

# REPTILES IN RESEARCH

*Investigations of Ecology, Physiology, and  
Behavior from Desert to Sea*



**William I. Lutterschmidt**  
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*Animal Science, Issues and Professions*

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**FROM DESERT TO SEA**

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**REPTILES IN RESEARCH**  
**INVESTIGATIONS OF ECOLOGY,**  
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**FROM DESERT TO SEA**

**WILLIAM I. LUTTERSCHMIDT, PH.D.**  
**EDITOR**



*New York*

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*Chapter 5*

## **REPTILE SPECIES RICHNESS AND DISTRIBUTION: WHAT CAN WE LEARN FROM ARID AND SEMIARID ENVIRONMENTS?**

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### **ABSTRACT**

Arid and semiarid environments of the world hold a remarkable richness of reptile species. Knowledge on richness, diversity and distribution is important for determining biogeographic and ecological processes that elucidate the structure of communities. At a local scale, ecological factors determine processes that influence species richness and its composition, and at a regional level, events such as extinction and speciation are considered the most important factors. In this chapter, we evaluated species richness and the taxonomic diversity of the reptile communities from arid and semiarid environments in the state of Hidalgo, México; and we also analyzed reptile communities of the central and northern regions of the country. The state of Hidalgo has six arid and semiarid environments; xeric scrub (XS), held the highest species richness with 42 species, followed by pine forest (PF), with 25 species, oak forest (OF) with 19 species, farmland (F) and secondary vegetation (SV) with 14 species each, and riparian vegetation (RV) with 13 species. With respect to the analysis of the taxonomic diversity, the SV and RV had the highest values, the XS and F values close to the average expected by a calculated null model, and PF and OF had the lowest values. When comparing Hidalgo region with regions from northern México, such as Sonora (SON), the latter had the highest species richness, followed by Tamaulipas (TAM), Hidalgo (HGO), and Guadalcázar (GDZ) with lowest number of species. The highest taxonomic diversity was found in TAM, followed by SON, and lowest value was reported in HGO and GDZ. The richness and diversity of reptiles from Hidalgo is characteristic of the regional pool of species from central Mexico, and is dissimilar from that reported in the northern section of the country. This suggests distinct conformation of the communities of reptiles which is likely due to environmental heterogeneity and different processes that regulate the establishment of the biological communities.

**Keywords:** Reptiles, Species richness, Hidalgo, Taxonomic diversity, México

## INTRODUCTION

Reptiles represent an interesting study group to assess species richness and diversity patterns (Vitt and Caldwell 2009), mainly due to the close association these species have with a wide range of the habitats and microhabitats (Vitt et al. 2003). Many reptile species occur in greatly diverse environments throughout the World (McCain 2010). For instance, in México, they are found inhabiting a wide range of ecosystems, going from tropical and temperate to arid and semiarid environments; the latter, mainly in the north, extending south to central México (Wilson et al. 2010), and it is in central México where a particular composition of reptile communities can be observed (Figure 1a and 1b), and subsequently, arid and semiarid environments that are remarkably rich in species and endemism (Figure 1c).



Figure 1. A lizard (a) *Sceloporus mucronatus* and snake (b) *Pituophis deppei* species found within the (c) xeric scrub habitat of Tilcuautla, Hidalgo, México. Photos (a) and (b) taken by Raciél Cruz Elizalde and (c) taken by Itzel Magno Benitez.

Patterns of spatial variation in species richness are still subject of study by different disciplines, such as biogeography and ecology (Rosenzweig 1995, Rabosky 2009), where it has been pointed out that species richness can vary substantially between areas with similar environments at different spatial scales, therefore, it is suggested that regional and historical factors play an important role on the richness and the structure of the biotic communities (Wiens and Donoghue 2004, Qian et al. 2007). Most studies about ecological communities at a local level (e.g., vegetation types, regions, etc.) consider ecological factors (competition, predation, etc.; Wiens and Donoghue 2004) as major causes of species richness; however, at larger spatial scales (provinces, continents, etc.), these patterns of diversity are better explained by biogeographic processes (see Wiens 2011).

For a better approach to the understanding of the structure of these communities, the species richness from a particular environment (alpha diversity) will form the foundation for contemplation and beta diversity will represent the degree of change in the species composition among communities (Whittaker 1972), however, with the methods previously mentioned, it is assumed that species contribute evenly to the community structure (Harper and Hawksworth 1995, Moreno et al. 2009).

In this sense, the design of methods, such as assessment of taxonomic diversity as proposed by Warwick and Clarke (1995), represents a complementary measure to the understanding of ecological communities (Somerfield et al. 2008). In this method, the assumption is that the community that contains a high ratio of closely related species will be less diverse than the community containing a low ratio of those species (Warwick and Clark 1995, Clarke and Warwick 1998). Such methods can provide useful tools to create or improve managements plans, ecological restoration, and establishment of areas under special protection (Somerfield et al. 2008).

In the case of communities of reptiles, the arrangement of the communities has been evaluated in different environments, from tropical (Vitt and Caldwell 1994, Vitt et al. 1999), to temperate (Scheibe 1987, Cruz-Elizalde and Ramírez-Bautista 2012) to desert habitats (Pianka 1973, Vitt, 1991). In the latter environment, a high species richness of reptiles has been observed (Pianka 1973, Qian 2009). Recent research with lizards from Europe (Chamaillé-Jammes et al. 2006), suggests that reptiles can benefit from occurrence of high temperatures on a global scale, and this result is similar to other studies showing that temperature is a determinant factor of high species richness of reptiles at regional scales (Vitt and Pianka 2005, Qian and Ricklefs 2007, Araújo et al. 2008). In response to elevated temperatures, this pattern of species richness is attributed to reptiles, mainly because they: (i) are more tolerant to the arid environments for their skin waterproof, (ii) show a higher vagility, (iii) have a high number of habitats and microhabitats they can occupy (Pianka 1986), and (iv) can have high population densities (Pough 1980, Jellinek et al. 2004).

In México, the herpetofauna is composed of 1,204 species (Johnson et al. 2010), with the highest diversity and endemism occurring in the highlands of central México, and in the Pacific Coast and Balsas Basin as well (García et al. 2007). Additionally, the greatest species turnover is associated between the Sierra Madre Occidental and the Yucatan Peninsula (García et al. 2007). With respect to northern México, the reptile richness is close to 299 species (Lavín-Murcio and Lazcano 2010), representing 31.5% of the total percentage for the country. These regions are characterized by a high percentage of arid and semiarid environments that extend toward the center of the country (Rzedowski 1978). In general, few studies have been developed to determine the species richness, diversity and distribution of reptile species, which eventually may contribute to recognition of areas of richness and biotic interchange. Furthermore, these studies would permit the identification of ecological and biogeographic patterns which encompass, in addition to the number of species, the ecological factors, and the biogeographical and phylogenetic processes (taxonomic relationships) for the establishment of complex communities in these environments (Wiens and Donoghue 2004).

Therefore, this chapter aims to describe and document the richness, diversity, and taxonomic diversity of the communities of reptiles in a portion of central México, particularly from the state of Hidalgo, located in a region characterized by a high percentage of arid and semiarid environments.

