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RESEARCH ARTICLE

Revealing hidden patterns in the potential distribution of *Leposternon polystegum* (Duméril, 1851) (Amphisbaenia, Amphisbaenidae) using fuzzy logic modeling

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Abstract

Leposternon polystegum is a fossorial reptile endemic to Brazil, distributed across several biomes. However, the environmental and spatial factors that shape its distribution remain poorly understood. Species distribution models provide useful insights into how different environmental gradients influence the occurrence of subterranean organisms. In this study, we applied fuzzy logic-based favorability models to identify the main environmental and spatial drivers of *L. polystegum* distribution. We compared the known distribution of the species with climatic, topographic, hydrographic, and spatial predictors to evaluate their relative influence on environmental suitability. The most favorable areas for the species' presence were concentrated in northeastern Brazil, particularly in semiarid regions with moderate elevation, stable humidity, and proximity to large rivers. The models showed good discrimination performance and revealed that temperature and precipitation gradients, along with spatial structure, affect the species' distribution strongly. Variation partitioning analysis further quantified the relative contribution of environmental and spatial components, confirming that both drivers play a significant role in explaining the occurrence patterns. These results indicate that both current environmental conditions and historical constraints may have influenced *L. polystegum*'s range. This approach provides a valuable tool for future studies, incorporating soil properties and serving to guide conservation strategies focused on fossorial biodiversity in South America.

Highlights

- Fuzzy logic-based favorability models effectively mitigate sampling biases and spatial uncertainties, providing a robust framework for mapping elusive and data-poor subterranean vertebrates.
- Variation partitioning revealed that environmental and spatial components jointly explain the distribution of *Leposternon polystegum*, highlighting the relative influence of contemporary climate and spatial constraints.
- Environmental suitability for fossorial reptiles is structured along continuous gradients of soil moisture and thermal stability, which act as physiological filters across heterogeneous Neotropical landscapes.
- The potential distribution of *Leposternon polystegum* transcends discrete biome boundaries, revealing high environmental favorability across transition zones between the Amazon, Cerrado, and Caatinga.
- Contemporary spatial patterns suggest the influence of historical geomorphological dynamics and dispersal constraints on the environmental favorability of South American open formations.

Keywords

Biogeography, biomes, distributional patterns, favorability model, Neotropical region, worm lizard

Introduction

One of the most significant challenges of modern biogeography is understanding the distribution patterns and ecological drivers of fossorial organisms, mainly amphisbaenians (Schröder 2008; Oliveira et al. 2025). Due to their subterranean lifestyle, these taxa are characterized by low detectability and often patchy sampling records, which limit field-based information and may produce biased distribution estimates (Sillero et al. 2014; Cruz-Arroyave et al. 2024). Identifying these environmental drivers is essential for understanding ecological connectivity and species distribution across heterogeneous landscapes. In Neotropical regions, environmental transitions between forested and open formations create complex mosaics of climatic and edaphic conditions that may strongly influence the distribution and population connectivity of fossorial organisms (Barbosa et al. 2010; Peterson and Soberón 2012; Sousa-Guedes et al. 2020).

To address the uncertainties inherent in presence-only data and irregular sampling, fuzzy logic-based favorability models have emerged as a robust alternative (Real et al. 2006; Romero et al. 2019). Unlike traditional probability-based models, favorability function allows for a direct comparison between different areas regardless of the species' prevalence. This approach provides a more nuanced interpretation of environmental suitability, particularly for species whose realized niche may be underrepresented in biological collections (Real et al. 2006; Hortal et al. 2008; Acevedo et al. 2012). By applying fuzzy logic it is possible to distinguish between environmentally restrictive areas and regions where the absence of records may primarily reflect sampling bias, thereby improving the interpretation of ecological factors influencing species distribution (Zadeh 1965; Real et al. 2006; Hortal et al. 2008).

A prime example of such a challenging study system is *Leposternon polystegum*, a fossorial amphisbaenian reptile endemic to Brazil. Amphisbaenians are specialized subterranean squamates characterized by elongated bodies, reduced visual systems, and strong associations with edaphic and microclimatic conditions (Gans 1971; Fraga et al. 2022). Despite its broad occurrence across diverse biomes, including the Amazon, Atlantic Forest, Caatinga, and Cerrado, the specific environmental and spatial factors shaping the distribution of *L. polystegum* remain poorly understood (Gans 1971; Ribeiro 2010).

In amphisbaenians, environmental factors such as temperature, precipitation, and soil properties influence ecological and physiological aspects directly, including activity cycles (Closel and Kohlsdorf 2012), morphology (Fraga et al. 2022), and thermoregulation (Taylor et al. 2020). These factors also affect the group's biology indirectly by shaping the availability of subterranean prey (Al-Sadoon et al. 2016). For *L. polystegum*, Amorim et al. (2019) documented a diet composed mainly of edaphic invertebrates whose presence is strongly tied to soil moisture and climatic stability. This highlights the importance of considering environmental variables including temperature, precipitation, soil characteristics, and proximity to water bodies when modeling the potential distribution of amphisbaenid species.

In this context, species distribution modeling acts as a strategic tool for evaluating how these variables influence occurrence (Guisan and Zimmermann 2000; Peterson and Soberón 2012). However, for poorly sampled fossorial species, uncertainties related to data scarcity and graded environmental boundaries often persist. Traditional models based on rigid suitability limits tend to oversimplify this complexity, potentially underestimating ecologically relevant areas. By applying the favorability function established by Real et al. (2006), we move beyond these limitations to provide a more consistent assessment of environmental suitability that is independent of species prevalence (Real et al. 2017).

Accordingly, this study adopts an explanatory framework using fuzzy logic favorability models to identify the main climatic, hydrographic, spatial, and topographic drivers of *L. polystegum* distribution. We hypothesize that the distribution of this fossorial reptile is not constrained by strict biome boundaries, but rather by a combination of environmental and spatial factors associated with soil properties and climatic stability across the Amazon, Atlantic Forest, Caatinga, and Cerrado transitions. Using variation partitioning procedures, our aim is to clarify the relative contribution of these drivers and provide a broader biogeographical understanding of how environmental gradients shape the distribution of fossorial amphisbaenians in the Neotropics.

