UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ

Colegio de Ciencias Biológicas y Ambientales

Spatial Patterns of Faunal Biodiversity in the Northwest of the Tropical Andes: Toward a Comprehensive Delimitation of Biogeographic Regions

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RESUMEN

Los bosques del noroeste de los Andes Tropicales, que se extienden a lo largo de la costa pacífica norte de América del Sur, abarcan regiones en Colombia, Ecuador, Perú y Panamá. Esta región biodiversa, conocida por sus altos niveles de endemismo, incluye diversas subregiones biogeográficas como bosques lluviosos de tierras bajas, bosques secos, bosques montanos y manglares. Aunque las delimitaciones biogeográficas existentes para esta área se basan principalmente en pocas especies, enfatizando con frecuencia la diversidad botánica y factores abióticos, este enfoque tiende a subrepresentar los factores faunísticos. Los animales de la región desempeñan roles ecológicos vitales, como la dispersión de semillas, el reciclaje de nutrientes y la indicación de cambios ambientales. Su representación incompleta en los modelos biogeográficos puede socavar los patrones espaciales de la región, lo que lleva a una representación inexacta de su biodiversidad. Esta tesis tuvo como objetivo investigar diversos aspectos de los patrones de diversidad espacial de las comunidades herpetofaunísticas en la región, utilizando todos los registros georreferenciados disponibles. El estudio emplea una rigurosa depuración de datos y modelado de distribución de especies para generar modelos robustos de distribución de herpetofauna. A partir de estos modelos, se calcularon la riqueza de especies y el endemismo, los cuales se usaron para determinar la diversidad alfa de la región. Asimismo, se modeló el recambio de especies a través del Modelado Generalizado de Dissimilaridad (GDM, por sus siglas en inglés) utilizando 20 capas predictoras bioclimáticas, lo que permitió generar mapas de distribución para 1093 especies a partir de más de un millón de puntos individuales. Este GDM se categorizó jerárquicamente para obtener regiones biogeográficas integradoras. Este enfoque centrado en la diversidad faunística busca evaluar la congruencia entre los modelos biogeográficos actuales basados en flora y las perspectivas basadas en fauna, con el objetivo de lograr una definición más integral de los límites biogeográficos basada en conjuntos de datos completos de clados (es decir, Reptilia, Amphibia). Estos hallazgos revelaron perspectivas biogeográficas que no fueron detectadas en modelos previos. Tales resultados pueden informar nuevas prioridades de conservación y garantizar que los modelos ecológicos reflejen mejor la composición de especies, el endemismo y el recambio de esta área.

Palabras clave: Chocó-Darién, Ecosistemas, Riqueza de Especies, Endemismo, Modelos de Disimilitud Genealizada (GDM)

ABSTRACT

The northwestern forests of the Tropical Andes, stretching along the northern Pacific coast of South America, encompass regions in Colombia, Ecuador, Perú, and Panama. This biodiverse region, known for its high levels of endemism, comprises various biogeographic subregions such as lowland rainforests, dry forests, montane forests, and mangroves. Whilst existing biogeographic delimitations for this area are primarily based on a few species, often emphasising botanical diversity and abiotic factors, this approach tends to underrepresent faunal factors. Animals in the region play vital ecological roles, including seed dispersal, nutrient cycling, and indicating environmental changes. Their non-comprehensive representation in biogeographic models potentially undermines the region's spatial patterns, misrepresenting the region’s biodiversity. This thesis aimed to investigate various aspects of the spatial diversity patterns of the herpetofaunal communities within the region utilising all available georeferenced records. The study employs rigorous data curation and species distribution modelling to generate robust herpetofaunal distribution models. Species richness and endemism was calculated based on these and were used to determine the alpha diversity of the region. Likewise, the species turnover of species was modelled through Generalised Dissimilarity Modelling (GDM) with 20 bioclimatic predictor rasters, producing 1093 species range maps using over a million individual points. This GDM was then categorised hierarchically to obtain integrative biogeographic regions. This focus on faunal diversity aims to assess the congruence between current flora-based biogeographic models and faunal-based insights, with the goal of a more comprehensive definition of biogeographical boundaries based on whole clade datasets (i.e. Reptilia, Amphibia). These findings revealed biogeographic insights that were not detected in previous models. These can inform novel conservation priorities and can ensure that ecological models better reflect the species composition, endemism, and turnover of this area.

Keywords: Chocó-Darién, Ecosystems, Species Richness, Endemism, Generalised Dissimilarity Modelling (GDM)

TABLE OF CONTENTS

INTRODUCTION **13**

RESEARCH QUESTION **16**

OBJECTIVES **17**

METHODOLOGY **18**

- **Area of Study** **18**
- **Data Curation and Data Mining** **20**
  - Sources 20
  - Occurrence Records Validation 20
  - Duplicate Detection 21
  - Georeferencing Process 21
  - Taxonomy 22
- **Species Distribution Models** **23**
  - Hexagonal Gridding 23
  - Convex Hull Generation and Clipping 24
  - Interactive Plotting and Confirmation 24
  - Species Richness and Endemism 25
  - Generalised Dissimilarity Modeling (GDM) 25
  - Community Composition Analysis 26

RESULTS **28**

- **Amphibians** **29**
  - Species Richness 29
  - Corrected Weighted Endemism 30
  - Areas of Endemism Based on Generalized Dissimilarity Modelling 33
- **Reptiles** **38**
  - Species Richness 38
  - Corrected Weighted Endemism 39
  - Areas of Endemism Based on Generalized Dissimilarity Modelling 41
- **Herpetofauna** **46**
  - Species Richness 46
  - Corrected Weighted Endemism 47
  - Areas of Endemism Based on Generalized Dissimilarity Modelling 49

DISCUSSION **53**

Amphibian Species Richness and Endemism 53
Reptile Species Richness and Endemism 59
GDMs **60**

CONCLUSIONS 69

REFERENCES 70

LIST OF FIGURES

Figure 1. Area of Study 19

Figure 2. Biodiversity measures for amphibians. 37

Figure 3. Biodiversity measures for reptiles. 45

Figure 4. Biodiversity measures for reptiles and amphibians. 52

In nature, nothing exists alone.

—Rachel Carson, Silent Spring

INTRODUCTION

Biogeographical regions are areas delimited based on the distribution patterns of biodiversity and their influencing abiotic factors. These patterns are shaped by the evolutionary history, dispersal, and ecological interactions of species within an area and often also reflect the environmental changes, geological events, and climatic shifts that biodiversity has evolved in over time (Lomolino et al., 2018). Naturalists like Alexander von Humboldt and Alfred Russel Wallace pioneered the discipline of biogeography and were the first to delimit global patterns of biodiversity distribution through their works in biomes/vegetation zones or biogeographic realms, respectively (Camerini, 1993; Hoorn et al., 2022; Keppel & Kreft, 2019; Schrodt et al., 2019). Since then, biogeography has expanded into a multifaceted field encompassing various methodologies and perspectives. Advances in species distribution modelling, phylogeography, and remote sensing have enabled the refinement of biogeographical delimitations and have led to a great variety of models (Champreux et al., 2024; Morrone, 2023).

A region of particular interest and biogeographic dissension is northwest (NW) of the Tropical Andes, spanning along the Pacific coast of South America, from eastern Panama to northern Peru. This area represents one of the most ecologically diverse regions on Earth and also displays some of the highest endemism due to its ecological diversity and variability (Fagua & Ramsey, 2019), including lowland tropical rainforests, montane forests, mangroves, coastal plains, etc. (Herrera et al., 2018). For instance, the botanical diversity of the region is estimated at over 11,000 species, with approximately 2,750 of these being endemic taxa (Christenhusz et al., 2017). Due to the area containing the only moist forests west of the Andes, it also plays critical roles in maintaining regional and global ecosystem functions, such as carbon sequestration, water cycle regulation, and climate stabilisation (Fagua & Ramsey, 2019; Mena-Mosquera & Andrade, 2021).

Nevertheless, this region has undergone a range of distinct models and classifications to regionalise it biogeographically. For instance, (Haffer, 1985) delineated *Trans-Andean Areas of Endemism* based on endemic bird distributions, establishing an early framework of biogeographical patterns in the region. Haffer established the *Tumbes* region. Similarly, Myers et al. (2000) defined *Biodiversity Hotspots*, incorporating both floral and faunal data but prioritising endemic species at risk of extinction, both these works eventually went on to influence the *Tumbes-Chocó-Magdalena Biodiversity Hotspot* (CEPF, 2005). Besides these, there have been numerous other different delimitation efforts, each utilising differing parameters and goals (Cabrera & Willink, 1973; Fittkau et al., 1969; Müller, 1973; Rivas-Martínez & Navarro, 1994; Rivas-Martínez & Tovar, 1983, 1983; Sick, 1969; Udvardy, 1975). However, some of the more recent and influential delimitations include the ecoregions defined by Dinerstein et al. (2017) and the biogeographic regions proposed by Morrone (2014). These models have undergone multiple iterations and remain widely used in conservation and biogeographic research (Morrone, 2001, 2006, 2006, 2014, 2015; Olson et al., 2001).

These models are critical for understanding biodiversity dynamics, identifying conservation priorities, and predicting ecosystem responses to environmental changes (Marske et al., 2023; Richardson & Whittaker, 2010). Nevertheless, they continue to rely on taxonomically limited species groups as they are based on few taxa, which may lead to biases and potential misrepresentations of biogeographic patterns. Thus, biogeographic models that rely on a limited set of species inevitably produce incomplete representations of biodiversity patterns (Fredricson Marquez et al., 2022). Utilising these non-comprehensive approaches may underrepresent certain regions' full biotic complexity and could limit the external validity of the models when applied to conservation planning. Hence, a comprehensive approach—one that incorporates as many species as possible from a given group—would address these limitations by providing a more accurate and integrative view of the ecosystem dynamics (Marske et al., 2023). These models mitigate the biases associated with the arbitrary selection of “indicator” or delimiting species, ensuring that all taxonomic groups are adequately represented, and reduce the discrepancy between biogeographic models and real spatial patterns of biodiversity, often also offering a higher degree of external validity. This is particularly important in regions like the NW of the Tropical Andes, where complex interactions between species drive ecological processes. For example, animals play essential roles in seed dispersal, nutrient cycling, and trophic regulation, contributing directly to ecosystem structure and resilience (Violle et al., 2014). Similarly, amphibians are highly sensitive to changes in humidity and temperature, serving as critical indicators of microclimatic conditions and ecosystem health (Hussain & Pandit, 2012; Siddig et al., 2016).

This thesis investigates the spatial diversity patterns, species richness, endemism, and faunal turnover of tetrapod species in the NW of the Tropical Andes. Using Generalized Dissimilarity Modelling (GDM)—a robust method for analysing biodiversity turnover across environmental gradients—this study aims to address the delimitations of existing biogeographic models comprehensively (Ferrier et al., 2007). The methodology employed in this study adapts and expands upon the approach used by Brown et al. (2016) in their analysis of spatial biodiversity patterns in Madagascar's amphibians and reptiles, incorporating modifications tailored to the unique characteristics of the NW of the Tropical Andes region, the scope of the data utilised, and the specific research aims of this thesis. By comparing the faunal patterns of tetrapod species with existing biogeographic models, this study evaluates the congruence between these perspectives and identifies potential discrepancies. In doing so, this work emphasises the need for a more inclusive and holistic approach to biogeographical delimitation, one that takes into account the full spectrum of biotic diversity in the clades used and their ecological interactions. By offering a more integrative representation of biodiversity patterns, this work aims to influence conservation strategies that align with the region's ecological realities, thereby safeguarding its exceptional and threatened biodiversity.

RESEARCH QUESTION

This thesis aims to investigate whether a Generalised Dissimilarity Modelling (GDM) of tetrapod faunal diversity patterns in the NW of the Tropical Andes reveals biogeographic insights not captured by existing biogeographic models, suggesting a need to redefine the region's boundaries. I hypothesise that incorporating faunal diversity within the definition of the NW of the Tropical Andes ecosystem will contribute to a more comprehensive understanding of the region's biodiversity and enhance conservation efforts. This investigation will be conducted utilising all available georeferenced occurrence data for tetrapods, irrespective of their collection date. The findings of this study will have significant implications for conservation policy and management, promoting a more holistic and effective approach to protecting the NW of the Tropical Andes’s invaluable natural heritage.

OBJECTIVES

1. To generate accurate and comprehensive species distribution maps (SDMs) for tetrapods within the NW of the Tropical Andes utilising all available georeferenced occurrence data, irrespective of their collection date.
2. To assess the spatial patterns of species richness and corrected weighted endemism within the NW of the Tropical Andes using the generated SDMs.
3. To compare the GDM-derived faunal diversity categories with existing biogeographic models to evaluate their congruence and identify potential areas of discrepancy.
4. To propose refinements to the definition of the NW of the Tropical Andes and surrounding delimitations if warranted by the findings of the faunal diversity analysis.

