
HERPETOFAUNA ALONG AN ELEVATIONAL GRADIENT IN THE SIERRA MADRE ORIENTAL, QUERÉTARO, MÉXICO

MAURICIO TEPOS-RAMÍREZ¹, RUBÉN PINEDA LÓPEZ, ALFEDO ACOSTA-RAMÍREZ,
ANGELA MARLENE SOTO CALDERÓN, AND ABIGAIL OCAÑA FERREGRINO

*Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Avenida de las Ciencias,
Delegación, 76230 Juriquilla, Qro, México*

¹Corresponding author, e-mail: teposmauricio@gmail.com

Abstract.—The spatial patterns of herpetofaunal diversity through elevational gradients have been little studied and therefore many aspects of their composition, arrangement, and functioning are unknown, especially in the mountainous areas of central Mexico. The Sierra Madre Oriental of Querétaro shows high environmental diversity in a small area with a range of vegetation, climate, and topography. This is reflected in the high vertebrate diversity, especially among amphibians and reptiles. We described and compared the diversity of amphibians and reptiles along an elevational gradient ranging from 1,028–3,100 m above sea level. Within seven segments along this gradient, we carried out systematic searches in microhabitats suitable for amphibians and reptiles. We conducted visual searches for a total of 680 person-hours during the rainy season of 2014 (July and August) and the dry season of 2015 (January, February, and March). We identified nine amphibian and 20 reptile species. Of these species, 41.1% are listed under some category of protection under Mexican law and 65.5% are endemic to Mexico. The communities above and below 1,900 m differed in their species composition with more species recorded at higher elevations; this change was associated with climatic and vegetation turnover. We found a significant nonlinear relationship between species richness and elevation with differences in community structure by elevation. Due to the high percentage of protected and endemic species and the dramatic turnover in community structure identified, we agree with proposals recommending the integration of the study area into a system of protected mountainous areas.

Key Words.—amphibians and reptiles; Detrended Correspondence Analysis (DCA); distribution; diversity; protected natural areas.

INTRODUCTION

Studies involving the diversity distribution of amphibians and reptiles are critical in the development of conservation plans as these species are an integral part of ecosystems (Gibbons et al. 2000). The diversity of amphibians and reptiles is threatened at different scales by a wide range of factors such as environmental contamination, exotic and introduced species, diseases and parasites, habitat loss and degradation, and climate change (Wilson et al. 2013a,b; Pyron 2018). Declines in their populations are especially alarming as the main drivers of these declines are fluctuating rapidly and unfavorable conditions for amphibians and reptiles are increasing due to climate change and anthropogenic environmental impacts (Huey et al. 2010; Alroy 2015).

Abiotic conditions are important in determining the distribution and radiation of some taxa of amphibians and reptiles (Péfaur and Duellman 1980; Halloy 1989). The primary conditions allowing high levels of reptile and amphibian diversity include suitable temperature, humidity, oxygen availability, solar radiation, and environmental heterogeneity (Hofer et al. 1999; Navas 2003; Rodríguez et al. 2019). Because ectothermic

organisms depend heavily on environmental conditions to regulate their physiological processes (Zug et al. 2001), it is of great importance to study them in regions where these conditions are changing to determine the factors that shape the richness and abundance of species on local and regional scales.

The mountainous areas of central Mexico are characterized by high levels of herpetofaunal diversity (Wilson and Johnson 2010; Rodríguez et al. 2019). The relevance of mountain ecosystems for the conservation of amphibians, reptiles, and other biological groups in this region (Flores-Villela and Geréz 1994) is currently unclear because they have been insufficiently studied and few studies have analyzed elevational patterns of herpetofaunal diversity in this region (but see Sánchez-Jasso et al., 2013). Species richness along an elevational gradient generally presents one of four patterns in vertebrates: (1) mid-elevation peaks, (2) decreasing richness with increasing elevation, (3) low-elevation plateaus, and (4) low-plateaus with mid-elevation peaks (Grytnes and McCain 2007; McCain 2010; McCain and Grytnes 2010). Each of these patterns is closely related to the biological, biogeographic, historic, and climatic characteristics of the particular region (Lomolino 2001;

Whittaker et al. 2001).

Due to their specific ecological requirements, amphibians and reptiles are ideal model taxa to test hypotheses related to the distribution of diversity across vegetation types and elevational distribution (Huey 1982; Navas 2003; Cruz-Elizalde and Ramírez-Bautista 2012). Within the Mexican biodiversity, amphibians and reptiles stand out on a global scale for their high percentage of richness and endemic species (67% for amphibians and over 57% for reptiles; Wilson et al. 2013a,b; Flores-Villela and García-Vázquez 2014; Parra-Olea et al. 2014; Johnson et al. 2017). Diversity analyses are useful tools to explore the relationships along elevational gradients between ecological/environmental factors and biological diversity (Lomolino 2001; Navas 2003). Therefore, we analyzed the diversity of amphibians and reptiles along an elevational gradient located in a portion of the Sierra Madre Oriental, within the Reserva de la Biosfera Sierra Gorda, Pinal de Amoles municipality, Querétaro, Mexico. We hypothesized that an elevational gradient changes species composition. We predict that we will find a gradual transition of amphibian and reptiles species along the gradient with decreasing richness at higher elevations.

