PPG Ecologia & Conservação

Universidade Estadual de Santa Cruz

UNIVERSIDADE ESTADUAL DE SANTA CRUZ - UESC

PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO

DA BIODIVERSIDADE - PPGECB

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ESTRUTURA DA ASSEMBLEIA DE ANUROS NO PARQUE NACIONAL SERRA DA CAPIVARA, PIAUÍ, BRASIL

ILHÉUS – BAHIA

2025

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Dissertação apresentada ao Programa de Pós-graduação em Ecologia e Conservação da Biodiversidade da Universidade Estadual de Santa Cruz como parte dos requisitos para obtenção do grau de Mestre em Ecologia e Conservação da Biodiversidade.
Linha de pesquisa: Ecologia e conservação de comunidades.
Orientador: Mirco Solé Kienle
Coorientador: Kássio de Castro Araújo
Coorientador: Etielle Barroso de Andrade

ILHÉUS – BAHIA

2025

R696 Rodrigues, Nayla Letícia Assunção.
Estrutura da assembleia de anuros no Parque Nacional Serra da Capivara, Piauí, Brasil / Nayla Letícia Assunção Rodrigues. – Ilhéus, BA: UESC, 2025.
68f.: il.

Orientador: Mirco Solé Kienle
Dissertação (Mestrado) – Universidade Estadual de Santa Cruz. Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade – PPGECB.
Inclui referências.

1. Anfíbios. 2. Diversidade. 3. Inventários. 4. Partilha de recursos (Ecologia). 5. Filogenia. 6. Competição (Biologia). I. Título.

CDD 597.8

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Ilhéus, 21 de fevereiro de 2025.

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AGRADECIMENTOS

Agradeço à Universidade Estadual de Santa Cruz e ao Instituto Federal do Piauí, por proporcionarem a infraestrutura necessária para o desenvolvimento desta pesquisa e para o meu crescimento pessoal. Sou grata ao Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, pela oportunidade de cursar o mestrado, e à Fundação Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), pelo apoio concedido por meio da bolsa de estudo.

Agradeço ao Dr. Mirco Solé, pela orientação atenciosa e pela confiança em mim depositada. Minha gratidão também ao Prof. Dr. Kássio Araújo e ao Prof. Dr. Etielle Barroso, pelo apoio constante e pelos valiosos ensinamentos.

À minha família, que sempre esteve ao meu lado, torcendo por mim: obrigada por todo amor e incentivo! Aos meus queridos amigos do grupo de oração, aos membros do BIOTECPI e aos meus amigos de sempre, sou imensamente grata pelo convívio, pelas risadas, pelo apoio e pelo encorajamento contínuos. Obrigada por acreditarem em mim. Por fim, agradeço às amizades cultivadas ao longo deste período: às colegas de mestrado e aos vizinhos em Ilhéus, obrigada por tornarem essa caminhada mais leve com sua companhia e alegria.

Como disse São Josemaria Escrivá: “Que a tua vida não seja estéril. Sê útil. Deixa rasto.” Que essa vitória seja um rastro de inspiração na vida de todos ao meu redor.
A todos, essa conquista é nossa! Muito obrigada!

RESUMO

A ecologia de comunidades investiga padrões de diversidade, abundância e composição de espécies, além dos fatores que moldam sua organização e dinâmica. A forma como as espécies utilizam os recursos disponíveis pode influenciar diretamente a estrutura da comunidade, enquanto a heterogeneidade local pode desempenhar um papel relevante na diversidade de espécies da comunidade. Este estudo analisou os padrões de estrutura da comunidade de nichos espaciais e tróficos de anuros no Parque Nacional Serra da Capivara (PNSC), e investigou como a heterogeneidade local afeta a abundância e a riqueza de espécies, além de apresentar uma lista atualizada de anuros do parque. Foram identificadas 16 espécies de anuros distribuídas em cinco famílias, sendo a maioria composta por espécies típicas da Caatinga ou amplamente distribuída. Registramos o uso de micro-habitat de 551 indivíduos e a dieta de 239 indivíduos pertencentes as 16 espécies registradas. Não identificamos padrões claros de estrutura espacial e trófica, sendo que a história evolutiva influenciou o nicho espacial, enquanto fatores ecológicos predominaram no nicho trófico. A maioria das espécies apresentou comportamento generalista em habitat e dieta, refletindo flexibilidade no uso dos recursos disponíveis, o que sugere a ausência de forças competitivas significativas para segregação de nichos. Além disso, nossos resultados indicam que a heterogeneidade local não influenciou significativamente a riqueza de espécies, mas teve um impacto relevante na abundância dos anuros do PNSC. Nosso estudo amplia o conhecimento sobre as comunidades de anuros da Caatinga e suas interações ecológicas, destacando a importância de áreas heterogêneas para suportar populações maiores, garantir a estabilidade ecológica e subsidiar estudos de conservação em ambientes semiáridos.

Palavras-chave: Anfíbios – Diversidade – Inventário – Partição de nicho – Filogenia - Competição

ABSTRACT

Community ecology examines patterns of species diversity, abundance, and composition, as well as the factors that shape their organization and dynamics. The way species utilize available resources can directly influence community structure, while local heterogeneity may play a significant role in community species diversity. This study analyzed the patterns of spatial and trophic niche structure of anurans in the Serra da Capivara National Park (SCNP) and investigated how local heterogeneity affects species abundance and richness, in addition to providing an updated list of the park's anurans. We identified 16 anuran species distributed across five families, most of which are typical of the Caatinga or widely distributed. We recorded microhabitat use by 551 individuals and analyzed the diet of 239 individuals belonging to the 16 recorded species. We did not identify clear patterns of spatial and trophic structure; evolutionary history influenced spatial niche, while ecological factors predominated in trophic niche. Most species exhibited generalist behavior in habitat and diet, reflecting flexibility in the use of available resources, suggesting the absence of significant competitive forces for niche segregation. Additionally, our results indicate that local heterogeneity did not significantly influence species richness but had a relevant impact on the abundance of anurans in the PNSC. Our study expands the knowledge of Caatinga anuran communities and their ecological interactions, highlighting the importance of heterogeneous areas in supporting larger populations, ensuring ecological stability, and informing conservation studies in semi-arid environments.

Keywords: Amphibians – Diversity – Inventory – Niche Partitioning – Phylogeny – Competition

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ACKNOWLEDGEMENTS .... **Erro! Indicador não definido.**
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1. INTRODUÇÃO GERAL

A ecologia de comunidades é a ciência que busca investigar os padrões de diversidade, abundância e composição das espécies, bem como os fatores que moldam a organização e a dinâmica dessas comunidades (Begon *et al*., 2007; Vellend, 2010). Nesse sentido, espécies coexistentes tendem a particionar seus nichos em algum aspecto, minimizando a competição direta, conforme o princípio da exclusão competitiva (Connell, 1980). Em razão disso, os recursos disponíveis e a estrutura do ambiente desempenham um papel crucial na distribuição das espécies, na utilização dos nichos ecológicos e nos padrões de interação entre os organismos (Morin, 2009; Souza; Eterovick, 2011). Assim, a ecologia de comunidades auxilia na compreensão dos sistemas ecológicos e no entendimento dos fatores envolvidos na estruturação das comunidades biológicas (Mesquita *et al*., 2006)

O nicho ecológico desempenha um papel fundamental na organização das comunidades (Hutchinson, 1959), pois a coexistência de espécies pode ser determinada pelas diferenças interespecíficas no uso de recursos (Morin, 2009). Além disso, a estrutura do ambiente pode influenciar a diversidade e a riqueza das espécies (MacArthur; MacArthur, 1961), dado que ambientes mais heterogêneos disponibilizam mais recursos e maior diversidade de nichos, suportando maior riqueza de espécies (Bazzaz, 1975). Ademais, as relações ecológicas (ex. predação e competição) afetam a estrutura da comunidade (MacArthur *et al*., 1972; Leite Filho *et al*., 2015). Isto pode estar relacionado aos processos ecológicos atuais e/ou relacionados às histórias evolutivas das espécies da comunidade (Losos, 1996; Vitt *et al*., 1999; Mesquita *et al*., 2006), conhecido como o “fantasma da competição passada” (Townsend *et al*., 2010). Dessa forma, fatores ambientais, tolerâncias fisiológicas e as interações bióticas influenciam a partição de recurso e organização das comunidades (Kopp; Eterovick, 2006).