METHODOLOGY

Area of Study

The study area was defined by a preliminary polygon selecting all areas north occidental to the Andes. The polygon was defined within bounds delimited by the Panama Canal in Panamá, the Sierra Nevada de Santa Marta (Pico Cristobal Colón) and the Serranía del Perijá in Northwest Colombia, and the Sechura Desert in northern Perú. In northern Colombia, the area consisted of the Western Cordillera, including the Cauca River Valley, but excluded the Magdalena River Valley and the Eastern Cordillera due to disconnectivity (only including the Llanura del Caribe region); the area between the Eastern Range Depression and the Cauca River Valley was connected following the Cauca, Nechí, and Magdalena Rivers (González-Orozco, 2021; Hazzi et al., 2018). In Perú, the area was delimited slightly south of the Marañon River due to its biogeographic importance and followed the western Andes until the Colombian Massif (Hazzi et al., 2018).

Then, a Digital Elevation Model (DEM) raster of South America—which provided the necessary altitudinal data—was used to cut the preliminary area of study to continental land borders and at 2000 masl. The altitudinal cutoff is supported by observed ecological transitions relating to vertebrate and plant data, with species turnover particularly elevated in both groups between 1750 and 2000 m, marking a clear transition zone between lowland and montane ecosystems (Jankowski et al., 2013). This 2000 masl threshold effectively captures the ecological shift from lowland to highly endemic montane communities, making it a suitable cutoff for regionalisation (Kessler, 2002).

These constraints excluded areas outside of significant altitudinal ranges or previously delimited biogeographic regions, focusing this analysis on interrelated elevation-restricted zones within the initial spatial bounds. The elevation mask was then converted to polygon format for ease of further spatial manipulation. The final polygon accurately represented the study area, constrained by geographic and elevation limits, and served as the foundation for biodiversity spatial pattern analyses (Figure 1).

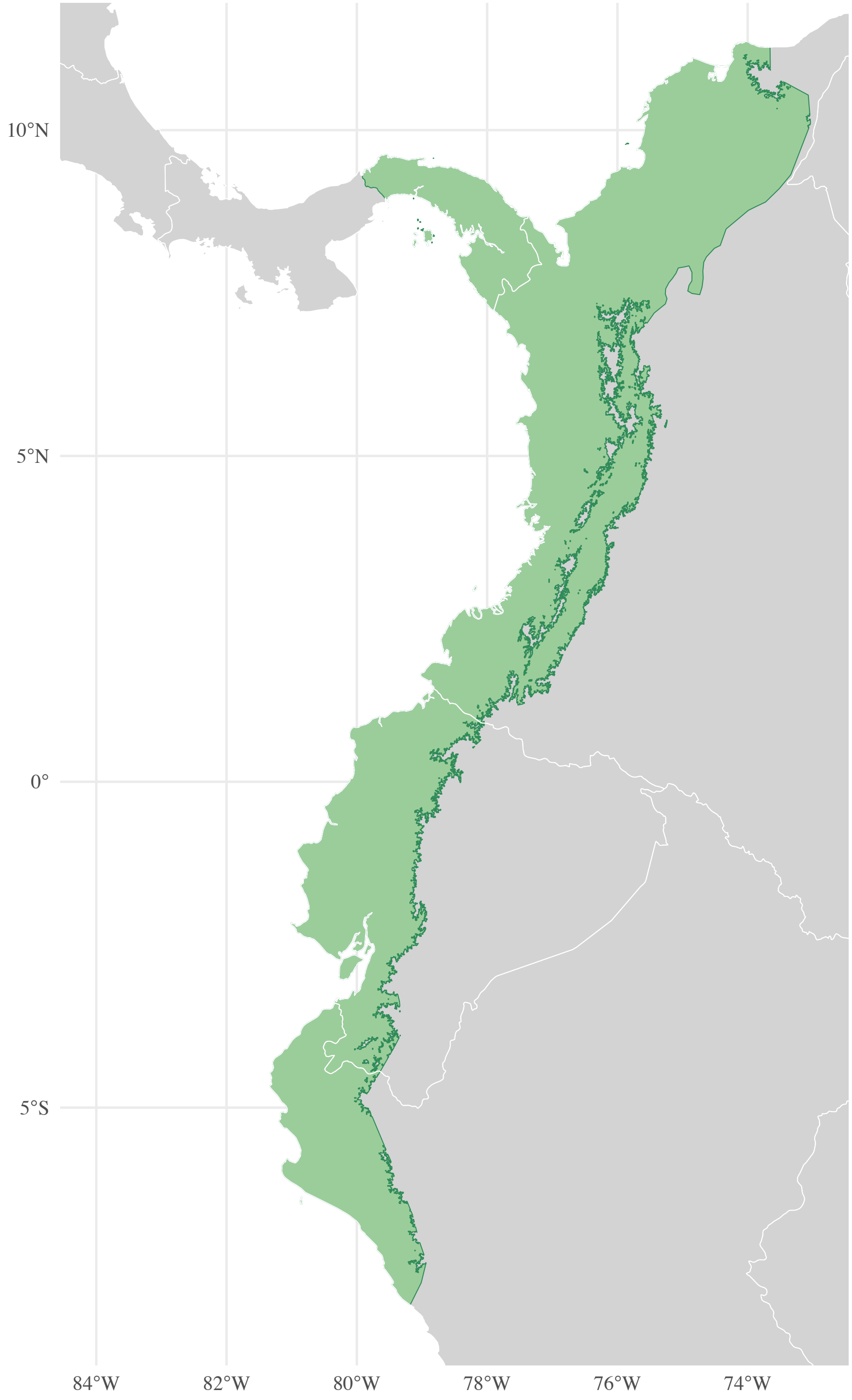

Figure 1. Area of Study

Data Curation and Data Mining

Sources

To compile a complete species list of amphibians and reptiles in the NW of the Tropical Andes, a variety of sources were utilised to find occurrence data for species within the study area. A previous compilation of occurrence records completed in 2019 by Diego F. Cisneros-Heredia (DFCH), as well as complete citizen science records from the Global Biodiversity Information Facility (GBIF) and iNaturalist, provided a preliminary thorough species list (Cisneros-Heredia, 2019; GBIF.Org User, 2024i; iNaturalist, 2024). Then, a thorough literature review was performed to find species not included in the aforementioned sources or species with few occurrence points. Based on this updated species list, all occurrence records were downloaded for each of the included species from GBIF and iNaturalist (GBIF.Org User, 2024a, 2024b, 2024c, 2024d, 2024e, 2024f, 2024g, 2024h, 2024i; iNaturalist, 2024); in this manner, the study area wouldn't influence the species distribution ranges. Recognising the critical importance of data quality and the challenges posed by heterogeneous data sources, a rigorous multi-stage protocol, based on Cisneros-Heredia (2019), was implemented for data curation and automised by a novel R pipeline.

This protocol encompasses the following sequential steps:

Occurrence Records Validation

A single dataset was compiled from all species occurrence data, and this data's trustworthiness was evaluated based on provenance, with scientific literature and the DFCH occurrence records considered the most reliable source, followed by natural history museums, photographic and sound databases, private expert databases, and finally, records-only databases. A standardised annotation mechanism was employed in R to meticulously review, evaluate, and correct all of the relevant metadata fields, ensuring transparency and traceability of any modifications made. Verbatim geographic data was obtained and compiled from their original sources; this was available as descriptions of the occurrence locality or other types of metadata. A critical evaluation and error correction were preliminarily conducted during data collection to identify and rectify any potential typographical inconsistencies or inaccuracies. Records devoid of essential geographic data were excluded from further analysis and assigned the error code "error 3."

Duplicate Detection

The dataset was rigorously examined to identify and eliminate duplicate occurrence records utilising the novel pipeline in R to automate this process. This involved a comprehensive scrutiny of fields such as "locality," "source code," "source reference," and "observation". Museum records were cross-referenced with scientific literature, global databases, and private databases using unique museum codes to detect duplicates and potential taxonomic discrepancies. Photographic records were subjected to visual comparison to identify duplicate occurrences. Following the identification of potential duplicates, a manual comparison was performed to verify the consistency and completeness of the records in question. Identical records were removed and assigned the error code "error 6," while non-identical records were evaluated to determine whether they contained unique and pertinent information that could be merged or if they harboured errors necessitating their exclusion.

Georeferencing Process

Considering the importance of accurate spatial data, especially in regions with significant altitudinal and climatic variations over short horizontal distances, a georeferencing process was implemented. Records lacking sufficient geographic information to pinpoint the species' locality were excluded and assigned the error code "error 4." Records containing coordinates were validated against locality descriptions, and any discrepancies were rectified, with the error code "error 1" assigned to inaccurate coordinates that were subsequently corrected. For records lacking coordinates but possessing locality data, a manual georeferencing protocol was employed. This protocol involved gathering additional information from diverse sources, including museum catalogues, field notes, and publications, to initially enhance the accuracy and precision of georeferencing. Then, the most probable position associated with the locality description and altitude was determined using the point-radius method and a collection of maps and databases (Cisneros-Heredia, 2019; Wieczorek et al., 2004). Finally, to ensure data quality and consistency, only occurrence records with an uncertainty of less than 5 km horizontally or 200 m in elevation were included in the final analysis. Records excluded due to high uncertainty were assigned the error code "error 7."

Taxonomy

Recognising the dynamic nature of taxonomic classifications and the potential for inconsistencies and uncertainties in species identifications, a comprehensive taxonomic validation process was undertaken. This process involved a thorough review of the identification of all occurrence records and a critical evaluation of any discrepancies or ambiguities (Cisneros-Heredia, 2019). The taxonomic standards used followed Frost (2024) and Uetz, (2024) for updated taxonomic information. Occurrences with potential taxonomic issues were flagged based on their locality, proximity to range boundaries, or known species complexes. Taxonomic errors were corrected and assigned the error code "error 5." Identifications that remained uncertain due to insufficient information, including putative novel or undescribed species, were excluded and assigned the error code "error 7."

Species Distribution Models

Following data curation and validation, the refined dataset was utilised for species distribution modelling and subsequent spatial analyses to investigate tetrapod diversity patterns in the NW of the Tropical Andes. All operations were carried out in Rstudio utilising R 4.4.1, and the following packages were utilised: sf, terra, ggplot2, rnaturalearth, rnaturalearthdata, dplyr, viridis, dbscan, readxl, stringr, paletteer, colourspace, ggsci, ggspatial, tidyverse, vctrs, gdm, geosphere, winch, & cluster (Dunnington et al., 2023; Fitzpatrick et al., 2024; Garnier et al., 2024; Hahsler et al., 2024; Hijmans, Bivand, et al., 2024; Hijmans, Karney, et al., 2024; Ihaka et al., 2024; Maechler et al., 2024; Massicotte et al., 2023; Müller & Lance Taylor, 2024; South et al., 2024; Wehrwein et al., 2024; Wickham, 2023a, 2023b; Wickham, Bryan, et al., 2023; Wickham et al., 2023a, 2024b; Wickham, Henry, et al., 2023; Xiao et al., 2024). This constituted the second novel pipeline in R and was fully automated but supervised, requiring approval of the generated map.

The automated pipeline performed the following steps:

Hexagonal Gridding

Within the study area, a hexagonal grid with individual 100,000km^2 hexagons was overlaid on the study area; this step was done once every time the automated pipeline was run, not for every species iteration. Hexagons were used to compose the lattice because they are the most complex regular polygon, due to their equidistant nature, data analysis is simplified, and statistical ambiguities are reduced, resulting in less orientation bias in analyses in comparison to square grids (Jurasinski & Beierkuhnlein, 2006). Additionally, hexagonal lattices are preferred for ecological mapping because they offer a better representation of connectivity and movement paths, making them more suitable for studies that require accurate neighbourhood relationships and spatial dynamics (Birch et al., 2007).

Convex Hull Generation and Clipping

The now valid data was subjected to the machine-learning algorithm, Hierarchical Density-Based Spatial Clustering of Applications with Noise (HDBSCAN), to determine occurrence clusterisation and detect spatial outliers (Campello et al., 2013). This algorithm was used because of its ability to utilise varying cluster densities and, identify spatial outliers and group them in clusters relating to density effectively. In HDBSCAN, the user does not need to specify the number of clusters in advance and can automatically detect regions of high-density data, making it well-suited for spatial data with irregular distributions and noise (Campello et al., 2015). This was well suited for the dataset because erroneous occurrences were determined, and I was able to discern whether certain clusters were, or were not, misidentified members of other allopatrically distinct groups.

Then, draft distribution maps were generated using convex hulls that were based on the remaining occurrence points, excluding invalid outliers, for each species. These hulls were then clipped using an elevation mask derived from a high-resolution DEM, depending on the occurrence’s interquartile altitudinal species range, to ensure that the predicted distributions aligned with the species' known ranges. This step helped to refine the models and reduce potential over-prediction in areas where the species is unlikely to occur due to elevational constraints.

Interactive Plotting and Confirmation

The resulting distribution maps and elevation violin plots showcasing the altitudinal distribution of each species were automatically presented for visual inspection and confirmation. This process allowed for the modification of the species ranges in case of discordance with literature. This automated pipeline also allowed for the identification and correction of any potential errors or inconsistencies in the models. In the case of approval, the range map would be saved, but in the case of disapproval, the parameters could be adjusted or points excluded from the map generation.

