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Snake functional traits are more influenced by microhabitat than by environmental gradients in the Upper Paraguay River Basin

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ABSTRACT

Understanding the mechanisms that shape species distributions and community structure is essential for biodiversity conservation. In this study, we investigate the functional diversity of snake species in the Upper Paraguay River Basin (UPRB), addressing four key questions: (1) Do environmental characteristics of the UPRB influence snake species distribution? (2) Do snake functional traits explain species' occurrence in specific communities? (3) How do environmental characteristics influence aspects of functional diversity? and (4) How are snake traits related to microhabitat use? We analyzed occurrence and trait data for 145 snake species using multivariate approaches to assess the contributions of environmental variables and functional traits. Our results demonstrate that environmental variables significantly shape species distributions across the UPRB. In contrast, functional traits alone did not predict community composition at broader spatial scales (habitat). However, functional diversity indices responded to environmental gradients, indicating that certain aspects of trait composition vary with local habitat conditions. Additionally, traits were strongly associated with microhabitat preferences, revealing fine-scale trait–environment relationships. These findings highlight the complexity of community assembly in Neotropical snake assemblages and the value of integrating environmental gradients, functional diversity metrics, and trait-microhabitat linkages into conservation strategies.

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Introduction

Biodiversity is broadly defined as the variability among living organisms from all sources, encompassing taxonomic, phylogenetic, and functional diversity, and covering levels of biological organization ranging from ecosystems to genes (Philbin 2007; CBD 2010). Ways of exploring biodiversity include complementary facets such as taxonomic, phylogenetic, and functional diversity. While taxonomic and phylogenetic diversities concern taxa and evolutionary lineages, functional diversity reflects the variety, value, and distribution of traits that mediate species-environment interactions (Petchey and Gaston 2002; Magneville et al. 2022). Functional traits are physiological, morphological, and natural history characteristics relevant to ecological adaptation (Violle et al. 2007), and they represent the basic units through which organisms interact with their environment.

Despite significant progress in understanding taxonomic and phylogenetic diversity, knowledge of functional diversity remains relatively limited (Luza et al. 2023), which hampers our ability to comprehend how species interact with their environments and respond to environmental change (Magurran 2004). Over the past two decades, functional diversity has nevertheless gained considerable prominence in ecology, biogeography, and conservation science (Magneville et al. 2022). For reptiles, studies have shown that variation among habitats and across seasons plays a key role in structuring functional diversity (e.g. Fraga et al. 2018; Barros et al. 2022, 2025; Rincón-Aranguri et al. 2023; Díaz-Marín et al. 2025; Fiorillo et al. 2025). In this context, snakes are particularly noteworthy because they possess unique functional traits, driven by variations in morphology, physiology, and behavior (O'Shea 2018), highlighting the relevance of incorporating their functional diversity into conservation strategies (Wan and Wei 2025).

Snake functional traits such as size, microhabitat, color, and diet enable them to exploit a range of ecological niches, making them essential to ecosystem dynamics (Shine and Bonnet 2000). However, there is a knowledge gap regarding snake functional diversity, mainly due to their secretive habits and the inherent

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challenges of detecting and sampling snakes in the field (Titley et al. 2017). As a result, relatively few studies have explored snake functional diversity, especially in Brazil, limiting our understanding of how traits influence their ecological roles and responses to environmental variables (e.g. Fraga et al. 2018; Cabral et al. 2022, 2024).

Environmental variables are known to influence multiple aspects of snake diversity, including species richness, composition, and community structure (Piatti et al. 2019; Fitschen-Brown et al. 2021; Cabral et al. 2022). As ectothermic reptiles, snakes are strongly affected by environmental conditions that shape their physiology, activity patterns, and distributions (Zimmerman and Tracy 1989; Clusella-Trullas et al. 2011; Moura et al. 2017; Jesus et al. 2023). Vegetation structure and habitat complexity, for instance, play a critical role in determining resource availability and microhabitat conditions (Duchesne et al. 2022). In tropical forest regions with moderate temperatures, arboreal snake species tend to be more diverse than in hotter, more open environments (Oliveira and Scheffers 2019). These habitat associations are closely linked to morphological traits: arboreal snakes typically exhibit slender, laterally compressed bodies, elongated tails, and prominent eyes (Guyer and Donnelly 1990; Pizzatto et al. 2007), whereas fossorial species are generally characterized by smaller body sizes, reduced tails, inconspicuous eyes, and specialized scale structures adapted for digging (Navas et al. 2004; Cyriac and Kodandaramaiah 2018). Soil characteristics, which often covary alongside climatic conditions, further influence habitat suitability by shaping microhabitat features relevant to snake occurrence (Feldman and Meiri 2014; Scheffers et al. 2017).

Environmentally heterogeneous and disturbance-driven landscapes provide valuable opportunities to examine how functional traits mediate species' responses to ecological filters and shape community structure (García-Llamas et al. 2019; Barros et al. 2022; Dayrell et al. 2024). One such region is the Upper Paraguay River Basin (UPRB) in central South America, home to the world's largest wetland, the Pantanal. Despite its ecological importance, the UPRB remains poorly studied (Neves et al. 2020; Pletsch et al. 2021) and has been increasingly impacted by human activities, including recurrent fires and agricultural expansion (Pletsch et al. 2021; Berlinck et al. 2022). The basin represents a major transition zone connecting the Pantanal to seven other South American ecoregions (Dinerstein et al. 2017), resulting in a unique convergence of flora and fauna from multiple biogeographic regions (Piatti et al. 2019).

Despite this ecological convergence, overall species richness in the UPRB is lower than in surrounding regions. This pattern has been linked to the basin's relatively recent geological origin, about 2.5 million years ago (Assine et al. 2015), as well as to the ecological constraints imposed by frequent and extensive flooding (Junk et al. 2011; Piatti et al. 2019). In addition, heterogeneous flooding regimes and limited accessibility across large portions of the basin have hindered biodiversity sampling efforts (Souza et al. 2017). In such dynamic and disturbance-prone landscapes, species persistence and spatial distributions are expected to depend strongly on functional traits that mediate responses to flooding, habitat alteration, and resource availability. This is particularly relevant for snakes, as arboreal species are strongly affected by deforestation (Galán-Acedo et al. 2021), and aquatic snakes accounted for a substantial proportion of vertebrate mortality during the 2020 Pantanal fires (Pletsch et al. 2021).