Material and methods

Occurrence data and study area

The geographic coordinates of specimen collection localities were obtained from multiple complementary sources, including digital biodiversity databases and specialized literature. A total of 452 records of *L. polystegum* preserved in biological collections were compiled from the GBIF (Global Biodiversity Information Facility; https://doi.org/10.15468/39omei, accessed via GBIF.org on October 27, 2024), supplemented with nine records from the speciesLink platform (specieslink.net/search; accessed on October 30, 2024), comprising specimens from three biological collections: MZUFBA-CH (Museum of Natural History of Bahia), US-Animalia (NMNH Extant Specimen and Observation Records), and NHM-London-ZOO (Zoological Collection). An additional 41 records were obtained from the specialized literature (Suppl. material 1).

The currently known distribution of *L. polystegum* is mainly concentrated in the northeastern region of Brazil, with additional occurrences in adjacent areas of the North and Central-West regions, including the states of Alagoas, Bahia (type locality), Ceará, Maranhão, Pará, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, Sergipe, and Tocantins (Suppl. material 1). These records encompass a wide range of environmental conditions across four Brazilian biomes: Amazon, Atlantic Forest, Caatinga, and Cerrado

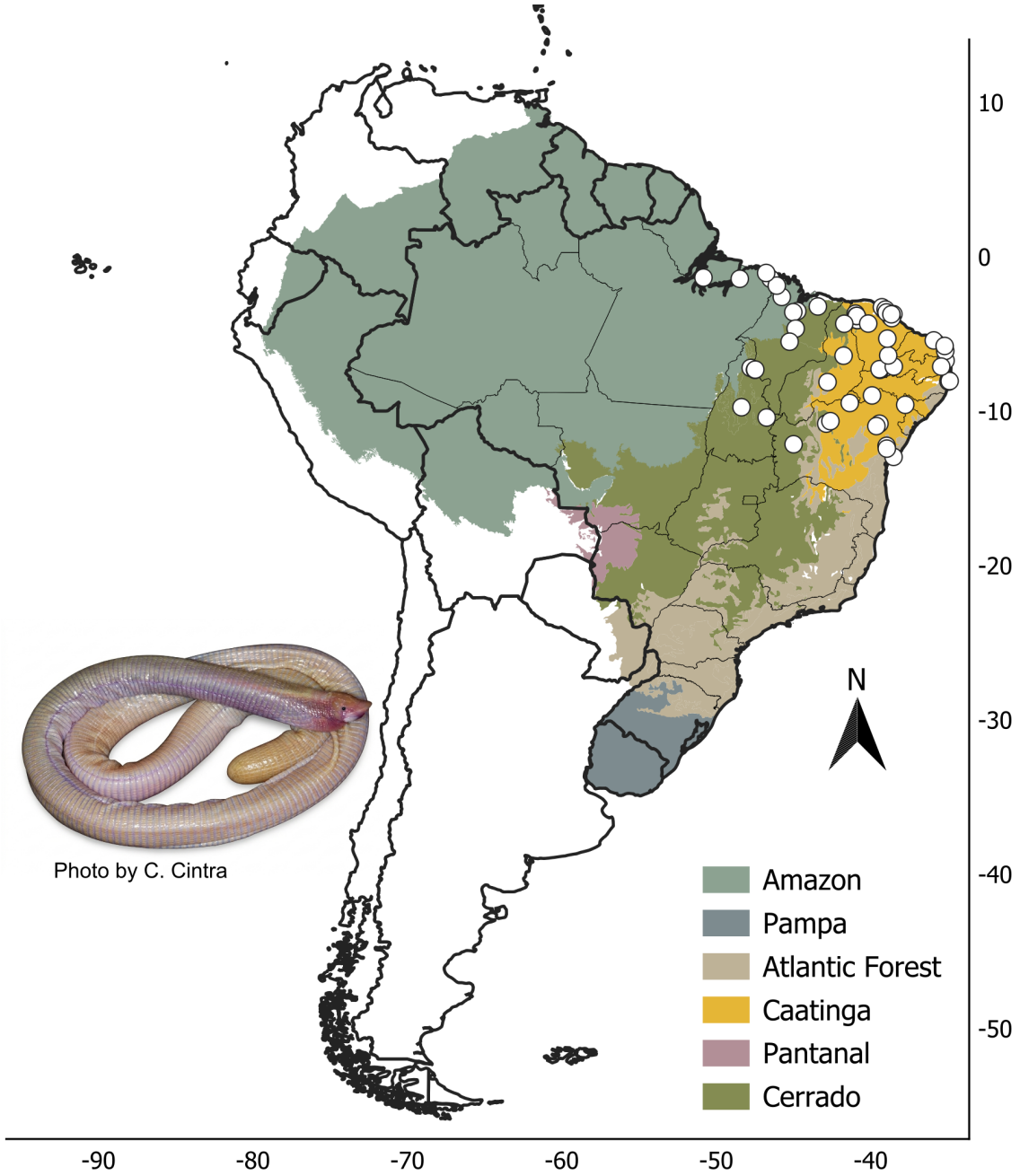

Figure 1. Map depicting the main biomes of Brazil, providing the environmental and biogeographical context for the distribution of *Leposternon polystegum* (adapted from Olson et al. 2001). White circles represent the empirical distribution of *L. polystegum* based on occurrence records. These markers are used for illustrative purposes and are independent of the hexagonal units used in the analysis.

(Fig. 1) (Perez and Ribeiro 2008; Tavares and Ribeiro 2014; Eleutério et al. 2023; Guedes et al. 2023).

To adequately capture the full range of environmental conditions potentially suitable for the species, the modelling extent was defined at the scale of South America. This broader spatial extent allows the inclusion of environmentally analogous areas beyond the currently known occurrences, thereby avoiding artificial truncation of the environmental space and improving the robustness of model predictions. This approach is particularly important for species with incomplete sampling and potentially underestimated distributions, as it enables a more realistic representation of the species' fundamental niche and reduces biases associated with geographically restricted calibration areas (Soberón 2007; Hortal et al. 2008).