## RESEARCH METHODS

The study area comprises various regions of arid and semiarid environments of the state of Hidalgo, which is located in central México (19.59777° and 21.41666°N, and 97.9575° and 99.86416°W; WGS 84; INEGI, 2011). The state has an average elevation of 1,660 m, with a maximum and minimum of 3,490 and 18 m, respectively (INEGI, 2011). The state has 13 vegetation types (Rzedowski, 1978), but due to topography of the region, there are several municipalities in the state that contain arid and semiarid environments. In this study, these environments were treated as different set communities to assess the taxonomic diversity of reptiles. These environments are pine forest (PF), farmland (F), desert scrub (DS), secondary vegetation (SV), riparian vegetation (RV), and oak forest (OF; Ramírez-Bautista et al., 2010).

### Data Collection

In this chapter records of the reptile species and the vegetation types from the state of Hidalgo were taken into account. These reptile records were obtained from data bases of scientific collections from México and foreign collections, and also from data taken from field work encompassing a period of nine years (2003-2012) during projects developed for the laboratory of Population Ecology of the herpetology area in Centro de Investigaciones Biológicas from Universidad Autónoma del Estado de Hidalgo. Due to the inclusion of historical records of these biological groups into this work, the database was purged by removing and updating scientific names and excluding synonymies according to Wilson and Johnson (2010), and all localities were georeferenced with the program ArcView<sup>®</sup> (ESRI, 1999), and by using cartographic maps of central México and adjacent areas (INEGI, 2011).

### Alpha Diversity and Similarity

Alpha diversity by vegetation types was determined by specific richness of reptiles found in the different vegetation types in each set (Whittaker 1972). To determine the similarity among communities, Jaccard's similarity coefficient was used and was based on qualitative data (presence and absence; Moreno, 2001). The formula is depicted as:  $J = c / (a+b) - c$ ; where  $a$  is the number of species present in the site A,  $b$  the number of species present in the site B, and  $c$  the number of species present in both A and B sites. The range of values for this index is 0 when there are not shared species between the two sites, and goes to 1 when the two sites have the same species composition. The analysis was performed by using the program EstimateS 7.5 (Colwell 2005).

Finally, in order to evaluate taxonomic distinctness of reptile communities, we calculated the mean (Delta =  $\Delta^+$ ) and variance (Lambda =  $\Lambda^+$ ; *sensu* Clark and Warwick 1998) of taxonomic diversity for each vegetation type, using the measures proposed by Warwick and Clark (1995, 2001). The formulas are represented by:  $\Delta^+ = [2\sum_{i<j}\omega_{ij}]/[S(S-1)]$ , and  $\Lambda^+ = [2\sum_{i<j}(\omega_{ij}-\Delta^+)^2]/[S(S-1)]$ ; where  $\omega_{ij}$  is the taxonomic distance between each pair of species  $i$  and  $j$ , and  $S$  is the species number observed in the sample (Warwick and Clark 1995). A high value of  $\Delta^+$  reflects low relatedness among species, and thus it is a direct measure of

taxonomic diversity. On the other hand,  $\Lambda^+$  is a measure of the unevenness in the structure across taxonomic units. Thus, a high value of  $\Lambda^+$  indicates over- or under- representation of taxa in the samples. Furthermore, we performed a randomization test (Clarke and Warwick 1998) from the expected values derived from the species pool from the combined species list for the region, with the aim of detecting differences (if present) in the taxonomic distinctness at each vegetation type. This null model uses the theoretical mean and variance values, with 95% confidence intervals, obtained by taking 1000 random samples from the pool. Since the theoretical mean remains constant while the variance decreases the number of species in the communities increases, the 95% confidence interval takes the form of a “funnel” (Clarke and Warwick 1998).

In this chapter, we used Liner classification (2007), considering six taxonomic categories: species, genera, family, suborder, order and class. The taxonomic diversity analysis was performed by using the PRIMER 5 program for Windows (Clarke and Gorley 2001).

Furthermore, to assess taxonomic richness and diversity of the analyzed environments, and evaluated it in an integrative framework with diverse arid and semiarid regions of México, we compared the results with the richness and diversity present in the northern region of the country that corresponds to desert of Sonora (western region of México), and Tamaulipas region (eastern region; Lavín-Murcio and Lazcano 2010), and a southern portion of the Chihuahuan Desert known as Guadalcázar (Hernández-Ibarra and Ramírez-Bautista 2006).

## RESULTS AND DISCUSSION

Species richness of reptiles from different arid and semiarid environments from Hidalgo state, was found to include 54 species (Table 1), which represent 45.4% of those reported by Ramírez-Bautista et al. (2010) for the entire state, and 6.3% for México (Wilson and Johnson 2010). Several studies have mentioned that desert environments contain a high richness and diversity of reptiles (McCain 2010). This species richness is reflected mainly by the environmental heterogeneity and vegetation types, as well as physiological and ecological characteristics of the species (Pianka 1986), because unlike other ectothermic vertebrates such as amphibians, reptiles exhibit impermeable skin, which favors them for their occurrence in habitats and microhabitats with a high incidence of heat (Vitt and Caldwell 2009). Furthermore, ecological phenomena such as competition for resources between species in arid and semiarid environments are a limiting factor on the population sizes of reptiles in desert ecosystems (Barbault et al. 1985).

With respect to vegetation assemblages, the XS had the highest species richness, with 42 species, followed by environments with a wide coverage in vegetation such as PF, with 25 species, OF with 19, and in a lesser extent were F and SV environments, with 14 species each, and RV with the lowest diversity (13 species only; Table 1). This result may be a reflection of a high heterogeneity of subgroups of vegetation types within the areas known as XS, furthermore, it is in this vegetation type where a high species richness and diversity of reptiles for México has been previously reported (Lavín-Murcio and Lazcano 2010). The above result can be reflected in the high number of exclusive species recorded for this type of

environment (Table 1), despite of its mean values of beta diversity according to all vegetation associations performed with the analyzed communities.

**Table 1. Species richness by vegetation types (X = occurrence, PF = Pine forest, F = Farmland, XS = Xeric scrub, SV = Secondary vegetation, RV = Riparian vegetation, and OF = Oak forest) in arid and semiarid regions from Hidalgo state, México**

