



Spatial variation of mammal richness, functional and phylogenetic diversity in the Mexican Transition Zone

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Abstract: The multi-dimensional analysis of biodiversity addresses several components, including the number of species, as well as their ecological and evolutionary identities. This approach can lead to key biodiversity patterns that remain covered when only species richness is studied. The convergence of the Nearctic and Neotropical biogeographic regions in Mexico suggests spatial variation in biodiversity patterns. In this study we analysed species richness, functional diversity, and phylogenetic diversity of mammal assemblages in relation to abiotic variables and their variation across the biogeographic regions. Our results showed contrasting patterns among biodiversity dimensions: 1) species richness followed the typical global pattern of a gradual increase from the Nearctic towards the Neotropical region, 2) phylogenetic diversity was highest in the Transitional region; and 3) functional diversity was highest in the Neotropical region, but not different between the Nearctic and Transitional regions. Abiotic variables had a significant relation with variation in biodiversity dimensions, but they had a higher contribution to explain functional diversity than species richness and phylogenetic diversity. The decoupled patterns of functional and phylogenetic diversity among the biogeographical regions highlight the complementarity between these dimensions and the importance of transitional regions, and suggest that several historical, environmental and ecological processes may be structuring mammal assemblages. Likewise, different approaches should be followed in accordance to variation of functional and phylogenetic traits among regions.

Nomenclature: Ramírez-Pulido et al. (2014).

Introduction

Spatial patterns of biodiversity and their associated processes have been of great interest to ecologists and biogeographers for several decades (Rosenzweig 1995). Traditionally, the study of biodiversity has focused on quantifying species richness, i.e., the number of species that occurs in ecosystems or communities. The main drawback of this approach is that species richness considers all species to be equally distinct. However in recent decades new approaches have emerged, incorporating other biodiversity dimensions to account for the ecological and evolutionary identity of species (Petchev et al. 2004, Davies and Buckley 2011, Stevens and Gavilanez 2015). On one hand, functional diversity incorporates the ecological identity of species to assess the variation of functional traits that influence species fitness and ecological processes (Petchev and Gaston 2002, Mlambo 2014). On the other hand, phylogenetic diversity incorporates the identity of species to measure the evolutionary history shared between taxa within communities (Faith 1992, Pellens and Grandcolas 2016). Thus, the interest to analyse functional and phylogenetic diversity in wildlife has increased, though birds and fish followed by mammals have been the most studied vertebrates, whilst reptiles and amphibians have been scarcely analysed (Gómez-Ortiz and Moreno 2017). This multi-dimensional approach constitutes a valuable tool that has been used to iden-

tify key species in ecosystem functioning and in systematic conservation planning (Dalerum 2013), to evaluate the quality of ecosystems and the loss of evolutionary history (Farias and Svensson 2014), and processes involved in community assembly (Davies and Buckley 2011, Safi et al. 2011).

The most studied spatial patterns of biodiversity are the increase of species richness with area, and the latitudinal gradient (Rosenzweig 1995), but the spatial variation of functional and phylogenetic diversity has been poorly described. Studies with mammals show that environmental factors such as temperature, precipitation, altitude, and evapotranspiration are significant predictors of functional or phylogenetic diversity (Safi et al. 2011, Stevens and Gavilanez 2015, González-Maya et al. 2016a, b).

Mexico is an interesting scenario for analysing biodiversity patterns and their related processes. The Mexican Transition Zone, where the Nearctic and the Neotropical regions converge, is a complex and evolutionarily active area where species from different biogeographical origins occur (Escalante et al. 2004, Morrone 2015). There are 564 mammal species in Mexico, and ca. 25% of them are medium and large sized (Sánchez-Cordero et al. 2014). They include species at key trophic levels in ecosystems; for example, some consumers have disproportionate impacts on ecosystems in relation to their abundance, and determine significant ecosystem effects (Dalerum et al. 2009). However, the use of a

multi-dimensional approach of mammal biodiversity patterns has been limited, especially for medium and large mammals, maybe due to difficulties in their monitoring and in the measurement of their functional traits.

In this study we used a multi-dimensional approach to analyse the species richness, functional and phylogenetic diversity of medium and large mammals in Mexico. Our aims were to describe the spatial variation of biodiversity dimensions across the biogeographic regions of the Mexican Transitional Zone, and to assess the influence of abiotic variables on each dimension, using ecoregions as spatial units for biodiversity analyses.