Species Richness and Endemism

Spatial patterns of species richness (SR) and endemism were investigated using the generated SDMs and the hexagonal grid. Species richness was calculated by overlaying the binary SDMs for all species within a given taxonomic group and counting the number of overlapping distributions within each hexagonal cell of the sampling grid. Corrected weighted endemism (CWE), a metric that weights the proportion of endemics inversely to range size, was employed to assess local endemism patterns similarly (Guerin et al., 2015). This approach gives greater weight to species with restricted ranges and thus is able to highlight areas with a concentration of range-restricted taxa, better-demonstrating endemism and requiring only georeferenced species records. Both models were run for each of the families in Reptilia and Amphibia that were considered in this work.

Generalised Dissimilarity Modeling (GDM)

GDM was used to analyse and predict spatial patterns of community turnover across the NW of the Tropical Andes. This approach quantifies the dissimilarity between communities at different locations based on their species composition and environmental characteristics. By identifying areas of high turnover, GDM reveals biogeographic boundaries and regions based on the distinct faunal assemblages and abiotic predictor variables at each point in the analysis (Ferrier et al., 2007). This modelling was based on the methodologies mentioned in Mokany et al. (2022). To avoid computer limitations associated with the pairwise comparison of very large datasets, I sampled 7000 points throughout the study area and then conducted the GDM at each locality using the aforementioned SDMs. To ensure the representativeness of the areas of endemism, the points were randomly selected based on a stratification of the CWE map. Thus, there existed representation of all endemism subareas, reducing sampling error and improving estimates. All three analyses (SR, CWE, and GDM) were integrated into a third R pipeline to generate all simultaneously for each group.

Community Composition Analysis

Principal Component Analysis (PCA) was employed on 20 bioclimatic rasters, yielding eight PCA-Rasters, these were sampled at the same 7000 localities to reduce the dimensionality of the predictor variables and still account for 99.7% of the variance. Species communities, as calculated by species occurrences at each of these sites, and the predictor environmental principal component vectors, were then input into a generalised dissimilarity model using the GDM package in R (Fitzpatrick et al., 2024). This model was then extrapolated based on the high-resolution PCA rasters previously used as predictor variables to their same resolution.

Finally, the GDM classification was done through subsampling and hierarchical clustering. From the extrapolated raster obtained from the continuous model, 500 grid cells were randomly sampled to estimate dissimilarities and classified into 50 distinct community types. Then, the ecological distances between all pairs of sampled grid cells were calculated using the environmental variables for each pair and transformed into a dissimilarity matrix based on the fitted GDM. Hierarchical clustering with Ward’s method was applied to this matrix and yielded clusters corresponding to unique community types (Ward, 1963). These clusters were joined based on similarity, allowing for comprehensive allocation of community types across the full extent of the environmental data.

To visualise the similarity between communities, mean environmental values for each community type were assigned, and dissimilarities were calculated and reduced to three dimensions using multidimensional scaling (Mokany et al., 2022). Each grid cell was assigned a scaled value for these three dimensions, normalised and colour-coded into RGB channels for intuitive visualisation, where each colour represented a unique community type, with similar colours indicating similar ecological characteristics in the R package ggplot2. Additionally, encountered communities were compared to theoretical communities derived from SDM overlap to evaluate detection probabilities and potential ecological specialisation among different taxa.

RESULTS

The results of this work provide a comprehensive analysis of species richness, endemism, and turnover within the northwest of the Tropical Andes. By applying generalised dissimilarity modelling (GDM), this research not only highlights the spatial patterns of biodiversity but also uncovers significant insights into the biogeographic boundaries and ecological dynamics of the region. This work represents one of the first attempts to utilise GDM for biogeographic regionalisation in South America, offering a novel approach to understanding the complex relationships between species composition and environmental factors in this biodiverse and ecologically unique region.

This work yielded a total of 1234 species distribution maps with 742 amphibians and 492 reptile species in total. Distribution maps were generated from 1,012,963 individual occurrence points, with 501,369 individual amphibian occurrences and 511,594 individual reptile occurrences. For amphibian species, 13 different taxonomic families were utilised, including Aromobatidae, Bufonidae, Centrolenidae, Ceratophrydae, Craugastoridae, Dendrobatidae, Eleutherodacctylidae, Hemiphractidae, Hylidae, Leptodactylidae, Microhylidae, Ranidae, and Strabomantidae. Likewise, for reptiles, ten families/subfamilies were considered, containing Alopoglossidae, Anolinae, Colubridae, Corytophaninae, Hoplocercinae, Iguaninae, Polychrotinae, Teiidae, and Tropidurinae. For each family, a SR and CWE map was generated, and a categorical and continuous GDM was obtained for the broader Amphibia and Reptilia. Similarly, SR, CWE, and GDM were also generated for the whole herpetofaunal assemblage.

Amphibians

Species Richness

The western piedmont forest of northwestern Ecuador holds the highest concentration of species of amphibians, with a particular increase near the Guayllabamba River Valley (Figure 2). However, species richness (SR) appears to be regularly distributed along the study area but concentrated in the northwestern regions, especially increasing when nearing the Andes Cordillera, in the Northwestern Andean Moist Forest Ecoregion, but decreasing dramatically near southern Ecuador and Northwestern Peru, near the Tumbes-Piura Dry Forests and the Secchura Desert. Amphibian SR in the NW of the Tropical Andes is highest in areas of growing elevation along the Colombian and Panamanian coast, especially near the Atrato River and the Uramba Bahía Málaga National Park/Buenaventura. Species richness is lowest in all dry forest areas within the study area and in a poorly surveyed area north of Guayaquil, Ecuador.

For the family Aramobatidae, the majority of species appear to be located in the northernmost section of the Study Area, displaying a predominantly Colombian and Panamanian distribution reaching up until Esmeraldas province. Similarly, Bufonidae also has a distribution mostly remaining near the northernmost areas, but the family is distributed more evenly, with a particular peak in the Valle del Cauca region near Buenaventura. Centrolenidae appears to be evenly distributed along the moist forest lowlands of Ecuador and Colombia; however, it also seems to have hotspots in the west of Pichincha and Antioquia. In the case of Ceratophrydae, the family only contained two species in the area, *Ceratophrys stolzmanni* and *Ceratophrys calcarata*, restricted to the western Coastal Cordillera in Ecuador and the Magdalena region in Colombia, respectively. Craugastoridae displayed a fundamentally Central American distribution with peaks in central Panama and a weaning prevalence southward. Dart Frogs (Dendrobatidae) displayed a somewhat uniform distribution with increasing richness in central Colombia and a peak in the north of the Chocó department. Eleutherodactilidae only contained species in the genus *Diasporus* and seemed to be most prevalent in northern Colombia and southeastern Panama. Hemiphractidae showed a high prevalence near Andean slopes, particularly in the western Imbabura, Cotopaxi, and Pichincha provinces in Ecuador, similarly in the west of Antioquia. Tree frogs in the family Hylidae displayed a slightly higher richness in central-northern Colombia but were distributed relatively uniformly among lower latitudes. The family Leptodacctylidae showed a clear prevalence in northern Colombia and eastern Panama, as well as the Guayas Gulf. Microhylid frogs displayed an increased prevalence in northern Colombia and eastern Panama, species further south were not usually distributed in the lowlands and were instead near Andean slopes. The family Ranidae had few representatives; however, these showed a clear pattern where no records were recorded in dry forests. There were two main hotspots for Ranidae, near the west of Cotopaxi province in Ecuador and along Southern Ecuador and Northern Peru. Finally, the family Stabomantidae had the highest number of species of any other amphibian family, particularly due to the genus *Pristimantis*; these displayed a clear pattern of richness near Andean slopes and had a *hotspot* in the western Cotopaxi and Pichincha provinces in Ecuador.

Corrected Weighted Endemism

Local endemism values only partly coincide spatially with SR (Figure 2). For amphibians, the largest extension of high-CWE cells coincides with that of SR in the Guayllabamba River Valley. CWE peaks are also observed in the Santa Marta montane forests and between Orquideas and Paramillo National Parks in Colombia. Besides these hotspots, endemism remains relatively uniform to the west of the Andres, decreasing primarily south of the Tumbes-Piura Dry Forests and east of the Magdalena-Urabá Moist Forests.

These patterns of endemism across amphibian families reveal distinct biogeographical dynamics among families. Aramobatidae has predominant endemic regions in northern Colombia and the border region between Esmeraldas Province (Ecuador) and Nariño Department (Colombia), highlighting the ecological importance of lowland forests as the family's biodiversity hotspots and corridors. Particularly, this family displays certain endemism patterns near the Atrato and Esmeraldas rivers, displaying possible diversification events near these. Likewise, Dendrobatidae displayed similar areas of endemism to Aromobatidae like the Atrato river basin and Buenaventura in Colombia; however, this family but tends to be more endemic than Aromobatidae and has a somewhat uniform pattern of endemism with increasing richness in central Colombia, but being more endemic in relation to Aromobatidae to the western Ecuadorian Andes even showing endemism to the Coastal Cordillera in Ecuador.

Similarly, Leptodactylidae demonstrates significant endemism in mountainous regions, particularly in the Coastal Cordillera and western Pichincha Province in Ecuador, as well as in southeastern Panama. Emphasising the role of sloping ecosystems in shaping the family's evolutionary processes, particularly those approaching lowland humid forests. However, it is notable that Ranidae displayed an endemism pattern where it seemed to be more endemic to the places Leptodactylidae was not endemic to and vice versa. For example, to the west of the Cotopaxi and Chimborazo provinces in Ecuador, Ranidae is quite endemic; however, Leptdactylidae is not. Moreover, Leptodactylidae appears to display high endemism to the west of the Coastal Cordillera in Ecuador and Ranidae to the east. Nevertheless, some areas are shared, like the south of the Guayas Gulf, the northwest of the Pichincha province (Ecuador), and the Cauca River valley in Colombia.

Similarly, the families Strabomantidae and Craugastoridae appear to have patterns of endemism that display similar niches. It appears that in the northmost region of the study area, Craugastoridae is the dominant terraranan, with most of its endemics near the border of Colombia and Panama and also some points near the Guayas Gulf with evident endemism. The family is also endemic to some areas in the northmost Western Cordillera in Colombia, displaying higher endemism near this area. Juxtaposed, Stabomantidae showed increasing endemism along the altitudinal gradient of the Andes, particularly in the southmost region of the area of study, with an evident endemism *hotspot* in the western Pichincha province in Ecuador and others near the Cauca River Valley where Craugastoridae is not endemic. However, Strabomantidae is also present in the Ecuadorian and southern Colombian lowlands. Another family that may also share a niche with these is Eleutherodactylidae; this family is most endemic in northern Colombia and southeastern Panama, similar to its richness distribution. However, it seems to be mostly endemic to the lowlands of northwestern Colombia, not intersecting with Craugastoridae in the northern highlands nor with Strabomantidae in the southern lowlands.

On the other hand, leaf and tree frogs (Hylidae) displayed a very uniform pattern of endemism throughout the study area, with particular hotspots of endemics near higher altitudes. This pattern was mostly noted in the northwestern Andean slopes and the Coastal Cordillera in Ecuador, in the Andean slopes of the Western Cordillera of Colombia, particularly the western side of it, and in the Serranía de Jungurudó and Pirre in Panama. Hemiphractidae and Centrolenidae showed a similar pattern to Hylidae, however, in the case of Hemiphractidae, there was a much higher endemism near mountains, not ranging far from the Andes and particularly endemic from western Cotopaxi province in Ecuador to the department of Antioquia in Colombia. Likewise, Centrolenidae is similarly endemic to the west of Pichincha to Antioquia, and on the south of Ecuador near the Jubones River, however, these frogs are also distributed in lowlands along the moist forest lowlands of northern Ecuador and western/central Colombia sharing areas of endemism with Hylidae like the Atrato and Esmeraldas rivers.

Bufonidae is most endemic in northwestern Ecuador near the Andes but displays a wide range of endemism, somewhat following the west of the Andes from northern Perú to the Antioquia department in Colombia. The family also displays degrees of endemism along lowlands, following the Colombian coast from Nariño to the Chocó Bay, along the Atrato River, and near Babahoyo and the eastern Guayas Gulf in Ecuador.

Microhylidae also displays significant endemism in northern Colombia and eastern Panama near the Andes and coastal mountains in Panama, with additional evidence near Buenaventura in Ecuador, reflecting the influence of lowland and foothill ecosystems on the diversification of this family.

In the case of Ceratophrydae, both species are endemic to their aforementioned respective regions and display, by far, the clearest endemism, with the species *Ceratophrys stolzmanni* only occurring in the northernmost and southernmost lowlands of the Guayas Gulf.

Areas of Endemism Based on Generalized Dissimilarity Modelling

Generalised Dissimilarity Modelling, as applied here, reconstructs for sites across the landscape the theoretical communities of species based on the overlap of their distribution ranges and then calculates pairwise differences between these communities. On this basis, it identifies changes in the communities which reflect high species turnover and can be interpreted as boundaries of biogeographic regions. Given that amphibians are mostly distributed in the humid and subhumid biomes, with few species in dry and subarid biomes, the main GDM boundaries display the boundaries of dry forests and moist forests. A trend is visible of more continuous community change in low elevations along the coasts. On the contrary, at higher elevations, a higher number of latitudinal breaks exist that mainly are located in the subhumid/montane biomes, and thus, more distinct patterns of turnover are observed.