White circles represent the empirical distribution of *L. polystegum* based on occurrence records. These markers are used for illustrative purposes and are independent of the hexagonal units used in the analyses.

Based on the occurrence points, a grid of regular hexagons with a spatial resolution of 6.1 km was created in QGIS 3.44 (QGIS Development Team 2025), where the resolution corresponds to the apothem of each hexagonal cell (i.e., the distance from the center to the midpoint of a side), totaling 181,221 hexagons. Hexagons containing

confirmed records of the species were classified as presence (1), whereas hexagons without records were treated as pseudo-absences (background), acknowledging that true absences cannot be guaranteed for fossorial species with low detectability and uneven sampling effort. Subsequent maps were also produced in QGIS 3.44.

Variables and variable selection

To model the distribution of *L. polystegum*, we compiled 33 predictors representing climatic, hydrographic, topographic, and spatial factors (Table 1). Climatic variables were obtained from CHELSA datasets (Karger et al. 2017) and ENVIREM variables (Title and Bemmels 2018), including standard bioclimatic descriptors as well as temperature- and water-related indices. Hydrographic variables were derived from HydroSHEDS datasets (https://www.hydrosheds.org/page/hydrorivers), whereas topographic variables were based on digital elevation models from Danielson and Gesch (2011). Spatial predictors were generated in QGIS using centroid geometry tools, with values assigned according to the latitude and longitude of grid centroids (WGS84).

All environmental variables were standardized to match the spatial resolution of the hexagonal grid (6.1 km). Continuous raster layers were resampled using bilinear interpolation to ensure consistency among predictors. To explicitly account for spatial structure, we derived a spatial predictor using a polynomial trend surface analysis (TSA) (Legendre and Legendre 1998), incorporating linear, quadratic, and cubic terms of latitude (La) and longitude (Lo) as well as their interactions (Lo, Lo^2, Lo^3, La, La^2, La^3, LaLo, La^2Lo, $LaLo^2$). This spatial component represents broad-scale geographic structure potentially associated

Table 1. Factors and variables used for modeling *Leposternon polystegum* distribution.

Factor	Code	Variable
Climatic (Bioclim)	Bio1[a]	Annual mean temperature (°C)
	Bio2[a]	Mean diurnal range (°C)
	Bio3[a]	Isothermality (%)
	Bio4[a]	Temperature seasonality
	Bio5[a]	Max temperature of warmest month (°C)
	Bio6[a]	Min temperature of coldest month (°C)
	Bio7[a]	Temperature annual range (°C)
	Bio8[a]	Mean temperature of wettest quarter (°C)
	Bio9[a]	Mean temperature of driest quarter (°C)
	Bio10[a]	Mean temperature of warmest month (°C)
	Bio11[a]	Mean temperature of coldest month (°C)
	Bio12[a]	Annual precipitation (mm)
	Bio13[a]	Precipitation of wettest month (mm)
	Bio14[a]	Precipitation of driest month (mm)
	Bio15[a]	Precipitation seasonality
	Bio16[a]	Precipitation of wettest quarter (mm)
	Bio17[a]	Precipitation of driest quarter (mm)
	Bio18[a]	Precipitation of warmest quarter (mm)
	Bio19[a]	Precipitation of coldest quarter (mm)
Climatic – Temperature	**GDD0[b]**	Growing degree days above 0 °C
	GDD5[b]	Growing degree days above 5 °C
Climatic – Water	ETP_Annual[b]	Annual potential evapotranspiration (mm)
	ETP_Season[b]	Seasonality of evapotranspiration
	ClimMoistu[b]	Climatic moisture index
Hydrographic	Sum_River[c]	Total number of nearby rivers
	Sum_BigRiv[c]	Total number of nearby large rivers
	Dist_BigRi[c]	Distance to nearest large river (m)
	Dist_AllRi[c]	Distance to nearest watercourse (m)
Spatial	**TSA[d]**	Spatial logit from a trend surface analysis
Topographic	**Altitude_mean[e]**	Mean altitude (m)
	OriNS_mean[e]	North–South orientation of terrain
	OriEW_mean[e]	East–West orientation of terrain
	Roughness[e]	Terrain roughness

Variables shown in bold correspond to the predictors retained in the final modelling procedure.
Sources of variables:
[a]Karger et al. (2017); [b]Title and Bemmels (2018); [c]HydroSHEDS (https://www.hydrosheds.org/page/hydrorivers); [d]Variables derived in QGIS using centroid geometry tools; values assigned based on the latitude and longitude of grid centroids (WGS84); and [e]Danielson and Gesch (2011).

with historical processes, unmeasured ecological factors, or uneven spatial distribution of occurrence records. Although the trend surface analysis (TSA) does not directly remove spatial autocorrelation from occurrence data, it allows the explicit incorporation of broad-scale spatial trends into the models, helping to distinguish environmentally driven patterns from geographically structured variation (Legendre 1993; Barbosa et al. 2010).

To ensure a robust selection of predictors, we followed a five-step protocol: (1) an initial set of 33 variables was selected based on theoretical relevance; (2) variables were filtered using pairwise Spearman correlation analysis ($|r| > 0.7$) to remove redundant pairs; (3) Variance Inflation Factor (VIF) analysis was applied to the remaining variables to mitigate multicollinearity (VIF > 10); (4) the False Discovery Rate (FDR) was used to control for Type I errors by adjusting p-values from individual explanatory assessments (Benjamini and Hochberg 1995), where the statistical significance of each variable was determined using Rao's score test; and (5) a multivariate stepwise logistic regression was performed using the multGLM function (Barbosa et al. 2013).

To avoid over-parameterization, the step 5 was first applied to each explanatory factor separately (climatic, hydrographic, spatial, and topographic). Only variables that remained significant within these factor-specific models were then included in the final integrated model through a recalibration procedure (Romero et al. 2016). This hierarchical approach, which incorporates a spatial component to account for broad-scale trends (Coelho et al. 2018), provides a robust framework for interpreting species–environment relationships across the environmental gradients of South America (Carvalho et al. 2025; Guerrero et al. 2025).