Order	Suborder	Family	Species	VegetationTypes					
				PF	F	XS	SV	RV	OF
Testudine		Kinosternidae	<i>Kinosternon herrerai</i>	0	0	0	X	X	0
			<i>K. hirtipes</i>	0	X	X	X	0	0
			<i>K. integrum</i>	0	0	X	0	0	0
Squamata	Sauria	Anguillidae	<i>Abronia taeniata</i>	0	0	0	0	0	X
			<i>Barisia imbricata</i>	X	X	X	0	0	X
			<i>Gerrhonotus infernalis</i>	0	0	X	0	0	0
		Phrynosomatidae	<i>Phrynosoma orbiculare</i>	X	0	X	0	0	X
			<i>Sceloporus aeneus</i>	X	X	0	0	0	X
			<i>S. bicanthalis</i>	X	0	0	0	0	X
			<i>S. grammicus</i>	X	X	X	X	0	X
			<i>S. minor</i>	X	0	X	0	X	X
			<i>S. mucronatus</i>	X	X	X	X	X	X
			<i>S. parvus</i>	X	X	X	X	0	X
	<i>S. scalaris</i>		X	0	X	0	0	X	
	<i>S. spinosus</i>		X	X	X	X	X	X	
	<i>S. torquatus</i>		X	0	X	X	0	X	
	<i>S. undulatus</i>	0	X	X	0	0	0		
	<i>S. variabilis</i>	X	0	X	0	X	0		
		Scincidae	<i>Plestiodon lynxe</i>	X	0	0	X	0	X
		Teiidae	<i>Aspidoscelis gularis</i>	0	0	X	X	X	0
		Xantusiidae	<i>Lepidophyma gaigeae</i>	X	0	X	0	0	0
	Serpentes	Colubridae	<i>Conopsis lineata</i>	X	X	X	X	0	X
			<i>C. nasus</i>	0	0	X	0	0	0
<i>Drymarchon melanurus</i>			0	0	X	0	0	0	
<i>Ficimia hardyi</i>			0	0	0	0	X	0	
<i>Lampropeltis mexicana</i>			0	X	0	0	0	0	
<i>Masticophis shotti</i>			0	0	X	0	0	0	
<i>M. taeniatus</i>			0	0	0	0	0	X	
<i>Pituophis deppei</i>			X	X	X	X	0	0	
<i>Salvadora bairdi</i>			0	0	X	0	0	0	
<i>S. grahamiae</i>			0	0	X	0	0	0	
		<i>Tantilla bocourti</i>	0	0	X	0	0	0	

Order	Suborder	Family	Species	VegetationTypes					
				PF	F	XS	SV	RV	OF
			<i>Trimorphodon tau</i>	0	0	X	0	0	0
		Viperidae	<i>Crotalus aquilus</i>	X	0	X	0	0	0
			<i>C. atrox</i>	0	0	X	0	0	0
			<i>C. molossus</i>	0	0	X	0	0	X
			<i>C. scutulatus</i>	0	0	X	0	0	0
			<i>C. triseriatus</i>	X	0	X	0	0	X
		Dipsadidae	<i>Geophis latifrontalis</i>	X	0	0	0	0	0
			<i>G. semiannulatus</i>	X	0	0	0	0	X
			<i>Hypsiglena jani</i>	0	0	X	X	X	0
			<i>H. torquata</i>	X	0	X	0	0	0
			<i>Tropidodipsas sartorii</i>	0	X	X	X	X	0
		Leptotyphlopidae	<i>Rena dulcis</i>	0	0	X	0	0	0
			<i>R. myopicus</i>	0	0	X	0	0	0
		Natricidae	<i>Nerodia rhombifer</i>	0	0	X	0	X	0
			<i>Thamnophis cyrtopsis</i>	X	X	X	0	0	0
			<i>T. eques</i>	0	0	X	0	X	X
			<i>T. melanogaster</i>	0	X	X	X	X	0
			<i>T. proximus</i>	X	0	X	0	0	0
			<i>T. pulchrilatus</i>	0	0	0	0	X	0
			<i>T. scalaris</i>	X	0	0	0	0	0
			<i>T. scaliger</i>	X	0	0	0	0	0
		Typhlopidae	<i>Ramphotyphlops braminus</i>	0	0	X	0	0	0
<b>Totals</b>				<b>25</b>	<b>14</b>	<b>41</b>	<b>14</b>	<b>13</b>	<b>19</b>

An important result is that among semiarid environments with influence of temperate environments, PF and OF showed the lowest beta diversity, reflecting a similar composition between these communities. This result highlights the inference that between temperate environments of central México, similar compositions in the reptile communities are maintained (Flores-Villela et al. 2010).

The study of the phylogenetic relationships of species in communities can provide an evolutionary interpretation (Wiens and Donoghue 2004). The taxonomic arrangement of assemblies, assumes that an assemblage with close phylogenetic relationships among species is less taxonomically diverse than one with distant phylogenetic relationships (Clark and Warwick 1998; Moreno et al. 2009). The results obtained in this chapter show a contrasting result with the high species number recorded for the analyzed communities, because the richest environments did not show the highest values of taxonomic diversity with respect to regional average expected by the model.

The XS had a value of taxonomic diversity similar to the average expected by the model, and the communities PF and OF were presented outside the confidence interval of 95% of the

model, showing the lowest values of taxonomic diversity (Figure 2). In this context, the communities less rich in species such as RV and SV had the highest values of taxonomic diversity, similar to the F community (Figure 2). In addition, most communities, except XS, showed high values of variation on taxonomic diversity (Figure 3). The above represents an interesting result for the composition of reptile community in the analyzed environments, since only a few types of vegetation (SV and RV) had a low richness and a higher value of taxonomic diversity. These values are given mainly by a distant phylogenetic relationship that occurs in each reptiles assemblage, as well as the processes driving this arrangement of species (Wiens 2012). That is, in these environments events such as colonization, extinction or immigration, and differential resource sharing may translate into different taxa (at the family level) using a range of specific microhabitats, food or particular spaces (Patterson and Brown 1991) even though they are found inhabiting environments with low representation relative to XS.

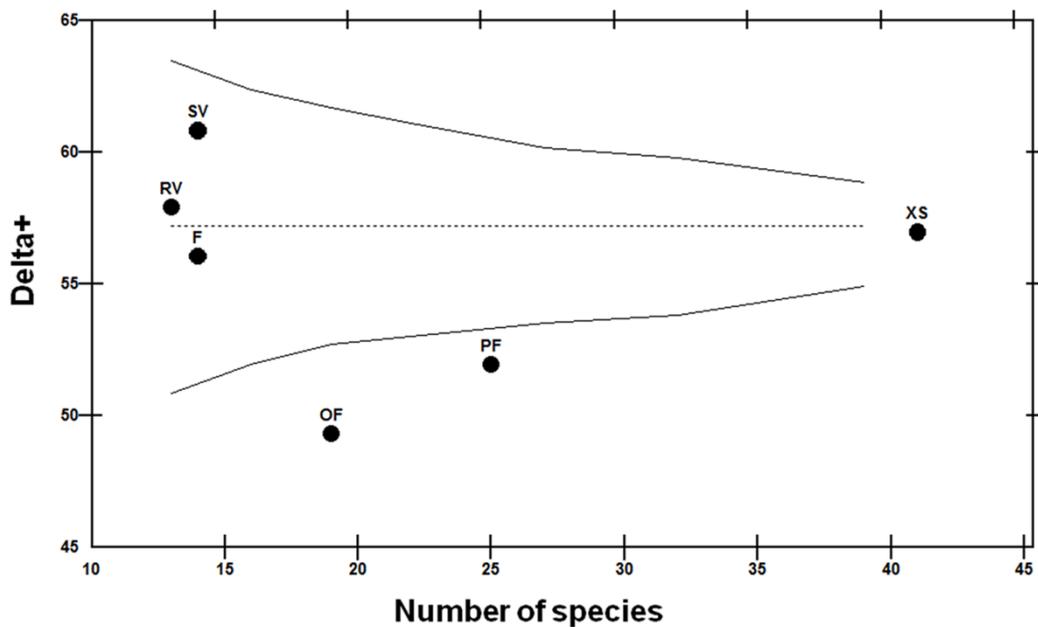


Figure 2. Average taxonomic diversity ( $\Delta^+$ ) for analyzed communities in Hidalgo, México (RV, SV, F, OF, PF, and XS); the curved line represents the confidence interval at 95% according to the model.