Particularly, for amphibian turnover, there are a variety of distinct regions that were elucidated using the GDM. Initially, for Panama, it was evident that the Serranía del Darién, Serranía del Sapo, and Serranía de Pirre had similar turnover patterns in amphibian composition with a similar region between them. Moreover, the regions with the most altitude in the Serranía del Darién and Pirre marked distinct regions of amphibian turnover, showing that the species in the highest points tended to be endemic. Likewise, between these two ranges, there was a distinct region of valley lowlands following the Chuncunaque River.

In the case of Caribbean Colombia, there were evident areas of species turnover delimiting Pico Cristobal Colón in the Serranía de Santa Marta. There was also a region of turnover to the west of this, corresponding accurately to the dry forests of the Sinú Valley. However, when reaching the Magdalena River, this region ends, and another begins spanning Caribbean Colombia until the Atrato River, where the river delimits this and the aforementioned turnover area in the Serranía del Darién in Panama. This appears to join the northernmost Chocó-Darién and Magdalena-Urabá moist forest ecoregions with the northernmost Northwest Andean montane forests.

Then, in now northwestern Colombia, the region follows the Atrato River and begins a transitional area that continues throughout the Western Cordillera in the Andes. The transitional area gives way to a lowland area where amphibian turnover is similar from the Tibuga Gulf until Tumaco Bay. In its south, the Rosario and Esmeraldas rivers delimit this area until the Andes. Within the Cauca River Valley, the transitional area continues along the montane regions, with the lowland dry forest being another distinct area of amphibian turnover.

In Ecuador, six occidental and distinct amphibian turnover regions were determined. The smallest of these consists of the regions surrounding the Esmeraldas River. This region follows the river inland and coastally. It was found to be very similar to the western Urabá Gulf, perhaps due to mangrove presence. Surrounding this region, there is an area that has as its southern limit the Mandariacu River from western Pichincha province and surrounds the Mache Chindúl Mountains. The northernmost border of this region follows the Mira River and ends in Tumaco Bay. Then, there appears to be a small montane area of turnover in the highest points of the Coastal Cordillera in Manabí province in the Chongón Colonche mountains. To the western side of these mountains, a region spans until the East of the Mache Chindúl Mountains and runs southward until it reaches the Andes near La Troncal, here it continues with the Andes to the east and the Guayas Bay to the west until the Puyango River, it is also located on the east of Puná Island; this region appears to be composed of mostly deciduous forests. To the northeast of this region and on the east side of Mache Chindul, there is another amphibian turnover region that has the Andes to the east, La Troncal at its south and the Mandariacu at its north; this is mostly lowland moist forests. Finally, there is a region to the west of Chongón Colonche and the southernmost Coastal Cordillera that reaches the coast and appears to include mostly dry forests. This region is located on three distinct coastlines: one in the north of the Guayas Gulf spanning north until Bahia de Caraquez, another in the westernmost of Puná Island, and yet another from the Jubones River delta to the Bocapán ravine delta in northern Perú.

In Perú, four main regions were elucidated, initially, the dry Ecuadorian forests in the Tumbes area span from the Bocapán ravine delta south until the Chira River. Then, the distinct dry forests in Piura span from the south and delta of the Chira River along the Andes until several rivers which the region follows through the Sechura Desert to the coast, initially, the Piura River, the Chancay and Zaña River where they both drive the region and then again from the Jequetepeque River southwards, occasionally interrupted. However, the region most associated with the coastline is the aforementioned Sechura Desert, this region spans most of the Blanco and Verde capes and reaches from Cape Blanco to the Chancay River, occasionally being interrupted by dry forests following the more humid river basins.

The biogeographic regions and turnover patterns observed in this study emphasise the intricate relationship between amphibian distributions and their surrounding ecological and topographical landscapes. The clear demarcation of turnover regions aligns with climatic gradients, habitat availability, and geographical barriers, such as rivers and mountain ranges, which act as filters or corridors for species dispersal. This is particularly evident in the Andes, where altitudinal variation creates numerous microhabitats fostering high endemism. For example, regions like the Serranía del Darién and the Coastal Cordillera highlight the role of isolated high-elevation areas as evolutionary hotspots, while lowland moist forests and dry forests reveal contrasting turnover dynamics due to differences in habitat connectivity and resource availability.

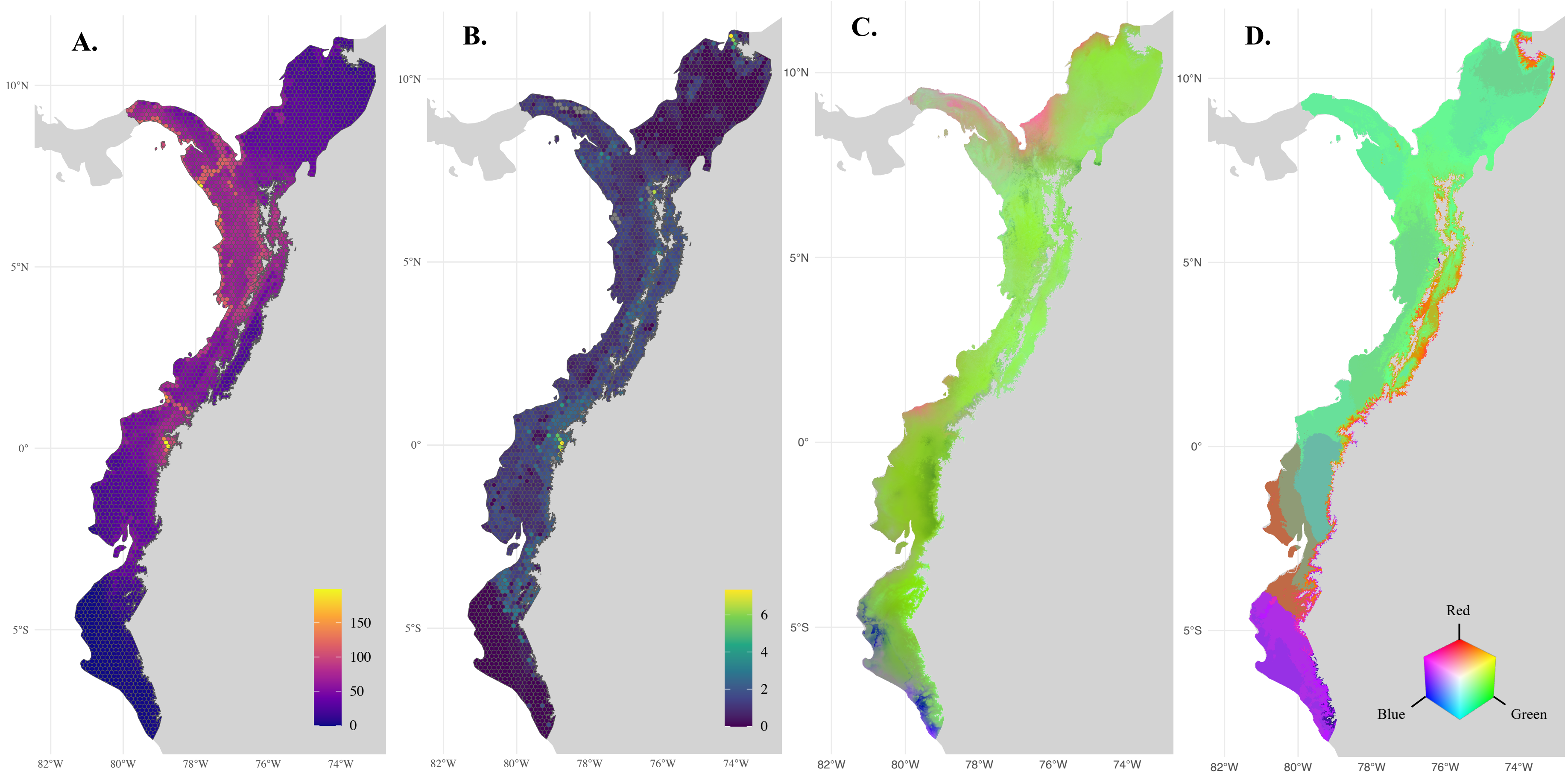

Figure 2. Biodiversity measures for amphibians.

A. Species richness (SR), **B.** endemicity (corrected weighted endemism, CWE), and turnover as measured by **C.** continuous and **D.** categorical general dissimilarity models (GDM), based on the distribution of 742 species of amphibians from the NW of the Tropical Andes. Species richness ranges from low (purple) to high (yellow) species per hexagon; Local endemism values range from low (blue) to high (yellow). GDM species turnover is graphed based on a RGB scale where every axis is a Principal Component (PC).

Reptiles

Species Richness

The northwesternmost piedmont forests of Ecuador, Colombia, and Panama appear to hold the highest concentration of species of reptiles, with a particular increase near the coast (Figure 3). Particularly, the points with the most species appear to be the montane forests in the Darién in Panama and Buenaventura in western Colombia. Species richness (SR) appears to be regularly distributed along the study area but decreases near drier regions like western and southern Ecuador and Northwestern Peru, near the Tumbes-Piura Dry Forests, the Ecuadorian Dry Forests, and the Secchura Desert. Reptile SR in the region is highest in areas of low elevation, particularly near coasts along Colombia and Panama, especially near the Darién Montane Forests, the Atrato River, and the Uramba Bahía Málaga National Park/Buenaventura.

For the family Alopoglossidae, the majority of species were located in northwestern Ecuador, displaying a predominantly humid lowland distribution. Anolinae has a distribution mostly remaining near the northernmost areas of the study area, particularly coastal areas. Nevertheless, the family is distributed evenly throughout humid lowlands and less in dry forests. Colubridae appears to be evenly distributed along the moist forest lowlands of Ecuador and Colombia. However, it also seems to have hotspots in the humid coastal regions in Guayas province in Ecuador, western Ecuador, northern Colombia, and southern Panama. In the case of Corytophaninae, the family only contained three species in the area, *Basiliscus galeritus, Basiliscus basiliscus* and *Corytophanes cristatus*, with the former being distributed along the NW of the Tropical Andes and the latter two in northern Colombia. Gymnophthalmidae displayed a fundamentally Andean distribution with peaks in central Colombia and western Pichicnha province in Ecuador and weaning presence toward lowland ecosystems. It may be important to note that the Coastal Cordillera in Ecuador is marked in Gymnophthalmidae distribution. The family Hoplocercinae only contained species in the genus *Enyalioides* and seemed to be most prevalent in northern Ecuador and southern Colombia, with another hotspot in the Colombia-Panama borders. Both Polychrotinae and Iguaninae had very few representatives and had very wide distributions. Both Teiidae and Tropidurinae displayed a notably particular distribution, with most species being located near drier lowlands. Teiidae is more prevalent in Northern Colombia and Tropidurinae in Southern Ecuador.

Corrected Weighted Endemism

Local endemism values only partly coincide spatially with SR (Figure 3). For reptiles, the largest extension of high-CWE shows a similar pattern to amphibians in the Guayllabamba River Valley. CWE peaks are also observed in the Andean slopes and areas of a higher elevation in general. Besides these hotspots, endemism remains relatively uniform to the west of the Andres, decreasing primarily in the Magdalena River Basin. Likewise, the data seems to have a generalised increase near the coasts of Colombia, possibly displaying a collection bias.

Similar to species richness, Both Teiidae and Tropidurinae displayed a notably similar endemism pattern, with most endemics being located in southern dry forest regions of southern Ecuador; likewise, both clades have endemic species that appear to relate to the Coastal Cordillera in Ecuador in the western side of Chongón Colonche. This mirrors how these are both families that have a variety of species adapted to drier conditions. In both these cases, the most evident *hotspot* for endemism was the Jubones River, with highly endemic species. There are various species in Tropidurinae from the Jubones River and southwards that are endemic to these regions, including *Stenocercus rhodomelas, S. simonsii, S. limitaris,* *S. ornatus,* and *S. carrioni*. Likewise, the critically endangered *Holcosus orcesi* in Teiidae is also endemic to the region of Santa Isabel in the Jubones River. These regions are quite dry and indicate that these families diversified in these areas of low precipitation. There are also hotspots for both families in the Cauca Valley and the Sinú Valley for Tropidurinae, further displaying the prevalence of these families in dry forest environments.

For the family Alopoglossidae and Hoplocercinae, there were certain similarities found in their areas of endemism. Particularly, these species both had high endemism on the west of Pichincha province and the Guayas Gulf in Ecuador, indicating endemic species in humid and dry forests. Likewise, Alopoglossidae displayed endemism from the Cerro Calima to the Farallones de Cali regions in the middle depression of the Western Cordillera in Colombia. Hoplocercinae appeared to also become endemic in lowlands such as those in the northernmost Western Cordillera (Colombia) and the Serranía del Sapo and Serranía de Pirre regions in southern Panama. Likewise, the endemism of Hoplocercinae was restricted to the easternmost part of the gulf, whereas Alopoglossidae displayed endemism throughout it. In the case of Polychrotinae, this family shared the same endemism pattern to the Guayas Gulf as Alopoglossidae and also seemed to be endemic to Puná Island similarly. Polychrotinae was prevalent and endemic in the Cauca Valley as well.