Os anfíbios anuros são um grupo interessante para estudos de ecologia de comunidade, pois atuam em processos ecológicos e teias tróficas do ambiente terrestre e aquático, além de serem um dos grupos de vertebrados com maior abundância e diversidade (Vitt; Caldwell, 2014; Frost, 2024). Estes animais têm elevada sensibilidade às condições do ambiente (Wells, 2010), assim, a heterogeneidade de habitats desempenha um papel importante na diversidade de anfíbios (Afonso; Eterovick, 2007; Mausberg *et al*., 2023). Nesse contexto, as características do ambiente podem determinar a distribuição desses indivíduos nos diversos ecossistemas naturais. Portanto, a heterogeneidade ambiental pode exercer forte influência na riqueza de espécies no ambiente (Haddad; Prado, 2005), já que uma grande diversidade de microhabitats permite a ocorrência de diferentes espécies (Vasconcelos *et al*., 2009; Araújo *et al*., 2018).

Além disso, a disponibilidade de recursos pode influenciar diretamente o modo como estes são explorados (Pianka, 1973), afetando, assim, a organização e a dinâmica da comunidade.

O Piauí está localizado em uma área de ecótono entre os biomas Caatinga e Cerrado (IBGE, 2019). Devido a isso, apresenta uma grande heterogeneidade de fitofisionomias (Castro, 2003), o que pode explicar alta diversidade de anfíbios do estado, com um total de 55 espécies registradas (Roberto *et al*., 2013). Até o momento, as áreas protegidas do Piauí abrigam a maior parte da herpetofauna conhecida na região (Araújo *et al*., 2020a, b; Pantoja *et al*., 2022). Apesar dos avanços nos estudos ecológicos na Caatinga nos últimos anos, ainda existem lacunas de conhecimento em diversas áreas desse bioma (e.g., Araújo et al., 2018; Lima et al., 2022). Entre as áreas protegidas, o Parque Nacional Serra da Capivara (PNSC) se destaca por ter sido o primeiro parque instituído no domínio morfoclimático da Caatinga, desempenhando um papel fundamental na proteção da fauna e flora local (Pagli et al., 2016). No entanto, o conhecimento sobre a anurofauna do PNSC ainda é insuficiente (Cavalcanti *et al*., 2014), o que evidencia a necessidade de mais estudos para compreender a dinâmica e os fatores ecológicos que moldam as comunidades de anfíbios nessa região.

Considerando que entender os fatores estruturantes das comunidades ainda é um dos desafios em Ecologia, assim como quais variáveis são predominantes na explicação dos padrões de diversidade de anuros, o presente estudo teve como objetivos principais descrever a diversidade de anuros e o papel da heterogeneidade local nesses padrões, além de descrever a estrutura e quais filtros determinam os padrões de estrutura em assembleias de anuros no PNSC.

Nesse sentido, essa dissertação de mestrado está organizada em dois capítulos, a seguir:

Capítulo 1 – Anuran assemblage structure in the Serra da Capivara National Park, Piauí State, Northeastern Brazil. Este manuscrito objetivou investigar os padrões de organização das assembleias de anuros do Parque Nacional Serra da Capivara quanto ao uso de recursos espaciais e tróficos, além de investigar o papel de filtros ecológicos e filogenéticos nessa organização. Esse manuscrito será submetido ao periódico científico *Austral Ecology*.

Capítulo 2 – Assessing the effect of local heterogeneity on anuran diversity in the Serra da Capivara National Park, Piauí State, Brazil. Este manuscrito objetivou descrever a diversidade de anfíbios do Parque Nacional Serra da Capivara e investigar como a heterogeneidade local influencia na riqueza e abundância de anfíbios da região. Esse manuscrito está aceito no periódico científico *Zookeys*.

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2. Chapter 1: Anuran assemblage structure in the Serra da Capivara National Park, Piauí State, Northeastern Brazil

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ABSTRACT. Biological communities are formed by species that coexist and interact with others and the environment in certain locals. Thus, how the species use the available resources can shape the community structure. This study investigated the community structure patterns of spatial and trophic niches of anurans in the Serra da Capivara National Park. We recorded the microhabitat used by 551 anurans and the diet of 239 anurans from 16 species. We also measured the spatial and trophic niche overlapping with null models to detect the presence of structure in the community, with a subsequent phylogenetic principal component analysis to detect the influence of phylogenetic and ecological filters. Overall, we found no spatial and trophic structure pattern in which evolutionary history exerted greater influence on the spatial niche while ecological factors predominated in the trophic niche. Most species had generalist behaviors regarding microhabitats and diet, reflecting flexibility in the resources used. The spatial and trophic resources were not limiting, given the absence of significant competitive forces for niche segregation. Our study increases the knowledge about the anuran networks and community structuring in the Caatinga biome, contributing to conservation studies in semi-arid environments.

KEYWORDS: Amphibians, Competition, Niche partitioning, Microhabitat-use, Phylogeny.

1. INTRODUCTION

A community can be defined as a group of different species coexisting and interacting with each other in a certain region (Morin, 2011). The natural resources used by the species might indicate structuring patterns in these communities (Pianka, 1973). Coexisting species generally tend to partition niches to reduce competition, according to the competitive exclusion principle (Connell, 1961). Therefore, the niches play an important role in the biological communities (Hutchinson, 1959) because the ecological interactions might lead to the partitioning or exclusion of species (Gause, 1932; Winemiller & Pianka, 1990).

The organization of communities might be a result of recent factors (ecological filters) such as competition (Protázio et al., 2015; Leite Filho et al., 2017; Gonçalves-Sousa et al., 2023). From this perspective, intraspecific and interspecific interactions are responsible for structuring how the species use natural resources. Furthermore, the species' evolutionary history may influence community structure (Cavender-Bares et al., 2009; Gonçalves-Sousa et al., 2019; Cavalcanti et al., 2023). Phylogenetically closer species tend to have similar ecological characteristics (Losos, 1996; Losos, 2008), and, consequently, they might compete by the available natural resources. Thus, grasping the community's evolutionary history could be valuable for understanding the effect of recent ecological filters on community structuring patterns (Losos, 1996).

Amphibians comprise one of the most diverse groups of vertebrates occurring across different regions worldwide (Vitt & Caldwell, 2014; Frost, 2025). Anurans may serve as an effective model for elucidating the influence of ecological niches on community organization, as these organisms possess a biphasic lifecycle, and occur that transpires across various microhabitats in arboreal, aquatic, and terrestrial environments (Duellman, 1988), thereby consuming a wide array of prey (Parmelee, 1999). The anuran lifecycle leads to a synchronized reproductive period in the rainy season (Wells, 2010), which might result in a high intraspecific and interspecific resource competition (Crump, 1994).

Studies dealing with herpetofauna species show that different filters might shape the community structure patterns (e.g., Winemiller & Pianka, 1990; Mesquita et al., 2006; Mesquita et al., 2007). In anurans, for instance, Leite Filho et al. (2015) observed no significant phylogenetic effect on the community structure of anurans from a Caatinga area. In contrast, other studies with anuran communities revealed historical and ecological effects on the diet and microhabitat use (Protázio et al., 2015; Caldas et al., 2019). Therefore, we investigate the anuran assemblage structure patterns in the Serra da Capivara National Park (SCNP), Piauí State, Northeastern Brazil. First, we described the spatial and trophic niche of the anuran species in the SCNP. Second, we searched for structuring patterns in the resources used (microhabitat and diet) by the anuran assemblage, in which we expected a low niche overlap because the SCNP interspecific competition can be reduced through niche partitioning, promoting coexistence among species. Lastly, we tested the influence of ecological and phylogenetic factors on resource use by anurans. We expected phylogenetic effects to be more relevant, as the extreme conditions of the semiarid region could act as an environmental filter, favoring lineages with adaptations to these conditions. Since closely related species tend to share similar ecological traits, these adaptations could be reflected in the community's organization.