Endemic species with specialized functional traits, such as large body size or narrow dietary specialization, often face elevated extinction risks (Violle et al. 2014; Pacifici et al. 2017). Consequently, approaches that focus exclusively on taxonomic diversity may overlook critical aspects of biodiversity, including functional distinctiveness and the loss of ecological strategies that underpin ecosystem functioning (Clavel et al. 2011; Brum et al. 2017; Cabral et al. 2024). Because functional traits mediate how species interact with environmental conditions and resources, linking functional diversity to environmental gradients provides key insights into the ecological processes that organize communities and influence species' capacity to persist under natural and anthropogenic disturbances. In snakes, functional traits are tightly associated with fitness, habitat use, and physiological performance (Lillywhite 2014), and their high ecological plasticity makes them particularly informative models for trait-based analyses (Shine and Bonnet 2000).

To address these knowledge gaps and inform conservation planning, this study assesses how environmental gradients drive the structure of snake communities in the Upper Paraguay River Basin, focusing on species composition, functional trait distributions, and multiple dimensions of functional diversity. We hypothesize that environmental gradients in the UPRB play a central role in structuring snake communities by shaping species composition and functional trait distributions. We predict that variation in species composition will be associated with environmental heterogeneity, reflecting the action of broad-scale ecological filters. Furthermore, we hypothesize that functional traits mediate species-environment relationships across spatial scales, such

that traits are nonrandomly associated with environmental conditions and microhabitat use. Finally, we predict that different components of functional diversity will respond independently to environmental variation, reflecting distinct underlying ecological processes.

Material and methods

Study area

The Upper Paraguay River Basin is situated in the center of South America, spanning approximately 600,000 km^2 across Brazil, Bolivia, and Paraguay (daRosa Oliveira et al. 2025; Figure 1). It comprises seven ecoregions: Pantanal, Cerrado, Humid Chaco, Dry Chaco, Southern Andean Yungas, Chiquitano Dry Forests, and a small portion of the Alto Paraná Atlantic Forests in the south (Dinerstein et al. 2017). The boundaries of the UPRB adopted here are based on Neves et al. (2020).

Occurrence data

Snake occurrence records were compiled from the literature, primarily through the Atlas of Brazilian Snakes (Nogueira et al. 2019). For species not covered by the Atlas or described after its release, additional records were obtained via Google Scholar and The Reptile Database (Uetz 2024). In total, 145 snake species were confirmed in the Upper Paraguay River Basin (UPRB) (Supplementary Table S1). We then downloaded species distribution data from the Global Assessment of Reptile Distributions (GARD; http://www.gardinitiative.org/data.html) and retained only species with at least one confirmed occurrence in the UPRB. The final dataset recorded species presence or absence across localities (Supplementary material 1). To define sampling units, we overlaid the data onto a 0.55° × 0.55° grid covering the entire basin. We chose a grid size that reflected macroecological patterns (Hurlbert and Jetz 2007), as we were interested in the entire UPRB.

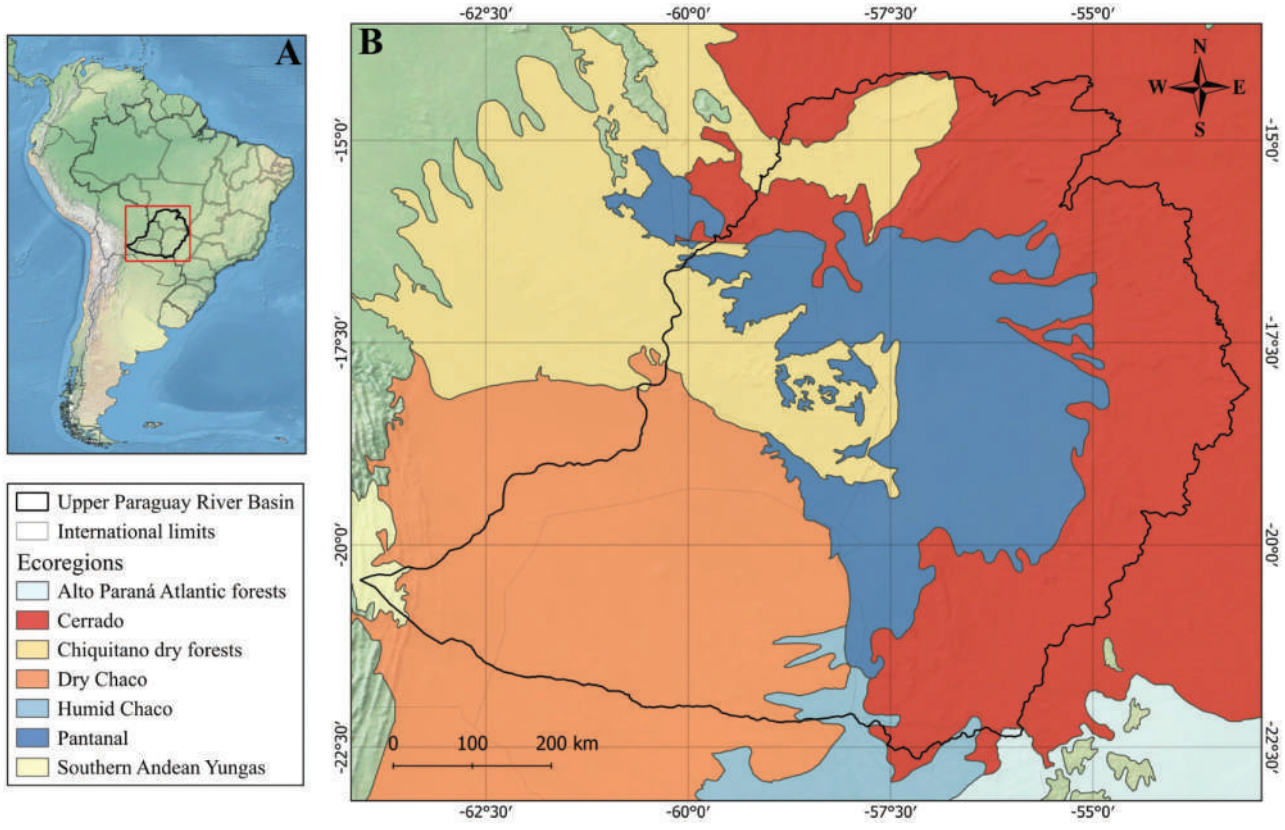

Figure 1. Ecoregions within the Upper Paraguay River Basin. (A) Location of the study area within South America. (B) Map showing the delineation of the Upper Paraguay River Basin (black outline) overlaid on distinct ecoregions. Ecoregions are color-coded, and international boundaries are indicated in gray.