MATERIALS AND METHODS

Study site.—Mexico is a country with significant topographic and climatic variation, within which lies the transition zone between the Nearctic and Neotropical biogeographic regions. Such variation allows a great diversity of environments and biodiversity to exist (Arita and Rodríguez 2002; Morrone and Márquez 2003; Escalante et al. 2005). These features come together in the state of Querétaro, located in the central region of Mexico. This region contains a diversity of vegetation types, such as Coniferous Forests, Tropical Dry Forest, and different types of xerophytic shrublands (Instituto Nacional de Estadística y Geografía [INEGI] 1986, 2014; Zamudio et al. 1992). These vegetation associations are linked with high biodiversity, especially with respect to amphibians and reptiles (Ochoa-Ochoa and Flores-Villela 2006; Wilson et al. 2013a,b; Flores-Villela and García-Vázquez 2014).

The Pinal de Amoles municipality is located in the northeastern region of the state of Querétaro, Mexico. It is part of the Sierra Madre Oriental and the Reserva de la Biosfera Sierra Gorda (INEGI 1986; Instituto Nacional de Ecología [INE] 1999). The sampling area was located between 21°9'29"–21°2'7"N and 99°37'5"W, along an elevational gradient ranging from 1,028 to 3,100 m above sea level (MASL). We divided a single elevational transect into seven segments of 300 m each to allow sufficient space for sampling and to follow the topography and vegetation types (Fig. 1).

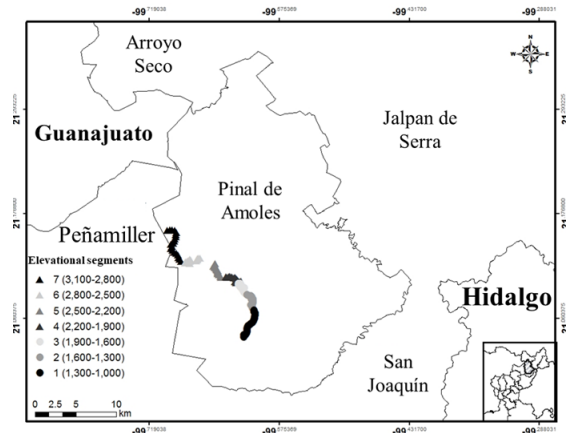


FIGURE 1. Region of study in the Pinal de Amoles municipality in Querétaro, Mexico, and the surveyed elevational segments in meters. Intervals of each elevational segment are indicated in parentheses. Surrounding municipalities and states (bold) are also shown.

Study system.—The climate below 1,800 m elevation (segments 1–3) is semi-warm and sub-humid (A)C(w0) and (A)C(w1) with rain in the summer (INEGI 1986). In segment 2, the steep slopes and soil type in the area do not retain water. Only the bottom segment (segment 1), below 1,250 m elevation, contains water, which is present in a permanent stream. At elevations higher than 1,800 m elevation (segments 4–7), the climate is temperate sub-humid with rain in the summer C(w2) and C(w2) (w), with warm summers, and with low precipitation in the winter. The annual rainfall in the region ranges from 313 mm at lower elevations up to 883 mm at the highest elevations (INE 1999). Although their presence is minimal in segments 6 and 7, there are towns and nearby crop fields throughout the area.

The predominant vegetation associations within the transect include riparian zones, xerophytic shrublands, and Juniper, Juniper-Oak, Oak, and Pine-Oak forests (Zamudio et al. 1992). In segment 1, riparian forest predominates with *Salix humboldtiana* (Humboldt's Willow), *Baccharis salicifolia* (Seepwillow), and *Platanus occidentalis* (Sycamores). Houses and fruit tree plantations are scattered along the stream, reaching the Extoraz River. Beyond the river channel, there are xerophytic shrublands and the village of Bucareli, with a population of 2,325 inhabitants (Secretaría de Desarrollo Social [SEDESOL]. 2010. Microregiones, Catálogo de Localidades. Available from <http://www.microrregiones.gob.mx/catloc/Default.aspx> [Accessed 30 January 2021]). Segment 2 is characterized by xerophytic shrubland, mainly rosetophilous (a type of vegetation composed of thorny plants with their leaves arranged in a rosette) in its higher elevations with settlements in the mid portion, as well as the steepest slopes in the transect. In segment 3, there is an open Juniper (*Juniperus* spp.)

Forest with xerophytic shrublands in the lower elevational portion and broad crop fields with settlements scattered throughout the segment. In segment 4, Juniper Forest predominates, with Oak (*Quercus* spp.) Woodland and crop fields in the upper portion and the town of Puerto del Derramadero in its mid portion. In segment 5, there are Oak-Juniper Woodland with the latter predominating in the lower section. Additionally, segment 5 contains abundant crop fields and the village of Derramadero de Bucareli, populated by 426 inhabitants (SEDESOL. 2010. *op. cit.*). Segment 6 is covered almost exclusively with Oak Forest and some junipers in the lower elevation part, as well as some invasive grasslands, meadows, crop fields, and isolated houses. Pine (*Pinus* spp.)-Oak Forest predominates segment 7 some firs (*Abies* spp.) and a few oaks in its upper part. Some isolated houses are in segment 7, although there is no evidence of major disturbances in land use (Fig. 2).

