Spatial scale and β-diversity of terrestrial vertebrates in Mexico

Escalas espaciales y diversidad beta de los vertebrados terrestres en México

Leticia M. Ochoa-Ochoa[1], Mariana Munguía[2], Andrés Lira-Noriega[3], Víctor Sánchez-Cordero[4], Oscar Flores-Villela[1], Adolfo Navarro-Sigüenza[1] and Pilar Rodríguez[2]✉

[1]*Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México. Apartado postal 70-399, 04510 México, D. F., Mexico.*
[2]*Comisión Nacional para el Conocimiento and Uso de la Biodiversidad. Av. Liga Periférico -Insurgentes Sur, Núm. 4903, Col. Parques del Pedregal, Delegación Tlalpan, 14010 México, D. F., Mexico.*
[3]*Department of Ecology and Evolutionary Biology. The University of Kansas. Lawrence, Kansas 66045.*
[4]*Instituto de Biología, Universidad Nacional Autónoma de México, Circuito Exterior s/n, Ciudad Universitaria, 04510 México, D. F., Mexico.*
✉ *pilar.rodriguez@conabio.gob.mx*

Abstract. Patterns of diversity are scale dependent and beta-diversity is not the exception. Mexico is megadiverse due to its high beta diversity, but little is known if it is scale-dependent and/or taxonomic-dependent. We explored these questions based on the self-similarity hypothesis of beta-diversity across spatial scales. Using geographic distribution ranges of 2 513 species, we compared the beta-diversity patterns of 4 groups of terrestrial vertebrates, across 7 spatial scales (from ~10 km^2 to 160 000 km^2), within 5 different (historically and environmentally) regions in Mexico: Northwest, Northeast, Centre, Southeast and the Yucatán Peninsula. We found that beta-diversity: *1)* was not self-similar along the range of scales, being larger than expected according to the null model at coarse scale, and lower, but not significantly different, to expected at intermediate and fine scales; *2)* varied across spatial scales, depending on the taxonomic group and on the region; *3)* was higher at coarser scales; *4)* was highest in the Centre and Southeast regions, and lowest in the Yucatán Peninsula, and *5)* was higher for amphibians and reptiles than mammals and birds. As a consequence, beta-diversity of each group contributes differentially to the megadiversity of Mexico, likely due to a variation in the biogeographical histories and the perception of each group to environmental heterogeneity. These results show the importance of identify the appropriate geographical scale for biodiversity conservation analyses, such as for example, the analysis of complementarity.

Key words: amphibians, self-similarity, birds, spatial scales, extent, grain, mammals, reptiles.

Resumen. Los patrones de diversidad son dependientes de la escala y la diversidad beta no es la excepción. Se ha propuesto que México es megadiverso por su alta diversidad beta, aunque existe poca información sobre si dicha diversidad es dependiente de la escala espacial, regiones geográficas y/o diferentes grupos taxonómicos. Aquí abordamos estas preguntas de manera cuantitativa, con base en la hipótesis de auto-similitud en el escalamiento de la diversidad. Utilizando áreas de distribución de 2 513 especies de vertebrados terrestres mexicanos, comparamos los patrones de diversidad beta de los 4 grupos taxonómicos, a lo largo de 7 escalas espaciales (de ~10 km^2 a 160 000 km^2) y en 5 regiones con diferentes características históricas y ambientales (Noroeste, Noreste, Centro, Sur y la Península de Yucatán). Se observó que la diversidad beta: *1)* no resultó auto-similar en el intervalo de escalas analizado, siendo, a escalas gruesas, mayor a lo esperado de acuerdo con el modelo nulo, y a escalas finas e intermedias menor aunque no significativamente diferente a lo esperado; *2)* varió a diferentes escalas espaciales según el grupo taxonómico y región; *3)* fue mayor a escalas geográficas gruesas; *4)* fue mayor en las regiones del centro y sureste y menor en la península de Yucatán, y *5)* fue mayor en anfibios y reptiles que en mamíferos y aves. En consecuencia, la diversidad beta de cada grupo taxonómico contribuye de manera distinta a la megadiversidad de México, probablemente debido a las diferencias en la historia biogeográfica y en la percepción de la heterogeneidad ambiental de cada grupo taxonómico. Los resultados muestran la importancia de la detección de la escala apropiada para optimizar análisis para la conservación de la biodiversidad, como es el caso del análisis de complementariedad.

Palabras clave: anfibios, auto-similitud, aves, escalas espaciales, extensión, grano, mamíferos, reptiles.

Introduction

Patterns of diversity and distribution of species are scale dependent (Whittaker et al., 2001; Willis and Whittaker, 2002; Rahbek, 2005), implying that form and properties of those patterns will change correspondingly to spatial scale. Beta diversity, the component of diversity that quantifies changes in species composition, is correlated with environmental heterogeneity, which is ultimately related to spatial scale. As geographical area increases, it is likely that additional habitat types and/or different geographic features are included (Rosenzweig, 1995), thus, beta diversity should be scale-dependent (Koleff et al., 2003; Tuomisto, 2010; Barton et al., 2013).

In addition to its sensitiveness to spatial scale, beta diversity is *per se* a scaling factor that relates 2 or more 'inventories' of species (Shmida and Wilson, 1985). Beta diversity detects the contribution of the diversity at finer spatial scales (alpha diversity) to coarse scales (gamma diversity). For example, in a region of high gamma diversity where alpha diversity is significantly low, beta diversity should be necessarily high in order to 'compensate' the low alpha diversity. Conversely, if alpha diversity is high, beta diversity has to be low.

Investigating patterns and processes explaining beta diversity across spatial scales is crucial for understanding structure and maintenance of biodiversity (Harte et al., 2005). Moreover, detailed information on how beta diversity is correlated with spatial scale improves the estimation of extinction rates due to habitat loss (e. g., Tanentzap et al., 2012), land protection policies for designing efficient and accurate monitoring strategies, and the understanding of the structural mechanisms of ecological diversity (Harte et al., 2005; Drakare et al., 2006; Barton et al., 2013).

There are different approaches to study beta diversity as a scaling factor of diversity. One of the most common approaches is centered in the use of the additive model relating alpha and gamma diversity (Loreau, 2000; Crist and Veech, 2006; Jost, 2007; Jost et al., 2010); that is $\gamma = \beta + \alpha_{mean}$, where γ is gamma diversity, the total number of species of the region and α_{mean} is alpha diversity, the average species number of the sites that conform the region. This approach allows the use of the same units (number of species) for alpha, beta and gamma diversity. However, results depend on the species richness of the system, thus comparisons among different systems are not straightforward. This disadvantage can be overcome by using the multiplicative formula, defined as the ratio between the gamma diversity to the mean of alpha diversity, $\beta_W = \gamma \alpha_{mean}^{-1}$ (Whittaker, 1960, 1972). Another alternative is to use the species-area relationship $S = cA^z$ (SAR, Crawley and Harral, 2001; Lennon et al., 2002; Šizling

and Storch, 2004), where S is the number of species, c is the intercept, A is the area of the sampled units, and z is the slope, that is, the rate at which new species accumulates as area increases. In its power function form (plotting the log values of species number and the log values of the area), the SAR produces straight lines. The slope z of the lines is related to beta diversity: a steeper slope corresponds to a faster accumulation of species, indicating higher beta diversity (Rosenzweig, 1995). This approach also allows a direct comparison between systems of different richness (Crawley and Harral, 2001). Arita and Rodríguez (2002) proposed a method that integrates the equations that relate alpha and gamma diversity in a multiplicative way, and the SAR. This method has the additional advantage of providing an explicit null hypothesis of self-similarity, that is, 'if the species area relationship is a power function, then beta diversity most be scale invariant' (Arita and Rodríguez, 2002; Harte et al., 1999).

