Ecological and taxonomic dissimilarity in species and higher taxa of reptiles in western Mexico (#101372)

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Ecological and taxonomic dissimilarity in species and higher taxa of reptiles in western Mexico

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The ecosystems in the neotropics are recognized for their great diversity of species, however, they are also the most threatened environments. Given this, ecologists have focused on designing robust methods to evaluate biodiversity, such as incorporating its multiple dimensions in the study of biological communities. This study presents the regional patterns of reptile diversity in western Mexico, incorporating analyzes at a local (alpha) and regional (beta) scale. An individual analysis is provided for lizards and snakes, as they are groups with different environmental requirements and their diversity patterns can change. We use current methods to describe the ecological processes that influence reptile communities, such as the taxonomic distinctness index and the dissimilarity of the taxonomic structure in each community. Beta diversity partitions were performed to identify components of turnover and differences in richness. We demonstrate the important representation of higher taxa in the regions of Jalisco, especially for the lizard group. The findings show that at the local level there are discrepancies between species richness and higher taxa, but at the regional level these two facets show similar results. In addition, discrepancies are also observed between the diversity patterns of snakes and lizards; where at the local level the diversity of lizards is greater, but at the regional level snakes influence the differentiation patterns of all reptiles to a greater extent. We conclude that reptile diversity is a result of richness and taxa turnover. These findings provides fundamental information for decision-makers regarding possible conservation strategies for reptiles.

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Abstract

The ecosystems in the neotropics are recognized for their great diversity of species, however, they are also the most threatened environments. Given this, ecologists have focused on designing robust methods to evaluate biodiversity, such as incorporating its multiple dimensions in the study of biological communities. This study presents the regional patterns of reptile diversity in western Mexico, incorporating analyzes at a local (alpha) and regional (beta) scale. An individual analysis is provided for lizards and snakes, as they are groups with different environmental requirements and their diversity patterns can change. We use current methods to describe the ecological processes that influence reptile communities, such as the taxonomic distinctness index and the dissimilarity of the taxonomic structure in each community. Beta diversity partitions were performed to identify components of turnover and differences in richness. We demonstrate the important representation of higher taxa in the regions of Jalisco, especially for the lizard group. The findings show that at the local level there are discrepancies between species richness and higher taxa, but at the regional level these two facets show similar results. In addition, discrepancies are also observed between the diversity patterns of snakes and lizards; where at the local level the diversity of lizards is greater, but at the regional level snakes influence the differentiation patterns of all reptiles to a greater extent. We conclude that reptile diversity is a result of richness and taxa turnover. These findings provide fundamental information for decision-makers regarding possible conservation strategies for reptiles.

Introduction

At the global level, the ecosystems located in the neotropics are the richest in species; however, they are also the environments most threatened by various factors, such as deforestation, the degradation of the remaining ecosystems and the effects of the landscape, which result in negative effects on biodiversity (Moreno et al., 2018). Due to these threats to global biodiversity, the application of robust ecological indicators is one of the concerns of ecologists, who have focused on unifying their analysis methods to obtain more complete assessments (Moreno et al., 2017).

One of the scales of biodiversity analysis with the most methodological contributions in recent years is beta diversity, which plays a very important role in shaping the richness of species, especially in heterogeneous landscapes with environmental, altitudinal and/or longitudinal gradients (Calderón-Patrón et al., 2012); this is the case in Mexico, where the constant replacement of species throughout a territory comprises its megadiversity (Koleff et al., 2008). This replacement of species better explains the high diversity of amphibians and reptiles in Mexico, surpassing birds and mammals (Koleff et al., 2008, Rodríguez et al., 2019), which also occurs at the state level (Calderón-Patrón et al., 2016) and at the regional level (Calderón-Patrón et al., 2013).

One of the most important states in Mexico in terms of biodiversity is Jalisco. This state has a large variety of ecosystems, ranging from temperate to tropical; combined, these ecosystems contain 23% of the flora of vascular plants in the country and 262 Pteridophytes, 24 Gymnosperms and 2,752 Angiosperms (Ramírez et al., 2010). Approximately 4.6% of these species are endemic to the state (Hernández-López, 1995; Meiners and Hernández-López 2007). There are 56 species of wild fauna, 143 species of reptiles (Cruz-Sáenz et al., 2017a), 438 species of birds (51% of the national total, Santana et al., 2017) and 173 species of mammals

(36% of the total) (Nacional, Guerrero et al., 2017). In Jalisco, there are also 19 protected natural areas, of which 11 are federal, covering 833,442 ha, which corresponds to 10.3% of the state area and 16.5% of the forested area; these include five AICAS and two areas for the protection of Jaguars (Jardel-Peláez et al., 2017).

However, despite being an state that dedicates an important area to biodiversity conservation, such as the case for reptiles, where 64.5% of the state's species are found in one of its Protected Natural Areas (ANP, Chávez-Ávila et al., 2015), it is also a state with great economic development; thus, approximately 61% of the territory is allocated to agricultural and forestry activities, and the large population concentration is the fourth largest at the national level, with 7.35 million inhabitants, and an urban population that represents 86.59% of the total population of the state (Aguirre-Jiménez and Castañeda Huizar, 2017). These factors result in threats to areas in which no biodiversity conservation strategies are implemented, and these threats are caused by changes in land use, pollution and urbanization (Aguirre-Jiménez and Castañeda Huizar, 2017).

