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Relação das assembleias de anuros com o ambiente em ecossistemas de areia branca na Amazônia: uma abordagem multi-escala

César de Andrade Fernandes

Manaus

2026

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Aos 27 dias do mês de fevereiro do ano de 2026, às 09:h00min, por videoconferência, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: Drª. **Kelly Cristhyna Torralvo**, do Instituto de Desenvolvimento Sustentável Mamirauá – IDSM, o Dr. **Sérgio Henrique Borges**, da Universidade Federal do Amazonas – UFAM e a Drª. **Amanda Batista da Silva de Oliveira** (UFAM), sendo as suplentes a Drª. Fernanda Magalhães da Silva, do Museu Paraense Emílio Goeldi – MPEG e o Dr. Janderson Batista Rodrigues Alencar (INPA), sob a presidência do orientador, a fim de proceder a arguição pública da **DISSERTAÇÃO DE MESTRADO** de **CÉSAR DE ANDRADE FERNANDES**, intitulada: **"RELAÇÃO DAS ASSEMBLEIAS DE ANUROS COM O AMBIENTE EM ECOSSISTEMAS DE AREIA BRANCA NA AMAZÔNIA: UMA ABORDAGEM MULTI-ESCALA"**, orientado pelo Dr. Igor Luís Kaefer (UFAM) e coorientado pela Drª. Jussara Santos Dayrell.

Após a exposição, o(a) discente foi arguido oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

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Sinopse: Nesta dissertação, investigamos como gradientes ambientais e fatores espaciais influenciam a estrutura de assembleias de anuros em ecossistemas de areia branca na Amazônia Central. Avaliamos padrões de riqueza, composição e diversidade beta em parcelas distribuídas em módulos RAPELD na Reserva de Desenvolvimento Sustentável do Rio Negro. Também examinamos a influência de variáveis ambientais, como estrutura da vegetação e profundidade do lençol freático, na organização das comunidades. Por fim, analisamos a contribuição relativa de fatores ambientais e espaciais para a diferenciação das assembleias de anuros na paisagem.

Palavras-chave: diversidade beta; anuros; ecologia de comunidades; gradientes ambientais; Amazônia.

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RESUMO

As florestas de areia branca da Amazônia Central constituem ecossistemas singulares, caracterizados por solos pobres em nutrientes, forte heterogeneidade ambiental e elevada diferenciação biológica em escala regional. Embora diversos estudos tenham documentado padrões de diversidade beta elevados nesses ambientes para diferentes grupos taxonômicos, ainda são escassas as investigações voltadas à estruturação das assembleias de anuros e aos processos ecológicos subjacentes a esses padrões. Neste estudo, avaliamos como gradientes ambientais e fatores espaciais influenciam a riqueza, a composição e a diversidade beta de assembleias de anuros associadas a ecossistemas de areia branca na Reserva de Desenvolvimento Sustentável do Rio Negro, Amazonas, adotando uma abordagem multi-escala. As comunidades foram amostradas em 43 parcelas distribuídas em três módulos RAPELD (KM18, KM26 e KM50), por meio de buscas ativas visuais e auditivas realizadas durante a estação chuvosa. Foram registradas 34 espécies de anuros, pertencentes a 18 gêneros e 10 famílias, com baixa variação na riqueza entre módulos e forte heterogeneidade composicional entre parcelas. A ordenação por escalonamento multidimensional não métrico (NMDS) indicou ampla sobreposição entre os módulos. A partição da diversidade beta revelou predominância de diferenças de abundância entre parcelas, enquanto a substituição completa de espécies desempenhou papel secundário. Modelos multivariados indicaram que a composição das assembleias foi significativamente influenciada pela profundidade do lençol freático e pela estrutura da vegetação, representada pelo índice de área foliar. Análises baseadas em matrizes de distância demonstraram que tanto a dissimilaridade ambiental quanto a distância geográfica contribuem para a diferenciação das comunidades, com maior influência dos processos espaciais. Conjuntamente, os resultados indicam que a diversidade beta das assembleias de anuros em florestas de areia branca emerge da atuação integrada de filtros ambientais e processos espaciais, refletindo respostas quantitativas das espécies aos gradientes locais e à limitação de dispersão ao longo da paisagem.

ABSTRACT

White-sand forests of Central Amazonia are unique ecosystems characterized by nutrient-poor soils, strong environmental heterogeneity, and high biological differentiation at regional scales. Although several studies have documented elevated beta diversity in these environments across different taxonomic groups, investigations focusing on anuran assemblages and the ecological processes underlying these patterns remain scarce. In this study, we evaluated how environmental gradients and spatial factors influence species richness, community composition, and beta diversity of anuran assemblages associated with white-sand ecosystems in the Rio Negro Sustainable Development Reserve, Amazonas, adopting a multi-scale approach. Anuran assemblages were sampled in 43 plots distributed across three RAPELD modules using visual and auditory active searches conducted during the rainy season. A total of 31 anuran species, belonging to 18 genera and 10 families, were recorded, with low variation in species richness among modules and strong compositional heterogeneity among plots. Non-metric multidimensional scaling (NMDS) acknowledges substantial overlap among modules, with no evidence of rigid compositional compartmentalization. Beta-diversity partitioning indicated a predominance of abundance differences among plots, whereas complete species replacement played a secondary role. Multivariate models showed that assemblage composition was significantly influenced by groundwater depth and vegetation structure, represented by the leaf area index. Distance-based analyses demonstrated that both environmental dissimilarity and geographic distance contribute to community differentiation, with a stronger influence of spatial processes. Together, these results indicate that beta diversity of anuran assemblages in Amazonian white-sand forests emerges from the integrated effects of environmental filtering and spatial processes, reflecting quantitative species responses to local gradients and dispersal limitation across the landscape.

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INTRODUÇÃO GERAL

As florestas de areia branca da Amazônia Central constituem ecossistemas únicos, caracterizados por solos pobres em nutrientes, alta heterogeneidade ambiental e conjuntos biológicos que diferem marcadamente daqueles encontrados em florestas de terra firme adjacentes (Adeney et al., 2016; Capurucho et al., 2020). Essas formações estão associadas a substratos arenosos antigos (Fig. 1) e exibem fortes restrições edáficas, que influenciam diretamente a estrutura da vegetação e a organização das comunidades biológicas (Rodrigues et al., 2024).

Figure 1. Substrato arenoso característico das florestas de areia branca da Amazônia Central, associado a solos pobres em nutrientes e fisionomias vegetais contrastantes, incluindo campinas abertas e campinaranas mais densas.

Nesse contexto, observam-se fisionomias vegetais contrastantes, como campinas abertas e campinaranas mais densas, que ocorrem como manchas naturalmente fragmentadas na paisagem. Esses habitats abrigam conjuntos faunísticos e florísticos altamente especializados, frequentemente com elevados níveis de endemismo, resultando em padrões pronunciados de diferenciação biológica em escalas regionais em múltiplos grupos taxonômicos nos ecossistemas de areia branca da Amazônia (Vicentini, 2016; Stropp et al., 2011; Borges et al., 2016).

Estudos focados na herpetofauna em florestas de areia branca na Amazônia ainda são escassos (Adeney et al., 2016). A Reserva de Desenvolvimento Sustentável Rio Negro (RDS

Rio Negro), localizada no estado do Amazonas, emergiu recentemente como uma importante área para pesquisa científica. Em 2020, um guia de identificação intitulado “Rãs da RDS Rio Negro – Região da Estrada Uga-Uga” foi publicado por pesquisadores envolvidos no projeto “Monitoramento da Diversidade de Anuros e Aves para Conservação e Inclusão Científica de Comunidades Rurais”. Este guia inclui fotografias, informações sobre distribuição geográfica e modos reprodutivos de 30 espécies (Lima et al., 2020). Mais recentemente, uma nova espécie de anuro, *Scinax albertinae* (Fig. 2), associada a habitats de campina contendo bromélias, foi descrita com base em espécimes coletados no RDS Rio Negro (Ferrão et al., 2022).

