

LIVING ON THE EDGE AND THE MANGROVE PARADOX: HERPETOFAUNAL DIVERSITY ACROSS THE COASTAL WETLANDS COMMUNITIES OF LOS PETENES, CAMPECHE, MEXICO

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Abstract.—Herpetofauna are a key component of global terrestrial vertebrate diversity. Because of its close association with the environment, it has been suggested that herpetofaunal diversity is higher in structurally heterogeneous plant communities (e.g., tropical forests) and lower in more homogeneous systems (e.g., mangroves). Despite being poorly studied, Los Petenes Biosphere Reserve (Campeche, Mexico) is an ideal system to test this hypothesis, as it harbors multiple plant communities within a single region. In this study, we used Hill numbers to assess whether amphibian and reptile diversity differs among six plant communities distributed along a transect: three heterogeneous (Disturbed Tropical Forest, Conserved Tropical Forest, and Tropical Forest Peten) and three homogeneous (Short Mangrove, Peten Mangrove, and Stripe Mangrove). We recorded 512 individuals representing 10 amphibian and 28 reptile species. Sample coverage estimates indicated adequate sampling completeness. In contrast to expectations, the Short Mangrove showed the highest abundance and species richness. β -diversity analyses revealed that this community is more similar to the heterogeneous communities than to the other homogeneous ones and indicated the existence of two assemblages within the regional herpetofaunal community. These findings suggest that factors such as geographic distribution or the availability of refuges may be more decisive than vegetation structural heterogeneity in shaping amphibian and reptile diversity patterns, encouraging a re-examination of the role of vegetation heterogeneity in tropical systems.

Key Words.—diversity; forest; heterogeneous/homogeneous vegetation; microhabitat; mangrove

INTRODUCTION

Herpetofauna are present in most terrestrial and aquatic environments, except the Arctic, making them one of the most important components of global biodiversity (Pough et al. 2004). Mexican herpetofauna are particularly remarkable: although Mexico represents only 1.3% of the continental area of the Americas, it harbors nearly 10% of the amphibian and reptile diversity of the world, with approximately 1,423 species recorded (Herpetología Mexicana 2021). A large proportion of these species are endemic (60.9%), and new species continue to be described year to year (Flores-Villela and Canseco-Márquez 2004; Ramírez-Bautista et al.

2023). This extraordinary herpetofaunal diversity has been associated with the wide geological and climatic variety that characterizes Mexico (Flores-Villela 1998; Camarillo and Rivera 1990; Morrone 2005; Koleff et al. 2019), which has also given rise to a mosaic of ecosystems (Rico-Gray 1982; Olmsted and Durán-García 1998; Comisión Nacional de Áreas Naturales Protegidas 2006).

The ecosystem diversity of Mexico includes a wide range of plant communities that differ in composition and structure. This variation directly influences amphibian and reptile richness patterns. For example, studies conducted in Mexico have reported higher herpetofaunal richness in structurally complex plant communities, such as evergreen and semi-deciduous

tropical forests, compared to more homogeneous communities dominated by a few plant species (Calderón-Mandujano 2006; Vargas-Santamaría and Flores-Villela 2006; Cruz-Sáenz et al. 2013; Ortiz-Medina et al. 2022). Similar patterns have also been documented in other Neotropical countries (Estrada 1998; Moreno-Bejarano and Álvarez-León 2003; Carvajal-Cogollo et al. 2007; Loc-Barragán et al. 2018). This evidence suggests a consistent pattern: heterogeneous plant communities harbor greater amphibian and reptile diversity than homogeneous ones (Mata-Silva 2003; Urbina-Cardona and Reynoso 2005; Wanger et al. 2010).

Los Petenes Biosphere Reserve, located on the northwestern coast of Campeche, Mexico, is a RAMSAR site and part of an ecoregion that includes Río Celestún and El Palmar (Comisión Nacional de Áreas Naturales Protegidas 2006). The *petenes* (from the Mayan word for vegetation islands) are unique ecosystems where mangroves, tropical forests, and seasonally flooded vegetation form a complex mosaic of habitats in which marine and terrestrial environments interact (Rico-Gray 1982; Olmsted and Durán-García 1998; Durán-García 1995; Flores-Verdugo et al. 2007; Koyoc-Ramírez et al. 2015). This interaction has resulted in heterogeneous plant communities, such as tropical forests (semi-evergreen and evergreen), being closely associated with more homogeneous communities, such as mangroves and Logwoods (*Haematoxylum campechianum*). This landscape in Los Petenes provides valuable opportunities to evaluate how the structure of plant communities influences amphibian and reptile diversity, although the herpetofauna diversity of Los Petenes remains poorly studied.

Despite the long history of herpetological research in Mexico (Ramírez-Bautista et al. 2023), and although Campeche is the state with the greatest herpetofaunal diversity in the Yucatán Peninsula (135 species; Flores-Villela and Pérez-Mendoza 2006; Wilson et al. 2013; Barão-Nóbrega et al. 2022), local information gaps persist. Most studies have focused on the Calakmul region in the southern part of the peninsula (Pozo-de la Tijera and Cedeño-Vázquez 1998; Calderón-Mandujano et al. 2003; Cedeño-Vázquez et al. 2006; Colston et al. 2015; Barão-Nóbrega et al. 2022), whereas other areas, such as the northern wetlands, have received little attention (Padilla and Perera-Trejo 2008, 2009; Padilla et al. 2021). This information gap underscores the importance of studying the herpetofauna of Los Petenes.