It is important to note that the knowledge of the biodiversity in Jalisco is still incomplete, as the best known and most studied ecosystems in the state for the last several decades have been the low and medium forests in the Chamela-Cuixmala region and the temperate forests of the Sierra de Manantlán region (Jardel-Peláez et al., 2017). The eastern and northeastern areas of the state have been less explored, and fewer conservation efforts have been implemented. For this reason, it is necessary to carry out analyses of biodiversity at the state level, considering all the regions in the state equally, which is the case for two recent publications that analyze the richness and distribution of herpetofauna in the state (Cruz-Sáenz et al., 2017b; Chávez-Ávila et al., 2015). Such studies providing possible strategies for conservation; however, both studies analyzed the richness of species and did not analyze beta diversity. This level analysis has the greatest influence on modeling biodiversity in heterogeneous areas, such as Jalisco. For this reason, for the first time, at the state level, we analyzed the taxonomic alpha diversity and beta diversity for the level of species and higher taxa of reptiles in Jalisco, incorporating the methods proposed by Baselga (2010), who separated the beta diversity into its replacement components and differences in richness. Based on the records provided by Cruz Sáenz et al. (2017b) for the reptiles of the physiographic subprovinces of the state of Jalisco, we also separated the analyses into reptiles with limbs and snakes to explore the ecological processes that drive the differentiation of the communities in each of the groups, including the capacity for locomotion, which can be related to the differences in community compositions.

Materials & Methods

Study area

The state of Jalisco (80208.29 km^2) is located in the western center of Mexico at the confluence zone between the Sierra Madre Occidental, Sierra Madre del Sur and the Trans-Mexican Volcanic Belt; this region features complex orography, with elevations between 0 and 4600 m asl. The area has dry, tropical and temperate climates, the latter predominating and the average temperature being between -3 °C and 22 °C; additionally, it has a high incidence of hydrometerological phenomena due to its location in the intertropical zone (Valero Padilla, et al., 2017; Figure 1). For this work, we use the reptile records reported by Cruz-Sáenz et al. (2017) in the seven physiographic regions of Jalisco, which are the Pacific Coastal Plain (PC), Sierra Madre Occidental (SO), Sierras Jaliscienses (SJ), the Trans-Mexican Volcanic Belt (TV), Sierra de Coalcomán (SC), the Central Plateau (CP), and the Tepalcatepec Depression (TD). Using the records of the reptiles in these regions, we built a database of presence and absence. A summary of the main characteristics of each physiographic region is shown in Table 1.

Data analysis

To determine the alpha taxonomic diversity of reptiles in physiographic regions, the average taxonomic distinctiveness index (AvTD) was used to evaluate the degree of taxonomic relationship between the species of an assemblage (Clarke and Warwick, 1998). For this purpose, an aggregation matrix was generated with seven taxonomic levels (order, suborder, superfamily, family, genus subfamily and species), which was related to the presence and absence of the reptile species in the seven physiographic regions. The taxonomic levels of the aggregation matrix were weighted according to the criteria established by Clarke and Gorley (2006). The average taxonomic distinctiveness and confidence intervals less than and greater than 95% were calculated based on 1,000 random interactions using the PRIMER V7® program (Clarke and Gorley, 2015). This analysis was also performed independently for groups of lizards and snakes following the same process and considering the same criteria.

The beta diversity analyses of the physiographic regions were performed independently for all reptiles, as well as for the group of lizards and snakes, as we believe that these groups have different environmental requirements and that their beta diversity patterns may change. For this purpose, the procedure of Carvalho et al. (2012, 2013), which is based on the approach of Baselga (2010, 2012; Baselga and Leprieur, 2015), is used to separate beta diversity into two components. According to this method, the total dissimilarity (β.sor) is 1 minus the Sorensen coefficient of similarity. This total dissimilarity was divided into two components: dissimilarity due to turnover (β.sim) and dissimilarity due to differences in richness (βsne). This analysis was carried out in R using the BAT package (Cardoso et al. 2015; R Core Team 2018).

We partitioned both the dissimilarity in the composition of species and the dissimilarity in the taxonomic structure, considering that the composition of taxa was greater than the species level. For the latter case, according to the methods of Bacaro et al. (2007), the total taxonomic dissimilarity, here β.sorT (1-ΔT *sensu* Bacaro et al. (2007), is equal to the dissimilarity of the Sorensen coefficient but considers more taxa. Taxonomic dissimilarity was measured as βsorT = 1- (Ta/Ta + Tb + Tc), where Ta is the total number of taxa shared between two communities, Tb is the number of taxa present only in the first community but absent in the second, and Tc is the number of taxa present exclusively in the second community. The values of β.sorT range from 0 when the taxonomic structure of both communities is identical to 1 when the taxonomic structure is completely different (Bacaro et al., 2007). The taxonomic data were calculated as the proportion of nonshared taxa relative to the total number of taxa in the two communities. Therefore, the partition of β.sorT with the procedure of Carvalho et al. (2013) shows a dissimilarity component due to the change in taxa (β.simT) and a compound number of dissimilarities due to the difference in the richness of taxa (β.sneT). The same methodology has been used to analyze the beta diversity of melolontid beetles in the Mexican Transversal Volcanic Belt (García-de Jesús et al., 2016) and terrestrial vertebrates, including amphibians, between ecoregions of the state of Hidalgo (Calderón-Patrón et al., 2016). To calculate the total taxonomic dissimilarity and its components, we used as many taxonomic levels as possible. In this case, the order, suborder, superfamily, family, subfamily, genus and species categories were used. The analysis was carried out in R (R Core Team 2018) following Carvalho et al. (2013).

To represent the species and taxonomic dissimilarity between the physiographic regions, cluster analyses were carried out, which were constructed by unweighted pair group method with arithmetic mean (UPGMA; Clarke and Gorley, 2015). Cluster analyses were performed independently for the reptile group and for the lizard and snake groups. Finally, to determine if there was a relationship between the beta diversity of species and higher taxa, simple linear regressions were performed for total beta diversity (β. sor), turnover (β. sim) and differences in richness (β. sne) in the seven physiographic regions. This analysis was carried out considering the totality of the reptiles as well as the groups of lizards and snakes.