The taxonomic diversity of reptiles in the analyzed environments of this chapter may be due to the history of the regional *pool* that conforms the biological communities and assemblages (Flores-Villela and Martínez-Salazar 2009, Morlon et al. 2011), as it has been observed in other studies (Heard and Cox 2007, Cavender-Bares et al. 2009). On the other hand, it could also be due to several factors such as (i) the ability of dispersal of species among areas, (ii) local extinctions, (iii) speciation *in-situ*, and (iv) evolution *in-situ* (Losos, 1996; Stephens and Wiens, 2003). These factors, in addition to ecological factors, are the main determinants for the taxonomic arrangement of the current assemblages of reptiles (Losos 1996, Vitt et al. 2003), other reptiles (Vitt 1995, Mesquita et al. 2006, França et al. 2008); with similar conditions reported for amphibians (Lowe and Bolger 2002, Welsh and

Lind 2002), mammals (Lindenmayer et al. 1999), birds (Rodewald and Yahner 2001, Bennett et al. 2004), and terrestrial invertebrates (Summerville et al. 2003).

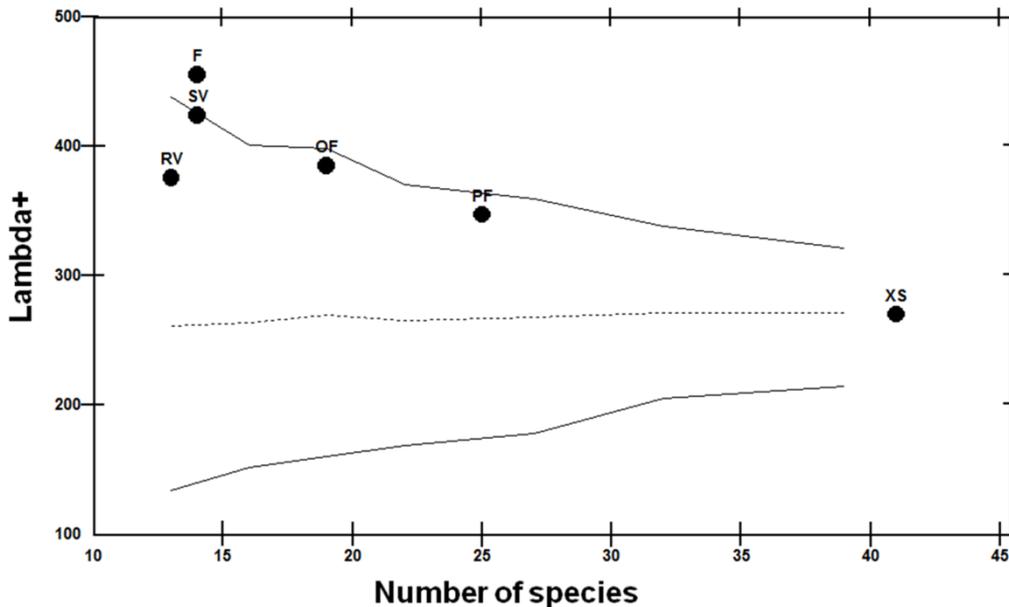


Figure 3. Variation in taxonomic diversity ( $\text{Lambda}^+$ ) for analyzed communities in Hidalgo, México (RV, SV, F, OF, PF, and XS); the curved line represents the confidence interval at 95% according to the model.

Studies that evaluate local levels of species richness, often determine the phenomena that give rise to the formation of the assemblages and/or biological communities (Harrison and Grace 2007), showing ecological processes such as competition for the resources (space, food, etc.), as the main cause of the arrangement of assemblages and communities at a local level (Wiens and Donoghue 2004). In contrast, at a regional or landscape level, processes of extinction in mass, immigration events, prolonged speciation events turn out to be the main factors to explain the large-scale variation (Wiens and Donoghue 2004); however, these two sets of phenomena are interrelated, because processes in one scale influence the other.

The results obtained for a single region, and in this case for arid and semiarid regions of the state of Hidalgo, highlight that they can be compared to other regions with similar environments. Thus, when comparing the studied region in this chapter with the arid and semiarid environmental regions from northern México, the region of the state of Hidalgo show a lower species richness of reptiles (Table 2). The Hidalgo (HGO) region contains greater richness (54 species) than the Guadalcázar region (GDZ; 44 species) located to the south of the Chihuahuan Desert ecoregion; however, compared to the Tamaulipas (TAM), and Sonora (SON) regions the HGO region has low richness values for reptiles, with 79 and 80, respectively (Table 2). These results suggest a strong influence by the regional *pool* of species in the reptile community characterized by environments, since the interaction between HGO and GDZ areas showed the lowest values of similarity ( $J = 0.69$ ), but HGO and SON showed the highest values ( $J = 0.94$ ). Therefore, the richness from HGO region is similar to that presented in central México, but differs substantially from that recorded for the northern

portion of the country (Ramírez-Bautista et al. 2009, Flores-Villela et al. 2010, Ramírez-Bautista et al. 2010). The above results show a similar pattern found in other studies, such as one done by Ramírez-Bautista and Moreno (2006), where these authors found a high association in species composition to the analyzed region for central México and Pacific regions and Gulf of México.

**Table 2. Species richness by regions (X = occurrence, HGO = Hidalgo, GDZ = Guadalcázar, SON = Sonora, TAM = Tamaulipas) whit arid and semiarid vegetation types in México**

Order	Suborder	Family	Species	Regions				
				HGO	GDZ	SON	TAM	
Crocodylia		Alligatoridae	<i>Alligator mississippiensis</i>	0	0	0	X	
		Crocodylidae	<i>Crocodylus moreletii</i>	0	0	0	X	
Testudines	Emydidae		<i>Pseudemys gorzugi</i>	0	0	0	X	
			<i>Terrapene carolina</i>	0	0	0	X	
			<i>T. nelsoni</i>	0	0	X	0	
			<i>T. ornata</i>	0	0	X	0	
			<i>Trachemys scripta</i>	0	0	X	X	
			Geoemydidae	<i>Rhinoclemmys pulcherrima</i>	0	0	X	0
			Kinosternidae	<i>Kinosternon alamosae</i>	0	0	X	0
			<i>K. flavescens</i>	0	0	X	X	
			<i>K. herrerae</i>	X	0	0	0	
			<i>K. hirtipes</i>	X	0	0	0	
			<i>K. integrum</i>	X	X	0	0	
			<i>K. sonoriense</i>	0	0	X	0	
		Testudinidae	<i>Gopherus agassizi</i>	0	0	X	0	
		Trionychidae	<i>Apalone spinifera</i>	0	0	0	X	
Squamata	Sauria	Anguillidae	<i>Abronia taeniata</i>	X	0	0	0	
			<i>Anguis attenuatus</i>	0	0	0	X	
			<i>Barisia imbricata</i>	X	0	0	0	
			<i>Gerrhonotus infernalis</i>	X	X	0	X	
			<i>G. ophiurus</i>	0	X	0	0	
			Crotaphytidae	<i>Crotaphytus dickersonae</i>	0	0	X	0
				<i>C. collaris</i>	0	X	0	0
				<i>C. nebrius</i>	0	0	X	0
				<i>C. reticulatus</i>	0	0	0	X
				<i>Gambelia wislizenii</i>	0	0	X	0
		Eublepharidae	<i>Coleonyx brevis</i>	0	0	0	X	
			<i>C. variegatus</i>	0	0	X	0	
		Dibamidae	<i>Anelytropsis papillosus</i>	0	X	0	X	
		Gekkonidae	<i>Hemidactylus frenatus</i>	0	0	0	X	
			<i>H. turcicus</i>	0	0	0	X	
			<i>Phyllodactylus homolepidurus</i>	0	0	X	0	
		Helodermatidae	<i>Heloderma horridum</i>	0	0	X	0	
			<i>H. suspectum</i>	0	0	X	0	
		Iguanidae	<i>Ctenosaura hemilopha</i>	0	0	X	0	
			<i>C. macrolopha</i>	0	0	X	0	
	<i>Dipsosaurus dorsalis</i>		0	0	X	0		
	<i>Sauromalus ater</i>		0	0	X	0		