Figure 2. Exemplar de Scinax albertinae registrado em habitat de campina na Reserva de Desenvolvimento Sustentável do Rio Negro, Amazônia Central. Esta espécie, descrita recentemente, está associada a ambientes de areia branca com bromélias. Foto de Rickelmy Holanda

Um estudo recente, baseado em dados de um único módulo de amostragem RAPELD, investigou a influência de variáveis ambientais na estrutura da comunidade de anuros e demonstrou que a composição de espécies ao longo de gradientes ambientais é fortemente influenciada pela estrutura da vegetação (Pereira et al., 2024). Após a instalação de dois

módulos RAPELD adicionais no RDS Rio Negro, uma expedição piloto foi realizada durante a estação chuvosa de 2023, liderada pela Dra. Albertina Lima.

Nesse contexto, ampliar o conhecimento sobre a herpetofauna associada às florestas de areia branca é essencial para a compreensão da biodiversidade desses ambientes e para orientar ações de conservação em áreas protegidas da Amazônia Central. Esta dissertação contribui para esse esforço ao investigar as assembleias de anuros em ecossistemas de areia branca dentro da Reserva de Desenvolvimento Sustentável do Rio Negro, fornecendo informações sobre a diversidade e a organização dessas comunidades em escala regional (Fig. 3).

Figure 3. Equipe de campo durante atividades de coleta de amostras de anuros na Reserva de Desenvolvimento Sustentável do Rio Negro, Amazônia Central. Foto de Rickelmy Holanda.

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Pereira E.A., Lima A.P., Magnusson W.E. & Menin M. (2024) Environmental variables shape anuran community structure in Amazonian white-sand forests. *Anais da Academia Brasileira de Ciências*, 96, e20230730.

Environmental and spatial drivers of anuran assemblage structure in Amazonian white-sand forests

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Abstract

White-sand forests of Central Amazonia are unique ecosystems characterized by nutrient-poor soils, strong environmental heterogeneity, and high biological differentiation at regional scales. Although several studies have documented elevated beta diversity in these environments across different taxonomic groups, investigations focusing on anuran assemblages and the ecological processes underlying these patterns remain scarce. In this study, we evaluated how environmental gradients and spatial factors influence species richness, community composition, and beta diversity of anuran assemblages associated with white-sand ecosystems in the Rio Negro Sustainable Development Reserve, Amazonas, adopting a multi-scale approach. Anuran assemblages were sampled in 43 plots distributed across three RAPELD modules using visual and auditory active searches conducted during the rainy season. A total of 31 anuran species, belonging to 18 genera and 10 families, were recorded, with low variation in species richness among modules and strong compositional heterogeneity among plots. Non-metric multidimensional scaling (NMDS) acknowledges substantial overlap among modules, with no evidence of rigid compositional compartmentalization. Beta-diversity partitioning indicated a predominance of abundance differences among plots, whereas complete species replacement played a secondary role. Multivariate models showed that assemblage composition was significantly influenced by groundwater depth and vegetation structure, represented by the leaf area index. Distance-based analyses demonstrated that both environmental dissimilarity and geographic distance contribute to community differentiation, with a stronger influence of spatial processes. Together, these results indicate that beta diversity of anuran assemblages in Amazonian white-sand forests emerges from the integrated effects of environmental filtering and spatial processes, reflecting quantitative species responses to local gradients and dispersal limitation across the landscape.

Keywords: Amazonia; white-sand ecosystems; anurans; beta diversity; water table depth

INTRODUCTION

Understanding how species assemblages are structured across environmental gradients remains a central challenge in community ecology. While local species richness (alpha diversity) has traditionally received considerable attention, variation in species composition among sites (beta diversity) provides deeper insights into the ecological and historical processes shaping biodiversity (Legendre et al., 2005; Gering & Crist, 2002). Beta diversity reflects how communities differentiate across space and may arise from species replacement (turnover), differences in species richness (nestedness), or quantitative variation in species abundances (Podani & Schmera, 2011). Disentangling these components is essential for identifying whether community differentiation is primarily driven by environmental filtering, spatial processes, or their interaction, which are fundamental questions to be answered in ecology (Sutherland et al., 2013).

Environmental gradients influence species distributions by imposing ecological filters related to habitat structure, resource availability, and microclimatic conditions. In contrast, spatial processes such as dispersal limitation and historical contingency may generate compositional differentiation even in the absence of strong environmental contrasts (Hubbell, 2001; Qian & Ricklefs, 2011). Because environmental and geographic distances are often correlated, assessing their independent contributions to beta diversity remains a key issue in ecological research (Peixoto et al., 2023). Empirical evidence from tropical ecosystems suggests that both niche-based mechanisms and spatial processes may operate simultaneously, with their relative importance varying according to spatial scale and taxonomic group.

In addition to niche-based mechanisms and environmental filtering, community structure may also be influenced by neutral processes, in which species are considered functionally equivalent on average and differences in composition and abundance emerge from stochastic processes associated with ecological drift, dispersal limitation, and historical contingency (Hubbell, 2001). Under this framework, local communities are viewed as probabilistic samples from a regional metacommunity, and compositional variation may arise even in the absence of strong environmental gradients. Empirical evidence across spatial scales suggests that such spatial processes can contribute substantially to beta diversity, often operating alongside environmental filters, reinforcing the need to integrate niche-based and neutral perspectives in community ecology (Qian & Ricklefs, 2011; Qian et al., 2013; Fraga et al., 2018; Peixoto et al., 2023).

Amazonian white-sand forests provide a particularly suitable system for investigating these mechanisms. These ecosystems are characterized by nutrient-poor sandy soils, pronounced environmental heterogeneity, and naturally fragmented vegetation mosaics composed mainly of open campinas and denser campinaranas (Adeney et al., 2016; Capurucho et al., 2020; Rodrigues et al., 2024). Although they typically harbor lower local richness compared to adjacent “terra firme” forests, they exhibit strong compositional differentiation at regional scales, a pattern documented for plants, birds, and invertebrates (Borges et al., 2016; Graça et al., 2017; Vicentini, 2016). However, investigations focusing on amphibian assemblages in these environments remain comparatively scarce.

Anurans are highly sensitive to environmental conditions, particularly to factors associated with moisture availability, vegetation structure, and soil characteristics (Haddad & Prado, 2005; Menin et al., 2007; Ribeiro et al., 2012). In Amazonian systems, small-scale variation in forest structure and hydrological conditions may strongly influence species occurrence and abundance (Guimaraes et al., 2021), shaping microclimatic conditions that are crucial for anurans' distribution. Groundwater depth can affect the formation and persistence of temporary water bodies used for reproduction, while vegetation structure modulates microclimatic conditions and habitat complexity. These environmental filters may structure assemblages locally, whereas dispersal limitation and spatial configuration of habitats may contribute to differentiation at broader scales.

Despite the ecological relevance of white-sand forests and the known environmental sensitivity of amphibians, it remains unclear to what extent beta diversity in these systems is primarily driven by environmental heterogeneity or by spatial processes. Moreover, few studies have simultaneously partitioned abundance-based beta diversity and evaluated the independent contributions of environmental and geographic distances in Amazonian amphibian assemblages.

To address these gaps, we employed a distance-based analytical framework integrating abundance-based beta diversity partitioning and variation partitioning approaches to disentangle the relative influence of environmental heterogeneity and spatial structure on anuran assemblages in white-sand ecosystems of Central Amazonia. Specifically, we aimed to: (i) describe patterns of species richness and compositional variation among sampling units; (ii) partition beta diversity into components associated with abundance differences and species replacement; (iii) evaluate the influence of vegetation structure, groundwater depth, soil properties, and litter depth on assemblage composition; and (iv) assess the relative contributions of environmental and geographic distances to community dissimilarity.

