

Published by the British
Herpetological Society<https://doi.org/10.33256/34.4.244255>

Small-scale geographic factors promote a high diversity of amphibians and reptiles in Colombia

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Analysing spatial biodiversity patterns in amphibians and reptiles is key to understanding the main drivers of community ecological structure, biogeography, and guiding conservation strategies. Our goal is to map patterns of taxonomic change and unravel the geographic and environmental factors driving species turnover among the biomes found in the Sogamoso river basin (SRB), which tributes to the inter-Andean middle Magdalena valley in Colombia, a hyperdiverse region at high-risk from human activities. The study area encompasses lowland forest, submontane, montane and high-elevation Andean habitats, with distinct biomes defined by elevation and physiographic characteristics. To do this, we compared species richness among different biomes and describe their variation along the altitudinal gradient. We collected data from literature and revision of specimens deposited in herpetological collections. Species distribution models were used to estimate geographic ranges and species composition was analysed among biomes using a presence/absence matrix. Generalised Dissimilarity Modelling (GDM) was employed to explore spatial turnover patterns of species composition. We observed that species richness of both amphibians and reptiles was the highest in the tropical humid forest biome and the lowest occurred mainly in the Sub-Andean semiarid vegetation. The spatial pattern of species turnover was the same for amphibians and reptiles and revealed an extreme similarity with the previous delimitation of the five biomes, which are supported by a combination of biotic, abiotic and anthropogenic factors. This study provides valuable baseline information for the conservation of amphibians and reptiles in the SRB and highlights the importance of considering geographic and environmental factors in understanding species distribution and turnover in the region.

Keywords: Sogamoso River, herpetofauna, richness patterns, turnover species, ecological structure

INTRODUCTION

Globally, the decline of many amphibian and reptile populations has been associated with important factors such as land-use change (Powers & Jetz, 2019; Cordier et al., 2021), introduced invasive species (Kraus, 2015), disease (Scheele et al., 2019), and global climate change (Hof et al., 2011; Mi et al., 2023). In Colombia, habitat loss and degradation are among the principal factors (Armenteras et al., 2014; Clerici et al., 2020). It is estimated that around 70% of Andean and 30% of lowland forests in Colombia have been lost (Etter et al., 2006), especially in the Magdalena river basin (Etter & van Wyngaarden, 2000). This basin is considered one of the most important regions of the country, due to its high economic productivity and population concentration. Furthermore, biologically and biogeographically, it represents an important reservoir of biodiversity, currently defined as the Province of Magdalena that belongs to the Pacific domain, sharing a composition of taxa with nearby provinces, such as Guajira, Chocó-Darién and Cauca (Hernández-Camacho & Sanchez, 1992; Kattan et al., 2004; Morrone, 2014).

One of the main tributaries of the Magdalena River is the Sogamoso River, which drains its waters on the western slope of the Cordillera Oriental and belongs to the great Magdalena-Cauca inter-Andean hydrographic area. The region is hydrographically delimited as a hydric subsystem with features of relief and homogeneous drainage, defined as the Sogamoso River Basin (SRB) (IDEAM, 2013). Located in north-eastern Colombia (Santander department), it is an important area for the extraction of oil, palm oil crops and cattle raising (Etter & van Wyngaarden, 2000; Etter et al., 2006), and it is the area of influence of one of the most important hydroelectric power plants in the country. This industrial development involves the establishment of new roads, petroleum wells, dams, and other infrastructure related to the economic activities that are developed in the region (Salgado et al., 2022).

In these terms, it is important to design conservation strategies that could reverse this trend in wild fauna populations, to prevent, mitigate, compensate or correct the negative effects of socio-economic activities on ecosystems (Schmeller et al., 2017). Hence, the starting point is to evaluate the state of biodiversity, generating

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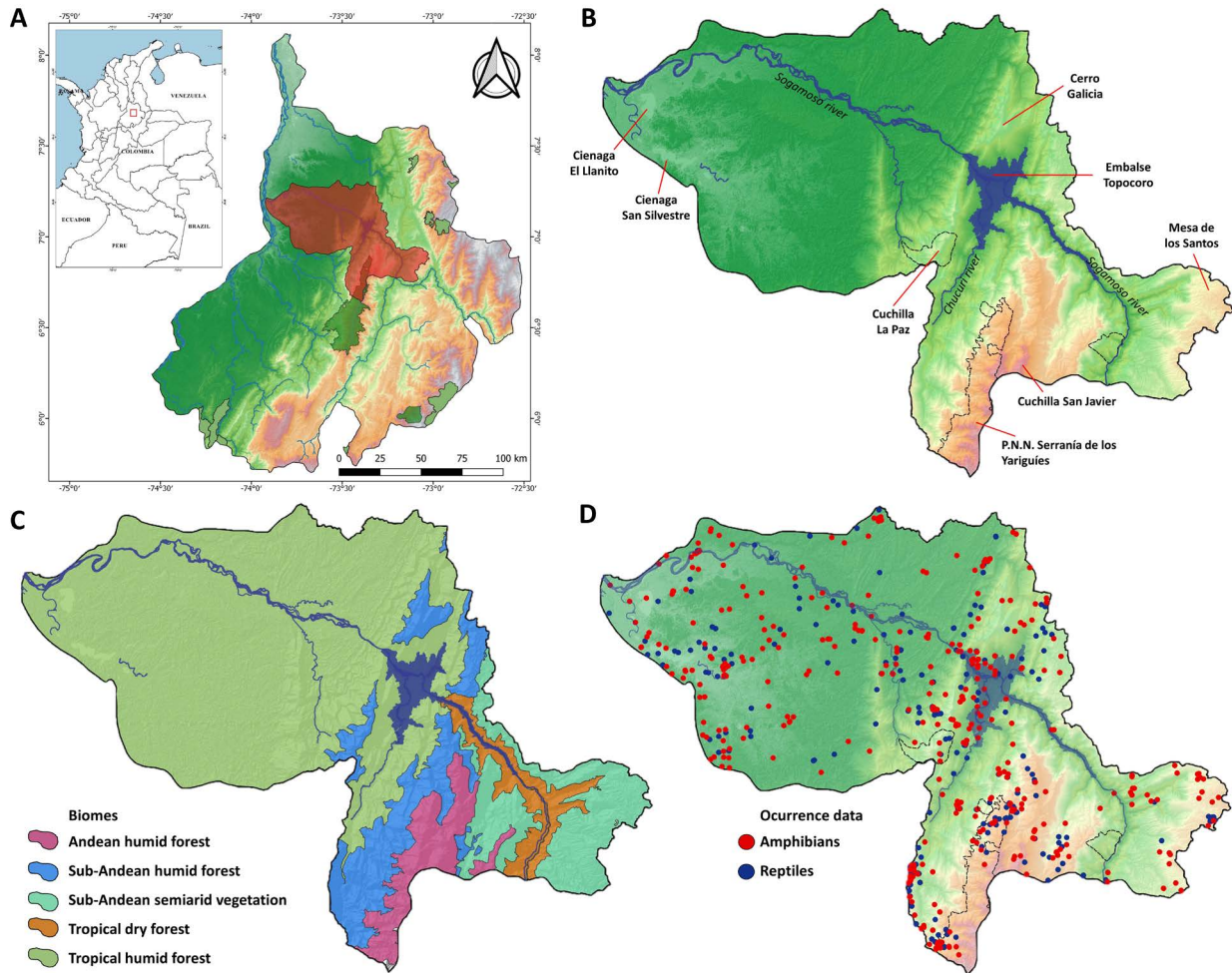


