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Spatial patterns of phylogenetic diversity of Mexican mammals for biodiversity conservation

Master's thesis in Natural Resources Management

Supervisor: Michael D. Martin

Co-Supervisor: James D.M. Speed

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Photo by Eduardo Lugo Cabrera

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ABSTRACT

Phylogenetic diversity (PD) is a biodiversity measurement that describes the total amount of evolutionary history contained by the taxonomic units in a particular region. PD has proven to be an important metric for determining conservation priorities, especially when the potential conservation area is small. Mammalian PD patterns have been suggested as potential surrogates of biodiversity for establishing priority areas to ensure the conservation of mammalian evolutionary diversity and of the other species with which they have co-evolved. Mexico is considered a megadiverse country, and it is one of world's richest in mammal species. This project aims to identify the areas of high mammalian phylogenetic diversity in Mexico and to assess if current protected areas in Mexico conserve this evolutionary diversity. Distribution data for 488 Mexican mammals were obtained from IUCN and used to estimate species richness based on a presence/absence grid with 10x10-km cells. Molecular data for these species was gathered from GenBank and from laboratory extractions and further sequencing of three molecular markers (*cytB*, *12S* and *COI*), which were used to reconstruct a maximum-likelihood phylogenetic tree. Diversity analyses were conducted in R by importing both the distribution data sets and the phylogenetic tree. PD was calculated by summing the branch lengths of the phylogenetic tree representing species presence in each cell of the grid. These results were compared to the map of Mexican protected areas (PAs) in order to quantify the proportion of evolutionary history that is effectively conserved. Patterns of PD and SR are similar and highly correlated, with the southeastern part of Mexico being the most highly diverse, likely because of its highly productive ecosystems and the higher abundance of chiropteran groups in southern areas. PAs conserve most of the mammalian SR and all the PD at the genus level. PAs can be divided into areas containing high levels of mammalian diversity and areas with low levels of it. This division may result from the many endemic species that occur in the country as well as the presence of PAs on islands. β -diversity analyses showed that the species composition between PAs and the rest of the country is very similar and that differences between the two of them are mainly due to species missing from the other sites rather than species missing from the PAs. Focusing conservation actions with PD can be useful when resources are limited as it allows conservation of the overall evolutionary history of a group, even though individual species may not be protected if they are closely related to others. We recommend further work on population viability within PAs, as well as the predicted effect of future climate change on PD patterns, in order to assess the effectiveness of PA in conserving the Mexican mammal community.

ACKNOWLEDGEMENTS

This master thesis in Natural Resources Management was written at the department of Natural History at the Norwegian University of Science and Technology (NTNU) University Museum. I want to thank my two supervisors, Mike and James. Thanks to Mike for teaching me how to extract and amplify DNA, and for all of the patience during the sequence alignment and building the phylogeny process. Thanks to James for always being available and for being super patient when answering my doubts about R. I also would like to thank Fernando Cervantes Reza from the National Collection of Mammals, Livia León Paniagua from the Museum of zoology "Alfonso L. Herrera", Celia López González, from CIIDIR, Durango, José Ramírez Pulido from UAMI as well as the Kansas Natural History Museum, the Smithsonian National Museum of Natural History and the Museum of Vertebrate Zoology at Berkeley for taking the time to prepare and send the samples we requested for this study. Thanks to Tania Escalante for sharing the database of the Biogeographical Atlas of North American Mammals, and for her wonderful advices. Thanks to Kristian for all of the technical help with R, for all of the late nights we spent eating delicious cookies and working on my results, for the proofreading, for helping me stay motivated and for bearing with me throughout the process, especially during the crazy Corona times! Thanks to Karla for always believing in me and being there for me all of these years. Finalmente, doy gracias a mis papás por siempre creer en mi y darme la increíble posibilidad de haber venido a Noruega, esto lo he logrado gracias a ustedes y siempre voy a estar profundamente agradecida por haberme apoyado con este proyecto.

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1 INTRODUCTION

1.1 Background

The importance of biological diversity has been broadly reviewed and cannot be understated. Beyond the intrinsic value that nature holds for itself, it is well known that the biodiversity strongly influences environmental conditions from local to global scales, as well as all of the ecosystem services (*i.e.* the benefits that humans derive from the nature) provided by biodiversity. The benefits include clean water, food, genetic resources, and cultural value, among many others (Naeem *et al.*, 2012). For this reason, preventing the loss of biodiversity should be of global urgency (Voskamp *et al.*, 2017). However, we are facing an era of huge biodiversity loss (including both genetic and functional diversity), and therefore proposing methods to quantify biodiversity in order to better conserve it are of high relevance (Voskamp *et al.*, 2017; Rapacciuolo *et al.*, 2019; Grumbs *et al.*, 2019).

To achieve conservation of the remaining biodiversity, it is necessary to know the processes that promote biodiversity patterns around the world, such as ecological and geological processes. It is also relevant to improve biological knowledge of the species ecosystems or any level of organization that is targeted for protection, as well as the areas that are particularly biodiverse. It is also of high relevance to understand and mitigate the complex socioecological and sociopolitical processes that lead to this biodiversity loss in order to develop successful conservation strategies.

Traditionally, conservation strategies for quantifying biodiversity in a certain region have focused on species richness (*i.e.* the number of species present in that area) and patterns of endemism (*i.e.* the overlap, recurrence or concentration of distribution areas of endemic species) (Fleishmann, Noss & Noon, 2006; McGoogan *et al.*, 2007; Naeem *et al.*, 2012; Noguera-Urbano 2017; Winter, Devicor & Schweiger; 2013; Schmidt-Lebuhn *et al.*, 2015; Voskamp *et al.*, 2017; Rosauer *et al.*, 2017; Karanth *et al.*, 2019). Although species richness has commonly been used as the main biodiversity surrogate for establishing priority areas of conservation, recently it has been more and more accepted that species richness alone cannot appropriately describe the spatial and temporal dynamics of biodiversity since it only represents the taxonomic dimension of biodiversity ((Safi *et al.*, 2011; Naeem *et al.*, 2012; Schmidt-Lebuhn *et al.*, 2015; Voskamp *et al.*, 2017; Karanth *et al.*, 2019; Grumbs *et al.*, 2019).

One of the reasons species richness has been so extensively used as the main measure of biodiversity (both on local and global scales) is the ease with which it can be calculated (Karanth *et al.*, 2019). However, it does not address the complete complexity of biodiversity (Fleishmann *et al.*, 2006; Karanth *et al.*, 2019). Species richness has also been so widespread for assessing conservation priorities because it has been assumed that it adequately captures other dimensions of biodiversity (Fleishmann *et al.*, 2006; Rapacciuolo *et al.*, 2019).

Nevertheless, recent studies suggest that the relation between SR and other biodiversity measures is not always so linear, so other methods need to be proposed in order to account for different dimensions of biodiversity and in order to be able to identify species irreplaceability (Rosauer *et al.*, 2017; Voskamp *et al.*, 2017; Grumbs *et al.*, 2019; Karanth *et al.*, 2019; Rapacciuolo *et al.*, 2019). Moreover, species richness is based on widespread and common species, so priority conservation areas based on this measure often fails to capture features of biodiversity that require the greatest conservation focus (Voskamp *et al.*, 2017). In addition, species richness *per se* does not distinguish between native and non-native species, and it does not provide information on endemism, rarity nor sensitivity to changes in land use, since it treats all species as taxonomically equivalent (Fleishmann *et al.*, 2006; Karanth *et al.*, 2019). Therefore, it underestimates true diversity value of an area, since it does not account for evolutionary or functional diversity, and it does not provide any information on how different species are from each other (Karanth *et al.*, 2019).

In response to this challenge, and under the light of limited resources for conservation action, other approaches for measuring biodiversity are increasingly being recognized as important components of biodiversity over the last decades, including functional and phylogenetic diversity (Faith 1992; Winter *et al.*, 2013; Rosauer *et al.*, 2017; Grumbs *et al.*, 2019). It is important to mention that these forms of measuring other dimensions of biodiversity do not aim to replace species richness but rather complement it (Fleishmann *et al.*, 2006). Any metric of biodiversity measurement should be regarded as an “*additional biodiversity component of nature conservation*”, since they add components to biodiversity which allow for a more complete conservation process (Winter *et al.*, 2013).

One of this alternative and complementary forms of measuring biodiversity is phylogenetic diversity (PD). PD is described as a biodiversity measurement that accounts for the total amount of evolutionary history that the taxonomic units have in a certain region contain (Safi *et al.*,

2011). It provides a metric of biodiversity that accounts for evolutionary distances between co-occurring species (Voskamp *et al.*, 2017). In other words, PD can be regarded the taxonomic distinctiveness or uniqueness of a species within a community and can be estimated by looking at the phylogenetic relations among taxa in order to assess irreplaceability in terms of evolutionary history and evolutionary potential (McGoogan *et al.*, 2007; Voskamp *et al.*, 2017). More technically, it can be quantified as the sum of the length of the branches of a phylogenetic tree relating all species occurring in a region (Faith, 1992). High values of PD can be expected to correspond to greater representation of phylogenetically distant taxa, which might be interpreted as indicative of refugia or competitive exclusion of relatives (Schmidt-Lebuhn *et al.*, 2015). On the other hand, low values of PD correspond to greater representation of phylogenetically close taxa, this might be interpreted as recent local radiations or phylogenetic habitat filtering that leads to the overaccumulation of closely related species with similar evolutionary conservative traits (Schmidt-Lebuhn *et al.*, 2015; Speed *et al.*, 2019).

PD has proven to be an important component for determining conservation priorities because it can be related to processes such as extinction, biotic invasion, ecosystem functioning and even ecosystem services (McGoogan *et al.*, 2007; Winter *et al.*, 2013; Grumbs *et al.*, 2019). Furthermore, it can be used to set conservation priorities at various biogeographical scales in order to maximize future biodiversity and evolutionary distinctiveness (McGoogan *et al.*, 2007). PD could be a useful metric to highlight areas of high irreplaceability and added value in conservation terms (Voskamp *et al.*, 2017). Likewise, PD is beneficial in systematic conservation planning processes when the area available for optimally conservation reserves declines (Safi *et al.*, 2011), making it an efficient way to set priority areas for conservation.

The motivations for incorporating PD into the conservation planning process are the same as for species richness conservation, or any metric of biodiversity: their utility to humans due to the ecosystem services that they provide, but also because of their intrinsic value because the conservation process should aim to conserve all components of biodiversity, including the evolutionary information (McGoogan *et al.*, 2007; Winter *et al.*, 2013; Rosauer *et al.*, 2017).

Although PD and species richness usually correlate, the patterns are not completely identical so different information can be obtained for the different methods (Voskamp *et al.*, 2017; Karanth *et al.*, 2019). One of the main advantages that PD has over species richness is that while species richness assigns equal value to all species in a community and fails to incorporate

information about relationships between species, PD accounts for differences between the taxonomic units (in this case species), and it considers the evolutionary processes that build contemporary biodiversity patterns (Safi *et al.*, 2011).

Another advantage is that PD takes into account the phylogenetic rarity of species measured as uniqueness of phylogenetic distinctiveness (Winter *et al.*, 2013). Phylogenetically unique taxa and the places where they occur must be prioritized in the allocation of conservation resources because their extinction would result in a larger loss of evolutionary history than species with numerous sister taxa (Rodrigues & Gaston, 2002; McGoogan *et al.*, 2007). Thus, increased understanding of the spatial distribution of phylogenetic diversity is an opportunity to support policymakers in the design of conservation strategies.

There has been some criticism of using PD measures to prioritize nature conservation, as it was claimed that the methods for assessing it are prohibitively expensive, and that the sequence data for assessing phylogenetic relationships between species tends to be scarce and very incomplete (Rodrigues & Gaston, 2002; Karanth *et al.*, 2019). But improvements in data sequencing have made molecular data more accessible so that in the recent years, more and more molecular data is available to use for any kind of studies, including PD studies, through use of online open databases such as GenBank¹ or Bold Systems². As mentioned above, the advantages of using this measure will contribute to a more informed conservation resources allocation.

Notwithstanding this, resources and time are finite, and it is not possible to measure all aspects of biodiversity (not to mention that, despite the great improvements in data availability, there is still a considerable lack of knowledge in terms of described species and understanding of the distribution ranges of most of the species (Linnean and Wallacean shortfalls respectively) (Whittaker *et al.*, 2005). Biodiversity conservation strategies involve estimating patterns of variation and then trying to conserve as much of that estimated variation as possible (Faith & Baker, 2006). Surrogates can be used to represent certain patterns of biodiversity variation that we are seeking to estimate. It has been suggested that PD patterns of mammals could be used as surrogates of biodiversity to establish priority areas of conservation that ensure the safeguarding not only of the mammalian evolutionary diversity, but also other species that have co-evolved along with them (Safi *et al.*, 2011).

¹ www.ncbi.nlm.nih.gov/genbank/

² <http://www.boldsystems.org>.

Both SR and PD are measures of the alpha diversity of a given area. In order to analyze differences in species composition, β -diversity can be calculated. β -diversity is a measure of how different or similar are species communities in different areas (Whittaker, 1960). If in one of the regions species occupy a small part of the territory (they have small distribution ranges), the sites would be different in terms of species composition, meaning that the β -diversity is high. On the other hand, if the species have broad distribution ranges, the sites will be similar in species composition and thus, have low β -diversity (Rodríguez *et al.*, 2003). β -diversity can also be calculated for phylogenetic dissimilarity. Phylogenetic β -diversity (phylo β -diversity) measures how phylogenetic relatedness changes across space in the same way β -diversity measures how species composition changes across space (Graham & Fine, 2008). It provides an evolutionary approach to evaluate how community structure changes as a function of both spatial and environmental gradients (Graham & Fine, 2008). Calculating SR, PD and both β and phylo β -diversity contributes to a broader understanding of the biodiversity dynamics of a given area.

1.2 Study Area

Mexico's biological diversity has been widely recognized, and it is considered to be a megadiverse country. A megadiverse country is that which contains the highest possible biodiversity (in terms of the number of both terrestrial and aquatic ecosystems, and of species and genetic richness) in comparison with its area; for example, Mexico occupies the third-place in the world for mammalian species richness in total (Espinosa *et al.*, 2008; Ceballos, 2013). Mexico is a megadiverse country not only for its high number of species but also for its number of endemic species, ecosystem richness, and its great genetic variability shown in many taxonomic groups as a result of natural and cultural diversification in the country (Espinosa *et al.*, 2008, Ceballos, 2013).

These patterns of distribution have been used to categorized geographical areas in terms of their biotas as well as paleontological features through a hierarchical system called bioregionalization (Escalante, 2009; Morrone, 2018). Biogeographic regionalization consists of hierarchical systems for categorizing biodiversity into realms, regions, dominions, provinces, and districts (Noguera-Urbano & Escalante, 2015). Mexico is the only continental country that

presents the complete intergradation of two biogeographical regions: the Nearctic and a Neotropical (Ceballos, 2013). This characteristic is one of the reasons the country has such species richness with features from both tropical and temperate zones.