We evaluated whether amphibian and reptile diversity differ among the plant communities present within a relatively small region. Specifically, we aimed to compile an updated checklist of herpetofauna for an area in northern Campeche, and to compare amphibian and reptile diversity among contrasting plant communities in a natural system that includes both heterogeneous and homogeneous habitats (Los Petenes Biosphere Reserve). Given the well-documented pattern associating vegetation heterogeneity with higher amphibian and reptile diversity, we expected that the heterogeneous tropical forest in northwestern Campeche would exhibit greater diversity than the homogeneous mangrove.

MATERIALS AND METHODS

Study site.—Los Petenes Biosphere Reserve is located in the municipality of Tenabo, on the northwestern coast of Campeche, Mexico (Fig. 1). This area is part of a coastal plain characterized by low-elevation soils (< 5 m) that are subject to permanent or seasonal flooding (Zamora-Crescencio 2003). The climate is warm sub-humid, with summer rains (Köppen classification as modified by García 1973). During the period from May 2008 to April 2009, mean temperature was 25.5° C, with a minimum of 15.4° C recorded between December 2008 and January 2009, and a maximum of 37° C in May 2008. Mean annual precipitation during the same period was 928.4 mm (http://hidrosuperf.imta.mx/sig_eric/).

We followed the classification proposed by Zamora-Crescencio (2003) to select six plant communities distributed along a transect. Based on their structural complexity, we studied herpetofauna in three heterogeneous communities (Fig. 1): (1) seasonally flooded semi-evergreen tropical forest with high abundance of Julub (*Bravaisia berlandieriana*), which we classified as Disturbed Tropical Forest (FTF-h); (2) seasonally flooded semi-evergreen tropical forest with low abundance of Julub classified as Conserved Tropical Forest (FTF-l); and (3) semi-evergreen tropical forest peten classified as Tropical Forest Peten (EFP); and three homogeneous communities: (4) dwarf mangrove dominated by *Conocarpus erectus* classified as Short Mangrove (SM); (5) peten mangrove dominated by Red Mangle (*Rhizophora mangle*) classified as Peten Mangrove (MP); and (6) stripe mangrove dominated by Black Mangrove (*Avicennia germinans*) that we classified as Stripe Mangrove (ST). We distinguished between

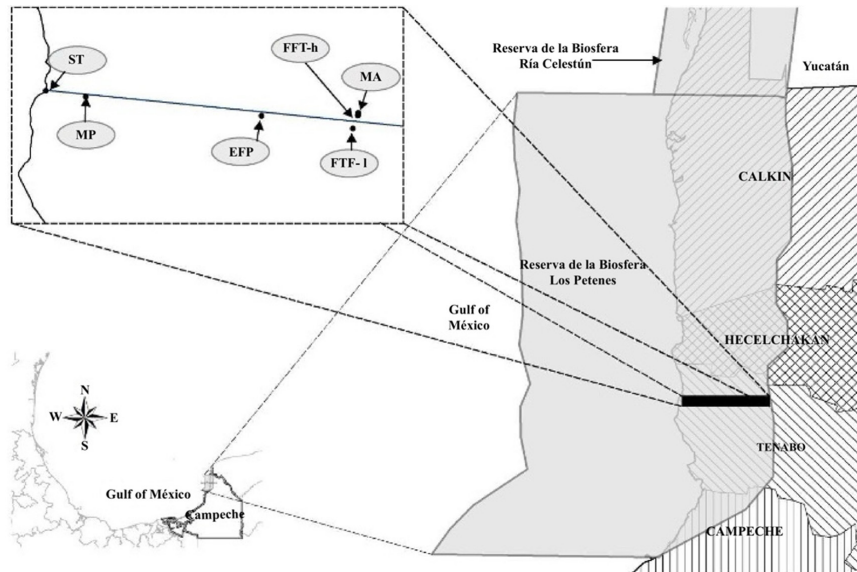


FIGURE 1. Location of the six plant communities sampled in this study within Los Petenes Biosphere Reserve, Campeche, Mexico. Abbreviations are FTF-h = Disturbed Tropical Forest (floodable semi-evergreen tropical forest with high presence of *Julub*), FTF-1 = Conserved Tropical Forest (floodable semi-evergreen tropical forest with low presence of *Julub*), SM = Short Mangrove (dominated by short mangrove), EFP = Tropical Forest Peten, MP = Peten Mangrove (dominated by red mangrove), and ST = Stripe Mangrove (dominated by stripe mangrove). Modified from Plan de Manejo de la Reserva de la Biosfera Los Petenes (Comisión Nacional de Áreas Naturales Protegidas 2006).

disturbed and Conserved Tropical Forest based on the presence of *Julub*, a plant species used as an indicator of disturbance (Lot 2004).

Data collection.—We conducted 11 consecutive monthly surveys from May 2008 to April 2009. During each survey, we performed active searches within 30 × 30 m quadrats established in each plant community. The total sampling effort amounted to 30 person-hours per month, with four people participating in each survey (1,320 cumulative person-hours), evenly distributed across sites. We carried out searches in two periods: morning (0700–1200) and night (1900–2400). We obtained records through visual encounters, auditory detections (for anurans), and direct captures.