Figure 1. Graphical representation of the study area – **A.** The geographic location of the Sogamoso river basin within the department of Santander and Colombia, **B.** topography with major mountain massifs and rivers, **C.** major bioclimatic zones or biomes, and **D.** occurrences for amphibians and reptiles within SRB.

a solid baseline that allows the correct direction of conservation actions (Mace, 2004). In general, the conservation status and distribution of amphibians and reptiles in the SRB is generally unknown, and until recently, few studies have examined species composition and diversity in this river basin. Those studies correspond to technical reports and environmental management plans. However, those studies have not been carried out with a scientific approach and are not publicly available, because they are reports for the exclusive use of companies or Colombian environmental legislation.

Here, we provide the first comprehensive analysis of the species richness and diversity of amphibians and reptiles species in an important geographical area in the middle Magdalena valley of Colombia. We compare the species richness among the biomes and describe their variation in the altitudinal gradient. This study aims to identify and understand the geographic and environmental factors that influence the presence and distribution of species, and contribute to species turnover in the region. We expect that geographic distance and climate have strong explanatory power, mainly when considering the whole basin assessed for differences between species turnover, as they may affect herpetofauna independently of their

ability to disperse, niche partitioning, and interspecific competition along environmental gradients.

MATERIALS & METHODS

Study area

The Sogamoso river basin is located in the Santander department, north-eastern Colombia between 7° 18'39.60"–6° 38'16.80" N and 73° 1'12.0"–73° 55'26.4" W from middle Magdalena valley to the western slope of the Cordillera Oriental, and covers 3400 km² of lowland forest, submontane, montane and high-elevation Andean habitats between 60 m and 3200 m elevation, which represents 0.3% of the national territory (Fig. 1). The temperature ranges between 11.7 and 29 °C and the annual rainfall is between 950 and 3150 mm (CAS & CDMB, 2016). For this work, we recognise five well-contrasting biomes or terrestrial ecosystems (tropical forest, tropical dry forest, Sub-Andean humid forest, Sub-Andean semiarid vegetation and high-Andean humid forest). These biomes are defined by their elevation range, and physiographic and physiognomic characteristics (Hernández-Camacho & Sanchez, 1992; Latorre et al., 2014) (Fig. 1) as described below.

The tropical humid forest biome covers an area of 231,617 ha (67% of SRB) and ranges in elevation from 60 to 850 m. It is a lowland ecosystem that currently consists mostly of agribusiness systems (extensive livestock, African oil palm crops and rubber crops, among others) and large infrastructure projects (oil extraction, a hydroelectric power plant and heavy transport roads). Additionally, within this area, we find large areas of wetlands, forests and tropical marshes (Supplementary Material Fig. 1). The annual average temperature is 28.5 °C and rainfall is 3150 mm (Latorre et al., 2014; CAS & CDMB, 2016).

The sub-Andean semiarid vegetation biome covers an area of 38,010 ha (11% of SRB) and ranges in elevation from 1200 to 1800 m. It is a tropical dry forest formed by the rain shadow on the leeward side of the 'Serranía de los Yariguíes'. The vegetation of this biome consists of trees of low and medium height, thorny thickets, dry grasslands, and some areas transformed into tobacco, pineapple, vegetables, and goat grazing areas (Supplementary Material Fig. 2). The annual average temperature is 18.5 °C and rainfall is 1700 mm (Latorre et al., 2014; CAS & CDMB 2016).

The sub-Andean humid forest biome covers an area of 38,160 ha (11.1% of SRB) and ranges in elevation from 850 to 2000 m. It is a mountain ecosystem located between the north-western zone of the Natural National Park Serranía de los Yariguíes (P.N.N. Serranía de los Yariguíes), and the upper area of the Serranía de la Paz, forming the Chucurí river basin. The vegetation cover currently present in this biome is small-scale agroforestry systems of cocoa, coffee plantations, livestock, and relicts of conserved forests in the highlands of the Serranía de la Paz and low marginal areas of the P.N.N. 'Serranía de los Yariguíes' (Supplementary Material Fig. 3). The annual average temperature is 25.5 °C and rainfall is 2600 mm (Latorre et al., 2014; CAS & CDMB, 2016).

The tropical dry forest biome covers an area of 15,750 ha (4.6% of SRB) and ranges in elevation from 220 to 1200 m. In this ecosystem, lands with steep slopes predominate, with low-organic matter soils, high erosion rates with high leaching processes, and where thorny and cardonal scrublands are established. This vegetation is typical of the Chicamocha and Suárez river basins that together form the SRB. At present, some areas withstand pressure from grazing goats (Supplementary Material Fig. 4). The annual average temperature is 24.6 °C and rainfall is 950 mm (Latorre et al., 2014; CAS & CDMB, 2016).

The Andean humid forest biome covers an area of 19890 ha (5.8% of SRB) and ranges in elevation from 2000 to 3200 m. In this work, this biome corresponds mainly to cloud forests; however, in this area, we also include small sub-paramo and paramo zones that are above 3000 meters, which cover less than 0.1% of the SRB area. Currently, the main land use of this ecosystem is the protected area of the P.N.N. Serranía de los Yariguíes (Supplementary Material Fig. 5). The annual average temperature is 18.5 °C and rainfall is 2100 mm (Latorre et al., 2014; CAS & CDMB, 2016).