Trait data

For the functional diversity analyses, a matrix of physiological, morphological, and behavioral attributes (Supplementary Table S2) of the snakes was constructed. Data were compiled primarily from the literature, with direct examination of specimens deposited in the Coleção Zoológica da Universidade Federal de Mato Grosso do Sul (ZUFMS-REP), Brazil, to fill specific data gaps when information was unavailable in published sources. Nine functional traits were gathered for all 145 species: 1 – size (maximum reported SVL, in mm); 2 – logMass (log10 body mass in grams, from Feldman et al. 2016); 3 – tail length (percentage of total body length); 4 – reproductive mode (viviparous or oviparous); 5 – diel activity (nocturnal, diurnal, or both); 6 – microhabitat use (fossorial, semifossorial, aquatic, semiaquatic, terrestrial, semiarboreal, and arboreal); 7 – eye size (classified as small, medium, or large, based on the relative width of the supralabial scale below the eye in relation to head size, following Cabral et al. 2022); 8 – predominant color pattern (brownish, ruby-black, coral pattern, reddish, and greenish), and 9 – diet (anurans, aquatic prey, arthropods, ectothermic prey, endothermic prey, generalist, serpentiform prey, or worms and snails/slugs) (Table 1; Supplementary Material 1).

Color categories were defined following the methodology proposed by Farooq and Uetz (2020, 2021). Initially, 10 colors were considered (including variations such as olive within green), but these were later simplified into five categories based on predominant coloration: brownish, ruby-black, coral pattern, reddish, and greenish. Species classified under 'coral pattern' exhibit a tricolored pattern of a light color (typically white or cream), red (or a similar hue), and black (or a dark equivalent), consistent with aposematic patterning criteria. Meanwhile, 'ruby-black' species display only red and black pigmentation, meeting the same criteria for distinct, contrasting coloration but lacking a third, lighter color.

Diet categories were defined based on prey type and specificity. Initially, 12 prey types were considered, later grouped into the following categories: 'generalist' – species consuming four or more distinct prey types; 'anurans' – frog-eating specialists; 'ectothermic prey' – species that feed on amphibians and reptiles only; 'endothermic prey' – species with diet composed on mammals and birds; 'arthropods' – species feeding primarily on insects or other arthropods; 'serpentiform prey' – species that feeds exclusively on snakes, amphisbaenians, legless lizards, and/or caecilians; 'aquatic prey' – species that feed on fish, tadpoles, and other prey strictly associated with aquatic environments; 'worms and snails/slugs' – species that feed primarily on oligochaetes and gastropods.

Environmental data

All 19 bioclimatic variables from WorldClim were gathered at a 10-arc-minute resolution (approximately 20 km; Fick and Hijmans 2017). Multicollinearity among environmental variables was assessed using Pearson correlation matrices (visualized with the 'corrplot' package) in R. Variables with pairwise correlation values higher than 0.7 were considered highly collinear and were excluded from subsequent analyses, resulting in the removal of BIO1, BIO3–BIO6, BIO10–BIO18. For each grid cell, we calculated the average value of each remaining variable (Table 2).

Forest cover was estimated in each grid cell by combining the areas of two specific land cover types: Evergreen and Deciduous Broadleaf Forests, based on data from the EarthEnv land cover dataset (www.earthenv.org/landcover; Tuanmu and Jetz 2014) (Table 2). These two categories represent nearly all forest types that provide arboreal habitat for snakes in the Upper Paraguay River Basin (Petry et al. 2012).

Flood intensity variables were derived by calculating the proportion of each grid cell classified as seasonally inundated, using floodplain data from the Global Lakes and Wetlands Database (Lehner and Döll 2004; www.worldwildlife.org/pages/global-lakes-and-wetlands-database) (Table 2). The resulting value represents the percentage of each grid cell covered by periodically flooded areas.

Table 1. Traits selection explanation.

Name	Reason
Size (mm)	Species presence/absence, metabolic rates, dispersal ability, mobility, and home range.
LogMass	Energy requirements, metabolic rate, prey size, thermoregulation, locomotion cost, and trophic interactions.
Tail length	Locomotion strategy, balance, microhabitat use, and predator evasion.
Reproductive mode	Parental investment, reproductive output, thermoregulation, and microhabitat use.
Diel activity	Exposure to predators, thermal environment, and prey availability.
Microhabitat use	Locomotion mode, refuge type, prey type, predator type.
Diet	Competition and microhabitat use.
Predominant color pattern	Crypsis and predator avoidance
Eye size	Sensory perception, prey detection, and microhabitat use.

Table 2. Description and sources of bioclimatic, vegetation, flood pulse, and edaphic variables from the Upper Paraguay River Basin used in the analysis after Pearson correlation filtering.

Variable	Name	Description	Source
Climatic	BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	WorldClim (Fick and Hijmans 2017)
	BIO7	Temperature Annual Range (BIO5-BIO6)	WorldClim (Fick and Hijmans 2017)
	BIO8	Mean Temperature of Wettest Quarter	WorldClim (Fick and Hijmans 2017)
	BIO9	Mean Temperature of Driest Quarter	WorldClim (Fick and Hijmans 2017)
	BIO19	Precipitation of Coldest Quarter	WorldClim (Fick and Hijmans 2017)
Vegetation	% Vegetation	Proportion of the grid cell covered by vegetation	EarthEnv (Tuanmu and Jetz 2014)
Hydrological	% Flood	Proportion of the grid cell that is seasonally floded	WWF (Lehner and Döll 2004)
Edaphic	% Sand	Proportion of sand particles (>0.05/0.063 mm) in the fine earth fraction	Soil Grids 250 m project (Hengl et al. 2017)
	Coarse fragments	Volumetric fraction of coarse fragments (>2 mm)	Soil Grids 250 m project (Hengl et al. 2017)

The mean value per grid cell was calculated for edaphic variables, including sand content (0–15 cm) and coarse fragments (0–15 cm), using SoilGrids 250 m 2.0 data (https://www.soilgrids.org) (Table 2).