We identified captured individuals to species level, and we recorded date, time, plant community, microhabitat, mass, snout-vent length (SVL), and total length (TL). For abundance counts, we relied on direct captures, and to avoid duplicate records, we marked individuals with nontoxic indelible ink before releasing them at the capture site. We preserved specimens found dead using standardized protocols (Pisani 1973) and deposited them in the scientific collection of Laboratorio de Vida Silvestre y Colecciones Científicas de la Universidad Autónoma de Campeche, Mexico.

We based taxonomic identification on specialized identification keys for the herpetofauna of Yucatan Peninsula (Lee 1996; Calderón-Mandujano et al. 1997; Cedeño-Vázquez et al. 1997; Campbell and Lamar 2004). Nomenclature follows González-Sánchez et al. (2017). To ensure comparability with other herpetofaunal inventories in Mexico (Vargas-Santamaría and Flores-Villela 2006; Gutiérrez-Mayén and Salazar-Arenas 2006), we report species abundances per plant community. We also classified each species according to its microhabitat use into six categories: (1) terrestrial, species found on the ground surface, excluding fossorial and water-associated species; (2) arboreal, associated with trees and shrubs; (3) fossorial, inhabiting subterranean environments; (4) riparian, occurring along water bodies; (5) saxicolous, using rocks, crevices, and rocky walls; and (6) anthropophilic, associated with human constructions (e.g., Vargas-Santamaría and Flores-Villela 2006; Gutiérrez-Mayén and Salazar-Arenas 2006).

Data analysis.—To estimate amphibian and reptile diversity in each plant community, we used Hill numbers (Jost 2006; Chao et al. 2014) implemented with the `hill_taxa` function in the `hillR` package (Li 2018) in R (R Core Team 2025). Similar to traditional indices such as Shannon Diversity Index (Magurran 1998), Hill numbers (qD) form a family of

diversity metrics that quantify the effective number of species in a community (Jost 2006). Unlike traditional indices, qD allows a direct interpretation in terms of the effective number of species, and this interpretation is consistent across metrics, facilitating comparisons among communities.

Hill numbers are parameterized by q , which controls sensitivity to rare or dominant species (Jost 2006; Roswell et al. 2021). Commonly, q is set to 0, 1, or 2: 0D measures species richness without considering relative abundances (${}^0D = S$), 1D weights richness by abundance and represents the number of equally common species in the community, and 2D reduces the influence of rare species and reflects the number of dominant species.

These metrics are applicable at the local level (α -diversity), the regional level (γ -diversity), and for species turnover between sites (β -diversity; Jost 2006; Chao et al. 2023). In contrast to qualitative indices such as Jaccard's (JI; Moreno 2001), β -diversity derived from Hill numbers is calculated as the ratio γ/α -diversity, where $\beta = 1$ indicates identical communities (100% similarity) and $\beta = 2$ indicates completely distinct communities (0% similarity). To compare species richness (0D), diversity (1D), and dominance (2D) among plant communities, we performed pairwise comparisons using the `hill_taxa_parti_pairwise` function (Li 2018) from `hillR` in R. This function computes α - and γ -diversity for each pair of communities, allowing estimation of β -diversity. In addition, to evaluate the diversity of the entire set of plant communities included in our study (γ -diversity), we applied a diversity partitioning approach using the `hill_taxa_parti` function (Li 2018) from the same package.

We assessed sampling completeness using sample coverage (SC; Chao and Jost 2012; Chao et al. 2020) calculated with the `DataInfo` function of the `iNEXT` package (Hsieh et al. 2016) in R. SC ranges from 0 to 1, where values < 0.90 indicate under-sampling and values > 0.95 indicate adequate sampling. Based on Hill numbers (0D , 1D , 2D) and observed SC, we extrapolated diversity to an SC of 0.99 using the `estimateD` function (Hsieh et al. 2016) from the same package. In this framework, steep slopes and $SC < 0.90$ indicate low representativeness, whereas flattened curves and $SC > 0.90$ indicate sufficient sampling effort (Chao et al. 2020), providing a clear and intuitive visualization of sampling completeness in each plant community.

RESULTS

We recorded 512 observations corresponding to 38 herpetofaunal species. Of this total, 180 individuals belonging to 10 species (26.3%) were amphibians and 332 individuals belonging to 28 species (73.7%) were reptiles (Supplemental Information Table S1). The complete taxonomic list is available in Supplemental Information Table S2. Three species were recorded outside the sampling sites: Green Sea Turtle (*Chelonia mydas*) on the beach, Road Guarder Snake (*Conopsis lineatus*) in semi-deciduous forest, and Cane Toad (*Rhinella horribilis*) in pasture. Additionally, two snakes could not be identified: one was represented only by skeletal remains and the other escaped rapidly into the vegetation. Therefore, these five species were not included in subsequent diversity analyses.