2. METHODS

2.1 Study area

The present study was conducted in the SCNP (8°40'58.3"S; 42°35'14.2"W), located in the southeast of Piauí State (Fig. 1). It comprises a total area of 130.000 ha within the municipalities of São Raimundo Nonato, Coronel José Dias, Brejo do Piauí, and João Costa

(ICMBio, 2019). The vegetation is typical of the Caatinga biome in the Northeastern semiarid, with a dense coverage of arboreal Caatinga, cacti, and bromeliads spread over the rocky outcrops (Lemos, 2004). The climate is dry, with irregular rainfall and average temperatures around 25 °C (Lemos & Rodal, 2002; Barros et al., 2012).

2.2 Sampling

We conducted four expeditions of five consecutive collection days from December to April 2024 in the SNCP, totaling 20 sampling days, during the rainy season. We used as sampling methodology visual and auditory searches (Heyer et al., 1994) in different environments used by anurans within SCNP. Five researchers carried out field activities, starting around 18:00 h and ending at 0:00 h. Our total sampling effort was 600 h. The voucher specimens were collected and deposited at the Coleção Biológica of the Instituto Federal de Ciência e Tecnologia do Piauí, Campus Pedro II (CBPII), Piauí State, Northeastern Brazil.

2.3 Spatial niche

We recorded the microhabitat used by each sampled anuran to evaluate the spatial niche, considering the microhabitat as the exact location where the individual was found (Eterovick, & Ferreira 2008): within the pond (WP), edge of the pond (EP), rocky outcrops (RO), litter leaf (LL), soil with herbaceous vegetation (SV), exposed soil (ES), inside dens (ID), perched on trees (PT), shrubs (SH), and herbaceous (HE). We used the inverse of Simpson's diversity index to calculate the spatial niche breadth (*Bspatial*) of each species (Simpson, 1994). The values of *Bspatial* can range from 1 (exclusive use of a single category of microhabitat) to 10 (use of all microhabitat categories by each species).

2.4 Trophic niche

In the lab, we removed the stomach contents of the collected individuals and analyzed them under a stereomicroscope to identify prey items to the lowest taxonomic level possible using specialized literature (Rafael et al., 2024). Then, we measured the length and width of prey items with a digital caliper (precision of 0.01 mm), and we used the ellipsoid formula to estimate their volume:

$$V = \frac{4}{3}\pi\left(\frac{L}{2}\right)\left(\frac{W}{2}\right)^2$$

Where V = volume, L = length, and W = width (Griffiths & Mylotte, 1987). We calculated each prey volumetric percentage to estimate the trophic niche breadth (*Bvol*) through the inverse of Simpson's diversity index. The values of *Bvol* can range from 1 (exclusive consumption of a single category of prey) to 24 (consumption of all prey categories by each species). In addition, we calculated the index of relative importance (IRI) to determine the relative contribution of each prey category to the diet of each species (Powell et al., 1990).

2.5 Data analysis

We used Pianka (1973) overlap index to calculate the spatial (microhabitat used) and trophic niche (sum of the volume of each prey category for each anuran species) overlap between all pairs of species:

$$\emptyset jk = \frac{\sum_{i=1}^{n} \rho ij \rho_i k}{\sqrt{\sum_{i=1}^{n} \rho ij^2 \sum_{i=1}^{n} \rho_i k^2}}$$

where ρij and $\rho_i k$ are the proportions of microhabitat used and prey volume of the category i, and j and k represent the pairs of compared species. The values of overlap range from 0 (without overlap) to 1 (total overlap).

We used null models by randomizing the data from the original matrix of niche overlap to investigate if the mean overlap in spatial and trophic niche dimensions was lower than expected by chance (Gotelli & Graves, 1996; Gotelli & Entsminger 2001). The presence or absence of structure in the community was established by comparing means of observed and simulated overlap, where the presence of nonrandom structuring patterns (organization) occurs when the mean niche overlap observed is lower than expected by chance ($p < 0.05$). We plot a matrix in which species correspond to a row and each microhabitat or prey category to a column. The values of each cell correspond to the proportion of microhabitat use or volume of each prey category. Thereafter, we used phylogenetic principal component analysis (pPCA) to investigate the effect of ecological or historical factors on the trophic and spatial niches. We used Pyron and Wiens (Pyron & Wiens, 2011) to encode the phylogeny, so that each group is coded separately as a binary variable. In this analysis, positive eigenvalues indicate a phylogenetic effect on the conservation of ecological traits, while negative eigenvalues indicate ecological convergence, resulting in variation of niche traits near the terminal branches (Jombart et al., 2010). Statistical analyses were performed using the R packages devtools (Wickham et al., 2022), spaa (Zhang, 2016), EcoSimR (Gotelli et al., 2015), ade4 (Dray et al., 2007), adephylo (Jombart & Dray et al., 2010), ape (Paradis & Schliep, 2019), picante (Kembel et al., 2010), Rcpp (Eddelbuettel & François, 2011), phylobase (Parker & Givnish, 2019), and ggplot2 (Wickham, 2016).

3. RESULTS

3.1 Species composition

We collected 239 anurans belonging to 16 species from four families (Table 1). The most abundant species were *Leptodactylus troglodytes* (N = 77), *Scinax x-signatus* (N = 72), and *Pithecopus gonzagai* (N = 65). In contrast, *Trachycephalus* cf. *nigromaculatus* (N = 7) and *Pleurodema diplolister* (N = 1) were the less abundant (Table 1). It is noteworthy that the observed individual of *P. diplolister* was captured, but not included in the statistical analyses.

3.2 Spatial niche

We recorded the microhabitat used by 551 individuals, corresponding to 15 species. The anuran assemblage used ten different categories of microhabitats in the SCNP. *Leptodactylus syphax* (*Bspatial* = 5.03) and *L. troglodytes* (*Bspatial* = 4.02) had the highest spatial niche breadth, whereas the lowest ones were found in *T.* cf. *nigromaculatus* (*Bspatial* = 1.0) occurring just perched on trees and *Physalaemus cuvieri* (*Bspatial* = 1.89) occurring just within the pond, litter leaf, and exposed soil (Table 1). Considering the species that share at least one type of microhabitat, niche overlap ranged from 0.01 (*P. cuvieri* vs. *P. gonzagai*; *P. cuvieri* vs. *Dendropsophus soaresi*) to 0.97 (*Leptodactylus macrosternum* vs. *Rhinella diptycha*; Table 2).

We have not detected niche partitioning in the microhabitat use (mean observed = 0.378, mean simulated = 0.415, p = 0.117). In addition, the species evolutionary history (phylogeny) had a greater influence on community structure than ecological filters, presenting higher eigenvalues for the global (historical) component than for the local (ecological) component (Fig. 2A).

3.3 Trophic niche

We found 24 prey categories consumed by the anurans in the SCNP, in which beetles, termites, and larvae were the most preyed items. In addition, we found plant material in the stomachs of 63 individuals that were not included in the statistical analyses due to their low volumetric quantity. Regarding the trophic niche breadth, *Dermatonotus muelleri* (*Bvol* = 1.16) was the most specialist species eating just ants and termites, whereas *Leptodactylus_fuscus* (*Bvol* = 6.27) and *Leptodactylus vastus* (*Bvol* = 6.19) were the most generalist species preying nine and 12 prey categories, respectively (Table 3). Although *L. syphax* consumed a wide variety of prey, its diet was dominated by beetles and termites (80%), resulting in a low trophic niche breadth (*Bvol* = 2.19; Table 3). Similarly, *R. diptycha* exhibited a low niche breadth (*Bvol* = 2.26; Table 3), with 70% of its diet comprising ants and beetles, although it also consumed a variety of prey. Considering the species of the community that share at least one type of prey category, the niche overlap ranged from 0.01 (*D. muelleri* vs. *D. soaresi*; *L. macrosternum* vs. *P. cuvieri*) to 0.96 (*Physalaemus cicada* vs. *Corythomantis greeningi*; *D. soaresi* vs. *L. macrosternum; L. syphax* vs. *D. muelleri*; Table 2).