Up to date no clear patterns regarding the self-similarity of beta diversity have emerged. Whereas some studies report that beta diversity is self-similar (e. g., Noguez et al., 2005), other studies found that beta diversity differs from self-similarity, at least in some ranges of the scales (Crawley and Harral, 2001; Arita and Rodríguez, 2002; Ulrich and Buszko, 2003; McGlinn et al., 2012; Jones et al., 2011). Clearly, more studies are needed for elucidating the spatial scaling of beta diversity and its conservation implications (Evans et al., 2005).

Mexico is one of the megadiverse countries in the world; however, unlike other megadiverse countries, its high biological diversity does not depend on high values of alpha diversity, but rather is explained by exceptionally high beta diversity (Arita and Rodríguez, 2002). Indeed, the empirical evidence for Mexican vertebrates shows consistent high beta diversity regardless of the spatial scale. Studies ranging from landscape scale (~1 to 10 km^2) (Moreno and Halffter, 2001) to coarse scales (~2 500 to 160 000 km^2), report high beta diversity for mammals (Arita and Rodríguez, 2002; Rodríguez and Arita, 2004; Koleff et al., 2008). Similar studies at coarse spatial scale for reptiles and amphibians (~2 500 km^2) (Flores-Villela et al., 2005; Koleff et al., 2008) and birds (Lira-Noriega et al., 2007; Koleff et al., 2008), have also found high beta diversity.

Nonetheless, on one side, the variety of methods applied to measure beta diversity, and the high variation in the scale of analyses in both elements of scale, extent and grain (*sensu* Barton et al., 2013), difficult comparisons between studies. Thus, there is a need to systematically explore the scaling patterns of beta diversity, in order to elucidate whether the hypothesis that Mexico is particularly high beta diverse is sustained at different spatial scales.

On the other side, it is well documented that the capacity of dispersion of the species is related to beta diversity (Baselga et al., 2012). Some studies have demonstrated the relatively low beta diversity of birds, the group of the highest dispersion capacity among vertebrates (Buckley and Jetz, 2008). Conversely, for amphibians and reptiles, in the groups with lower dispersal capacity, the studies report the highest beta diversity (e. g., Qian, 2009; Dobrovolski et al., 2012). This tendency was clearly documented for the vertebrates of Mexico at the country level (scale of $2\ 500\ km^2$): amphibians and reptiles have the highest beta diversity, followed by mammals, while birds have the lowest beta diversity (Koleff et al., 2008). Recently, Calderón-Patrón et al. (2013) found that in the Isthmus of Tehuantepec, southern Mexico, at fine and intermediate scales (cells of 10 x 10 km and 20 x 20 km respectively), birds have higher dissimilarities that amphibians, contrarily to the idea that vagility and beta diversity are negatively related. These new findings reinforce the necessity to investigate the effect of the scale in the beta diversity patterns of different taxonomic groups, and to find out whether the tendency found at the scale of $2\ 500\ km^2$ (Koleff et al., 2008) is sustained at other spatial scales.

Herein, we explore systematically and quantitatively the scaling patterns of beta diversity for Mexican terrestrial vertebrates. Specifically, *1)* we test the hypothesis of self-similarity in beta diversity; *2)* identify the spatial scale or scales where beta diversity is higher or lower than the expected self-similar value; *3)* explore whether the pattern is maintained in different geographic regions, and *4)* identify general patterns of beta diversity between taxonomic groups.

Materials and methods

Databases. We used 3 comprehensive databases of distribution maps based on Environmental Niche Models (ENM) of 2 513 terrestrial vertebrates distributed in Mexico. Data were compiled from different sources, including: 883 resident land birds (Navarro-Sigüenza et al., 2003; Navarro-Sigüenza and Peterson, 2007), 344 mammals (Ceballos et al., 2002), 364 amphibians, and 811 reptiles (Ochoa-Ochoa et al., 2006). The distribution models ranged between 70 and 97% of the total species of each group of terrestrial vertebrates occurring in Mexico. These models have been considered robust and an adequate approximation to the Mexican distribution range for terrestrial vertebrates, and have been used for biogeography and conservation studies (e. g., Sánchez-Cordero et al., 2005; Lira-Noriega et al., 2007; Pronatura-Mexico and The Nature Conservancy, 2007; Conabio-Conanp-TNC-Pronatura-FCF, UANL, 2007; Munguía et

al., 2008; Koleff et al., 2008; Ochoa-Ochoa et al., 2014; Villalobos et al., 2013).

Regions. We selected 5 regions representing contrasting environmental conditions in Mexico: Northwest (NW), Northeast (NE), Centre (C), Southeast (SE) and the Yucatán Peninsula (P) (Fig. 1). Two of those regions were placed within the Nearctic realm, 2 were located in the Neotropic realm, and 1 was positioned in the Trans-Mexican Volcanic Belt. The extent of each region was 160 000 km^2 (400 x 400 km side). A brief description of the each region can be found in Table 1.

Scales. We fixed the 'extent' of our study (squares of 160 000 km^2) and varied the 'grain' (*sensu* Barton et al., 2013) as follows. Seven spatial scales were obtained by dividing the regions in successively smaller squares following the method proposed by Arita and Rodríguez (2002). Overall, it is a nested design, where the unit of study is a square, and the scales are subdivisions of the square that are progressively smaller. Following this procedure, we started with a 400 x 400 km square, the coarsest region (A_1); then, we subdivided it in 4 squares, 200 x 200 km (A_2). The next scale was constructed by subdividing each 200 x 200 km squares in 4 squares, 100 x 100 km, obtaining 16 squares of 100 x 100 km (A_3). We repeated the procedure in the next 5 scales. The finest spatial scale corresponds to 16 384 squares of 3.12 x 3.12 km (A_8). We subdivided the initial square 7 times, then, the scales ranged from around 160 000 km^2 to around 10 km^2 (Fig. 2).

Presence-absence matrices (PAM). We constructed presence-absence matrices (PAM) by intersecting all distributional maps with the set of grids in ArcView 3.2 (ESRI, 1999), and run all analyses in geographic coordinates. The intersected databases were exported to
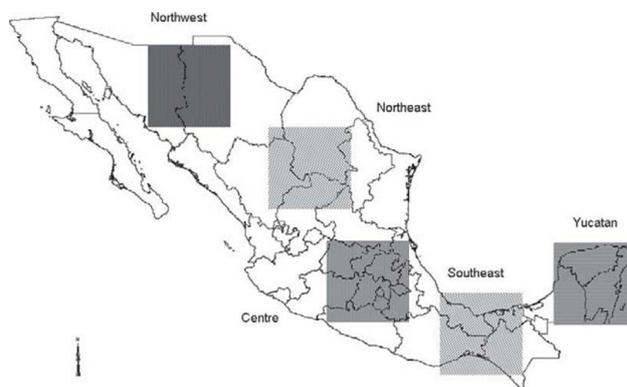
Figure 1. Location of the 5 regions of Mexico analyzed in this study: Northwest (NW), Northeast (NE), Centre (C), Southeast (SE), and Yucatán Peninsula (P).