Materials and methods

Mammal composition and ecoregions selection

We used the ecoregions proposed by the World Wildlife Fund (Olson et al. 2001), as units of analysis. They are units of land with distinctive assemblages of natural communities that share species and environmental conditions. This regionalization offers a biogeographic delineation less sensitive to heterogeneity in data distribution, compared with grid analysis (Loyola et al. 2009). We grouped the ecoregions in Mexico according to the biogeographical region they belong to (Nearctic, Transitional or Neotropical). The Nearctic region includes the arid subtropical areas in the north of the country; the Transitional region is immersed in the middle of both Nearctic and Neotropical regions and includes the highlands of central Mexico; and the Neotropical region extends to the south of the country, including humid and sub-humid tropical areas (Escalante et al. 2004, Morrone 2005, Fig. 1).

The mammal assemblage composition was determined from georeferenced records available at the Global Biodiversity Information Facility species database (www.gbif.org). We selected geographical records acquired between 1990 and 2015, in order to represent current distribution of mammals, and drew a map with 5207 geographic records of terrestrial and continental aquatic species (>1000 g) using ArcGIS 10.2.2 (ESRI 2014). We excluded small mammals (i.e., small terrestrial and flying mammals) because they are functionally different and have dissimilar dispersal capabilities. The geographic records were overlapped with the digital polygons of ecoregions to build a species presence matrix by ecoregion, i.e., the mammal community composition at each ecoregion. In order to select the well sampled ecoregions, we used the total number of records per species in each ecoregion to estimate the inventory completeness based on the sample coverage (Chao and Jost 2012), and selected only the ecoregions with more than 74% of inventory completeness. Data for 59 species, belonging to 21 families and 43 genera were used for the analysis (the rest included marine species and terrestrial species with few records). Thirty-seven terrestrial ecoregions were selected, and eight ecoregions were not included due to insufficient data (low inventory completeness and less than three species; Appendix 1, Appendix 2).

Mammal biodiversity dimensions

We calculated three dimensions of mammal biodiversity: species richness (S), functional diversity (FD) and phylogenetic diversity (PD). The species richness was the total number of species in each ecoregion. Functional diversity was calculated with the FD index, which measures the total branch length of species in a dendrogram of functional traits (Petchey and Gaston 2002, 2006). FD measures the functional diversity of species traits, so that functionally different

Figure 1. Ecoregions and biogeographical classification used (Nearctic, Transitional and Neotropical) for the multi-dimensional analysis of biodiversity of medium and large mammals of Mexico.

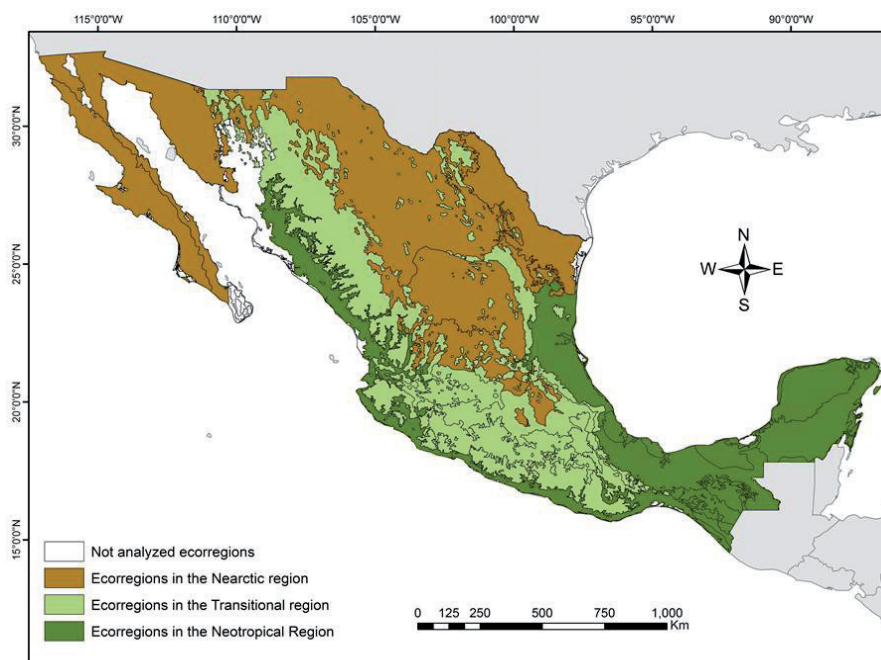


Table 1. Functional traits used to quantify functional diversity (FD) of medium and large mammals of Mexico.