Gymnophthalmidae displayed mostly Andean endemics following the Western Cordillera in Pichicnha province in Ecuador and Antioquia department in Colombia. The family also showed peaks in some lowland highlands following the Coastal Cordillera and the Esmeraldas River basin in Ecuador and the Serranía del Darién in Panama. Within Colubridae, a similar pattern was found, appearing to be evenly distributed along the moist forest lowlands of Ecuador and Colombia but with a slight increase near the Andean slopes, near the Coastal Cordillera in Ecuador, in the middle depression of the Western Cordillera in Colombia, and in both the Serranía del Sapo and Serranía del Darién in Panama. This shows that Colubridae endemism increases altitudinally, with many endemic species in the highlands. Anolinae also displayed some of the phenomena from the aforementioned two families, such as the Andean, Coastal Cordillera, and Serranía del Sapo increases in endemism. However, near Colombian coasts, there is a large increase in endemism that may be related to bias in the distributional data.

Finally, the families Iguaninae and Corytophaninae displayed fairly empty CWE maps as the few representatives of these groups show a wide distribution, not allowing for much endemism to be appreciated.

Areas of Endemism Based on Generalized Dissimilarity Modelling

As mentioned previously, the GDM applied here identifies changes in the communities, which reflect high species turnover and can be interpreted as boundaries of biogeographic regions. In the case of reptiles, the main GDM boundaries display the boundaries of several different areas but indicate an important pattern relating to altitude. This trend is visible in more continuous community change in low elevations along the coasts with coastal cordilleras such as those in the Darién or Manabí in Panamá and Ecuador, respectively. The regions delimited for reptile turnover seem to be somewhat similar to amphibian regions in some respects and quite distinct in others, particularly given that reptiles are distributed more commonly than amphibians in dry and subarid biomes.

Particularly, for reptile turnover, there are a variety of distinct regions that were elucidated using the GDM. Initially, in Panama, the Serranía del Darién, Serranía del Sapo, and Serranía de Pirre had similar turnover patterns in reptile composition with a similar region between them but defined more in accordance to altitude than in the amphibian GDM; the highest regions in the Serranía del Darién and Pirre also marked distinct regions of reptile turnover showing endemism in these points. Likewise, between these two ranges, there was a distinct region of valley lowlands following the Chuncunaque River, however, concerning amphibian turnover, this region is more southbound with a pacific lowland area relating to isthmian moist forests in the north.

In the case of Caribbean Colombia, there were evident areas of species turnover delimiting Pico Cristobal Colón in the Serranía de Santa Marta very similar to those accounted for in amphibian GDM. However, to the north of this peak near Santa Marta, there appeared to be a xeric scrub region that was undefined in amphibians. There was also a region of reptile turnover to the west of Pico Cristobal Colón corresponding to the dry forests of the Sinú Valley but with a larger western extension toward the Momposina Depression. When reaching this depression, the dry forest region transitions throughout Caribbean Colombia until the Atrato River, with two distinct areas. The northmost eastern area includes the Momposina Depression with numerous other floodplains and is a transition from xeric scrub to more humid environments. Gradually, the southmost western area interconnects to this while bordering the Momposina floodplains, changing into moist forests. This area is delimited by the Western Cordillera and the Gulf of Urabá. On the other side of the Western Cordillera in Pacific Colombia, to the south of the aforementioned area in the Serranía del Darién in Panama, a small area of turnover is delimited by the Atrato River and is related to the lowland isthmian moist forests. Between this area and the Gulf of Urabá, another region forms related to both moist forest and Andean montane forest, in a lesser way than in amphibian GDM. This region only reaches the Pacific Ocean in the Cupica Gulf and then forms a montane forest covering the Western Cordillera and until the Cauca River Valley. This montane transitional area is bordered to the Pacific side by a lowland area where reptile turnover is similar, ranging from the coast of the Tibuga Gulf until the Tumaco Bay In. its south, the Rosario and Esmeraldas rivers delimit this area until it reaches the Andes (homologous to amphibian turnover). Within the Cauca River Valley, the lowlands display a similar turnover area to the Western Cordillera montane forests; however, these regions are distinct, probably displaying lowland dry forests.

In Ecuador, eight occidental and distinct reptile turnover regions were determined, these are somewhat similar to the amphibian zones; moreover, they display an intermediate zone in between the humid and deciduous forests. A similar region to the northernmost area in amphibian turnover has, as its southern limit, the Guayllabamba River from western Pichincha province and follows the Esmeraldas River to the West of the Mache Chindúl Mountains. The northernmost border of this region begins at the western slopes of the Cotacahi Volcano and ends in northern Tumaco Bay. Then, another quite distinct turnover zone, relating to premontane/cloud forests, ranges from the Intag Valley to the Toachi-Pilatón Valley, with slight remnants remaining near the montane Western Cordillera. To the west of the Intag Valley, and following the Guayllabamba River until Mache Chindul, is a transitional zone from moist forest to deciduous forest. As this region extends southward, it contains the eastmost and westmost areas of the amphibian GDM's, deciduous and moist forest areas. The area shows components intermediate to both of these amphibian turnover regions and displays the greater prevalence of reptile species in more arid or seasonal climates. To the west of this region, there is an area of turnover that spans the east of the Mache Chindul until it reaches Naranjal and runs southward, following the Andes to the east and the Guayas Bay until the Puyango River, it is also located on the east of Puná Island and appears to be composed of deciduous forests. To the east of the transitional zone, from moist forest to deciduous forest, there is an area of moist forest reaching the Andes to its east, this area is surrounded on all other sides by the transitional zone. Then, there appears to be a small montane area of turnover in the highest points of the Coastal Cordillera in Manabí province in the Chongón Colonche mountains. To the west of Chongón Colonche and the southernmost Coastal Cordillera, there is an area that reaches the coast and appears to include mostly dry forests. This region is located on three distinct coastlines: one in the north of the Guayas Gulf spanning north until Bahia de Caraquez, another in the westernmost of Puná Island, and yet another from the Jubones River delta to the Bocapán ravine delta in northern Perú.

In Perú, there are five main regions that were elucidated, initially, the dry Ecuadorian forests in the Tumbes area that spans from the Bocapán ravine delta south until Cerros de Amotape, Following this area, another turnover zone reaches the Andes to the eastern Chira River. Then, the dry forests in Piura that span from the south of the aforementioned areas along the Andes, tapering until the to the Zaña River Valley. However, the region most associated with the coastline is the Sechura Desert, spanning from Punta Pariña to the lower limit of the study area.

The GDM analysis of reptile turnover across these diverse regions highlights distinct biogeographic patterns influenced by altitude, climate, and vegetation types. The variation between areas, such as the coastal dry forests and montane ecosystems, reflects the complex interactions between species and their environments. While some turnover regions align closely with amphibian patterns, others reveal unique distinctions, particularly in the preference of reptiles for more arid or seasonal climates. This differentiation underscores the importance of considering both ecological and geographical factors when defining biogeographic boundaries, offering valuable insights into the conservation and study of species distributions in these dynamic landscapes.

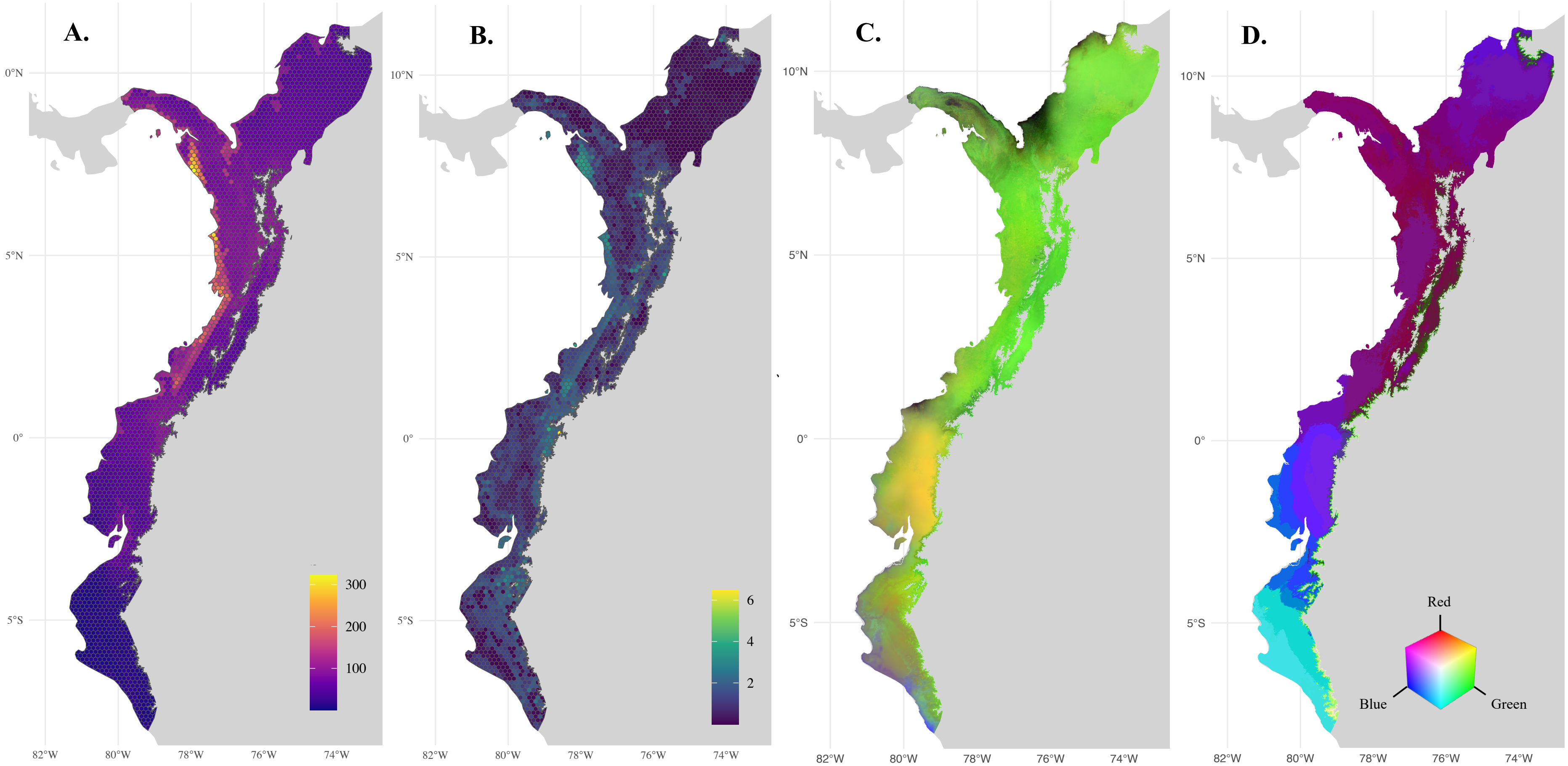

Figure 3. Biodiversity measures for reptiles.

A. Species richness (SR), **B.** endemicity (corrected weighted endemism, CWE), and turnover as measured by **C.** continuous and **D.** categorical general dissimilarity models (GDM), based on the distribution of 492 species of reptile from the NW of the Tropical Andes. Species richness ranges from low (purple) to high (yellow) species per hexagon; Local endemism values range from low (blue) to high (yellow). GDM species turnover is graphed based on a RGB scale where every axis is a Principal Component (PC).

Herpetofauna

Species Richness

The levels of species richness when considering the whole herpetofaunal assemblage displayed a larger amount of species generally concentrated near the Western Cordillera and in the moist lowland forests (Figure 4). In particular, the forests in the Seranía del Darién, Serranía del Sapo, and Serranía de Pirre in Panama, Buenaventura in western Colombia, Western Pichincha Valleys in Ecuador, and overall Andean slopes displayed higher species richness.

All these regions have significant richness *hotspots* in comparison to other more evenly distributed areas, such as dry forests. These more arid regions, located in Southwestern Ecuador, Caribbean Colombia, and Northwestern Peru, displayed a lesser amount of species due to the areas’ decreased availability of resources and increased competition. Herpetofaunal richness in this region had evident patterns, such as the increase in reptile diversity and a decrease of amphibian species along these lower and drier localities. For example, Teiidae and Tropidurinae, which are prevalent in the drier lowlands of northern Colombia and southern Ecuador, contribute importantly to the richness of these ecosystems; however, very few species of amphibians can even be found in the area.

In contrast, the humid regions in the NW of the Tropical Andes, especially those associated with altitudinal strata nearing the Andes, displayed a massive increase in richness for both amphibians and reptiles. Notably, regions like Serranía del Sapo, the Atrato and Guayllabamba Rivers, and the Colombian Buenaventura region are epicentres of richness for the entire assemblage. For example, tree-dwelling species of anurans like Centrolenidae, Hylidae, and Hemophractidae, were distributed in the moist forest lowlands of Ecuador and Colombia, as well as in hotspots in Pichincha and Antioquia. This led to them contributing largely to the elevated richness in these areas along an altitudinal gradient. Likewise, Dendrobatidae and Aromobatidae, which are also abundant in these humid areas, add considerably to the diversity of lowland regions. Lastly, Stabomantidae, and especially the genus *Pristimantis*, is prominent in the Andean slopes and added massively to the species diversity of the humid forest and montane regions. As for examples of reptiles, speciose groups like Colubridae and Anolinae also had increased richness in humid lowlands, and their increased diversity contributed heavily to the map's peaks. Finally, Alopoglossidae and Gymnophthalmidae, predominantly found in the humid lowlands and highlands of northwestern Ecuador, respectively, further enrich the species diversity in the moist forest areas of the NW of the Tropical Andes.