Order	Suborder	Family	Species	Regions			
				HGO	GDZ	SON	TAM
		Phrynosomatidae	<i>Callisaurus draconoides</i>	0	0	X	0
			<i>Cophosaurus texanus</i>	0	X	X	X
			<i>Holbrookia approximans</i>	0	X	0	0
			<i>H. lacerta</i>	0	0	0	X
			<i>H. maculata</i>	0	0	X	0
			<i>H. propinqua</i>	0	0	0	X
			<i>Phrynosoma cornutum</i>	0	0	X	X
			<i>P. ditmarsii</i>	0	0	X	0
			<i>P. hernandesi</i>	0	0	X	0
			<i>P. mcallii</i>	0	0	X	0
			<i>P. modestum</i>	0	X	0	X
			<i>P. orbiculare</i>	X	X	0	0
			<i>P. platyrhinos</i>	0	0	X	0
			<i>P. solare</i>	0	0	X	0
			<i>Sceloporus aeneus</i>	X	0	0	0
			<i>S. bicanthalis</i>	X	0	0	0
			<i>S. clarki</i>	0	0	X	0
			<i>S. cowlesi</i>	0	0	X	X
			<i>S. horridus</i>	0	0	X	0
			<i>S. grammicus</i>	X	X	0	X
			<i>S. magister</i>	0	0	X	0
			<i>S. marmoratus</i>	0	0	0	X
			<i>S. minor</i>	X	X	0	0
			<i>S. mucronatus</i>	X	0	0	0
			<i>S. nelsoni</i>	0	0	X	0
			<i>S. olivaceus</i>	0	X	0	X
			<i>S. parvus</i>	X	X	0	0
			<i>S. scalaris</i>	X	X	0	0
			<i>S. serrifer</i>	0	0	0	X
			<i>S. spinosus</i>	X	X	0	0
			<i>S. torquatus</i>	X	0	0	0
			<i>S. undulatus</i>	X	0	0	0
			<i>S. variabilis</i>	X	X	0	0
			<i>Uma notata</i>	0	0	X	0
			<i>Urosaurus bicarinatus</i>	0	0	X	0
			<i>U. graciosus</i>	0	0	X	0
			<i>U. ornatus</i>	0	0	X	0
			<i>Uta stansburiana</i>	0	0	X	0
		Polychrotidae	<i>Anolis carolinensis</i>	0	0	0	X
		Scincidae	<i>Plestiodon brevirostris</i>	0	X	0	0
			<i>P. callicephalus</i>	0	0	X	0
			<i>P. lynxe</i>	X	0	0	0
			<i>P. obsoletus</i>	0	0	0	X
			<i>P. tetragrammus</i>	0	X	0	X
			<i>S. lateralis</i>	0	0	0	X
			<i>S. silvicola</i>	0	X	0	0
		Teiidae	<i>Ameiva undulata</i>	0	0	0	X
			<i>Aspidoscelis burti</i>	0	0	X	0
			<i>A. gularis</i>	X	0	0	X
			<i>A. inornata</i>	0	X	0	0

Table 2. (Continued)

Order	Suborder	Family	Species	Regions			
				HGO	GDZ	SON	TAM
			<i>A. laredoensis</i>	0	0	0	X
			<i>A. opatae</i>	0	0	X	0
			<i>A. sexlineata</i>	0	0	0	X
			<i>A. sonora</i>	0	0	X	0
			<i>A. tigris</i>	0	0	X	0
			<i>A. uniparens</i>	0	0	X	0
		Xantusiidae	<i>Lepidophyma gaigeae</i>	X	0	0	0
			<i>Xantusia vigilis</i>	0	0	X	0
Serpentes		Boidae	<i>Boa constrictor</i>	0	0	X	X
			<i>Charina trivirgata</i>	0	0	X	0
		Colubridae	<i>Arizona elegans</i>	0	X	X	X
			<i>Chilomeniscus stramineus</i>	0	0	X	0
			<i>Chionactis occipitalis</i>	0	0	X	0
			<i>Ch. palarostris</i>	0	0	X	0
			<i>Coluber constrictor</i>	0	0	0	X
			<i>Conopsis lineata</i>	X	0	0	0
			<i>C. nasus</i>	X	0	0	0
			<i>Drymarchon melanurus</i>	X	X	X	X
			<i>Drymobius margaritiferus</i>	0	0	X	X
			<i>Ficimia hardyi</i>	X	X	0	0
			<i>F. streckeri</i>	0	0	0	X
			<i>Gyalopion canum</i>	0	0	X	0
			<i>G. quadrangulare</i>	0	0	X	0
			<i>Lampropeltis calligaster</i>	0	0	0	X
			<i>L. getula</i>	0	0	X	X
			<i>L. mexicana</i>	X	X	0	0
			<i>L. pyromelana</i>	0	0	X	0
			<i>L. triangulum</i>	0	X	0	X
			<i>Masticophis bilineatus</i>	0	0	X	0
			<i>M. flagellum</i>	0	X	X	X
			<i>M. shotti</i>	X	X	0	X
			<i>M. taeniatus</i>	X	0	0	0
			<i>Opheodrys aestivus</i>	0	0	0	X
			<i>Oxybelis aeneus</i>	0	0	X	X
			<i>Pantherophis emoryi</i>	0	X	0	X
			<i>Phyllorhynchus browni</i>	0	0	X	0
			<i>P. decurtatus</i>	0	0	X	0
			<i>Pituophis deppei</i>	X	X	0	0
			<i>P. catenifer</i>	0	0	X	X
			<i>P. obsoleta</i>	0	0	0	X
			<i>Rhinocheilus lecontei</i>	0	X	X	X
			<i>Salvadora bairdi</i>	X	0	0	0
			<i>S. deserticola</i>	0	0	X	0
			<i>S. grahamiae</i>	X	X	X	X
			<i>S. hexalepis</i>	0	0	X	0
			<i>Senticolis triaspis</i>	0	X	X	0
			<i>Sonora aemula</i>	0	0	X	0
			<i>S. semiannulata</i>	0	0	X	X
			<i>Sympholis lippiens</i>	0	0	X	0