Field work.—We carried out sampling during both the rainy season (summer) in July and August of 2014 and the dry season (winter) during January and March 2015. During each season, we performed 15 sampling trips of three to four days each in diurnal (0900–1400) and nocturnal (1700–2200) outings with the aim of including species with day, night, and crepuscular activity patterns (Casas-Andreu et al. 1991). We divided the sampling effort evenly between day and night searches to have

equal possibility of capturing diurnal, nocturnal, and crepuscular species. A rotating group composed of four to five individuals carried out each sampling effort. In total, we accumulated approximately 680 person-hours, split evenly between the two sampling seasons with 340 person-hours during the rainy season and 340 person-hours during the dry season.

We opportunistically captured amphibians and reptiles through visual detection within each segment, searching different habitats (native vegetation, crop fields, and urban areas) and microhabitats (trunks, rocks, bodies of water, cracks, among others) in which these organisms are known to occur (Casas-Andreu et al. 1991; Foster 2011). We captured, photographed, and identified the specimens at the species level using the taxonomic keys for amphibians and reptiles of Queretaro (Dixon and Lemos-Espinal 2010). Subsequently, we returned all specimens to the location from which they had been collected. Species names were updated according to Wilson et al. (2013a,b) and Duellman et al. (2016).

Inventory completeness and species diversity.—To assess inventory completeness, we used the non-parametric estimator Chao2 (Chao 1987) in the software EstimateS 9.1 (<http://viceroy.eeb.uconn.edu/estimates/>) for each segment and the whole transect. Non-parametric estimators have proven to be good methods to evaluate species completeness because they are the most rigorous

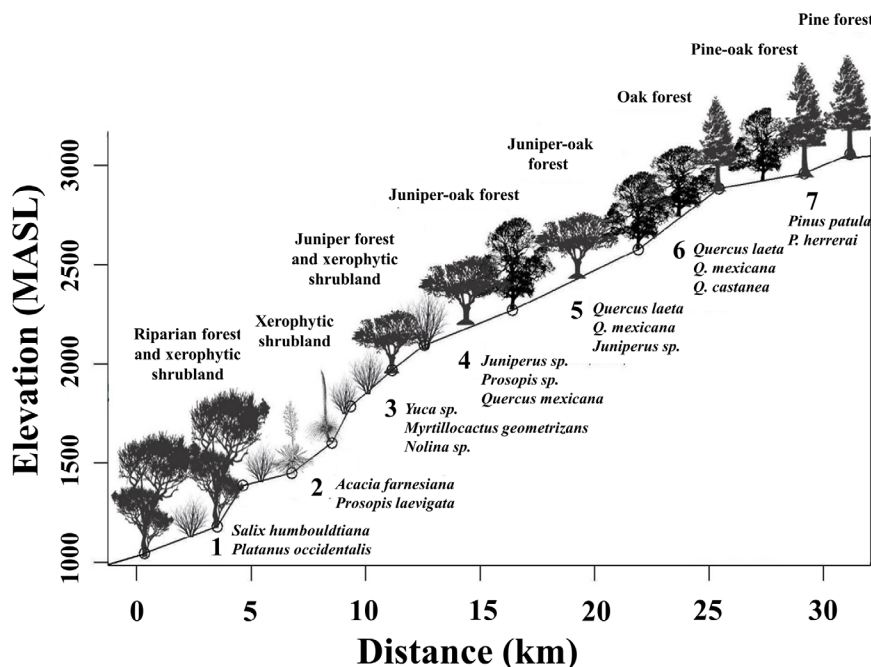


FIGURE 2. Sampled elevational gradient. Elevation segments (numbers) are indicated, as well as main vegetation types and defining floral taxa. Common names by elevations are as follows: 1. Humboldt's Willow (*Salix humboldtiana*); American Sycamore (*Platanus occidentalis*). 2. Sweet Acacia (*Acacia farnesiana*); Smooth Mesquite (*Prosopis laevigata*). 3. Yucca (*Yucca* sp.); Billberry Cactus (*Myrtillocactus geometrizans*); beargrass (*Nolina* sp.). 4. Junipers (*Juniperus* sp.); mesquite (*Prosopis* sp.); Red Oak (*Quercus mexicana*). 5. White Oak (*Quercus laeta*), *Q. mexicana*; Juniperus sp. 6. *Quercus laeta*; *Q. mexicana*; Beech (*Q. castanea*).

and have less bias for small sample sizes compared with other estimators (Gotelli and Chao 2013). To compare the diversity among different segments, we used effective numbers of species because it represents a simple measure, and its mathematical properties make the results directly comparable (Jost 2006; Moreno et al. 2011). For this analysis, we used first (1D) and second (2D) orders of diversity. These estimate the effective number of species according to their total abundance and give higher weight to the effective species numbers (Jost 2006). We carried out these analyses using the software PAST 2.17 (Hammer et al. 2001), which calculates 95% confidence intervals through the bootstrap technique with 1,000 randomizations, and we used non overlap of confidence intervals to determine significance. We then compared species richness to elevation using Regression Analysis ($\alpha = 0.05$) for amphibians separately, reptiles separately, and for amphibians and reptiles together.