Table 1. Brief description of each region selected for the analyses of scaling beta diversity

Region	States included	Major topographic formations	Vegetation types (in order of amount of area)
Northwest (NW)	Sonora and Chihuahua	Sierra Madre Occidental	Coniferous forests, prairies, tropical dry forest, xerophytic vegetation and thorny shrubs
Northeast (NE)	Chihuahua, Coahuila, Nuevo León, Durango, Zacatecas and San Luis Potosí	Altiplano Central and Sierra Madre Oriental	*Pinus-Quercus* forests, prairies, tropical dry forest, and xerophytic vegetation
Centre (C)	Guanajuato, Querétaro, San Luis Potosí, Estado de México, Distrito Federal, Morelos, Cuernavaca, Puebla, Veracruz, Michoacán, Guerrero	Trans-Mexican Volcanic Belt	*Pinus-Quercus* forests, prairies, tropical dry forest, thorny shrubs, xerophytic vegetation, cloud montane forest, tropical rain (evergreen) and deciduous forests, aquatic and sub-aquatic vegetation
Southeast (SE)	Oaxaca, Veracruz, Chiapas, Tabasco and part of Campeche	Tehuantepec Isthmus, Sierra Madre del Sur, Sierra Norte de Oaxaca	*Quercus* forests, prairies, thorny shrubs, cloud montane forest, tropical rain (evergreen) and deciduous forests, aquatic and sub-aquatic vegetation
Yucatán Peninsula (P)	Campeche, Yucatán and Quintana Roo		Shrubs, tropical rain (evergreen) and deciduous forests, aquatic and sub-aquatic vegetation

Access, performing a crosstab query to create each PAM. All steps were done for each taxonomic group and region at each spatial scale. Using PAM, we calculated the total species number for the coarsest scale (200 x 200 km) and the average species number for the 7 subsequent spatial scales.

The beta diversity model. We followed a method proposed by Arita and Rodríguez (2002), consisting in constructing 'species-scale plots'. Details of the analytical procedure area presented elsewhere (Arita and Rodríguez, 2002), but briefly, the data required to construct the plots is the average species number (S_i) at each scale, except the first point (A1) that corresponds to the total species number of the region (gamma diversity; S_0). Beta diversity is the slope resulting from connecting 2 adjacent points in the plot; consequently we obtained values of beta diversity for 7 spatial scales (1-2, 2-3, 3-4, 4-5, 5-6, 6-7, and 7-8). Measured in this way, and in agreement with the system of fully nested squares, beta diversity ranges from 1 (when $S_i = S_{i-1}$) to 4 units (when each of the nested regions has a completely different set of species).

The model predicts that if the slope of the line connecting 2 adjacent points of the graph is constant along all the scales, beta diversity is self-similar (Arita and Rodríguez, 2002). In order to evaluate if the observed values of beta diversity differ significantly or not from the expected beta diversity, we calculated an expected value simply by dividing the total species number of the region, by the average species number at the finest scale, and dividing that value by 4 ($\beta = (S_0/S_8)/4$) (Arita and Rodríguez, 2002, p. 544). We generated the expected beta diversity for each taxonomic group, for the 5 regions.

We tested if there were significant differences between the observed and expected values of beta diversity using Chi-square tests. Due to the non-independence of beta diversities among spatial scales, the comparisons were performed at each spatial scale separately. The first test included all regions and all the taxa in order to obtain a general trend of beta diversity across scales. After that, in order to evaluate if each taxonomic groups followed that general trend among regions, we performed the test separately for each region. We do not include these results due the small sample size (N= 4), which can lead to inaccuracy in the tests.

For a straightforward interpretation of the results, we plotted the observed beta diversity directly in 'beta diversity-scale plots'. In this plot, if beta diversity is self-similar, we would observe a parallel line to the X-axis.

Results

Overall, beta diversity was not self-similar across the range of scales, and the patterns varied along the scales,
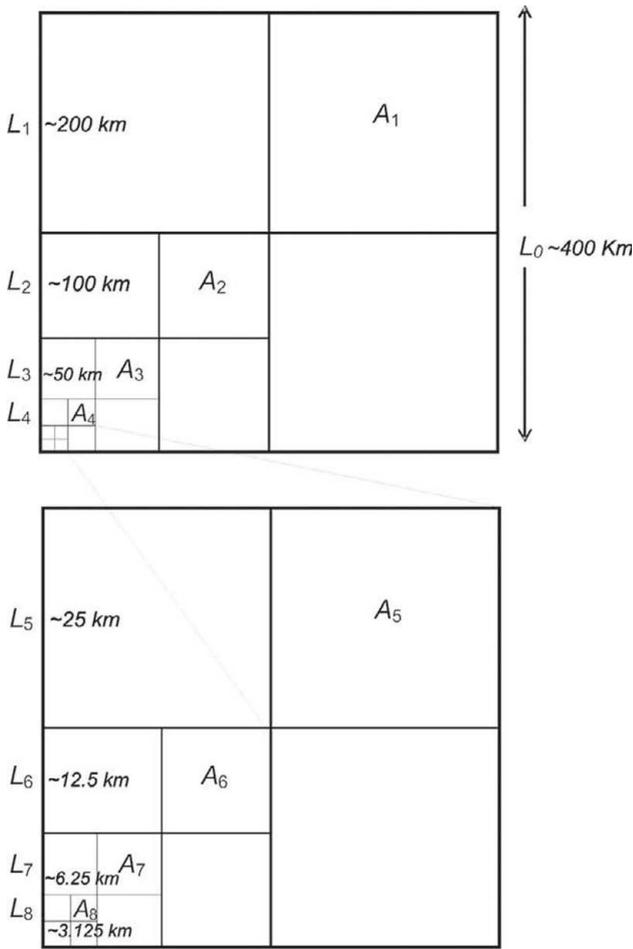
Figure 2. System of nested squares designed to analyze the scaling of species diversity proposed by Arita and Rodríguez (2002). A square-shaped region of side L_0 and area $A_0 = L_0{}^2$, is divided into 4 squares of side $L_1 = L_0/2$ and area $A_1 = L_1{}^2 = A_0/2^2$. By iterating the division i times, a series of increasingly smaller squares of side $L_i = L_0/2^i$ and area $A_i = L_i{}^2 = A_0/2^{2i}$ is obtained. The nested design for this study comprise a wide range of scales, as the region $A_0 = 400 \times 400$ km (~160 000 km^2) is divided 7 times: $A_1 = 200 \times 200$ km (~40 000 km^2), $A_2 = 100 \times 100$ km (~10 000 km^2), $A_3 = 50 \times 50$ km (~2 500 km^2), $A_4 = 25 \times 25$ km (~625 km^2), $A_5 = 12.5 \times 12.5$ km (~156.25 km^2), $A_6 = 6.25 \times 6.25$ km (~39.06 km^2), $A_7 = 3.12 \times 3.12$ km (~9.76 km^2) (for clarity, the progressively finer squares are illustrated only in the lower left corners of squares).

depending on the geographic region and the taxonomic group (Figs. 3, 4; Table 2).