Order	Suborder	Family	Species	Regions			
				HGO	GDZ	SON	TAM
			<i>Tantilla atriceps</i>	0	X	0	X
			<i>T. bocourti</i>	X	0	0	0
			<i>T. gracilis</i>	0	0	0	X
			<i>T. hobartsmithi</i>	0	0	X	0
			<i>T. rubra</i>	0	0	0	X
			<i>T. wilcoxi</i>	0	X	0	0
			<i>T. yaquia</i>	0	0	X	0
			<i>Trimorphodon tau</i>	X	X	0	0
			<i>T. wilkinsonii</i>	0	0	X	0
		Viperidae	<i>Agkistrodon taylori</i>	0	0	0	X
			<i>Crotalus aquilus</i>	X	X	0	0
			<i>C. atrox</i>	X	X	X	X
			<i>C. cerastes</i>	0	0	X	0
			<i>C. lepidus</i>	0	X	0	0
			<i>C. mitchelli</i>	0	0	X	0
			<i>C. molossus</i>	X	X	X	0
			<i>C. scutulatus</i>	X	0	X	0
			<i>C. tigris</i>	0	0	X	0
			<i>C. totonacus</i>	0	0	0	X
			<i>C. triseriatus</i>	X	0	0	0
			<i>Sistrurus catenatus</i>	0	0	0	X
		Dipsadidae	<i>Coniophanes imperialis</i>	0	0	0	X
			<i>Diadophis punctatus</i>	0	0	X	0
			<i>Geophis latifrontalis</i>	X	0	0	0
			<i>G. semiannulatus</i>	X	0	0	0
			<i>Hypsiglena jani</i>	X	0	0	0
			<i>H. torquata</i>	X	X	X	X
			<i>Leptodeira septentrionalis</i>	0	0	0	X
			<i>Tropidodipsas sartorii</i>	X	0	0	0
		Elapidae	<i>Micruroides euryxanthus</i>	0	0	X	0
			<i>Micrurus tener</i>	0	X	0	X
		Leptotyphlopidae	<i>Rena dulcis</i>	X	X	X	X
			<i>R. humilis</i>	0	0	X	0
			<i>R. myopicus</i>	X	0	0	0
		Natricidae	<i>Nerodia erythrogaster</i>	0	0	0	X
			<i>N. rhombifer</i>	X	0	0	X
			<i>Storeria dekayi</i>	0	0	0	X
			<i>Thamnophis cyrtopsis</i>	X	X	X	0
			<i>T. eques</i>	X	X	0	0
			<i>T. marcianus</i>	0	0	X	X
			<i>T. melanogaster</i>	X	0	0	0
			<i>T. proximus</i>	X	0	0	X
			<i>T. pulchrilatus</i>	X	0	0	0
			<i>T. scalaris</i>	X	0	0	0
			<i>T. scaliger</i>	X	0	0	0
			<i>T. validus</i>	0	0	X	0
		Typhlopidae	<i>Ramphotyphlops braminus</i>	X	0	0	X
		Xenodontidae	<i>Heterodon kennerlyi</i>	0	0	X	X
<b>Totals</b>				<b>54</b>	<b>44</b>	<b>89</b>	<b>70</b>

Several studies suggest the influence of the evolutionary history of the species or the regional history of the environment on the biodiversity of reptile communities (Vitt and Pianka 2005). The diversity of reptile species recorded for México (854 species), differs among regions, and particularly for the environments occurring in northern México with respect to those found in the central and southern portions of the country (Wilson et al. 2010). From other analyzed regions of México, TAM represents the highest value of taxonomic diversity, followed by SON, HGO, and GDZ (Figure 4), however these regional values did not show contrasting variation in taxonomic diversity (Figure 5). These results refer to the high number of supraspecific member levels (genera, families, and orders) occurring in the northern Mexican regions (SON and TAM), since these contain different families and genera of turtles, lizards, and snakes that do not occur in central México.

The change in the composition of species, genera, and families among areas, is an important phenomenon in studies of biogeography and macroecology (Gaston et al. 2007, Qian and Ricklefs, 2007). Knowledge of the processes that give rise to this phenomenon is crucial for understanding the origins and the presence of the diversity of these groups at different spatial scales (Janzen 1967, Whittaker 1972, Gaston et al. 2007). Studies involving analyses of richness and diversity of reptiles at different spatial scales, particularly those from arid and semiarid environments, are needed to map the biogeographic patterns in different regions. This will allow subsequent assessment of any changes in reptile community composition and/or assemblages that take into account ecological, biogeographic and phylogenetic processes.

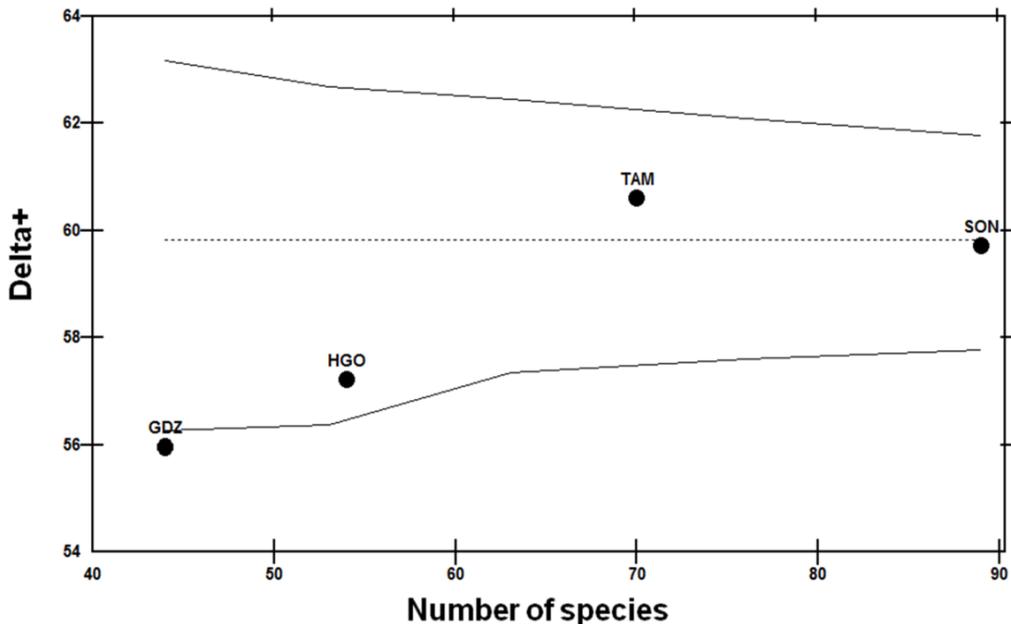


Figure 4. Average taxonomic diversity ( $\Delta^+$ ) for analyzed regions (GDZ, HGO, TAM, and SON); the curved line represents the confidence interval at 95% according to the model.