The area where both the Neotropical and Nearctic biota intersect is known as the Mexican Transition Zone (MTZ), and there has been broad study of the great amount of endemism and species richness presented in the area (Escalante, 2009; Ceballos, 2013; Morales *et al.*, 2016; Morrone *et al.*, 2017; Morrone, 2018), as well as the characteristics given by this zone that allow the country to have great diversity of ecosystems, from very unproductive ecosystems such as deserts to evergreen tropical rainforests (Ceballos, 2013, Morrone *et al.*, 2017). The great complexity in the distribution ranges and patterns of species in Mexico is related to the great heterogeneity of the physical environment which is product of the country's geological and climatic history (Ceballos, 2013). In accordance, some vegetation classification systems have recognized up to 50 different vegetation types (see González-Medrano, 2003).

The distribution range of a taxon is determined by both historic and current factors (Noguera-Urbano & Escalante, 2015), therefore, mammals' distribution patterns are consistent with the great diversity of vegetation types in Mexico as well as with the geological history of the area (Ceballos, 2013). Thus, the MTZ holds the biggest majority of mammals' endemism (Morales *et al.*, 2016). Some endemic mammals of the MTZ have very small ranges (can be as small as few square kilometers) and are rare, therefore catalogued under risk categories (Morales *et al.*, 2016). Species richness, tends to increase to the south of the country, having its highest value in the north-east of Oaxaca, where four mountainous systems (the Sierra Madre Occidental in the west, the Transmexican Volcanic Belt, the Sierra Madre Oriental, the Sierra of North-Oaxaca, and the Tehuacán-Cuicatlán valley) converge (Espinosa *et al.*, 2008). The aforementioned mountainous systems plus the Sierra Madre Occidental and the Balsas Basin also constitute the MTZ. One of the reasons Mexico has such a mammalian species richness is because it is the only continental country with a complete intergradation of two biogeographical regions (Espinosa *et al.*, 2008; Ceballos, 2013).

According to Ramírez-Pulido *et al.* (2014), Mexico has 496 species of terrestrial mammals (plus 47 marine species) contained in 168 genera. Besides being a country with high amount of species richness, Mexico also has high levels of endemism of mammals (34%), this means that 170 species have a spatial range that does not extend outside Mexico (Ceballos, 2013; Ramírez-

Pulido *et al.*, 2014). The order with greatest species richness is Rodentia with 146 species followed by bats and carnivores (Ceballos, 2013; Ramírez-Pulido *et al.*, 2014).

Despite the great diversity of all mammalian taxonomic groups in the country, the conservation status of Mexico is not optimal (Sisk, Castellanos & Koch, 2007; Figueroa *et al.*, 2008; Valdez *et al.*, 2006; Pisanty *et al.*, 2016). In the last decades, economic development has caused significant perturbations, such as soil erosion and deforestation, to Mexican ecosystems (Pisanty *et al.*, 2016). As a response, the government developed environmental policy instruments such the Protected Area (PA) network, among others (Pisanty *et al.*, 2016). In Mexico, a PA is a representative portion of the different ecosystems in the national territory where the original environment has not been highly modified by human activities, and that has certain ongoing activities related to protection, conservation or restoration (Conanp, 2016). There are 182 PAs in Mexico, and they are managed at three levels; federal, which involves all of the IUCN management categories, regional and private, which have laxer management regimes. The total protected area of Mexico represents 11% of the national territory (Conanp, 2016). The PAs in Mexico most gather some biological requirements in order to belong to the National Natural Protected Area System (SINAP), such as high levels of SR, endemism and functional integrity of the ecosystems, among others (Conanp, 2016). In this way, SINAP ensures that PAs are representative of the relevant biological features of the area they are located.

Based on the aforementioned, this project aims to identify the areas of high mammalian evolutionary diversity in Mexico as well as to compare species richness patterns with phylogenetic diversity. On the other hand, it also aims to compare if current protected areas in Mexico conserve this evolutionary diversity and to identify if Protected Areas are complementary in terms of phylogenetic representativeness. We hypothesize that some unprotected regions of Mexico will be identified as having higher PD. We also expect the PD and SR patterns to correlate, and that β -diversity analyses reveal hidden patterns of the protected and non-protected mammal communities.

2 MATERIALS AND METHODS

Several methodological steps were undertaken in order to assess the spatial patterns of mammalian phylogenetic diversity. First the species selection was done based on data availability. Species distribution ranges were obtained from Mexican and international repositories in order to assess the species richness status in the country. Subsequently the molecular data for the selected species were assembled both from a repository and from DNA extraction and Sanger sequencing. Once all the sequences were aligned, they were used to generate a maximum-likelihood phylogenetic tree. Then, the species richness data and the phylogenetic tree were utilized for the phylogenetic diversity analysis. The phylogenetic diversity map was overlapped with the map of Mexican PAs in order to assess if phylogenetic diversity is being conserved. Finally, β and phylo β -diversity was calculated for the PAs mammal community and the rest of the country to assess the turnover between these two communities and to inform the proposal of novel areas for protection. β and phylo β -diversity were also calculated within the PA community in order to assess phylogenetic complementarity. A flowchart of the methods used for this thesis can be found in Supplementary material *Figure B6*.

2.1 Species selection and Spatial Data analyses

The species selection was done based on the list of Mexican terrestrial mammals of Ramirez-Pulido et al. (2014), which is one of the most recognized taxonomic authorities in the country. Out of an initial list of 497 terrestrial mammals, 479 species were selected for use in this study (Supplementary *Table A1*). The other 18 species were removed from the study due to lack of distribution data. For the phylogenetic analysis, another 34 species were excluded from the study due to a lack of molecular data on open-source repositories or because loans from biological collections were not possible. Species with a synonym already included on the initial list were also removed. Both molecular and species range data were based on the same species name.

For this final list of 479 species, geographical distribution maps were obtained from the IUCN Red List (IUCN, 2020) and from the Biogeographical Atlas of North American Mammals (Escalante, 2013; Escalante, Noguera-Urbano & Corona, 2018). Range maps were downloaded

as shapefiles and converted into a rasterized, 10x10 km equal-area grid. Grid cells were considered occupied by those species where the grid cell center intersects with the species range, as suggested by Safi *et al.* (2011). Species richness was calculated utilizing the R packages ‘*rasterVis*’, ‘*rgdal*’ and ‘*sp*’, as the number of occurrences of species per grid cell.

The PA maps were originally downloaded as polygons in the form of three different maps. Only federal PA polygons were used. Regional and private PA were excluded from the study because the resolution used in this study does not allow to analyze PA smaller than 100 km². Some federal PA were smaller than 100 km² as well, so they were also excluded from the study (see Supplementary *Table A3*). 182 PA vector files were obtained from the CONABIO database (Conabio, 2018).

All maps used for the spatial data analyses (the species’ distribution ranges, the protected area map, and the Mexican transition zone map) were re-projected into a Lambert conformal conic projection.

2.2 Molecular Data processing

Molecular data of 434 species was obtained from NCBI’s GenBank public repository for sequence data. GenBank sequences were obtained using MatrixMaker, a custom Python script (Freyman & Thornhill, 2016). Three mitochondrial markers were found to have broad coverage over the 434 species: cytochrome b (*cytB*), cytochrome oxidase subunit 1 (*COI*), and the *12S* ribosomal RNA gene (*12S*). When multiple sequences were available for a single species, the longest sequence was selected. At least one of the relevant markers was obtained from GenBank for the 434 species.

For the remaining 63 species, we attempted to obtain representative samples via institutional loan from various institutions in Mexico and the US. However, we were only able to obtain destructive sampled specimen fragments (either tissue, hair or bone samples or DNA extracts) from 30 species (Supplementary *Table A2*). Most of the samples were obtained from the Museum of Zoology “Alfonso L. Herrera” of the Faculty of Sciences (MZFC), and Institute of Biology (IB), both from the National autonomous university of Mexico (UNAM), and from the National Polytechnic Institute (IPN). One of the samples was provided as a genomic DNA

extract. The molecular data for the remaining 29 species was generated from DNA extraction, and subsequent Sanger sequencing (Supplementary *Table A2*).

Once samples were received, DNA extractions were performed with Qiagen DNeasy Blood & Tissue® Kit. For each of the 29 samples, a bone/tissue fragment of between 10-25 mg was homogenized using a Qiagen TissueLyser II for 1 min at a frequency of 25 Hz. The DNA extraction protocol followed the manufacturer's recommended protocol. The only adjustment of this protocol was that the incubation period for the cell lysis was ca. 20 hours. The extracted DNA was measured with a Qubit™ dsDNA HS assay kit and Qubit 2.0 Fluorometer. Extractions were performed in three sets of samples, and one negative control (blank) was included in each extraction. All non-control DNA extractions were successful.

Polymerase Chain Reaction (PCR) was performed for each of the extracted products for three mitochondrial markers: *cytB*, *12S* and *COI*. Each PCR sample had a final volume of 50 µL, consisting of: 5 µL of PCR Buffer II, 3 µL of MgCl₂ (25 mM), 0.40 µL of dNTPs (25 mM), 1 µL of bovine serum albumin (20 mg/ml), 1 µL of each primer, both forward and reverse (10 µM each), 0.25 µL of AmpliTaq Gold™ polymerase (5 U/µL), 33.35 µL of molecular grade H₂O and 5 µL of the template DNA.

For *12S* and *cytB*, two primers were used, whereas for the *COI* marker, two primers and one degenerate primer cocktail were used since two regions of it were amplified (*Table 1*). The thermocycling protocols varied depending on the primers. The different protocols are described in *Table 1*. However, for the *COI* markers, most of the samples failed to amplify in the initial PCR, so a “prime” PCR was conducted for these samples. That is, a second, identical PCR round was conducted, except that the template DNA was the failed PCR product from the first round of PCR.

Table 1. The selected oligonucleotide primers and the PCR thermocycling protocols used for the amplification of the markers *12S*, *COI* and *cytB*.

Marker	Target taxa	Source	Primer IDs	PCR Protocol
<i>cytB</i> (68-bp fragment)	vertebrates	(Parson, Pegoraro, Niederstätter, Föger, & Steinlechner, 2000)	L14816-F, H15173-R	10 min of denaturation at 95°C; 40 cycles: 95°C 45s, 50°C 45s, 72°C 45s; final extension at 72°C 10 min.
<i>COI</i> (121-bp fragment)	mammals	(Ivanova et al., 2012; Pfunder, Holzgang, Frey, & Pfunder, 2004)	RonM_t1, C_VR1LRt1 (primer cocktail)	5 min of denaturation at 95°C; 40 cycles: 95°C 45s, 54°C 45s, 72°C 1min; final extension at 72°C 10 min.
<i>COI</i> (200-bp fragment)	mammals	(Ivanova, Clare, & Borisenko, 2012)	AquaF2, C_VR1LRt1 (primer cocktail)	10 min of denaturation at 95°C; 40 cycles: 95°C 45s, 54°C 45s, 72°C 60s; final extension at 72°C 10 min.
<i>12S</i> (up to 132-bp fragment)	vertebrates	(Riaz et al., 2011)	Vert01-F, Vert01-R	10 min of denaturation at 95°C; 40 cycles: 95°C 45s, 49°C 45s, 72°C 45s; final extension at 72°C 10 min.

For visualizing the PCR products, electrophoresis was conducted by first combining 10 μ L of PCR product with 1.67 μ L of dense gel solution (6X loading DNA gel), and then electrophoresing in a 2% TAE gel stained with 9 μ L Invitrogen™ SYBR safe. The PCR products were compared to a 100-bp ladder. Not all PCR reactions were successful. Only 105 samples (70.5%) of PCR reactions were successfully amplified. The successful products were purified, and Sanger sequenced by Eurofins Genomics.

2.3 Phylogenetic analysis

In order to generate the phylogenetic tree of the Mexican mammals, an alignment of the overall sequences was performed using the program Geneious (version 2019.2.3). First the newly generated sequences for each of the three markers were independently aligned. The forward and reverse chromatograms, obtained by DNA extraction and subsequent sequencing were both manually and automatically edited and subsequently trimmed, in order to keep only high-

quality sequences. These were then aligned, and the consensus nucleotide sequence for each sample was exported to text format. Low quality sequences were eliminated from subsequent analysis. The automated alignment was performed with ‘MAFFT Alignment’ by including the generated sequences and the ones obtained from GenBank. Alignments were manually adjusted in problematic regions.

The three marker alignments were then concatenated into a single, 3727-bp multiple sequence alignment (MSA), which was used to infer the phylogenetic tree with RAxML-HPC BlackBox (v 8.2.12) via the CIPRES Science Gateway v 3.3 online platform (Miller, Pfeiffer & Schwartz, 2010). A partitioned maximum-likelihood analysis was conducted with RAxML (3 partitions, 500 bootstraps) based upon a nucleotide substitution model with gamma-distributed among-site variation (‘GTRGAMMA’).

The reconstructed evolutionary relationships between the species were compared against the topology of a reference phylogeny produced by TimeTree (Supplementary *Figure B*), since it generates a phylogenetic tree based on recently published literature on evolutionary relation of the selected taxa. The first tree did not conform to the accepted topology, and particularly two mammalian orders (Rodentia and Lagomorpha) were paraphyletic. This was resolved by constraining all orders to be monophyletic groups in accordance to Speed et al. (2019). The constraint tree defines relationships between selected taxa and afterwards determines the highest-likelihood tree that conforms to this constraint. In analyzing the resulting phylogeny, if a node had low support (<70%), but the resulting phylogeny was congruent to the reference tree, each of the tree branches were not inspected further. FigTree v 1.4.4 was employed to visualize the dendrograms. The final constraint tree included 437 species and was exported as a Newick file format for further analysis. The topology of the phylogenetic tree is displayed in *Figure 1*.

2.4 Biodiversity analyses

The biodiversity analyses were conducted using R and by importing both the distribution data sets and the phylogenetic trees. The script for running all the biodiversity analyses described on this section is available in GitHub³.

Species richness and phylogenetic diversity were calculated for all 72,594 raster grid cells (equal area 10x10 km) in R. Species richness was calculated a sum of a raster stack, where all individual species had a value of one in their distribution areas, resulting in a numeric value indicating the number of species per grid cell. Phylogenetic diversity was calculated by utilizing the '*picante*' package (Kembel et al., 2010) in R. This package calculates the phylogenetic diversity of an area as the sum of the total branch length for the subset of species present within each cell.

The β and phylo β analysis were conducted in order to assess the compositional and phylogenetic dissimilarity between the PA's mammal community and the rest of the country. Phylo β diversity offers a complementarity approach to phylogenetic community assembly. β -diversity was calculated in R using the '*betapart*' package for each of the cells outside protected areas and all the cells of the protected areas, merged as one single community, and for each PA. For assessing the phylogenetic complementarity between PA, a hierarchical cluster analysis was carried out based on the phylo β -diversity of the PA. The cluster analysis was also carried out based on the compositional β -diversity of the PA. The cluster analysis was carried out with the '*stats*' package.