We also not detected niche partitioning regarding prey items consumed by the anuran assemblage (mean observed = 0.388, mean simulated = 0.379, $p > 0.05$). However, ecological filters have a greater influence on the community structure than phylogeny, presenting higher eigenvalues for the local (ecological) component than for the global (historical) component (Fig. 2B).

4. DISCUSSION

We sampled about 30% of the anuran species registered in Piauí State (Roberto et al., 2013), which is relatively low compared to the total richness of the state. However, the anuran richness in the SCNP was similar to other studies carried out in the Caatinga *strictu sensu* (Vieira et al., 2007; Benício et al., 2015; Freire et al., 2023). In addition, we increased the number of known anuran species for the SCNP (Cavalcanti et al., 2014). Although some of these species are typical from Caatinga, most of them are geographically widely distributed in the Brazilian biomes (Garda et al., 2017; Frost, 2025).

Most anuran species of the SCNP had a broader niche breadth than those from other areas of Caatinga (Leite Filho et al., 2015, Protázio et al., 2015), and from an area of Atlantic

Rainforest (Leite Filho et al., 2017) reflecting more generalist habits of microhabitat use (Clavel et al., 2010). The spatial niche plasticity may offer advantages for exploring the environment in scenarios of challenging environmental conditions, such as the low and irregular precipitation associated to relatively high temperatures found in the Caatinga (Lima et al., 2015; Eterovick & Barros, 2003). Additionally, the species tend to expand their spatial niches in depauperate communities (Rodda & Dean-Bradley, 2002; Pianka, 2011; Gonçalves-Sousa et al., 2023). Although resource availability plays an important role in community organization (Pianka, 1973), more studies are still needed to understand better which factors have influenced the spatial niche breadth observed in the SCNP.

Our results suggested that spatial competition weakly influenced the assemblage organization. We observed a random use of the available spatial resources (a non-structure pattern), similar to other studies dealing with anurans in the Atlantic Forest and Caatinga biomes (Leite Filho et al., 2015; Protázio et al., 2015; Caldas et al., 2019). Additionally, most species used at least three microhabitat types which suggest the spatial resources seem not be a limiting factor (Pianka, 1973). Thus, the observed niche-overlapping may reflect a similar resource use but does not imply competition since the spatial niche space is not completely occupied (Oliveira & Eterovick, 2010). Anurans usually have a high plasticity and variability in the use of microhabitats (Eterovick et al., 2010; Leite Filho et al., 2017), contributing to the use of the spatial resource available without the need to segregate their niches.

Our analysis revealed that phylogeny is the main driver of microhabitat use in the studied community, as observed in other Caatinga areas (Protázio et al., 2015). By the way, phylogenetically closest species tend to share similar trait characteristics (Wiens & Graham, 2005), which may explain why they explore microhabitats similarly. We found three main guilds: arboreal anurans formed by hylids (for example, *D. soaresi*, *S. x-signatus*, *P. gonzagai*, and *T.* cf. *nigromaculatus*); semiaquatic anurans formed predominantly by leptodactylids (for example, *L. macrosternum*, *L. vastus*, *P. cuvieri*); and terrestrial anurans formed by bufonids, microhylids, and also some leptodactylids (for example, *Rhinella diptycha*, *R. granulosa*, *L.* s*yphax*, *Pleurodema diplolister*, and *D. muelleri*). This partitioning regarding the use of microhabitats is typically observed for other anuran assemblages (Afonso & Eterovick., 2007; Leite Filho et al., 2017; Caldas et al., 2019). This result reflects the evolutionary history, which promoted the separation between arboreal, semiaquatic, and terrestrial species (Báez et al., 2009).

Our findings indicate that most anurans in the SCNP exhibit an opportunistic feeding behavior, consuming a diverse array of prey items, eating 24 prey categories. Likewise, other anuran communities in the Caatinga biome presented a high variety of consumed prey (Leite Filho et al., 2015; Protázio et al., 2015). Particularly in the SCNP, only *D. muelleri* presented a specialized diet, eating ants and termites, which is a common pattern for microhylids (Blanco-Torres et al., 2015; Machado et al., 2020). In contrast, *T.* cf. *nigromaculatus* cannot be considered a specialist, although its diet was based on only two specimens, which limits the characterization of its feeding habits. Overall, anurans are classified as generalist and opportunistic predators eating whatever is available in the environment (Duellman & Trueb, 1994; Parmelee, 1999). This variety of prey items is usually associated with their foraging behaviors, microhabitats, and prey availability (Toft, 1980; Blanco-Torres et al., 2015; Blanco-Torres et al., 2020). As observed in other anuran communities in the Caatinga biome (Leite Filho et al., 2015; Caldas et al., 2019), beetles were the most consumed prey by the anurans of the SCNP, ranked among the most important prey items for the majority of species. This usually occurs due to their diversity and abundance in various environments (Leite Filho et al., 2017;

Bernardes et al., 2020), and their chitinous exoskeleton, which slows digestion and prolongs their presence in anuran stomachs (Mahan & Johnson, 2007).

The observed niche overlapping between some species in the SCNP may not imply competition because we did not identify a structured assemblage based on available trophic resources. There is no evidence of a significant competitive force in the studied assemblage, suggesting that food resources are not limiting (Pianka, 1973; Connor & Simberloff, 1979). In Brazilian semiarid regions, rainfall plays an important role in the diet of anuran communities because it increases insect abundance (Vasconcellos et al., 2010). In this context, the high availability of food resources allows different species to consume the same prey items without resulting in direct competition. It is a pattern already observed for other anuran communities in the Caatinga biome (Leite Filho et al., 2015; Protázio et al., 2015).

Additionally, we observed that ecological processes seem to be more significant in determining the use of trophic resources than historical factors. This result has also been observed in other anuran communities (Leite Filho et al., 2015; Caldas et al., 2019). Although some anurans, such as microhylids, maintain dietary patterns related to their phylogeny (Parmelee, 1999; Solé et al., 2002), the observed food plasticity for most anuran species indicates that their diet is influenced by prey availability in the environments (Almeida-Gomes et al. 2007). Therefore, the dietary pattern observed for the anurans of the SNCP is to be more affected by the local ecological conditions, reinforcing the importance of environmental filters in the dynamics of these systems.

Our results suggest that the available resources are not a limiting factor, leading to the absence of spatial and trophic niche partitioning. It is noteworthy, however, that the structure of the assemblage may be shaped by other factors or interactions. Most of these anurans were generalists in their use of microhabitats and exhibited opportunistic feeding habits.

Furthermore, phylogenetic and ecological filters play a fundamental role in shaping the structure of anuran assemblages in the SCNP. Additionally, phylogenetic and ecological filters drive the anuran assemblage structure in the SCNP. This National Park provides a protected environment with diverse and abundant resources, increasing the species' fitness in the studied community. Our study contributes to a better understanding of the anuran assemblage structure in the SCNP and provides important information about anuran networks in the Caatinga biome.

