Patterns of alpha, beta and gamma diversity of the herpetofauna in Mexico's Pacific lowlands and adjacent interior valleys

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Abstract

Patterns of alpha, beta and gamma diversity of the herpetofauna in Mexico's Pacific lowlands and adjacent interior valleys.— The latitudinal distribution patterns of alpha, beta and gamma diversity of reptiles, amphibians and herpetofauna were analyzed using individual binary models of potential distribution for 301 species predicted by ecological modelling for a grid of 9,932 quadrants of ~25 km^2 each. We arranged quadrants in 312 latitudinal bands in which alpha, beta and gamma values were determined. Latitudinal trends of all scales of diversity were similar in all groups. Alpha and gamma responded inversely to latitude whereas beta showed a high latitudinal fluctuation due to the high number of endemic species. Alpha and gamma showed a strong correlation in all groups. Beta diversity is an important component of the herpetofauna distribution patterns as a continuous source of species diversity throughout the region.

Key words: Latitudinal distribution pattern, Diversity scales, Herpetofauna, Western Mexico.

Resumen

Patrones de diversidad alfa, beta y gama de la herpetofauna de las tierras bajas y valles adyacentes del Pacífico de México.— Se analizaron los patrones de distribución latitudinales de la diversidad alfa, beta y gama de los reptiles, anfibios y herpetofauna utilizando modelos binarios individuales de distribución potencial de 301 especies predichas mediante un modelo ecológico para una cuadrícula de 9.932 cuadrantes de aproximadamente 25 km^2 cada uno. Se organizaron los cuadrantes en 312 bandas latitudinales para las cuales se determinaron los valores de alfa, beta y gama. Las tendencias latitudinales de todas las escalas de diversidad eran similares en todos los grupos. Alfa y gama respondieron inversamente a la latitud mientras que beta registró una gran fluctuación latitudinal debida al alto número de especies endémicas. Alfa y gama mostraron una fuerte correlación en todos los grupos. La diversidad beta es un componente importante de los patrones de distribución de la herpetofauna como una fuente constante de diversidad de especies a lo largo de la región.

Palabras clave: Patrón latitudinal de distribución, Escalas de diversidad, Herpetofauna, Oeste de México.

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Introduction

Mexico is one of the richest countries in the world in herpetofauna, with about 1,165 reptile and amphibian species (Flores–Villela & Canseco–Márquez, 2004). It is one of the 17 megadiverse countries that jointly account for more than two thirds of the earth's plant and animal diversity (Mittermeier et al., 1988; Ramamoorthy et al., 1993; Sánchez–Cordero et al., 2005 among others). The distribution of Mexican herpetofauna is not homogeneous. The highest number of reptile and amphibian species and endemics are found in two regions, Central Mexico and Western Mexico (Flores–Villela, 1993a, 1993b; Flores–Villela & Goyenechea, 2003; Garcia, 2003, 2006). Western Mexico and specifically the Pacific lowlands and adjacent interior valleys are home to almost a third of the Mexican herpetofauna species and a fourth of the endemic species (Flores–Villela & Goyenechea, 2003; García, 2006; Ochoa–Ochoa & Flores–Villela, 2006). Previous studies on the diversity and distribution of plant and terrestrial animal species rank this region as one of the most diverse in Mexico both in species richness and endemics (Ramamoorthy et al., 1993; Bojorquez–Tapia et al., 1995; Ceballos & García, 1995; García–Trejo & Navarro, 2004).