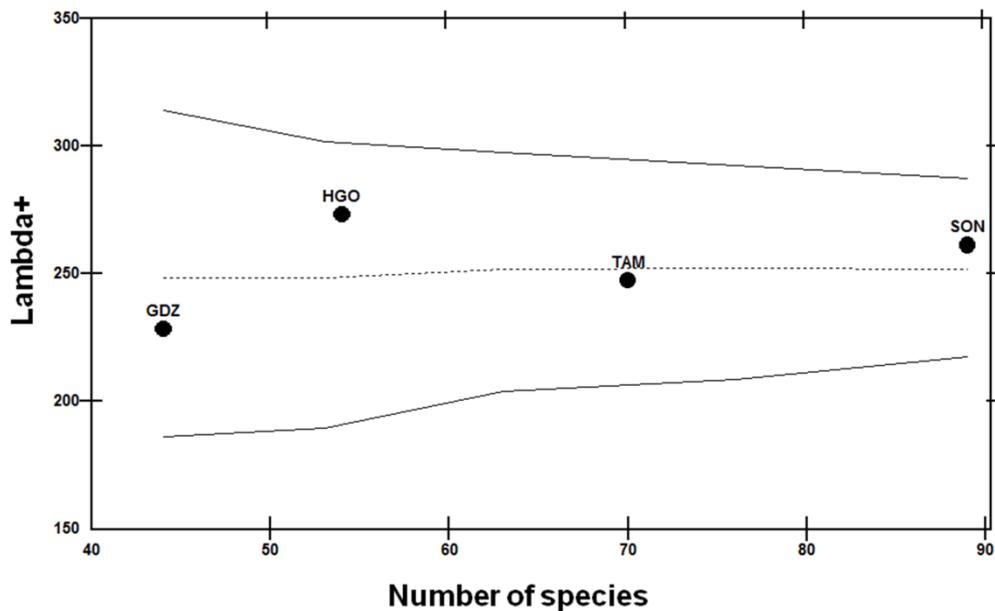


Figure 5. Variation in taxonomic diversity ( $\text{Lambda}^+$ ) for analyzed regions (GDZ, HGO, TAM, and SON); the curved line represents the confidence interval at 95% according to the model.

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## REFERENCES

- Araújo, MB, D Nogués-Bravo, JAF Diniz-Filho, AM Haywood, PJ Valdés, and C Rahbek. 2008. Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography* 31:8-15.
- Barbault R, A Ortega, and ME Maury. 1985. Food partitioning and community organization in a mountain lizard guild of Northern Mexico. *Oecologia* 65:550-554.
- Bennett, AF, SA Hinsley, PE Bellamy, RD Swetnam, and R MacNally. 2004. Do regional gradients in land-use influence richness, composition and turnover of bird assemblages in small woods? *Biological Conservation* 119:191-206.
- Cavender-Bares, J, KH Kozak, PVA Fine, and SW Kembel. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12:693-715.
- Chamaillé-Jammes, S, M Massot, P Aragón, and J Clobert. 2006. Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. *Global Change Biology* 12:392-402.

- Clarke, KR and RM Warwick. 1998. A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology* 35:523-531.
- Clarke, KR and RN Gorley. 2001. PRIMER v5: user manual/tutorial.-PRIMER-E, Plymouth, UK.
- Colwell, RK. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5.
- Cruz-Elizalde, R and A Ramírez-Bautista. 2012. Diversidad de reptiles en tres tipos de vegetación del estado de Hidalgo, México. *Revista Mexicana de Biodiversidad* 83:458-467.
- ESRI. 1999. ArcView 3.2 GIS. Enviromental Systems Research Institute. Inc. New York.
- Flores-Villela, O and EA Martínez-Salazar. 2009. Historical explanation of the origin of the herpetofauna of Mexico. *Revista Mexicana de Biodiversidad* 80:817-833.
- Flores-Villela, O, L Canseco-Márquez, and LM Ochoa-Ochoa. 2010. Geographic distribution and conservation of the Mexican central highlands herpetofauna, Pp. 303-321. In LD Wilson, JH Townsend, and JD Johnson (Eds.), *Conservation of the Mesoamerican Amphibians and Reptiles*, Eagle Mountain Publ., L. C. Eagle Mountain, Utah. 812 Pp.
- França, FGR, DO Mesquita, CC Nogueira, and AFB Araújo. 2008. Phylogeny and Ecology Determine Morphological structure in a snake assemblage in the Central Brazilian Cerrado. *Copeia* 2008:23-38.
- García, A, H Solano-Rodríguez, and O Flores-Villela. 2007. Patterns of alpha, beta and gamma diversity of the herpetofauna in Mexico's Pacific lowlands and adjacent interior valleys. *Animal Biodiversity and Conservation* 30:169-177.
- Gaston, KJ, KL Evans, and JJ Lennon. 2007. The scaling of spatial turnover: pruning the thicket, Pp 181-222. In D Storch, PM Marquet, and JJ Brown (Eds.), *Scaling biodiversity*. Cambridge University Press, Cambridge.
- Harrison, S and JB Grace. 2007. Biogeographic affinity helps explain productivity-richness relationships at regional and local scales. *The American Naturalist* 170:5-15.
- Harper, JL and DL Hawksworth. 1995. Preface, Pp 5-12. In DL Hawksworth (Ed.), *Biodiversity: measurement and estimation*. Chapman and Hall, London, UK.
- Heard, SB and GH Cox. 2007. The shapes of phylogenetic trees of clades, faunas, and local assemblages: experimental spatial pattern in differential diversification. *American Naturalist* 169:107-118.
- Hernández-Ibarra, X and A Ramírez-Bautista. 2006. Herpetofauna del municipio de Guadalcázar, San Luis Potosí, México, Pp. 58-73. In A Ramírez-Bautista, L Canseco-Márquez, and F Mendoza Quijano (Eds.), *Inventarios herpetofaunísticos de México: avances en el conocimiento de su biodiversidad*. Sociedad Herpetológica Mexicana. México, D. F. No. 3 y Benemérita Universidad Autónoma de Puebla. 346 Pp.
- INEGI. 2011. Cartas digitales, México.
- Janzen, DH. 1967. Why mountain passes are higher in the tropics. *American Naturalist* 101:233-49.
- Jellinek, S, DA Driscoll, and JB Kirkpatrick. 2004. Environmental and vegetation variables have a greater influence than habitats fragmentation in structuring lizards communities in remnant urban bushland. *Austral Ecology* 29:294-304.
- Johnson, JD, V Mata-Silva, and A Ramírez-Bautista. 2010. Geographic distribution and conservation of the herpetofauna of southeastern Mexico, Pp. 323-369. In LD Wilson, JH

