Warwick, R. M., & Clarke, K. R. (1995). New "biodiversity" measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology Progress Series, 129*, 301–305.

Warwick, R. M., & Clarke, K. R. (1998). Taxonomic distinctness and environmental assessment. *Journal of Applied Ecology, 35*, 532–543. https://doi.org/10.1046/j.1365-2664.1998.3540532.x

Webb, R. G. (1984). Herpetogeography in the Mazatlán-Durango Region of the Sierra Madre Occidental, Mexico. *Vetrebrate Ecology and Systematics, 1*, 217–241.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., & Bentivenga, S. (2011). Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society b: Biological Sciences, 366*, 2403–2413. https://doi.org/10.1098/rstb.2011.0056

Wilson, L. D., Mata-Silva, V., & Johnson, J. D. (2013a). A conservation reassessment of the reptiles of Mexico based on the EVS measure. *Amphibian & Reptile Conservation, 7*, 97–127.

Wilson, L. D., Mata-Silva, V., & Johnson, J. D. (2013b). A conservation reassessment of the reptiles of Mexico based on the EVS measure. *Amphibian & Reptile Conservation, 7*, 1–47.

Zug, G., Vitt, L., & Caldwell, J. (2001). *Herpetology*. San Diego: Academic Press.