The most species-rich family was Colubridae, with seven species, followed by Dipsadidae with five. In contrast, families such as Corytophanidae, Eublepharidae, Iguanidae, Scincidae, Chelonidae, Kinosternidae, Bataguridae, Crocodylidae, Rhinophrynidae, and Ranidae were each represented by a single species (Supplemental Information Table S1). Among amphibians, Stauffer's Treefrog (*Scinax staufferi*), Gulf Coast Toad (*Incilius valliceps*), and Sabinal Frog (*Leptodactylus melanonotus*) were the most abundant species, together accounting for 29% (148 of 512) of all records (Fig. 2). Among reptiles, the most abundant species were Morelet's Crocodile (*Crocodylus moreletii*), Brown Basilisk (*Basiliscus vittatus*), Rodriguez's Anole (*Anolis rodriguezii*), and the introduced Common House Gecko (*Hemidactylus frenatus*), which together accounted for 41% (210 of 512) of total records (Fig. 2). Nine amphibian species were recorded across five plant communities (no amphibians were recorded in Stripe Mangrove). The greatest number of amphibian species was found in Short Mangrove (eight species), followed by Disturbed Tropical Forest (six species), conserved tropical forest (four species), Tropical Forest Peten (three species), and Short Mangrove (three species). Reptiles were present in all communities, with the highest number of species in Tropical Forest Peten (17 species) and Short Mangrove (15 species), and the lowest number in Conserved Tropical Forest (seven species; Table 1).

The plant community with the highest abundance of herpetofauna was Short Mangrove, with 174 of 512 (34%) recorded individuals, while Conserved Tropical Forest had the lowest abundance with 59

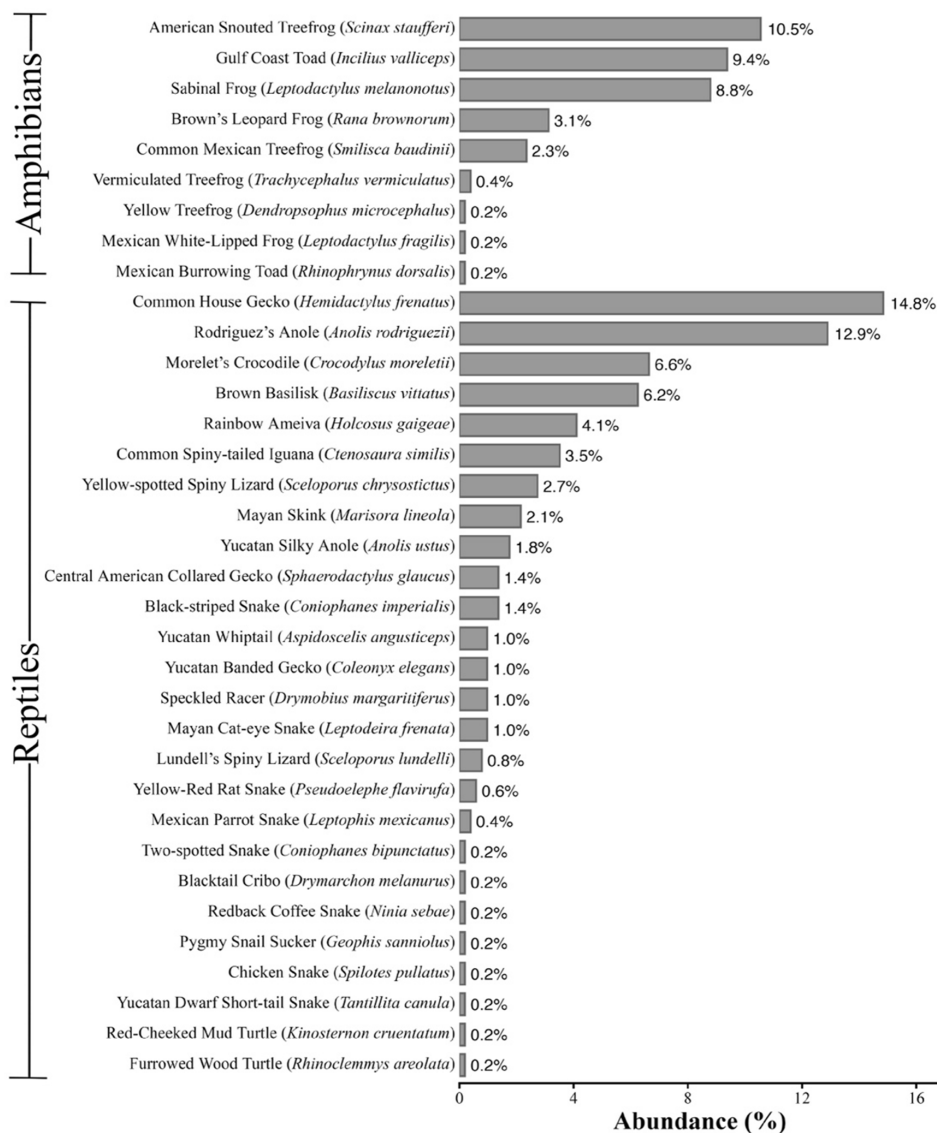


FIGURE 2. Relative abundance (%) of amphibian and reptile species recorded in the municipality of Tenabo, Campeche, Mexico. Bars represent the percentage of individuals per species relative to the total number of individuals recorded.