Species composition.—We performed a Detrended Correspondence Analysis (DCA; Hill and Gauch 1980) as a beta diversity measure, which represents the sampling sites and species in a two-dimensional axis where the obtained values for each axis provide an index of species composition for each site and their affinity to them (Liebermann et al. 1996; Legendre and Legendre 1998). To calculate if the differences among observed groups in the DCA were significant, we used the Analysis of Similarities (ANOSIM), which is a non-parametric test applied to the similarity matrix that uses permutations to tests the null hypothesis that there are no differences in the composition of the community among sites (McCune et al. 2002; Magurran 2004). We used the

Bray-Curtis Similarity Index, which considers the species abundance highlighting the inclusion of low abundance representatives (Gauch 1982):

$$d_{ij} = 1 - \frac{\sum_{i=1}^n |y_{ij} - y_{ik}|}{\sum_{i=1}^n (y_{ij} + y_{ik})}$$

where y_{ij} and y_{ik} represents the abundance for the i th species in the j th and k th sample. Subsequently, we used the Similarity Percentage Analysis (SIMPER) to evaluate the taxa with higher weight in the observed differences among groups (Clarke 1993). We carried out all analyses using software PAST ver.4 (Hammer et al. 2001).

RESULTS

Inventory.—We recorded 29 species: nine amphibians, one turtle, and 19 squamates. The amphibian diversity found represents two orders, seven families, and eight genera; while the reptile diversity (lizards, snakes, and turtles) comprises two orders, nine families, and 15 genera (Table 1). The best represented families were Colubridae and Phrynosomatidae with three and six species, respectively (Table 1). All of the species were encountered in rainy season, whereas only 13 were found during the dry season. We estimated 93% inventory completeness for the whole transect. While most segments were sampled with a completeness of over 80%, completeness of segments 2 and 7 were 78% each and segment 3 was 52%.

Fourteen percent of the species we encountered showed a wide distribution range, defined as presence in three or more segments along the elevational gradient (Fig. 3). On the other hand, 62% of the species were

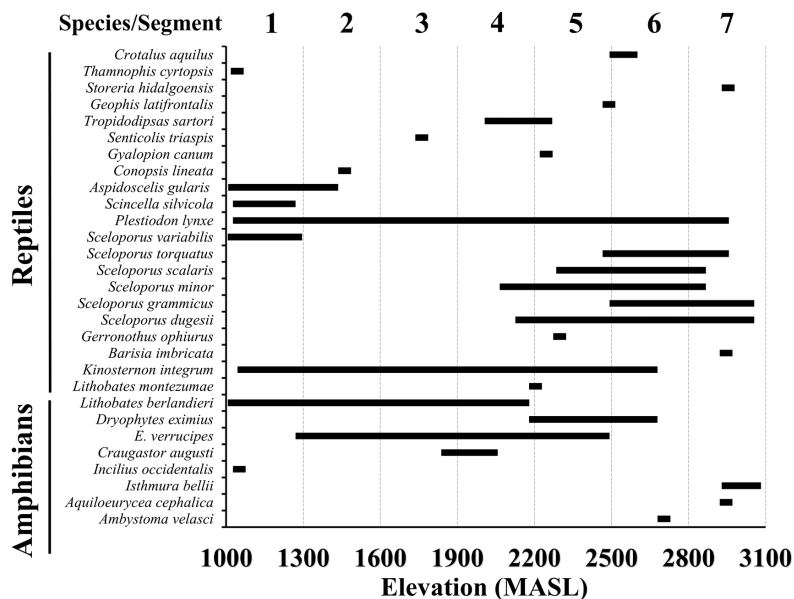


FIGURE 3. Elevational distribution of herpetofauna in this study. Ranges indicated by the bars represent lowest and highest elevational records for each species. Species are ordered by taxonomy. Common names are presented in Table 1.