Functional traits	Categories	Values
Trophic level	carnivore	binary
	omnivore	binary
	herbivore	binary
Habitat	aquatic	binary
	semiaquatic	binary
	terrestrial	binary
	arboreal	binary
Activity cycle	nocturnal	binary
	diurnal	binary
	crepuscular	binary
Sociality	solitary	binary
	in couples	binary
	in group	binary
Body sized	g	Continuous
Home range	km ²	Continuous
Density	ind/km ²	Continuous
Longevity	years	Continuous

species account for higher values in FD. We used Gower distance (Pavoine et al. 2009), which is an adequate multivariate distance to use with both quantitative and qualitative variables (Podani and Schmera 2006) and average linkage was used in the analysis to maximize cophenetic relationships and maintain the structure of the original dissimilarity (Petchev and Gaston 2002, 2006).

Functional traits were obtained from published literature (Ceballos and Oliva 2005, Aranda 2012) and databases such as PanTheria (Jones et al. 2009) and Animal Diversity Web (Myers et al. 2015). In cases where data were not available, we derived trait information from closely related species with near distributions. We deleted highly correlated functional traits to prevent overestimation in analysis (Pearson test, $R > 0.80$, $p < 0.05$) and generated a species-trait matrix including eight functional traits with 17 categories (Table 1; Appendix 3).

Phylogenetic diversity was calculated with the PD index, which works in an analogous manner to FD. It is based on a distance matrix and measures the sum of branch lengths in the phylogeny (Faith 1992, 2016). We used the mammal phylogeny of Bininda-Emonds et al. (2007). The names of the species were used according to the nomenclature of the phylogeny and some were replaced by their synonyms or phylogenetically closest species (*Puma yagouaroundi* was changed by *Herpailurus yagouaroundi*, *Coendu mexicanus* by *Sphiggurus mexicanus*, *Vulpes macrotis* by *V. velox*, *Mazama temama* by *M. americana* and *Cuniculus paca* by *Agouti paca*). *M. pandora* is not included in this phylogeny and was excluded from the PD analysis. The FD and the PD indices were performed in the FDiversity software (Casanoves et al. 2011).

Data analysis

We used five abiotic variables as the environmental explanatory data set that could explain biodiversity patterns: ecoregion area (obtained from WWF polygons), variation in altitude (calculated as standard deviation, HYDRO1k; Verdin 2011), temperature seasonality (measured as standard deviation*100, BIO4 from BIOCLIM, Hijmans et al. 2005), net primary productivity (measured as the range, Imhoff et al. 2004) and annual evapotranspiration (measured as standard deviation, Trabucco and Zomer 2009). All abiotic variables were processed using a Geographic Information System and resampled to an equal area grid of 1 km². All variables were standardized to have a mean of 0 and variance of one before the analysis. We tested spatial autocorrelation between these abiotic variables in ecoregions in order to delete those highly correlated, using Global Moran's I (all values were close to 0, $p > 0.05$, in all cases). We also eliminated the abiotic variables that showed multicollinearity (Pearson test, $R > 0.8$, $p > 0.05$).

We applied an ordinary least squares (OLS) regression analysis to test the relationship between S and the abiotic variables. Since PD and FD measures maintain a monotonic relationship with S, we used a partial regression analysis to evaluate the relationships between functional and phylogenetic diversity with environmental data set taking into account for S effect (diversity measures data set; Legendre and Legendre 2003). Similarly, FD and PD may be closely related to each other because of the variation in S and evenness (Pavoine et al. 2013), thus, we also analysed the FD taking into account the PD effect (diversity measures data set).

To evaluate the variation of richness, functional and phylogenetic diversity among the biogeographical regions, we used the dispersion of residuals approach (PD and FD taking into account S or PD). Higher residual values than expected from S, suggest regions with high FD or PD. In contrast, lower residual values than expected from S indicate regions with low FD or PD. In the case of FD (taking PD into account), higher residual values may suggest regions without phylogenetically conserved traits (Cisneros et al. 2014). Finally, we performed analysis of variance (ANOVA, $p = 0.05$), using the residual values of biodiversity dimensions of each ecoregion as dependent variables, and the Nearctic, Transitional and Neotropical regions as factors. We applied post-hoc tests between biogeographical regions for each biodiversity dimension when significant results were found (Fisher-LSD, $p = 0.05$). The same analyses were performed taking into account the abiotic variables effect when these predictors showed a significant relationship with biodiversity dimensions in regression analysis. All statistical analyses were carried out in the XLSTAT (2014).