Variation partitioning

To evaluate the relative contribution of predictor groups, we performed a variation partitioning analysis (Borcard et al. 1992; Muñoz et al. 2005) using the varpart function in the vegan R package. Predictors were grouped into four sets: climatic, hydrographic, topographic, and spatial.

This analysis partitioned the explained variation into: (i) a purely environmental component (climatic + hydrographic + topographic), (ii) a spatially structured environmental component, and (iii) a purely spatial component. This approach provides an explanatory framework to disentangle environmental and spatial drivers of species distribution patterns.

Modelling and evaluation

Unlike conventional probabilistic approaches, favorability-based modeling estimates the degree to which environmental conditions favor a species independently of its prevalence (Real et al. 2006). Within a fuzzy logic framework, species distributions are represented as continuous gradients of environmental suitability, which is particularly relevant for fossorial taxa with low detectability, such as *L. polystegum*. However, the favorability function does not directly eliminate spatial autocorrelation in occurrence data. Instead, it reduces the influence of species prevalence and improves the interpretation of environmental suitability under conditions of uneven sampling effort (Real et al. 2006; Acevedo and Real 2012).

Models were fitted using multivariate logistic regression based on a presence–absence matrix, implemented in the fuzzySim R package (Barbosa 2015). Model parameters (β coefficients) were estimated by maximum likelihood using an iterative gradient-based optimization algorithm.

The favorability function (F) was calculated from the probability (P) obtained in the logistic models as:

$$F = [P/(1-P)]/\,[(n_1/n_0) + (P/(1-P))]$$

where P is the predicted probability of occurrence, n_1 is the number of presences, and n_0 is the number of absences (Real et al. 2006; Acevedo and Real 2012).

Model construction followed a forward–backward stepwise procedure based on the significance (p-value), excluding variables that did not significantly improve model fit ($p > 0.05$) to obtain the most parsimonious model.

Model performance was evaluated using the modEvA package (Barbosa et al. 2013). Discriminatory capacity was assessed using the Area Under the Receiver Operating Characteristic curve (AUC; Hanley and McNeil 1982). Classification performance was evaluated using sensitivity, specificity (Liu et al. 2009), and the Correct Classification Rate (CCR), based on the threshold that maximizes the True Skill Statistic (TSS) (Allouche et al. 2006). The relative importance of predictors was assessed using Wald statistics (Wald 1943). All analyses were conducted in R (R Core Team 2025). A detailed description of the modeling workflow is provided in Suppl. material 2.

Results

Modeling for environmental and spatial factors

A total of 502 occurrence records of *L. polystegum* were compiled, corresponding to 327 hexagonal cells with confirmed presence (Fig. 1). Following the variable-selection procedures described in the Methods, eleven predictors were retained from the initial set of thirty-three variables (Table 1), including climatic, hydrographic, topographic, and spatial components. A detailed summary of the excluded variables and the selection process is provided in Suppl. material 3.

Partial multivariate models were fitted for each explanatory factor, and the retained predictors were subsequently incorporated into the final logistic model for species occurrence (Table 2). The final combined model showed high performance, with an Area Under the Curve (AUC) of 0.825 and a total explained deviance of 76.8%.

Table 2. Coefficients (β) and Wald statistics for predictors included in the combined logistic model for *Leposternon polystegum*.

Factor	Variable	β (Estimate)	Std. Error	Wald	*p*-value	Exp(B)
Climatic	Bio3[(9)]	0.0244	0.0379	0.415	0.519	1.0247
	Bio5[(8)]	-0.1852	0.1076	2.963	0.085	0.831
	Bio6[(7)]	0.1555	0.1771	0.771	0.38	1.1682
	GDD0[(11)]	-0.00005	0.00005	1.045	0.307	0.9999
	Bio8[(6)]	0.6237	0.1719	13.171	< 0.001	1.8658
	Bio18[(10)]	0.0017	0.0018	0.813	0.367	1.0017
Hydrographic	Sum_BigRiv[(3)]	0.00008	0.00004	4.768	0.029	1.0001
	Dist_BigRi[(2)]	-0.000003	0.000001	4.982	0.026	0.9999
Spatial	TSA[(1)]	0.931	0.1754	28.162	< 0.001	2.5371
Topographic	Altitude_mean[(5)]	0.001	0.0016	0.405	0.525	1.001
	OriNS_mean[(4)]	0.0103	0.0052	4.019	0.045	1.0104
—	Intercept	-10.8992	6.6894	2.655	0.103	< 0.0001

The order in which variables were entered into the model is indicated by superscript numbers. The sign of the regression coefficient indicates the direction of the effect: (+) when an increase in the variable is associated with a higher probability of occurrence, and (−) when it is associated with a lower probability. Wald values and corresponding *p*-values refer to the combined multivariate logistic model and indicate the relative weight of each predictor and statistical significance. Variables included in the model are: Bio3 (Isothermality, %); Bio5 (Maximum temperature of the warmest month, °C); Bio6 (Minimum temperature of the coldest month, °C); Bio8 (Mean temperature of the wettest quarter, °C); Bio18 (Precipitation of the warmest quarter, mm); GDD0 (Growing degree days above 0 °C); TSA (spatial trend surface); Dist_BigRi (Distance to the nearest large river, m); Sum_BigRiv (Total number of nearby large rivers); Altitude_mean (Mean altitude, m); and OriNS_mean (North–south terrain orientation).

Variation partitioning analysis (Fig. 2) indicated that the explanatory variables jointly accounted for 54.821% of the total variation in the distribution of *L. polystegum*, whereas the unexplained fraction represented 45.172%. Among the pure fractions, spatial variables explained the largest proportion of variation (29.878%), followed by climatic variables (22.869%). Topographic and hydrographic predictors contributed comparatively smaller unique fractions, accounting for 1.272% and 0.782% of the explained variation, respectively. Shared fractions among predictor groups were negligible, with only a minor overlap detected between hydrographic and topographic components (0.020%).