ACKNOWLEDGEMENTS

We are grateful to the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Fundação Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and Fundação de Amparo à Pesquisa do Estado do Piauí (FAPEPI) for financial support (Finance Code 001; 150013/2023-0), and the ICMBio for the collection license (Permit: ICMBio 87498-1). NLAR thanks the CAPES for granting a research grant (8888.7827305/2023-00) and Programa de Pós-graduação em Ecologia e Conservação da Biodiversidade, da Universidade Estadual de Santa Cruz (PPGECB UESC) for their financial support. JGGS thanks the Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico for a postdoc fellowship granted to JGGS (FUNCAP/CNPq: FC3-0198-00136.01.00/22; 150110/2023-5). We thank the Federal Institute of Piauí for the logistical support in the field and for the use of the laboratory. This study was approved by the Ethics Committee on the Use of Animals of the Instituto Federal do Piauí (CEUA/IFPI – 02/2024).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

N.L.A.R. – research, methodology, project administration, writing-original draft, writing-review and editing. K.C.A. – research, methodology, project administration and resources, formal analysis, writing-review and editing. J.G.G.S. – formal analysis, research, and writing-review & editing. E.B.A. – contributed to supervision and writing-review, editing. M.S. – contributed to supervision and writing-review and editing.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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FIGURE LEGENDS

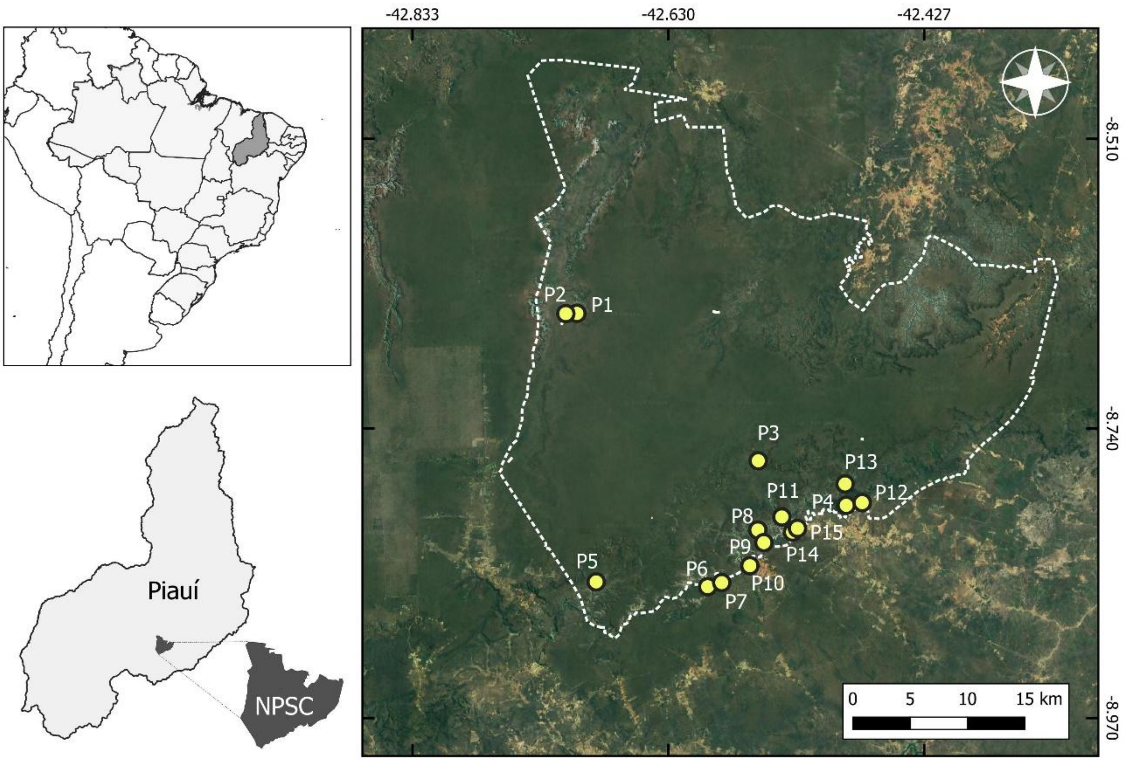

Figure 1. Geographical location of the Serra da Capivara National Park (SCNP), Piauí state, Northeastern Brazil. Yellow points representing the sampling sites

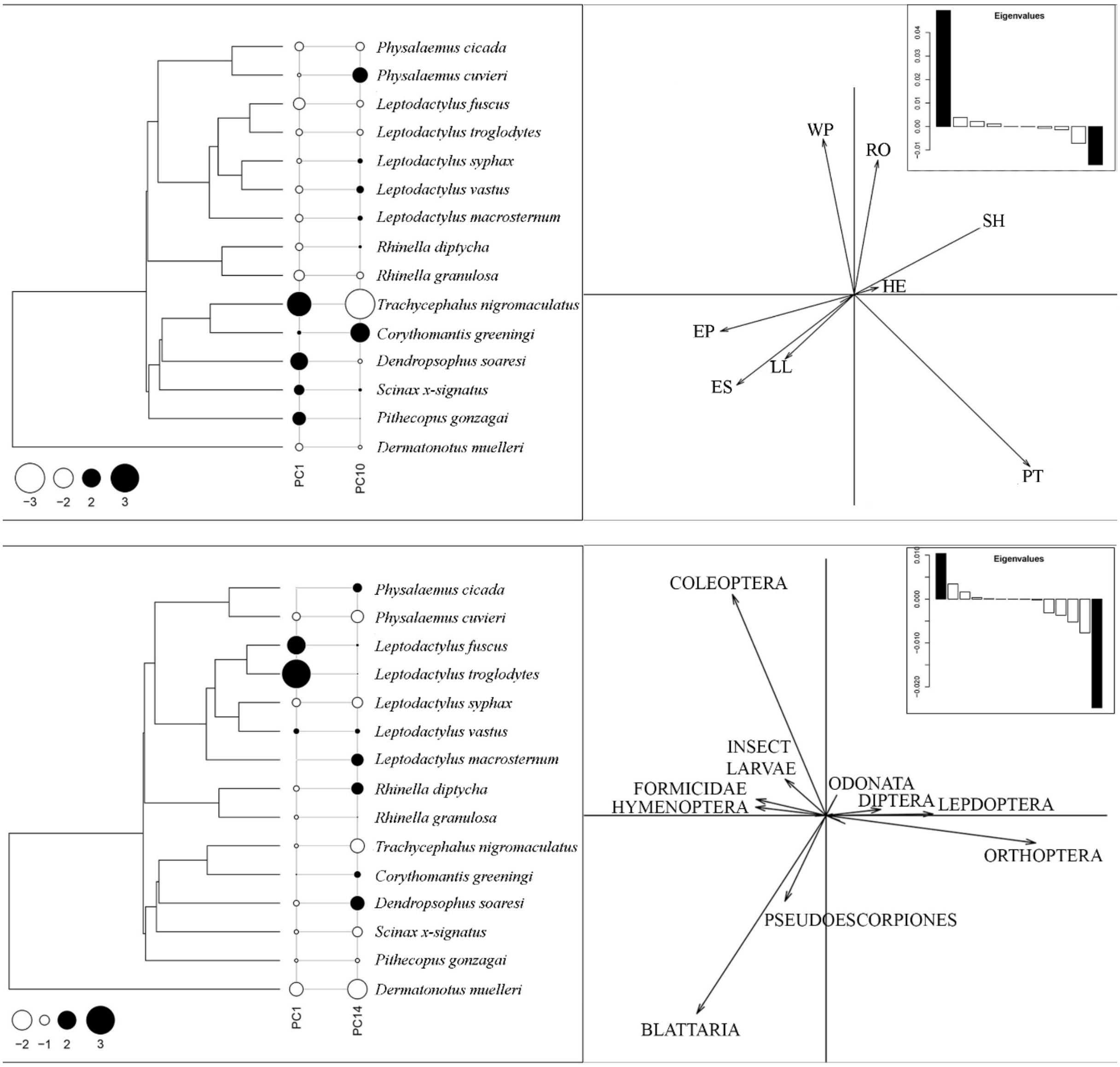

Figure 2. Phylogenetic principal component analyses for anuran microhabitat use (A) and diet (B) in the Serra da Capivara National Park. The left-hand panels show trees built for the anuran assemblage that incorporate the first global (black circles) and local (white circles) principal components. Circle size is proportional to score value. Eigenvalue bar plots in the right-hand panels correspond to global (left) and to local (right) principal components. Trophic categories close to 0 on both X and Y axes were omitted. Acronyms for microhabitat types were presented in material and methods.