Results

Alpha diversity of species and higher taxa

The physiographic region with the highest reptile richness was TV with 85 species, followed by PC with 75 species (Figure 2a). The regions with the lowest richness were the SC and TD regions, with 24 and 23 species, respectively. The remaining regions had a richness of reptiles between 63 and 68 species. The taxonomic distinctiveness followed a different pattern than the species richness; the PC region presented the highest distinctiveness value (64.81), and it was significantly higher than expected ($p \leq 0.05$). The rest of the regions maintained distinctiveness values between 52.97 and 56.18, with the exception of the TD region, which obtained the lowest distinctiveness value (49.15). Notably, the CP, SJ and TV regions are completely outside the probability funnel, which indicates that their taxonomic distinctiveness is significantly lower than expected ($p \leq 0.05$).

For the lizard group, TV was the physiographic region with the highest richness, with 29 species, followed by CP, with 26 species (Figure 2b). For reptiles, the regions with the lowest lizard richness were the SC and TD regions, with 8 and 7 species, respectively. The remaining regions had a total of 21 to 24 species of reptiles. Regarding taxonomic distinctiveness, the PC region presented the highest value (46.83), which was significantly greater than expected ($p \leq 0.05$). The rest of the regions had values between 32.65 and 40.63, with the TD region having the least taxonomic distinctiveness. For the lizard group, all regions with the exception of the PC region remained within the probability funnel, indicating that the taxonomic distinctiveness of the regions was consistent with expectations ($p > 0.05$).

The TV region with the highest species richness (54) was also highlighted, followed by the SJ region (45) (Figure 2c). For reptiles and lizards, the regions with the lowest richness of snakes were SC and TD, with 15 and 16 species, respectively. The remaining regions presented a richness of reptiles between 37 and 42 species. The results of the taxonomic distinctiveness showed that the SO region presented the highest value (98.70). The regions with the least taxonomic distinctiveness were SC and TD, with values of 25.14 and 27.92, respectively. For the snake group, all regions remained within the probability funnel, indicating that the taxonomic distinctiveness of the snakes was consistent with what was expected ($p > 0.05$).

Beta diversity of species at multiple site levels

At the species level, the total beta diversity of the reptiles was 75% (βSOR = 0.75), that of the lizards was 77% (βSOR = 0.77), and that of the snakes was 73% (βSOR = 0.74). In the three groups, turnover was the most important component, followed by differences in richness (reptiles: βSIM = 0.64, βSNE = 0.11; lizards: βSIM = 0.66, βSNE = 0.11; snakes: βSIM = 0.61, βSNE = 0.12; Figure 3a) .

Beta diversity of species by region pairs

In the case of reptiles, the greatest dissimilarity occurred in five pairs of physiographic regions: PC/CP βsor = 0.76, CP/TD βsor = 0.758, PC/TD βsor = 0.755, TV/TD βsor = 0.74, and PC/SC βsor = 0.737. The replacement had the highest values for PC/CP βsim = 0.75, PC/SO βsim = 0.65, and PC/TV βsim = 0.64. Furthermore, 18 pairs of regions exhibited greater turnover than differences in richness. Only three pairs showed differences in richness greater than the exchange: TV/SC βsne = 0.44, SJ/SC βsne = 0.38 and SJ/TD βsne = 0.34 (Figure 3b).

Beta diversity was greater in lizards than in reptiles, as six pairs of regions presented values greater than 70% dissimilarity (SO/TD βsor = 0.81, PC/TD βsor = 0.79, PC/CP βsor = 0.79, TV/TD βsor = 0.78, PC/TV βsor = 0.76, CP/TD βsor = 0.76). Regarding the exchange, 19 pairs presented higher values than the differences in richness, with the highest values occurring for PC/CP βsim = 0.77, PC/TV βsim = 0.73, PC/SO βsim = 0.64 and SJ/CP βsim = 0.62. Only two pairs of regions showed differences in richness greater than turnover (TV/SC βsne = 0.50, SJ / SC βsne = 0.39; Figure 3c).

For the snakes, four pairs presented a total beta greater than 70% (CP/TD βsor = 0.75, PC/CP βsor = 0.73, PC/SC βsor = 0.72, TV/TD βsor = 0.71). Turnover prevailed over differences in richness in 17 pairs of regions, two of which had dissimilarities greater than 60% (PC/CP βsim =

0.73, PC/SO βsim = 0.65). Three pairs presented differences in richness greater than exchange: TV/SC βsne = 0.41, SJ/SC βsne = 0.37, and SJ/TD βsne = 0.36 (Figure 3d).

Beta diversity of higher taxa at multiple site levels

At the level of higher taxa, the beta diversity of reptiles was 66% (βSORT = 0.66), that of lizards was 64% (βSORT = 0.64), and that of snakes was 64% (βSORT = 0.64). Among the three groups analyzed, the turnover was greater than the difference in richness (reptiles: βSIMT = 0.46, βSNET = 0.19; lizards: βSIMT = 0.47, βSNET = 0.17; snakes: βSIMT = 0.46, βSNET = 0.18; Figure 3e).

Beta diversity of higher taxa by region pairs

For reptiles, the highest total taxonomic dissimilarity occurred in two pairs of physiographic regions with values greater than 60%: PC/TD βsorT = 0.62 and PC/SC βsorT = 0.62. The turnover was low since only three pairs presented turnover values higher than 35% (PC/CP βsimT = 0.42 and PC/TV βsimT = 0.39, PC/SO βsimT = 0.35). In addition, 11 pairs presented a greater turnover than differences in richness, while the opposite was true in the remaining 10 pairs, where four pairs presented dissimilarity values greater than 40% (TV/SC βsneT = 0.44, PC/TD βsneT = 0.43, PC/SC βsneT = 0.42, TV/TD βsneT = 0.40; Figure 3f).