Data analysis

The correlations among species functional traits, environmental factors, and species occurrences were examined using RLQ analysis, implemented via the 'rlq' function in the ade4 R package (Dray and Dufour 2007). This multivariate method integrates three data tables through ordination: environmental variables (Table R), species traits (Table Q), and species presence/absence across grids (Table L). Table R was subjected to a Principal Component Analysis (PCA), which accommodates datasets combining continuous and categorical variables. Table L was analyzed through Correspondence Analysis (CA). Table Q was analyzed using Hill – Smith analysis, an adaptation of PCA for mixed data types. The CA scores were then used as weighting factors for the ordination of Tables R and Q, effectively linking species-level occurrence (Table L) to their corresponding environmental conditions (Table R) and functional traits (Table Q) (Dray et al. 2014).

To investigate whether species distributions were shaped by functional traits and/or environmental variables, two permutation-based models integrating the RLQ and fourth-corner methods were implemented, following the protocol outlined by Dray et al. (2014). Model 2 tests the assumption that species distributions, when traits are fixed and independent of location, are unaffected by environmental variation. Model 4, in contrast, tests whether distributions under constant environmental conditions are independent of species traits. The significance of each model was evaluated using the 'randtest' function, while the combined analysis of both models was carried out with the 'fourthcorner2' function from the 'ade4' (Kembel et al. 2010) R package, using 49.999 permutations.

The relationship between functional traits and environmental variables was further assessed by integrating the results of the fourth-corner analysis with the first two axes from the RLQ, using the 'fourthcorner.rlq' function. The statistical significance of trait – environment associations was again evaluated using 49.999 permutations, with *p*-values adjusted using the False Discovery Rate (FDR) correction method (Dray et al. 2014).

To assess whether microhabitat influences species traits, an analysis of variance (ANOVA) was applied to continuous traits (size, logMass, and tail percentage) and chi-square tests were used for categorical traits (activity, reproduction mode, diet, eye size, and color). The attribute matrix was also used to calculate three functional diversity indices for each community: Functional richness (FRic), which is the volume of the convex hull shaping the species present in the assemblage; Functional evenness (FEve), which is the regularity of biomass-density distribution along the minimum spanning tree for the studied assemblage; and Functional dispersion (FDis), which represents the weighted deviation to center of gravity of species in the assemblage (Magneville et al. 2022). Functional distances among species were calculated using the Gower distance, which integrates mixed trait data (continuous and categorical variables). These distances were then used to perform a Principal Coordinates Analysis (PCoA), and two axes were retained, as they best captured the structure of the data, following the criteria proposed by Mouillot et al. (2012) for selecting the dimensionality of the functional space. A functional dendrogram was constructed by applying the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) agglomeration method to the two primary PCoA axes. These analyses were conducted using the 'mFD' (Magneville et al. 2022) package in R.

The influence of environmental predictors, including bioclimatic variables selected based on Pearson correlation (5 variables), as well as edaphic (SAND, COARSE), hydrological (FLOOD), and vegetation cover (VEG) (Table 2), was assessed in relation to three functional diversity indices: functional richness

(FRic), functional dispersion (FDis), and functional evenness (FEve). These relationships were explored using RLQ analysis, and the resulting patterns were visualized by plotting the indices in its PCA.

Results

The final dataset of snake traits in the UPRB includes snakes with SVL ranging from 149 mm to 4770 mm, with a mean logMass of 2.2 and tail percentages ranging from 1.8% to 38.2%. Among categorical traits, 119 (82.1%) of the 145 species are oviparous, and 26 (17.9%) are viviparous, 46.2% (67 species) are nocturnal, 38.6% (56 species) are diurnal, and 15.2% (22 species) are both. Regarding the diet, 45 species (31%) are generalist, 21 (14.5%) are specialized in serpentiform prey, 19 (13.1%) are anuran specialists, 18 (12.4%) are specialized in ectothermic prey, 16 (11%) are aquatic prey specialists, 10 (6.9%) are specialized in arthropods, seven (4.8%) are endothermic prey specialists, six (4.1%) are mollusks specialists, and the last three (2.1%) are worms specialists. Regarding eye size, 51 species (35.2%) have large eyes, 50 (34.5%) have medium-sized eyes, and 44 (30.3%) have small eyes. Finally, 68.3% (99 species) are brownish, 11% (16 species) are greenish, 8.3% (12 species) are ruby-black, 6.9% (10 species) are reddish, and 5.5% (eight species) have a coral pattern (detailed in supplementary material).

The first two axes of the RLQ analysis accounted for 78.3% of the total inertia between functional traits and environmental variables (Table 3). The R matrix showed high explanatory power (98.8% across both axes), indicating that most environmental variation was well represented. In contrast, the Q matrix explained 66.1% of trait variation, suggesting a weaker relationship between traits and the main RLQ axes.

The fourth-corner analysis did not return any significant associations after p-values adjustment. Species composition of snakes in the Upper Paraguay River Basin was significantly associated with environmental variables (model 2: $p = 0.002$), but not with functional traits (model 4: $p = 0.82$). These combined models also showed no significant trait–environment relationships ($p = 0.82$) (Figure 2).