TABLE LEGENDS

Table 1. Anuran species observed in the Serra da Capivara National Park, Piauí State, Northeastern Brazil.

Taxa	**Nmh**	**Ncl**	**Bspatial**	**Bvol**
BUFONIDAE				
Rhinella diptycha (Cope, 1862)	122	11	3.88	2.26
Rhinella granulosa (Spix, 1824)	21	11	2.15	3.81
HYLIDAE				
Corythomantis greeningi Boulenger, 1896	25	14	2.99	3.42
Dendropsophus soaresi (Caramaschi and Jim, 1983)	31	22	2.67	2.11
Scinax x-signatus (Spix, 1824)	51	22	3.51	2.70
Pithecopus gonzagai Andrade, Haga, Ferreira, Recco-Pimentel, Toledo, and Bruschi, 2020	38	27	3.25	4.09
Trachycephalus cf. *nigromaculatus* Tschudi, 1838	7	2	1	1.91
LEPTODACTYLIDAE				
Leptodactylus fuscus (Schneider, 1799)	36	27	2.61	6.27
Leptodactylus macrosternum Miranda-Ribeiro, 1926	10	07	3.57	2.60
Leptodactylus syphax Bokermann, 1969	22	16	5.03	2.19
Leptodactylus troglodytes Lutz, 1926	52	26	4.02	2.29

Leptodactylus vastus Lutz, 1930	81	10	3.40	6.19
Physalaemus cicada Bokermann, 1966	14	14	3.05	2.96
Physalaemus cuvieri Fitzinger, 1826	25	18	1.89	2.21
Pleurodema diplolister (Peters, 1870)	1	1	-	-
MICROHYLIDAE				
Dermatonotus muelleri (Boettger, 1885)	21	11	3.21	1.16

Legends: number of microhabitats used by the anurans (Nmh), number of collected specimens (Ncl), spatial niche breadth (Bspatial), and volumetric trophic niche breadth (Bvol).

Table 2. Spatial (above the diagonal) and trophic (below the diagonal) niche overlap indices between pairs of anuran species observed in the Serra da Capivara National Park, Piauí State, Northeastern Brazil. Rd - *Rhinella diptycha*; Rg - *Rhinella granulosa*; Cg - *Corythomantis greeningi*; Ds - *Dendropsophus soaresi*; Ss - *Scinax x-signatus*; Tn - *Trachycephalus* cf. *nigromaculatus*; Lf - *Leptodactylus fuscus*; Lm - *Leptodactylus macrosternum*; Ls - *Leptodactylus syphax*; Lt - *Leptodactylus troglodytes*; Lv - *Leptodactylus vastus*; Pc - *Physalaemus cicada*; Pcu - *Physalaemus cuvieri*; Dm - *Dermatonotus muelleri*; Pg - *Pithecopus gonzagai*.

Species	Rd	Rg	Cg	Ds	Ss	Tn	Lf	Lm	Ls	Lt	Lv	Pc	Pcu	Dm	Pg
Rd		0.67	0.54	0.08	0.23	0.00	0.86	**0.97**	0.88	0.59	0.85	0.54	0.33	0.53	0.07
Rg	0.29		0.21	0.15	0.23	0.00	0.72	0.55	0.49	0.76	0.46	0.85	0.35	0.88	0.13
Cg	0.63	0.47		0.20	0.26	0.13	0.10	0.54	0.65	0.18	0.56	0.13	0.65	0.28	0.15
Ds	0.85	0.50	0.62		0.87	0.58	0.09	0.05	0.04	0.11	0.03	0.11	0.01	0.12	0.85
Ss	0.13	0.49	0.53	0.03		0.18	0.22	0.19	0.23	0.32	0.14	0.26	0.06	0.25	0.75
Tn	0.05	0.19	0.13	0.00	0.48		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.36
Lf	0.33	0.29	0.56	0.38	0.24	0.09		0.84	0.62	0.61	0.74	0.58	0.11	0.52	0.08
Lm	0.77	0.46	0.62	**0.96**	0.03	0.00	0.49		0.84	0.45	**0.93**	0.42	0.39	0.41	0.05
Ls	0.28	0.40	0.40	0.20	0.87	0.52	0.09	0.19		0.64	0.75	0.58	0.45	0.54	0.04
Lt	0.13	0.24	0.45	0.13	0.22	0.00	0.53	0.13	0.05		0.34	0.94	0.26	0.89	0.09
Lv	0.53	0.28	0.51	0.44	0.15	0.00	0.30	0.40	0.10	0.23		0.35	0.60	0.40	0.03

Pc	0.69	0.45	**0.96**	0.68	0.40	0.06	0.54	0.65	0.30	0.57	0.54		0.40	**0.96**	0.10
Pcu	0.16	0.49	0.45	0.02	**0.95**	0.50	0.12	0.01	**0.92**	0.16	0.14	0.32		0.57	0.01
Dm	0.13	0.36	0.24	0.01	0.88	0.54	0.00	0.00	**0.96**	0.00	0.02	0.12	**0.94**		0.10
Pg	0.29	0.75	0.66	0.35	**0.91**	0.42	0.40	0.35	0.83	0.26	0.25	0.55	0.86	0.77	

Table 3. Diet composition of the anuran species in the Serra da Capivara National Park, Piauí State, Northeastern Brazil. Values represent the index of relative importance of each prey category. See Table 2 for definition of species abbreviations

Prey categories	Species														
	Rd	Rg	Cg	Ds	Ss	Tn	Lf	Lm	Ls	Lt	Lv	Pc	Pcu	Dm	Pg
Invertebrates															
Acarina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.67
Araneae	0.88	-	4.96	-	-	-	3.31	-	2.39	-	-	-	9.77	-	-
Blattaria	13.65	27.95	20.27	-	26.06	56.42	-	-	47.43	-	-	16.72	46.16	85.12	34.68
Coleoptera	33.53	12.08	30.96	42.80	12.28	-	20.41	33.20	15.19	20.28	26.48	25.72	4.07	-	15.06
Diplopoda	1.23	-	-	-	-	-	-	-	-	-	1.78	-	-	-	-
Dermaptera	-	-	-	-	-	-	-	-	1.15	-	-	-	-	-	-
Diptera	-	-	4.52	-	17.36	-	21.22	-	-	-	-	-	-	-	7.08
Formicidae	36.54	28.08	-	25.41	5.98	-	1.97	15.23	11.68	-	14.56	26.07	24.82	14.88	-
Gastropoda	-	-	-	-	-	-	-	9.33	-	-	3.53	-	-	-	-
Hemiptera	0.85	-	-	-	-	-	-	-	-	-	2.22	-	-	-	-
Hymenoptera	0.90	21.76	-	31.79	-	-	5.19	16.02	4.05	-	3.42	4.96	-	-	12.76
Insect larvae	6.18	10.13	35.28	-	27.89	-	12.36	-	4.65	52.90	13.50	18.86	15.20	-	22.50
Lepidoptera	4.36	-	4.01	-	-	-	17.67	26.21	2.37	-	10.23	-	-	-	4.24
Mantodea	-	-	-	-	-	-	-	-	2.49	-	-	-	-	-	-
Odonata	-	-	-	-	-	-	-	-	1.17	-	9.83	-	-	-	-

Orthoptera	-	-	-	-	-	-	11.97	-	-	26.82	-	7.67	-	-	-
Scolopendromorpha	-	-	-	-	-	-	-	-	-	-	4.65	-	-	-	-
Scorpiones	0.96	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phasmatodea	-	-	-	-	-	-	-	-	3.36	-	-	-	-	-	-
Plecoptera	-	-	-	-	10.42	-	-	-	-	-	-	-	-	-	-
Pseudoescorpiones	-	-	-	-	-	43.58	5.91	-	-	-	-	-	-	-	-
Vertebrates															
Anura (adult)	-	-	-	-	-	-	-	-	-	-	7.78	-	-	-	-
Anura (larvae)	0.91	-	-	-	-	-	-	-	2.30	-	-	-	-	-	-
Lizard	-	-	-	-	-	-	-	-	1.73	-	2.03	-	-	-	-
Prey total	11	5	6	3	6	2	09	5	13	3	12	6	5	2	7