Data collection

The records presented here come mainly from literature, global databases (Gbif) and specimens collected in the study area and deposited in the herpetological collections of Universidad Industrial de Santander (MHN-UIS), Instituto de Ciencias Naturales (ICN), Museo de Herpetología Universidad de Antioquia (MHUA), and in the biological collections of the Instituto de Investigaciones de Recursos Biológicos Alexander von Humboldt (IAvH). Most of the specimens reviewed come from the collections made during the different phases of construction of the Sogamoso hydroelectric power project led by the company ISAGEN S.A. All procedures were conducted under collecting permit #4120-E1-29166, issued by ANLA (Autoridad Nacional de Licencias Ambientales) on 16 June 2014.

For the revision and identification of the specimens, the original descriptions of the species, taxonomic revisions, reference material and type series available in the collections visited were used. Amphibian nomenclature follows Frost (2024), and reptile nomenclature follows Uetz et al. (2024). We included in the list only the species having voucher specimens or photographs that allow unambiguous identification of taxa. All records were tabulated and organised in the standard template Darwin Core (version 2015-06-05), which contains the elements required for the documentation of biological records of amphibians and reptiles that were developed by Biodiversity Information Standards (TDWG, 2011). Additionally, the threat categories for each species were consulted in the IUCN Red List of Threatened Species (IUCN, 2023).

Species Richness

Because the distribution ranges of SRB's amphibians and reptiles have not been comprehensively mapped and distribution records are scattered, we used species distribution models (SDMs) to obtain an estimate of the geographic ranges. Species distribution models were limited to species that had, at minimum, three unique occurrence points at the spatial resolution (0.91 km²). The models were generated in MaxEnt v3.3.3e (Phillips et al., 2004) using the following parameters: random test percentage = 25, regularisation multiplier = 1, the maximum number of background points = 10000, replicates = 10, replicated run type = cross-validate, threshold = minimum training presence. Species distributions were modelled for the current climate using the 19 standard bioclimatic variables of WorldClim 2.1 (Fick & Hijmans, 2017). Non-climatic variables (geology, aspect, elevation, solar radiation and slope) were included. Before SDM analysis, using SDMtoolbox (Brown, 2014) we checked and removed highly correlated variables. All layers were projected to Colombian projection in ArcMap at a resolution of 0.91 km². Continuous SDMs were converted to binary models using the minimum training presence threshold to represent the potential habitat of each species based on its fundamental niche (Guisan & Zimmermann, 2000). We stacked SDM predictions separately for reptiles,

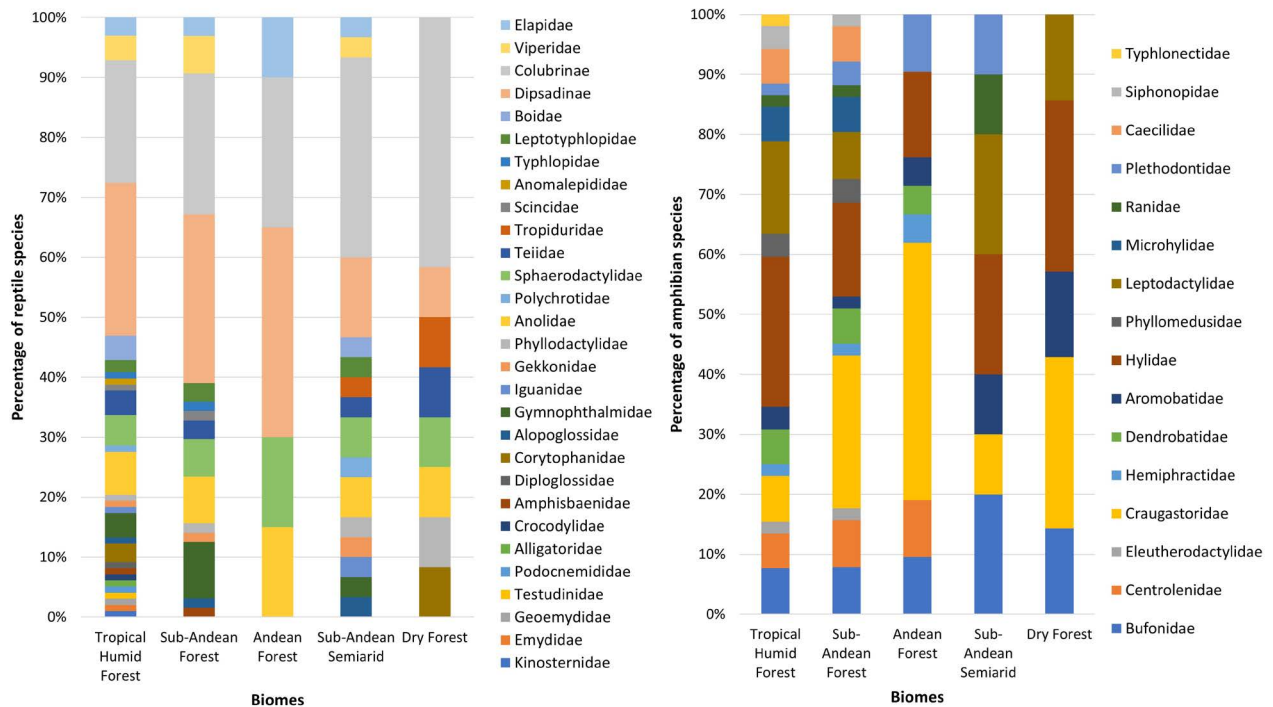


Figure 2. Bar graphics showing the reptile (left) and amphibian (right) families represented in each of the five major biomes of Sogamoso river basin. The percentage shows the representation of the species of each family within each biome with respect to the total number of species of the same biome.

amphibians, and both together using SDMtoolbox v1 (Brown, 2014) to estimate a threshold-based richness map. This methodology is useful as a baseline for analysing the abiotic deterministic processes that may shape and affect community assembly (Pouteau et al., 2019), and to define a reference pool against which null models or hierarchical analyses can be performed (Carstensen et al., 2013) for hypothesis testing modelling of biodiversity dynamics (Grenié et al., 2020).