Seasonal tropical dry forest is the dominant vegetation type in the Mexican Pacific lowlands and adjacent interior valleys (Trejo–Vazquez & Dirzo, 2000; García, 2006). Despite its importance for Mexican biodiversity conservation, such forest is at high risk since it has the second highest annual deforestation rate (2%) in Mexico, and only 27% of the original forest remains intact (Trejo–Vazquez & Dirzo, 2000; Trejo–Vazquez, 2005; García, 2006). Disappearance of this ecosystem and its associated vegetation types places Mexican biodiversity at risk of extinction (Ramamoorthy, et al., 1993; Sarukhán & Dirzo, 1995; Trejo–Vazquez, 2005; García, 2006). Several studies have established conservation strategies for the Mexican herpetofauna at both national and regional levels based on the distributional patterns of species richness, endemism and endangerment. In some cases ecological modelling has been used as a tool to determine such patterns (e.g. Flores–Villela, 1993b; Garcia, 2006; Ochoa–Ochoa & Flores–Villela, 2006). In the specific case of tropical dry forest in the Mexican Pacific lowlands and adjacent interior valleys, conservation strategies for the associated herpetofauna and other fauna have included the establishment of a net of protected areas. These incorporate new reserves with those already established, prioritizing areas that are unique in terms of species turn–over or habitat quality (Sonora and Sinaloa: García, 2006) and also those with high diversity (e.g. in Jalisco, Michoacán and Oaxaca).

Recently, beta diversity or species turnover has received attention as an important component of the diversity patterns of Mexican mammals, especially for terrestrial species (Rodriguez et al., 2003), birds (García–Trejo & Navarro, 2004), flowering plants (Trejo–Vazquez, 2005) and the herpetofauna in general (Flores–Villela et al., 2005). Analysis of the herpetofauna found no correlation between beta diversity and species richness or endemism, though this may have been influenced by an insufficient inventory effort and an incomplete database for the study area (Flores–Villela et al., 2005). Ecological modelling has been proposed as a tool to determine spatial patterns of diversity for those areas with inadequate inventory efforts due to time and financial constraints (e.g. Bojorquez–Tapia et al., 1995; Illoldi–Rangel et al., 2004; Sánchez–Cordero & Martínez–Meyer, 2000; Peterson et al., 2002; Midgley et al., 2003; Peterson & Kluza, 2003; Ortega–Huerta & Peterson, 2004; García, 2006; Ochoa–Ochoa & Flores–Villela, 2006).

This study presents the latitudinal distribution patterns of alpha, beta and gamma diversity of the herpetofauna in México's Pacific lowlands and adjacent interior valleys of México using ecological modelling. The correlation of potential patterns of different diversity scales among reptiles, amphibians and latitude was analysed. We used individual binary models of the herpetofauna species' potential distributions predicted by GARP (Generic Algorithm for Rule set Prediction – Stockwell & Peters, 1999) produced in a previous work in the same study area (García, 2006).

Material and methods

The study area encompasses the tropical lowlands of the Pacific coast and adjacent valleys of the Balsas Basin and Central Depression of Chiapas in Mexico. It contains seven tropical dry forest ecoregions (García, 2006): 1. Sonoran–Sinaloan transition subtropical dry forests; 2. Sinaloan dry forests; 3. Jalisco dry forests; 4. Balsas dry forests; 5. Southern Pacific dry forests; 6. Central American dry forests; and 7. Chiapas Depression dry forests (fig. 1). With a total estimated surface area of ~250,000 km^2, the study area has a latitudinal extension of ~16° with altitudes from 0 to 1,100 m above sea level. General information on the area's physical and biological characteristics can be found elsewhere (Bullock, 1986; Murphy & Lugo, 1986; Rzedowsky, 1990; Bullock et al., 1995; Trejo–Vazquez, 1999; Robichaux & Yetman, 2002; Trejo–Vazquez & Dirzo, 2000, 2002; Noguera et al., 2002; García, 2006). Tropical dry forest is the main vegetation type, though other natural ecosystems also occur, such as tropical semi–deciduous forest, mangroves, shrubs, or human–induced plant communities such as grasslands, cultivated fields, and urban areas. Mean annual temperatures and precipitation vary from 16 to 30°C and from 300 to 2,000 mm respectively, whereas the dry season lasts from six to 10 months a year.