In lizards, the highest dissimilarity occurred in four pairs of regions, with a value greater than 55% (PC/SC: βsorT = 0.60, PC/TD: βsorT = 0.59, SO/SC: βsorT = 0.56, TV/TD: βsorT = 0.55). The turnover was low, and the highest values were presented as follows: PC/TV: βsimT = 0.42, PC/CP: βsimT = 0.41, and SC/TD: βsimT = 0.41. However, 11 pairs presented higher values than did the differences in richness, whose highest values were obtained for five pairs: TV/SC = βsneT = 0.48, SJ/SC: βsneT = 0.44, PC/SC: βsneT = 0.42, TV/TD: βsneT = 0.42, and PC/TD:

βsneT = 0.41; in addition, the other five pairs presented values of differences in richness greater than the exchange (Figure 3g).

For snakes, the three pairs with the greatest dissimilarity were PC/SC: βsorT = 0.588, TV/TD: βsorT = 0.54, and PC/TD: βsorT = 0.531. Only one pair presented a value greater than 40% (PC/CP: βsimT = 0.44); however, 13 pairs exceeded the difference in richness, which was also low since only one pair exceeded 40% dissimilarity (TV/SC: βsneT = 0.42) and eight pairs presented values higher than the turnover value (Figure 3h).

Cluster analysis of species dissimilarity

The cluster analysis revealed a 65% dissimilarity of species (βsor = 0.65) in the physiographic regions considering all reptiles. Similarly, two groups are observed, one formed by SC, TV, and CP (βsor = 0.59) and the other by SO, PC and SJ (βsor = 0.56). Within the first group, SC and TV tie at a level of 35% dissimilarity (βsor = 0.35), and in the second, SO and PC tie at 41% dissimilarity (βsor = 0.41, Figure 4a).

In the cluster analysis considering only the lizards, a maximum dissimilarity of 71% was observed (βsor = 0.71). The CP and PC regions were not grouped with any other region, maintaining a dissimilarity of 69% and 71%, respectively (βsor = 0.69 and βsor = 0.71), with respect to the remainder of the regions. The other regions formed a group consisting of SJ, SO, SC and TV (βsor = 0.61 dissimilarity) and were divided into two groups: SJ and SO (βsim = 0.43) and SC and TV (βsor = 0.38 Figure. 4b).

For snakes, the regions were grouped with 62% dissimilarity (βsor = 0.62), and two groups were separated: one formed by SC, TV, and CP (βsor = 0.57) and the other by SO, PC and SJ (βsor =

0.53). In the first group, SC and TV and SO and PC presented 33% dissimilarity (βsor = 0.33. Figure 4c).

Cluster analysis of taxa with greater dissimilarity

The maximum taxonomic dissimilarity in the physiographic regions comprising all the reptiles was 50% (βsorT = 0.50). The same groupings were observed as those at the species level, where the regions SC, TV, CP (βsorT = 0.47) and the regions SO, PC and SJ were grouped (βsorT = 0.37). Within the first group, SC and TV showed the least dissimilarity (βsorT = 0.24), and in the second group, SO and PC showed the least dissimilarity (βsorT = 0.28. Figure 4d).

CP was the most dissimilar region among the lizards, with 52% taxonomic dissimilarity (βsorT = 0.52). The remaining regions formed a group with 47% dissimilarity (βsorT = 0.47). This was divided into two groups: a group formed by three subprovinces, SJ, SO, and PC, with a dissimilarity of 35% (βsorT = 0.35); within this group, SJ and SO were grouped (βsorT = 0.24); and the other group was composed of SC and TV, 24% (βsorT = 0.35; Figure 4e).

In the case of snakes, all regions showed 47% dissimilarity (βsorT = 0.47), and two groups are presented, one formed by SC, TV, and CP (βsorT = 0.40), where SC and TV are grouped (βsorT = 0.24). The other group is composed of SO, PC and SJ (βsorT = 0.37), where SO and PC are grouped (βsorT = 0.22; Figure 4f).

Relationships between beta diversity of species and higher taxa

The linear regression analyses revealed a positive and significant relationship between the beta diversity of species and higher taxa for both total beta diversity (βsor = 0.87, $p < 0.001$) and for its replacement components (βsim = 0.78, $p < 0.001$) and for differences in richness (βsne = 0.91, $p < 0.001$). This relationship was also observed in the lizard (βsor = 0.68, $p < 0.001$; βsim = 0.57,

$p < 0.001$; βsne = 0.88, $p < 0.001$) and snake (βsor = 0.91, $p < 0.001$; βsim = 0.78, $p < 0.001$; βsne = 0.91, $p < 0.001$) groups (Figure S1).

Discussion

The state of Jalisco has a variety of reptiles within the different physiographic regions that it contains, with TV and PC having the highest number of species and SC and TD having the least number of species. These contrasts may be a reflection of the fact that some subprovinces have large tropical forest areas, which have higher amounts of reptiles (Chávez-Ávila et al., 2015), and of the difference used in the collection effort between regions or between areas of the state, as evidenced by a geographical analysis of the herpetofauna of Jalisco; the points of greatest species richness are located in the municipality of Guadalajara, in the Chamela-Cuitzmala Biosphere Reserve, in the Ejido Toxin and the Sierra de Manantlán Biosphere Reserve and in areas with low deciduous and subdeciduous forests (Chávez-Ávila et al., 2015). At these sites, more collections and studies have been carried out within the state, meaning that richness can increase in poor areas, such as in the Sierra Madre Occidental area (Chávez-Ávila et al., 2015), if the collection effort is increased. Another important factor influencing the richness of the regions was the area, as SC and TD had the smallest surface areas (SC: 2, 714.9 km^2, TD: 1,571.9 km^2). The same trend occurred in Oaxaca, where the subprovinces with the smallest surface area presented the least richness of the amphibians (Mata-Silva et al., 2015).