Species richness among biomes and generalised dissimilarity modelling

Because the species richness of biological communities changes as the environment changes, we used species as an indicator of the state of the environment and evaluated the variation of species richness across biomes with distinctive physiognomic and physiographic characteristics. To do this, we first extracted the species richness of each grid from the threshold-based richness map to obtain a presence/absence matrix of species for each grid cell. We assigned each matrix grid cell to one of the biome categories. Then, with the species list for each grid cell and biome, was defined each biome's characteristic species as those that have the maximum proportion of their range in that biome. This approach is useful to assess a directional taxonomic overlap among biomes (see Echeverría-Londoño et al., 2018 for further details and use of this methodology).

Additionally, we calculate the Sørensen similarity index (Magurran, 2004) to estimate the similarity in species composition among biomes and extracted the maximum, minimum and mean elevations predicted for each species from the adjusted SDMs for calculating the

number of species estimated by the models to occur at intervals of 200 m above sea level. This analysis was performed in R v 4.2.3 (R Core Team, 2023). On the other hand, we explore the spatial turnover patterns of species composition using Generalised Dissimilarity Modelling (GDM, Ferrier et al., 2007), this analysis is a nonlinear matrix regression technique between pairs of locations as a function of environmental dissimilarity and geographical distance. GDM accommodates (i) variation in the rate of compositional turnover at different positions along a given gradient, and (ii) the curvilinear relationship between compositional dissimilarity and increasing environmental/geographical distance between sites (Ferrier et al., 2007). To fit GDMs, we used the site-by-species matrix obtained from previous analysis and the same environmental predictors used for the species distribution models (SDMs). This analysis was performed in R v 3.2.2 (R Core Team, 2023) with the package “gdm” (Manion et al., 2017).

RESULTS

General results

Currently, there are 2953 amphibian and reptile specimens registered that were collected between the 1940s and 2020 in the SRB and deposited in the herpetological collections visited during this work. With this review, we generated a list of 197 species, 76 of which are amphibians (16 families, 43 genera) and 121 reptiles (28 families, 83 genera; Supplementary Material Table 1, Fig. 2). Of these species, 49 are endemic to Colombia (35 amphibians, 14 reptiles), and 19 endemics to the Santander department (17 amphibians, 2 reptiles), indicating high levels of

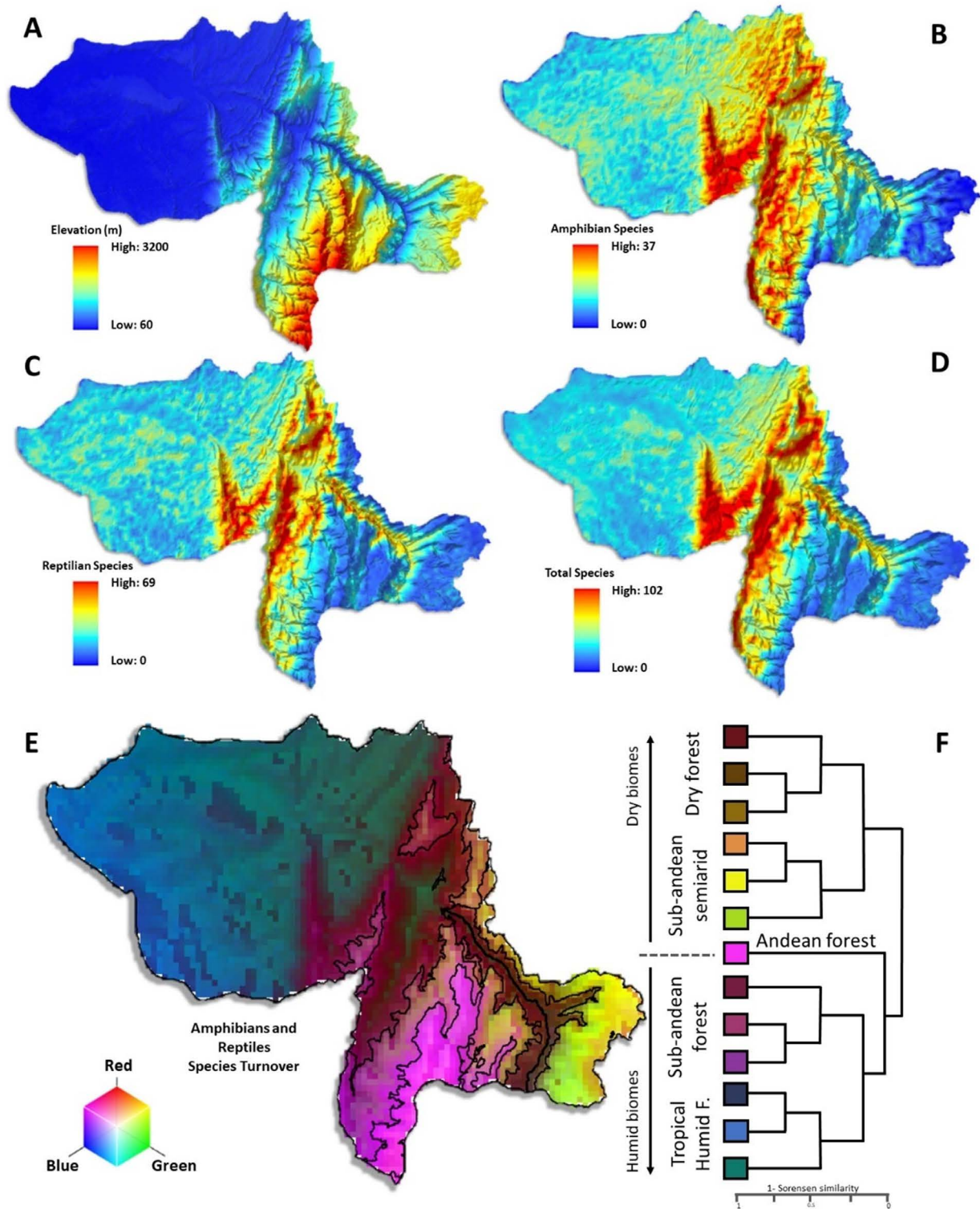


Figure 3. Biodiversity measures for reptiles and amphibians in the SRB – **A.** Elevation gradient, **B.** species richness of amphibians, **C.** species richness of reptiles, **D.** species richness of both, and **E.** visual representation of the turnover as measured by generality dissimilarity models (GDM), based on the distribution of 194 amphibian and reptile species from SRB. Similarity in colour represents similarity in species composition. The dendrogram depicts the relationships of each of the five biomes, where sister groups comprise communities of the highest similarity (1- Sørensen similarity) in species composition among biomes.