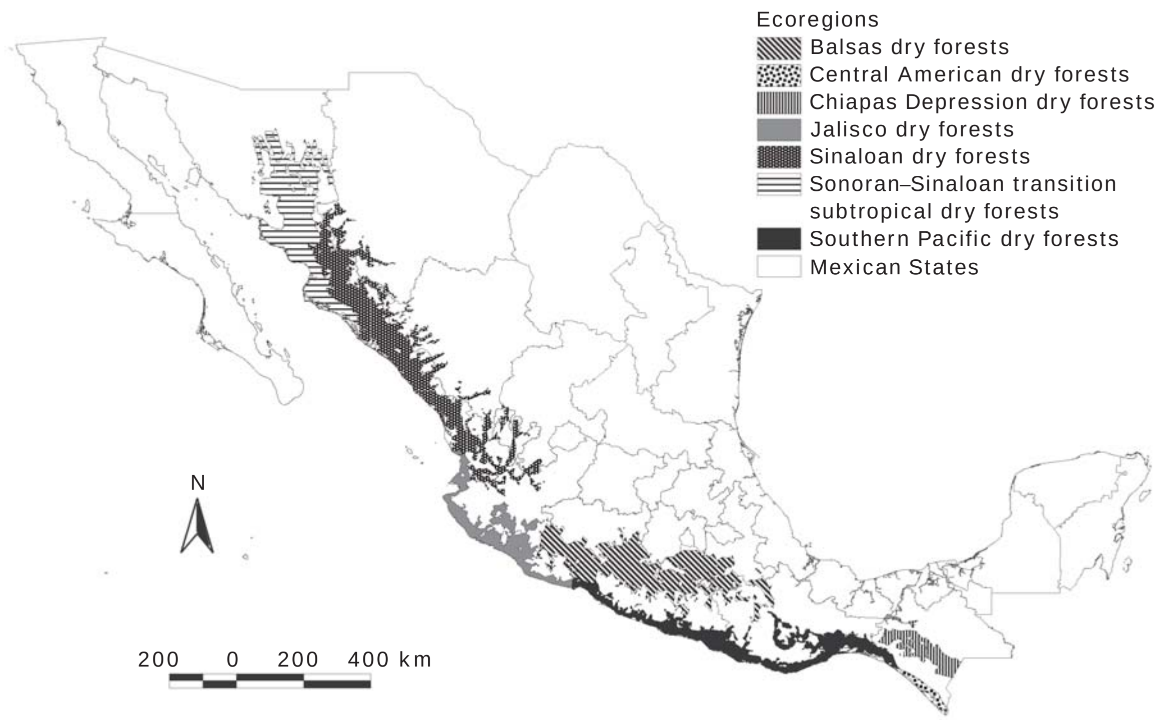

Fig. 1. Localisation of tropical dry forest ecoregions within the study area.

Fig. 1. Localización de las ecoregiones de selva tropical seca dentro del área de estudio.

A previous study reported 301 herptile species in the study area (63 amphibians and 238 reptiles; see Appendix I, in García, 2006). The authors used a data base that included 29,271 species locality records to produce 267 individual binary models of species potential distributions predicted by GARP using a grid covering the total surface of the study area, with 9932 quadrants of ~25 km^2 each (or 0.05 x 0.05 degrees pixel size). Details regarding how the database and GARP binary models were constructed can be consulted in García (2006). In this paper we used the same grid and binary models to determine species composition and richness for each quadrant in order to determine the latitudinal gradient of alpha, beta and gamma diversity for reptiles, amphibians and herpetofauna in the study area. For 34 herpetile species there was insufficient data to run a binary model of potential distribution. We therefore simply assigned their locality records into the corresponding quadrants (these species are identified in Appendix I, of García, 2006).

The analysis of latitudinal patterns at different scales of diversity is based on the shape and latitudinal extension of the study area (~15.025° to 30.075° degrees of latitude north). We arranged each of the 9,932 quadrants in 302 latitudinal bands of 0.05 degrees. We used a latitudinal approach to analyse these patterns due to the considerable latitudinal extension of the region, and its ecological and geological isolation (Ceballos, 1995), in view of which, the area has been considered a biogeographic unit in several studies (e.g. Escalante–Pliego et al., 1993; Fa & Morales, 1993; Flores Villela, 1993a, 1993b; Ceballos & García, 1995; Trejo–Vazquez, 1999; García, 2006). Alpha diversity was determined as the average number of species in each quadrant in a certain latitudinal band, whereas gamma diversity was measured as the total number of species in that band. Beta diversity in each latitudinal band was calculated as the coefficient between gamma and alpha diversity as suggested by Rodríguez et al. (2003) as follows:

$$\beta = S\gamma \;/\; S\alpha$$

where $S\gamma$ is the species number in each band, $S\alpha$ is average alpha in each band based on the values of alpha from those quadrants included within and β values could be from 1.0 (without species turn over) to $S\gamma$.