We hypothesized that environmental filtering, driven by vegetation structure and hydrological conditions, would significantly influence assemblage composition. Additionally, we expected that both environmental and spatial processes would contribute to beta diversity, reflecting the combined effects of local habitat heterogeneity and dispersal limitation across the landscape.

METHODS

Study area

The study was conducted in the Rio Negro Sustainable Development Reserve (RDS Rio Negro; 60°44′27″ W, 3°04′14″ S), located in the state of Amazonas, Brazil, encompassing the municipalities of Novo Airão, Iranduba, and Manacapuru (Figure 4). Established in 2008, the reserve covers approximately 103,086 hectares and is part of the Amazonas State System of Protected Areas (SEUC) and the Amazon Region Protected Areas Program (ARPA).

The regional climate is classified as humid equatorial, with consistently high temperatures and rainfall throughout the year. Long-term climatological data (1991–2020) indicate mean annual temperatures around 27 °C and annual precipitation exceeding 2,000 mm, with a wetter season typically extending from December to May and a comparatively drier period between June and November (INMET, 2022).

The reserve includes extensive white-sand ecosystems, comprising campinas and campinaranas, which are associated with highly sandy, nutrient-poor, and intensely leached soils that support structurally distinct vegetation compared to adjacent terra firme forests (Anderson, 1981; Adeney et al., 2016). These ecosystems exhibit pronounced structural heterogeneity driven by variations in microtopography and hydrological conditions, which influence soil drainage and water table depth, resulting in a fine-scale mosaic of vegetation physiognomies (Damasco et al., 2013; Adeney et al., 2016). Campinaranas encompass shrubby and forested formations with discontinuous canopies (Fine et al., 2010), whereas campinas are characterized by open vegetation with exposed sandy soils, dominated by low-stature shrubs and sparsely distributed trees (Adeney et al., 2016).

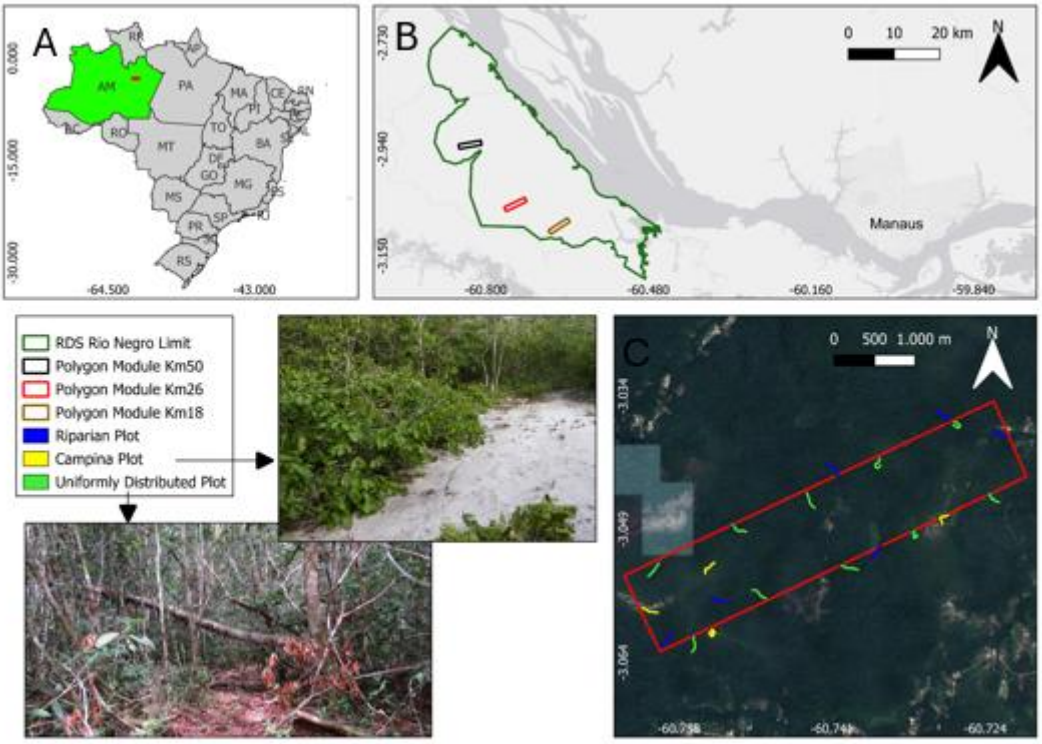

Figure 4. Study area in the Rio Negro Sustainable Development Reserve (RDS Rio Negro), Central Amazonia, Brazil. (A) shows the location of the state of Amazonas (AM) within Brazil. (B) illustrates the geographic position of the reserve in relation to the city of Manaus and major river systems. (C) presents the spatial distribution of sampling plots within a RAPELD module, including riparian, campina, and uniformly distributed plots. Photographs depict representative white-sand vegetation physiognomies (campina and campinarana) occurring within the study area.

Sampling Design

We followed the RAPELD standardized sampling protocol (Magnusson et al., 2013). Anuran assemblages were surveyed in three sampling modules (KM18, KM26, and KM50), each consisting of two parallel 5-km transects spaced 1 km apart. Standard RAPELD plots (250 m × 10 m) were established along these transects. Non-riparian plots followed contour lines to minimize internal topographic variation, whereas riparian plots were positioned along watercourses.

Each plot was subdivided into 25 consecutive 10-m segments, which were used as the basic units for recording species occurrences and relative abundances during surveys. A total of 43 plots were sampled: 13 in KM18, 16 in KM26, and 14 in KM50, encompassing riparian, campina, and non-riparian habitats.

Anuran sampling

The anuran assemblages was sampled following the standardized terrestrial herpetofauna sampling protocol in RAPELD modules (Dayrell et al. 2025), developed by PPBio to ensure spatial and temporal comparability in biodiversity studies. This protocol combines methodological standardization and operational flexibility, allowing its application in different Amazonian ecosystems and ensuring the provision of consistent and replicable data in the long term (Dayrell et al. 2025). The use of a unified method is essential to reduce variations associated with sampling effort, differences between observers, and intrinsic environmental characteristics, increasing the reliability of ecological inferences (Magnusson et al. 2013; Dayrell et al., 2025).

Sampling was carried out through active visual and auditory searching (Heyer et al. 1994; Dayrell et al. 2025), methods that complement each other and expand the ability to detect species with different behavioral patterns. Visual searching involves the systematic inspection of leaf litter, trunks, branches, temporary and urban marshes up to about 5 m in height, with the aim of locating active individuals or those in refuge. Auditory searching, in turn, was based on the identification of vocalizations emitted by individuals, which are species-specific and allow recognition even without direct observation (Menin et al. 2007; Gingras et al., 2013). The combination of these approaches is widely recommended in inventories of tropical amphibians, due to the differences in the activity and detection modes of the species.

The field campaigns were conducted at two intervals of the day, twilight (4–6 pm) and night (7–10 pm), in order to include species with different periods of activity, including those that are predominantly diurnal, twilight, and nocturnal. This temporal planning maximizes the probability of detection in the Amazon, where the vocalization, movement, and reproductive activity of anurans are strongly influenced by variations in photoperiod and microclimatic conditions (Zigler et al. 2023). Collections were carried out during the rainy season (December to March), a period of greater reproductive activity and greater detectability of Amazonian species (Menin et al. 2008; Pereira et al. 2024). In total, three independent campaigns were carried out throughout this interval, following the recommendation of Dayrell et al. (2025) to capture seasonal variations in the composition of the assemblages.