Although all partial models (Fig. 3: A–Topographic; B–Hydrographic; C–Climatic; D–Spatial) incorporated relevant environmental information, most predictions were ecologically unrealistic (Fig. 3A–C), as the indicated areas were unlikely to be suitable for fossorial reptiles. Among the evaluated models, the one based on the spatial predictor (Fig. 3D) produced the most ecologically plausible pattern.

In the final global multivariate logistic model (Table 2), several predictors showed statistically significant contributions to species occurrence. Among the retained climatic variables, Bio3, Bio6, Bio8, and Bio18 showed positive effects, whereas Bio5 and GDD0 showed negative effects. For hydrographic predictors, the total number of nearby large rivers (Sum_BigRiv) had a positive effect, while distance to large rivers (Dist_BigRi) had a negative effect. Within the set of topographic predictors, mean altitude (Altitude_mean) and north–south terrain relief orientation (OriNS_mean) also had positive effects on species occurrence.

Model performance and predictions

The models showed a substantial reduction in deviance from the null model (from 1.473 to residual values between 1.026 and 1.027). AIC values ranged from 1.023 to 1.033, reflecting differences in model parsimony among the competing partial and combined models rather than absolute goodness of fit. Consequently, models with lower AIC values were considered more parsimonious, effectively balancing explanatory power and model complexity. Overall, these results indicate that the selected predictors adequately explain the distribution of *L. polystegum* across the analyzed environmental and spatial gradients. Predicted occurrence probabilities reached values close to 0.9 in the most favorable areas, reinforcing the model's capacity to clearly discriminate between regions of high and low environmental suitability.

Among the variables included in the final model, the spatial trend TSA showed the highest positive coefficient (+0.931) and the highest Wald value (28.162), indicating that broad-scale spatial structure contributed substantially to the observed distribution pattern. Interpreting this coefficient as an odds ratio (Exp(B) = 2.537), the odds of occurrence increased by approximately 153.7% for each additional unit in the spatial trend. This spatial component may reflect a combination of historical processes, dispersal limitations, and geographically uneven sampling effort not fully captured by the environmental predictors.

On the other hand, the distance to the nearest large river (Dist_BigRi) showed a negative coefficient (-3.316×10^{-6}; $p = 0.026$), indicating that the probability of species

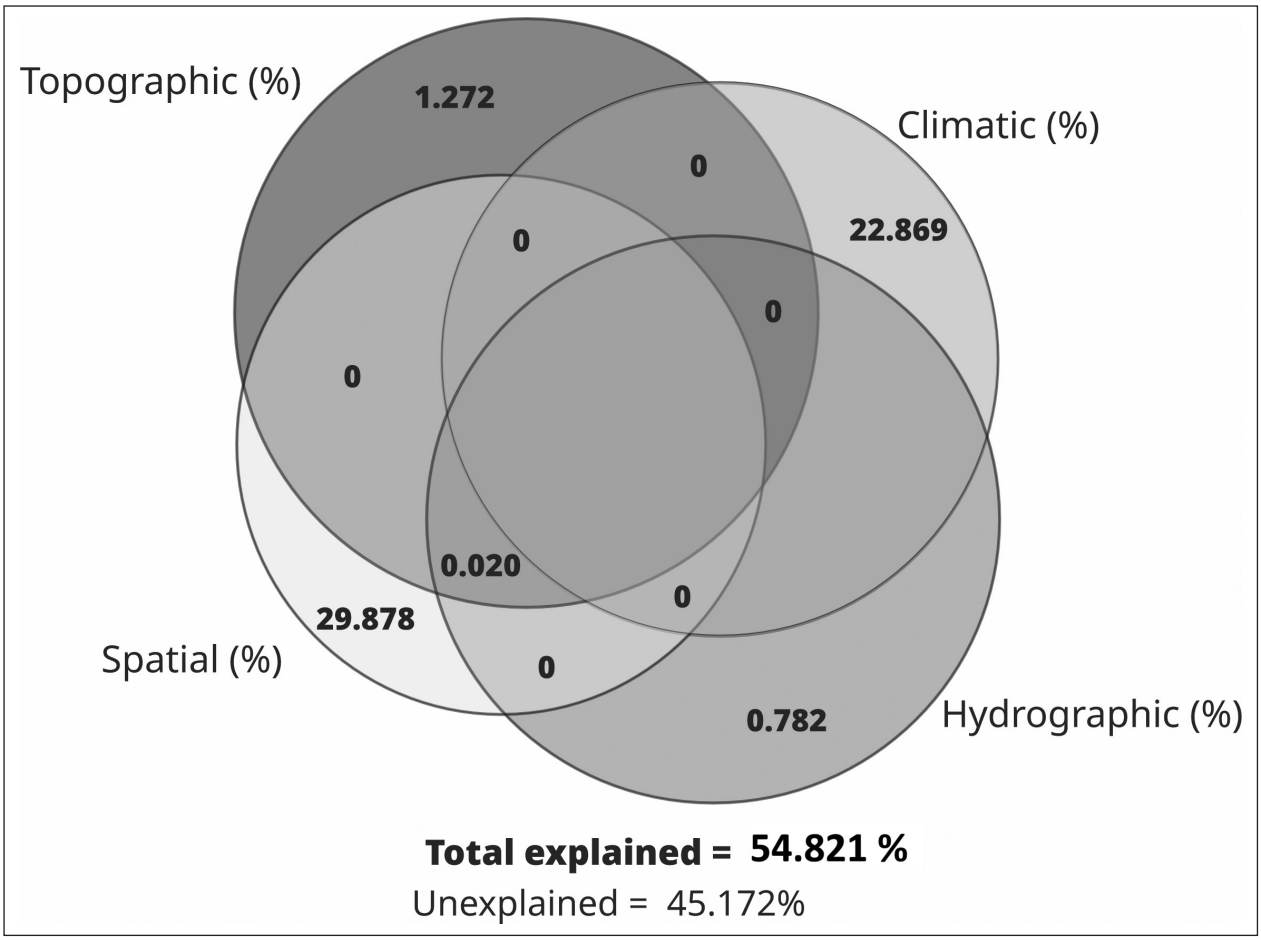

Figure 2. Venn diagram representing variation partitioning of the *Leposternon polystegum* favorability model. Bold numbers indicate the percentage of variation explained by each pure or shared fraction of the model. Values inside non-overlapping regions represent pure contributions of each predictor group, whereas values in overlapping regions represent shared contributions among groups. The total explained variation was 54.821%, and the unexplained fraction was 45.172%.

occurrence decreases as the distance to major rivers increases. This contributes to a continuous ecological gradient determining broad-scale suitability for *L. polystegum*.