Results

We found different patterns in the distribution of mammal biodiversity dimensions among the biogeographical regions of Mexico (Fig. 2). First, S followed the typical latitudinal pattern, of a gradual increase from the Nearctic to the

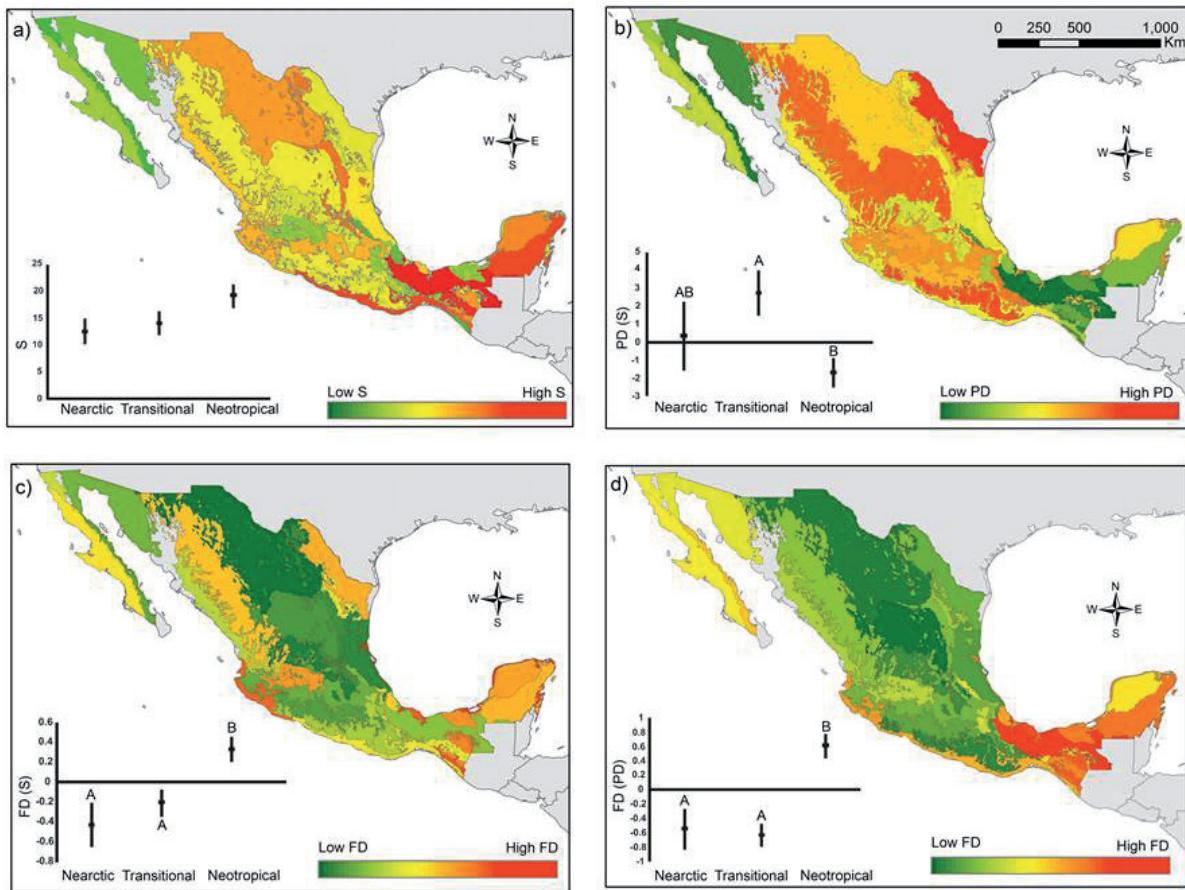


Figure 2. Biogeographical variation of biodiversity dimensions of mammals in Mexico. (a) Species richness, (b) phylogenetic diversity taking S into account, (c) functional diversity taking S into account, (d) functional diversity taking PD into account. Capital letters indicate statistical difference among biogeographical regions (mean and standard error; LSD, p -values < 0.05).