3. Chapter 2: Assessing the effect of local heterogeneity on anuran diversity in the Serra da Capivara National Park, Piauí State, Brazil

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Abstract. Anurans are among the most diverse groups of vertebrates globally, and environmental heterogeneity plays a key role in shaping their diversity patterns. This study aimed to update the anuran checklist of the Serra da Capivara National Park, Piauí State, northeastern Brazil, and investigate the influence of local heterogeneity on anuran abundance and richness. We recorded 16 anuran species across five families - Bufonidae, Hylidae, Leptodactylidae, Microhylidae, and Phyllomedusidae - most of which are typical Caatinga species or widely distributed taxa. Our results indicate that local heterogeneity did not significantly affect species richness; however, it had a notable impact on anuran abundance. We highlight the importance of heterogeneous habitats in supporting larger anuran populations and enhancing population stability. This study contributes to the understanding of biodiversity patterns and the primary environmental factors affecting anuran communities in Serra da Capivara National Park, offering insights to inform current and future conservation strategies.

Keywords. abundance, amphibians, biodiversity patterns, Caatinga, checklist, conservation unit, semiarid, species richness

Introduction

Amphibians are among the most diverse vertebrate groups, with 8827 species registered worldwide (Frost 2024). They were the first vertebrates to colonize terrestrial environments in the Devonian period, approximately 300 million years ago (Bray and Lawson 1985). Morphophysiological adaptations enabled amphibians to occupy a wide range of habitats, including aquatic, terrestrial, and arboreal environments (Vitt and Caldwell 2013), and their varied reproductive strategies (Crump 2015) have contributed significantly to the group's diversification. Most amphibian species are found in Neotropical regions (Duellman and Trueb

1994), with Brazil hosting the highest amphibian diversity worldwide, where anurans dominate in terms of species richness (Segalla et al. 2021).

Anurans play vital ecological roles, participating in various trophic interactions (Toledo et al. 2007; Ceron et al. 2019) and serving as bioindicators of environmental quality (Lebboroni et al. 2006; Calderon et al. 2019). As such, they contribute to maintaining ecosystem stability and functions (Hocking and Babbitt 2014). Anurans are present in all Brazilian biomes, including the semiarid Caatinga biome (Garda et al. 2017) in northeastern Brazil, which, despite being historically understudied, harbors a high diversity of species. To date, 116 anuran species have been cataloged in the Caatinga, including several endemic taxa (Silva 2022).

Among the states within the Caatinga biome, Piauí is one of the few to have an anuran checklist with 54 species registered (Roberto et al. 2013). The last decade has seen a surge in herpetofaunal research in the state, primarily conducted within Conservation Units (UCs) such as National Parks (e.g., Dal-Vechio et al. 2016; Araújo et al. 2020a; Marques et al. 2023) and Environmental Protection Areas (e.g., Andrade et al. 2016; Araújo et al. 2020b). Nevertheless, unprotected areas outside these UCs also harbor a rich anuran fauna (Benício et al. 2014, 2015). Of the 44 UCs in Piauí, herpetological studies have been conducted in only eight (Pantoja et al. 2022), and some of these are still considered under-sampled, as is the case with Serra da Capivara National Park, where only seven anuran species have been documented so far (Calvacanti et al. 2014).

Understanding the main drivers of anuran diversity is a complex task, as these animals are highly sensitive to environmental conditions (Hopkins 2007). Local habitat heterogeneity has been identified as a key factor influencing anuran diversity in otherwise homogeneous landscapes (e.g., Afonso and Eterovick 2007; Silva et al. 2011; Andrade et al. 2019; Mausberg et al. 2023), including in Piauí State (Andrade et al. 2016; Araújo et al. 2018). According to this hypothesis, more heterogeneous areas tend to support greater species diversity (MacArthur and MacArthur 1961). However, it remains unclear which specific environmental variables play the most significant role in shaping anuran diversity patterns. To address this knowledge gap, we (i) characterized the anuran fauna of Serra da Capivara National Park (SCNP), Piauí State, Brazil, and (ii) tested how local habitat heterogeneity influences anuran abundance and species richness.

Material and methods

Study area

This study was conducted in the Serra da Capivara National Park (SCNP), located in the state of Piauí, northeastern Brazil (Fig. 1). The park, established by Federal Decree No. 83.548 on June 5, 1979, spans a total area of 130,000 hectares (BRASIL 1990). Although SCNP is situated within the Caatinga biome (IBGE 2019), it is characterized by a mosaic of vegetation types with high species richness. The area includes a variety of vegetation forms, such as tall and dense shrublands, arboreal communities, medium-density woodlands, low shrublands, and mixed shrub-arboreal habitats (Lemos 2004). Rainfall is concentrated primarily between November and April, with an average annual precipitation exceeding 600 mm and a mean temperature of 26 °C (Lemos and Rodal 2002; Aquino and Oliveira 2017).

Sampling

We conducted four expeditions, each lasting five consecutive days, from December 2023 to April 2024 in SNCP, totaling 20 sampling days. We used as sampling methodology visual and auditory searches (Heyer et al. 1994) in different environments used by anurans within the park. A total of 15 sampling points were randomly chosen according to the vocalization activities of the anurans (Table 1). Fieldwork was carried out by five researchers, beginning at 18:00 h and concluding at 00:00 h each night. We surveyed three points per night, spending approximately 1.5 hours at each site. This resulted in a total sampling effort of 600 hours (5 researchers x 120 hours). A single voucher specimen for each species was collected and deposited in the Coleção Biológica of the Instituto Federal de Ciência e Tecnologia do Piauí, Campus Pedro II (CBPII), Piauí State, northeastern Brazil.

Environmental variables of sampling points

We measured a set of nine abiotic and biotic variables at each of the 15 sampling points (Table 2). These variables were selected as they are considered strong indicators of local heterogeneity in anuran communities (e.g., Silva et al. 2011; Araújo et al. 2018; Mausberg et al. 2023). The sampling points were distributed across different habitats: three in natural ponds, three in artificial ponds, and eight in modified ponds (Fig. 2). To minimize observer bias, all variables were consistently measured by the same researcher (NLRA).

Statistical analyses

We used sample-based accumulation curves (Gotelli and Colwell 2001) with 1000 randomizations based on an incidence matrix to evaluate our sampling efficiency. To estimate expected species richness in SCNP, we applied the non-parametric estimators CHAO 2 and JACKKNIFE 1 (Magurran and McGill 2011), each with 100 randomizations. To compile abundance data and avoid biases in interpretation, we used the highest abundance value recorded among the four expeditions (Andrade et al. 2019).

Considering the SCNP is a UC located in the Caatinga biome, we compared the diversity of anurans registered in the present study with 13 other localities within this biome characterized by the Caatinga *sensu stricto* as the predominant plant physiognomy: Picos municipality (PICOS), Piauí State (Benício et al. 2015); Seridó Ecological Station (SERID), Rio Grande do Norte State (Caldas et al. 2016); Catimbau National Park (CATNP) and Serrita municipality (SERR), Pernambuco State (Pedrosa et al. 2014; Pereira et al. 2015); São João do Cariri (SJCA) and Cabaceiras (CABAC) municipalities, Paraíba State (Vieira et al. 2009; Leite-Filho et al. 2015; Protázio et al. 2015; Cascon and Langguth 2016); Aiuaba Ecological Station

(AIUAB), Rio Salgado Basin (BHRS), Middle Jaguaribe River (JAGUA), and the municipalities of Farias Brito (FBRIT) and Itapipoca (ITAP), Ceará State (Santana et al. 2015; Ávila et al. 2017; Costa et al. 2018; Castro et al. 2018; Silva-Neta et al. 2018; Oliveira et al. 2021); and Raso da Catarina Ecological Station (RCAT) and Nordestina municipality (NORD), Bahia State (Garda et al. 2013; Leite et al. 2019). For this analysis, we constructed a matrix with presence and absence data for 43 anuran species, excluding species having an uncertain specific identification ("gr." – group, "aff." – affinity with a known species, and "sp." – exact species is unknown) and considering only species with an identification to be confirmed ("cf."). Thereafter, we performed a cluster analysis by Unweighted Pair Group Average Method (UPGAM) to illustrate the similarity between the anuran composition of the SCNP and other Caatinga areas.