The integration of RLQ and fourth-corner analyses revealed three significant trait–environment associations (Figure 3): fossorial microhabitat, serpentiform diet, and small eyes were positively correlated with the first RLQ environmental axis (AxR1). Trait axis

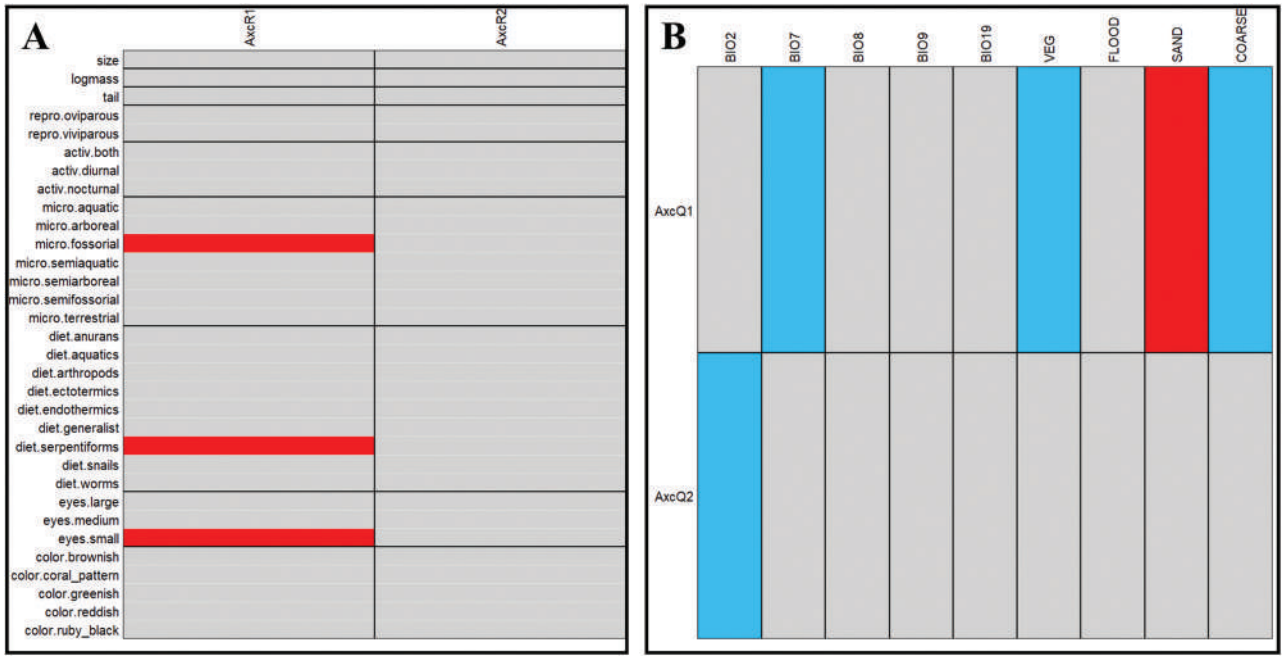

Figure 2. Results of RLQ and fourth-corner analyses testing relationships between environmental variables and biological traits at the species level in UPRB snakes. (A) Fourth-corner tests of association between the first two RLQ axes for environmental gradients (AxisR1 and AxisR2) and individual trait variables. (B) Fourth-corner tests of associations between the first two RLQ axes for trait gradients (axis Q1 and axis Q2) and individual environmental variables. Blue cells represent significant negative association, red cells represent positive association, and grey cells represent no significant association. The environmental variables are: BIO2 = mean diurnal range; BIO7 = temperature annual range; BIO8 = mean temperature of wettest quarter; BIO9 = mean temperature of driest quarter; BIO19 = precipitation of coldest quarter; veg = proportion of the grid cell covered by vegetation; FLOOD = proportion of the grid cell that is seasonally flooded; SAND = proportion of sand particles in the fine earth fraction; coarse = volumetric fraction of coarse fragments.

Table 3. Summary of RLQ results testing relationships between environmental variables and biological traits of snake species in the Upper Paraguay River Basin.

RLQAxis	Eigenvalues	Covariance	Contribution to Total Inertia (%)	corrL (Correlation between trait-based species scores and site-based environmental scores)
1	0.0386	0.1964	51.89	0.088
2	0.0196	0.14	26.39	0.058

(AxQ1) was negatively associated with BIO7, forest cover, and coarse substrates, and positively associated with sandy soils. Trait axis (AxQ2) was negatively associated with BIO2.

Among the 145 snake species in the UPRB, there are nine aquatic, seven arboreal, 24 fossorial, 11 semiaquatic, 29 semiarboreal, 10 semifossorial, and 55 terrestrial species. Microhabitat significantly influences both continuous and categorical traits. Log-transformed body mass ($f = 9.093$), tail length ($f = 31.3$), and body size ($f = 4.096$) varied across habitats ($p < 0.001$ for all). Dorsal background color ($\chi^2 = 88.56$), as did activity period ($\chi^2 = 55.88$), diet ($\chi^2 = 258.57$), and eye size ($\chi^2 = 102.39$) also differed significantly by microhabitat ($p < 0.001$).

Species richness ranged from 36 to 94 per grid cell, enabling the calculation of functional diversity indices. Functional Richness (Fric) ranged from 0.32 to 0.86 (mean = 0.72); functional dispersion (FDis) ranged from 0.59 to 0.64 (mean = 0.62) and functional evenness (FEve) ranged from 0.67 to 0.78 (mean = 0.71) (Figure 4).

In the PCA, FRic was positively associated with sandy soils and negatively associated with temperature of the wettest quarter (BIO8) and vegetation. FDis showed positive associations with floodplains, precipitation of the coldest quarter (BIO19), temperature of the driest quarter (BIO9), and negatively associated with mean diurnal range (BIO2), temperature annual range (BIO7), and coarse soil. FEve was positively associated with BIO8 and vegetation and negatively associated with sandy soils (Figure 5).

Discussion

Environmental characteristics of the UPRB and the distribution of snake species

Our results indicate that snakes in the Upper Paraguay River Basin (UPRB) are strongly influenced by environmental variables, particularly climate, soil, vegetation, and flooding regimes. In our study, while environmental factors explained species distributions, trait – environment relationships were weak in this region, at least as measured by the selected functional traits. However, snake functional traits were strongly associated with microhabitat types, which, apparently, acted as ecological filters shaping species' morphology, behavior, and physiology. For instance, fossorial species are predominantly smaller, whereas arboreal and semi-arboreal species have a higher tail percentage than species in other microhabitats. These findings show that environmental conditions determine which species are found in a given area, but the traits of those species are more closely linked to the microhabitats they use than to larger-scale environmental gradients.