We determined that the taxonomic distinctiveness of the reptiles was greater than that reported in other studies in which reptiles were also evaluated in different regions within and outside Jalisco (Cruz-Elizalde et al. 2014; Cruz-Elizalde et al. 2022; Peña-Joya et al. 2018). For example, Cruz-

Elizalde et al. (2014) reported approximately 65 taxonomic distinctions, which was attributed to the presence of certain families of reptiles with a high number of species; for example, the Colubridae family in the snake group and Phrynosomatidae in the lizard group. On the other hand, Cruz-Elizalde et al. (2022) reported taxonomic distinctiveness values of less than 60, which was attributed to the presence of certain genera of reptiles with a high number of species, as well as a high degree of endemism. Compared to the above results, in our study, only the PC subprovince had a greater value than did those reported by these studies, which indicates that this subprovince holds a high variety of taxa above the species level. The high distinctiveness of CP for the reptiles and for the group of lizards responds to the variety of ecosystems presented in this subprovince, as well as the presence of tropical environmental conditions and its proximity to the sea, which allows it to be the only physiographic region where the presence of marine reptiles is recorded, highlighting the families Cheloniidae and Dermochelyidae; similarly, the Crocodylia order, with the sole representative *Crocodylus acutus*, inhabits estuarine ecosystems and mangrove vegetation (Cruz-Sáenz et al., 2017b). These results coincide with those of Maciel-Mata (2013), who noted that the areas with the greatest taxonomic diversity are characterized by being mainly in warm climates.

On the other hand, it was determined that for the group of reptiles, the CP, SJ and TV regions had low variety of higher taxa, with taxonomic distinctiveness values similar to those reported by Cruz-Elizalde et al. (2014) in the region of the Chihuahuan Desert. This low representativeness of taxa shows that some families and genera are overrepresented in these regions, such as the Phrynosomatidae family and particularly the *Sceloporus* genus*,* whose species are mostly distributed at high, medium and high elevations (Cruz-Sáenz et al., 2017b), which are prevailing conditions in the subprovinces CP, SJ and TV, respectively. In the case of snakes, the SW subprovince stands out for having few species, but they are more distant taxonomically, as of the 63 species that are present, 21 belong to different genera and families, so this subprovince is highly important for the conservation of snakes and their evolutionary history (Calderón-Patrón et al., 2016).

The beta diversity at the species level for multiple sites presented average values among the three groups of reptiles analyzed (75%), which exceeded that of the reptiles of six ecoregions in Hidalgo (83%) and between quadrants at the fine scale and average (82 and 79%, respectively) in the Isthmus of Tehuantepec in Oaxaca (Calderón-Patrón et al., 2013) and those registered at the national level where reptiles and amphibians present higher dissimilarity values than birds and mammals (Koleff et al. al., 2008; Ochoa-Ochoa et al., 2014; Rodríguez et al., 2019). In all the groups of reptiles analyzed, turnover prevailed over differences in richness, with values ranging between 61 and 64% dissimilarity (Fig. 4a). These values are similar to those presented for the reptiles in the six ecoregions in Hidalgo (62% replacement) (Calderón-Patrón et al., 2016) and for those obtained by Villegas-Patrac et al. (2022) for reptiles from eight protected natural areas of the Cucapá region in Baja California (change from 0.46 to 0.78%). However, in the case of the reptiles of the Isthmus of Tehuantepec, turnover and differences in richness contribute in very similar proportions (Calderón-Patrón et al., 2013).

In the case of total beta diversity between pairs of subprovinces for all reptiles as a whole, the highest values were presented for five pairs (PC/CP, CP/TD, PC/TD, TV/TD, and PC/SC). These results coincide with those recorded for the herpetofauna (amphibians and reptiles) of Jalisco

(Cruz-Sáenz et al., 2017b) that estimated a coefficient of biogeographic similarity and recorded the lowest similarities in these same five pairs of regions. In both studies, the highest dissimilarity value and the lowest similarity value were presented between PC and SC, since they are located at opposite ends of the state and within a considerable geographical distance from each other; in addition, they present notable environmental differences. Furthermore, both subprovinces are separated by the Trans-Mexican Volcanic Belt (TV), which is composed of reptiles that are more similar to those of CP (0.66) (Cruz-Sáenz et al., 2017b). At the level of pairs of subprovinces, turnover prevailed over differences in richness in 18 pairs of subprovinces, while the differences in richness were greater in only three pairs. These results coincide with those recorded for ecoregions in Hidalgo and for quadrants in the Isthmus of Tehuantepec in Oaxaca, where the most distant ecoregions and the most distant quadrants and important environmental differences are those that present the greatest dissimilarity in their species compositions of reptiles due to replacement (Calderón-Patrón et al., 2013; Calderón-Patrón et al., 2016).

The intermediate beta diversity values found for the reptiles in this study coincide with those recorded by Ochoa-Ochoa et al. (2014) and Rodríguez et al. (2019), who analyzed the beta diversity of terrestrial vertebrates on a national scale. The highest beta diversity of amphibians and reptiles occurs in the southern region of the country, while in mountain ranges, such as the Sierra Madre Oriental and Occidental, there are intermediate values, and in the Yucatan Peninsula, there are lower values. On broad spatial scales, the complex interactions of habitat heterogeneity, contrasting vegetation types, and biogeographic histories are increasingly important in explaining extraordinary beta diversity, while on finer spatial scales, the ecological processes related to topography, environmental heterogeneity and local environmental conditions seem to be more important in explaining beta diversity (Ochoa-Ochoa et al., 2014).

On a national scale, the beta diversity of reptiles is associated with heterogeneity in temperature and its correlation with elevation since at intermediate elevations and at short distances, there are important differences in temperature and most reptile species. Due to their ectothermic nature, reptiles appear to be sensitive to rapid changes in temperature along elevational gradients (Rodríguez et al., 2019). It has also been reported that the beta diversity of reptiles is the product of the similarity of habitats and ecosystems present in physiographic provinces, in addition to the proximity between them (Lemos-Espinal and Smith, 2023). Notably, the lizard group presented higher dissimilarity values at multiple sites, possibly because the average size of the distribution areas and dispersal capacity were lower than those of the snakes, as they exhibit greater habitat specialization (Koleff et al., 2008; Vitt and Cadwell, 2014; Calderón-Patrón et al., 2016; Cruz-Sáenz et al., 2017a).