Corrected Weighted Endemism

Local endemism values only partly coincide spatially with SR (Figure 4); nevertheless, CWE offers a complementary perspective by emphasising species with restricted ranges, thereby mitigating some biases present in species richness data. When comparing CWE to species richness, distinct patterns emerge, highlighting less apparent areas of conservation significance, such as regions with range-restricted species. Through this endemism metric, it is evident that there were very high peaks of endemism in the Guayllabamba River Valley for both reptiles and amphibians. This peak shows the unique composition of the area, particularly when considering the relative endemism of the area in comparison to the NW of the Tropical Andes. CWE peaks were also observed in Andean slopes and Piedmont forests when compared to lowland forests. This is evident in the Buenaventura region of Ecuador, the Paramillo Massif, and the Sierra Nevada de Santa Marta, which all are somewhat species-poor but have highly endemic species.

For reptiles, as mentioned previously, endemism patterns reveal ecological and geographical causality. The Jubones River Valley and Buenaventura stood out with high endemism across families, particularly in Tropidurinae and Teiidae, which thrive in drier conditions. These groups exhibit strong endemism in the southern dry forests of Ecuador, such as the Jubones River region, home to highly range-restricted species like *Stenocercus rhodomelas* and *Holcosus orcesi*. These findings highlight the importance of arid ecosystems in shaping reptile diversity, particularly in groups adapted to these areas; similar endemism patterns are seen in dry forest areas of the Cauca and Sinú Valleys, emphasising the adaptability of these groups to low-precipitation environments. Conversely, families like Gymnophthalmidae and Colubridae show stronger Andean affinities, with endemism concentrated in the Western Cordillera from Ecuador to Colombia, the Coastal Cordillera in Ecuador, and the Sapo and Pirre Serranias. These patterns underscore the role of montane and lowland humid forests as diversification areas and display the effect of altitudinal gradients on reptile evolution.

Amphibian endemism also reflects varied ecological niches and species' evolutionary history. Endemism peaks were observed in the Guayllabamba River Valley, Santa Marta forests, and the northern Western Cordillera in Colombia. Families such as Aromobatidae and Dendrobatidae displayed clear areas of endemism in lowland forests near the Atrato and Esmeraldas Rivers, suggesting historical diversification events in these corridors. Meanwhile, montane specialists like Craugastoridae and Strabomantidae demonstrate niche-specific endemism along altitudinal gradients, with Craugastoridae being dominant in northern montane regions, whereas Strabomantidae was dominant in southern Andean slopes and lowlands. Tree-dwelling families belonging to Hylidae, Hemiphractidae, and Centrolenidae also exhibit unique patterns with broad and altitude-linked endemism with hotspots in the Andean slopes and the Coastal Cordillera.

These patterns collectively emphasise the complex interplay of ecological, topographical, and historical factors driving endemism in the region and underscore the need for tailored conservation strategies to protect both well-known and cryptic biodiversity across this unique landscape.

Areas of Endemism Based on Generalized Dissimilarity Modelling

The GDM applied in this case, implementing all species of both reptiles and amphibians within the area, is a comprehensive biogeographic regionalisation that provides delimitations representing the spatial patterns of fauna within these groups. The delimitations shown display novel patterns that had not previously been detected in literature using other methods. These patterns surprisingly reveal a lot more than the amphibian or reptile maps did on their own and are highly representative of species distribution patterns.

Initially, for Panama, it was evident that the Serranía del Darién, Serranía del Sapo, and Serranía de Pirre had similar turnover patterns in herpetofaunal composition with a shared turnover region between all three. In this region, the areas with the most altitude in the Serranía del Darién and Pirre marked other distinct turnover regions, showing that the species at the highest points tended to be endemic. Likewise, between these two ranges, there was a distinct region of valley lowlands following the Chuncunaque River that extended toward central Panama and had both Caribbean and Pacific shores.

In the case of Caribbean Colombia, there were evident areas of species turnover delimiting Pico Cristobal Colón in the Serranía de Santa Marta as there were for amphibian and reptile assemblages prior. The turnover region to the west of this, corresponding to the dry forests of the Sinú Valley, was present but further stratified, demonstrating initial dry forests transitioning to more humid areas. In the coastal regions of the Magdalena Peninsula, the northernmost region (similar to that in reptilia) represented some of the xeric ecosystems reaching north Santa Marta; this was the north boundary of the Sinú dry forests. The next region began and followed the Magdalena River, spanning Caribbean Colombia until the

Morrosquillo Gulf. This area bifurcates into two floodplains following the Cauca and Magdalena Rivers further south, corresponding to the Momposina Depression. Between this bifurcation and reaching the northernmost point near Isla Tortuguilla is a transitional moist lowland region. This area eventually transitions into a Caribbean and Pacific Colombia region encompassing the Western Cordillera, the east of the Serranía del Darién, the northmost Cauca River Valley, and the Atrato River composing the Tibuga Gulf. This region appears to be similar to the montane forest of the Western Cordillera, but it is distinct in the integrative herpetofaunal assemblage, as opposed to reptiles and amphibians individually. To the south of this region is another area that is very distinct and uniform, spanning from the south of the Tibuga Gulf until the Patía and Mira Rivers, this is an area composed of moist forest that spans nearly all of western Colombia from the coast up to the Western Cordillera. In the south of the Cauca River Valley, a somewhat uniform lowland region appears to correspond to a dry forest ecosystem with montane ecosystems surrounding it. Additionally, in the Patía Valley, a dry forest region was detected.

South of the latter two regions, eight occidental and distinct herpetofaunal turnover regions were determined for Ecuador. The northmost of these is a region with its southern limit at the Guayllabamba River from the westernmost Pichincha province and reaching the northern Mache Chindúl Mountains along the Mache River; the northernmost border of this region continues until the Patía River. Alongside this region’s limit in the Guayllabamba River, two distinct montane/cloud forest regions are noticeable, one spanning north slightly and another spanning south more significantly, divided by this river. Further south, the Coastal Cordillera separates four main regions. In its altitudinal maxima, small montane areas of herpetofaunal turnover appear significant in Manabí province in Chongón Colonche mountains. To the western side of these mountains, a region spans north from Punta Ballena, southeast of the Mache Chindúl Mountains, and runs southward along the Ecuadorian coast.

It continues to the southeast of Guayas Bay and ends west on the Bocapán ravine delta in northern Perú and is also located on the east of Puná Island; this region appears to be composed of mostly dry forests. The only coastal regions this dry forest ecosystem does not encompass are the Punta Santa Elena region, likely due to the xeric and arid ecosystems and the affinities of Punta Jama. East of the Coastal Cordillera, two forest ecosystems remain, the most distant is a moist forest ecosystem near the Andes and enclosed by the Coastal Cordillera, it reaches the northmost Guayas Gulf and is surrounded in the east and south by the region proximal-most to the Coastal mountain range. This area is a deciduous forest region ranging inland from Punta Jama across the south of Mache Chindúl and east of Chongón Colonche. The deciduous region spans toward the northeastern Guayas Gulf to the Chanchan River and continues south along the Andes until the inland Bocapan Ravine.

In Perú, five main regions were elucidated, initially, the dry Ecuadorian forests in the Tumbes area that spans from the Bocapán ravine delta south until the Tumbes National Reserve. Then, Ecuadorian deciduous forests in the inland area from the Tumbes National Reserve to the Chira River. South of these, a transitional region of dry forests spans a narrow band from the Zorritos Ravine to the Quiroz River. Following this transitional area and the Andes, the dry forests in Piura span from the south of the aforementioned areas along the Andes, tapering until the Zaña River Valley. However, the region most associated with the coastline is the Sechura Desert from Punta Pariña to the lower limit of the study area.

The GDM revealed novel biogeographic regions in the NW Tropical Andes, with distinct turnover regions in Panama's Serranías, Colombia's forests, Ecuador’s Cordilleras, and Perú’s dry forests and deserts. These results highlight the complex biodiversity patterns and the importance of using comprehensive species groups in biogeographical modelling.

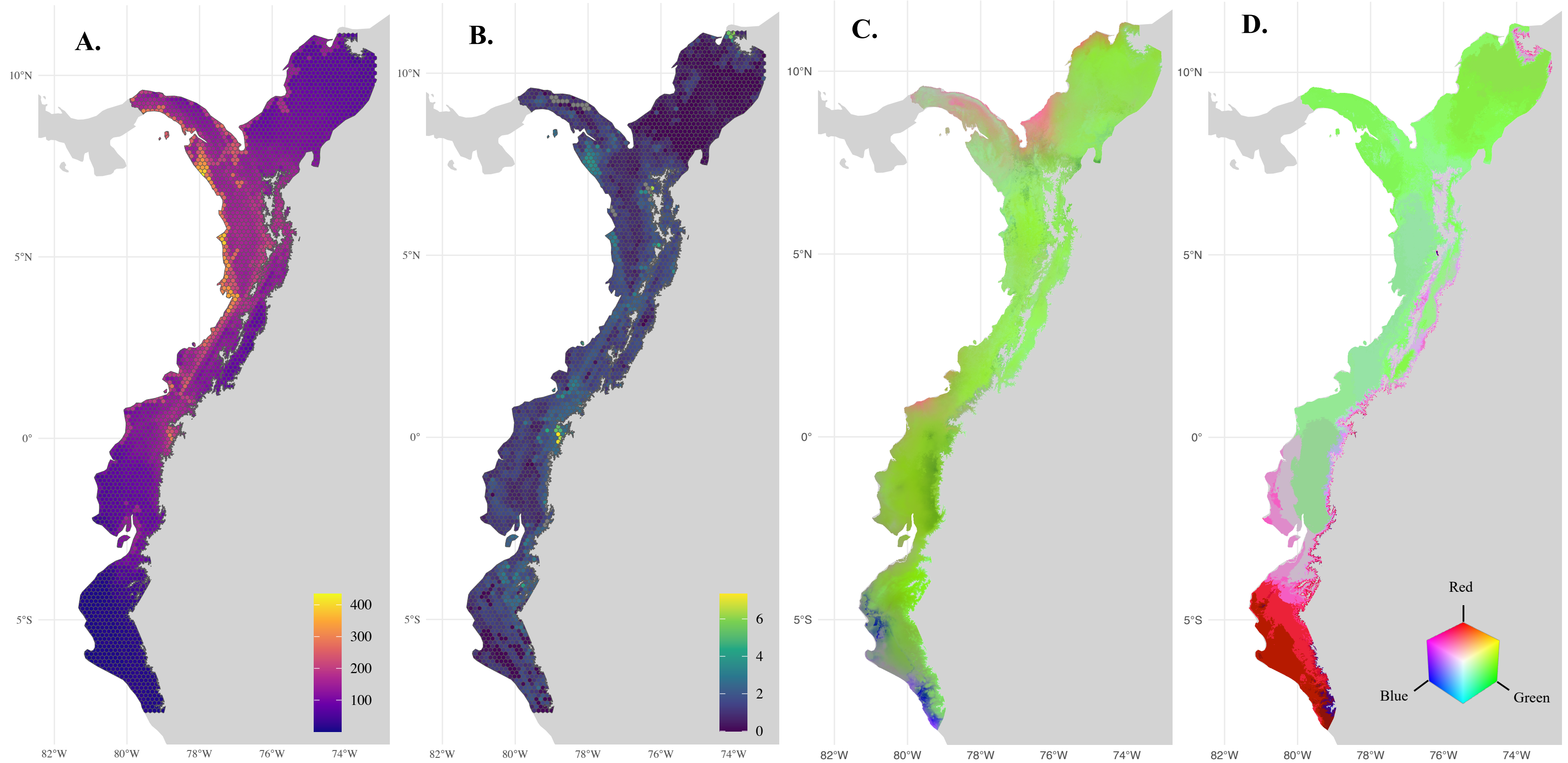

Figure 4. Biodiversity measures for reptiles and amphibians.

A. Species richness (SR), **B.** endemicity (corrected weighted endemism, CWE), and turnover as measured by **C.** continuous and **D.** categorical general dissimilarity models (GDM), based on the distribution of 1093 species of the herpetofauna from the NW of the Tropical Andes. Species richness ranges from low (purple) to high (yellow) species per hexagon; Local endemism values range from low (blue) to high (yellow). GDM species turnover is graphed based on a RGB scale where every axis is a Principal Component (PC).