Beta diversity was higher at the coarsest scales (1-2, 2-3) and tended to decrease as the scale became finer in all groups. At the finest scales (5-6, 6-7, 7-8), beta diversity was relatively low for all terrestrial vertebrates (Figs. 3, 4). For example, at the coarsest scales, beta diversity of
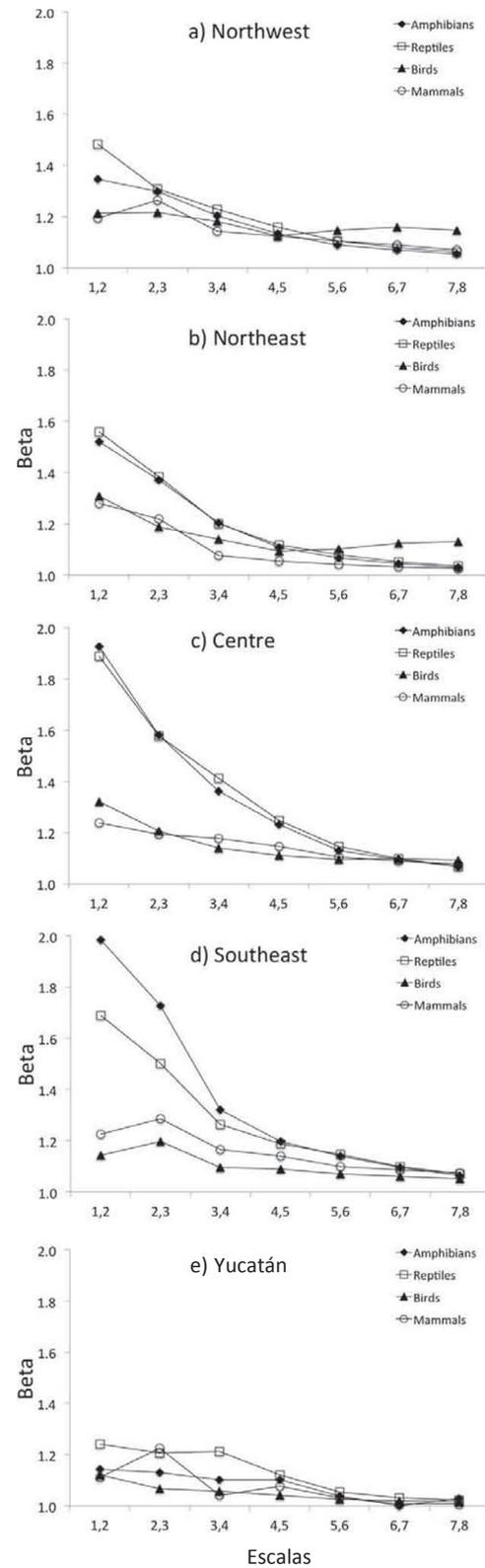
Figure 3. Beta diversity for the 5 regions: a) Northwest, b) Northeast, c) Centre, d) Southeast and e) Yucatán Peninsula.
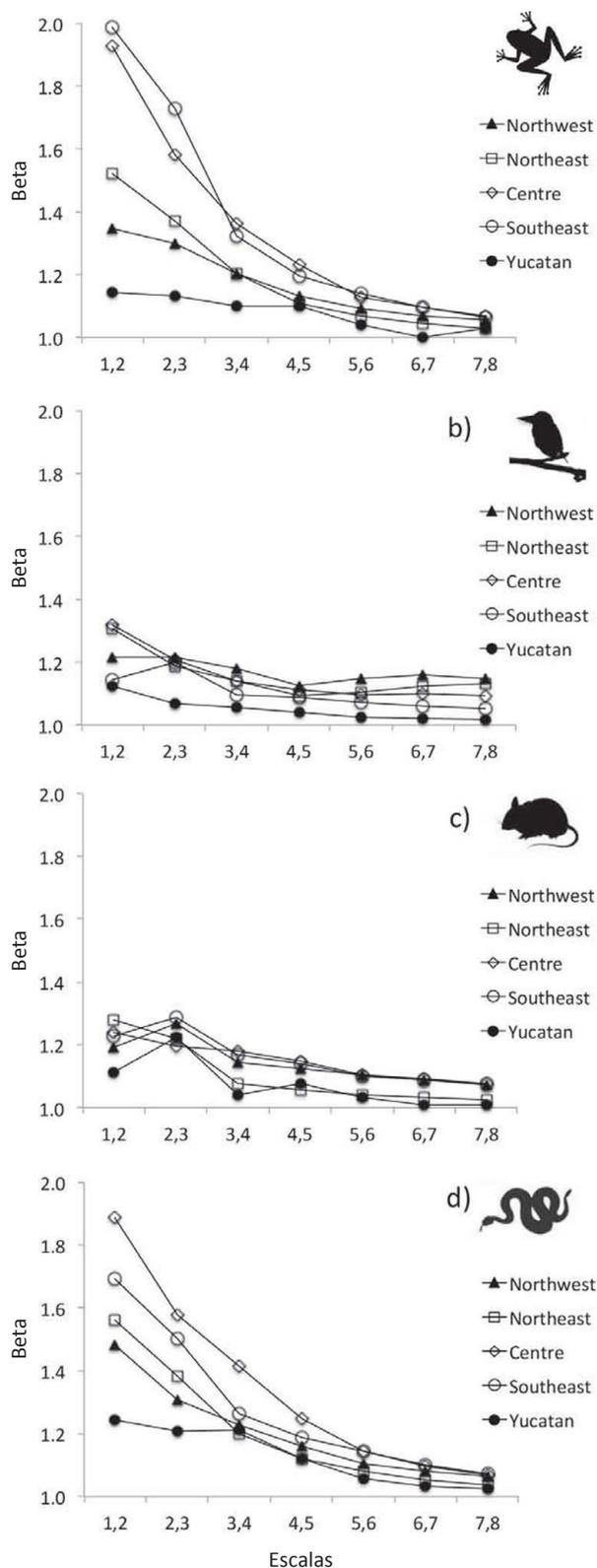
Figure 4. Beta diversity by taxonomic group: a) amphibians, b) birds, c) mammals, and d) reptiles.

amphibians in Centre region was around 2 units; for the second-largest scales was lower (1.6 units), and at the finest scale resulted much lower (1.2 units) (Fig. 3). Overall, we observed similar trends in all the regions even in the Yucatán Peninsula region, where beta diversity was low along all spatial scales, but even lower at the finer scales.

Some exceptions to this general tendency were found in NW and NE regions, where beta diversity of the scale 2-3 resulted higher than the scale 1-2 for birds and mammals; in NW, beta diversity increased in 5-6 and 6-7 scales, and in NE, beta diversity increased in 7-8 scale for birds. In SE and the Yucatán Peninsula, beta diversity was higher in scales 2-3 than in previous scales for mammals. In the Yucatán Peninsula, beta diversity increased in scales 7- 8 for amphibians compared to previous scales (Fig. 3).

The results of global Chi-square tests (performed for each individual scale and including all the regions and all the groups) showed that at coarser scale, beta diversity was significantly higher that the expected: 1-2 (7.73, df= 1, $p < 0.01$), and 2-3 (5.52, df=1, $p < 0.025$). In contrast, at finer spatial scales beta diversity resulted not significantly different than expected: and 3-4 (3.07, df=1, $p < 0.1$), 4-5 (2.18, df=1, $p < 0.9$), 5-6 (1.65, df=1, $p < 0.9$), 6-7 (1.41, df=1, $p < 0.9$) and 7-8 (1.28, df=1, $p < 0.9$), that is, it tended to be self-similar within this range of spatial scales (Table 2).

The results of individual regions Chi-square test, showed that observed beta diversity resulted higher than the expected null hypothesis in all individual cases of the NW, NW and Yucatán Peninsula. This is also the case of birds and mammals in the Centre and SE regions. In all the cases, for amphibians and reptiles the observed beta diversity resulted higher than the null hypothesis at coarser scales, but lower at finer scales (Table 2). Nonetheless, it is worth mentioning that although the values resulted higher than the null hypothesis, at lower scales the values were not significantly different according to the Chi-tests.

Reptiles and amphibians showed the highest beta diversity in most of the regions and scales, and resulted particularly notorious at coarser scales (Fig. 3). Some few exceptions were found, for example, birds showed higher beta diversity than reptiles and amphibians in NW region, in the scales 5-6, 6-7 and 7-8 in NW. When we compare the beta diversity between mammals and the birds, we obtain mixed results: mammals tended to show higher beta diversity than birds in the Centre region (at spatial scales 3-4, 4-5, 5-6, 6-7 and 7-8), and in SE and the Yucatán Peninsula region (scale 2-3) (Fig. 3).