The total beta diversity, turnover and differences in richness of reptiles at the level of higher taxa were lower in all the cases than at the species level because as we move up in the taxonomic categories, the dissimilarity decreases drastically, as each category increasingly includes more species and/or taxa (Calderón-Patrón et al., 2016). These findings led to the correlation analysis results between the beta diversity at the species level and the higher taxa being high and positive for the total beta diversity, the turnover and the differences in richness in the three groups of reptiles analyzed. This finding coincides with those for the reptiles in the ecoregions of Hidalgo and for quadrants at different spatial scales in the Isthmus of Tehuantepec (Calderón-Patrón et al., 2013; Calderón-Patrón et al., 2016). This result indicates that the beta diversity assessments of higher taxa are good surrogates for analyzing beta diversity at the species level (Calderón-Patrón et al., 2016).

The dendrograms indicate that the snake dissimilarity among regions has an important influence on the dendrogram topology for all reptiles (Figure 4a). The groups that formed are associated with the subprovinces with close dissimilarity values, less geographical distance, and greater environmental similarity to each other, such as CP, TV and SW, which are contiguous and share tropical deciduous forests, xerophilous scrubs, and pine and oak forests. SJ and PC both have dry forests, while CP and TV share the tropical deciduous forest and pine and oak forests. These results coincide with clusters of ecoregions in Hidalgo that share some types of vegetation and which have similar composition of terrestrial vertebrates (Calderón-Patrón et al., 2016).

Conclusions

This study shows the important representation of more taxa in the regions of Jalisco at the state level, especially for the group of lizards. The beta diversity presented average values, and turnover was more important than was the difference in richness at both the level of species and higher taxa. The values of total beta diversity and turnover were greater in lizards than in snakes, probably due to a smaller area of distribution, greater specialization of the habitat and greater competition for resources; however, the differentiation patterns of the reptiles between the regions is influenced to a greater extent by the group of snakes. Therefore, in this state, conservation strategies focused on the protection of the regions with the greatest diversity of species and those with the greatest dissimilarity between them should be considered to ensure biological connectivity between the different physiographic regions.

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Table 1(on next page)

Surface, elevation, annual average temperature, precipitation, and percentage of land use and land cover of the physiographic regions of Jalisco (Cruz-Sáenz et al., 2017)

Physiographic regions: Pacific Coastal Plain (PC); Sierra Madre Occidental (SO); Sierras Jaliscienses (SJ); Trans-Mexican Volcanic Belt (TV); Sierra de Coalcomán (SC); Central Plateau (CP); Tepalcatepec Depression (TD). Source: [1]Cruz-Sáenz et al., (2017b); [2]INEGI (2013); [3]Fick and Hijmans (2017); [4]INEGI (2018). Abbreviations Vegetation and Land Use. CBF: Coniferous and broadleaf forests; TF: Tropical forests, AGR: Agriculture; PA: Pastures.

Table 1. Surface, elevation, annual average temperature, precipitation, and percentage of land use and land cover of the physiographic regions of Jalisco (Cruz-Sáenz et al., 2017): Pacific Coastal Plain (PC); Sierra Madre Occidental (SO); Sierras Jaliscienses (SJ); Trans-Mexican Volcanic Belt (TV); Sierra de Coalcomán (SC); Central Plateau (CP); Tepalcatepec Depression (TD).

Physiographic region	**Area (km^2)[1]**	**Elevation (m a.s.l.)[2]**			**Annual average temperature (°C)[3]**	**Annual precipitation (mm)[3]**	**Vegetation and Land Use (LU) (%)[4]**	
		Min	**Mean**	**Max**			**Vegetation**	**LU**
PC	3818.5	0	96.29	680	25.3	950.5	63.1%; TF (57.1%)	36.9%; AGR (18.4%)
SO	15712.4	273	1673.10	2863	19.6	774.0	64.7%; CBF (36.1%)	35.3%; AGR (21.2%)
SJ	15070.3	0	1030.94	2880	20.8	1335.0	82.2%; CBF (57.2%)	17.8%; PA (11.4%)
TV	18733.2	144	1522.32	4260	19.7	897.8	53.3%; CBF (33.2%)	46.7%; AGR (33.2%)
SC	2714.9	484	1367.62	2725	21.0	938.8	86.1%; CBF (64.6%)	13.9%; PA (11.2%)

CP	20702.8	1252	1839.61	2957	18.2	716.7	24.3%; TF (10.4%)	75.7%; AGR (53.4%)
TD	1551.9	327	715.57	1704	25.1	843.8	70.7%; TF (68.2%)	29.3%; AGR (15.5%)

Source: [1]Cruz-Sáenz et al., (2017b); [2]INEGI (2013); [3]Fick and Hijmans (2017); [4]INEGI (2018). Abbreviations Vegetation and Land Use. CBF: Coniferous and broadleaf forests; TF: Tropical forests, AGR: Agriculture; PA: Pastures.

Figure 1

Location map of physiographic regions of the state of Jalisco; A) elevation is shown and B) vegetation and land use are shown.