During sampling, each plot was traversed by two observers walking parallel to each other, separated by approximately 10 m and covering the segments independently. In each plot, the observers recorded all species visualized or blocked by vocalization on standardized forms,

including information on location, environmental conditions, location within the plot, and number of individuals collected.

To standardize sampling effort and minimize biases associated with detectability, the maximum record of one individual per species in each 10 million segment was reconsidered, regardless of the number of individuals observed or heard. In this way, the maximum relative abundance of each species in a plot corresponded to 25 records, equivalent to 25 sampled segments. This standardization is a fundamental element of the RAPELD method (Dayrell et al. 2025), especially relevant for small and highly detectable species, such as the genus Adenomera.

At the end of the three campaigns, the highest value of relative abundance recorded per species in each plot was selected for analysis, according to the approach used by Pereira et al. (2024) and recommended in long-term anuran monitoring protocols (Dayrell et al. 2025). This strategy aims to reduce the effect of variations in detectability and more reliably represent the potential occurrence of species throughout the reproductive season (Dayrell et al., 2021).

Environmental variables

Environmental predictors were selected based on their ecological relevance for Amazonian anurans, particularly in white-sand ecosystems where microhabitat structure and water availability are highly variable. We focused on variables related to vegetation structure, hydrological conditions, and soil characteristics, as these factors are known to influence species distribution and local abundance.

The vegetation structure variables were obtained using a portable terrestrial LiDAR remote sensing system (Light Detection and Ranging; Riegl LD90-3100VHS-FLP). LiDAR is recognized as an effective tool for characterizing the three-dimensional structure of vegetation, as it allows recording the vertical distribution of structural elements based on the time elapsed between the emission and return of laser pulses (Lefsky et al. 2002; Parker et al. 2004).

Measurements were taken during constant-speed walks along the 250-meter centerline of each plot, ensuring standardization in collection effort and comparability between sampling units. This procedure allowed for the systematic recording of canopy height, the distribution of plant elements along with the vertical profile, and the relative density of the understory. The raw data obtained by the sensor was subsequently processed using standardized scripts in the R software (R Core Team 2022), resulting in the final values used in the analyses. This processing

step included filtering the laser returns, extracting the structural metrics of interest, and organizing the data into a database compatible with subsequent ecological analyses. Fourteen vegetation structure variables were obtained by LIDAR, but it is not necessary to use all of them.

The structure of vegetation is a central element for understanding the ecology and distribution of anurans, especially in Amazonian environments where microclimatic factors and structural heterogeneity exert a strong influence on species persistence (Pereira et al., 2024). The density and complexity of vegetation determine the availability of micro-habitats along the vertical and horizontal profile, directly affecting the use of the environment by different species, whether for shelter, reproduction, vocalization, or food acquisition (Menin 2007; Pereira et al., 2024). In environments where water availability is highly variable, as frequently occurs in white sand formations, vegetation structure plays an even more critical role in creating microenvironments suitable for survival (Malagoli et al. 2013).

Given this ecological relevance, a variable related to vegetation structure and potentially associated with the local structuring of anurans was selected: the leaf area index along the vertical profile. These variable captures complementary dimensions of forest structure, reflecting both the complexity of the canopy and the vegetation density at different heights.

The depth of the water table can represent one of the most important environmental factors for the ecology and distribution of anurans, especially in white sand environments, where the availability of surface water is highly variable throughout the year (Adeney et al., 2016). Many species depend directly on the presence of temporary water bodies for reproduction and larval development, so variations in the water table level influence both the formation and persistence of these pools (Haddad and Prado 2005; Camacho-Rozo and Urbina-Cardona 2021).

The depth of the water table was monitored monthly using piezometers installed at the beginning of each plot, always positioned at points with the same altimetric level as the centerline. These piezometers allowed recording the height of the groundwater column in relation to the ground level, providing direct estimates of water availability in the subsoil and the proximity between saturated layers and the surface. Measurements were taken between January and March of 2025, a period that coincides with the highest reproductive activity of anurans in the region (Pereira et al., 2024). As a final proxy for groundwater depth, we used the highest value recorded among the three sampling campaigns. Very deep measurements, less than -2 m, were standardized to -2 m, since values beyond this limit exceed the detection

capacity of the method and represent ecologically equivalent conditions in terms of water availability for the surface stratum (Baccaro et al. 2013). A similar procedure was adopted by Baccaro et al. (2013), who also standardized excessively high depths to ensure comparability between plots and restrict the analysis to ecologically relevant hydrological variations.

Soil composition plays an important role in the ecology of anurans by indirectly influencing species distribution, microhabitat availability, and water retention dynamics. In white sand environments, where soils are highly sandy and have low water retention capacity, this influence is even more evident, as high permeability affects the formation of humid microenvironments necessary for maintaining the behavioral and physiological activities of anurans (Menin 2007; Anderson et al. 1981). Soil texture, particularly clay and silt content, modifies this relationship by increasing moisture retention capacity, conferring greater stability to the microhabitat and contributing to the persistence of species more sensitive to dehydration (Juo and Franzluebbers 2003).

Topsoil samples were collected in all plots using a standardized six-point scheme along the transect (0, 50, 100, 150, 200, and 250 m). The collection was carried out in the 0 to 10 cm layer, corresponding to the interface most directly associated with the litter layer and the microhabitat used by anurans. The samples were sent for physical and chemical analyses, including pH and clay content, with granulometric determination by sedimentation methods and chemical analyses following conventional laboratory protocols. These measurements allowed for a robust characterization of the edaphic variability between plots, providing essential information to understand how soil attributes relate to the ecological patterns observed in the assemblages.

The depth of the litter layer was measured in a standardized way along each plot, with records taken every 50 meters along the transect (0, 50, 100, 150, 200 and 250 m). At each point, a graduated ruler was inserted vertically through the litter layer until it reached the mineral soil, recording the total thickness of the accumulated layer. This procedure allows for an accurate estimate of litter depth, which is directly related to the availability of microhabitats, moisture retention, and thermal dynamics in the environment—crucial attributes for anuran ecology (Siqueira et al., 2009). From the six values obtained per plot, the average depth was calculated, which was used as a continuous environmental variable in subsequent analyses. This approach ensures that the measurement represents the internal heterogeneity of the plot, reducing the influence of point variations and allowing for robust comparison between sampling units.

These data provide a detailed overview of soil conditions in the study area and are essential for understanding how physical characteristics, such as water retention capacity, and chemical characteristics, such as pH and nutrient availability, can affect the presence, abundance, and diversity of anurans along the investigated environmental gradients.

Data analysis

Plots were used as sampling units in all analyses. Multicollinearity among environmental variables was assessed using the variance inflation factor (VIF), and variables with values greater than 10 were removed to avoid redundancies. The VIF (Variance Inflation Factor) is a widely used metric in regression analysis to quantify the degree of multicollinearity among independent variables (Park et al., 2019). The presence of multicollinearity indicates that two or more variables have a high correlation with each other, which compromises the interpretation of regression coefficients and can generate inaccurate estimates; therefore, the application of the VIF contributes to the selection of environmentally informative and statistically independent variables (Cheng et al., 2021). Multicollinearity was initially assessed among the vegetation structure variables obtained by LiDAR (Table S1); of the fourteen metrics generated, only one was selected. Next, this variable was incorporated into the set of environmental predictors, and all variables in the overall model were reassessed using the VIF (Table S2)

Species richness per plot was used as a measure of alpha diversity. Sample-based rarefaction curves were generated using the iNEXT package (Hsieh, Ma, & Chao, 2016). Abundance-based beta diversity was partitioned into similarity (S), replacement (R), and abundance difference (D) components following Podani & Schmera (2011). This procedure allows for the decomposition of beta diversity into three main components: similarity, species replacement, and difference in richness. The approach also makes it possible to derive relative measures of nestedness and variation in richness, offering a more detailed characterization of the composition patterns and structure of communities along the studied gradient (Podani and Schmera, 2011). Indices were calculated using SDRSimplex and visualized in ternary plots.