Discussion

Self-similarity patterns of diversity have been associated to a single process driving the scaling of

Table 2. Values of beta diversity between scales. Beta diversity was calculated as the ratio of species diversity measured at adjacent scales resulting from the iterative procedure detailed in figure 2. For example 4, 5 is equal to $S_{4average}/S_{5average}$. Expected values of the self-similarity hypothesis were calculated as $(S_{1average}/S_{8average})/4$ according to Arita and Rodríguez (2002). The highest values per scale are shown in bold and *italics* indicate the cases in which beta diversity resulted higher than the previous spatial scale

	Amphibians	Birds	Mammals	Reptiles
Northwest				
Scale/Expected	0.74	0.75	0.63	0.88
1, 2	1.35	1.21	1.19	**1.48**
2, 3	1.30	*1.22*	*1.27*	**1.31**
3, 4	1.21	1.18	1.14	**1.23**
4, 5	1.13	1.13	1.13	**1.16**
5, 6	1.09	*1.15*	1.11	1.11
6, 7	1.07	*1.16*	1.09	1.08
7, 8	1.05	**1.15**	1.07	1.06
Northeast				
Scale/Expected	0.80	0.68	0.49	0.85
1, 2	1.52	1.31	1.28	**1.56**
2, 3	1.37	1.19	1.22	**1.38**
3, 4	**1.20**	1.14	1.08	**1.20**
4, 5	1.11	1.09	1.06	**1.12**
5, 6	1.07	**1.10**	1.04	1.08
6, 7	1.04	**1.12**	1.03	1.05
7, 8	1.03	*1.13*	1.03	1.04
Centre				
Scale/Expected	1.69	0.67	0.65	1.77
1, 2	**1.93**	1.32	1.24	1.89
2, 3	**1.58**	1.21	1.20	**1.58**
3, 4	1.36	1.14	1.18	**1.41**
4, 5	1.23	1.11	1.15	**1.25**
5, 6	1.13	1.10	1.10	**1.15**
6, 7	1.09	**1.10**	1.09	**1.10**
7, 8	1.07	**1.09**	1.08	1.07
Southeast				
Scale/Expected	1.81	0.49	0.68	1.29
1, 2	**1.99**	1.14	1.23	1.69
2, 3	**1.73**	1.20	*1.29*	1.50
3, 4	**1.32**	1.10	1.17	1.26
4, 5	**1.20**	1.09	1.14	1.19
5, 6	1.14	1.07	1.10	**1.15**
6, 7	1.10	1.06	1.09	**1.10**
7, 8	1.06	1.05	1.08	**1.07**
Yucatán				
Scale/Expected	0.42	0.35	0.40	0.57
1, 2	1.14	1.12	1.11	**1.24**
2, 3	1.13	1.07	*1.23*	**1.21**
3, 4	1.10	1.06	1.04	**1.21**
4, 5	1.10	1.04	1.08	**1.12**
5, 6	1.04	1.03	1.03	**1.06**
6, 7	1.00	1.02	1.01	**1.03**
7, 8	*1.03*	1.02	1.01	1.02

diversity. Conversely, a non-self-similar pattern implies more than one driving process in the scaling of diversity (Crawley and Harral, 2001; Drakare et al., 2006). Our results provides further solid evidence that beta diversity is scale dependent in all terrestrial vertebrates in Mexico; at coarser scales, beta diversity is high, but decreases as spatial scales decreases, consequently different processes that acts at different scales are explaining the beta diversity of Mexico.

Beta diversity is higher at coarse scales. High beta diversity at coarser spatial scales was observed for all groups of terrestrial vertebrates and was significantly different from the expected null hypothesis. Larger spatial scales of 2º grids (~40 000km^2) likely include different vegetation types, ecoregions, and unrelated biota assemblages with contrasting biogeographic histories (Crawley and Harral, 2001; Sánchez-Cordero et al., 2005; Drakare et al., 2006; Barton et al., 2013). Thus, the trend of high beta diversity at coarse spatial scales is likely a result of a complex interplay of habitat heterogeneity, contrasting types of vegetation and biogeographic histories as area increases (Crawley and Harral, 2001; Drakare et al., 2006; Barton et al., 2013). Exceptionally high values were found in the Centre and SE, both of these regions fall within the 'Mexican Transition Zone' defined by Halffter (1987), a highly complex area where the Neotropical and Nearctic realms overlap. This supports the previous argument of different biogeographic histories generating high values of beta diversity.

According to previous studies (Koleff et al., 2008), beta diversity of amphibians and reptiles tended to be significantly higher than for mammals and birds. In general, low dispersal capacity and the small distributional range of the species of these groups (Ochoa-Ochoa and Flores-Villela, 2006) explains the extraordinary high beta diversity, particularly at the coarse scale. Indeed, amphibians showed the highest beta diversity in the Centre and SE regions, being congruent with the fact that in those regions amphibians have the smallest range size. Conversely, reptiles showed the highest beta diversity in NW, NE and the Yucatán Peninsula, where they have restricted distributional range sizes, in congruence with the biogeographical history and the endemism pattern of reptiles in Mexico (Marshall and Liebherr, 2000; Ochoa-Ochoa and Flores-Villela, 2006; Ochoa-Ochoa et al., 2014).

Contrarily to the pattern reported in previous analyses (Koleff et al., 2008), birds showed higher beta diversity than mammals in all the regions, except in SE. We find these results counter-intuitive, but provide a preliminary explanation. It is possible that the distributional ranges of birds tend to be ecoregion-restricted (Vázquez et al., 2009), whereas mammals can occur in 1 or more ecoregion

included in the region. An alternative, but not mutually exclusive explanation, is that the relatively low beta diversity of the mammals is due to the effect of volant mammals which were not excluded from the analyses. Bats have significantly larger distributional range sizes compared to non-volant mammals (Arita, 1997). For example, it is well documented that rodents show restricted non-overlapped distributions along the western, central and eastern regions of the Transvolcanic Belt (e. g., Sánchez-Cordero et al., 2005; Escalante et al., 2007; Navarro-Sigüenza et al., 2007).

The highest beta diversity values for terrestrial vertebrates occurred in the SE region (amphibians), and Centre (birds, reptile and mammals). The SE region includes the southernmost part of the Sierra Madre Oriental, a region that holds a complex topography with highly diverse plant associations (Table 1), as for example the montane cloud forest. This type of forest contains the highest diversity of birds partly due to an exceptional number of endemism and ecologically restricted bird species in Mexico (Escalante-Pliego et al., 1998; Sánchez-González and Navarro-Sigüenza, 2009). This region has been also identified as a centre of endemism for amphibians and reptiles (Ochoa-Ochoa and Flores-Villela, 2006, 2011). The fact that amphibians always have higher beta diversity than birds, even though the former have lower gamma diversity (i. e., 148 species in SE) than the latter (433 species), does not support the idea that the higher the species richness, the higher beta diversity as reported in other studies (Gaston et al., 2007). The restricted range size of the species of amphibians that inhabit the SE region explains the extraordinary high beta diversity of this group. In other words, beta diversity is not directly associated to the species richness *per se* but to the size of the distribution areas.

The lowest beta diversity values at coarse spatial scales observed in the Yucatán Peninsula for all terrestrial vertebrates can be explained as the 'Yucatán Peninsula effect', that is the tendency of the species to have large range sizes. Indeed, in this region, the proportion of the distributional ranges between groups tend to be large (Vázquez-Domínguez and Arita, 2010; e. g., Cortés-Ramírez et al., 2012, for birds; Lee, 1980, for amphibians and reptiles; Arita and Vázquez-Domínguez, 2003, for mammals), likely as a consequence of the low environmental heterogeneity, similar vegetation types (Ibarra-Manríquez et al., 2002; White and Hood, 2004), topography and its relatively recent history (Ward et al., 1985). The species tend to occupy a high proportion of the Yucatán Peninsula, and as a consequence, beta diversity tends to be low, as previously reported for mammals (Arita and Rodríguez, 2002).

Beta diversity is lower at finer scales. Beta diversity was

low at finer spatial scales for all terrestrial vertebrates. Further, beta diversity was, in general, higher but not significantly different from the expected null hypothesis, that is, it tended to be self-similar but with higher values.