The relationship between alpha, beta and gamma with the latitudinal gradient of species richness was analyzed by Spearman correlations and linear regressions (Rodríguez et al., 2003).

Table 1. Spearman correlation coefficients for different types of diversity for reptiles, amphibians and herpetofauna with respect to latitude and quadrants. Bold numbers indicate statistical significance at $P < 0.05$: L. Latitude; Q. Quadrants.

Tabla 1. Coeficientes de correlación de Spearman para los diferentes tipos de diversidad de reptiles, anfibios y la herpetofauna con respecto a la latitud y los cuadrantes. Los números en negritas indican una significancia estadística de P < 0,05: L. Latitud; Q. Cuadrante..

			Reptiles			Amphibians			Herpetofauna		
	L	Q	Alpha	Beta	Gamma	Alpha	Beta	Gamma	Alpha	Beta	Gamma
L	1.00										
Q	–0.10	1.00									
Reptiles											
Alpha	**–0.86**	0.19	1.00								
Beta	0.04	**0.56**	–0.22	1.00							
Gamma	**–0.80**	0.40	**0.86**	0.17	1.00						
Amphibians											
Alpha	**–0.83**	0.07	**0.97**	–0.28	**0.82**	1.00					
Beta	–0.03	0.33	–0.14	**0.73**	0.18	–0.19	1.00				
Gamma	**–0.84**	0.30	**0.87**	0.11	**0.95**	**0.86**	0.21	1.00			
Herpetofauna											
Alpha	**–0.86**	0.17	1.00	–0.23	**0.86**	**0.98**	–0.14	**0.88**	1.00		
Beta	0.06	**0.50**	–0.24	**0.97**	0.14	–0.30	**0.87**	0.10	–0.25	1.00	
Gamma	**–0.82**	0.35	**0.87**	0.14	**0.99**	**0.85**	0.20	**0.98**	**0.88**	0.12	1.00

Results

Alpha and gamma diversity in reptiles, amphibians and herpetofauna have a statistically significant and negative inverse relationship with latitude, whereas beta diversity showed no correlation with latitude in any case (table 1). The correlation coefficients of alpha and latitude were slightly higher than those of gamma and latitude, except for amphibians. Neither alpha nor gamma diversity latitudinal gradients were statistically affected by the number of quadrants or the total surface area within each latitudinal band in any taxonomic group. As suggested by the statistically significant correlation coefficients, however, the number of quadrants had an apparent effect on the latitudinal distribution of beta diversity in both reptiles and herpetofauna.

There were several positive, statistically significant correlations of the different scales of diversity among taxonomic groups, as shown by the cross–group analysis (table 1). Beta diversity in each taxonomic group was statistically significant and correlated positively with the beta diversity of the two other groups. Both alpha and gamma diversity of amphibians were correlated with reptile and herpetofauna alpha and gamma diversity. Herpetofauna gamma diversity was correlated with reptile alpha and gamma diversity, and herpetofauna alpha diversity was correlated with reptile gamma diversity (table 1).

The latitudinal gradient of different scales of diversity in reptiles, amphibians and herpetofauna followed a similar trend (fig. 2). Alpha and gamma diversity tended to decrease with latitude, whereas beta diversity tended to increase towards higher latitudes (about 28°), especially in amphibians.

Fig. 2. Latitudinal gradient of reptile (A), amphibian (B) and herpetofauna (C) alpha, beta and gamma diversity.

Fig. 2. Gradiente latitudinal de la diversidad alfa, beta y gama en reptiles (A), anfibios (B) y herpetofauna (C).