proportional endemism. Additionally, *Niceforonia aderca* (Lynch, 2003a), *Pristimantis ixalus* (Lynch, 2003b), *Bolitoglossa yariguiensis* Meza-Joya et al., 2017, and *Gonatodes chucuri* Meneses-Pelayo and Ramírez, 2020, are restricted to small areas in the SRB. We also included species that we have identified as putatively

new in molecular and morphological analyses, which are currently being described. This species richness represents 13% of the Colombian herpetofauna. The families with the highest proportions of richness are Hylidae (21.9%, 16 species), Craugastoridae (17.8%, 13 species), and Leptodactylidae (10.9%, 8 species)

for amphibians. For reptiles, richness is the highest in Colubridae (46.2%, 56 species), followed by Anolidae (8.2%, 10 species), Gymnophthalmidae (6.6%, 8 species), and Sphaerodactylidae (4.9%, 6 species). However, this representativeness of the families changes throughout different biomes of the SRB. In amphibians, 100% of the families (16) were registered in the tropical humid forest showing a gradual decrease across the biomes until the dry forest where only 5 families occur (31%). For reptiles, the humid tropical forest again supports 100% of the families, followed by the semiarid Sub-Andean biome with 16 families (57%) and the Sub-Andean forest with 15 (53.5%), in the dry forest biome 8 families (28.5%), and 5 families (17.8%) in the Andean forest (Fig. 2).

Species richness and overlap between biomes

The mapping of the modelled distribution of 194 amphibians and reptiles species (with 3 or more occurrences; Supplementary Material Table 2) showed that the tropical humid forest near the foothills of the mountains and the Sub-Andean forest biome in the middle basin of the Sogamoso River holds the highest concentration (101.6 species per cell) of species richness of both amphibians and reptiles, and the lowest species richness occurring mainly in the sub-Andean semiarid vegetation with only 6 species per cell, the mean species richness per cell was 43.5 (± 18.7 SD) in the SRB (Fig. 3D). In amphibians, the highest richness is found in the upper zones of the western flank of the Serranía de los Yariguíes with 37 species per cell and the lowest richness (3 species per cell) occurring in the dry forest and sub-Andean semiarid biomes, with the mean richness in 15.3 (± 6.5 SD) (Fig. 3B). For reptiles, the highest richness occurred in the dry forest with 69 species per cell, and the lowest richness (5 species per cell) in sub-Andean semiarid biomes, with the mean richness in 28.2 (± 12.8 SD) (Fig. 3C).

We found an important overlap in the total species composition across biomes, based on the intersection of modelled species distribution maps (Fig. 4). This taxonomic overlap is greater within all the biomes. Despite the high proportion of species characteristic of tropical humid forest (91%), this biome also shares large numbers of species with the sub-Andean forest biome. The high taxonomic overlap of arid biomes such as dry forest and sub-Andean semiarid suggests the potential for low functional distinctiveness (Fig. 4), with the dry biomes representing a poorer subset of the more species-rich, functionally diverse humid biomes (Fig. 3F).

Altitudinal distribution

We sampled the altitudinal species richness (SR) of amphibians and reptiles as the number of species predicted to occur in altitudinal sections of 200 m according to their modelled distributions (Fig. 5). With this, we analysed three important aspects of these data. First, we compared the variation in SR along the altitudinal gradient and found that the SR of amphibians increases slightly with increasing elevation, reaching a maximum between 400–800 m a.s.l., with the highest value at 600 m a.s.l. Above 600 m a.s.l., SR is negatively correlated

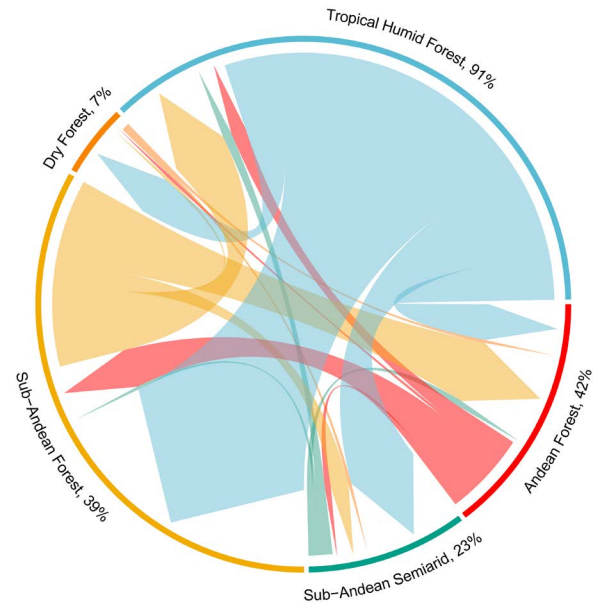


Figure 4. Overlap of species among biomes from Sogamoso river basin. Percentage values express the fraction of species occurring in a biome that has the greatest proportion of their geographic range in that biome, $N = 196$. The base of each branched arrow is positioned to show the biome that includes the greatest proportion of a species range, while the width represents the number of species shared with the biomes at the tips of the arrow.

with elevation, with a gradual reduction between each altitude interval. The altitudinal SR of reptiles shows the same trend in the lowland intervals, with the maximum SR value at 600 m a.s.l., and a moderately continuous decrease of SR with increasing elevation. In this case, the SR decreased dramatically above 1600 m, with amphibian SR being higher in the highland intervals above 2000 m a.s.l., relative to reptiles. The differences seen between amphibians and reptiles are statistically significant, with both minimum and maximum elevation per species, and altitudinal range, being on average higher in reptiles (t-test: $P = 0.002$, $P < 0.001$, $P < 0.001$).