TABLE 1. Recorded species in the sampling performed along an elevational gradient in the municipality of Pinal de Amoles, Querétaro, Mexico. An asterisk (*) indicates an endemic species to Mexico. Conservation statuses (in parentheses) follow SEMARNAT (2010), where A = Threatened and Pr = subject to special protection. Species are Mexican Plateau Tiger Salamander (*Ambystoma velasci*), Chunky False Brook's Salamander (*Aquiloerycea cephalica*), Bell's Salamander (*Isthmura belli*), Mexican Plateau Toad (*Incilius occidentalis*), Barking Frog (*Craugastor augusti*), Big Ear Chirping Frog (*Eleutherodactylus verrucipes*), Mountain Treefrog (*Dryophytes eximius*), Rio Grande Leopard Frog (*Lithobates berlandieri*), Mexican Mud Turtle (*Kinosternon integrum*), Imbricate Alligator Lizard (*Barisia imbricata*), Snake Lizard (*Gerrhonotus ophiurus*), Duge's Spiny Lizard (*Sceloporus dugesii*), Mesquite Lizard (*Sceloporus grammicus*), Light-Bellied Bunch Grass Lizard (*Sceloporus scalaris*), Crevice Swift (*Sceloporus torquatus*), Rosebelly Lizard (*Sceloporus variabilis*), Oak Forest Skink (*Plestiodon lynxe*), Taylor's Ground Skink (*Sciincella silvicola*), Eastern Spotted Whiptail (*Aspidoscelis gularis*), Lined Toluacan Ground Snake (*Conopsis lineata*), Western Hooknose Snake (*Gyalopion canum*), Green Rat Snake (*Senticolis triaspis*), Terrestrial Snake Sucker (*Tropidodipsas sartorii*), Potosí Earth Snake (*Geophis latifrontalis*), Mexican Yellowbelly Brown Snake (*Storeria hidalgoensis*), Blackneck Garter Snake (*Thamnophis cyrtopsis*), and Queretaran Dusky Rattlesnake (*Crotalus aquilus*).

Amphibia		Reptilia	
Caudata		Testudines	Colubridae
Ambystomatidae		Kinosternidae	<i>Conopsis lineata</i> *
<i>Ambystoma velasci</i> * (Pr)		<i>Kinosternon integrum</i> * (P)	<i>Gyalopion canum</i>
Plethodontidae		Squamata	<i>Senticolis triaspis</i>
<i>Aquiloerycea cephalica</i> * (A)		Anguidae	Dipsadidae
<i>Isthmura belli</i> * (A)		<i>Barisia imbricata</i> * (Pr)	<i>Tropidodipsas sartorii</i> (Pr)
Anura		<i>Gerrhonotus ophiurus</i>	<i>Geophis latifrontalis</i> * (Pr)
Bufo		Phrynosomatidae	Natricidae
<i>Incilius occidentalis</i>		<i>Sceloporus dugesii</i> *	<i>Storeria hidalgoensis</i> *
Craugastoridae		<i>Sceloporus grammicus</i> (Pr)	<i>Thamnophis cyrtopsis</i> (A)
<i>Craugastor augusti</i>		<i>Sceloporus minor</i> *	Viperidae
Eleutherodactylidae		<i>Sceloporus scalaris</i> *	<i>Crotalus aquilus</i> * (Pr)
<i>Eleutherodactylus verrucipes</i> * (Pr)		<i>Sceloporus torquatus</i> *	
Hylidae		<i>Sceloporus variabilis</i>	
<i>Dryophytes eximius</i> *		Scincidae	
Ranidae		<i>Plestiodon lynxe</i> * (Pr)	
<i>Lithobates berlandieri</i> (Pr)		<i>Sciincella silvicola</i> * (A)	
<i>Lithobates montezumae</i> * (Pr)		Teiidae	
		<i>Aspidoscelis gularis</i>	

found only in the higher segments of the transect (between 2,200–3,000 m elevation). For amphibians, we found a higher number of species in the higher segments of the transect. We found six reptiles species limited to < 2,000 m, 12 only above 2,000 m (especially lizards), and two species across the range of elevations we surveyed (Fig. 3).

Community diversity.—Based on overlap of confidence intervals, diversity values between 1D and 2D were not significantly different, but elevational segments differed significantly where segment two and three showed lower diversity values than the other segments (Fig. 4). Species richness did not differ significantly across elevations for either amphibians and reptiles combined ($F_{1,5} = 2.130$; $P = 0.204$), amphibians separately ($F_{1,5} < 0.001$; $P = 1.000$), or reptiles separately ($F_{1,5} = 3.780$; $P = 0.109$).

Species composition.—When contrasting species composition among the different segments, the DCA showed two groups of segments split on axis one, one comprising the lower segments (1–4, although segment 4 is separated from the first three on axis two), and another formed by the higher segments (5–7). The first included 17 associated species, while nine were recovered in the second (Fig. 5). The difference between these two groups was large ($R = 0.713$) and significant ($P = 0.031$). Most of the primary species contributing to the difference between groups of segments show an affinity for the higher segments (4–7), except for the Big Ear Chirping Frog (*Eleutherodactylus verrucipes*). The species that explained most of the variation percentage among segments were the Duge's Spiny Lizard (*Sceloporus dugesii*), the Oak Forest Skink (*Plestiodon lynxe*), the Plateau Tiger Salamander (*Ambystoma velasci*), and the Mountain Treefrog (*Dryophytes eximius*; see Supplemental Information for SIMPER analysis).