Several studies have shown that environmental variables strongly influence reptile distribution (Guisan and Hofer 2003; Qian et al. 2007; Mulhall et al. 2023) and snake taxonomic and phylogenetic diversity (Moura et al. 2017; Fraga et al. 2018; Piatti et al. 2019; Whiting and Fox 2020), indicating that these animals are highly affected by environmental conditions. This pattern was also observed for snakes in the UPRB, where *model 2* of the RLQ analysis, which rejects the null hypothesis of independence, indicated that species distributions with fixed traits are influenced by environmental conditions. The strong influence of environmental conditions on snake distributions reflects squamates' narrow thermal tolerances (Huey et al. 2009; Buckley et al. 2012). Additionally, variables, such as temperature, vegetation, and soil type have long been recognized as environmental filters that shape reptile diversity (Luiselli and Capizzi 1997; Jackson et al. 2008; Moura et al. 2016).

Functional traits among different communities

In our study, functional traits did not explain snake distributions in the UPRB. These results diverge from studies in other areas, where traits such as body size and diet are closely linked to environmental gradients (Burbrink and Myers 2015; Rincón-Aranguri et al. 2023). The lack of association between traits and spatial distribution may be due to the predominance of floodplains in the UPRB, which support mostly generalist reptile species (Mesquita et al. 2015; Silva et al. 2022).

Nevertheless, we found that some specific traits aligned with environmental gradients, especially those related to soil type and temperature, as well as other environmental factors, such as vegetation cover (i.e. the first two axes of the RLQ). We found that fossorial

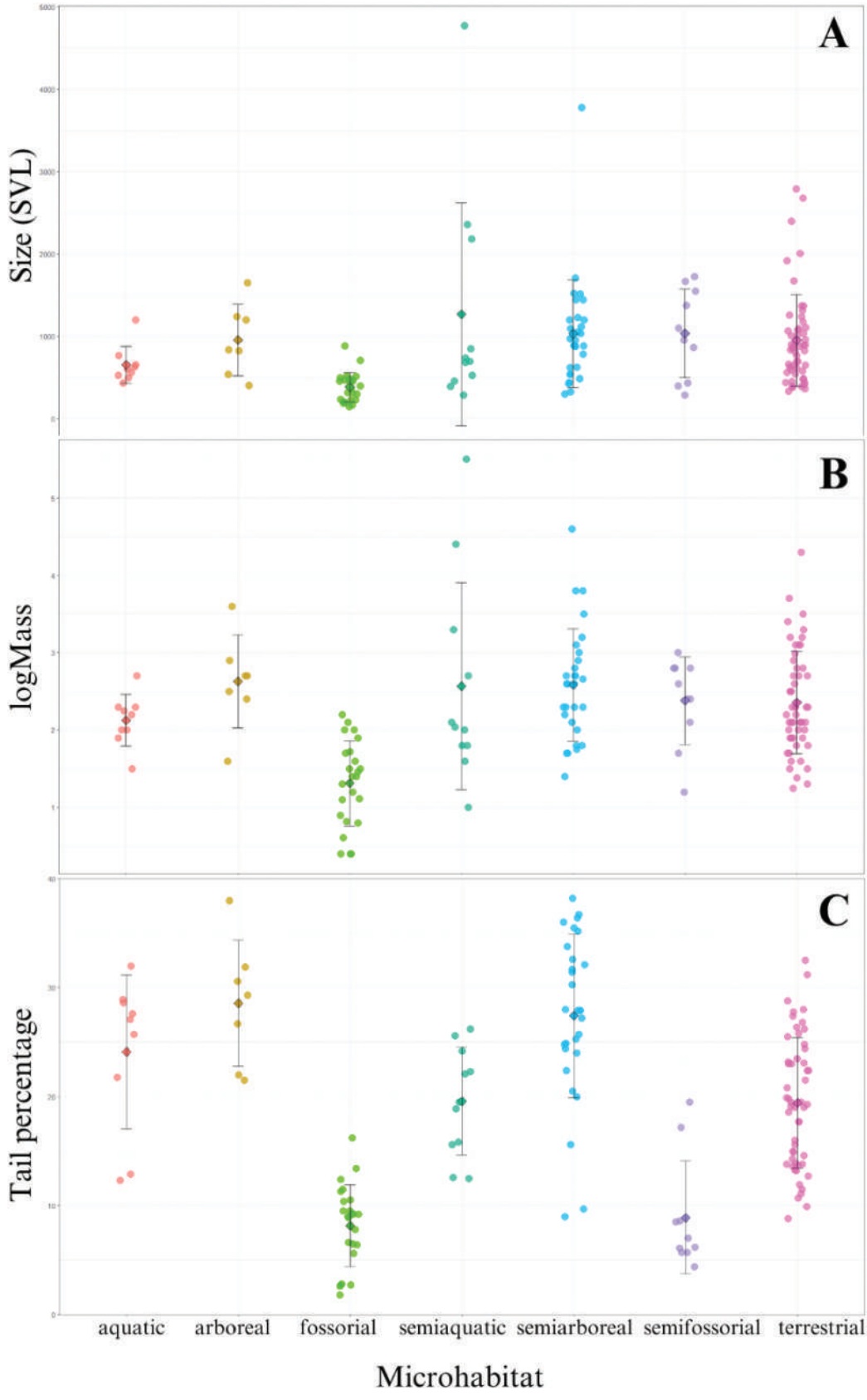

Figure 3. Comparison of size (A), logMass (B), and tail proportion (C) across different habits. Points represent species, with distinct colors for each habit. Black diamonds indicate the average of each group, and the black error bars represent the standard deviation.