Later, we graphically represent the distribution ranges of each species with vertical bars coloured according to their degree of threat or endemism. Also, these bars were placed on the biomes in which each species is distributed. We found that in amphibians the presence of endemic and threatened species increases with altitude but only in humid biomes; in dry biomes, we found only common species with wide altitude distribution ranges (Fig. 5A). In reptiles, the trend is similar, but the altitude distribution ranges of the species are wider than in amphibians (Fig. 5B). Finally, the altitudinal gradient showed a high turnover in species composition in mid-altitude intervals between 1400 to 1600 m a.s.l., both for amphibians and reptiles. These species clusters, along the altitudinal gradient, largely correspond to the different biomes present in the SRB.

Generalised Dissimilarity modelling

We applied Generalised Dissimilarity Modelling (GDM) to identify important areas for conservation

in the SRB, based on turnover patterns for reptiles and amphibians together. This method identifies changes in the communities that reflect high species turnover and can be interpreted as boundaries of biogeographic regions or biomes. The GDM model based on the data from amphibians and reptiles together captured 85.2% of deviance explained, and separately for each group 83.3% and 85.1%, respectively (Fig. 3E). In all cases, the distribution pattern of species turnover was generally the same. However, the level of importance of the predictors was moderately different between amphibians and reptiles. The top climatic predictors of species turnover (and percent of contribution to the model) for amphibians were, the maximum temperature of the warmest month (73.4%), elevation (72%), radiation of the warmest quarter (25.1%), annual mean radiation (23.4%), and precipitation of the coldest quarter (20.2%). For reptiles, the top predictors were the highest period moisture index (65.7%), the maximum temperature of the warmest month (41.2%), the mean moisture index of the warmest quarter (41.2%), the mean temperature of the wettest quarter (38.5%), and moisture index seasonality (35%). Given that the explained deviance is like other GDM models that are known for their robustness, but it is not close to 100%, indicating that the model does not capture all the variation present, the non-climatic species-specific idiosyncrasies were retained in input data, and thus, supported the use of GDM methods. The spatial pattern of species turnover reconstructed herein results largely mirrors the biomes previously delineated by Latorre et al. (2014), and the similarity relationships found with Sorensen's analysis show a strong separation between dry and humid biomes consistent with the turnover distribution pattern of species in the altitudinal gradient (Fig. 3F).

Conservation status

According to their IUCN status, in the SRB 129 species (64.7%) are of Least Concern (LC), 42 (21.4%) are listed as Not Evaluated (NE), 8 (4%) as Data Deficient (DD), 3 (1.5%) as Near Threatened, 8 (4%) as Vulnerable (VU), 4 (2%) as Endangered (EN) and 2 (1%) as Critically Endangered (CR). It was possible to show that species with significant degrees of threat or endemism tend to be more associated with highland biomes. In amphibians, 33 endemic species were found, of which 11 have a threat category between vulnerable, threatened and critically endangered. For reptiles, 20 endemic species were reported, and only two of them were within a threat category. This scenario may not represent the current reality in the region because for most species there are no population studies that provide evidence of the current status of their potential threats at a local scale.

DISCUSSION

The study of the spatial biodiversity patterns of Colombian amphibians and reptiles has been rarely addressed (Ortiz-Yusty et al., 2013, Herrea-Lopera et al., 2023; Saboyá & Urbina-Cardona, 2023). An important factor

to focus effective conservation strategies on territories with high rates of deforestation is the collection and analysis of basic information on the variation of richness and diversity of species from a spatial perspective, based on explicitly modelled distributions from a complete dataset of species as possible (Brown et al., 2016). In this work, we illustrate how herpetofauna communities are structured according to the main bioclimatic regions or biomes in the Sogamoso river basin and demonstrate an important effect of some geographic and environmental predictors in the variation of these patterns.

The first and most important result of this study is the compilation, depuration, and review of all records and specimens that have been collected within the SRB and deposited in the main scientific collections of the country and registered in global databases (Gbif). At this point, we list a total of 197 species between amphibians and reptiles, this being the largest currently reported herpetofauna for the Santander department (80% of the total, Meneses-Pelayo, 2024) and one of the most representative for the middle Magdalena valley and north-western Colombia. However, we are aware of several difficulties in this work. Such as the effects of taxonomic uncertainty, with some species included in this study belonging to species complexes that contain deep mitochondrial and nuclear lineages that might turn out to correspond to distinct species upon taxonomic revision. Some of these are currently in the process of description and are referenced in Supplementary Material Table 1 at the genus level. But, despite these, we are convinced that the results presented here reflect true biological patterns.

The spatial distribution of SR in amphibians and reptiles suggests a clear concentration of species around the Serranía de la Paz, foothills of the Serranía de los Yariquies, between 400 and 800 m a.s.l (Fig. 3B, C & D). This accumulation of species richness (up to 102 species per cell of 0.91 km²) is found within the tropical humid forest biome and its transition to the sub-Andean humid forest. This altitudinal pattern could be partly explained by the species-area relationship since the tropical humid forest of the SRB has 56% more available area than the sub-Andean humid forest (Fig. 5A & B). Species-area relationships have been extensively studied in metapopulation dynamics and have demonstrated the importance of diversity analyses at a spatial scale (Rahbek, 1997; Lawton, 1999; Lomolino, 2000; McCain, 2007). Additionally, there is a strong contrast to dry biomes in which species richness is very low and is mostly represented by common and widely distributed species with some exceptions of endemic species found in tropical dry forests and the sub-Andean semiarid vegetation, such as *Bolitoglossa nicefori*, *Micrurus sangilensis*, *Stenocercus santander* and *Alopoglossus bicolor* (Fig. 3B & C). Therefore, the high degree of importance of the foothills of the tropical humid forest is evident, as it offers a bank of species with wide altitude distribution ranges that facilitate a large taxonomic overlap between the biomes (Figs. 3 & 5). This taxonomic overlap is complemented by the contribution of Andean and sub-Andean forests, which do not have a high species richness but are home