The resulting components are expressed through standardized indices, which were graphically represented in ternary diagrams, allowing visualization of relationships between beta diversity and similarity, between replacement and nestedness, and between difference and richness concordance (Podani and Schmera 2011). In the context of these analyses, richness concordance corresponds to the maximum subset of species shared between two locations that have the same richness, while richness difference expresses the sum of discrepancies between pairs of plots that do not share species. The calculation of the indices was performed using the

SDRSimplex program (Podani and Schmera 2011), and the graphical representations were produced using the SYN-TAX 2000 software (Podani 2001), following the procedures described by the authors.

The influence of environmental variables on assemblage structure was tested using multivariate generalized linear models (manyGLM), according to Warton et al. (2012), implemented in the mvabund package (Wang et al. 2017). This approach employs distributions appropriate for count data, such as Poisson or negative binomial, and takes into account the correlation between species, resulting in more realistic estimates of multispecific responses (Jupke & Schäfer, 2020). The significance of the predictors was evaluated through residual-based permutations, totaling 999 permutations, using the anova.manyglm function. The chosen model was as follows.

Composição de espécies = Área foliar ~ Profundidade do lençol freático ~ Estrutura do solo ~ Ph do Solo ~ Profundidade da serrapilheira

Histograms of species distributions (Dambros 2014) throughout the environmental gradients were generated to describe the responses of each species to the environmental variables.

To identify the factors that structure the variation in species composition between plots, two complementary analytical approaches were used, following the design proposed by Peixoto et al. (2023). The first approach consisted of applying the Mantel test, using Pearson's correlation coefficient with 999 permutations, to evaluate the correlation between matrices of taxonomic dissimilarity and geographic and environmental distances. The environmental distance matrix was calculated from differences between plots in leaf area, litter depth, groundwater depth, soil structure, and soil pH, representing continuous environmental heterogeneity across the landscape. A geographic distance matrix was calculated with the linear spatial separations between plots, obtained from the UTM coordinates of each plot. We used Mantel tests with 999 permutations to evaluate the correlation between taxonomic dissimilarity and these sets of distances, verifying whether species turnover follows environmental variations or reflects spatial autocorrelation. Next, we applied Multiple Regression on Distance Matrices (MRM) to quantify the independent contribution of each factor and distinguish the effects of spatial isolation from those associated with environmental gradients (Lichstein 2007). This approach makes it possible to determine whether the assemblage structure is driven primarily by environmental filters, related to the availability of micro-habitats, edaphic conditions and humidity, or by spatial processes limiting dispersal.

Bray–Curtis dissimilarity matrices were calculated for species composition. Environmental and geographic distance matrices were computed separately. Mantel tests (999 permutations) were used to assess correlations between compositional dissimilarity and both environmental and geographic distances. Multiple Regression on distance Matrices (MRM) was then applied to quantify their independent contributions.

All analyses were performed in R 4.4.1 using the vegan (Oksanen et al., 2013) and ecodist packages ((Goslee & Urban, 2007).

RESULTS

We recorded 31 anuran species belonging to 18 genera and 10 families across the 43 sampled plots (Table 1). Total species richness was similar among modules, with 22 species\ recorded in KM50 and 21 species in each of KM18 and KM26. At the plot level, observed richness ranged from 1 to 14 species.

Two species, *Adenomera andreae* and *Trachycephalus cunauaru*, were widely distributed, occurring in at least 75% of plots. Ten species showed intermediate occurrence frequencies (25–60% of plots), including *Allobates femoralis*, *Osteocephalus vilarsi*, and *Rhinella* aff. *proboscidea*. In contrast, nine species were recorded in fewer than 20% of plots, indicating restricted spatial distributions or low detectability.

Rarefaction and extrapolation curves showed similar patterns of species accumulation across modules, suggesting comparable sampling effort (Figure S1).

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Table 1. Anuran species recorded in the KM18, KM26, and KM50 modules of the Rio Negro Sustainable Development Reserve, and the number of plots in which each species was recorded.

Táxon	**KM18**	**KM26**	**KM50**
Aromobatidae			
Allobates femoralis (Boulenger, 1884)	11	5	8
Allobates paleovarzensis Lima, Caldwell, Biavati & Montanarin, 2010	5	1	5
Bufonidae			
Rhinella marina (Linnaeus, 1758)	6	4	7
Rhinella aff. *proboscidea*	8	4	8
Centrolenidae			
Vitreorana ritae (Lutz, 1952)	1	1	1

Táxon	KM18	KM26	KM50
Craugastoridae			
Pristimantis campinarana Mônico, Ferrão, Moravec, Fouquet & Lima, 2023	11	7	4
Oreobates quixensis Jiménez de la Espada, 1872	1		
Eleutherodactylidae			
Phyzelaphryne miriamae Heyer, 1977	9	8	11
Phyzelaphryne sp.		1	
Hylidae			
Boana boans (Linnaeus, 1758)	1		2
Boana lanciformis (Cope, 1871)		1	
Dendropsophus marmoratus (Laurenti, 1768)			
Dendropsophus sarayacuensis (Shreve, 1935)	2	1	0
Osteocephalus taurinus Steindachner, 1862	2	4	5
Osteocephalus vilarsi (Melin, 1941)	5	10	8
Trachycephalus cunauaru Gordo et al., 2013	11	12	13
Scinax aff. *cruentomma*			2
Scinax albertinae Ferrão, Moravec, Ferreira, Moraes & Hanken, 2022		4	2
Leptodactylidae			
Adenomera albarena Martins, Mônico, Mendonça, Dantas, Souza, Hanken, Lima & Ferrão, 2024	10	5	8
Adenomera andreae (Müller, 1923)	11	13	12
Adenomera hylaedactyla (Cope, 1868)	1	2	7
Leptodactylus pentadactylus (Laurenti, 1768)	5	4	5
Leptodactylus mystaceus (Spix, 1824)	1	2	2
Leptodactylus petersii (Steindachner, 1864)	1	0	0
Leptodactylus rhodomystax Boulenger, 1884	2	4	7
Leptodactylus riveroi Heyer & Pyburn, 1983	0	2	3

Táxon	KM18	KM26	KM50
Microhylidae			
Chiasmocleis hudsoni Parker, 1940	3	1	6
Synapturanus sp.	1	1	
Phyllomedusidae			
Callimedusa tomopterna (Cope, 1868)			
Phyllomedusa aff. *vaillantii*	2	3	2
Pipidae			
Pipa pipa (Linnaeus, 1758)			2

Rarefaction and extrapolation curves showed similar patterns of species accumulation across modules, suggesting comparable sampling effort (Figure S1).

Non-metric multidimensional scaling (NMDS) did not reveal clear segregation in species composition among modules KM18, KM26, and KM50. Plots largely overlapped in ordination space, indicating the absence of strong compositional compartmentalization at the module scale (Figure 5).