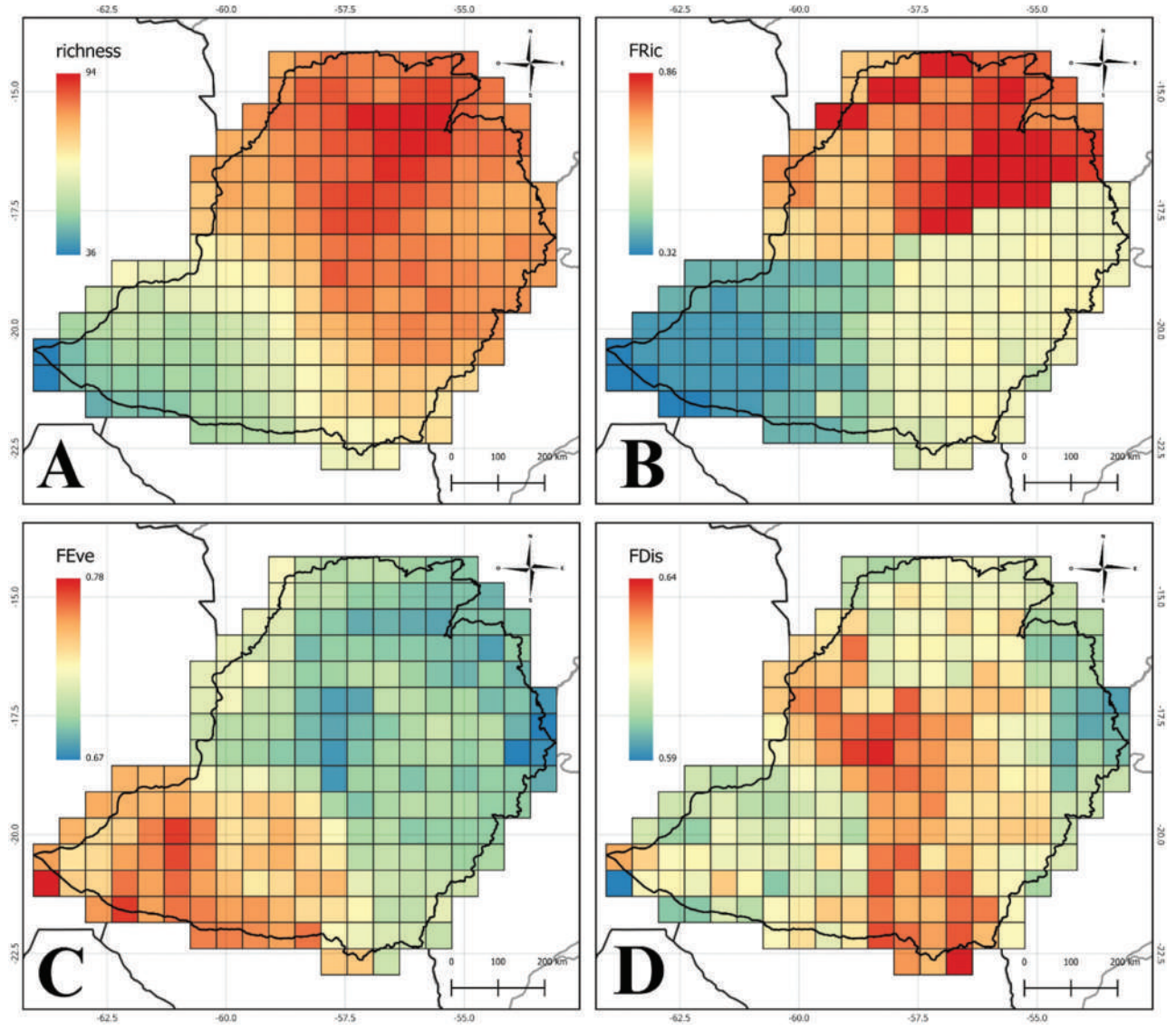

Figure 4. Spatial distribution of taxonomic and functional diversity metrics for snake species in the Upper Paraguay River Basin. (A) Snake species richness; (B) functional richness; (C) functional evenness; and (D) functional dispersion, across 0.55º grids in the UPRB. Values are represented as a gradient, with blue indicating low values and red indicating high values for each functional diversity index.

traits (e.g. small eyes, serpentiform body) are primarily associated with sandy soils, areas of low forest cover, and low-temperature variation, matching known adaptations of fossorial species to these conditions (Kinlaw 1999; Cyriac and Kodandaramaiah 2018). Soil texture (sandy vs. coarse) is especially relevant: sandy soils facilitate burrowing, whereas coarse substrates act as physical barriers for snakes. These findings agree with the findings of Cabral et al. (2022) and Chen et al. (2025), that sand predicts the richness of fossorial species. We also found that vegetation and climatic variables influence different dimensions of functional diversity (i.e. the first two axes of the RLQ), likely by mediating species coexistence through niche complementarity or redundancy (Hernández-Salinas et al. 2023; Rincón-Aranguri et al. 2023).

We found that areas with a lower temperature annual range tend to host more fossorial snake species, likely because it shapes snake distribution (Karamiani et al. 2018; Huang et al. 2025), influences phylogenetic pattern (Pyron and Burbrink 2009), and affects fossorial microhabitat selection (Terribile et al. 2018). Other studies have shown that tree cover has little effect on fossoriality (Cabral et al. 2022). Likewise, coarse soil fragments can negatively affect fossorial snakes (Cabral et al. 2022). Since sandy soils are strong indicators of fossorial snake presence, rockier soils with larger particles are expected to be negatively associated with