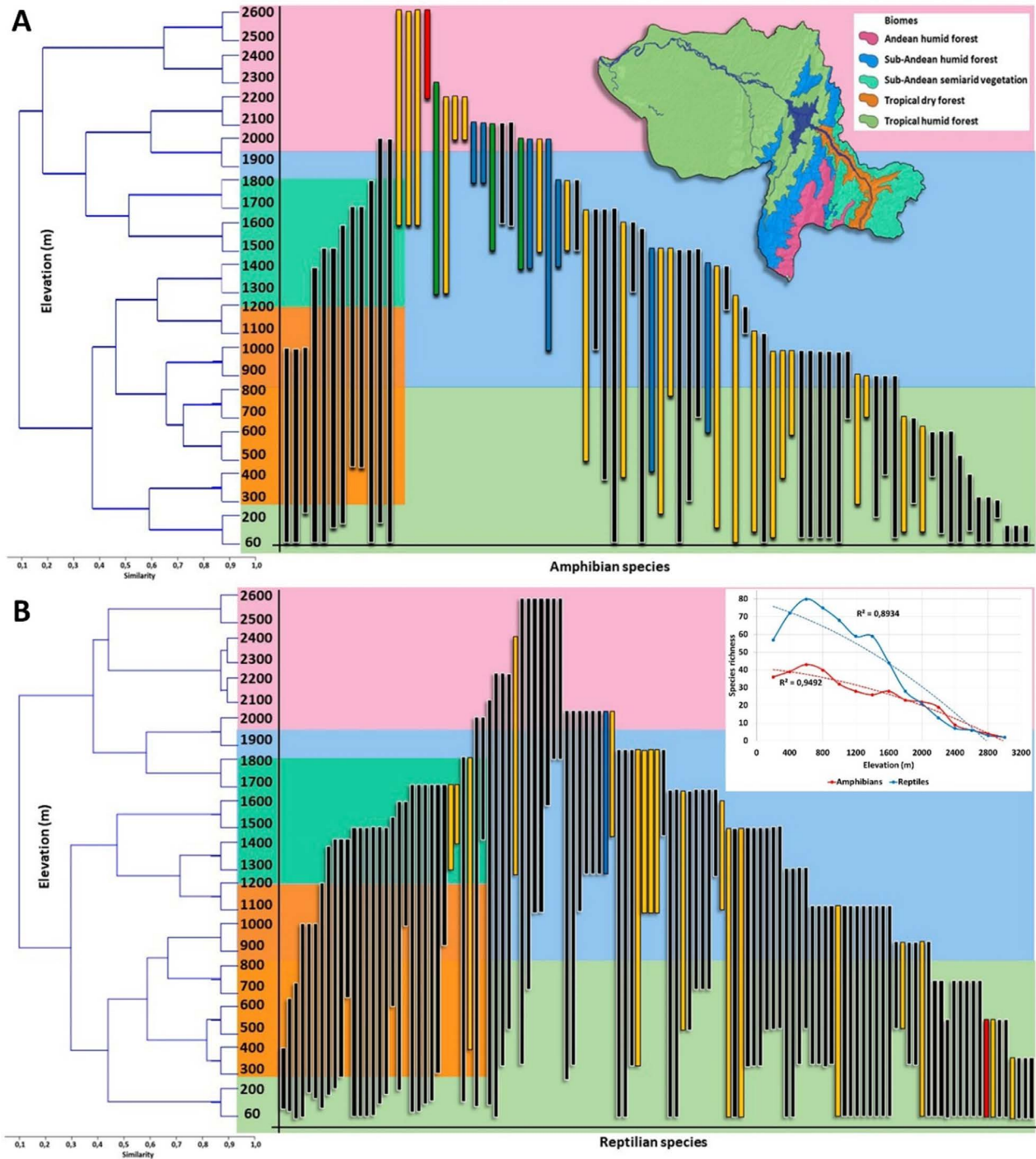


Figure 5. Distribution profiles of each species – **A.** amphibians and **B.** reptiles, based on the original records ordered according to their presence in each biome. The dendrogram represents the relationships of each of the five biomes, where the sister groups comprise communities of greater similarity (Jaccard similarity) in the composition of species between biomes. The colours of the bars represent endemic species (yellow bars), endemic and vulnerable species (green bars), endemic and threatened species (blue bars), and critically endangered species (red bars). The colours of the background stripes represent the spatial distribution of the biomes and coincide with their respective colour on the SRB map.

to 49% of endemic and threatened species, in only 17% of the total area of the SRB (Fig. 5A & B).

Moreover, whereas the patterns of species richness can give us a basis for directing conservation strategies to the areas, spatial analyses of species turnover, that integrate geographic and environmental information, could anticipate and mitigate the impacts of biodiversity threats. Since we can expect that areas with high

turnover (where the colours on the map contrast) and climatic stability, retain biodiversity in a scenario of climate warming or shifts in rainfall regimes (Sandel et al., 2011; Garcia-Rodríguez et al., 2021). In the SRB we found that areas of high species turnover identified by the GMD dissimilarity model agree remarkably well with the previously delimited biomes of Latorre et al. (2014) used in this study. However, we identified