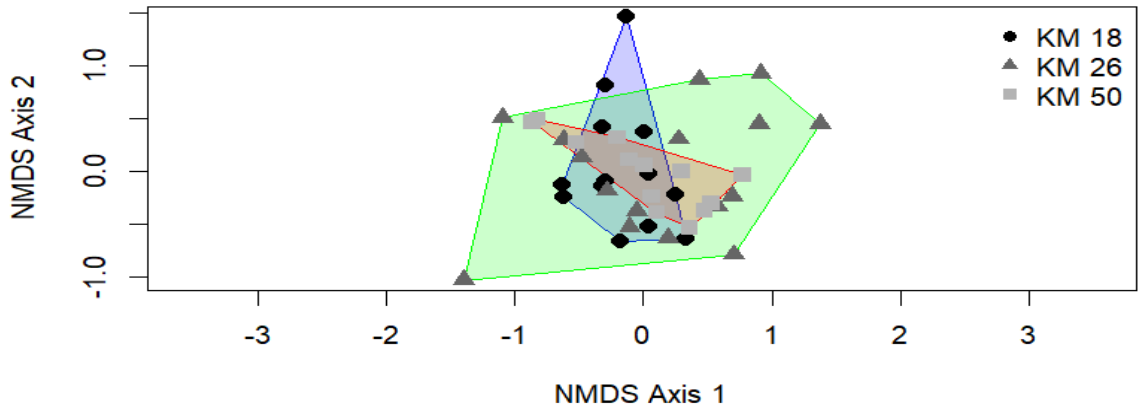

Figure 5. Non-metric multidimensional scaling (NMDS) ordination of plots based on anuran assemblage composition. Each point represents a sampled plot, and symbols indicate sampling modules (KM18, KM26, and KM50). NMDS 1 and NMDS 2 correspond to the two ordination axes.

Partitioning of abundance-based beta diversity revealed that variation in anuran assemblages among plots was predominantly structured by abundance differences (D = 60.72%), which represented the largest component of the index (Table 2). Species replacement contributed moderately (R = 15.19%), whereas relativized similarity (S = 24.10%) was comparatively low.

Total beta diversity (R + D) reached 75.9%, indicating high spatial heterogeneity among plots. Abundance agreement (S + R) remained low (39.28%), reinforcing that most variation among sampling units was driven by differences in abundance and richness rather than consistent patterns of species co-occurrence.

Table 2. Components of abundance-based beta diversity partitioning between pairs of plots in the Rio Negro Sustainable Development Reserve, obtained using the SDR Simplex method (Podani & Schmera, 2011). S represents relativized similarity between plots; R corresponds to abundance replacement among communities; and D expresses abundance difference resulting from variation in species richness and unequal species distribution. Derived values include total beta diversity (R + D) and abundance agreement (S + R), which summarizes, respectively, the degree of compositional heterogeneity and the level of shared structural consistency among assemblages.

Component	Value (%)
S	24.1
R	15.19
D	60.72
R+D	75.9
S+R	39.28

The ternary plot illustrates the predominance of the abundance difference component, with most pairwise comparisons concentrated towards the D vertex (Figure 6). Few comparisons approached the similarity vertex, and intermediate dispersion along the R axis indicates moderate species replacement among plots.

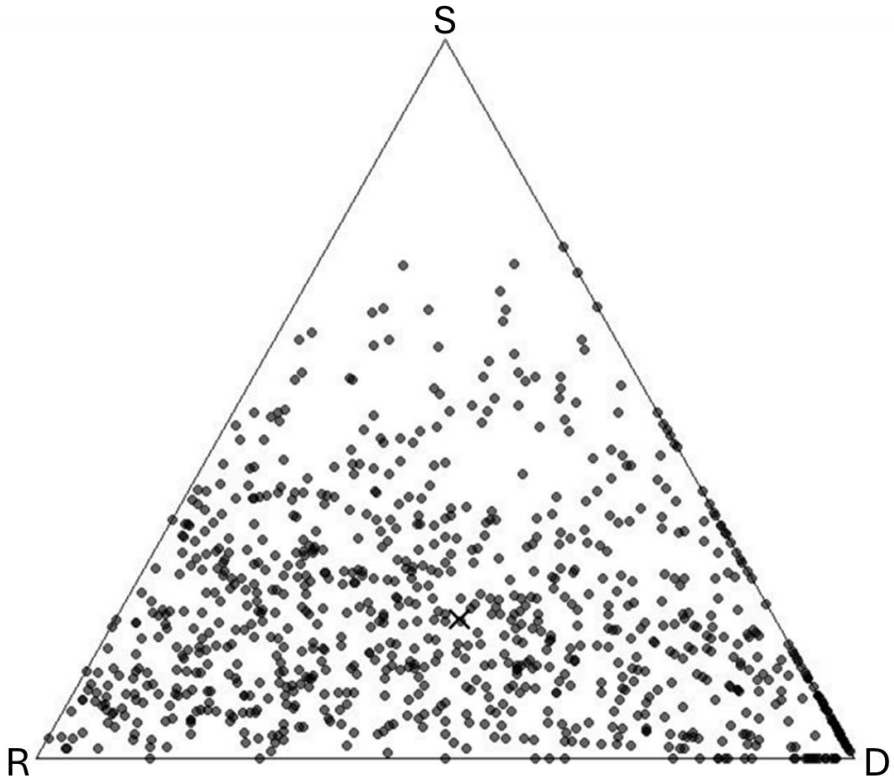

Figure 6. Ternary plot representing the relativized components of anuran beta diversity between pairs of plots: similarity (S), replacement (R), and abundance difference (D). Each point corresponds to a pairwise comparison between plots and is positioned according to the relative contribution of each component. Points located near the vertices indicate high values for the respective metric, whereas points distributed along the edges reflect extreme combinations between two components.

Multivariate generalized linear models (manyGLM) indicated that assemblage composition was significantly influenced by groundwater depth (Wald = 7.312, p = 0.012) and Leaf Area Index (LAI) (Wald = 7.157, p = 0.015). Litter depth showed a marginal effect (Wald = 6.717, p = 0.07), whereas soil pH and clay proportion were not significantly associated with community structure (Table 3).

Table 3. Results of the multivariate test assessing the association between anuran assemblage composition and environmental variables, obtained using the manyGLM model (mvabund). Wald statistics indicate the strength of the effect of each predictor on multivariate species variation, whereas p-values indicate statistical significance after correction for multiple tests. Variables with $p < 0.05$ were considered significantly associated with species composition, reflecting their contribution to assemblage organization across the sampled modules.

Environmental variables	Wald	P
LAI (Leaf Area Index)	7.157	**0.015**
Water table depth	7.312	**0.012**
Clay proportion	4	0.87

pH	5.312	0.329
Litter depth	6.717	0.07

Ordering plots along the LAI gradient revealed variation in species abundances across structural conditions (Figure 7). Plots with lower LAI values generally exhibited lower relative abundances, whereas intermediate and higher LAI values concentrated greater abundances of particular species. Although most species occurred across broad portions of the gradient, some exhibited more restricted abundance patterns along specific LAI intervals.