(11.5%) individuals (Fig. 3). The specific abundance pattern varied among communities: Stauffer's Treefrog was the most abundant species in Conserved Tropical Forest (27%) and Short Mangrove (20%). Rodriguez's Anole dominated in Disturbed Tropical Forest (42%) and Tropical Forest Peten (19%) and was also the second most abundant species in Disturbed Tropical Forest (25%) and Short Mangrove (13%). Finally, the Common House Gecko was the dominant species in Peten Mangrove (46%) and Stripe Mangrove (62%; Table 1).

Species richness (0D) was highest in Short Mangrove, followed by Tropical Forest Peten,

Disturbed Tropical Forest, Peten Mangrove, and Conserved Tropical Forest, with the lowest value recorded in Stripe Mangrove (Fig. 4; Table 1). We recorded the highest diversity (1D) and dominance (2D) in Tropical Forest Peten, followed by Short Mangrove and Disturbed Tropical Forest. Peten Mangrove and Conserved Tropical Forest showed similar diversity and dominance values, while Stripe Mangrove had the lowest values for both (Fig. 4; Table 1). Pairwise β -diversity analyses (Appendix Table) showed that, in terms of richness (0D), the highest similarity was between conserved and Disturbed Tropical Forest (72%), followed by Disturbed Tropical Forest and

TABLE 1. Abundance (n), species richness (0D), diversity (1D), and dominance (2D) of amphibians and reptiles across six plant communities in Los Petenes Biosphere Reserve, Campeche, Mexico. Values of 0D , 1D , and 2D represent Hill numbers and are expressed as effective numbers of species, allowing direct comparison among communities. The last row shows the overall γ -diversity (regional diversity) considering all communities combined.

Plant community	Composition	n	0D	1D	2D
Short Mangrove	Homogeneous	176	23	12.06	8.78
Tropical Forest Peten	Heterogeneous	72	20	13.59	10.2
Disturbed Tropical Forest	Heterogeneous	64	14	8.35	5.76
Peten Mangrove	Homogeneous	68	12	6.05	3.91
Conserved Tropical Forest	Heterogeneous	59	11	6.03	4.06
Stripe Mangrove	Homogeneous	73	9	3.75	2.42
Total (γ)	–	512	35	15.71	10.72

Short Mangrove (64.9%). In contrast, the lowest similarity was between Tropical Forest Peten and Stripe Mangrove (27.6%), followed by Conserved Tropical Forest and Peten Mangrove (34.8%).

For diversity (1D), Peten Mangrove and Stripe Mangrove exhibited the highest similarity (75.2%), followed by disturbed and Conserved Tropical Forest (69.7%). Conversely, the lowest similarity occurred between Conserved Tropical Forest and Stripe Mangrove (13.4%), followed by Disturbed Tropical Forest and Stripe Mangrove (14%; Appendix Table). Dominance-based similarity (2D) was highest between Peten Mangrove and Stripe Mangrove (90.3%), followed by Conserved Tropical Forest and Tropical Forest Peten (70%). The lowest similarity was between Disturbed Tropical Forest and Stripe Mangrove (2.3%), followed by Conserved Tropical

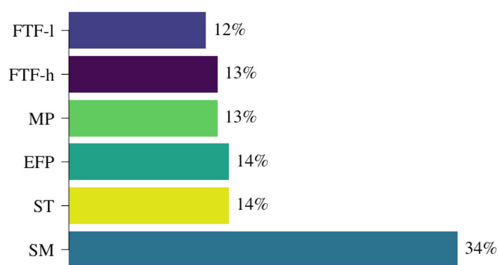


FIGURE 3. Relative abundance (%) of amphibians and reptiles recorded in six plant communities of Los Petenes Biosphere Reserve, Campeche, Mexico. Abbreviations are FTF-h = Disturbed Tropical Forest (floodable semi-evergreen tropical forest with high presence of *Julub*), FTF-l = Conserved Tropical Forest (floodable semi-evergreen tropical forest with low presence of *Julub*), SM = Short Mangrove (short mangrove), EFP = Tropical Forest Peten, MP = Peten Mangrove (*red mangrove*), and ST = Stripe Mangrove (stripe mangrove).

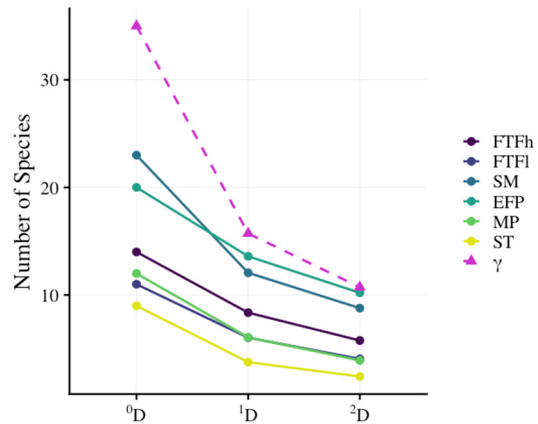


FIGURE 4. Species richness (0D), diversity (1D), and dominance (2D) of amphibians and reptiles across six plant communities in Los Petenes Biosphere Reserve. Abbreviations are FTF-h = Disturbed Tropical Forest, FTF-l = Conserved Tropical Forest, SM = Short Mangrove (*Conocarpus erectus*), EFP = Tropical Forest Peten, MP = Peten Mangrove (*Rhizophora mangle*), and ST = Stripe Mangrove (*Avicennia germinans*). Values represent Hill numbers, expressed as effective numbers of species.