At these spatial scales, the pattern of beta diversity ranging: mammals> birds> reptiles> amphibians, does not hold in all the regions. Surprisingly, at finer spatial scales, birds showed the highest beta diversity values among terrestrial vertebrates in NE, NW, and the Centre. This unexpected trend can be explained as an artifact due to the fact that only resident birds were considered in the study. The distribution of the resident birds limits in both NE and Centre regions and, as a consequence, at finer spatial scales several sites do not contain species, mirroring in low mean alpha diversity and then in high beta diversity.

Our results suggest that at finer scales (beyond 2 500 km^2; 0.5º lat-long) beta diversity is more influenced by ecological than historical factors (Crawley and Harral, 2001; Barton et al., 2013). The ecological interactions and dynamics are probably more related to the complex topography of the country (Ferrusquia-Villafranca, 1993). Environmental heterogeneity allows different vegetation types to share a reduced geographical region; however, the effect of environmental heterogeneity depends on the taxa and the scale. For example, a landscape unit from the human perspective may be defined from 30 to 300 km^2 (Fischer and Lindenmayer, 2007), for an amphibian it is probably around 100 km^2 (Gardner et al., 2007), but for a beetle a landscape unit can be restricted to a few square meters (Wiens and Milne, 1989). Differences in the patterns of diversity between taxonomic groups could be associated with species' different spatial scale perceptions of environmental heterogeneity.

Other possible factors that explain beta diversity at fine scales come from the Species-Area relationship (SAR) topology. Recently, Triantis et al. (2012) showed that when the spatial range analyzed exceeds 3 orders of magnitude (as does this study ~10 km^2 to 160 000km^2), SAR are best represented by a sigmoid curve (Lomolino et al., 2010) with 3 main slopes with different values, equivalent to different values in beta diversity. Factors proposed to explain this pattern referred as "small-island effect" (Lomolino and Weiser, 2001), are resources availability, dispersal abilities, and degree/time of isolation. Some of these factors might contribute to the fact that the Centre and SE regions have a high proportion of endemic and range restricted species, increasing the possibility of recording high beta diversity.

The low beta diversity at finer spatial scales can also be explained as an extension the 'Yucatán Peninsula effect', mentioned above, that is the tendency of the species to have large range sizes. At the finer scales (i. e., squares

of 3.12 x 3.12 km, 6.25 x 6.25 km, 12.5 x 12.5 km), the species tend to occupy a high proportion of the squares in which the region was subdivided, mirroring in low values of beta diversity in all the groups.

At these finer spatial scales, an additional and related explanation to the effect describe above is proposed. The sources of information used in our study (species range distribution generated using climatic niche models) are restrained by the spatial autocorrelation of the environmental variables used for producing species distribution models. Thus, distributions tend to over-fill areas, whereas at a landscape scale, distributions would be more fragmented. It is possible that some of the detailed habitat preferences are not captured by our modeling approach resulting in an underestimation of beta diversity values. We assumed that all terrestrial vertebrates are affected similarly at finer scales, which is highly unlikely.

Scale dependence of Beta diversity. This study provides further solid evidence that beta diversity is scale dependent in all terrestrial vertebrates in Mexico; at coarser scales, beta diversity is high, but decreases as spatial scales decreases. Scale dependency of beta diversity was also observed by Lira-Noriega et al. (2007) with the resident avifauna of central Mexico. As far as we know, there are no other studies attempting to analyses beta diversity for all of Mexico and along the large range of scales considered in this study.

In contrast to the pattern found here, other studies reported the opposite pattern, that is, lower beta diversity at coarse scales (Vellend, 2001; Qian, 2009; Qian and Ricklefs, 2000, 2012; Keil et al., 2012; Calderón-Patrón et al., 2013). Keil et al. (2012) reported that dissimilarity decreases when increasing spatial scale using dissimilarity/distance metrics with plants, birds, herps and butterflies in Europe. In a study situated in the Isthmus of Tehuantepec, southern Mexico, for vertebrates, Calderón-Patrón et al. (2013), reported higher values of dissimilarity at fine grain, while a coarse grain returns lower values of dissimilarity. The apparent contradiction of the results can be explained mainly by differences in conceptual terms and, in consequence, in the methods applied to measure beta diversity. The studies that focus on the 'differentiation' aspect of beta diversity (Tuomisto, 2010; Moreno and Rodríguez, 2010, 2011) use indices based on the dissimilarity/distance family. The number of species shared between 2 squares increases as the resolution decreases (i. e., larger areas), and occurs mainly because larger areas have more species or because the degree of aggregation of species is reduced (Gaston et al., 2007). In contrast, when the study of beta diversity is focused in the 'proportional' aspect of beta diversity (Moreno and Rodríguez, 2010), the indices used are, for example, the

Species- Area relationship (the method used in this study is based on the SAR). Scale in this case is the size of the area and, the slope of the SAR unavoidably became steeper with increasing the area (i.e. scale), or, as the exception found in this study, in the Yucatán Peninsula, practically z does not increases with increasing the area.

Implication for conservation of biodiversity. Our results suggest that the spatial scale to perform complementarity analysis for conservation purposes needs to be taken into consideration. Overall, there is a break in the values of beta diversity at the spatial scale 4-5 (from 50 x 50 km to 25 x 25 km), where beta diversity decreases drastically and become similar along the remaining finer spatial scales. Thus, the optimal scale to capture the maximum dissimilarity across communities using models of species distributions are squares of 625 km^2.

Large protected areas are more suitable for conservation, such as Calakmul or Sian Ka'an in the Yucatán Peninsula; conversely, conservation area networks are more suitable in regions holding high beta diversity, as in the Centre or SE regions. Moreover, recent approaches of rarity-complementarity for selecting priority areas for conservation of terrestrial vertebrates can be adjusted to an adequate spatial scale as proposed in our study.

This study presents the first set of analyses of beta diversity across a wide range of 7 spatial scales (from ~160 000 km^2 to ~10 km^2) for the Mexican terrestrial vertebrates. The simultaneous analyses for 5 different regions allowed us to make suggestions about the generality of the pattern of scaling of beta diversity and, more importantly, to generate specific predictions regarding the factors that might explain the patterns of diversity in Mexico.

Our study showed that beta diversity varies among regions and spatial scales, suggesting some processes that act differentially between spatial scales and taxonomic groups. Drivers of beta diversity vary along spatial scales, and both historical and ecological processes shape the patterns of biological diversity of vertebrates of Mexico. At coarser spatial scales, complex interplay of habitat heterogeneity, contrasting types of vegetation and biogeographic histories as area increases seem to be important to explain the extraordinary beta diversity, whereas, in turn, at finer spatial scales ecological processes related to topography, environmental heterogeneity and in general the local environmental conditions seem to be the important to explain the beta diversity. Also, the information used in the study (niche models) and other decisions, such as considering resident birds only, might also affect the results.

Beta diversity of each group contributes to the megadiversity of Mexico in different ways. Amphibians and reptiles are important at coarse scale, whereas, surprisingly, birds contribute to high values of beta diversity at finer scales. The general pattern of beta diversity found at the scale of 2 500 km^2 following the dispersal capacity of the 4 groups, amphibians > reptiles > mammals> birds (Koleff et al., 2008), does not hold at other scales, opening new and interesting question to be investigated.

Findings of this study set the basis for more elaborated hypotheses that need to be tested regarding the biogeographic affinity of these taxonomic groups in spatially explicit ways, and with respect to the environments in which their species occur. Finally, our study may help to determine the spatial scale which is better suited for the assessment and design of protected areas in the context of the diversity patterns of the 4 taxonomic groups evaluated.

Acknowledgments

Literature cited

Arita, H. T. 1997. The non-volant mammal fauna of Mexico: species richness in a megadiverse country. Biodiversity and Conservation 6:787-795.

Arita, H. T. and P. Rodríguez. 2002. Geographic range, turnover rate and the scaling of species diversity. Ecography 25:541-553.