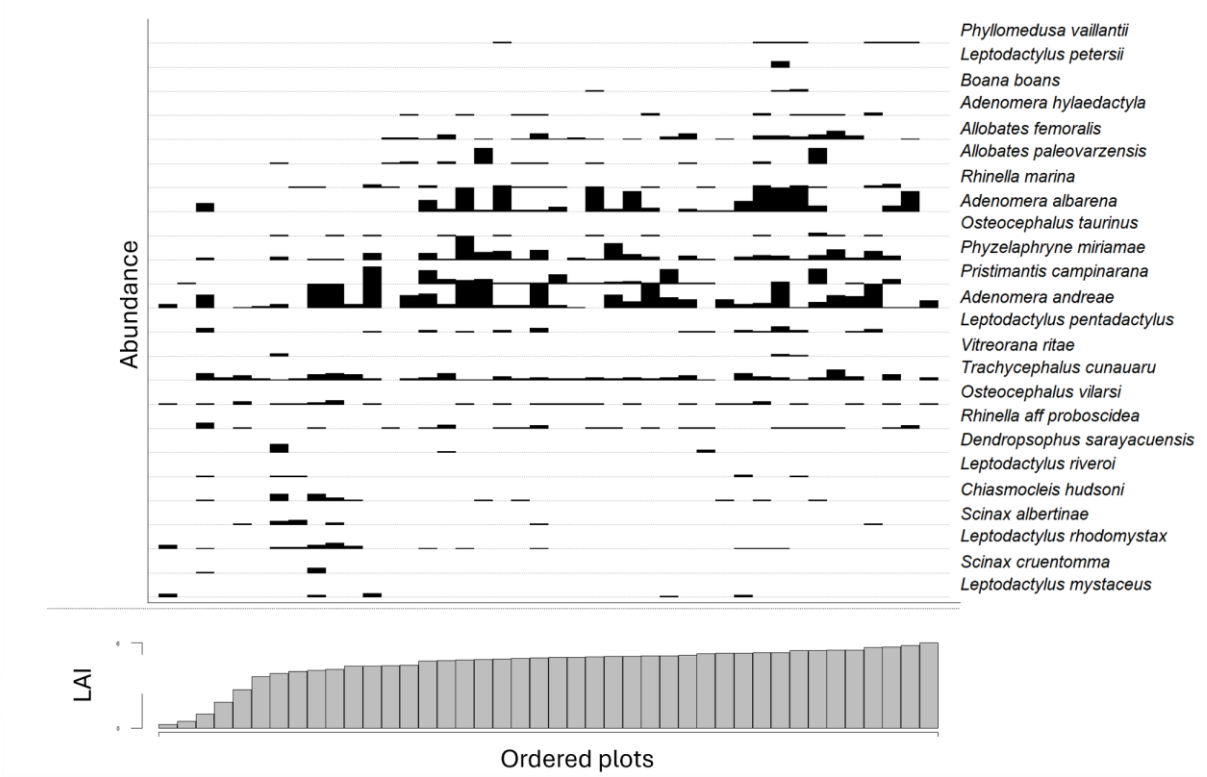

Figure 7. Distribution of anuran species abundances across plots ordered by increasing Leaf Area Index (LAI) values. In the upper panel, each horizontal bar represents the relative abundance of a species in each plot. In the lower panel, the corresponding LAI values for the ordered plots are shown as vertical bars, illustrating the structural vegetation gradient.

Similarly, ordering plots by groundwater depth revealed changes in abundance distributions along the hydrological gradient (Figure 8). Plots associated with shallower groundwater levels concentrated higher abundances of certain species, while deeper groundwater levels were associated with a quantitatively distinct assemblage structure.

Although several species occurred across most of the gradient, some showed abundance patterns restricted to plots with relatively superficial water tables.

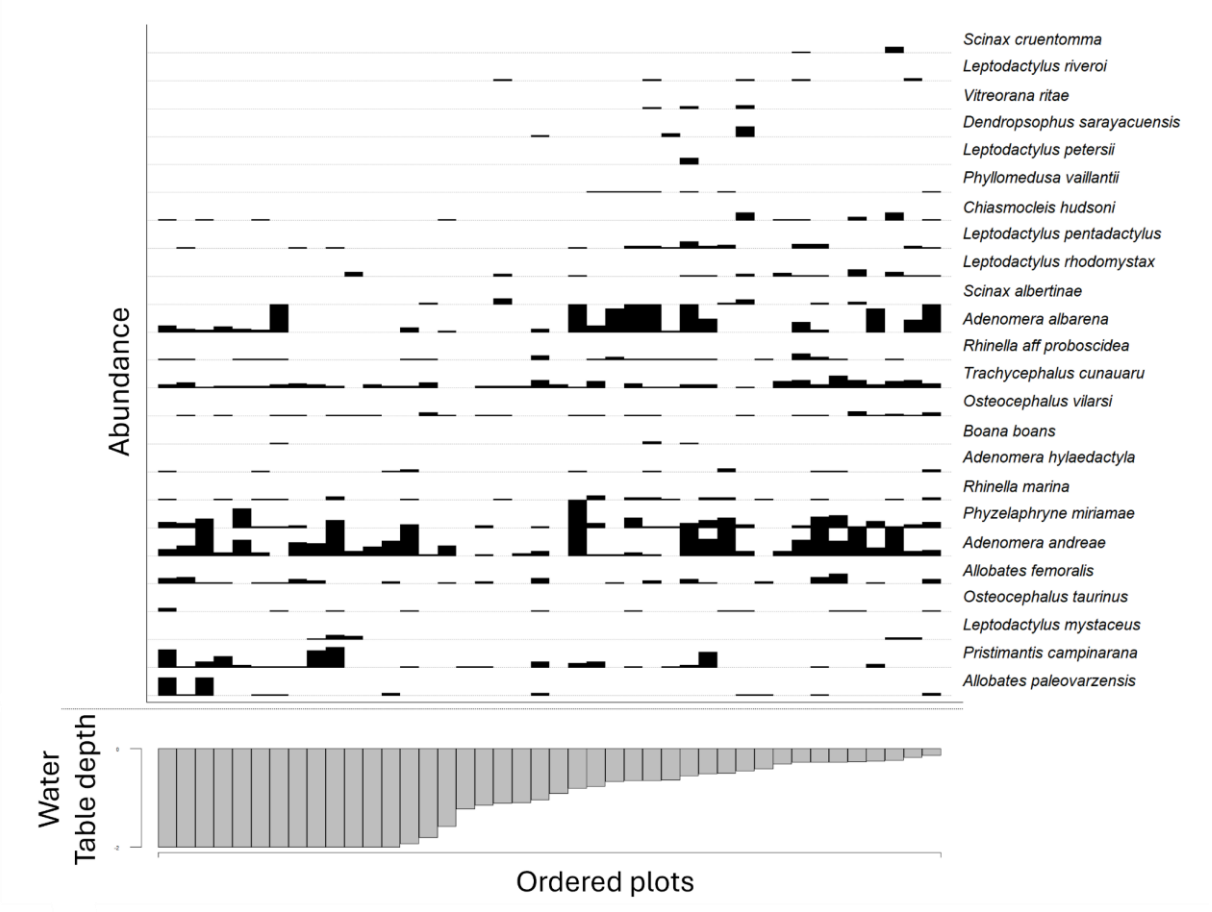

Figure 8. Distribution of anuran species abundances across plots ordered according to groundwater depth. In the upper panel, each horizontal bar represents the relative abundance of a species in each plot. The lower panel shows the corresponding groundwater depth values (m) for the ordered plots.

Multiple regression on distance matrices (MRM) indicated that both environmental and geographic distances contributed to compositional dissimilarity among plots. Environmental distance significantly influenced community differentiation ($\beta = -5.56 \times 10^{-4}$; $p = 0.030$), and geographic distance also showed a significant effect ($\beta = 5.45 \times 10^{-6}$; $p = 0.001$). The full model explained approximately 9% of variation in compositional dissimilarity ($R^2 = 0.091$; $p = 0.002$), indicating that environmental gradients and spatial processes jointly structure assemblage variation across the landscape.

DISCUSSION

The results of this study indicate that anuran assemblages associated with white-sand forests in the Rio Negro Sustainable Development Reserve exhibit high compositional heterogeneity among sampling units, expressed by elevated beta diversity values. This variation is predominantly structured by differences in species abundance and relative richness, whereas species replacement plays a secondary role. This pattern indicates that many species are shared among localities, but with marked differences in their distribution and dominance across space.

The high beta diversity observed is consistent with patterns described for other taxonomic groups associated with Amazonian white-sand ecosystems, such as birds, invertebrates, and plants (Borges et al., 2016; Graça et al., 2017; Vicentini, 2016). However, unlike systems in which differentiation among areas results primarily from complete species turnover, our results indicate that, for anurans in the RDS Rio Negro, spatial heterogeneity emerges predominantly from quantitative differences in abundance and relative richness among plots (D = 60.72%), whereas species replacement contributed secondarily (R = 15.19%). This pattern is consistent with the broad overlap observed in the NMDS ordination, which did not showclear compositional segregation among modules, suggesting that differentiation occurs at a finer spatial scale, among plots, rather than among large spatial blocks.