Note: The horizontal line for PD and FD (value of 0) represents the expected values for the diversity dimensions according to S or PD.

Neotropical region ($F = 2.57$, d.f. = 2, 34, $p = 0.09$; Fig. 2a). Second, PD values peaked at the Transitional region, and were significantly higher than those at the Neotropical region ($F = 3.59$, d.f. = 2, 34, $p < 0.05$; Fig. 2b). Finally, FD showed a similar pattern than S, increasing from the Nearctic to the Neotropical region; nonetheless, there was no significant difference in FD pattern between the Nearctic and Transitional regions. These patterns persisted when either S or PD were taken into account ($F = 7.15$, d.f. = 2, 34, $p < 0.01$; and $F = 15.34$, d.f. = 2, 34, $p < 0.01$ respectively; Fig. 2c, 2d) or when taken into account the abiotic variables effect ($F = 7.15$, d.f. = 2, 34, $p < 0.01$ and $F = 15.34$, d.f. = 2, 34, $p < 0.01$; respectively; except for PD pattern due to the lack of significance of the regression model; $R^2 = 0.24$; $p > 0.05$, Table 2).

Abiotic variables contribution

The three partial regression models showed high R^2 values (full); this value is the sum of the variation explained by the abiotic variables, the diversity measures and the combined effect of them (“a”, “b” and “c” fractions; Legendre and Legendre, 2003). The variation explained by the environ-

mental data set accounted for 34 percent of species richness pattern, 24 percent of PD when taking S into account, and about 43 percent of FD when taking both S and PD into account (Table 2). However, as the PD and FD measures we used are intrinsically correlated with S, the species richness captured most of the variation, and consequently, the partial R^2 for the relative unique contribution of abiotic variables was naturally low (fraction “a”, Table 3). Regarding the variables contribution, only the net primary productivity range was a marginal predictor of S (Table 2). No abiotic variable showed a significant relation with PD when taking S into account, but the ecoregion area, altitude and temperature seasonality showed a significant association with FD (Table 2). In short, these results indicate that abiotic variables may contribute to explain FD, but not the PD in the ecoregions.

Discussion

The spatial variation in FD and PD supports the idea that these biodiversity dimensions may differ substantially between species assemblages with the same species richness (Petchey and Gaston 2006). Thus, different historical, envi-

Table 2. Slope of abiotic variables related with richness (S), phylogenetic diversity (PD) and functional diversity (FD), taking in account for S and PD effects. Abiotic variables with significant effects are in bold (p-values < 0.05, *p = 0.056).

Abiotic variable	S	PD (S)	FD (S)	FD (PD)
R ²	0.34	0.24	0.43	0.43
Ecoregion area	0.21	-0.29	0.54	0.55
Variation in altitude (SD)	-0.07	0.26	0.42	0.10
Temperature seasonality (SD)	-0.18	-0.18	0.22	0.34
Net primary productivity (Range)	0.34*	-0.09	-0.12	-0.07
Annual evapotranspiration (SD)	0.20	-0.42	-0.14	0.23

Table 3. Partition of the variation of phylogenetic diversity (PD) and functional diversity (FD) among the abiotic variables and diversity measures (S and PD). The sum of a, b, c and d corresponds to 100% of the variation in each biodiversity dimension PD taking into account S and FD taking into account PD (significant effects of fitted models are in bold, p-values < 0.05).

	Explanatory data set (R ²)			Partition of the variation of biodiversity dimensions (R ²)			
	Environmental data set (a+b)	Diversity measures data set (b+c)	Full	a	b	c	d
				Abiotic variables	Combined	Diversity measures (S, PD)	Unexplained variation
PD (S)	0.24	0.92	0.95	0.03	0.21	0.71	0.05
FD (S)	0.43	0.96	0.97	0.01	0.42	0.54	0.03
FD (PD)	0.43	0.91	0.94	0.03	0.41	0.50	0.06

ronmental and ecological processes may be structuring the mammal assemblages in the Mexican Transitional Zone, as has been reported in other regions (Davies and Buckley 2011, Cisneros et al. 2014, González-Maya et al. 2016a).