³ GitHub repository: <https://github.com/JamesDMSpeed/Mexican-mammal-phylogenetic-diversity/blob/master/MexicanMammals.R>

3 RESULTS

3.1 Phylogenetic analysis

The total data completeness (proportion of species used in this study with genetic data) per marker varied. The markers with the highest completeness were *cytB* and *COI* with 82.5% and 54.3%, respectively. The coverage of *12S* was 46.3%. The tree conformed to known topology, and the resulting clades were all monophyletic (*Figure 1*). The node support in the resulting tree ranges from 100% to 12%, with lower support in shallow nodes that distinguish highly related species.

3.2 Biodiversity pattern analysis

Two mammalian biodiversity maps were generated based on the distribution ranges and the phylogenetic tree (*Figure 1*). The resulting maps have a total of 72,594 cells. The cell with the highest mammal richness contains 145 species and is in the southeastern part of the country (Chiapas), whereas the cell with the lowest species richness has only two species and is in the Baja California Peninsula. The states of Oaxaca and Chiapas⁴ hold the highest diversity, containing around the 31% of all the mammal species of the country. On the other hand, Baja California and Baja California Sur are the least diverse states, with only the 7% of the mammal species. The mean mammal SR in Mexico is of 7.8 species per 10 km². The SR analysis was done with the initial species selection of 479 species.

⁴ For the geographical location of the Mexican states see Supplementary material *Figure B7*

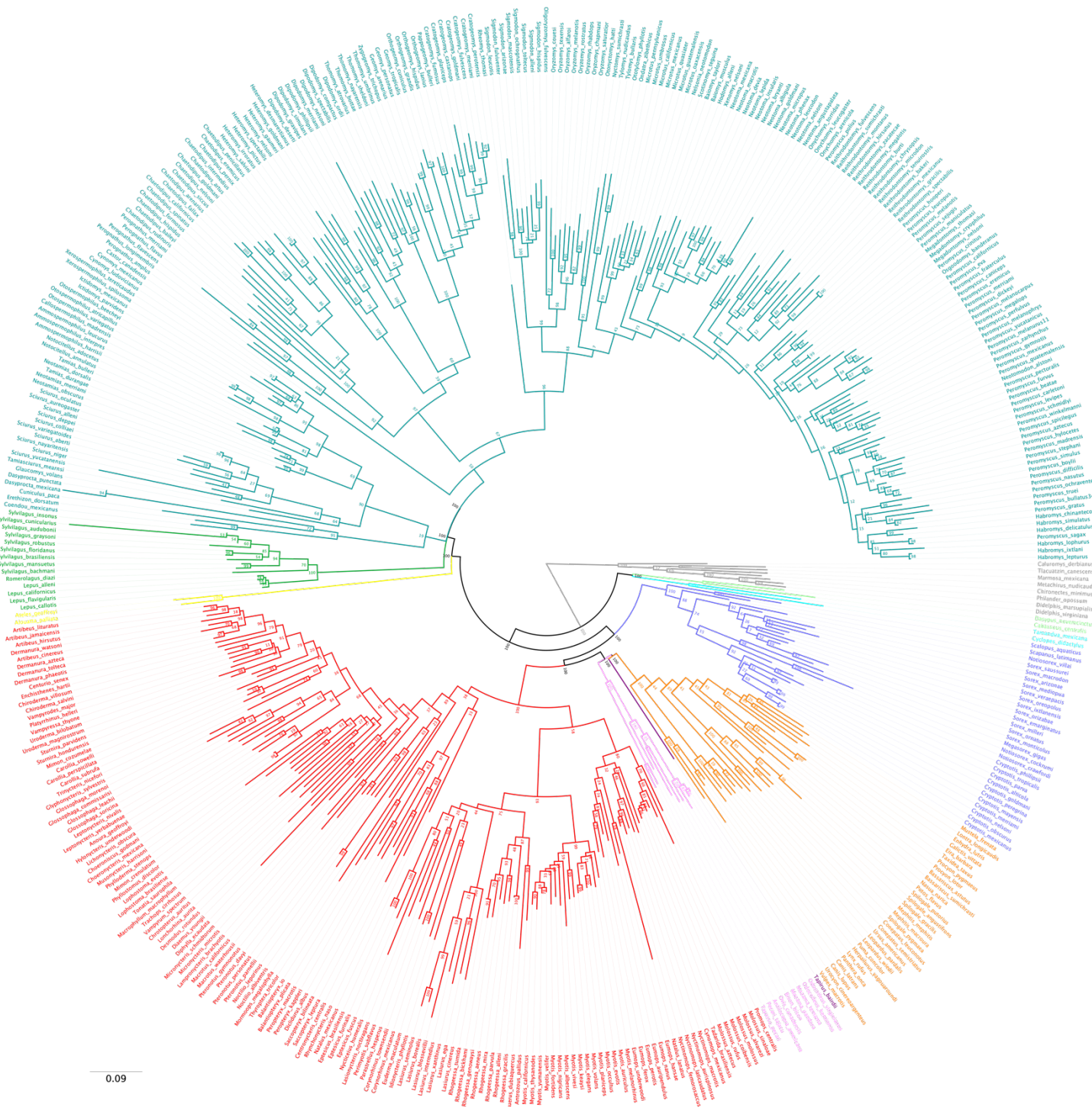


Figure 1. The topology of the maximum-likelihood phylogenetic tree of Mexican mammals based on the mitochondrial markers *cytB*, *COI* and *12S*. The length of the scale bar indicates the branch length in number of substitutions per site according to the evolutionary model 'GTRGAMMA'. The numbers at the nodes indicate bootstrap values. The branch colors show species of the same order; grey branches correspond to the order Didelphimorphia, light green to Cingulata, light blue to Pilosa, purple to Soricomorpha, pink to Atiodactyla, magenta to Perissodactyla, orange to Carnivora, red to Chiroptera, yellow to Primates, green to Lagomorpha and blue to Rodentia.

The observed PD patterns are similar, although not identical to the SR pattern, as expected. Both diversity measures are highly correlated (Supplementary *Figure B2*). In general, PD has higher values than SR across Mexico, although they tend to correspond across the country (*Figure 2*). However, phylogenetic diversity increases slightly more in the Mexican transition zone, whereas species richness is highly concentrated towards the southeast of the country. In agreement with SR, the highest amount of PD is located in the southeast of the country, in the states of Chiapas and Oaxaca. The lowest amount of PD is located at the northwest of the country, in the Baja California Peninsula. For the phylogenetic diversity analysis, only 451 species were used because the remaining 29 species used also for the SR lacked molecular data.

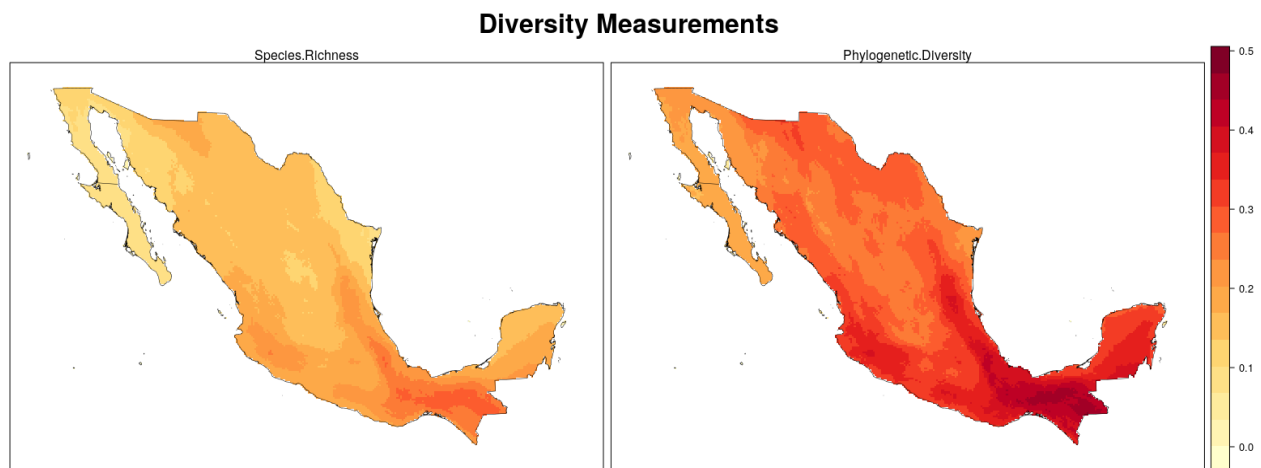


Figure 2. Distribution maps of species richness and phylogenetic diversity of Mexican mammals. Maps are presented as a proportion of the total diversity pattern. SR is presented as the sum of species found in a cell and PD as the sum of branch lengths in a cell. The maps are projected in Lambert Conformal Conic projection. A total of 72,594 cells with 10 by 10 km dimensions.

3.3 Protected areas and PD conservation

Protected areas conserve 90% of Mexican mammal PD and SR. There are 48 distribution ranges of species that are not being conserved by Mexican protected areas. 68% (33) of these species are under any IUCN endangered category, 75% (36) are endemic to Mexico, whereas the remaining 25% (12) are broadly distributed outside the political borders of Mexico, particularly towards the US. 75% (36) belong to the order Rodentia, and of these 36 rodent species, 30.5% (11) are from the endemic genus *Peromyscus* (Supplementary *Table A4*).

The PA with the highest mammal richness and PD was the Biosphere Reserve *Selva El Ocote*, and presented 144 species in one cell, in the southeastern part of the country (Chiapas), whereas Biosphere Reserve *Lagunar Ojo de Liebre* was the one with the least species richness per cell had only two species, in the Baja California Peninsula. The mean mammal species richness in the PA is of 77 species per 100 km². The species richness analysis was done with the initial species selection of 479 species. PD patterns across PA behave just like SR, being *Selva El Ocote* the PA with the greatest PD and *Lagunar Ojo de Liebre* with the least (Supplementary Table A5).

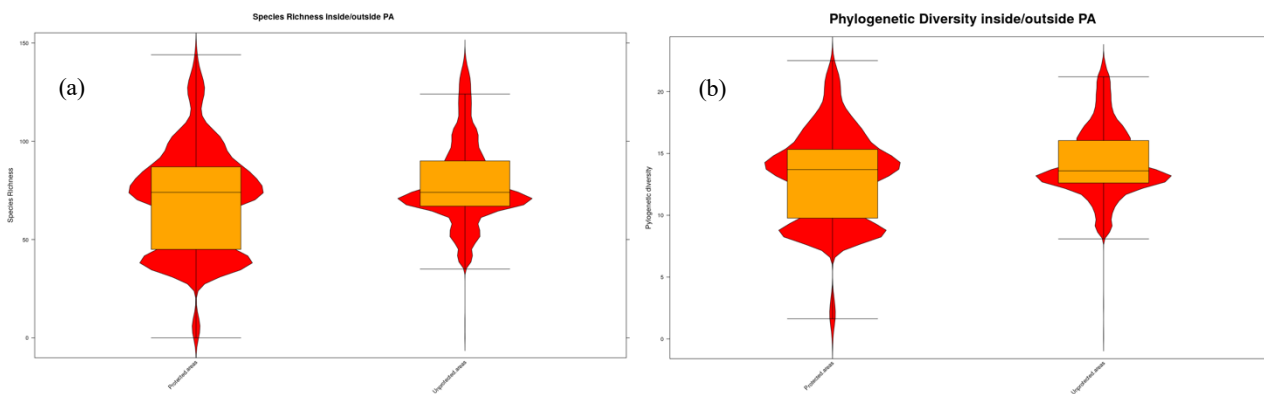


Figure 3. Diversity measurements' boxplots of species richness (a) and phylogenetic diversity (b) in protected and non-protected areas. The violin plots represent the distribution of the number of species/branch lengths respectively per cell both inside and outside protected areas.

As mentioned before, the patterns of PD and SR inside and outside PA is very similar (for example the mean of 77 and 78 species, respectively). The distribution of both PD and SR inside PAs is multimodal, meaning that the data has two wider sections (*Figure 3*). Wider sections of the violin plot represent a higher probability of observations taking a given value, the thinner sections correspond to a lower probability. Most of the cells outside PAs have values closer to the median, whereas the PAs have cells with values further away from the median. The highest concentration was on the first quartile, between ca 30 and 50 species, and on the third one closer to the median for both PD and SR. The cells inside PAs have broader range of possible values whereas the cells outside PAs have a narrower range of possible values, therefore the SR and PD of cells inside PAs are more variable than those outside PAs.

Protected areas were also ranked based on the amount of total PD that they conserve. The ten most relevant PAs for conserving PD are listed in *Table 2*. The first three PAs are *Selva el Ocote* (59%), *Lagunas de Montebello* (58%) and *Montes Azules* (54%) (Supplementary Table A5).

These PAs are mostly located towards the southeastern part of the country, Chiapas and in the MTZ.

Table 2. The 20 most relevant protected areas in terms of phylogenetic diversity conservation. First column indicates the ranking position of the PA from highest PD to lowest. Second column indicates the name of the PA. Third and fourth indicate the management categories of the area according to IUCN and the Mexican systems accordingly. The fifth column indicates the location of the PAs. The last column shows the percentage values of PD that the PA hold. Values have been normalized to the mean.

Rank	Name	IUCN	Mexico ⁵	State	PD [%]
1	Selva El Ocote	IV	RB	Chiapas	59
2	Lagunas de Montebello	II	PN	Chiapas	58
3	Montes Azules	IV	RB	Chiapas	54
4	La Sepultura	IV	RB	Chiapas	50
5	Lacan-Tun	IV	RB	Chiapas	48
6	Yaxchilán	III	MN	Chiapas	46
7	Z.P.F. en los mpios. de La Concordia, Ángel Albino Corzo, Villa Flores y Jiquipilas	VI	APRN	Chiapas	46
8	Chan-Kin	VI	APFyF	Chiapas	43
9	Palenque	II	PN	Chiapas	42
10	Tehuacán-Cuicatlán	IV	RB	Puebla, Oaxaca	41
11	Cañón del Río Blanco	II	PN	Veracruz, Puebla	41
12	El Triunfo	IV	RB	Chiapas	41
13	Cañón del Usumacinta	VI	APFyF	Tabasco	40
14	Pico de Orizaba	II	PN	Veracruz, Puebla	38
15	Volcán Tacaná	IV	RB	Chiapas	37
16	Cofre de Perote o Nauhcampatépétl	II	PN	Veracruz	34
17	Calakmul	IV	RB	Campeche	33
18	El Jabalí	VI	APFyF	Colima	31
19	Los Tuxtlas	IV	RB	Veracruz	30
20	Sierra de Manantlán	IV	RB	Jalisco, Colima	27

⁵ Mexican management categories:

RB: Biosphere Reserve

PN: National Park

MN: natural monument

APRN: Protection area for natural resources

APFyF: protection area of flora and fauna

3.4 β -diversity analysis

The β and phylo β -diversity analyses show that the islands in the Baja California Peninsula and Cozumel (in the Caribbean part) are, in terms of species and phylogenetic composition, the most different non-protected places from the PA community, with Cozumel being the most relevant for future conservation action. The areas of highest (phylo) β -diversity are located towards the northwest part of the country and the lowest to the southeast (*Figure 4*), which is an opposite pattern from the one in *Figure 2* for PD and SR.