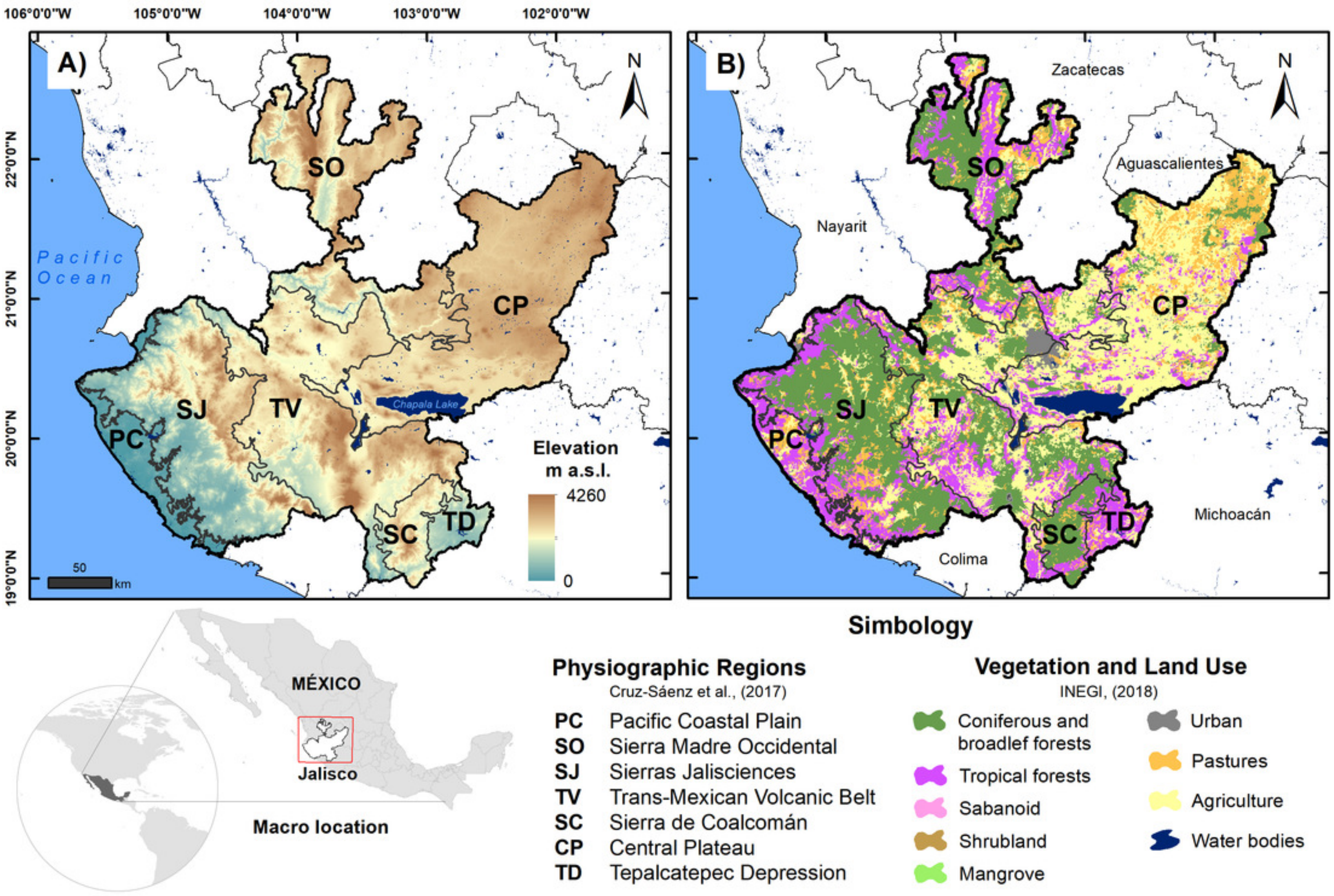

Figure 2

Analysis of taxonomic distinctness of the of the physiographic regions for Reptiles (a), Lizards (b) and Snakes (c).

The dotted line represents the average taxonomic distinctness; the solid lines represent the lower and upper confidence intervals at the 95% level.