Forest and Stripe Mangrove (2.7%; Appendix Table). The γ -diversity analysis for the entire set of plant communities indicated a richness (0D) of 35 species, a diversity (1D) of 15.71 species, and a dominance (2D) of 10.72 species (Table 1). β -diversity analysis further indicated that approximately 2.35 effective communities can be distinguished based on species richness, 2.07 communities based on diversity, and 2.32 communities based on dominance.

The analysis of sampling completeness indicated that only Short Mangrove (0.96) and Conserved Tropical Forest (0.95) reached estimated coverage values that reflect adequate sampling effort (> 0.95). The remaining plant communities showed intermediate values: Stripe Mangrove (0.94), Disturbed Tropical Forest (0.93), Peten Mangrove (0.92), and Tropical Forest Peten (0.90). These values indicate acceptable sampling effort but with potential for improved representativeness. No community had $SC < 0.90$, indicating that none were undersampled (Fig. 5). Extrapolated diversity curves showed a consistent pattern among communities. For richness (0D), all plant communities displayed steeper slopes than those observed for diversity (1D), whereas dominance (2D) curves were nearly flat. Among richness curves, Short Mangrove exhibited the steepest slope, whereas among diversity and dominance curves, Tropical Forest Peten was the steepest (Fig. 5). At the regional level, the estimated sampling coverage was high (approximately 0.98), indicating that the overall inventory was well represented. The extrapolated richness curve (0D)

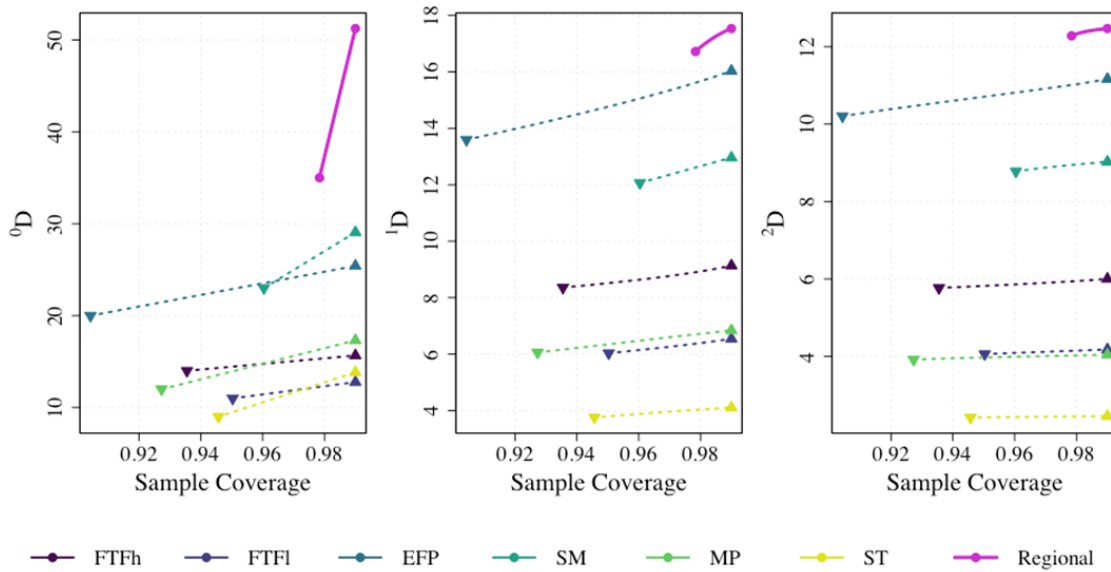


FIGURE 5. Sample coverage-based extrapolation curves of species richness (0D), diversity (1D), and dominance (2D) for amphibians and reptiles across six plant communities and at the regional level in Los Petenes Biosphere Reserve, Campeche, Mexico. Curves show the relationship between sample coverage (SC) and Hill numbers, extrapolated up to SC = 0.99. Steeper slopes indicate lower representativeness, whereas flatter curves indicate adequate sampling effort. Abbreviations are FTF-h = Disturbed Tropical Forest, FTF-l = Conserved Tropical Forest, SM = Short Mangrove, EFP = Tropical Forest Peten, MP = Peten Mangrove, and ST = Stripe Mangrove.

retained a steeper slope than the diversity (1D) and dominance (2D) curves, which were nearly identical to the observed values (Fig. 5).

DISCUSSION

Our sampling in the Tenabo transect recorded 80% of the amphibians and 72% of the reptiles previously reported for the southern portion of Los Petenes Biosphere Reserve (Padilla and Perera-Trejo 2009; Padilla et al. 2021). These numbers represent 41.6% of the amphibians and 26.9% of the reptiles documented for the state of Campeche (González-Sánchez et al. 2017), as well as 26.2% of the herpetofauna reported for the Yucatán Peninsula (González-Sánchez et al. 2017). In terms of taxonomic composition, the higher representation of Colubridae, followed by Dipsadidae, is consistent with patterns reported for other regions of the peninsula, where both families usually dominate in species richness (González-Sánchez et al. 2017). In contrast, the presence of families represented by a single species reflects the relative rarity of some lineages in the region and highlights the importance of long-term monitoring to confirm the presence of poorly represented taxa.