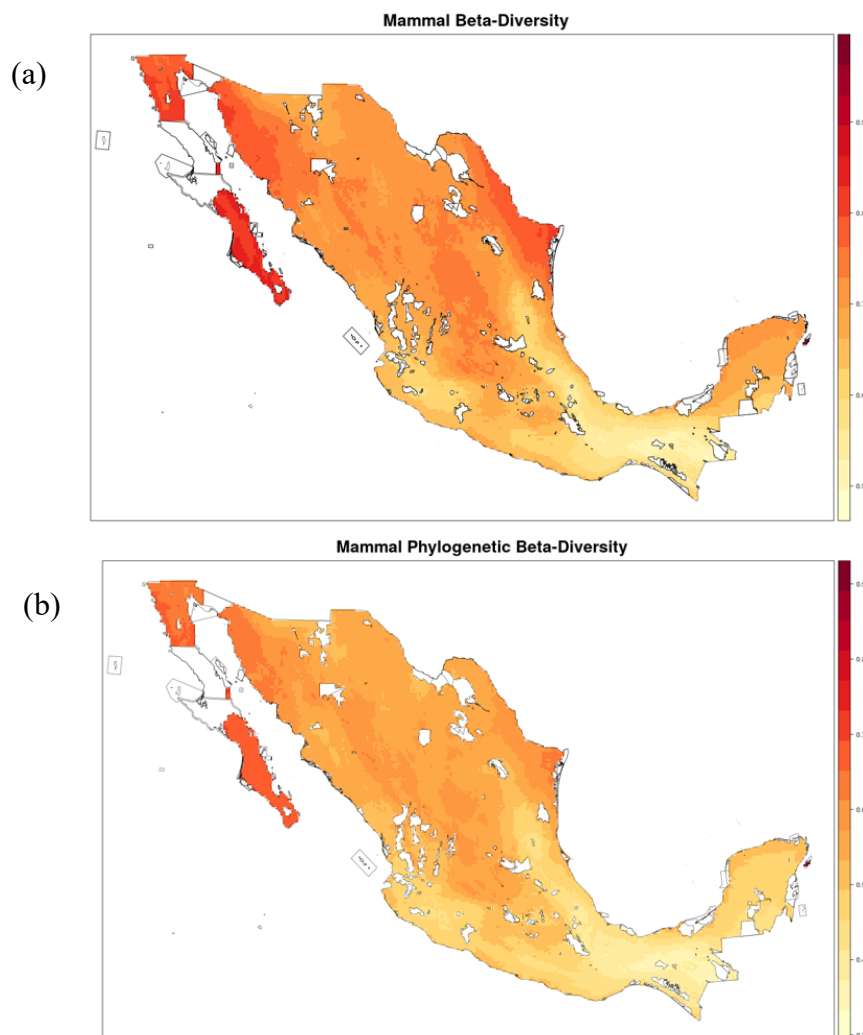


Figure 4. β -diversity (a), phylogenetic β -diversity (b) between protected and non-protected areas. Low values of (phylo) β -diversity represent less dissimilarity between the two communities whereas high levels show greater dissimilarity. The polygons without color represent the PAs that constitute the federal PA network.

In order to assess the complementarity of phylogenetic composition of PA, a hierarchical clustering analysis was conducted based on phylo β -diversity. The optimal number of clusters determined by the 'ward.D' method was 10. Clusters were categorized based on the biogeographical regions proposed by Morrone *et al.* (2017) in Neartic (blue), Neotropical (red) and the Mexican Transition Zone (green). The clusters were represented as a dendrogram (Figure 5 (a)) but also in a map (Figure 5 (b)) to visualize them geographically.

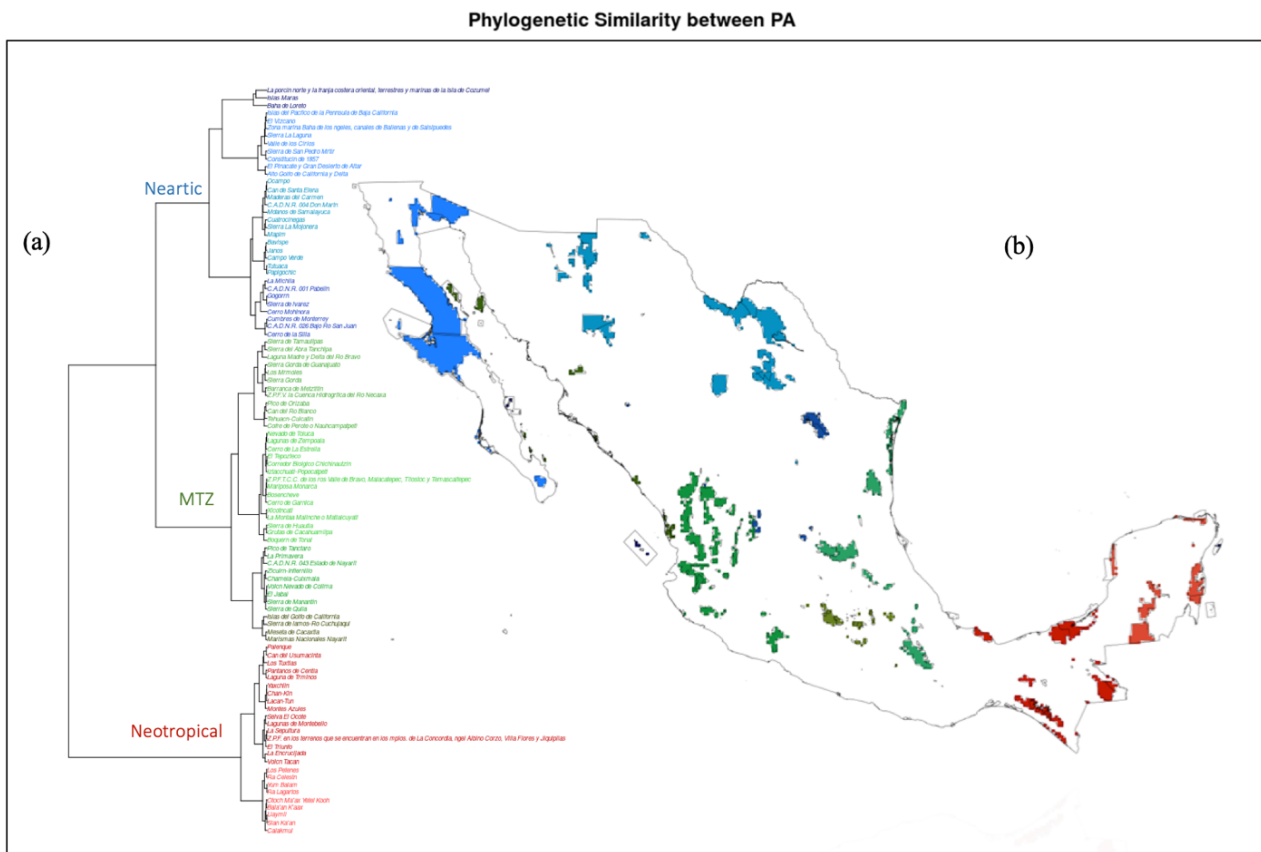


Figure 5. Hierarchical clustering of the PA of Mexico based on the phylo β similarity index of the Mexican mammals. PA were grouped into 3 clusters. Hierarchical dendrogram (a) and geographical representation of the three clusters of PAs (b). Colors correspond to the clustering based on the biogeographical regions of Mexico in both figures. Blue represents the Neartic region, green the Mexican Transition Zone and Red the Neotropical region.

4 DISCUSSION

This is the first attempt to incorporate different taxonomic measures, SR, PD and phylogenetic β -diversity, at a national scale and within the PAs, with a complete taxonomic group at the class level (Mammalia) in Mexico. This is also the first study to use multidimension biodiversity analysis at the national scale in Mexico using a relatively high resolution. The patterns of PD and SR are highly correlated, with the southeast part of Mexico being the most highly diverse area. PAs overlap with most of the species ranges used for this study, and they can be divided into three main groups based on their phylogenetic similarity. This study functions as a basis for a more informed conservation-planning and decision-making process as it advances our understanding on the current conservation status of the mammal phylogenetic diversity based on the Mexican PA network/system. The present study also emphasizes the importance of basing conservation efforts not only on highly species-rich areas, but on areas deemed valuable for the evolutionary history that they contain.

4.1 Diversity analyses: PD and SR

Species richness and β -diversity have been previously calculated for communities of several taxonomic groups at national scale in Mexico (Rodríguez, Soberón & Arita, 2003; Escalante *et al.*, 2007; Koleff & Soberón, 2008; Martín-Regalado *et al.*, 2020). That being said, phylogenetic diversity is a relatively novel and promising biodiversity measure that has also been assessed for some taxonomic groups in Mexico at very local scales and with narrow taxonomic levels, usually at the family level (Martín-Regalado *et al.*, 2020).

This study assessed PD for the whole Mexican territory for the class Mammalia. The results of this study show high similarity between PD and SR, which is due to their linear relationship and their high correlation (0.97). Their mirroring patterns in the country (Supplementary *Figure B2*) can be explained in that when SR increases, it adds more taxa (more branches) to a phylogeny, which increases the total sum of the branches and therefore PD (Karanth *et al.*, 2019).

Both PD and SR patterns show greatest diversity towards the southeastern part of the country and least towards the northwest (*Figure 2*). This is likely due to the environmental heterogeneity of Mexico, particularly the distinct types of vegetation and great climatic and elevational variability (Rodríguez *et al.*, 2003). The most productive ecosystems (*e.g.* the *Lacandona* rainforest) are found on the southeast, mainly in the state of Chiapas, which can explain the greater number of species and the higher levels of phylogenetic diversity. The least productive ecosystems (*e.g.* the Sonora desert) are located in the north and northeast, where the least diverse cells were found. A consequence of this heterogeneity is the presence of a high number of endemic species and, in general, species with small distribution ranges. This implies that the species turnover must be high and thus explains the high α -diversity of Mexico as a whole (Valdez *et al.*, 2006; Koleff & Soberón, 2008).

Likewise, Rodríguez *et al.* (2003) suggest that the high levels of SR in the southern part of Mexico are mainly due to diversity within the chiropterans, as they presented different geographical patterns than the rest of the terrestrial mammals. The diversity of chiropterans tends to increase towards the southern part of Mexico (and other tropical latitudes of America), while the patterns of the other terrestrial mammals are not so pronounced, indicating that the high diversity patterns of the mammals is driven mainly by chiropterans (Rodríguez *et al.*, 2003), suggesting that the high PD diversity patterns towards the southeast is also driven mainly by the order Chiroptera.

4.2 Protected Areas and PD conservation

The PA network in Mexico overlaps with some part of the ranges of 90% (431 species) of mammal species in Mexico. In an attempt to understand why the remaining 48 species are not being conserved by the PA systems, we can divide them in two types: those that are restricted (endemic) to certain areas of Mexico and those whose distribution ranges extend beyond the Mexican borders. This last group constitutes 25% of the non-protected species. None are considered as threatened according to the IUCN (IUCN, 2020), and most of them only slightly distribute in Mexico (*i.e.* Mexico is a small part of their total range). For this reason, the fact that they are not being conserved in Mexico does not imply that other countries are not taking conservation actions to protect and maintain the status of these species. Such is the case of *Ondatra zibethicus*, which occurs all across the US and only slightly extends beyond the

Mexican border. Some parts of the distribution range of this species are covered by American PAs (IUCN, 2020).

For the other type of species (the ones endemic to Mexico), 95% are assigned to an endangered category from IUCN, 1.7% are categorized as '*Least Concern*' and 2% as '*Data Deficient*' (Supplementary Table A4). One of the main reasons why these endangered species are not being conserved is because they are all small rodents and moles (Supplementary Table A4). Small species in general are poorly known. The lack of protection of the small endemic mammals is therefore associated with the Linnean and Wallacean shortfalls: the absence of biological data about them, such as their systematics, distributions, relative abundances, natural histories and ecologies (González-Ruíz *et al.*, 2005). For example, *Peromyscus bullatus* is one of the species listed on Supplementary Table A4. *P. bullatus* is an endemic mouse with a very restricted distribution range in the Oriental basin in the eastern part of Mexico (state of Veracruz). What is interesting of this mouse is that in the species report of IUCN, it is stated that *this species is protected in Mexico* (Álvarez-Castañeda, 2018) by the NOM-059-ECOL-2001⁶ but no more information is available on the topic.

A quick literature review revealed that, at least until 2005, there were none ongoing conservation actions in the country for the protection of *P. bullatus*. According to González-Ruíz *et al.* (2005), *P. bullatus* is a highly threatened species by land use change processes in the area where it is distributed, particularly changes from natural vegetation to agricultural land. Even though information of the conservation status has been available for some years now and the species is listed on the NOM-059 since 2001, this endangered species remains unprotected. It has been suggested that this could be because the species occupies an area with low SR (González-Ruíz *et al.*, 2005). However, the region has two endemic (and currently unprotected) species: *Peromyscus bullatus* and *Neotoma nelsoni* which are endangered (Supplementary Table A4). In the same region other endemic species have been recorded⁷: *Dipodomys phillipsii*, *Peromyscus mekisturus*, and *Reithrodontomys chrysopsis* (González-Ruíz *et al.*, 2005). The closest PA to the distribution of this species would be *Cofre de Perote*, which happens to be one of the PAs with the highest values of PD (number 16 in Table 2). Unfortunately, its area does not protect this mouse at all.

⁶ The Official Mexican Norm for the environmental protection of native species of Mexico. An official Mexican norm is a series of official compulsory standards and regulations for diverse activities in Mexico.

⁷ Species endemic to Mexico, not restricted to the state of Veracruz

Nevertheless, the PA system is conserving almost the totality of the Mexican mammals. The PD of Mexican mammals at the genus level is fully protected as one of the unprotected species in Supplementary *Table A4* are within unprotected genera. As presented in *Figure 3*, both the median and the average number of species and phylogenetic diversity inside and outside PAs are not significantly different. This suggests that the Mexican PA network is conserving (at least some parts) of the distribution ranges of the Mexican mammal community. However, other factors should be studied in order to address the effectiveness of PA in conserving mammals⁸.

PAs conserve areas with very diverse values of PD and SR. The bimodal distribution in the PAs (*Figure 3*) shows that PAs can be divided into mainly two types: those with higher PD and SR, and those with lower. The fact that PAs are not only conserving the areas of the highest diversity (both compositional and phylogenetic) is important due to the heterogeneity of the country. As explained above, the elevational and climatic heterogeneity of Mexico, as well as the presence of islands, has favored the establishment of many endemic and range-restricted species, which means that there are many species that are distributed in only very small areas due to their high environmental specificity. For this reason, it is relevant to establish a widespread network of several PAs across the Mexican territory that protects and represents the highest possible diversity with the available resources. This can explain the distribution of the data in *Figure 3*, where PAs are conserving areas with both very high and very low values of PD and SR. This also explains the more even distribution of the per-cell PD and SR in non-protected cells.