Arita, H. T. and E. Vázquez-Domínguez. 2003. Fauna y la conformación de la provincia biotíca yucateca: Biogeografía y macroecología. *In* Naturaleza y sociedad en el área maya, pasado, presente y futuro, P. Colunga-García Marín and A. Larqué- Saavedra (eds.). Academia Mexicana de Ciencias, CICY, Mexico. p. 60-80.

Baselga, A., C. Gómez-Rodríguez and J. M. Lobo. 2012. Historical legacies in world amphibian diversity revealed by the turnover and nestedness components of Beta diversity. PloS One 7:e32341.

Barton, P. S., S. A. Cunningham, A. D. Manning, H. Gibb, D. B. Lindenmayer and R. K. Didham. 2013. The spatial scaling of beta diversity. Global Ecology and Biogeography 22:639-647.

Buckley, L. B. and W. Jetz. 2008. Linking global turnover of species and environments. Proceedings of the National Academy of Sciences USA 105:17836-17841.

Calderón-Patrón, J. M., C. E. Moreno, R. Pineda-López, G. Sánchez-Rojas and I. Zuria. 2013. Vertebrate dissimilarity due to turnover and richness differences in a highly beta-diverse region: the role of spatial grain size, dispersal ability and distance. PloS one, 8:e82905.

Ceballos, G., J. Arroyo-Cabrales and R. A. Medellín. 2002. The mammals of Mexico: composition, distribution and conservation status. Occasional Papers, Museum of Texas Tech University 218:1-27.

Conabio-Conanp-TNC-Pronatura-FCF, UANL. 2007. Análisis de vacíos y omisiones en conservación de la biodiversidad terrestre de México: espacios y especies. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Comisión Nacional de Áreas Naturales Protegidas, The Nature Conservancy- Programa México, Pronatura, A. C., Facultad de Ciencias Forestales, Universidad Autónoma de Nuevo León, Mexico.

Cortés-Ramírez, G., A. Gordillo-Martínez and A. G. Navarro-Sigüenza. 2012. Patrones biogeográficos de las aves de la Península de Yucatán. Revista Mexicana de Biodiversidad 83:530-542.

Crawley, M. J. and J. E. Harral. 2001. Scale dependence in plant biodiversity. Science 291:864-868.

Crist, T. O. and J. A. Veech. 2006. Additive partitioning of rarefaction curves and species–area relationships: unifying α-, β- and γ-diversity with sample size and habitat area. Ecology Letters 9:923-932.

Dobrovolski, R., A. S. Melo, F. A. Cassemiro and J. A. F. Diniz-Filho. 2012. Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. Global Ecology and Biogeography 21:191-197.

Drakare, S., J. J. Lennon and H. Hillebrand. 2006. The imprint of the geographical, evolutionary and ecological context on species–area relationships. Ecology Letters 9:215-227.

Escalante, T., G. Rodríguez, N. Gámez, L. León-Paniagua, O. Barrera and V. Sánchez-Cordero. 2007. Biogeografía y conservación de los mamíferos. In Biodiversidad de la Faja Volcánica Transmexicana, I. Luna, J. J. Morrone and D. Espinosa (eds.). FES-Zaragoza and Instituto de Biología, UNAM, México, D. F. p. 485-502.

Escalante-Pliego, P., A. G. Navarro-Sigüenza and A. T. Peterson. 1998. Un análisis geográfico, ecológico e histórico de la diversidad de aves terrestres de México. In Diversidad biológica de México: orígenes y distribución, T. P. Ramammoorthy, R. Bye, A. Lot, y J. Fa (eds.). Instituto de Biología, UNAM, México, D.F. p. 279-304.

ESRI, 1999. ArcView 3.2. Environmental Systems Research Institute. Redlands, California, USA.

Evans, K. L., P. H. Warren and K. J. Gaston. 2005. Species–energy relationships at the macroecological scale: a review of the mechanisms. Biological Reviews 80:1-25.

Ferrusquia-Villafranca, I. 1993. Geology of Mexico: a synopsis.

In Biological diversity of Mexico: origins and distribution, T. P. Ramamoorthy, R. Bye, A. Lot and J. Fa (eds.). Oxford University Press. New York. p. 3-107.

Fischer, J. and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16:265-280.

Flores-Villela, O., L. M. Ochoa-Ochoa and C. Moreno. 2005. Variación latitudinal y longitudinal de la riqueza de especies y la diversidad beta de la herpetofauna mexicana. In Sobre diversidad biológica: el significado de las diversidades alfa, beta y gama, G. Halffter, J. Soberón, P. Koleff and A. Melic (eds.). Monografías tercer milenio. SEA, Conabio, Grupo Divesitas and Conacyt, Zaragoza. p. 143-152.

Gardner, T. A., J. Barlow and C. A. Peres. 2007. Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. Biological Conservation 138:166-179.

Gaston, K. J., Evans, K. and J. Lennon. 2007. The scaling of spatial turnover: pruning the thicket. In Scaling biodiversity, D. Storch, P. M. Marquet and J. H. Brown (eds.). Cambridge University Press, Cambridge. p. 181-222.

Halffter, G. 1987. Biogeography of the montane entomofauna of Mexico and Central America. Annual Review of Entomology 32:95-114.

Harte, J., A. Kinzig and J. Green. 1999. Self-similarity in the distribution and abundance of species. Science 284:334-336.

Harte, J., E. Conlisk, A. Ostling, J. L. Green and A. B. Smith. 2005. A theory of spatial structure in ecological communities at multiple spatial scales. Ecological Monographs 75:179-197.

Ibarra-Manríquez, G., J. L. Villaseñor, R. Durán and J. Meave. 2002. Biogeographical analysis of the tree flora of the Yucatán Peninsula. Journal of Biogeography 29:17-29.

Jones, K. E., T. M. Blackburn and N. J. Isaac. 2011. Can unified theories of biodiversity explain mammalian macroecological patterns?. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2554-2563.

Jost, L. 2007. Partitioning diversity into independent alpha and beta components. Ecology 88:2427-2439.

Jost, L., P. DeVries, T. Walla, H. Greeney, A. Chao and C. Ricotta. 2010. Partitioning diversity for conservation analyses. Diversity and Distributions 16:65-76.

Keil, P., O. Schweiger, I. Kühn, W. E. Kunin, M. Kuussaari, J. Settele, K. Henle, L. Brotons, G. Pe'er, S. Lengyel, A. Moustakas, H. Steinicke and D. Storch. 2012. Patterns of beta diversity in Europe: the role of climate, land cover and distance across scales. Journal of Biogeography 39:1473-1486.

Koleff, P., K. J. Gaston and J. J. Lennon. 2003. Measuring beta diversity for presence–absence data. Journal of Animal Ecology 72:367-382.

Koleff, P., J. Soberón, H. Arita, P. Dávila, O. Flores-Villela, G. Halffter, A. Lira-Noriega, C. E. Moreno, E. Moreno, M. Munguía, M. Murguía, A. Navarro-Sigüenza, O. Téllez, L. M. Ochoa-Ochoa, A. T. Peterson and P. Rodríguez. 2008. Patrones de diversidad espacial en grupos selectos de especies.

In Capital natural de México, Vol. I, Conocimiento actual de la biodiversidad. Conabio, México, D. F. p. 323-364.

Lee, J. C. 1980. An ecogeographic analysis of the herpetofauna of the Yucatán Peninsula. Miscellaneous Publications of the University Kansas Museum of Natural History 67:1-75.

Lennon, J. J., W. E. Kunin and S. Hartley. 2002. Fractal species distributions do not produce power-law species-area relationships. Oikos 97:378-386.

Lira-Noriega, A., J. Soberón, A. G. Navarro-Sigüenza, Y. Nakazawa and A. T. Peterson. 2007. Scale dependency of diversity components estimated from primary biodiversity data and distribution maps. Diversity and Distributions 13:185-195.