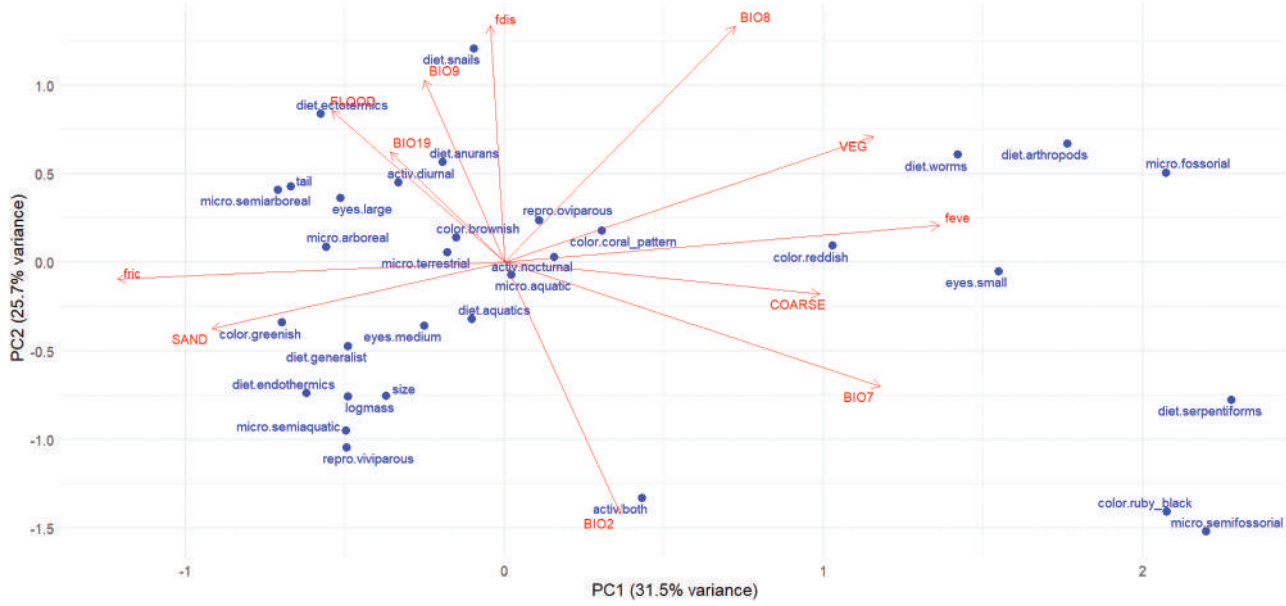

Figure 5. Principal component analysis (PCA) showing the ordination of functional traits (blue points) in relation to environmental variables and functional diversity indices (red arrows).

these species. Moreover, sand can also influence snake species richness, especially for fossorial species (Chen et al. 2025).

The relation between traits and microhabitats

Snakes in the UPRB largely conform to expected trait – microhabitat patterns, with fossorial species showing reduced eyes and tail length, and arboreal species displaying larger eyes and cryptic coloration (Pizzatto et al. 2007; Cabral et al. 2022). An exception is the presence of large semiaquatic snakes, such as *Eunectes murinus* and *Hydrodynastes gigas*. This deviation may reflect the ecological opportunities offered by the Pantanal's vast, seasonally flooded plains, where prolonged inundation, extensive suitable habitat, and abundant aquatic prey allow large semiaquatic snakes to persist and thrive, overriding general trait – microhabitat constraints observed in other environments (Strüssmann and Sazima 1993).

Traits such as body size, eye size, tail length, and coloration are significantly associated with arboreal, fossorial, aquatic, or terrestrial lifestyles, confirming that microhabitat exerts a strong selective pressure on trait evolution and community assembly (Guyer and Donnelly 1990; Banci et al. 2022). The consistency of trait – microhabitat associations reinforces the assumption that microhabitats can act as evolutionary filters (Cadle and Greene 1993; Greene 1997). Moreover, in this study, all nine traits tested showed little variance within microhabitat groups, reinforcing the role of local habitat structure in shaping snake functional traits.

Environmental characteristics of the UPRB and functional diversity

In our study, functional richness (FRic) in snakes from the UPRB is negatively associated with the temperature of the wettest quarter (BIO8) and vegetation cover and positively correlated with sandy soils. In this region, areas dominated by sandy substrates are typically less vegetated. The restriction of fossorial species, characterized by highly specialized morphological traits, to these sandy and open environments may have contributed to the observed relationships between FRic, vegetation, and soil type, as the presence of trait-specialized fossorial strategies can expand the overall functional trait space occupied by local assemblages, thereby increasing functional richness in these communities.

Functional dispersion (FDis) is positively associated with floodplain environments, precipitation during the coldest quarter, and higher temperatures in the driest quarter, while showing negative relationships with mean diurnal temperature range, annual temperature range, and coarse soils. These environmental conditions likely promote spatiotemporal heterogeneity, allowing species with contrasting functional strategies to co-occur within the same assemblages. For example, periodically flooded areas that retain aquatic habitats due to higher precipitation may allow typically aquatic species, such as *Eunectes* and *Hydrodynastes*, to persist

alongside terrestrial taxa. Given their highly specialized aquatic traits and large, often extreme body sizes, the presence of these species can substantially increase functional dispersion by expanding functional distances among co-occurring species. This illustrates how environmental heterogeneity can increase functional divergence without necessarily increasing functional richness.

In the UPRB, areas with higher vegetation cover exhibit higher functional evenness, indicating a more even distribution of functional traits among co-occurring species. Forested environments in the region appear to support assemblages in which distinct ecological strategies, such as terrestrial, arboreal, and semi-arboreal habits, are represented in more balanced proportions. In contrast, open environments dominated by sandy substrates are associated with lower functional evenness. These habitats strongly favor fossorial taxa while restricting arboreal and semi-arboreal species (Cabral et al. 2022). Such environmental filtering reduces the regularity of trait distributions, even when species richness remains high, leading to the dominance of functionally similar strategies and lower functional evenness (FEve).

Functional evenness was also positively associated with the temperature of the wettest quarter (BIO8). This pattern suggests that warmer and wetter conditions may relax environmental constraints on community assembly, allowing multiple functional strategies to coexist in more even proportions, potentially through indirect effects on habitat structure, prey availability, and microhabitat diversity during periods of peak snake activity.

Concluding remarks

Together, our findings indicate that while environmental characteristics strongly influence snake species composition and multiple dimensions of functional diversity in the UPRB, broad-scale environmental gradients do not directly structure species-level functional trait distributions. Instead, functional traits are more closely linked to microhabitat use, as evidenced by strong associations between microhabitat categories and both continuous and categorical traits. This decoupling between the drivers of species distributions and those shaping functional traits highlights the importance of spatial scale in functional biogeography. While broad environmental gradients filter which species occur in different parts of the landscape, microhabitat conditions appear to play a dominant role in shaping the functional strategies of snakes within local communities. By integrating trait-based ecology with spatial environmental data, our study demonstrates how microhabitat filtering and environmental heterogeneity jointly, but non-redundantly, can structure snake functional diversity in tropical wetlands.

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Author contributions

CRediT: **Vanessa Nocelli:** Conceptualization, Data curation, Formal analysis, Investigation, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing; **Liliana Piatti:** Conceptualization, Methodology, Validation, Writing – review & editing; **Diego José Santana:** Conceptualization, Writing – review & editing; **Simone J. Cardoso:** Formal analysis, Methodology, Validation, Visualization, Writing – review & editing; **Henrique C. Costa:** Conceptualization, Data curation, Project administration, Supervision, Validation, Visualization, Writing – review & editing.

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Data availability statement

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials.

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