The predominance of the D component indicates that a large proportion of assemblages share a relatively similar regional species pool, but that species varies strongly in dominance along environmental and spatial gradients. This result suggests that the available taxonomic pool may be partially filtered by the restrictive edaphic conditions typical of white-sand forests (Adeney et al., 2016), while the internal organization of assemblages is structured by local variation in habitat structure and water availability.

Local environmental gradients exerted a significant influence on assemblage composition, as indicated by the multivariate models (manyGLM). Groundwater depth ($p = 0.012$) and Leaf Area Index ($p = 0.015$) were the main predictors of compositional variation, whereas edaphic variables related to soil pH and clay proportion did not show significant effects. These results indicate that, within the context of the white-sand forests studied, factors directly associated with water availability and vertical vegetation structure are more determinant for anuran assemblage organization than soil chemical properties.

The influence of vegetation structure is corroborated by the pattern observed in the ordering of plots along the LAI gradient. Plots with lower LAI values showed lower concentration of abundances, whereas plots with intermediate and higher values concentrated greater relative abundances of some species. Species such as *Phyllomedusa vaillantii* were more strongly associated with structurally denser areas, whereas *Leptodactylus mystaceus* occurred

more frequently in more open plots. In contrast, widely distributed species such as *Adenomera andreae* and *Trachycephalus cunauaru* occurred across nearly the entire gradient, indicating broader ecological tolerance. These patterns suggest differentiated responses to habitat structural conditions, reinforcing the role of vegetation structure in influencing understory microclimate and the availability of refuges and calling sites (Menin, 2007; Ribeiro et al., 2012; Pereira et al., 2024).

Similarly, groundwater depth constituted an environmental axis strongly associated with variation in species relative abundance. Plot ordering revealed that areas with shallower groundwater levels concentrated on a higher number of records of some species, whereas plots with deeper groundwater exhibited a quantitatively distinct composition. Considering the dependence of anurans on humid environments for reproduction and larval development (Haddad & Prado, 2005; Menin, 2007), this pattern suggests that small variations in groundwater proximity may alter the microenvironmental suitability of plots, influencing species' persistence and relative dominance.

In addition to environmental effects, the significant relationship between compositional dissimilarity and geographic distance indicates that spatial processes additionally contribute to assemblage structuring. Although the MRM model explained a relatively small proportion of total variation ($R^2 = 0.091$), the simultaneous significance of environmental distance ($p = 0.030$) and geographic distance ($p = 0.001$) demonstrates that differentiation among plots cannot be attributed exclusively to the local ecological filters investigated in our study. Thus, the organization of anuran assemblages across the RDS Rio Negro reflects the joint influence of environmental variation and dispersal limitation at the landscape scale.

From a theoretical perspective, these patterns can be interpreted under neutral approaches to community ecology, in which differences in species composition and abundance emerge from stochastic processes associated with ecological drift and limited dispersal (Hubbell, 2001). In this study, this interpretation is supported by the stronger association between compositional dissimilarity and geographic distance among plots, compared to environmental distance. Similar results have been reported for other Amazonian vertebrates, in which dispersal limitation and landscape spatial configuration explain a substantial portion of beta diversity, as demonstrated for snake assemblages in the Amazon (Fraga et al., 2018; Peixoto et al., 2023). These findings reinforce the importance of spatial processes in structuring communities in naturally fragmented ecosystems.

Taken together, our results indicate that beta diversity of anuran assemblages in white-sand forests results from the combined influence of local environmental gradients and spatial processes operating at multiple scales. Environmental heterogeneity modulates species

abundance and dominance among plots, whereas dispersal limitation contributes to compositional differentiation across the landscape. These complementary mechanisms help explain the elevated beta diversity observed and highlight the complexity of processes structuring anuran communities in singular Amazonian ecosystems.

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SUPPLEMENTARY MATERIAL

Table S1. Variance Inflation Factors (VIF) for environmental variables obtained from LiDAR measurements. The variable with the lowest collinearity and greatest ecological relevance to the focal organisms was selected for subsequent analyses.

Environmental variables	VIF
H.MAX.Max	17.366791
H.MAX.0.995	25.361595
H.Max.Loess	6.008928
H.MEAN.Max	775.514882
H.MEAN.0.995	803.453110
H.MEAN.Loess	29.123997
P.skyshots	16.814505
P.P.skyshots	7.180214
Gap.5m	19.271590
Gap.10m	47.246500
Gap.15m	13.303133
LAI	8.225192
LAI_0_15	17.117322
LAI_m_15	25.146838

Table S2. Variance Inflation Factors (VIF) for environmental variables included in the analyses. All variables showed VIF values below 2, indicating low multicollinearity and supporting their simultaneous inclusion in the models.

Environmental variables	VIF
Profundidade da Serrapilheira	1.34
Profundidade do lençol freático	1.27
Índice de área foliar (LAI)	1.69
Argila no solo	1.26

pH do solo	1.31

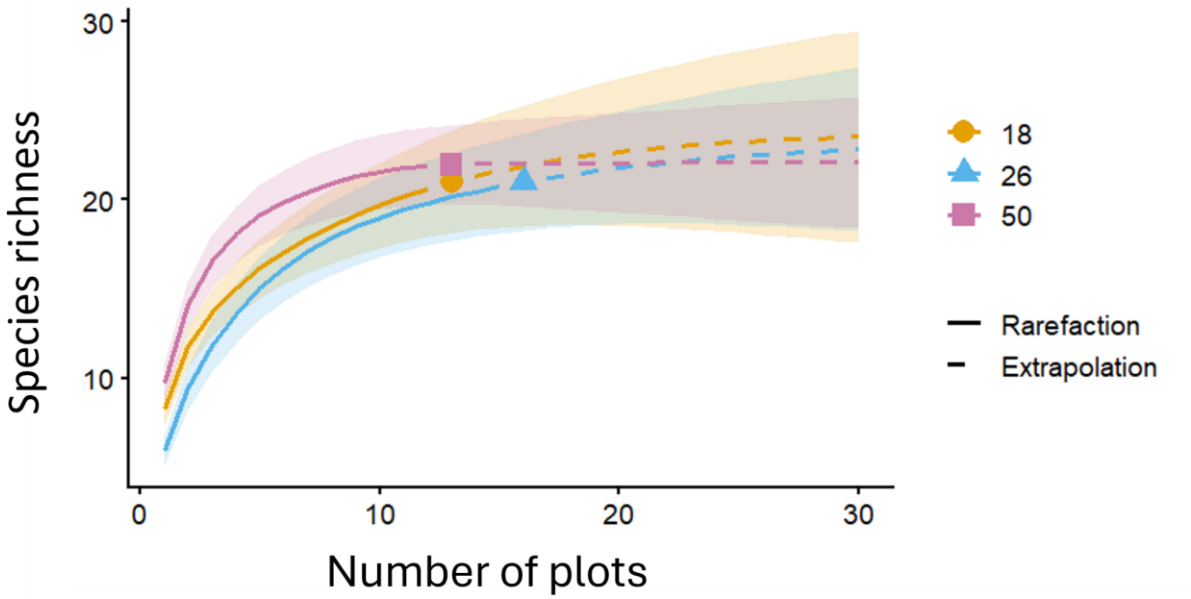

Figure 9. Rarefaction and extrapolation curves of anuran species richness based on the number of sampled plots in modules KM18, KM26, and KM50. Solid lines represent rarefaction (interpolation) up to the observed number of plots in each module, and dashed lines represent extrapolation. Shaded areas indicate confidence intervals (1,000 bootstrap replicates). Points represent the observed species richness in each module.