From the perspective of model evaluation, sensitivity–specificity trade-offs were analyzed using probability-based thresholds. With a threshold of 0.01, the model achieved high specificity (98.9%) but relatively low sensitivity (35.0%). However, spatial predictions were interpreted using continuous favorability values rather than binary classifications. Because favorability functions are independent of species prevalence, no fixed threshold was applied to the favorability maps (Fig. 3). Consequently, occurrence records remained spatially associated with regions of high environmental favorability even though sensitivity values were lower under probability-based threshold evaluation.

Favorable areas

The distribution of *L. polystegum* is associated with regions of moderate to high altitude, proximity to large rivers with constant humidity, stable climatic conditions characterized by hot, humid summers, and mild winters. It also exhibits a strong spatial structure, possibly resulting from historical constraints and limited dispersal across the landscape. Areas of highest predicted suitability were concentrated mainly in northeastern Brazil and, consistent with known occurrence records of the species, included coastal regions (Fig. 4).

Discussion

Our results reinforce the importance of integrating fuzzy logic-based methods into biogeographical analyses of poorly sampled and cryptic taxa, particularly for understanding both distributional patterns and their underlying ecological drivers. Fossorial organisms are inherently difficult to detect and are typically underrepresented in biodiversity datasets, leading to substantial uncertainty in distributional inferences. In this context, favorability modeling provides a robust alternative to traditional probabilistic approaches. By adopting a favorability value of F = 0.5 as a neutral classification threshold, mathematically equivalent to a probability value equal to species prevalence, occurrence probabilities can be interpreted relative to random expectation. This framework distinguishes areas according to the degree to which they are favored by environmental

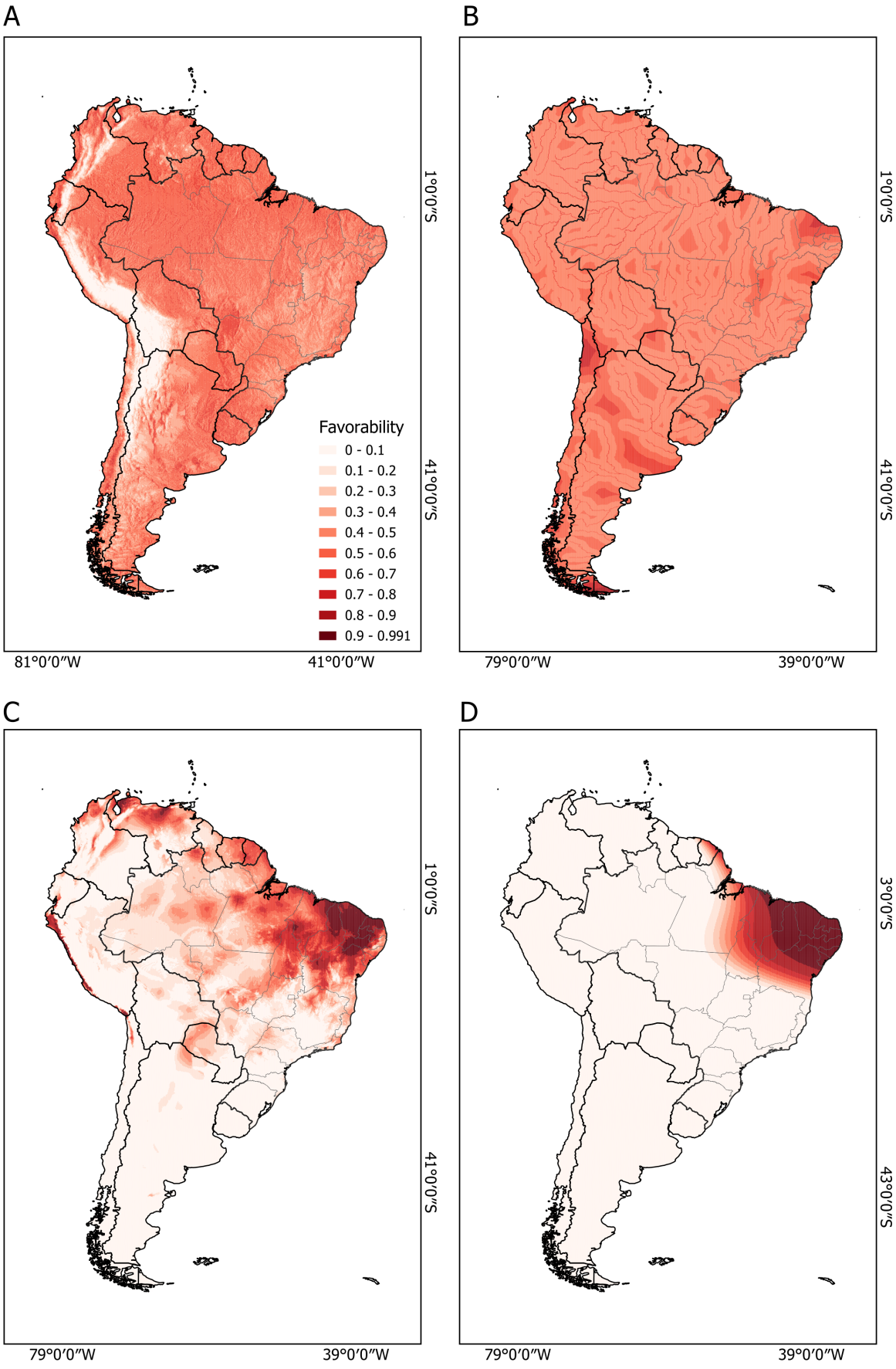

Figure 3. Environmental favorability models categorized by factor: **A.** Topographic; **B.** Hydrographic; **C.** Climatic; and **D.** Spatial. Darker red areas indicate higher values, while lighter shades represent lower favorability. Maps are based on partial models fitted separately for each explanatory factor.