Lomolino, M. V. and M. D. Weiser. 2001. Towards a more general species-area relationship: diversity on all islands, great and small. Journal of Biogeography 28:431-445.

Lomolino, M. V, B. R. Riddle, R. J. Whittaker and J. H. Brown. 2010. Biogeography. Fourth edition. Sinauer, Sunderland, Massachusetts. 878 p.

Loreau, M. 2000. Are communities saturated? On the relationship between α, β and γ diversity. Ecology Letters 3:73-76.

Marshall, C. J. and J. K. Liebherr. 2000. Cladistic biogeography of the Mexican transition zone. Journal of biogeography 27:203-216.

McGlinn, D. J. and A. H. Hurlbert. 2012. Scale dependence in species turnover reflects variance in species occupancy. Ecology 93:294-302.

Moreno, C. E. and G. Halffter. 2001. Spatial and temporal analysis of alpha, beta, and gamma diversities of bats in a fragmented landscape. Biodiversity and Conservation 10:367-382.

Moreno, C. E. and P. Rodríguez. 2010. A consistent terminology for quantifying species diversity? Oecologia 163:279-282.

Moreno, C. E. and P. Rodríguez. 2011. Do we have a consistent terminology for species diversity? Back to basics and toward a unifying framework. Oecologia 167:889-892.

Munguía, M., A. T. Peterson and V. Sánchez-Cordero. 2008. Dispersal limitation and geographical distributions of mammal species. Journal of Biogeography 35:1879-1887.

Navarro-Sigüenza, A., A. T. Peterson and A. Gordillo-Martínez. 2003. Museums working together: the atlas of the birds of Mexico. Bulletin of the British Ornithologist's Club 123: 207-225.

Navarro-Sigüenza, A. G. and A. T. Peterson. 2007. Mapas de las aves de México basados en WWW. Informe final Snib-Conabio. Proyecto Núm. CE015. México D. F.

Navarro-Sigüenza, A. G., A. Lira-Noriega, A. T. Peterson, A. Oliveras de Ita and A. Gordillo-Martínez. 2007. Diversidad, endemismo y conservación de las aves del Eje Neovolcánico Transversal, México. *In* Biodiversidad de la Faja Volcánica Transmexicana, I. Luna, J. J. Morrone and D. Espinosa (eds.). FES-Zaragoza and Instituto de Biología UNAM, México, D. F. p 461-483.

Noguez, A. M., H. T. Arita, A. E. Escalante, L. J. Forney, F. García-Oliva and V. Souza. 2005. Microbial macroecology: highly structured prokaryotic soil assemblages in a tropical deciduous forest. Global Ecology and Biogeography 14:241-248.

Ochoa-Ochoa, L. M. and O. Flores-Villela. 2006. Áreas de diversidad y endemismo de la herpetofauna mexicana. Jiménez Editores/Conabio/UNAM. México, D. F. 259 p.

Ochoa-Ochoa, L. M. and O. Flores-Villela. 2011. Endemismo de la herpetofauna de Veracruz: análisis y problemáticas. *In* La biodiversidad en Veracruz, estudio del estado, Vol. II. Diversidad de especies: conocimiento actual, A. Cruz Angón (ed.). Conabio, México, D. F. p. 545-558.

Ochoa-Ochoa, L. M., O. Flores-Villela, U. García-Vázquez, M. E. Correa-Cano and L. Canseco-Márquez. 2006. Áreas potenciales de distribución de la herpetofauna de México. Conabio, México. http://www.conabio.gob.mx/ informacion/gis/?vns=gis_root/biodiv/distpot ; last access: 29.IV.2013.

Ochoa-Ochoa, L. M., J. A. Campbell and O. Flores-Villela. 2014. Richness and endemism of the Mexican herpetofauna, a matter of spatial scales? Biological Journal of the Linnean Society 111:305-316.

Pronatura México A. C. and The Nature Conservancy. 2007. Biodiversidad del centro y occidente de México planeación ecorregional: avances y próximos pasos. Parques en peligro / USAID, Mexico. 80 p.

Qian, H. 2009. Global comparisons of beta diversity among mammals, birds, reptiles, and amphibians across spatial scales and taxonomic ranks. Journal of Systematics and Evolution 47:509-514.

Qian, H. and R. E. Ricklefs. 2000. Large-scale processes and the Asian bias in species diversity of temperate plants. Nature 407:180-182.

Qian, H. and R. E. Ricklefs. 2012. Disentangling the effects of geographic distance and environmental dissimilarity on global patterns of species turnover. Global Ecology and Biogeography 21:341-351.

Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecology Letters 8:224-239.

Rodríguez, P. and H. T. Arita. 2004. Beta diversity and latitude of North American mammals: testing the hypothesis of covariation. Ecography 27:547-556.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge. 436 p.

Sánchez-Cordero, V., V. Cirelli, M. Munguía and S. Sarkar. 2005. Place prioritization for biodiversity content using species ecological niche modelling. Biodiversity Informatics 2:11-23.

Sánchez-González, L. A. and A. G. Navarro-Sigüenza. 2009. History meets ecology: a geographic analysis of ecological restriction in the Neotropical humid montane forests avifaunas. Diversity and Distributions 15:1-11.

Shmida, A. and M. V. Wilson. 1985. Biological determinants of species diversity. Journal of Biogeography 12:1-20.

Šizling, A. L. and D. Storch. 2004. Power-law species–area relationships and self-similar species distributions within finite areas. Ecology Letters 7:60-68.

Tanentzap, A. J., S. Walker, R. T. T. Stephens and W. G. Lee.

2012. A framework for predicting species extinction by linking population dynamics with habitat loss. Conservation Letters 5:149-156.

Triantis, K. A., F. Guilhaumon and R. J. Whittaker. 2012. The island species–area relationship: biology and statistics. Journal of Biogeography 39:215-231.

Tuomisto, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography 33:2-22.

Ulrich, W. and J. Buszko. 2003. Self-similarity and the species–area relation of Polish butterflies. Basic and Applied Ecology 4:263-270.

Vázquez, L., H. Moya and M. C. Arizmendi. 2009. Avifauna de la selva baja caducifolia en la cañada del río Sabino, Oaxaca, México. Revista Mexicana de Biodiversidad 80:535-549.

Vázquez-Domínguez, E. and H. Arita. 2010. The Yucatán Peninsula: biogeographical history 65 million years in the making. Ecography 33:212-219.

Vellend, M. 2001. Do commonly-used indices of beta diversity measure species turnover? Journal of Vegetation Science 12:545-552

Villalobos, F., A. Lira-Noriega, J. Soberón and H. T. Arita. 2013. Range-diversity plots for conservation planning: using richness and rarity in priority setting, the case of Mexican avifauna. Biological Conservation 158:313-320.

Ward, W. C., A. E. Weidie, W. Back and A. P. Andrews. 1985. Geology and hydrogeology of the Yucatán and quaternary geology of northeastern Yucatán Peninsula. New Orleans Geological Society, New Orleans. p. 160.

White, D. A. and C. S. Hood. 2004. Vegetation patterns and environmental gradients in tropical dry forests of the northern Yucatán Peninsula. Journal of Vegetation Science 15:151-160.

Whittaker, R. H. 1960. Vegetation in the Siskiyou Mountains, Oregon and California. Ecological Monographs 30:279-338.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21:213-251.

Whittaker, R. J., K. J. Willis and R. Field. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography 28:453-470.

Wiens, J. A. and B. T. Milne. 1989. Scaling of "landscapes" in landscape ecology, or, landscape ecology from a beetle's perspective. Landscape Ecology 3:87-96.

Willis, K. J. and R. J. Whittaker. 2002. Species diversity- Scale matters. Science 295:1245-1248.