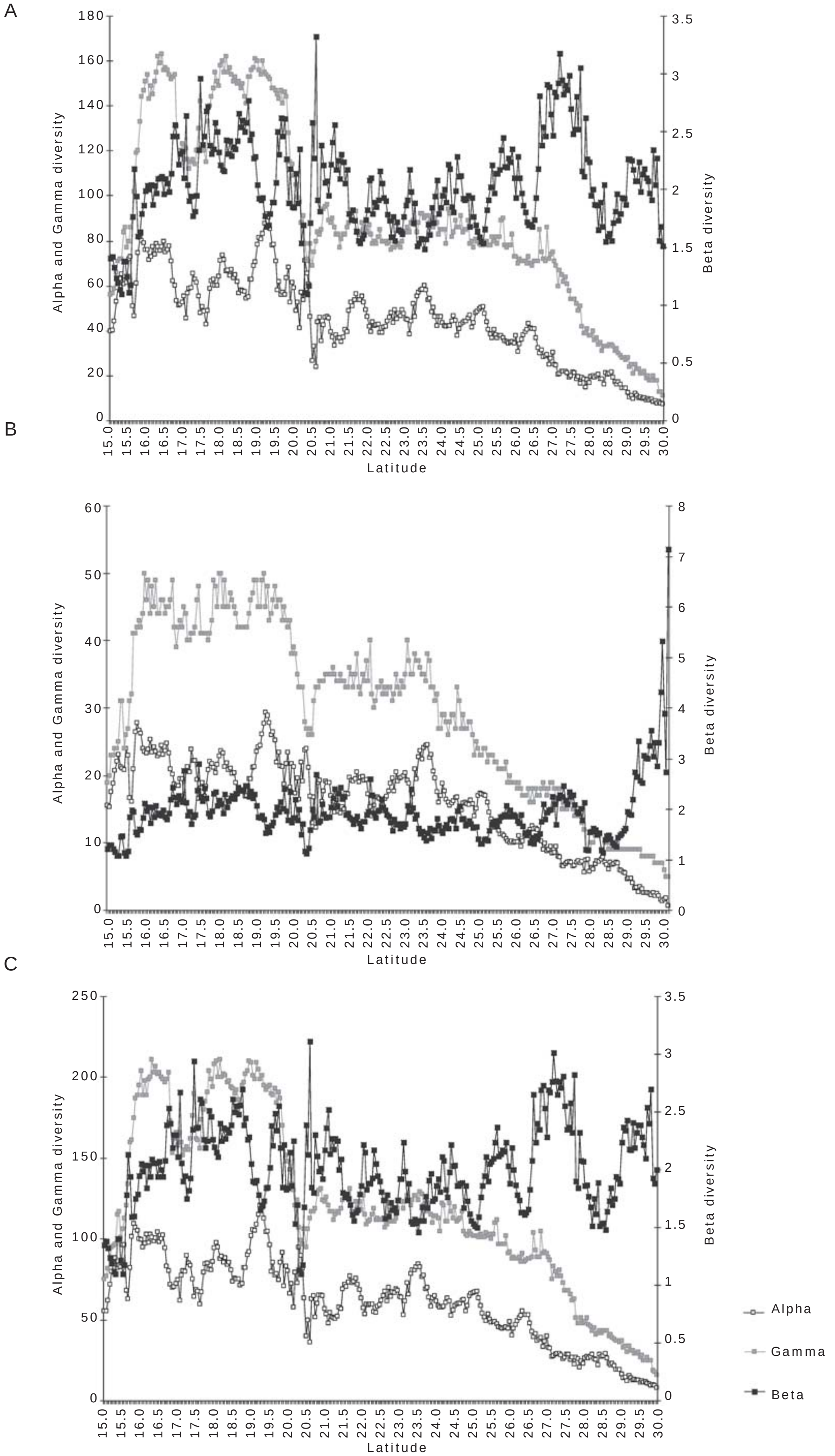
A
Alpha and Gamma diversity
Beta diversity
Latitude
B
Alpha and Gamma diversity
Beta diversity
Latitude
C
Alpha and Gamma diversity
Beta diversity
Latitude
Alpha
Gamma
Beta

Table 2. Results of the linear regression of alpha and gamma diversity with latitude in the three groups. All results were statistically significant (P < 0.001), except for beta diversity.