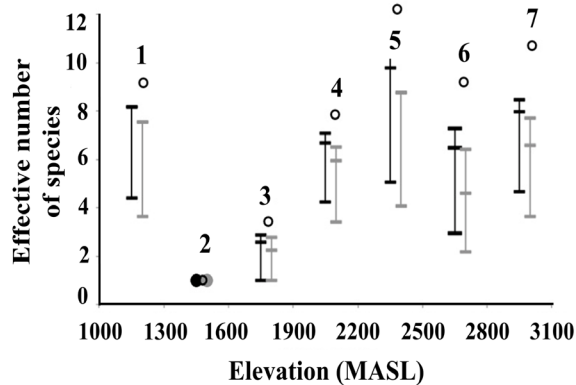


FIGURE 4. Species diversity found in the different elevational segments: black lines represent 1D diversity while gray lines represent 2D diversity. The 84% confidence intervals, segment numbers, and the observed richness (circles) are indicated for comparison.

DISCUSSION

We found that there was no gradual replacement of species among segments along an elevational gradient; the richness and composition of species changed dramatically above 1,900 m elevation, indicating two communities significantly different from each other. Although numerous studies show the relationship between reptile and amphibian diversity and elevation, we did not find significant relationships for amphibians and reptiles combined or analyzed separately. We think this is because of the great difference in the number of species registered in some segments of the gradient that may have masked the elevation-diversity relationship. Additionally, the scale of the study or the sampling methods may not have been sufficient to detect all possible species. Therefore, these results must be interpreted cautiously.

The high inventory completeness found in the sampling indicates that it is representative of the study area. Other species previously registered in the municipality may be present in the study area. These include the Tamaulipan False Brook Salamander (*Aquiloerycea scandens*), the Toothy Splayfoot Salamander (*Chiropoterotriton multidentatus*), the Long Footed Frog (*Eleutherodactylus longipes*), the Small-eared Hyla (*Rheohyla myotimpanum*), the Toluca Bunch Grass Lizard (*Sceloporus aeneus*), the Minor Lizard (*Sceloporus minor*), the Gage’s Tropical Night Lizard (*Lepidophyma gageae*), the Madrean Tropical Night Lizard (*Lepidophyma sylvaticum*), the Eastern Milksnake (*Lampropeltis triangulum*), the Gage’s Pine Forest Snake (*Rhadinaea gageae*), the Great Plain’s Ratsnake (*Pantherophis emoryi*), the Long Tail Alpine Gartersnake (*Thamnophis scalaris*), and the Western Black-tailed Rattlesnake (*Crotalus molossus*; Dixon and Lemos-Espinal 2010). Lack of detection of these

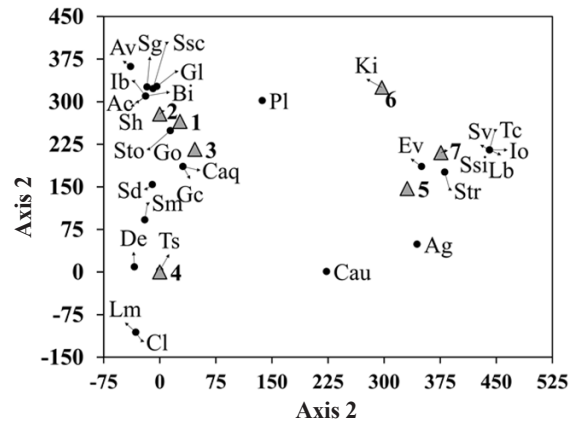


FIGURE 5. Detrended Correspondence Analysis of the first two axes. Elevational segments are indicated with grey triangles and bolded numbers, while black circles and their acronyms show representative species (see Table 1).

species during sampling may be due to particularities of the study area, the inherent detectability of each species, or the sampling techniques used in this study.

Some studies demonstrate the effectiveness of transects over other sampling techniques (Rödel and Ernst 2004; Hutchens and DePerno 2009). There is also evidence, however, that other sampling techniques, such as pit fall traps and fences, are useful to generate more complete inventories (Sung et al. 2011; Carpio et al. 2015) because they improve detection of species with secretive, fossorial, or arboreal habits. Despite the overall high level of inventory completeness, species that may not have been detected in this study for this reason include the Bromeliad Arboreal Alligator Lizard (*Abronina taeniata*), the Braminy Blind Snake (*Ramphotyphlops braminus*), the Black Threadsnake (*Leptotyphlops goudotti*) and the Highlands Earth Snake (*Geophis multitorques*).

Species reported in this study correspond to 21% of the registered species for the state (Cruz-Elizalde et al. 2016), which is relatively high considering the size of the study area in relation to the entire state. Of the total registered species, 41.1% of these species are listed in some category of protection under Mexican law (four listed as Threatened and 11 as Under Special Protection), and 65.6% of these species are endemic to Mexico. The following species records are of particular interest, given that they represent an elevational range expansion of at least 120 m (Hammerson y Santos-Barrera 2007; Ponce-Campos and García-Aguayo 2007; Dixon and Lemos-Espinal 2010; Lee et al. 2020). *Sceloporus dugesii* is listed as at 1,800–2,679 m elevation; we found it at 3,056 m. The Western Hooknose Snake (*Gyalopion canum*) is listed at 305–2,100 m and we found it at 2,221 m elevation, and the Terrestrial Snail Sucker (*Tropidodipsas sartorii*) is listed at sea level to 2,000 m and we found it at 2,269 m.