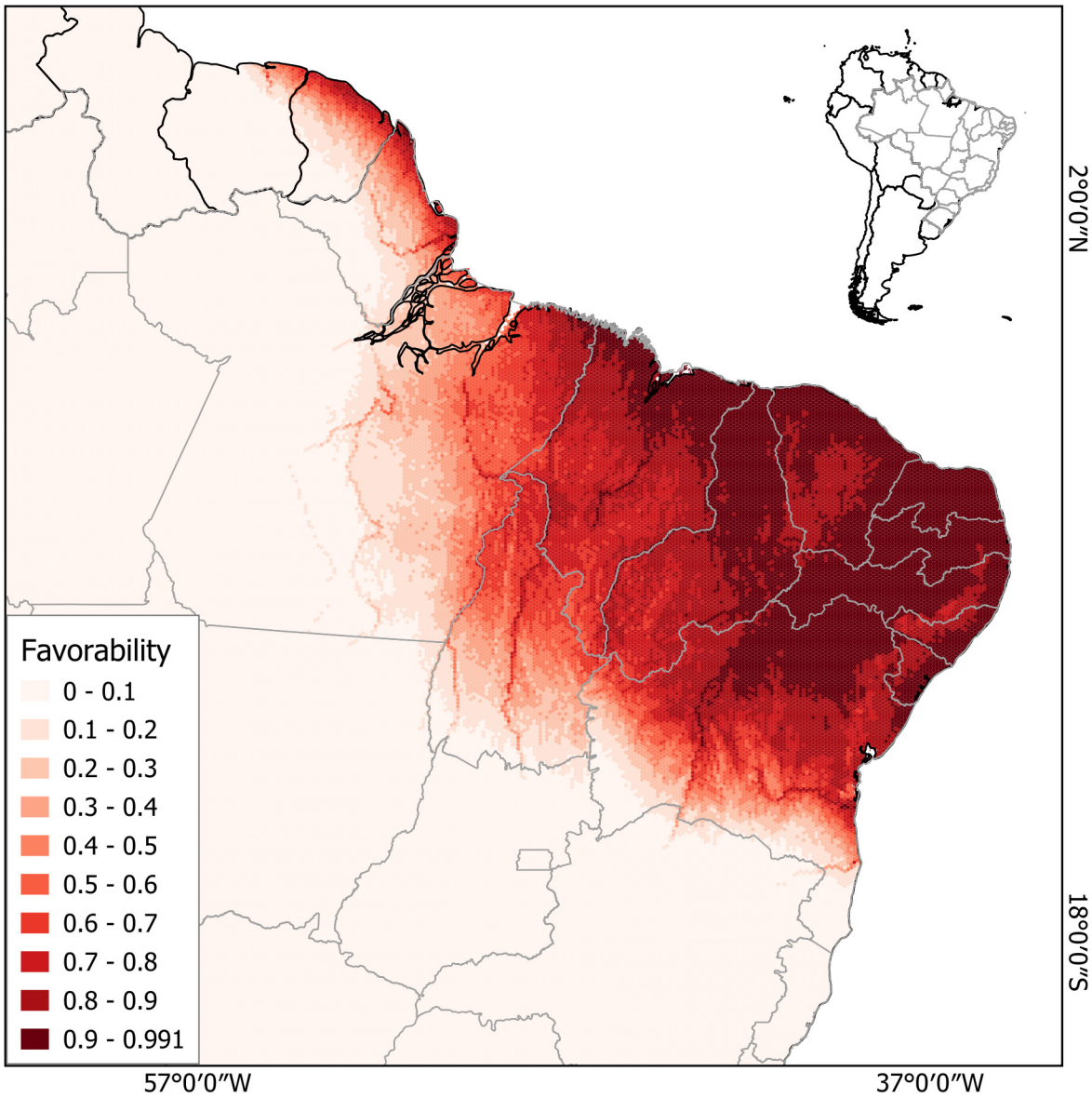

Figure 4. Potential distribution map of *Leposternon polystegum*. The map illustrates favorability values derived from the fuzzy logic model based on climatic, hydrographic, spatial, and topographic predictors. Values range from 0 (low favorability; light pink) to 0.991 (high favorability; dark red), with darker shades indicating higher environmental favorability, particularly concentrated in semiarid regions of northeastern Brazil.

and spatial conditions, regardless of the low prevalence and sampling biases typical of fossorial taxa (Real et al. 2006; Acevedo and Real 2012; Cruz-Arroyave et al. 2024). This is particularly relevant for taxa whose realized distributions are likely to be underestimated due to methodological constraints and sampling biases (Soberón 2007; Hortal et al. 2008; Cruz-Arroyave et al. 2024; Abecassis et al. 2026). Long-term comparisons of species distribution models have further demonstrated that predicted ranges can vary substantially depending on data availability, temporal context, and modeling approach (Guerrero et al. 2025).

The high performance of the final model indicates that the selected predictors effectively captured key ecological gradients influencing the occurrence of *L. polystegum*. Model selection was supported by the lowest AIC values and significant reductions in Deviance, indicating a parsimonious combination of predictors. Variation partitioning revealed that spatial and climatic components accounted for the largest pure fractions of explained variation, whereas topographic and hydrographic predictors contributed comparatively smaller fractions. Shared fractions among predictor groups were negligible, suggesting limited overlap among the evaluated components. Together, these results reinforce the importance of environmental gradients and spatial structure acting simultaneously to shape species distributions, a pattern widely reported in large-scale biogeographical studies (Borcard et al. 1992; Barbosa et al. 2010).