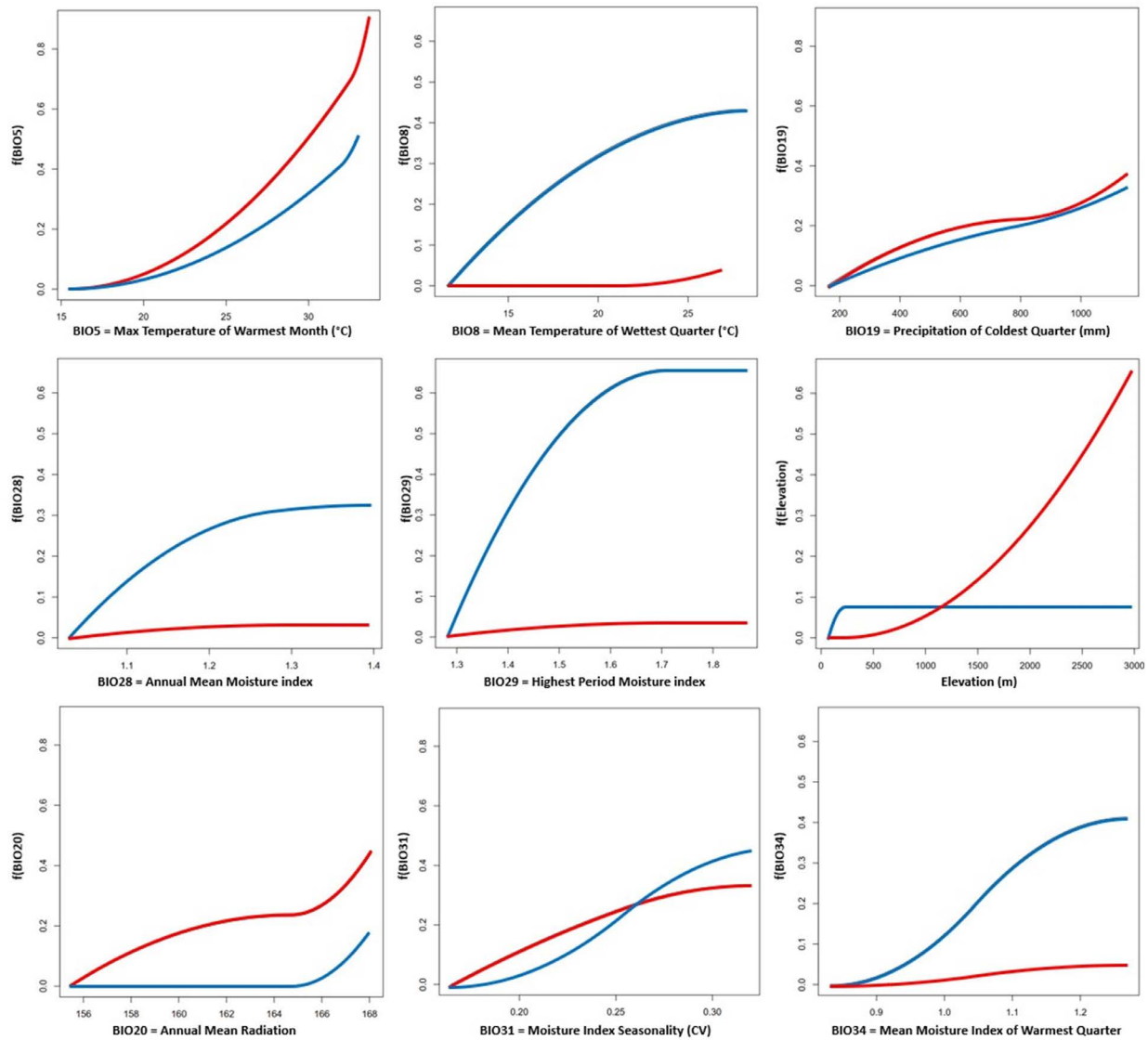


Figure 6. I-splines derived from a generalised dissimilarity model (GDM) for amphibians (red line) and reptiles (blue line). The maximum height of each spline indicates the total degree of community turnover predicted by that variable while holding the others constant. The shape of the spline corresponds to how the rate of turnover changes over the ecological gradient.

differences between amphibians and reptiles regarding the importance of the environment concerning species composition, which could show that small-scale habitat preferences and ecophysiological requirements can result in detectable patterns in the geographical distribution of different lineages. For example, in amphibians, abrupt changes in geography related to the elevation gradient facilitate the availability of many types of microhabitats. Each one of them, with differences in temperature and precipitation (Fig. 6), enhances the effects on the metabolism and demands additional physiological and behavioural adaptations (Wells, 2007; Hillman et al., 2009; Cunningham et al., 2016), potentially supporting a hypothesis of niche-filtering process (Carnicer et al., 2008). In contrast, in reptiles, the greater compositional turnover was explained by the temperature and moisture indexes (Fig. 6). These predictors have been widely accepted as important determinants of the distribution of reptile species (Huey, 1982), in which these variables

affect the hydoregulation and thermoregulatory behaviour (Rozen-Rechels et al., 2019). For example, competition for thermal and hydric resources can shape interactions between syntopic lizard species (Žagar et al., 2015) or be indirectly affected by dramatic thermal fluctuations that influence the adaptive capacity to cushion these fluctuations (Diele-Viegas & Rocha, 2018). These effects need to be monitored to plan effective long-term conservation strategies in the SRB, considering trends observed elsewhere in the world (Gibbons et al., 2000; Bickford et al., 2010; Dayananda et al., 2021).

Patterns of amphibians and reptiles diversity in the SRB cannot be attributed to a single combination of explanation hypotheses, but rather to multiple biotic, abiotic and anthropogenic factors (Dainese & Poldini, 2012). The relation between species richness, turnover, and distribution of the threatened species between different biomes suggests that conservation efforts should focus on the whole gradient rather than just portions of

it. Currently, a large part of the sub-Andean humid forest and the entire Andean forest biome is protected within the Serranía de los Yariguíes National Park and civil society reserves. These areas are of vital importance for conservation because they are home to 49% of endemic and threatened species (Supplementary Material Table 1; Fig. 5A & B). However, in the tropical humid forest, where the highest values of species richness are concentrated, there are not enough areas designated for conservation, and where the greatest anthropogenic pressure is due to changes in the use of land destined for agriculture, livestock, and large infrastructure projects that put at risk the few relicts of forests that still exist. Consequently, it becomes imperative to implement more conservation actions, with a specific focus on creating and maintaining nature reserves in this area of the Sogamoso river basin and the broader middle Magdalena valley.

ACKNOWLEDGEMENTS

We want to thank all the collectors who have contributed for many years to the collection of specimens in the Sogamoso river basin. In the same way, we thank Professor Juan Daza, curator of the Herpetology Museum of the University of Antioquia; Professor John Lynch and Professor Martha Calderón, curators of the amphibian and reptile collection of the Institute of Natural Sciences, respectively; and the researcher Sandra Galeano, curator of the Amphibian and Reptile Collection of the Alexander von Humboldt Institute. To the company ISAGEN S.A.S. for contributing to the data obtained in the different phases of construction and biological monitoring of the Topocoro reservoir. To S. Bolívar, O. Alvarado and S. Londoño for their help in solving problems with data management and recommendations. Especially to Erika Tatiana Rueda and colleagues, A. Gutiérrez, D.M. Díaz, J. Quiroga, R. Useche, J. Pinzón, and L. Meneses who provided valuable support and information for this study. Finally, we would like to thank the Universidad Industrial de Santander and the Grupo Estudios en Biodiversidad (GEBIO) for funding this research.

Author contributions

Conceptualisation: EM-P, VHS-C, MPR-P; Methodology: EM-P; Formal analysis: EM-P, Resources: VHS-C, M.P.R.-P.; Data curation: EM-P; Writing - original draft: EM-P; Writing - review & editing: EM-P, VHS-C, M.P.R.-P.; Supervision: VHS-C, M.P.R.-P.

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Accepted: 26 March 2024