DISCUSSION

This study investigated whether Generalized Dissimilarity Modelling (GDM) of tetrapod faunal diversity patterns in the northwest of the Tropical Andes revealed biogeographic insights not captured by existing models. The research provided a comprehensive analysis of species richness, endemism, and turnover within the NW Tropical Andes, highlighting significant biogeographic patterns and ecological dynamics. Key findings included the identification of distinct biogeographic regions and turnover zones using GDM, revealing novel insights into the spatial distribution of tetrapod species. Notable hotspots of species richness and endemism were found in areas such as the Guayllabamba River Valley, the Serranías of Darién and Pirre, and the Western Cordillera. The study emphasised the critical role of both lowland and montane ecosystems in shaping biodiversity patterns, underscoring the importance of considering a wide range of species and ecological interactions in biogeographic studies to enhance conservation strategies and ensure the protection of the region's unique and threatened biodiversity.

Amphibian Species Richness and Endemism

One of the key findings of this work is the spatial patterning of species richness to identify regions of ecological significance. In terms of amphibian species richness, this study, like Duellman (1988) and Savage (1982), found significant concentrations of species in the moist forests of the western piedmont and Andean slopes within the NW of the Tropical Andes.

Duellman (1988) identified homologous SR hotspots along the Guayllabamba River or the Quebrada Zapadores and various of the foothills of the western Andes, such as those in this study. Likewise, he also observed a gradient of species richness with increasing elevation in these regions, with peaks near the northern Andes. However, while Duellman emphasised a more general distribution of species across the Tropical Andes, the current study offers a more granular understanding of these patterns by focusing on individual families such as Aromobatidae, Bufonidae, and Dendrobatidae, which exhibit clear regional richness peaks that align with Duellman's findings but also reveal finer distinctions within specific areas like the Chocó and Pichincha provinces. The endemism patterns of Leptodactylidae and Ranidae also display distinct geographic distributions in this study, with significant endemism along the Ecuadorian western slopes, echoing his general observations but refining them with a more localised focus. However, interestingly, Duellman (1988) also noted a decrease in species diversity near drier regions such as the Tumbes-Piura Dry Forests, which is corroborated by this study's findings, where SR significantly drops near these areas. These phenomena align quite well with the obtained results and can be observed in several of the detailed SR maps produced in this research (Figure 2Figure ***4***).

Similarly, Savage (1982) proposed a vicariance model to explain the distribution of Neotropical herpetofaunal groups, suggesting that the uplift of the Andes played a crucial role in isolating populations and driving speciation. This hypothesis aligns with the findings of this study, which demonstrate the significant influence of Andean uplift on the distribution and endemism of many amphibian and reptile families. This work observes that amphibian species richness is concentrated in the northwestern regions, particularly along the foothills of the Andes, but decreases dramatically in the southern regions and areas of drier ecosystems. This corroborates many of the hypotheses he proposes in accordance with families such as Aromobatidae and Bufonidae. These exhibit similar distributions to those proposed by Savage (1982) Aromobatidae concentrated in northern Colombia and Panama, and Bufonidae showing a broader but still northern range, particularly near the Cauca River Valley.

Although this work corroborates Savage's hypotheses in various aspects, it also fails to do so in others, such as most speciose, Strabomantidae. It is not certain whether the families that follow Savage's predictions are due to a speciation event in that direction or due to environmental factors. It is certainly the case in a variety of genera, such as those in the family Hemiphractidae (Kok et al., 2017); however, it may also be possible that various phylogeographic lineages are uncertain and may yet be uncovered (Santos et al., 2009).

Other studies also identified key families within the amphibian assemblage of South America, focusing on the spatial patterns of species richness and endemism in a different tropical region (Rivas et al., 2021). For families such as Stabomantidae and Craugastoridae, this study revealed clear endemism hotspots in the western Andes of Ecuador and Colombia. These findings are consistent with Rivas et al. (2021) who highlighted similar endemism patterns within the same families in the lowland-to-montane gradient, although our study suggests that Craugastoridae has a more extensive Central American distribution. The families Aromobatidae and Bufonidae in this study showed a distribution concentrated in the northern parts of the region, with Aromobatidae showing a pronounced hotspot around the Atrato River basin. This pattern of distribution mirrors the findings of Rivas et al. (2021), who observed similar trends in their study areas in terms of lowland richness and endemism. Similarly, compared to Vasconcelos et al. (2019), findings in both studies show that species richness is highest in the western piedmont forest of northwestern Ecuador, especially near the Colombian and Panamanian coasts. Vasconcelos et al. (2019) identify a similar richness hotspot in the northwestern Andes, especially along the Colombian and Panamanian coasts, which corroborates the results from this study. In particular, the NW Andes moist forests appear to support high SR values, which are consistent with findings in the present study for amphibians.

When considering endemism, both Duellman (1988) and this work highlight a strong correlation between endemism and elevation, particularly in montane regions of the Andes. Nevertheless, Duellman (1988) generally placed more emphasis on latitudinal gradients of endemism, focusing on broad biogeographical patterns. Although this method appears to have a general trend, the current study incorporates the concept of CWE and offers a more nuanced view of local endemism. For example, Duellman (1988) findings on Aromobatidae show a higher concentration of species in the northernmost regions, extending into Colombia and Panama, a pattern also noted in this study. However, the incorporation of CWE reveals that Aromobatidae, in particular, demonstrates significant endemism hotspots along the Guayas Gulf and the western slopes of the Andes, also highlighting these areas as critical biodiversity refuges.

Similarly, when comparing the findings from this thesis to those of Savage (1982), several key patterns in species richness (SR) and endemism (CWE) in amphibians and reptiles across the Tropical Andes emerge, with both similarities and distinguished differences across taxonomic families. For amphibians, Savage (1982) highlighted the importance of the western piedmont forests of the Tropical Andes as biodiversity hotspots, particularly for species richness and herein, the western piedmont forests in northwestern Ecuador, particularly near the Guayllabamba River Valley, also show high SR. Moreover, this study observes that amphibian species richness is concentrated in the northwestern regions, particularly along the foothills of the Andes, but decreases dramatically in the southern regions and areas of drier ecosystems in concordance with Savage (1982). Similarly, families such as Aromobatidae and Bufonidae exhibit similar distributions to those in Savage (1982) with Aromobatidae concentrated in northern Colombia and Panama and Bufonidae showing a broader but still northern range, particularly near Valle del Cauca. However, utilising CWE's nuanced hotspots of endemism, these families are noticeable. For example, the unique endemism observed in Dendrobatidae near the Atrato River basin in Colombia and the increased endemism in western Ecuador, particularly in the Andes and Coastal Cordillera. These results support and extend Savage's (1982) observations of the biogeographic richness of Dendrobatidae but also provide additional details about the ecological corridors influencing species persistence.

Rivas et al. (2021) identified key families within the amphibian assemblage, their work focused on the spatial patterns of species richness and endemism in a different tropical region. Similar to these findings, their study emphasised the importance of lowland humid forests and montane regions in sustaining high species richness. For families such as Stabomantidae and Craugastoridae, both studies found clear endemism hotspots in the western Andes of Ecuador and Colombia. The families Aromobatidae and Bufonidae in this study showed a distribution concentrated in the northern parts of the region, with Aromobatidae showing a pronounced hotspot around the Atrato River basin. This pattern of distribution mirrors the findings of Rivas et al. (2021), who observed similar trends in their study areas in terms of lowland richness and endemism. However, this research found a more distinct separation in the endemism of these two families, with Dendrobatidae exhibiting a more uniform pattern of richness but stronger endemism across the western Ecuadorian Andes, particularly in the Coastal Cordillera in the genera *Epipedobates* and *Hyloxalus*. This aligns with the broader patterns of richness and endemism observed in Rivas et al. (2021), where species endemism was often correlated with elevation and proximity to the Andes but extends to minor mountain ranges as well.

Likewise, for families such as Stabomantidae and Craugastoridae, this study revealed clear endemism hotspots in the western Andes of Ecuador and Colombia. These findings are consistent with Rivas et al. (2021), who highlighted similar endemism patterns within the same families in the lowland-to-montane gradient, although this study suggests that Craugastoridae has a more extensive Central American distribution. These families appear to share ecological niches in montane and lowland forest ecosystems, reinforcing the importance of these habitats in driving speciation and maintaining high levels of biodiversity.

In contrast, the families Leptodactylidae and Ranidae displayed inverse patterns of endemism, with Leptodactylidae being highly endemic to the west Coastal Cordillera and Ranidae more prevalent in the east. This contrasts with the more homogeneous distribution of these families observed by Rivas et al. (2021), indicating possible regional differences in ecological drivers and evolutionary histories.

Vasconcelos et al. (2019) suggest that areas of high endemism are found in isolated montane regions, while this study finds that endemism is more concentrated continuously along the western Andean slopes, particularly in regions such as the western Pichincha and Cotopaxi provinces of Ecuador or near the department of Antioquia in Colombia. For example, Leptodactylidae shows high endemism along the Coastal Cordillera and the western Andean slopes, a finding that corresponds with the regional patterns described by Vasconcelos et al. (2019), who also noted high endemism in similar montane areas. However, this study, provides a finer resolution of endemism hotspots within families, such as the relatively uniform endemism of Hylidae throughout the region. This contrasts with the more variable endemism patterns observed in other families like Craugastoridae, which display a contrasting distribution pattern.

Nevertheless, both studies highlight the importance of different lowland forests in supporting endemism. This study discusses Andean slopes, the Atrato River basin in Colombia, and the Guayas Gulf in Ecuador, serving as key biodiversity hotspots, however, Vasconcelos et al. (2019) discuss lowland forest endemism. Although families such as Dendrobatidae and Eleutherodactylidae exhibit endemism patterns closely aligned with these lowland ecosystems, particularly in the tropical forests of Colombia and Panama, others do not, particularly families like Hemphractidae.

Reptile Species Richness and Endemism

In this study, reptile species richness was highest in the lowland regions near the Pacific coast, with Andean altitudinal gradients also in place, particularly around the Darién Montane Forests, which is consistent with the findings of Rivas et al. (2021) that also noted the importance of coastal regions in maintaining high reptile biodiversity.

In reptiles, the thesis echoes many of the observations made by Savage (1982) regarding species richness in lowland moist forests and the decline of richness in drier areas. For example, Alopoglossidae and Anolinae families show similar distributions, with high species richness in humid lowland ecosystems near the coast. However, this study finds that Anolinae has a more concentrated presence in the northern parts of the study area, particularly in coastal regions, extending further into Panama and Colombia, aligning with Savage (1982) and Rivas et al. (2021) and broader recognition of lowland forest ecosystems as critical for reptile diversity. Notably, Corytophaninae, mentioned in both studies for its specific distribution along the northern Andes, shows slightly divergent patterns from Savage (1982). This work points out a particularly strong presence in Ecuador’s northwestern regions, however, this issue may is probablu due to taxonomical inaccuracy.

Moreover, in terms of endemism, both studies show a convergence in the importance of mountainous ecosystems for shaping species distributions. Families such as Gymnophthalmidae and Hoplocercinae exhibit a clear concentration of endemism along the Andes and in the foothills, particularly in regions with complex altitudinal gradients (Savage, 1982). These findings are in line with Savage et al.'s observations of the importance of Andean montane ecosystems in fostering species isolation and endemism. Considering

Teiidae and Tropidurinae reveals distribution patterns more influenced by lowland dry forest ecosystems, particularly in the south of Ecuador and northern Colombia. Savage (1982) had noted similar patterns of dryness-associated reptiles, but this thesis highlights a more precise delineation of these species' ranges and suggests that drier ecosystems could serve as refugia for reptiles that have adapted to these harsher environments, further emphasising the need to consider such ecosystems in conservation planning.

Richness and endemism in the NW of the Tropical Andes exhibit distinct spatial patterns. Nonetheless, these patterns raise questions about the plausible accuracy and biases inherent in the data. For instance, regions with higher reported richness often coincide with areas that are more accessible or politically significant, even though political boundaries were not explicitly used in the analysis. This observation highlights the potential influence of sampling efforts and accessibility on species distribution datasets. And is one of the reasons SR and CWE are not the most useful biogeographical delimitation tool.

GDMs

This Generalized Dissimilarity Modelling (GDM) represents the first attempt at a biogeographic regionalisation in the NW of the Tropical Andes. In South America particularly, this study is among the first to use GDM for this purpose, setting a precedent for future biodiversity research. From the three GDM obtained, important patterns in species turnover and biogeographic delineation were obtained. While the amphibian and reptile-specific GDMs independently provide valuable insights, the combined model demonstrates a more nuanced and comprehensive understanding, reducing inaccuracies observed in the taxon-specific models.

The amphibian-specific GDM primarily reflects turnover patterns associated with humid and subhumid biomes, consistent with amphibians' ecological dependence on moist environments. The model effectively delimits boundaries for species turnover corresponding to distinct biogeographic regions, such as the humid lowlands and montane areas of the Andes. However, it demonstrates limitations in capturing transitions in drier or subarid biomes, where amphibians are less prevalent. This narrow focus provides an understanding species turnover in ecotonal areas, particularly in regions like the Sinú Valley dry forests or the Sechura Desert, where species distributions are more heterogeneous.

In contrast, the reptile-specific GDM excelled in characterising turnover in dry and subarid biomes, reflecting Reptilia's greater ecological plasticity and prevalence in these environments. Noteworthy distinctions include the distinct delineation of xeric scrub regions near Santa Marta and a more detailed characterization of transitional zones in the Momposina Depression. However, the reptile model struggles with resolution in regions dominated by humid biomes, particularly in montane areas where amphibians exhibit higher endemism. This discrepancy likely arises from the differences in species richness and ecological preferences between the taxa.