The main processes structuring diversity patterns are related to equilibrium and non-equilibrium dynamics. In a global study, Oliveira et al. (2016) found evidence showing that mammal species richness and functional diversity are decoupled in America, with species richness being explained by environmental factors (equilibrium processes), whilst functional diversity is related to evolutionary time (non-equilibrium processes). Our results agree with these findings, and also with the general pattern of species richness increase towards the tropics (Rosenzweig 1995, Brown 2014). Functional diversity in the Mexican Transitional Zone is weakly explained by environmental factors, which suggest that non-equilibrium dynamics may be driving the community structuring, according to the intrinsic characteristics of our study area. First, we are analysing the geographical extremes of both the Nearctic and Neotropical biogeographical zones, which may affect differently the functional pattern of the species in relation to their affinities. For the Neotropical species we are analysing the most environmentally heterogeneous portion of their distribution; such conditions may favour functional divergence (Safi et al. 2011). In counterpart, for the Nearctic species, we are analysing the most stable environmental conditions, which may decrease the functional divergence; moreover, the Nearctic region has lower mammal richness than the Neotropical region (Cole et al. 1994, Davies et al. 2008).

Several environmental factors have been used to explain the spatial biodiversity patterns. At regional scales, seasonality,

productivity and climatic stress have resulted significant indicators of biodiversity variation (Brown 2014). In this study, S has a marginal relationship with net primary productivity, PD is not related to any of the abiotic variables we tested and FD is weakly explained by the area, and environmental heterogeneity (variation in altitude and temperature seasonality).

In a global analysis, mammal functional diversity was associated with temperature seasonality, indicating that tropical areas are characterized by a functional deficit and suggesting that in tropical regions, niche conservatism may be dominant over niche evolution (Safi et al. 2011). Our results suggest that functional diversity in the Neotropical portion we analysed is different from the global pattern observed for all terrestrial mammals in the tropics, as we found that environmental heterogeneity may explain functional diversity. Our results agree with the findings reported for mammals in South America by Fergnani and Ruggiero (2015), and suggest that competition, high environmental heterogeneity, and niche partitioning are among the ecological process that may act in the community structuring (Safi et al. 2011, Cisneros et al. 2014). These opposite patterns may be explained by merge of biological groups with different dispersal capabilities or groups with disproportionate number of species (e.g., rodents and flying mammals), which affect the estimation of diversity (Fergnani and Ruggiero 2015).

Phylogenetic diversity in our study area peaks in the Mexican Transitional Zone, which is characterized by high elevations and temperate environments. According to Oliveira et al. (2016) we would expect that the old colonized areas had the highest phylogenetic diversity (Nearctic zone in our study area), nonetheless, our results are congruent with expecta-

tions, considering three main reasons: 1) this region gathers the phylogenetic histories from Nearctic and Neotropical regions, 2) the greatest mammal species richness in Mexico is located in temperate mountains (Sánchez-Cordero et al. 2014), and 3) the Transitional region is considered an evolutionarily active zone with high rates of speciation and endemism (Escalante et al. 2002, Morrone 2015).

High phylogenetic diversity has been associated with the hypothesis of niche evolution as driver in the assemblages (Safi et al. 2011, Cisneros et al. 2014), thus indicating that historical factors, such as dispersal events, speciation and extinction may have shaped the phylogenetic relationships among extant species (Davies and Buckley 2011); nonetheless we must be cautious when the phylogenetic signal is not explicitly evaluated (Losos 2008). In contrast, other environmental processes (e.g., low trait evolution, relaxed competition) may be driving the biodiversity dimensions in the Nearctic and the Neotropical regions.

The comparison between geographic regions clearly shows that biodiversity dimensions are not interchangeable measures, but complementary surrogates of biodiversity (Devictor et al. 2010, Safi et al. 2011). The endemism and richness in the ecoregions have been also suggested as useful surrogates for conservation (Orme et al. 2005). In Mexico, the Neotropical region harbours the highest richness and functional diversity of mammals, and the convergence of both biogeographical regions in the Transitional region seems to favour higher phylogenetic diversity; thus highlighting the particularities of this zone and may be other transitional zones around the world. Our results also show the importance of tropical and temperate zones in Mexico as reservoirs of functional traits and evolutionary history, respectively. Thus, further conservation strategies should take into account the spatial variation of biodiversity dimensions.

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Appendix 1. Species richness (S), functional diversity (FD) and phylogenetic diversity (PD) of mammals in 37 ecoregions of Mexico.

Appendix 2. Mammal species composition for each ecoregion.

Appendix 3. Information source for functional traits of mammal species.