- Towsend, and JD Johnson (Eds.), Conservation of the Mesoamerican Amphibians and Reptiles, Eagle Mountain Publ., L. C. Eagle Mountain, Utah. 812 Pp.
- Lavín-Murcio, PA and D Lazcano. 2010. Geographic distribution and conservation of the herpetofauna of northern México, Pp. 274-301. In LD Wilson, JH Townsend, and JD Johnson (Eds.), Conservation of the Mesoamerican Amphibians and Reptiles, Eagle Mountain Publ., L. C. Eagle Mountain, Utah. 812 Pp.
- Lindenmayer, DB, RB Cunningham, and ML Pope. 1999. A large-scale “experiment” to examine the effects of landscape context and habitat fragmentation on mammals. *Biological Conservation* 88:387-403.
- Liner, EA. 2007. Checklist of the amphibians and reptiles of México. *Occasional Papers of the Museum of Natural Science* 80(1):1-59.
- Losos, JB. 1996. Phylogenetic perspectives on community Ecology. *Ecology* 77:1344-1354.
- Lowe, WH and DT Bolger. 2002. Local and landscape-scale predictors of salamanders abundance in New Hampshire headwater streams. *Conservation Biology* 16(1):183-193.
- McCain, CM. 2010. Global analysis of reptile elevational diversity. *Global Ecology and Biogeography* 19:541-553.
- Mesquita, DO, GR Colli, FGR França, and LJ Vitt. 2006. Ecology of a Cerrado Lizard Assemblage in the Jalapão Region of Brazil. *Copeia* 2006:460-471.
- Moreno, CE. 2001. Métodos para medir la biodiversidad. *M&T-Manuales y Tesis Sociedad Entomológica Aragonesa*, vol. 1, Zaragoza. 84 Pp.
- Moreno, CE, G Castillo-Campos, and JR Verdú. 2009. Taxonomic diversity as complementary information to assess plant species diversity in secondary vegetation and primary tropical deciduous forest. *Journal of Vegetation Science* 20:935-943.
- Morlon, H, DW Schwikl, JA Bryant, PA Marquet, AG Rebelo, C Taus, BJM Bohannan, and JL Green. 2011. Spatial patterns of phylogenetic diversity. *Ecology Letters* 14:141-149.
- Patterson, BD and JH Brown. 1991. Regionally nested patterns of species composition in granivorous rodent assemblages. *Journal of Biogeography* 18:395-402.
- Pianka, ER. 1973. The structure of lizard communities. *Annual Review Ecology Systematic* 4:53-74.
- Pianka, ER. 1986. Ecology and Natural History of Desert Lizards. Princeton University Press, Princeton, New Jersey.
- Pough, FH. 1980. The advantages of ectothermy for tetrapods. *American Naturalist* 115:92-112.
- Qian, H and RE Ricklefs. 2007. A latitudinal gradient in large-scale beta diversity for vascular plants in North America. *Ecology Letters* 10:737-744.
- Qian, H, X Wang, S Wang, and Y Li. 2007. Environmental determinants of amphibian and reptiles species richness in China. *Ecography* 30:471-482.
- Qian, H. 2009. Beta diversity in relation to dispersal ability for vascular plants in North America. *Global Ecology and Biogeography* 18:327-332.
- Rabosky, DL. 2009. Ecological limits on clade diversification in higher taxa. *American Naturalist* 173:662-674.
- Ramírez-Bautista, A and C Moreno. 2006. Análisis comparativo de la herpetofauna de cuatro regiones geográficas de México, Pp. 74-98. In A Ramírez-Bautista, L Canseco-Márquez, and F Mendoza-Quijano (Eds.), Inventarios herpetofaunísticos de México: avances en el conocimiento de su biodiversidad. Sociedad Herpetológica Mexicana. México, D. F. No. 3 y Benemérita Universidad Autónoma de Puebla. 346 Pp.

- Ramírez-Bautista, A, U Hernández-Salinas, UO García-Vázquez, A Leyte-Manrique, and L Canseco-Márquez. 2009. Herpetofauna del Valle de México: diversidad y conservación. Universidad Autónoma del Estado de Hidalgo, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. 213 Pp.
- Ramírez-Bautista, A, U Hernández-Salinas, F Mendoza-Quijano, R Cruz-Elizalde, VD Vite-Silva, BP Stephenson, and A Leyte-Manrique. 2010. Lista anotada de los anfibios y reptiles del estado de Hidalgo, México. Universidad Autónoma del Estado de Hidalgo, *Comisión Nacional para el Conocimiento y Uso de la Biodiversidad*. 104 Pp.
- Rodewald, AD and RH Yahner. 2001. Influence of landscape composition on avian community structure and associated mechanism. *Ecology* 82:3493-3502.
- Rosenzweig, ML. 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge. 436 Pp.
- Rzedowski, J. 1978. Vegetación de México. Limusa, México D. F. 432 Pp.
- Scheibe, JS. 1987. Climate, competition, and the structure of temperate zone lizard communities. *Ecology* 68:1424-1436.
- Somerfield, PL, KR Clarke, RM Warwick, and NK Dulvy. 2008. Average functional distinctness as a measure of the composition of assemblages. *ICES Journal of Marine Science* 65:1-7.
- Stephens, PR and JJ Wiens. 2003. Explaining species richness from continents to communities: The time-for-speciation effect in Emydid turtles. *The American Naturalist* 161:112-128.
- Summerville, KS, MJ Boulware, JA Veech, and TO Crist. 2003. Spatial variation in species diversity and composition of forest Lepidoptera in eastern deciduous forest of North America. *Conservation Biology* 17:1045-1047.
- Vitt, LJ. 1991. An introduction to the ecology of cerrado lizards. *Journal of Herpetology* 25:79-90.
- Vitt, LJ and JP Caldwell. 1994. Resource utilization and guild structure of small vertebrates in the Amazon forest leaf litter. *Journal of Zoology* 234:463-476.
- Vitt, LJ, PA Zani, and MC Espósito. 1999. Historical ecology of Amazonian lizards: Implications for community ecology. *Oikos* 87:286-294.
- Vitt, LJ. 1995. The ecology of tropical lizards in the Caatinga of northeast Brazil. *Occasional Papers Oklahoma Museum Natural History* 1:1-29.
- Vitt, LJ, ER Pianka, WE Cooper Jr, and K Schwenk. 2003. History and the global ecology of squamate reptiles. *American Naturalist* 162:44-60.
- Vitt, LJ and ER Pianka. 2005. Deep history impacts present-day ecology and biodiversity. *Proceeding National Academic Science*. USA 102:7877-7881.
- Vitt, LJ and JP Caldwell. 2009. Herpetology. An introductory biology of amphibians and reptiles. Third Edition. Academic Press. 697 Pp.
- Warwick, RM and KR Clarke. 1995. New biodiversity measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology Progress Series* 129:301-305.
- Warwick, RM and KR Clarke. 2001. Practical measures of marine biodiversity based on relatedness of species. *Oceanography Marine Biology Annual Review* 39:207-231.
- Welsh, HH and AJ Lind. 2002. Multiscale habitat relationships of stream amphibians in the Klamath-Siskiyou region of California and Oregon. *Journal of Wildlife Management* 66:581-602.

- Whittaker, RH. 1972. Evolution and measurement of species diversity. *Taxon* 21(2):213-251.
- Wiens, JJ. 2011. The causes of species richness patterns across space, time and clades and the role of “ecological limits”. *The Quarterly Review of Biology* 86:1-20.
- Wiens, JJ. 2012. Why biogeography matters: historical biogeography vs. phylogeography and community phylogenetics for inferring ecological and evolutionary processes. *Frontiers of Biogeography* 4:128-135.
- Wiens, JJ and MJ Donoghue. 2004. Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution* 19:639-644.
- Wilson, LD, and JD Johnson. 2010. Distribution patterns of the herpetofauna of Mesoamerica, a biodiversity hotspot, Pp. 32-235. In LD Wilson, JH Townsend, and JD Johnson (Eds.), *Conservation of the Mesoamerican Amphibians and Reptiles*, Eagle Mountain Publ., L. C. Eagle Mountain, Utah. 812 Pp.
- Wilson, LD, JH Townsend, and JD Johnson. 2010. *Conservation of the Mesoamerican Amphibians and Reptiles*. Eagle Mountain Publisher, L. C. Eagle Mountain, Utah. 812 Pp.