The most phylogenetically diverse PAs are concentrated in Chiapas (*Table 2*), where the highest SR is also localized, confirming once again the link between these two biodiversity measurements. The second most diverse set of PAs in Mexico corresponds to the MTZ area. This is because the MTZ contains biota with the evolutionary history from both the Nearctic and neotropical biogeographical regions (Morales *et al.*, 2016). Out of those, 50% are Biosphere Reserves, suggesting that this management category might be the most appropriate for conserving mammal PD. This ranking has implications for the conservation of Mexican mammals as it proposes a set of areas that can be prioritized for the conservation of the mammalian phylogenetic tree. Nevertheless, because Mexico possesses a high β -diversity (Rodríguez *et al.*, 2003), allocating resources only to, for example, the first three most phylogenetically diverse PAs won't succeed in better protecting the mammalian PD of the

⁸ This is discussed in depth in sections 4.4 and 4.5

country. A phylogenetic dissimilarity analysis of the PA network's mammal community would be more informative in assessing how to better allocate conservation resources for Mexican mammals (*Figure 5*). This will be discussed in more depth in 4.3.1.

This study addresses the conservation status of the Mexican mammals based on the federal protected area system. Not all of the federal PA's were included because of their small sizes (smaller than 10x10 km) and because most of them do not have any management plans (Supplementary *Table A3*). An example of this is *El Histórico de Coyoacán*, a national park of 5 km² located in the center of Mexico City. This is mainly used as a park and running tracks as well as a nursery garden. The flora of this national park is composed of mainly alien species, mostly eucalyptus. The only mammal species distributed there is *Sciurus aureogaster*⁹. For this reason, the PAs excluded from this study do not belong to National Natural Protected Area System (SINAP). In order to belong to the SINAP, a PA must have some of the following characteristics: (1) SR, (2) endemism, (3) presence of range-restricted species, (4) ecosystem diversity, (5) functional integrity of the ecosystems, (6) high relevance of the generated ecosystem services, and (7) social viability for its preservation (Conanp, 2016). Based on these points, the SINAP ensures a good allocation of resources for conservation of the relevant features inside the PA.

4.3 β and phylo β diversity analysis: Complementarity and priority areas of conservation

Because of the high α -diversity of Mexico inside and outside PAs, and both in terms of number of species and the sum of branch lengths in a given area, it is interesting to analyze to which degree are the two communities (inside vs. outside PAs) similar. Analyzing the species composition as well as the phylogenetic similarity between the two communities and within the PA area community can reveal more information about the Mexican mammal conservation status.

The results showed that, contrary to our hypothesis, the (phylo) β analyses were not informative. The analysis both present the lowest values towards the southeast area and the highest values to the northwest, a mirroring effect with respect to PD and SR patterns. This is because the

⁹ For more information see <https://www.gob.mx/semarnat/articulos/el-historico-coyoacan>

highest number of species/branch lengths are concentrated towards the Chiapas region. Comparing those areas with the protected mammal community, they share more features than in the areas with lower PD/SR values. Furthermore, meaning that the proportion of the total species (and thus the branch lengths) in the PAs is so high that the differences between protected and non-protected communities are dominated by species missing from the other sites, rather than species missing from the protected areas.

Previous studies show that β and phylo β patterns might be highly correlated (Leprieur *et al.*, 2012). This was also verified in this study as the β and phylo β indices were highly correlated, based on the Sørensen's dissimilarity index (Supplementary *Figure B3*). The correlated patterns of β and phylo β can be explained by the expected variation of β and phylo β from Graham & Fine (2008). The areas of the south and southeastern part of Mexico with low levels of both β and phylo β meaning that there are similar species composition between the two sites, *i.e.* widespread species. On the contrary, the areas of the Baja California Peninsula, and especially, the island of Cozumel, with high and very high levels of (phylo) β , respectively, show that there is a high proportion of small-ranged species, with higher than expected average divergence times (Graham & Fine, 2008). The areas with higher β and lower phylo β can be explain by the high proportion of small ranged species that had diversified recently (Graham & Fine, 2008). For the particular case of Cozumel, it is important to remember that this study is only analyzing federal PAs. A small part of the Cozumel island is covered by a federal PA¹⁰, which mainly aims to protect the marine area. However, most part of the rest of the island is protected by a regional PA, so the mammal species located in that area are currently under a protection scheme, just not by a federal PA. This is the only case in which a regional or private area are conserving species not included in the federal PA community.

The phylogenetic complementarity analysis within the PA community reveals that none of the PAs has a particularly distinct phylogenetic composition. Instead, they group into biogeographical regions: the Nearctic region to the north, the MTZ in the center and in the principal mountain systems, and the Neotropical to the south and southeast (*Figure 5*). At the same time, the PAs form subgroups within the biogeographical regions that would correspond to the Mexican biogeographical provinces proposed by Morrone *et al.* (2017) (Supplementary *Figure B4*). The complementarity analysis was also conducted based on species composition,

¹⁰ La porción norte y franja costera de la Isla de Cozumel

and it presented the same patterns of PA grouping as phylogenetic complementarity (Supplementary *Figure B5*). This shows that protected areas indeed complementary in terms of their phylogenetic and species composition and that it is important to maintain the geographical spread of the current PAs network. The hierarchical dendrogram suggests that the Neartic PAs are the most distinct in terms of phylogenetic composition. One of the clusters within the Neartic region is composed of PAs located in islands, which can be explained by the high proportion of mainly paleoendemic species with small ranges (Graham & Fine, 2008), as the compositional complementarity analysis also grouped this three PAs as the most distinct in terms of species composition.

4.4 Conservation Implications

The results of this study are in agreement with the suggestion that areas selected by species-based conservation also perform well for PD conservation (Rosauer *et al.*, 2017). PD of Mexican mammals overlaps with the PA network in a very similar way as SR does, which indicates that same conservation actions can be taken for preserving both PD and SR.

Despite the fact that PAs overlap with the distribution ranges of most of the Mexican mammals, further work is needed in order to assess the effectiveness of PA in conserving mammals' populations, as the PA establishment does not guarantee effective protection of threatened species. PA effectiveness analysis can be based on, for example, population dynamics, ecosystem integrity and land use change inside PAs, as well the effects that climate change will have on species' distributions and how current conservation actions should be conducted.

Analysis of population viability within the PAs allow assessment regarding if PAs ensure the long-term preservation of the species. For example, the jaguar (*Panthera onca*) is considered an endangered species in Mexico mainly due to habitat loss and illegal extraction (Quigley *et al.*, 2017). It is distributed in the southeastern part of Mexico, and many protected areas overlap with its distribution. However, only two protected areas (*Calakmul* and *Sian Ka'an*) are large enough to sustain jaguar viable populations (Valdez *et al.*, 2006). Nevertheless, it is important to mention that there are species that do not need to be within PAs to have viable populations, as their populations tend to perform well outside PAs. Examples of these are the Mexican wolf (*Canis lupus baileyi*) (Lara-Díaz *et al.*, 2015), coyote (*Canis latras*), gray fox (*Urocyon cinereoargenteus*), and the coati (*Nasua narica*), among others (Coronel-Arellano *et al.*, 2016).

Another way to ensure conservation actions in the PAs would be through PA's management plans. Unfortunately, prior to 1994 most of NPAs lacked management plans, and between 1994 and 2000, management plans were developed for only around 30% of PAs (Valdez *et al.*, 2006). More management plans have been developed, but still not all PAs have one. In addition, due to the actual circumstances of rapid change (*i.e.* climate change and accelerated land use change processes), management plans should be adaptive in terms of the monitoring and evaluation of the plan implementation and modifying goals according to the changing condition in order to better achieve the PA's conservation goals.

In terms of the PA network geographic location and the goal of conserving the overall PD of the country, it is important to keep a network of spread protected areas so that most the biodiversity features are covered. This is particularly relevant for places with high levels of β -diversity as Mexico. In an area with high β - and phylo β -diversity (large compositional and phylogenetic turnover), only a system of widespread PAs all over the territory would be capable of accounting for all the diversity within it. Grouping the PAs in terms of phylogenetic similarity can also be important for future conservation actions as they could be managed as the groups based on their phylogenetically similarity. For example, promote connectivity between the PAs within a group (*e.g.* the Neartic PAs), but avoid connectivity between PAs of different groups, since each biogeographical province has its own evolutionary history, and excessive connectivity between different provinces might promote the fusion of biotas with different histories that are naturally disjoint (Morales *et al.*, 2016).

It is also relevant to restate the fact that although not all the mammal species distributed in Mexico are within a PA, the overall PD of the group is within the PA network as all of the mammal genera are being preserved by the PAs. This is relevant for a conservation point of view since, in the current scenario where resources are limited and the protection of some species needs to be prioritized over others, PD provides a framework for deciding in which areas to allocate resources in order to conserve the evolutionary history of a group, even though not all the species will be protected. This way of prioritizing is relevant, since the extinction of species that are closely related to others would not represent such a disproportionate loss of evolutionary and genetic diversity as it would the extinction of a species that is not closely related to any other living ones (Rodrigues & Gaston, 2002).

4.5 Limitations and further work

This study assessed the PD and SR of Mexican mammals in the whole country and inside the federal PA network, both in terms of turnover and absolute values per unit area. Although this is very valuable information contributing to the knowledge of the taxonomic group (Mammalia) and its conservation status in Mexico, the incorporation of more dimensions of biodiversity (e.g. functional diversity, both in its α and β dimensions) promises to yield an even better understanding of mammals' diversity in Mexico.

Most of the diversity analyses in Mexico are calculated at a medium resolution of the grain, usually 0.5^{011} or larger (Rodríguez *et al.*, 2003; Escalante *et al.*, 2007; Escalante *et al.*, 2010; Martín-Regalado *et al.*, 2020). The resolution of this study (10 by 10 km) allowed to calculate α and β SR and PD for Mexico. It was the highest resolution that consumed the least computational time. We tried to use a 1 by 1 km equal area grid cell to run the necessary analyses, but it was not possible for the program as it was too computationally intensive. We tried 5 by 5 km and then 100 km², and 10 by 10 km was the most optimal grid size for running the analyses. Based on this, it is important to propose that for further work, a higher resolution analysis at smaller scales would be the next step in implementing on-the-ground conservation strategies based on PD. If possible, a 1 by 1 km grid cell would be preferable, since for many species, in particular rodents, the distribution ranges are very small. Thus, analyzing possible ways to conserve them at finer scales would result in proper conservation strategies and a better and more informed allocation of resources. This scale would also be beneficial in terms of regional and private PAs, whose areas tend to be very small, so an analysis at an even higher resolution than this one could include them. The same occurs with islands; some islands or portions of them can only be analyzed at higher scales.

Further work at higher resolution in more local areas could also be helpful in order to assess mammal status in traditionally managed areas by local groups, which presumably tend to do sustainable practices that are beneficial for biodiversity conservation (Valdez *et al.*, 2006). This is especially promising, since some of the traditionally managed areas are localized in Chiapas, where the highest levels of PD/SR were found.

¹¹ 0.5° correspond to approximately 55.5 km

Moreover, it would also be relevant to analyze and predict the possible effects of climate change on the PD and SR patterns in the country. For example, the effects of climate change are especially relevant for very range-restricted species, such as *Romerolagus diazi*. This lagomorph is endemic to the MTZ, more specifically from the grass tussocks in the high part of four volcanos (*Popocatepetl*, *Iztaccíhuatl*, *El Pelado* and *Tláloc*) around the southern part of Mexico City (Monroy-Vilchis *et al.*, 2020). It is also the only member of its genus. The principal threats for this species are human disturbances, mainly land use change to agricultural land and residential development, and climate change, which affects the species even inside the PAs that are conserving it. In the last 10 years, the *Iztaccíhuatl-Popocatepetl* national park has done relatively well in conserving its natural vegetation, although with small rate of change. The principal type of vegetation that is changing is grasslands, which is the main habitat of *R. diazi* (Escalante, Aguilar-Tomasini & Farfán-Gutiérrez, 2020; Monroy-Vilchis *et al.*, 2020). These alpine grasslands are mainly changing to pine and oak forests. This is presumably an effect of warmer temperatures that allow this kind of vegetation to advance and distribute higher, where it replaces high grasslands, which results in a huge threat for *R. diazi* (Escalante *et al.*, 2020). Therefore, even though the distribution range of this species is covered by this and other PAs, they are not effectively conserving the species as they cannot take action to prevent the effects of global climate change.

Finally, we believe that extending the exercise of calculating PD for other taxonomic groups in Mexico is relevant for improving the knowledge of the status of Mexico's biodiversity. This could include the analysis of other taxa (such as reptiles, birds, amphibians) in the phylogenetic tree, or calculation of PD of the biota of a whole ecosystem, which would reveal complex patterns of the PD in the country that could provide insightful tools for the conservation management of the area.

5 CONCLUSION

This is the first study that attempts to calculate the PD of a complete taxonomic group at the class level in Mexico. The results obtained here can contribute to a more informed decision-making during the conservation process as they offer a multidimensional approach of the diversity of the Mexican mammal community as well as their status in the federal PA network in Mexico.

The results showed that PD and SR are highly correlated biodiversity measures. The areas of highest mammalian PD correspond with the highest SR. They locate towards the southeastern part of Mexico, especially in the state of Chiapas. The areas with the lowest PD also correspond with the SR patterns, being the Baja California Peninsula the least phylogenetically and compositionally diverse in terms of mammals.

In terms of conservation, the federal PAs are overlapping with most of the species ranges of the Mexican mammal community. PAs can be divided in two groups: those containing high levels of PD/SR, and those containing low levels of PD/SR. This last group is relevant because they conserve endemic species, mainly from islands. The PAs that contain the highest PD, and thus are more relevant in the conservation resources allocation, were *Selva El Ocote*, *Lagunas de Montebello* and *Montes Azules*, which are all located in the state of Chiapas. These PAs also hold the highest levels of SR.

The mammalian phylogenetic composition between protected and the non-protected areas is very similar. Differences between the mammal community of protected and non-protected areas are driven by species missing from the non-PA, rather than species missing from the protected areas. This pattern repeats with species composition: both PA and non-PA are very similar.

The Mexican PAs are complementary in terms of phylogenetic composition: the different PAs geographically spread across Mexico conserve different parts of the Mexican mammal phylogenetic tree. Based on their phylogenetic composition they can be divided into 10 subgroups within three main groups that represent the evolutionary history of the Neartic mammal biota in the north, the Neotropical in the south, and the intergradation of these two biotas, known as the MTZ, in the center and in the mountainous region.

Although the federal PA network seems to be conserving the Mexican mammal PD, we recommend further work on population viability within the PAs. We also suggest that analysis of predicted range shifts and other possible effects of climate change would be helpful for a better understanding of the conservation status of Mexico's mammals.

