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Spatial scale and β-diversity of terrestrial vertebrates in Mexico

Escalas espaciales y diversidad beta de los vertebrados terrestres en México

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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.

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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.