The combined GDM, utilising all herpetofauna, provides a more balanced representation of turnover patterns across diverse biomes and elevational gradients. By synthesising the complementary strengths of the taxon-specific models it reduces the inaccuracies observed in the other two models. For instance, in the Andes, the combined model captures both the high-altitude endemism characteristic of amphibians and the broader distribution patterns of reptiles in drier areas. Likewise, in the Sechura Desert, the herpetofauna GDM delineates turnover boundaries that align more accurately with ecological gradients, accounting for the contributions of both taxa. The combined GDM identifies novel biogeographic regions and transitional zones that were less apparent in the taxon-specific models. For example, intermediate zones between humid and deciduous forests in western Ecuador are more distinctly resolved, reflecting the overlapping yet distinct ecological preferences of amphibians and reptiles, similarly, the delimitation of the Coastal Cordillera in

Ecuador was clearly observed in the combined GDM in relation to the weak signals of the other two. Similarly, the combined model aligned its delimitations better to other biogeographic features like rivers or mountains. These findings underscore the importance of integrating data from multiple taxa to enhance the resolution and accuracy of biogeographic models.

Thus, the combined GDM classifications is an accurate biogeographic model of herpetofaunal turnover and assemblage. In relation to the most relevant and latest existing biogeographic models, notably those by Dinerstein et al. (2017) and Morrone et al. (2022) it was revealed that both congruence and divergence is evident. Particularly, the model by Morrone et al. (2022) reveals a very broad biogeographic regionalization, possibly losing valuable information. Likewise, although Dinerstein et al. (2017) has a similar scope to the GDM, many evident features are not present.

Initially, when considering the delimitations obtained for Panama, the Serranía del Darién, Serranía del Sapo, and Serranía de Pirre had similar turnover patterns in herpetofaunal composition with a shared turnover region between all three. This was classified by Dinerstein et al. (2017) as *Chocó-Darién moist forests* and was not individually delimited like in this study. Likewise, in the highlands of this area, in the Serranía del Darién and Pirre, there was a distinct turnover region. This region was classified by Dinerstein et al. (2017) as *Eastern Panamanian montane forests*, nevertheless, the delimitations did not follow the altitudinal patterns of the Serraías. None of these areas were detected in Morrone et al. (2022) and were all classified as *Chocó-Darién Province.* Likewise, between these two detected ranges, there was a distinct region of valley lowlands following the Chuncunaque River that extended toward central Panama and had both Caribbean and Pacific shores. This region was detected by both Dinerstein et al. (2017) and Morrone et al. (2022) and was classified as *Isthmian Atlantic moist forests* and *Guatuso–Talamanca province*, respectively.

Although the limits for this lowlands region were coarser in the aforementioned studies, the limits were somewhat similar showing congruence in this area.

In the case of Caribbean Colombia, there were evident areas of species turnover delimiting Pico Cristobal Colón in the Serranía de Santa Marta. These were delimited as *Santa Marta montante forests* and *Santa Marta páramo* in Dinerstein et al. (2017), sharing similar limits to those seen in this study. Likewise, the turnover region to the west of this, corresponding to the dry forests of the Sinú River Valley, was present but stratified, demonstrating initial dry forests transitioning to more humid areas. This shows that this is a transition area or an ecotone and is not a *sensu stricto* biogeographical zone. Dinerstein et al. (2017) classifies it as *Sinú Valley dry forests* and displays limits beyond the delimitations obtained in this work. In the coastal regions of the Magdalena Peninsula, the northernmost region represented xeric ecosystems reaching north Santa Marta; this was the north boundary of the Sinú dry forests. Dinerstein et al. (2017) classifies it as *Guajira-Barranquilla xeric scrub* but includes an ecoregion not detected for the present study, *Amazon-Orinoco-Southern Caribbean mangroves*. These non-detected delimitations were likely due to the use of plant data in the model, however, for the detected model, Dinerstein et al. (2017) displayed a southwestern extrusion not present in this work. However, Morrone et al. (2022) depicted this region as *Guajira province*, and included within all of the aforementioned Carribbean Colombia regions. The next region began delimited by the Magdalena River, spanning Caribbean Colombia until the Morrosquillo Gulf. This area bifurcates into two floodplains following the Cauca and Magdalena Rivers further south, corresponding to the Momposina Depression. Between this bifurcation and reaching the northernmost point near Isla Tortuguilla is a transitional moist lowland region. Both of these areas were delimited by Dinerstein et al. (2017) as *Magdalena-Urabá moist forests*, but in this study were revealed to be a floodplain region and a moist forest region. Morrone et al. (2022) depicted this area as the *Magdalena province*. The next area to the west, transitions into a Caribbean and Pacific region encompassing the Western Cordillera, the east of the Serranía del Darién, the northmost Cauca River Valley, and the Atrato River composing the Tibuga Gulf. This area is considered to be the middle of the *Chocó-Darién moist forests*, north of the *Northwest Andean montane forests*, and west of the *Magdalena-Urabá moist forests* (Dinerstein et al., 2017). Likewise, is region is the middle of the *Chocó-Darién*, north of the *Cauca*, and west of the *Magdalena provinces* in Morrone et al. (2022). In this work, this region is similar to montane forest the Western Cordillera. To the south of this region is another area that is very distinct and uniform, spanning from the south of the Tibuga Gulf until the Patía and Mira Rivers, this is an area composed of moist forest that spans nearly all of western Colombia from the coast up to the Western Cordillera. This corresponds to the midsection of the *Chocó-Darién moist forests* and the *Chocó-Darién province* in Dinerstein et al. (2017) and Morrone et al. (2022), respectively. It is evident that in this analysis this region no longer is within the Darién province of Panamá and that its lower limit is consistently straight in Dinerstein et al. (2017) and Morrone et al. (2022), but it is diagonal in this study. In the south of the Cauca River Valley, a somewhat uniform lowland region appears to correspond to a dry forest ecosystem with montane ecosystems surrounding it. This region is part of the *Cauca province* in Morrone et al. (2022) and contains the *Cauca Valley montane forests* and *Cauca Valley dry forests* in Dinerstein et al. (2017). Additionally, the *Patía Valley Dry forests* were detected corresponding exactly to Dinerstein et al. (2017) in this work.

South of the latter two regions, in Ecuador, the northmost of these has its southern limit at the Guayllabamba River from the westernmost Pichincha province and reaches the northern Mache Chindúl Mountains along the Mache River; the northernmost border of this region continues until the Patía River. It was not detected in either Dinerstein et al. (2017) or Morrone et al. (2022) and was included in the *Western Ecuador moist forests* and *Western*

Ecuador province, respectively. Alongside this region's limit in the Guayllabamba River, two distinct montane/cloud forest regions are noticeable, one spanning north slightly and another spanning south more significantly, divided by this river. Also, further south, the Coastal Cordillera in its altitudinal maxima has a small montane area turnover in the Chongón Colonche mountains. This was also not detected in either Dinerstein et al. (2017) or Morrone et al. (2022) and was included in the *Northwest Andean montane forests* and *Cauca province*, respectively. To the west of these mountains, a region spans north from Punta Ballena, southeast of the Mache Chindúl Mountains, and runs southward along the Ecuadorian coast to the southeastern Guayas Bay and ends west on the Bocapán ravine delta in northern Perú, also in the east of Puná Island. This region appears to be composed of mostly dry forests and would be equivalent to *Ecuadorian dry forests* (Dinerstein et al., 2017) and *Western Ecuador province* (Morrone et al., 2022). Dinerstein et al. (2017) classifies this region as distinct from that across the Guayas Bay, but it is found to be equivalent in this work. The coastal region this dry forest ecosystem does not encompass is the Punta Santa Elena region, likely due to the xeric and arid ecosystems and the affinities of Punta Jama, also *Ecuadorian dry forests* (Dinerstein et al., 2017). East of the Coastal Cordillera, two forest ecosystems remain, one moist forest ecosystem near the Andes and enclosed by the Coastal Cordillera, reaching the northmost Guayas Gulf and surrounded in the east and south the other deciduous forest region proximal-most to the east Coastal mountain range ranging inland from Punta Jama across the south of Mache Chindúl and toward the northeastern Guayas Gulf to the Chanchan River, continuing south along the Andes until the inland Bocapan Ravine. This region encapsulates the *Western Ecuador moist forests* and the east of the *Tumbes-Piura dry forests* (Dinerstein et al., 2017). Morrone et al. (2022) classifies this area as the *Western Ecuador province* and the *Ecuadorian province*. Dinerstein et al. (2017) also classifies the Guayaquil flooded grasslands and South American Pacific mangroves, neither of these areas were detected using the methods in this study, however it is possible that thes results may arise with the use of flora and historic data.

In Perú, five main regions were elucidated, initially, the aforementioned dry Ecuadorian forests in the Tumbes area spanning from the Bocapán ravine delta south to the Tumbes National Reserve. Then, the also aforementioned Ecuadorian deciduous forests in the inland area from the Tumbes National Reserve to the Chira River. However, south of these, a transitional region of dry forests spans a narrow band from the Zorritos Ravine to the Quiroz River. This is all considered the *Tumbes-Piura dry forests* (Dinerstein et al., 2017) and the *Ecuadorian province* (Morrone et al., 2022). This transitional area then gives way for the dry forests in Piura, spanning from the south of the aforementioned areas alongside the Andes, tapering until the Zaña River Valley this area corresponds closely to the Tumbes-Piura dry forests (Dinerstein et al., 2017) and the *Ecuadorian province* (Morrone et al., 2022), however it is thinner and more affected by bodies of water like rivers. Finally, the region most associated with the coastline is the Sechura Desert from Punta Pariña to the lower limit of this work's study area. It corresponds to the Sechura desert and Páramo province in Dinerstein et al. (2017) and Morrone et al. (2022), respectively.

A key difference between the obtained delimitation and these studies is the fragmentation of the traditionally unified *Chocó-Darién* lowland rainforest into multiple distinct forest types. This divergence from the established models reflects the power of GDM to detect fine-scale ecological variations that may be overlooked in more generalised models. Likewise, the model found that in the highlands of the Ecuadorian coast, particularly along the Coastal Cordillera in Manabí, there emerged a novel distinct region—an observation not previously identified in any existing biogeographic delimitation (Fernández, 2013; Strang, 1999). These findings suggest that current models may underestimate the ecological complexity and diversity of the region.

The implications of these results for conservation are profound. By identifying previously unrecognised ecosystems and refining biogeographic boundaries, this study highlights areas that warrant further investigation and potential protection. Should new protected areas be proposed based on these methods? The evidence suggests that integrative approaches like GDM can provide a robust foundation for conservation planning, guiding the designation of protected areas that more accurately reflect ecological realities. For instance, conservation strategies could prioritise fragmented lowland forests and distinct coastal highland ecosystems, ensuring the preservation of unique community types that are critical for regional biodiversity (Hoffmann, 2021). Likewise, the method adapted to novel changes in ecosystems, not detecting certain extinct ecosystems such as those detected near the Guayas province in Ecuador.

However, using a comprehensive approach based on a full species dataset—rather than a select subset—has important implications for conservation planning. By incorporating all species that could potentially inhabit the NW of the Tropical Andes, the analysis offers a broader, more accurate representation of biodiversity patterns. This enables the identification of regions critical to conservation that may have been overlooked in studies using limited species lists. Areas identified as having high species richness, high levels of endemism, or significant community turnover may warrant priority for protection, as they are likely to contain vulnerable or rare species that are critical to maintaining ecological integrity. This comprehensive approach increases the likelihood that conservation efforts will address biodiversity needs more fully, ensuring that protected areas encompass both species-rich hotspots and unique ecosystems that contribute to overall ecosystem health. Such methods could reshape how protected areas are proposed, moving beyond traditional boundaries and considering the full spectrum of species and ecological processes. By using more complete datasets and integrative metrics, conservation strategies can better account for the complexities of biodiversity, offering more effective and targeted solutions for long-term conservation success in the NW of the Tropical Andes.

CONCLUSIONS

In conclusion, this study successfully obtained range maps for all 1,093 species of reptiles and amphibians, providing a comprehensive dataset for analysing the spatial distribution patterns of these species within the region. By examining SR, CWE, and GDM, it was possible to uncover complex biogeographical patterns and gain valuable insights into the ecological dynamics of the study area. This research represents the first comprehensive biogeographic delimitation of entire groups in the NW of the Tropical Andes, offering a whole-group perspective that contrasts with previous subset-based approaches such as those proposed by Dinerstein et al. (2017) or Morrone et al. (2022) and has notable areas of discrepancy and similarity. The results from this approach also revealed distinct biogeographic boundary refinements, highlighting the finer-scale ecological nuances that were not captured in earlier models and that are of enormous ecological, social, and political importance.

While the findings from this study contribute significantly to this understanding of the region's biogeography, it is likely that an even more integrative approach, incorporating a broader spectrum of taxa such as all tetrapods, fauna, and potentially even fungi and flora, could further refine these biogeographic classifications. Implementing such a comprehensive delimitation would allow for a more holistic understanding of the region's ecological complexity and contribute to the development of more effective conservation strategies.

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