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APPENDICES

Appendix A:

Table A1. List of mammal species used in this study

<i>Alouatta palliata</i>	<i>Corynorhinus mexicanus</i>	<i>Eumops ferox</i>
<i>Ammospermophilus harrisii</i>	<i>Corynorhinus townsendii</i>	<i>Eumops hansae</i>
<i>Ammospermophilus interpres</i>	<i>Cratogeomys castanops</i>	<i>Eumops nanus</i>
<i>Ammospermophilus leucurus</i>	<i>Cratogeomys fulvescens</i>	<i>Eumops perotis</i>
<i>Anoura geoffroyi</i>	<i>Cratogeomys fumosus</i>	<i>Eumops underwoodi</i>
<i>Antilocapra americana</i>	<i>Cratogeomys goldmani</i>	<i>Galictis vittata</i>
<i>Antrozous pallidus</i>	<i>Cratogeomys merriami</i>	<i>Geomys arenarius</i>
<i>Artibeus hirsutus</i>	<i>Cratogeomys perotensis</i>	<i>Geomys personatus</i>
<i>Artibeus jamaicensis</i>	<i>Cratogeomys planiceps</i>	<i>Geomys tropicalis</i>
<i>Artibeus lituratus</i>	<i>Cryptotis alticola</i>	<i>Glaucomys volans</i>
<i>Ateles geoffroyi</i>	<i>Cryptotis goldmani</i>	<i>Glossophaga commissarisi</i>
<i>Baiomys musculus</i>	<i>Cryptotis mayensis</i>	<i>Glossophaga leachii</i>
<i>Baiomys taylori</i>	<i>Cryptotis merriami</i>	<i>Glossophaga morenoi</i>
<i>Balantiopteryx io</i>	<i>Cryptotis mexicanus</i>	<i>Glossophaga soricina</i>
<i>Balantiopteryx plicata</i>	<i>Cryptotis nelsoni</i>	<i>Glyphonycteris sylvestris</i>
<i>Bassariscus astutus</i>	<i>Cryptotis obscurus</i>	<i>Habromys chinanteco</i>
<i>Bassariscus sumichrasti</i>	<i>Cryptotis parva</i>	<i>Habromys delicatulus</i>
<i>Bauerus dubiaquercus</i>	<i>Cryptotis peregrina</i>	<i>Habromys ixtlani</i>
<i>Bison bison</i>	<i>Cryptotis phillipsii</i>	<i>Habromys lepturus</i>
<i>Cabassous centralis</i>	<i>Cryptotis tropicalis</i>	<i>Habromys lophurus</i>
<i>Callospermophilus madrensis</i>	<i>Cuniculus paca</i>	<i>Habromys simulatus</i>
<i>Caluromys derbianus</i>	<i>Cyclopes didactylus</i>	<i>Herpailurus yagouaroundi</i>
<i>Canis latrans</i>	<i>Cynomops mexicanus</i>	<i>Heteromys desmarestianus</i>
<i>Canis lupus</i>	<i>Cynomys ludovicianus</i>	<i>Heteromys gaumeri</i>
<i>Carollia perspicillata</i>	<i>Cynomys mexicanus</i>	<i>Heteromys irroratus</i>
<i>Carollia sowelli</i>	<i>Dasyprocta mexicana</i>	<i>Heteromys nelsoni</i>
<i>Carollia subrufa</i>	<i>Dasyprocta mexicana</i>	<i>Heteromys pictus</i>
<i>Castor canadensis</i>	<i>Dasyprocta punctata</i>	<i>Heteromys salvini</i>
<i>Centronycteris centralis</i>	<i>Dasybus novemcinctus</i>	<i>Heteromys spectabilis</i>
<i>Centurio senex</i>	<i>Dermanura azteca</i>	<i>Hodomys alleni</i>
<i>Chaetodipus arenarius</i>	<i>Dermanura phaeotis</i>	<i>Hylonycteris underwoodi</i>
<i>Chaetodipus artus</i>	<i>Dermanura tolteca</i>	<i>Ictidomys mexicanus</i>
<i>Chaetodipus baileyi</i>	<i>Dermanura watsoni</i>	<i>Idionycteris phyllotis</i>
<i>Chaetodipus californicus</i>	<i>Desmodus rotundus</i>	<i>Lampronnycteris brachyotis</i>
<i>Chaetodipus eremicus</i>	<i>Diaemus youngii</i>	<i>Lasionycteris noctivagans</i>
<i>Chaetodipus fallax</i>	<i>Didelidurus albus</i>	<i>Lasiurus blossevillii</i>
<i>Chaetodipus formosus</i>	<i>Didelphis marsupialis</i>	<i>Lasiurus borealis</i>
<i>Chaetodipus goldmani</i>	<i>Didelphis virginiana</i>	<i>Lasiurus cinereus</i>
<i>Chaetodipus hispidus</i>	<i>Diphylla ecaudata</i>	<i>Lasiurus ega</i>
<i>Chaetodipus intermedius</i>	<i>Dipodomys deserti</i>	<i>Lasiurus intermedius</i>
<i>Chaetodipus nelsoni</i>	<i>Dipodomys gravipes</i>	<i>Lasiurus seminolus</i>
<i>Chaetodipus penicillatus</i>	<i>Dipodomys merriami</i>	<i>Lasiurus xanthinus</i>
<i>Chaetodipus pernix</i>	<i>Dipodomys nelsoni</i>	<i>Leopardus pardalis</i>
<i>Chaetodipus rudinoris</i>	<i>Dipodomys ordii</i>	<i>Leopardus wiedii</i>
<i>Chaetodipus siccus</i>	<i>Dipodomys phillipsii</i>	<i>Leptonycteris nivalis</i>
<i>Chaetodipus spinatus</i>	<i>Dipodomys simulans</i>	<i>Leptonycteris yerbabuena</i>
<i>Chiroderma salvini</i>	<i>Dipodomys spectabilis</i>	<i>Lepus alleni</i>
<i>Chiroderma villosum</i>	<i>Eira barbara</i>	<i>Lepus californicus</i>
<i>Chironectes minimus</i>	<i>Enchisthenes hartii</i>	<i>Lepus callotis</i>
<i>Choeroniscus godmani</i>	<i>Eptesicus brasiliensis</i>	<i>Lepus flavigularis</i>
<i>Choeronycteris mexicana</i>	<i>Eptesicus furalis</i>	<i>Lichonycteris obscura</i>
<i>Chrotopterus auritus</i>	<i>Eptesicus fuscus</i>	<i>Lonchorhina aurita</i>
<i>Coendou mexicanus</i>	<i>Erethizon dorsatum</i>	<i>Lontra longicaudis</i>
<i>Conepatus leuconotus</i>	<i>Euderma maculatum</i>	<i>Lophostoma brasiliense</i>
<i>Conepatus semistriatus</i>	<i>Eumops auripendulus</i>	<i>Lophostoma evotis</i>

Lynx rufus
Macrophyllum macrophyllum
Macrotus californicus
Macrotus waterhousii
Marmosa mexicana
Mazama pandora
Mazama temama
Megadontomys cryophilus
Megadontomys nelsoni
Megadontomys thomasi
Megasorex gigas
Mephitis macroura
Mephitis mephitis
Metachirus nudicaudatus
Micronycteris microtis
Micronycteris schmidtorum
Microtus californicus
Microtus guatemalensis
Microtus mexicanus
Microtus oaxacensis
Microtus pennsylvanicus
Microtus quasiater
Microtus umbrosus
Mimon cozumelae
Mimon crenulatum
Molossus alvarezi
Molossus aztecus
Molossus coibensis
Molossus molossus
Molossus rufus
Molossus sinaloae
Mormoops megalophylla
Musonycteris harrisoni
Mustela frenata
Myotis albescens
Myotis auriculus
Myotis californicus
Myotis elegans
Myotis evotis
Myotis fortidens
Myotis keaysi
Myotis melanorhinus
Myotis nigricans
Myotis occultus
Myotis planiceps
Myotis thysanodes
Myotis velifer
Myotis vivesi
Myotis volans
Myotis yumanensis
Nasua narica
Natalus lanatus
Natalus mexicanus
Nelsonia neotomodon
Neotamias dorsalis
Neotamias merriami
Neotamias obscurus
Neotoma albigula
Pteronotus davyi
Pteronotus gymnonotus

Neotoma angustapalata
Neotoma bryanti
Neotoma devia
Neotoma goldmani
Neotoma insularis
Neotoma lepida
Neotoma leucodon
Neotoma macrotis
Neotoma mexicana
Neotoma micropus
Neotoma nelsoni
Neotoma phenax
Neotomodon alstoni
Noctilio albiventris
Noctilio leporinus
Notiosorex cockrumi
Notiosorex crawfordi
Notiosorex villai
Notocitellus adocetus
Notocitellus annulatus
Nycticeius humeralis
Nyctinomops aurispinosus
Nyctinomops femorosaccus
Nyctinomops laticaudatus
Nyctinomops macrotis
Nyctomys sumichrasti
Odocoileus hemionus
Odocoileus virginianus
Oligoryzomys fulvescens
Ondatra zibethicus
Onychomys arenicola
Onychomys leucogaster
Onychomys torridus
Orthogeomys cuniculus
Orthogeomys grandis
Orthogeomys hispidus
Orthogeomys lanius
Oryzomys alfaroi
Oryzomys chapmani
Oryzomys couesi
Oryzomys melanotis
Oryzomys rhabdops
Oryzomys rostratus
Oryzomys saturator
Oryzomys texensis
Osgoodomys banderanus
Otonyctomys hatti
Otospermophilus atricapillus
Otospermophilus beecheyi
Otospermophilus variegatus
Otodylomys phyllotis
Ovis canadensis
Panthera onca
Pappogeomys bulleri
Parastrellus hesperus
Pecari tajacu
Perimyotis subflavus
Perognathus amplus
Sorex mediopua
Sorex milleri

Perognathus flavescens
Perognathus flavus
Perognathus longimembris
Perognathus merriami
Peromyscus aztecus
Peromyscus beatae
Peromyscus boylii
Peromyscus bullatus
Peromyscus californicus
Peromyscus caniceps
Peromyscus carletoni
Peromyscus crinitus
Peromyscus difficilis
Peromyscus eremicus
Peromyscus eva
Peromyscus fraterculus
Peromyscus furvus
Peromyscus gratus
Peromyscus guatemalensis
Peromyscus gymnotis
Peromyscus hooperi
Peromyscus hylocetes
Peromyscus leucopus
Peromyscus levipes
Peromyscus madrensis
Peromyscus maniculatus
Peromyscus megalops
Peromyscus melanocarpus
Peromyscus melanophrys
Peromyscus melanotis
Peromyscus melanurus
Peromyscus merriami
Peromyscus mexicanus
Peromyscus nasutus
Peromyscus ochraventer
Peromyscus pectoralis
Peromyscus perfulvus
Peromyscus polius
Peromyscus sagax
Peromyscus schmidlyi
Peromyscus sejugis
Peromyscus simulus
Peromyscus spicilegus
Peromyscus stephani
Peromyscus truei
Peromyscus winkelmanni
Peromyscus yucatanicus
Peromyscus zarhynchus
Peropteryx kappleri
Peropteryx macrotis
Philander opossum
Phylloderma stenops
Phyllostomus discolor
Platyrrhinus helleri
Potos flavus
Procyon lotor
Procyon pygmaeus
Promops centralis

<i>Pteronotus_parnellii</i>	<i>Sorex_monticolus</i>
<i>Pteronotus_personatus</i>	<i>Sorex_oreopolus</i>
<i>Puma_concolor</i>	<i>Sorex_orizabae</i>
<i>Reithrodontomys_bakeri</i>	<i>Sorex_ornatus</i>
<i>Reithrodontomys_chrysopsis</i>	<i>Sorex_saussurei</i>
<i>Reithrodontomys_fulvescens</i>	<i>Sorex_ventralis</i>
<i>Reithrodontomys_gracilis</i>	<i>Sorex_arizonae</i>
<i>Reithrodontomys_hirsutus</i>	<i>Sorex_emarginatus</i>
<i>Reithrodontomys_megalotis</i>	<i>Sorex_ixtlanensis</i>
<i>Reithrodontomys_mexicanus</i>	<i>Sorex_macrodon</i>
<i>Reithrodontomys_microdon</i>	<i>Spilogale_pygmaea</i>
<i>Reithrodontomys_montanus</i>	<i>Sturnira_hondurensis</i>
<i>Reithrodontomys_spectabilis</i>	<i>Sturnira_parvidens</i>
<i>Reithrodontomys_sumichrasti</i>	<i>Sylvilagus_audubonii</i>
<i>Reithrodontomys_tenuirostris</i>	<i>Sylvilagus_bachmani</i>
<i>Reithrodontomys_zacatecae</i>	<i>Sylvilagus_brasiliensis</i>
<i>Reithrontomys_burti</i>	<i>Sylvilagus_cunicularius</i>
<i>Rheomys_thomasi</i>	<i>Sylvilagus_floridanus</i>
<i>Rhogeessa_aeneus</i>	<i>Sylvilagus_graysoni</i>
<i>Rhogeessa_alleni</i>	<i>Sylvilagus_insonus</i>
<i>Rhogeessa_bickhami</i>	<i>Sylvilagus_mansuetus</i>
<i>Rhogeessa_genowaysi</i>	<i>Sylvilagus_robustus</i>
<i>Rhogeessa_gracilis</i>	<i>Tadarida_brasiliensis</i>
<i>Rhogeessa_mira</i>	<i>Tamandua_mexicana</i>
<i>Rhogeessa_parvula</i>	<i>Tamias_bulleri</i>
<i>Rhogeessa_tumida</i>	<i>Tamias_durangae</i>
<i>Rhynchonycteris_naso</i>	<i>Tamiasciurus_mearnsi</i>
<i>Romerolagus_diazi</i>	<i>Tapirus_bairdii</i>
<i>Saccopteryx_bilineata</i>	<i>Taxidea_taxus</i>
<i>Saccopteryx_leptura</i>	<i>Tayassu_pecari</i>
<i>Scalopus_aquaticus</i>	<i>Thomomys_bottae</i>
<i>Scapanus_latimanus</i>	<i>Thomomys_umbrinus</i>
<i>Sciurus_aberti</i>	<i>Thyroptera_tricolor</i>
<i>Sciurus_alleni</i>	<i>Tlacuatzin_canescens</i>
<i>Sciurus_arizonensis</i>	<i>Tonatia_saurophila</i>
<i>Sciurus_aureogaster</i>	<i>Trachops_cirrhosus</i>
<i>Sciurus_colliaei</i>	<i>Trinycteris_nicefori</i>
<i>Sciurus_deppei</i>	<i>Tylomys_bullaris</i>
<i>Sciurus_nayaritensis</i>	<i>Tylomys_nudicaudus</i>
<i>Sciurus_niger</i>	<i>Urocyon_cinereoargenteus</i>
<i>Sciurus_oculatus</i>	<i>Uroderma_bilobatum</i>
<i>Sciurus_variegatoides</i>	<i>Uroderma_magnirostrum</i>
<i>Sciurus_yucatanensis</i>	<i>Ursus_americanus</i>
<i>Scotinomys_teguina</i>	<i>Ursus_arctos</i>
<i>Sigmodon_alleni</i>	<i>Vampyressa_thyone</i>
<i>Sigmodon_arizonae</i>	<i>Vampyrodes_major</i>
<i>Sigmodon_fulviventer</i>	<i>Vampyrum_spectrum</i>
<i>Sigmodon_hispidus</i>	<i>Vulpes_macrotis</i>
<i>Sigmodon_leucotis</i>	<i>Xenomys_nelsoni</i>
<i>Sigmodon_mascotensis</i>	<i>Xerospermophilus_spilosoma</i>
<i>Sigmodon_ochrognathus</i>	<i>Xerospermophilus_tereticaudus</i>
<i>Sigmodon_toltecus</i>	<i>Zygoeomys_trichopus</i>