Our findings demonstrate that environmental suitability is structured along continuous gradients that transcend formal biome boundaries, particularly across transition zones between the Amazon, Atlantic Forest, Cerrado, and Caatinga. This pattern supports the hypothesis that

distributional limits in fossorial taxa are not strictly constrained by surface-defined ecoregions. Instead, soil properties and microenvironmental stability likely buffer the effects of macroclimatic variability. Recent studies have emphasized the importance of edaphic factors in shaping the distribution and diversity of fossorial squamates, highlighting how soil structure, moisture, and temperature interact to define suitable habitats (Fraga et al. 2022; Chen et al. 2025). Consequently, ecological boundaries may be diffuse and not necessarily aligned with aboveground patterns, reinforcing the concept of "hidden biogeography" (Civantos et al. 2003).

Climatic predictors related to temperature and precipitation regimes emerged as major drivers of environmental suitability, indicating that hydric and thermal stability are essential conditions for fossorial organisms. These findings are consistent with the physiological constraints documented for amphisbaenians, which show strong sensitivity to fluctuations in temperature and humidity due to their limited thermoregulatory capacity (Weber et al. 1981; Abe and Johansen 1987). Additionally, the negative relationship with extreme temperature conditions supports the hypothesis that fossorial reptiles avoid thermal extremes, since soil environments buffer, but do not completely eliminate, temperature variability (Closel and Kohlsdorf 2012; Taylor et al. 2020).

Hydrographic variables also contributed substantially to environmental suitability, particularly proximity to water bodies. Riparian environments and floodplains provide friable, moisture-retentive soils that facilitate burrowing, gas exchange, and locomotion, all essential for fossorial lifestyles (Dorgan 2015; Hohl et al. 2017). These environments also tend to support higher densities of edaphic invertebrates, which constitute the primary food source for many amphisbaenians (Al-Sadoon et al. 2016; Amorim et al. 2019). Together, these factors reinforce the importance of integrating hydrographic and edaphic variables when modeling the distribution of fossorial taxa.

Topographic variables revealed context-dependent effects, suggesting that intermediate elevations may provide optimal conditions by balancing drainage and moisture retention. This pattern is consistent with studies indicating that soil structure and aeration are critical for fossorial organisms, as both waterlogging and excessive desiccation can impose physiological constraints (Lavelle et al. 1997; Fraga et al. 2022). Overall, these results reinforce the idea that habitat suitability in fossorial species emerges from the interaction of multiple environmental dimensions rather than isolated factors.

Beyond environmental drivers, the strong spatial component detected in the models suggests that distribution patterns are also influenced by broad-scale spatial and historical processes. This structure likely reflects the combined influence of past climatic fluctuations, geomorphological dynamics, dispersal barriers, and geographically uneven sampling effort not fully captured by the environmental predictors. Similar patterns have been reported for other Neotropical fossorial and open-area squamates, in which landscape dynamics and environmental heterogeneity contributed to lineage diversification and spatial structuring across South American dry-diagonal regions (Nogueira et al. 2011; Werneck 2011; Graboski et al. 2022). Even in environmentally suitable areas, such processes may limit colonization and contribute to the patchy distribution patterns commonly observed in fossorial taxa (Barbosa et al. 2010; Romero et al. 2016).

Within this broader biogeographical framework, *L. polystegum* serves as a model for understanding how fossorial organisms respond to environmental gradients in heterogeneous landscapes. Its distribution across the South American diagonal of open formations reflects the interaction between climatic stability, soil properties, and spatial constraints rather than strict biome boundaries. The continuity of environmentally favorable areas across transition zones between the Amazon, Cerrado, Caatinga and Atlantic Forest suggests that these regions may have functioned as connectivity corridors for fossorial taxa under past climatic conditions. This supports the view that fossorial biodiversity is structured by a combination of ecological filtering and historical processes operating across multiple spatial scales.

Overall, fuzzy logic and favorability modelling provide a powerful framework for representing species distributions as continuous gradients of environmental suitability. By decoupling favorability from species prevalence, this approach reduces biases associated with uneven sampling and enhances the interpretation of distributional patterns (Real et al. 2006; Acevedo and Real 2012). As demonstrated here, such methods are particularly valuable for advancing the biogeography of data-poor taxa, offering new insights into hidden biodiversity and supporting the identification of priority areas for research and conservation in the Neotropics.

Conclusion

This study demonstrates that the distribution of *L. polystegum* is shaped by the interaction of climatic, hydrographic, and spatial factors, highlighting the importance of environmental gradients and broad-scale spatial structure in fossorial taxa. By applying a fuzzy logic favorability framework, our results provide new insights into the biogeography of subterranean reptiles across South American transition regions.

More broadly, this study reinforces the usefulness of favorability-based approaches for investigating the distribution of poorly sampled organisms, contributing to a better understanding of hidden biodiversity patterns and supporting future research and conservation strategies for fossorial taxa.

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Author contributions

All authors contributed to the conception and planning of the study. Data collection was performed by Jady Eleutério, and data analysis was conducted by Jady Eleutério and José C. Guerrero. The first version of the manuscript was written by Jady Eleutério, with all authors providing comments and suggestions on subsequent versions. All authors read and approved the final version of the manuscript.

Use of AI

The authors declare that artificial intelligence (AI) tools were used exclusively to assist with language revision, grammar correction, and improvement of text clarity during manuscript preparation. All scientific interpretations, analyses, results, and conclusions were developed and reviewed by the authors, who take full responsibility for the content of the manuscript

Data accessibility statement

The data used in this article for analysis are available in Suppl. material 1, where references are also provided for records obtained from the literature when these publications are not already included in the reference list.

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Supplementary materials

Supplementary material 1

Distribution records of *Leposternon polystegum* (.xlsx)
Link: https://doi.org/10.21425/fob.19.179470.suppl1

Supplementary material 2

Favorability modeling script (.txt)
Link: https://doi.org/10.21425/fob.19.179470.suppl2

Supplementary material 3

Selection and exclusion steps of the environmental, topographic, hydrographic, climatic and spatial variables used in the favorability models of *Leposternon polystegum* (.docx)
Link: https://doi.org/10.21425/fob.19.179470.suppl3