The elevational distribution of amphibians and reptiles is linked to environmental factors, which directly influence the physiological and behavioral responses of organisms and also influence dispersal potential in some taxa (Halloy 1989; Navas 2003; Woolrich-Piña et al. 2006). In addition to climatic and vegetation factors, anthropogenic influences can modify distributions of species. Human structures (i.e., roads, towns, crop fields, and others) create unnatural conditions that alter the composition and spatial distribution of the vegetation as well as affecting abiotic factors (e.g., temperature and humidity), resulting in environmental heterogeneity that can lead to differences among species composition, abundance, and richness (Becker et al. 2007; García and Cabrera-Reyes 2008; Moreno-Rueda and Pizarro 2009; Birx-Raybuck et al. 2010; Palis 2018).

The effects of environmental heterogeneity on herpetofaunal diversity at different scales are well known (Ochoa-Ochoa and Flores-Villela 2006; Koleff et al. 2008; Ochoa-Ochoa et al. 2014). In amphibians, species turnover is associated with heterogeneity in precipitation, whereas it is associated with temperature in reptiles (Rodríguez et al. 2019). This pattern is clearly represented in the elevational distribution of both groups, where we find few species with a wide distribution across the gradient as a reflection of environmental heterogeneity. The low dispersal capacity of both groups can be explained from an eco-physiological perspective. In the case of amphibians, their reproductive strategies keep them linked to sites with high humidity and to permanent or temporary water reservoirs. On the other hand, reptiles are highly susceptible to temperature changes over short distances typical of mountain environments (0.6°C per 100 m elevation; Barry 1992).

Our regression analysis revealed no significance differences regarding the relationship between species richness (amphibians, reptiles, or combined) and elevation; however, the trends observed in this study are similar to previous works in the nearby mountainous regions of Hidalgo, where Hernández-Salinas and Ramírez-Bautista (2013) described a pattern with the lowest number of species in the mid-elevation sections and an increasing number of species towards higher elevations. Regardless, the patterns described herein are not consistent with others observed at similar or larger scales (Grytnes and McCain 2007; Smith et al. 2007; Kozak and Wiens 2010; McCain 2010). There may exist a decrease in reptile species above 3,100 m elevation, which was the highest elevation surveyed in this study. This trend was described by Vega-López and Álvarez-Castañeda (1992) in the Popocatepetl and Iztaccihuatl volcanoes, where they found the upper limit for amphibians where the tree coverage is reduced at 3,500 m elevation, and at 4,000 m elevation for most reptiles due to low temperatures. Because of the high diversity and endemism in the region as a result of vicariance by climatic fluctuations during

the Pleistocene (Ochoa-Ochoa and Flores-Villela 2006; Flores-Villela and Martínez-Salazar 2009; Wilson et al. 2013a,b), it is possible that more species with secretive habits may exist across the gradient due to restrictions imposed by their respective tolerance limit zones.

Some studies suggest a gradual replacement of species across a gradient (Fischer and Lindenmayer 2005); however, we found that species replacement was evident above and below 1,900 m elevation. The remarkable differences in the DCA with respect to species composition between upper and lower segments in the gradient, corresponding to semi-warm and temperate climates, respectively (INEGI 2014), coincides with the abrupt change in vegetation composition marked by temperate forests at higher elevations (pine forest, oak, *Juniperus* sp.; from 3,100 to 1,800 m elevation).

Species with affinities for temperate climates were found at higher elevations, such as the amphibians the Chunky False Brook Salamander (*Aquiloerycea cephalica*) and the Bell's False Brook Salamander (*Isthmura belli*) and the reptile the Mexican Yellowbelly Brownsnake (*Storeria hidalgoensis*; Dixon and Lemos-Espinal 2010), while the Pine Toad (*Incilius occidentalis*), a species found in semi-warm climates in Queretaro (Dixon and Lemos-Espinal 2010), was found at lower elevations. These distributions are correlated with the segment groupings recovered, including the relative distinctiveness of segment 4 on axis two of the DCA exhibited by species exclusive to the middle section of the gradient such as the Green Ratsnake (*Senticolis triaspis*) and the Barking Frog (*Craugastor augustii*). The Rosebelly Lizard (*Sceloporus variabilis*), which we found only in segment 1, has been reported in Querétaro to be associated with mesquite branches and low shrubs, in seasonally dry areas at mid-to-low elevations (Dixon and Lemos-Espinal 2010). Likewise, we only registered the Blackneck Gartersnake (*Thamnophis cyrtopsis*) in segment 1, as it is associated with Mountain Thornscrub and permanent water bodies (Rossman et al. 1996). Additionally, these differences in habitat associations are related to the biogeographic affinities of the taxa present in each segment grouping. For example, the families Craugastoridae and Hylidae have a predominantly tropical origin (Duellman 2016), while Caudata has a predominantly temperate origin (Wake and Lynch 1976).