Table A2. Details of the received museum samples that were used to extract the DNA for species not found on GenBank

Species name	Species Key	Date collected	Country of Origin	Museum of Origin	Institution Code	Preservation Method
<i>Dasyprocta mexicana</i>	18304	1980	Mexico	Institute of Biology	IBUNAM	skin
<i>Nelsonia neotomodon</i>	19699	1982	Mexico	Institute of Biology	IBUNAM	Skin and hair
<i>Neotoma phenax</i>	3362	1954	Mexico	Institute of Biology	IBUNAM	Skin
<i>Sciurus nayaritensis</i>	26179	1966	Mexico	Institute of Biology	IBUNAM	Skin
<i>Sciurus yucatanensis</i>	36668	1994	Mexico	Institute of Biology	IBUNAM	Skin
<i>Sorex ventralis</i>	26254	1974	Mexico	Institute of Biology	IBUNAM	Skin
<i>Sorex veraepacis</i>	44746	2006	Mexico	Institute of Biology	IBUNAM	Skin
<i>Sylvilagus cunicularius</i>	40388	1998	Mexico	Institute of Biology	IBUNAM	Skin
<i>Sylvilagus graysoni</i>	26446	1982	Mexico	Institute of Biology	IBUNAM	Skin
<i>Sylvilagus insonus</i>	40390	1998	Mexico	Institute of Biology	IBUNAM	Skin
<i>Tylomys bullaris</i>	3096	1955	Mexico	Institute of Biology	IBUNAM	Skin
<i>Oryzomys chapmani</i>	9136	1998	Mexico	Museum of zoology "Alfonso L. Herrera"	MZFC	Skin
<i>Oryzomys couesi</i>	10148	2009	Mexico	Museum of zoology "Alfonso L. Herrera"	MZFC	Skin
<i>Pecari tajacu</i>	10703	2004	Mexico	Museum of zoology "Alfonso L. Herrera"	MZFC	Skin and hair
<i>Sorex macrodon</i>	10047	2004	Mexico	Museum of zoology "Alfonso L. Herrera"	MZFC	Skin and hair
<i>Sorex oreopolus</i>	10728	2008	Mexico	Museum of zoology "Alfonso L. Herrera"	MZFC	Skin and hair
<i>Sorex orizabae</i>	10565	2003	Mexico	Museum of zoology "Alfonso L. Herrera"	MZFC	Skin and hair
<i>Tamandua mexicana</i>	5639	1987	Mexico	Museum of zoology "Alfonso L. Herrera"	MZFC	skin, skull
<i>Peromyscus melanurus</i>	10993	2010	Mexico	Museum of zoology "Alfonso L. Herrera"	MZFC	Tissue ethanol
<i>Spilogale angustifrons</i>	1401	1985	Mexico	Museum of zoology "Alfonso L. Herrera"	MZFC	Skin and hair
<i>Cabassous centralis</i>	10095	2007	Mexico	Museum of zoology "Alfonso L. Herrera"	MZFC	skin
<i>Natalus lanatus</i>	7646	2009	Mexico	CIIDIR	CIIDIR-IPN	Tissue ethanol
<i>Notiosorex villai</i>	54932	1953	Mexico	Kansas Natural History Museum	KUNHM	
<i>Procyon pygmaeus</i>	92565	NA	Mexico	Kansas Natural History Museum	KUNHM	Skin and hair
<i>Reithrodontomys burti</i>	96106	1963	Mexico	Kansas Natural History Museum	KUNHM	Skin and hair
<i>Sorex ixtlanensis</i>	136575	1975	Mexico	Kansas Natural History Museum	KUNHM	Skin and hair
<i>Sorex mediopua</i>	111372	1967	Mexico	Kansas Natural History Museum	KUNHM	Skin and hair
<i>Sciurus arizonensis</i>	250906	1932	Mexico	Smithsonian National Museum of Natural History	NMNH-SI	Skin and hair
<i>Peromyscus bullatus</i>	13928	1990	Mexico	Autonomous University of Mexico	UAMI	Skin and hair
<i>Tylomys bullaris</i>	141786	1971	Mexico	Museum of Vertebrate Zoology at Berkeley	MVZ	DNA extract

Table A3. List of excluded protected areas. 63 PA were excluded from this study because their total area was smaller than the resolution grain of this analysis.

Federal Protected Areas	Federal Protected Areas
Balandra	Molino de Flores Netzahualcoyotl
Barranca del Cupatitzio	Nah
Benito Juárez	Rayn
Bonampak	Ro Bravo del Norte
Cañón del Sumidero	Sacromonte
Cascada de Agua Azul	Sierra de rganos
Cascada de Bassaseachic	Tula
Cerro de Las Campanas	Tulum
Cinegas del Lerma	Yagul
Costa Occ. de I. Mujeres, Pta. Cancn y Pta. Nizuc	El Chico
Cumbres de Majalca	El Potos
Cumbres del Ajusco	Islas Marietas
Desierto de los Leones	Metzabok
Desierto del Carmen o de Nixcongo	Playa Mexiquillo
El Cimatarío	Playa de Maruata y Colola
El Histórico Coyoacan	Playa de Rancho Nuevo
El Sabinal	Playa Piedra de Tlacoyunque
El Tepeyac	Playa El Verde Camacho
Fuentes Brotantes de Tlalpan	Playa Ceuta
General Juan lvarez	Playa de Tierra Colorada
Insurgente Miguel Hidalgo y Costilla	Playa Teopa
Insurgente Jos Mara Morelos	Playa Cuitzmala
Isla Contoy	Playa de Puerto Arista
Isla Isabel	Playa de Mismaloya
Islas La Pajarera, Cocinas, Mamut, Colorada, San Pedro, San Agustn, San Andrs y Negrita y los Islotes Los Anegados, Novillas, Mosca y Submarino	Playa adyacente a la localidad denominada Ro Lagartos
Lago de Camcuaro	Playa de la Isla Contoy
Lagunas de Chacahua	Playa de Escobilla
Las Huertas	Playa El Tecun
Lomas de Padierna	Playa de la Baha de Chacahua
Los Novillos	El Veladero
Los Remedios	Dzibilchantn
Manglares de Nichupt	

Table A4. Species distribution within Mexican borders without any conservation category. Conservation status according to IUCN, Endemism status and geographical distribution (Co- Continental and In-Insular) of the species is also provided here

Species	Order	Conservation Status	Endemism	Geographical Distribution
<i>Procyon pygmaeus</i>	Carnivora	CE	E	In
<i>Lasiurus seminolus</i>	Chiroptera	LC		Co
<i>Rhogeessa bickhami</i>	Chiroptera	LC		Co
<i>Lepus flavigularis</i>	Lagomorpha	EN	E	Co
<i>Sylvilagus mansuetus</i>	Lagomorpha	CE	E	In
<i>Cratogeomys fulvescens</i>	Rodentia	LC	E	Co
<i>Geomys tropicalis</i>	Rodentia	EN	E	Co
<i>Habromys chinanteco</i>	Rodentia	CE	E	Co
<i>Habromys ixtlani</i>	Rodentia	CE	E	Co
<i>Habromys lepturu</i>	Rodentia	CE	E	Co
<i>Habromys schmidlyi</i>	Rodentia	CE	E	Co
<i>Heteromys spectabilis</i>	Rodentia	EN	E	Co
<i>Megadontomys cryophilus</i>	Rodentia	EN	E	Co
<i>Megadontomys thomasi</i>	Rodentia	EN	E	Co
<i>Microtus oaxacensis</i>	Rodentia	EN	E	Co
<i>Microtus pennsylvanicus</i>	Rodentia	LC		Co
<i>Microtus umbrosus</i>	Rodentia	EN	E	Co
<i>Neotamias merriami</i>	Rodentia	LC		Co
<i>Neotoma lepida</i>	Rodentia	LC		Co
<i>Neotoma nelsoni</i>	Rodentia	CE	E	Co
<i>Ondatra zibethicus</i>	Rodentia	LC		Co
<i>Orthogeomys cuniculus</i>	Rodentia	DD	E	Co
<i>Orthogeomys lanius</i>	Rodentia	CE	E	Co
<i>Otospermophilus atricapillus</i>	Rodentia	EN		Co
<i>Peromyscus bullatus</i>	Rodentia	CE	E	Co
<i>Peromyscus caniceps</i>	Rodentia	CE	E	In
<i>Peromyscus interparietalis</i>	Rodentia	CE	E	In
<i>Peromyscus melanocarpus</i>	Rodentia	EN	E	In
<i>Peromyscus melanurus</i>	Rodentia	EN	E	Co
<i>Peromyscus pseudocrinitus</i>	Rodentia	CE	E	In
<i>Peromyscus schmidlyi</i>	Rodentia	LC		Co
<i>Peromyscus sejugis</i>	Rodentia	EN	E	In
<i>Peromyscus slevini</i>	Rodentia	CE	E	In
<i>Peromyscus stephani</i>	Rodentia	CE	E	In
<i>Peromyscus winkelmanni</i>	Rodentia	EN	E	Co
<i>Reithrodontomys spectabilis</i>	Rodentia	CE	E	In

<i>Rheomys mexicanus</i>	Rodentia	EN	E	Co
<i>Sciurus arizonensis</i>	Rodentia	DD		Co
<i>Sciurus griseus</i>	Rodentia	LC		Co
<i>Tamiasciurus mearnsi</i>	Rodentia	EN	E	Co
<i>Tylomys tumbalensis</i>	Rodentia	CE	E	Co
<i>Cryptotis griseoventris</i>	Soricomorpha	EN	E	Co
<i>Cryptotis peregrina</i>	Soricomorpha	DD	E	Co
<i>Cryptotis phillipsii</i>	Soricomorpha	VU	E	Co
<i>Notiosorex cockrumi</i>	Soricomorpha	LC		Co
<i>Scapanus latimanus</i>	Soricomorpha	LC		Co
<i>Sorex sclateri</i>	Soricomorpha	CE	E	Co
<i>Sorex stizodon</i>	Soricomorpha	CE	E	Co

Table A5. Ranking of all PA based on their PD percentage. Values are normalized to the mean. Positive values indicate greater than the mean and negative values indicate lower than the mean.

Federal Protected Areas	Maximum Value of the Phylogenetic Diversity normalized to the mean [%]
Selva El Ocote	58,5
Lagunas de Montebello	57,9
Montes Azules	53,9
La Sepultura	50,4
Lacan-Tun	48,4
Yaxchiln	45,7
Z.P.F. en los terrenos que se encuentran en los mpios. de La Concordia, ngel Albino Corzo, Villa Flores y Jiquipilas	45,6
Chan-Kin	42,9
Palenque	42,3
Tehuacn-Cuicatln	41,4
Can del Ro Blanco	41,3
El Triunfo	41,0
Can del Usumacinta	39,5
Pico de Orizaba	37,9
Volcn Tacan	37,3
Cofre de Perote o Nauhcampatpetl	34,0
Calakmul	32,5
El Jabal	30,9
Los Tuxtlas	29,9
Sierra de Manantln	27,3
Volcn Nevado de Colima	27,0
Z.P.F.V. la Cuenca Hidrogrfica del Ro Necaxa	26,9
Sierra del Abra Tanchipa	26,5
La Encrucijada	26,0
Pico de Tanctaro	24,0
Sierra Gorda	24,0
Sistema Arrecifal Veracruzano	23,3
C.A.D.N.R. 043 Estado de Nayarit	21,8
Bala'an K'aax	21,7
Uaymil	20,2
Sian Ka'an	19,5
Zicuirm-Infiernillo	19,1
La Primavera	19,1
Barranca de Metztitln	18,7
Sierra de Quila	18,7
Pantanos de Centla	17,7
Iztacchuatl-Popocatpetl	15,6

El Tepozteco	14,7
Boquem de Tonal	14,7
Corredor Biológico Chichinautzin	13,7
Otoch Ma'ax Yetel Kooh	13,6
Laguna de Trminos	13,0
Huatulco	12,9
Chamela-Cuixmala	11,6
Lagunas de Zempoala	10,8
Cerro de La Estrella	10,6
La Montaa Malinche o Matlalcuyatl	9,9
Sierra de Tamaulipas	9,3
Nevado de Toluca	9,3
C.A.D.N.R. 026 Bajo Ro San Juan	9,1
Z.P.F.T.C.C. de los ros Valle de Bravo, Malacatepec, Tilostoc y Temascaltepec	8,9
Los Petenes	8,0
Los Mrmoles	8,0
Janos	7,4
Cumbres de Monterrey	7,1
Bavispe	7,1
Marismas Nacionales Nayarit	7,1
Grutas de Cacahuamilpa	6,8
Mariposa Monarca	6,6
Yum Balam	5,2
Ra Lagartos	5,0
Sierra Gorda de Guanajuato	5,0
Bosencheve	4,8
Xicotncatl	4,3
Sierra de Huautla	4,2
Cerro de Garnica	4,2
Arrecife de Puerto Morelos	4,0
Ra Celestrn	2,7
Can de Santa Elena	2,0
Sierra de lamos-Ro Cuchujaqui	1,7
Ocampo	1,0
Meseta de Cacaxtla	0,6
C.A.D.N.R. 004 Don Martn	0,6
Maderas del Carmen	0,4
Campo Verde	0,3
Cerro de la Silla	0,6
Tutuaca	-3,7
Papigochic	-4,1
La Michila	-4,4
Sierra La Mojonera	-5,5

Sierra de Ivarez	-6,0
Mdanos de Samalayuca	-6,1
C.A.D.N.R. 001 Pabelln	-6,8
Mapim	-7,5
Gogorrn	-8,2
Islas del Golfo de California	-10,3
Cuatrocinegas	-11,0
Cerro Mohinora	-11,2
Laguna Madre y Delta del Ro Bravo	-15,3
El Pinacate y Gran Desierto de Altar	-22,3
Alto Golfo de California y Delta del Ro Colorado	-22,7
Constitucin de 1857	-26,6
Valle de los Cirios	-30,5
Sierra de San Pedro Mrtir	-30,6
El Vizcano	-32,1
Sierra La Laguna	-34,2
Islas del Pacfico de la Pennsula de Baja California	-36,0
Cabo Pulmo	-37,5
Cabo San Lucas	-37,5
Baha de Loreto	-38,7
Zona marina Baha de los ngeles, canales de Ballenas y de Salsipuedes	-39,8
Complejo Lagunar Ojo de Liebre	-41,7
La porcin norte y la franja costera oriental, terrestres y marinas de la Isla de Cozumel	-81,4
Islas Maras	-84,1
Isla Guadalupe	-100
Isla San Pedro Mrtir	-100
Banco Chinchorro	-100