Tabla 2. Resultados de la regresión linear de la diversidad alfa, beta y gama con la latitud en los tres grupos. Todos los resultados, con excepción de la diversidad beta, fueron estadísticamente significativos (P < 0,001).

	Reptiles			Amphibians			Herpetofauna		
	Alpha	Beta	Gamma	Alpha	Beta	Gamma	Alpha	Beta	Gamma
R–Sq(adj)	72.6	0.08	65.7	73.1	2.9	73.5	73.8	1.1	69.3
F	797.54	2.33	577.02	817.12	8.84	836.24	848	3.29	679.23

According to the regression analysis, both alpha and gamma diversity were influenced by latitude in all groups while beta diversity showed no statistically significant response to latitude (table 2). Both in reptiles and herpetofauna latitude had a slightly greater effect on alpha diversity (72.6% and 73.8% respectively) than on gamma diversity (65.7% and 69.3% respectively). In comparison, in amphibians latitude had a greater effect on gamma diversity than on alpha diversity, although this was less marked. There was practically no response of beta diversity to latitude.

Discussion

Our results show that latitudinal patterns of alpha, beta and gamma diversity of reptiles and amphibians in particular, and the herpetofauna in general, followed similar trends at a national level to those observed in other studies for these groups (Flores–Villela et al., 2005), and for terrestrial mammals (Rodríguez et al., 2003). Alpha and gamma diversity are correlated and both decreased with latitude, whereas beta diversity fluctuates across the latitudinal bands but with no clear latitudinal gradient. A recent analysis of the biogeographic patterns of avian species richness and endemism from western Mexico also reported a lack of latitudinal trend of beta diversity (García–Trejo & Navarro, 2004). The present study found a fluctuating pattern in beta diversity, corresponding to that found for other studies for mammals and the herpetofauna in Mexico (Rodríguez et al., 2003; Flores–Villela et al., 2005), as well as studies reporting a lack of simple gradients in beta diversity (Koleff et al., 2003).

It may be more complex than expected to establish a spatial pattern of beta diversity (e.g. Koleff et al., 2003; Rodríguez et al., 2003), but its influence as an important component of gamma diversity and Mexican biodiversity is well accepted (Rodríguez et al., 2003; García–Trejo & Navarro, 2004; Flores–Villela et al., 2005). The high latitudinal fluctuation of beta diversity across the study area could be explained by the high number of reptile and amphibian species, endemic and microendemic (Flores–Villela & Goyenechea, 2003; García, 2006; Ochoa–Ochoa & Flores–Villela, 2006), which result in a constant species turn–over throughout the region, especially at higher latitudes (central coastal Sonora for amphibians). There are two peaks of beta diversity for reptiles and herpetofauna, one in western Jalisco near the border with Nayarit (latitude 20.5) and the other in southern Sonora (between 27.0 and 28.0). The occurrence of these two peaks may be due to the poor knowledge of the herpetofauna in these states. A similar trend was found for other northern states, such as Durango that has no published herpetofauna (Flores–Villela et al., 2005; Flores–Villela & Pérez–Mendoza, 2006).

The inverse relationship of gamma diversity (species richness at each latitudinal band) with latitude found in this study is not surprising since the latitudinal decrease of species richness has been reported in a wide variety of organisms (e.g. Fischer, 1960; Simpson, 1964; Schall & Pianka, 1978; Macpherson & Duarte, 1994; Davidowitz & Rosenzweig, 1998; Kaufman & Willing, 1998; Lyons & Willing, 1999), as in the particular case of Mexican mammals (Ceballos, 1995; Rodríguez et al., 2003; Vázquez & Gaston 2004) and the herpetofauna (Flores–Villela et al., 2005). The latitudinal gradient of gamma diversity estimated in this study showed a similar trend to that recorded in a previous study in the same area. The mentioned study, however, used latitudinal bands of a larger scale (one degree versus 0.05 degree in this study) and only species locality records were considered (García, 2003).