The high number of species listed under some category of protection and/or endemic to Mexico and the dramatic turnover in community structure registered in this study highlights the importance of the study area for amphibian and reptile conservation. As such, we recommend that this area should be integrated into a system of mountainous protected areas (Meza-Parral and Pineda 2015; Lara-Tufiño et al. 2019), taking into account that endemic and range-restricted species are especially vulnerable to environmental disturbances and constitute one of the main criteria for the designation of

priority conservation areas (Ochoa-Ochoa and Flores-Villela 2006; Wilson et al. 2013a; Wilson et al. 2013b). It is important to highlight, however, that the trends shown in this study may not be consistent when extrapolated to other mountainous areas in Mexico or elsewhere and much more research is required to untangle the elevational trends of herpetological diversity, specifically in central Mexico.

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APPENDIX TABLE. Percentage species contribution to the difference between groups of segments (see Fig. 5), according to the SIMPER analysis. Species are the Duge’s Spiny Lizard (*Sceloporus dugesii*), the Oak Forest Skink (*Plestiodon lynxe*), the Mexican Plateau Tiger Salamander (*Ambystoma velaci*), the Mountain Tree Frog (*Dryophytes eximius*), the Minor Lizard (*S. minor*), the Mezquite Lizard (*S. grammicus*), the Big Ear Chirping Frog (*Eleutherodactylus verrucipes*), the Montezuma Leopard Frog (*Lithobates montezuma*), the Toluca Ground Snake (*Conopsis lineata*), and the Crevice Swift (*S. torquatus*).

Species	Contribution (%)	Cumulative (%)	Elevational affinity
<i>Sceloporus dugesii</i>	10.81	10.81	upper
<i>Plestiodon lynxe</i>	10.12	20.93	undefined
<i>Ambystoma velaci</i>	8.153	29.08	upper
<i>Dryophytes eximius</i>	7.812	36.89	upper
<i>Sceloporus minor</i>	6.777	43.67	upper
<i>Sceloporus grammicus</i>	6.053	49.72	upper
<i>Eleutherodactylus verrucipes</i>	5.058	54.78	lower
<i>Lithobates montezumae</i>	3.655	58.44	upper
<i>Conopsis lineata</i>	3.655	62.09	upper
<i>Sceloporus torquatus</i>	3.182	65.27	upper



MAURICIO TEPOS RAMÍREZ is a Biologist with a Master’s degree in Biological Sciences from the Universidad Autónoma de Querétaro, Mexico. His research interests include amphibians and reptile diversity from central Mexico, population ecology and systematics of Mexican snakes such as the Blunt-headed Tree Snake (*Imantodes cenchoa*) in southern Veracruz and Mexico, as well as highland pitvipers (*Metlapilcoatlus* spp.). (Photographed by Mauricio Tepos Ramírez).



RUBÉN PINEDA LÓPEZ is a Biologist with a Master’s degree from the Universidad Nacional Autónoma de México (UNAM) and a Ph.D. from the University of Alicante, Spain. He is a full-time Professor at the Autonomous University of Querétaro, Mexico. His current focus is on the study of bird diversity patterns, especially how birds are affected in urban and aquatic environments. Rubén teaches graduate courses related to the analysis of biodiversity at the Faculty of Natural Sciences. He has authored 19 peer-reviewed articles, five books, and six book chapters. He is currently the Technical Manager of the Biological, Management, and Conservation Network of Native Fauna in Anthropogenic Environments, supported by Consejo Nacional de Ciencia y Tecnología. (Photographed by Rubén Pineda López).



ALFREDO ACOSTA RAMÍREZ is a Biologist from Queretaro State University, Mexico. His work is focused on evaluating avian and reptile diversity in Mexico. Specifically, he participated in the research project, Avian community response to a mountain pine beetle outbreak in ponderosa pine forests, surveying and monitoring woodpecker nests and measuring vegetation with the Ecology Department at Montana State University, Bozeman, USA, and the Rocky Mountain Research Station in the Helena National Forest, Montana, USA. He has led private and public tours of the Sierra Gorda Biosphere Reserve, Querétaro, México, and worked as a volunteer monitoring Yellow Headed Parrots (*Amazona oratrix*) for the Belize Bird Conservancy. He currently works at the Universidad Autónoma de Querétaro, Mexico, researching the distribution, ecology, and behavior of exotic and invasive bird species. (Photographed by Iván Méndez Rubio).



ANGELA MARLENE SOTO CALDERÓN is a Biology student at the Universidad Autónoma de Querétaro, Mexico. Her interests include the analysis of faunal diversity in human-disturbed environments with an emphasis on birds. Angela joined the specialized professional services unit (USPAE) of the Instituto de Ecología (INECOL) as part of the annual bird monitoring team in the Tehuantepec Isthmus, Mexico, where she currently participates in the raptor migratory count of the Mesoamerican corridor. (Photographed by Fernando Díaz).



ABIGAIL OCAÑA FEREGRINO is a Biologist with a degree from the Universidad Autónoma de Querétaro, Mexico. She has collaborated in various projects at the same university studying Querétaro bird species as a part of the outreach team of the Science and Technology Council of the State of Querétaro that runs projects for high school students. Her current research is focused on the interaction between agriculture and biodiversity at this same university. (Photographed by Miriam Lerma).