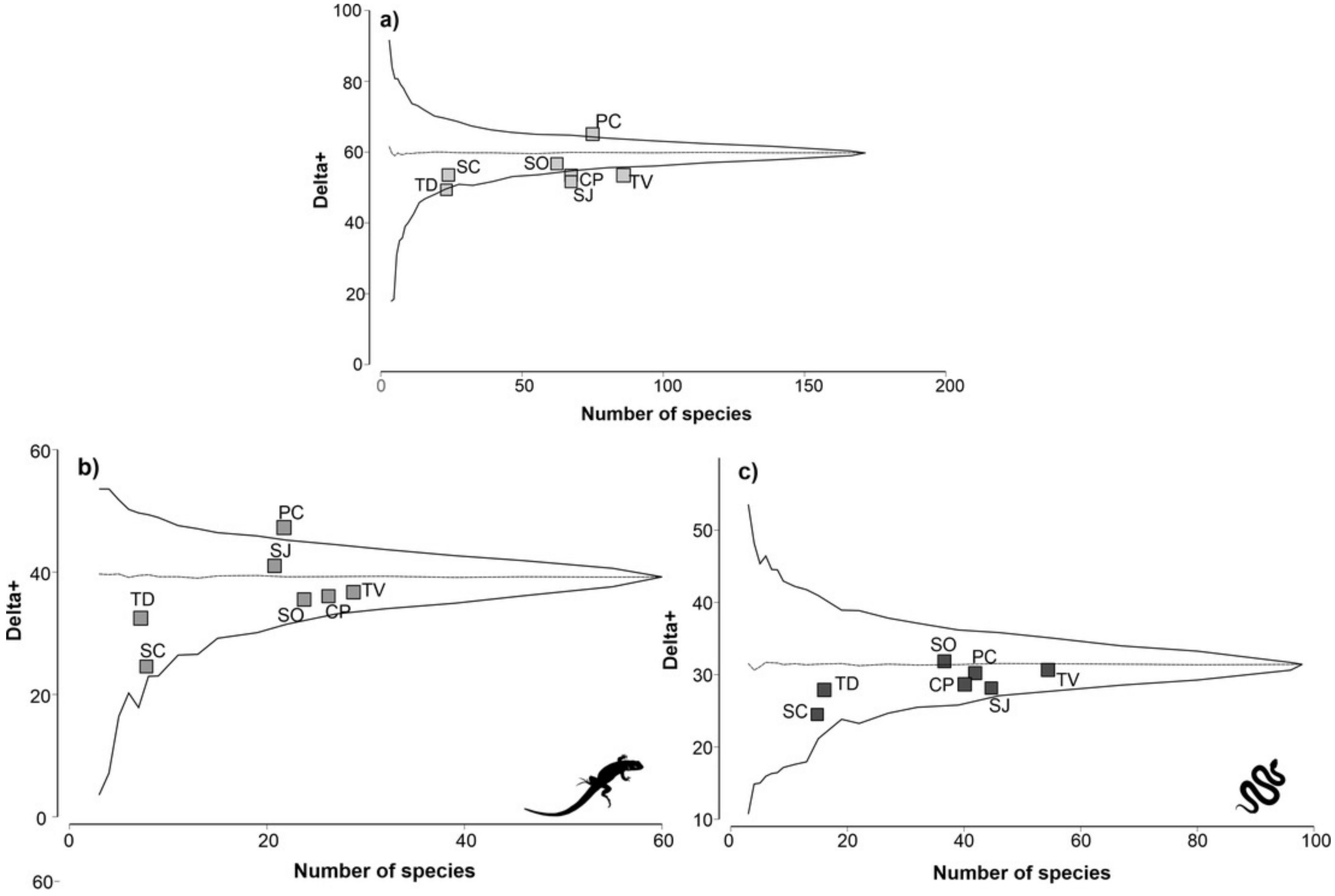

Figure 3

Total beta diversity for species and higher taxa of reptiles in the physiographic regions of the Jalisco state.

(a, e) Total beta diversity (beta.sor), replacement (beta.sim), and richness differences (beta.sne) for species and higher taxa of reptiles, lizards, and snakes in the entire set of physiographic regions of the state of Jalisco. (h, f) Total beta diversity, replacement, and richness differences for species and taxa of reptiles, (c, g) lizards, and (d, h) snakes for the all-possible combinations between pairs of the seven physiographic regions present in the Jalisco state.

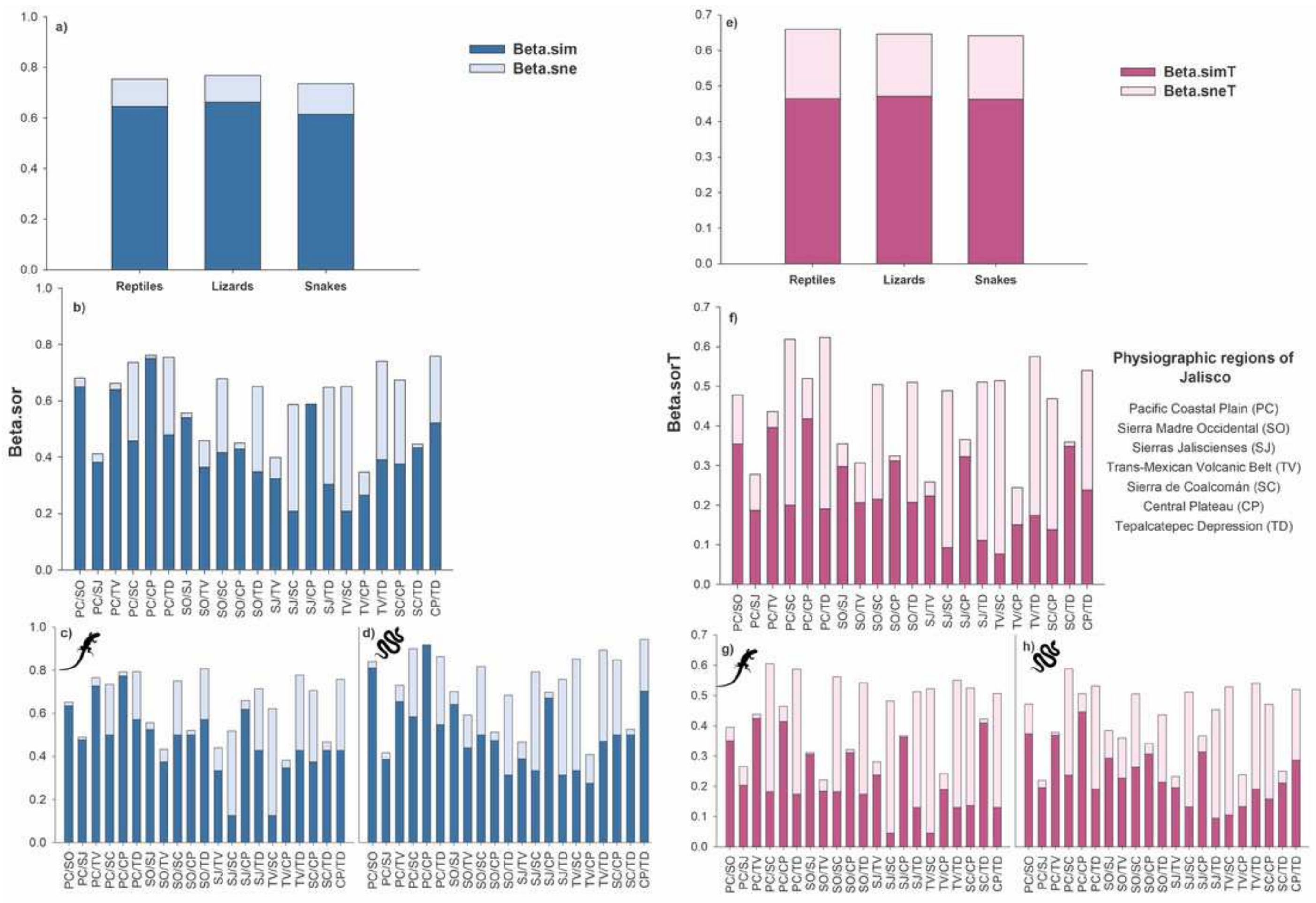

Figure 4

Cluster analysis of species and taxonomic dissimilarity of reptiles (a, b), lizards (c, d) and snakes (e, f) between physiographic regions present in the Jalisco state.