Alpha diversity was an important component of gamma diversity in all analyzed taxonomic groups (reptiles, amphibians, and herpetofauna) in this study, indicating that a latitudinal increase in gamma diversity could be the result of a similar increment in alpha diversity, as has been suggested for Mexican mammals (Rodríguez et al., 2003). The important relationship between alpha and gamma diversity in amphibians and reptiles could also be explained by the high proportion of endemic species in the study area (Flores–Villela, 1993a, 1993b;

Flores–Villela & Goyenechea, 2003; García, 2006) and by the high correlations of the distribution patterns of richness and endemism of the herpetofauna in this region in particular (Flores–Villela & Goyenechea, 2003; García, 2006) and in Mexico in general (Flores–Villela, 1993b; Ochoa–Ochoa & Flores–Villela, 2006).

As we have shown, tropical dry forest is an important ecosystem with high alpha, beta and gamma diversity, and it is also one of the areas of Mexico with a rich herpetofauna as well as high endemism (Flores–Villela, 1993a, 1993b; Flores–Villela & Goyenechea, 2003; García, 2006). Nevertheless, this ecosystem once occupied 14% of the vegetation in the country, while today it is at high risk of disappearance, since only 28% of the original forest remains intact today (Trejo–Vazquez, 2005). It has been suggested that the rate of deforestation of this vegetation type is comparable to that of the tropical rain forest; which in the Los Tuxtlas region is 4.2% (Dirzo & García, 1992). Official statistics from the Mexican government estimate the annual deforestation rate for tropical vegetation at 1.58% (Flores–Martínez, 2002). Recent information for the high Balsas Basin states the annual rate of deforestation at 1.3% (Trejo–Vazquez & Drizo, 2000), indicating the high rates of transformation of tropical dry forest in Mexico. Another factor that worsens the situation is that few areas in this ecosystem are protected. Other published data report the disappearance of this vegetation type in some parts of Mexico such as the Central Depression of Chiapas (Trejo–Vazquez, 2005).

Some of the regions where high rates of beta diversity were determined have no protected areas, and in others they are relatively few. Large extensions of territory with relatively high beta diversity with no protected areas include the coastal areas of the states of Nayarit, Colima, Michoacán, as well as large portions of Sinaloa, Guerrero and Oaxaca. In Sonora where two areas of high beta diversity were determined there is only one protected area (Garcia, 2006). The only state where a high representation of tropical dry forest is in protected areas is Chiapas which has two biosphere reserves (La Seputura and La Encrucijada). We have no direct information on how the deforestation rate of tropical dry forest has affected the herpetofauna inhabiting this ecosystem. A recent study in the southern coast of Michoacán comparing species richness in tropical dry forests with adjacent natural and human–induced vegetation types have shown the negative effects of deforestation and habitat transformation in tropical dry forest herpetofauna (Vargas–Santa María & Flores–Villela, 2006). Such study reports that introduced grasslands have the lowest number of amphibian and reptile species in the area (6 spp.), tropical semideciduous forest has 11 species, followed by croplands and orchards with 29 species, and tropical dry forest with 36 species. Trejo–Vazquez (2005) pointed out that only half of all tropical dry forests in Mexico maintain their original arboreal structure whereas herbs and bushes are the dominant life plant forms in the others. It is likely that such transformation of the vegetation structure of these ecosystems would affect the conservation of associated herpetofauna.

In conclusion, latitudinal patterns of alpha and gamma diversity of the herpetofauna from the Pacific lowlands and adjacent interior valleys of Mexico are strongly correlated probably due to a high proportion of both endemic species to Mexico and species geographically restricted to the study area. Beta diversity is an important component of the herpetofauna distribution patterns as a continuous source of species diversity throughout the region. Tropical dry forest in Mexico faces enormous conservation problems despite being one of the richest ecosystems. The main threat appears to be deforestation and there is little information available on the impact of this process on the herpetofauna.

Studies on the effects of deforestation and habitat fragmentation at different temporal and spatial scales should be promoted 1) to determine patch size and connectivity of remaining intact and disturbed tropical dry forest throughout the study area, in relation to hotspots of herpetofauna diversity and endemism and protected areas; and 2) to measure the responses of the reptile and amphibian community structure to perturbation of tropical dry forest.

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