Plant communities differed markedly in herpetofaunal abundance, richness, and diversity. Short Mangrove and Tropical Forest Peten had the highest abundance, richness (0D), diversity (1D),

and dominance (2D) compared with the other plant communities. β -diversity analysis showed that Short Mangrove was more similar to the heterogeneous plant communities (Tropical Forest Peten, Conserved Tropical Forest, and Disturbed Tropical Forest) than to the other homogeneous communities (Peten Mangrove and Stripe Mangrove). Furthermore, although sampling coverage was adequate for Short Mangrove, extrapolation indicated that this community would still yield the highest species richness if additional sampling were performed. This pattern is counterintuitive, as structurally heterogeneous communities are generally expected to harbor greater diversity compared to homogeneous ones such as mangroves (Cruz-Sáenz et al. 2013; Loc-Barragán et al. 2018; Ortiz-Medina et al. 2022), although cases in which homogeneous plant communities exhibit higher-than-expected diversity have been reported (Rog et al. 2017; Rosas-Espinoza et al. 2024).

Although Short Mangrove is dominated by *Conocarpus erectus*, its broad representation throughout Los Petenes Biosphere Reserve may provide greater opportunities and reduced competition, resulting in higher abundance and richness than in structurally complex but more spatially restricted communities such as tropical forest. In addition, many observations were made along trails, which have been described as small ecotones that not only

harbor more individuals but also facilitate dispersal (Andrews 1980; Urbina-Cardona et al. 2006; Kurz et al. 2014). Tropical Forest Peten ranked second in abundance and richness (0D) but first in diversity (1D) and dominance (2D), reflecting a community with fewer rare species and greater evenness. Extrapolated sampling coverage confirmed this pattern (second in maximum richness, first in maximum diversity and dominance). Its structure and composition, typical of tropical evergreen forest (high plant diversity and cover, thick leaf litter layers, high humidity, and stable temperatures), make it a favorable habitat for amphibians and reptiles, as previously reported (Mata-Silva 2003; Urbina-Cardona and Londoño-Murcia 2003). Thus, whereas Short Mangrove illustrates an atypical case of high diversity in a homogeneous environment, Tropical Forest Peten confirms the classic expectation that structural heterogeneity promotes more balanced and diverse communities (Vargas-Santamaría and Flores-Villela 2006; Cruz-Sáenz et al. 2013; Ortiz-Medina et al. 2022).

Disturbed and Conserved Tropical Forest, along with Peten Mangrove, formed a group of communities with intermediate values of abundance, richness (0D), diversity (1D), and dominance (2D). Extrapolated sampling coverage confirmed that effort was adequate in all cases, with no substantial differences between observed and expected values. Pairwise β -diversity revealed that, in terms of richness, Peten Mangrove was most similar to Tropical Forest Peten (50%), whereas in diversity and dominance it was most similar to Stripe Mangrove (75.2% and 90.3%, respectively).

Although the homogeneous structure of Peten Mangrove (dominated by Red Mangrove) might limit diversity, microhabitats associated with fallen logs and aerial roots may provide opportunities for some species (Heatwole 1982). The high similarity in diversity and dominance between Peten Mangrove and Stripe Mangrove appears to be driven by the shared abundance of Black Spiny-tailed Iguana (*Ctenosaura similis*) and Common House Gecko. This similarity may be reinforced by their geographic proximity. The coexistence of Common House Gecko with the native Least Gecko (*Spherodactylus glaucus*) is particularly noteworthy, as the invasive species has been reported to displace native species elsewhere (Hoskin 2011), suggesting a conservation concern for the region.

Conserved and Disturbed Tropical Forests exhibited differences in richness, diversity, and dominance.

Nevertheless, β -diversity analysis revealed high similarity between them (> 60%), which is expected given that they represent the same plant community in different conservation states. The lower diversity observed in Conserved Tropical Forest suggests that resource stability does not necessarily translate into greater herpetofaunal richness. In this herpetofaunal community, the difference between diversity and dominance was relatively small, with several species occurring in similar numbers, which tempers the impression of low richness.

In Disturbed Tropical Forest, the presence of Julub, typical of disturbed areas, appears to generate a heterogeneous understory that provides multiple niches. This has been associated with greater refuge availability and microhabitat diversity, favoring the coexistence of several species (Ortega-Esquinca 2000). This pattern is consistent with the high abundance of Rodríguez's Anole, which responds positively to moderate disturbance (Calderón-Mandujano 2006).

Stripe Mangrove was the least diverse community, with only nine recorded species and strong dominance of Common House Gecko. Extrapolated sampling coverage suggested that, in terms of richness (0D), this community might even surpass Conserved Tropical Forest; however, no meaningful changes were observed in diversity (1D) or dominance (2D). As noted earlier, β -diversity analysis showed that this community was markedly different from all others except Peten Mangrove. The direct influence of tides and salinity restricts the presence of amphibians and many reptile species (Moreno-Bejarano and Álvarez-León 2003), consistent with the absence of amphibians recorded for this community. Together, these patterns suggest that low diversity and high dominance in Stripe Mangrove are driven primarily by harsh physical conditions rather than by vegetation structural homogeneity.