Appendix B:

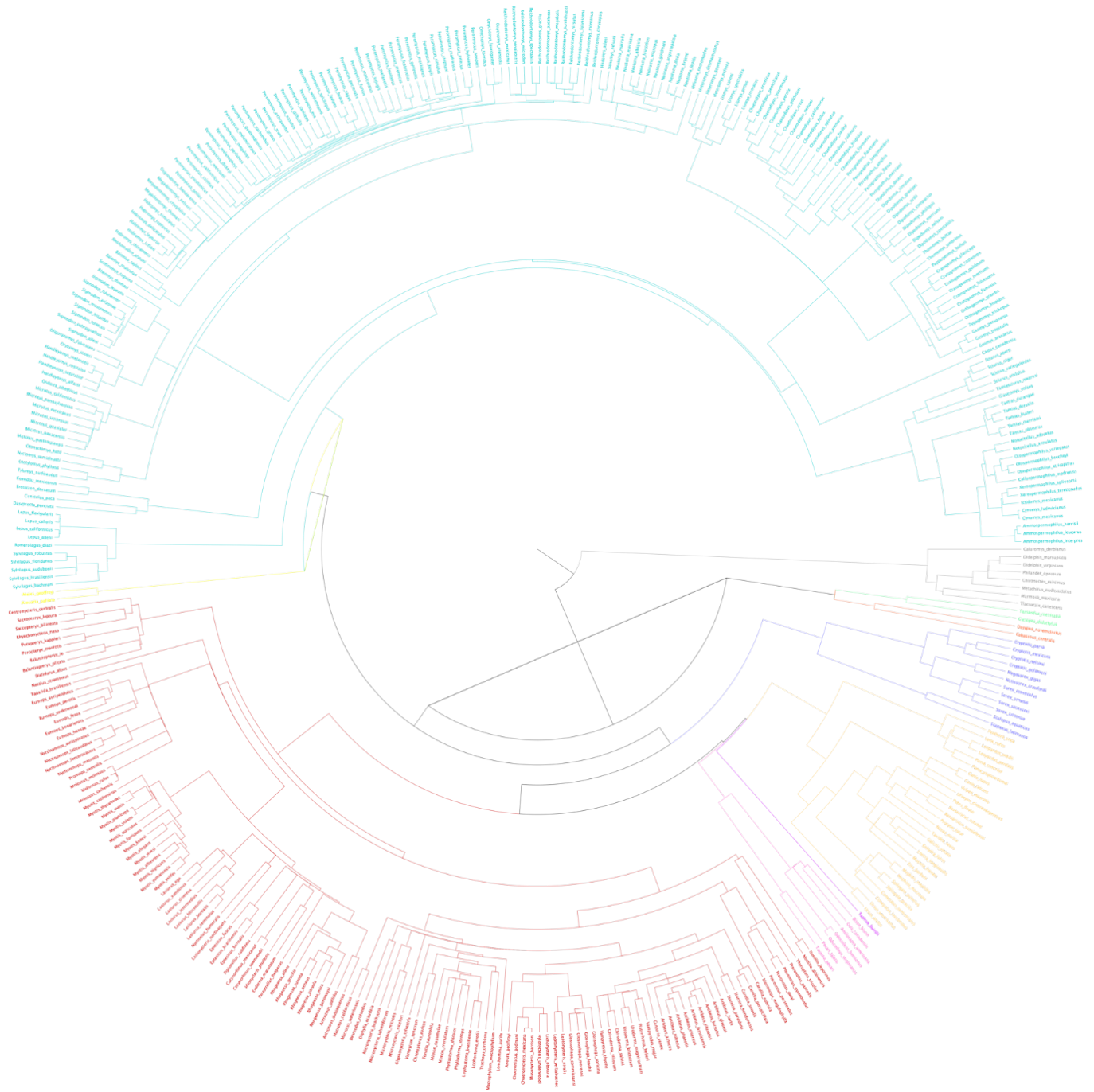


Figure B1. Phylogenetic relationships of Mexican mammals based on TimeTree

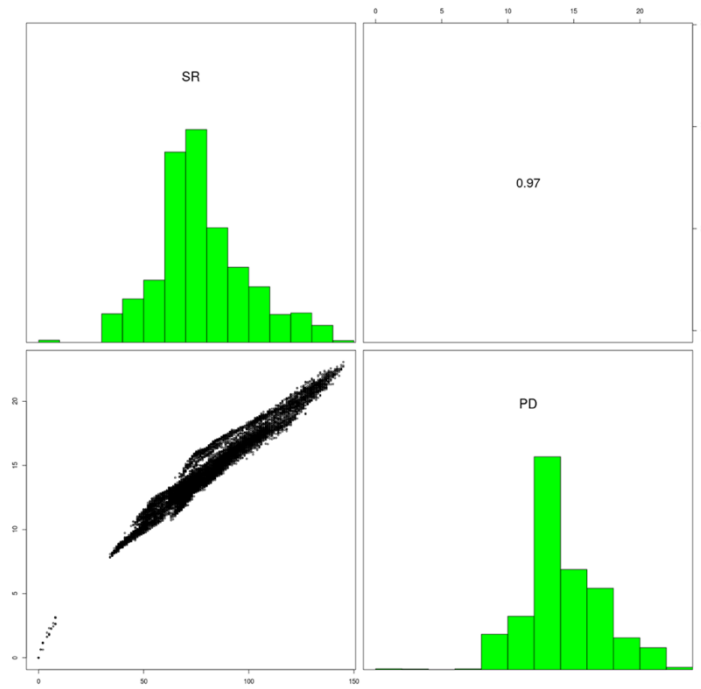


Figure B2. Pair plot of Species richness and phylogenetic diversity. The histograms show the frequency distribution of the different diversity patterns. The number in the upper panel is the correlation coefficient with 1 being fully correlated and 0 having no correlation at all.

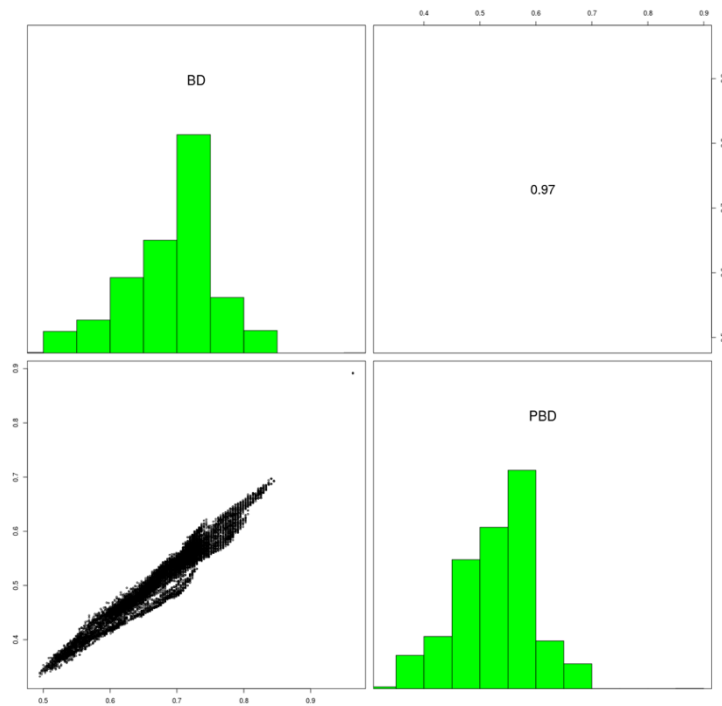


Figure B3. Pair plot of β -diversity and phylogenetic β -diversity. The histograms show the frequency distribution of the different diversity patterns. The number in the upper panel is the correlation coefficient with 1 being fully correlated and 0 having no correlation *at all*.



Figure B4. Biogeographical provinces of Mexico. Image taken from Morrone *et al.* (2017). Blue polygons belong to the Nearctic region, Red and orange to the neotropical and green to the Mexican Transition Zone.

Compositional Similarity between PA

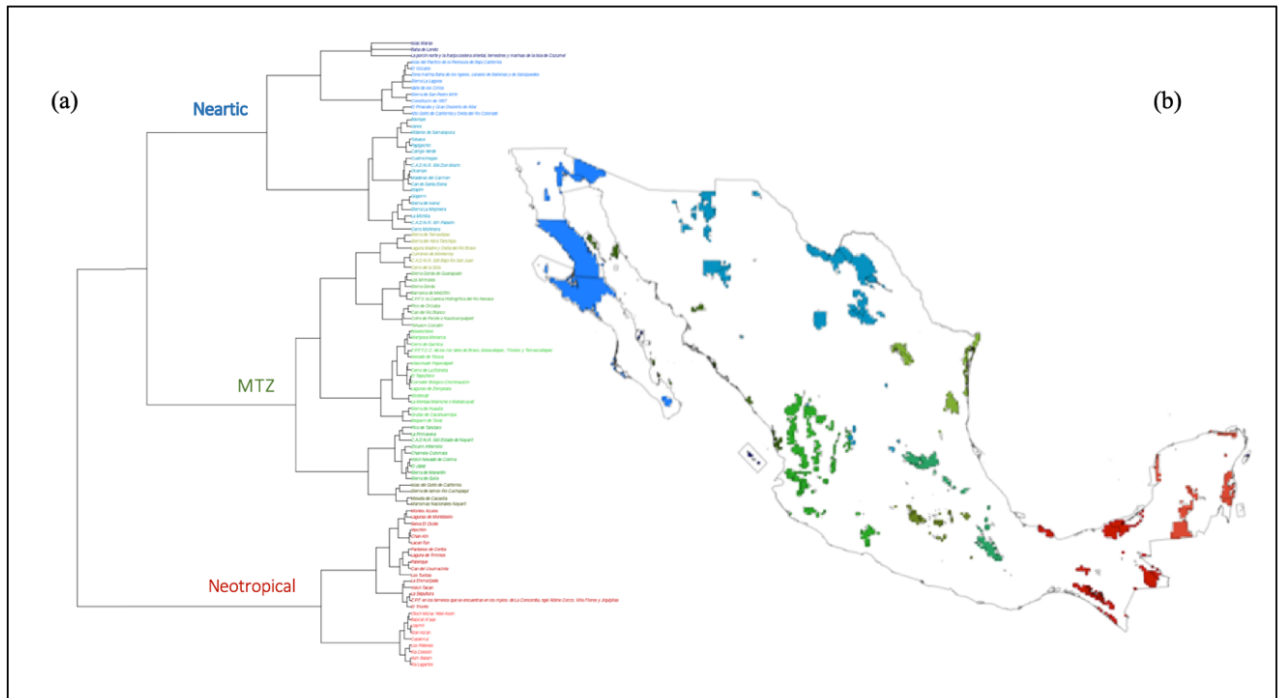


Figure B5. Hierarchical clustering of the PA of Mexico based on the compositional β similarity index of the Mexican mammals. PA were grouped into 3 clusters. Hierarchical dendrogram (a) and geographical representation of the three clusters of PAs (b). Colors correspond to the clustering based on the biogeographical regions of Mexico in both figures. Blue represents the Neartic region, green the Mexican Transition Zone and Red the Neotropical region.

Figure B6. High-level flowchart of the methods used for this thesis project.

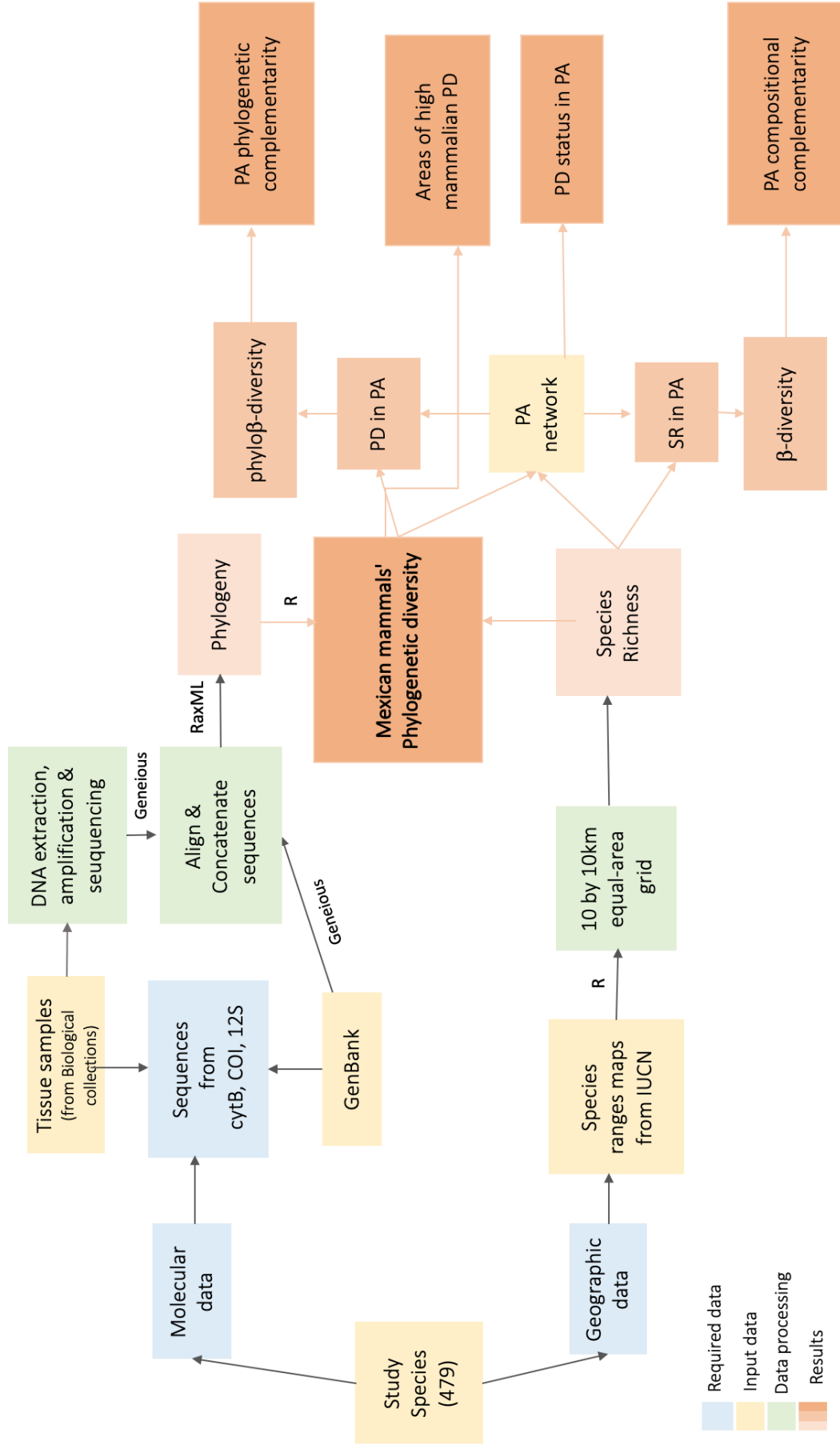




Figure B7. Mexican administrative states. Map published by Inegi, 2018.