Regional γ -diversity analysis showed that of the 35 species recorded in the region, only about 16 contribute evenly to effective diversity, while around 11 species dominate the assemblage. Although our inventory adequately reflects regional patterns (72% of amphibians and 80% of reptiles reported for the reserve; Padilla and Perera-Trejo 2009; Padilla et al. 2021), the estimated sample coverage for richness, although high (98%), suggests that with coverage extended to 99%, richness could increase to 51 species and diversity to 18 species. This is consistent with species recorded in nearby areas (Padilla and Perera-Trejo 2009; Padilla et al. 2021), with those

whose ranges include the region (Lee 1996; Díaz-Gamboa et al. 2020), and with our opportunistic observations of unidentified snakes. Overall, these results indicate that, although our sampling was sufficient to characterize the regional herpetofauna, additional species (particularly rare ones) are likely to be recorded with increased sampling effort in underrepresented communities.

Regional β -diversity analysis suggests that, in terms of richness, diversity, and dominance, the region is structured into approximately two assemblages. Based on pairwise similarity among communities, disturbed and Conserved Tropical Forest, Tropical Forest Peten, and Short Mangrove form one assemblage, whereas Peten Mangrove and Stripe Mangrove constitute the second. This pattern may be influenced by spatial proximity and geographic position: lower diversity is observed in communities closest to the coast and tends to increase toward the interior of the peninsula, as previously reported (Moreno-Bejarano and Álvarez-León 2003).

In summary, our results show that the higher diversity observed in Short Mangrove and its low similarity with other homogeneous communities contradict the classical expectation that vegetation structural complexity is positively associated with amphibian and reptile diversity (Mata-Silva 2003; Urbina-Cardona and Londoño-Murcia 2003; Urbina-Cardona and Reynoso 2005; Calderón-Mandujano 2006). These findings suggest that large-scale factors, such as geographic distribution and spatial extent of the communities, and local-scale factors, such as refuge availability and microhabitat quality, may play a more decisive role than vegetation structural heterogeneity in explaining herpetofaunal diversity patterns. Future studies in other systems could test these results and contribute to a better understanding of amphibian and reptile diversity patterns, with direct implications for the designation of conservation areas (Urbina-Cardona and Flores-Villela 2010).

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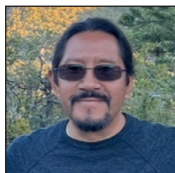
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APPENDIX

APPENDIX TABLE. Pairwise comparison of herpetofaunal diversity between plant communities in Los Petenes Biosphere Reserve, Campeche, Mexico. The table shows α -diversity, γ -diversity, β -diversity (expressed as the ratio γ/α), and similarity (%) for each pair of communities, calculated using Hill numbers (0D = richness, 1D = diversity, 2D = dominance). Plant community abbreviations are FTF-h = Disturbed Tropical Forest (floodable semi-evergreen tropical forest with high presence of *Julub*), FTF-l = Conserved Tropical Forest (floodable semi-evergreen tropical forest with low presence of *Julub*), SM = Short Mangrove (*Conocarpus erectus*), EFP = Tropical Forest Peten, MP = Peten Mangrove (*Rhizophora mangle*), ST = Stripe Mangrove (*Avicennia germinans*).

Pairwise	0D	α	γ	β	Similarity %
	0	16	24	1.5	50
EFP - MP	1	9.075	13.649	1.504	41
	2	5.663	9.312	1.644	21
	0	21.5	30	1.395	60
EFP - SM	1	12.806	17.555	1.371	54
	2	9.439	13.169	1.395	43
	0	14.5	25	1.724	27
EFP - ST	1	7.148	12.878	1.802	15
	2	3.917	7.541	1.925	3
	0	17	25	1.471	52
FTFh - EFP	1	10.661	14.009	1.314	60
	2	7.371	9.411	1.277	56
	0	12.5	16	1.28	72
FTFh - FTFI	1	7.103	8.765	1.234	69
	2	4.767	5.726	1.201	66
	0	13	21	1.615	38
FTFh - MP	1	7.116	11.201	1.574	34
	2	4.667	7.733	1.657	20
	0	18.5	25	1.351	64
FTFh - SM	1	10.042	13.448	1.339	57
	2	6.963	9.204	1.322	51
	0	11.5	18	1.565	43
FTFh - ST	1	5.605	10.171	1.815	14
	2	3.413	6.67	1.954	2
	0	15.5	25	1.613	38
FTFI - EFP	1	9.058	11.744	1.297	62
	2	5.811	6.835	1.176	70
	0	11.5	19	1.652	34
FTFI - MP	1	6.046	9.675	1.6	32
	2	3.989	6.395	1.603	24
	0	17	24	1.412	58
FTFI - SM	1	8.532	11.566	1.356	56
	2	5.554	8.42	1.516	31
	0	10	16	1.6	40
FTFI - ST	1	4.762	8.68	1.823	13
	2	3.036	5.909	1.946	2

APPENDIX TABLE, Continued

Pairwise	qD	α	γ	β	Similarity %
	0	10.5	17	1.619	38
MP - ST	1	4.772	5.666	1.187	75
	2	2.995	3.147	1.051	90
	0	17.5	27	1.543	45
SM - MP	1	8.549	13.46	1.575	34
	2	5.419	9.47	1.748	14
	0	16	25	1.562	43
SM - ST	1	6.733	11.367	1.688	24
	2	3.798	7.149	1.882	6