We first tested the normality of the variables using the SHAPIRO-WILK test and log-transformed those that did not meet normality assumptions (Shapiro-Wilk $p < 0.05$), which applied only to species abundance data. To detect collinearity among the variables, we calculated the Variance Inflation Factors (VIF) and excluded any variable with a VIF ≥ 10 (James et al. 2013), resulting in the removal of pond size from the analysis. We then constructed Generalized Linear Models (GLMs) to assess the effect of predictor variables—pond margin profile, percentage of vegetation within the pond, vegetation types within the pond, types of marginal vegetation, pond location, number of ponds at the sampling point, depth of the largest pond, and pond type—on response variables (anuran richness and abundance). Our general model was defined as: Response variable (richness or abundance) ~ predictor variables, family = poisson (link = "log").

We then used Akaike's Information Criterion with second-order bias correction for small samples (AICc) to compare models for each response variable alone or in combination (Burnham and Anderson 2002). We considered both ΔAICc and Akaike's weight (w) of each model. Models with ΔAICc lower than 2 were interpreted as having the strongest support (Burnham and Anderson 2002). Statistical analyses were performed using the R packages vegan (Oksanen et al. 2019), bbmle (Bolker 2020), dendextend (Leonnardi et al. 2018), factoextra (Kassam et al. 2020), ggplot2 (Wickham 2016), and usdm (Naimi 2015).

Results

We recorded a total of 551 individuals representing 16 anuran species across five families: Bufonidae (*N* = 2), Hylidae (*N* = 4), Leptodactylidae (*N* = 8), Microhylidae (*N* = 1), and Phyllomedusidae (*N* = 1) (Table 3, Fig. 3). The most abundant species were *Leptodactylus troglodytes* (*N* = 77), *Scinax x-signatus* (*N* = 72), and *Pithecopus gonzagai* (*N* = 65), while *Trachycephalus* cf. *nigromaculatus* (*N* = 7) and *Pleurodema diplolister* (*N* = 1) were the least abundant. All species are classified as "Least Concern" (LC) according to the IUCN Red List Categories and Criteria (IUCN, 2024).

The species accumulation curve indicated a strong tendency toward stabilization (Fig. 4), with observed species richness accounting for approximately 90% of the richness estimated by the non-parametric JACKKNIFE 1 estimator (17.9 ± 1.34) and about 95% of that estimated by CHAO 2 (16.9 ± 2.19). Consequently, we anticipate the discovery of at least two additional species in the study area.

We observed the formation of four clusters regarding the anuran composition of the Caatinga *sensu stricto* areas analyzed: the first one was formed by São João do Cariri and the Cabaceiras municipalities, Paraíba State, and the Itapipoca municipality, Ceará State. The second one is the largest cluster with seven areas within Ceará, Pernambuco, Piauí, and Rio Grande do Norte states. The anuran composition of the SCNP was more similar to those registered in the Catimbau National Park, Pernambuco State, and Nordestina municipality, Bahia State. The Raso da Catarina Ecological Station was isolated in the cluster analysis (Fig. 5).

Regarding the variables analyzed, we found that local habitat heterogeneity did not significantly influence anuran richness in SCNP ($P > 0.05$); however, it played a crucial role in explaining anuran abundance. Specifically, significant variables included margins profile (z-value = 2.907, $P = 0.003$), types of marginal vegetation (z-value = 2.304, $P = 0.021$), percentage of vegetation cover within ponds (z-value = 4.070, $P < 0.001$), number of ponds at the sampling point (z-value = 5.600, $P < 0.001$), depth of the largest pond at the sampling point (z-value = 2.991, $P = 0.002$), and type of ponds at the sampling point (z-value = -3.211, $P = 0.001$; Supplementary material, Appendix 1). Furthermore, based on Akaike's Information Criterion, the model incorporating all significant variables together provided a better explanation of anuran abundance in SCNP than models considering each variable in isolation (Supplementary material, Appendix 2).

Discussion

We identified 16 anuran species in the Serra da Capivara National Park (SCNP), which accounts for approximately 30% of the anurans known from Piauí State (Roberto et al. 2013). In addition, we recorded more than double the number of anuran species previously documented for the SCNP (Calvacanti et al. 2014). This level of species richness is considered moderate when compared to other studies conducted in areas of Caatinga *stricto sensu* (e.g., Pedrosa et al. 2014; Benício et al. 2015). It is interesting to highlight that the anuran composition of the SCNP was more similar to those recorded in the Catimbau National Park, Pernambuco State (Pedrosa et al. 2014) and Nordestina municipality, Bahia State (Leite et al. 2019). It is unclear why these locations are more similar, given their geographical distances. Thus, Brazilian state divisions did not seem to be predominant regarding differences in the composition of anurans in the Caatinga biome. In addition, we suggest further studies aiming to investigate the main factors filters driving the anuran composition dissimilarity in different localities of this biome.

When focusing solely on conservation units in Piauí State, the number of species in SCNP is lower than in other protected areas, such as Uruçuí–Una Ecological Station (Dal-Vechio et al. 2013; 26 species), Sete Cidades National Park (Araújo et al. 2020a; 30 species), Serra das Confusões National Park (Marques et al. 2023; 29 species), and the Environmental Protection Area Delta do Parnaíba (Araújo et al. 2020b; 33 species). Notably, except for SCNP and Uruçuí–Una Ecological Station, all other conservation units are situated within ecotonal regions of the Caatinga and Cerrado biomes. Ecotones are typically characterized by high biodiversity (Kark 2013), which may help explain the observed variation in species richness.

In terms of anuran species composition, most species identified are considered widespread across Brazilian biomes, including *Rhinella diptycha*, *Scinax x-signatus*, *Leptodactylus fuscus*, *L. macrosternum*, *L. syphax*, *L. vastus*, *Physalaemus cuvieri*, and *Dermatonotus muelleri* (Frost 2024). Although we did not document any endemic species, we did encounter several species commonly associated with the Caatinga biome, such as *Corythomantis greeningi*, *Pleurodema diplolister*, *Pithecopus gonzagai*, *Physalaemus cicada*, and *Rhinella granulosa* (Garda et al. 2017).

Overall, the families Leptodactylidae and Hylidae exhibited the highest diversity within the SCNP, a pattern that is frequently observed in the Neotropical region (Duellman 1978). Similar findings have been reported in the Caatinga biome (Arzabe 1999; Vieira et al. 2007; Pedrosa et al. 2014), including various conservation units in Piauí State (e.g., Araújo et al. 2020a; Marques et al. 2023). Due to the spatial segregation between leptodactylids and hylids (Protazio et al. 2015; Leite-Filho et al. 2017; Caldas et al. 2019), anurans from these families typically coexist habitually and stably in diverse environments.

We found that anuran richness in the Serra da Capivara National Park (SCNP) was not significantly influenced by local heterogeneity, regardless of whether the sampling ponds were natural, modified, or artificial. While some studies have similarly reported a lack of support for this relationship (e.g., Vasconcelos et al. 2009; Gouveia and Faria 2015), such a pattern is atypical since more heterogeneous environments generally support higher species richness (e.g., Tews et al. 2004; Lorenzón et al. 2016; Andrade et al. 2016; Araújo et al. 2018; Piña et al. 2019), particularly among anuran communities (e.g., Silva et al. 2011; Couto et al. 2017; Andrade et al. 2016, 2019; Figueiredo et al. 2019). The absence of a relationship between richness and local heterogeneity may be attributed to the prevalence of habitat-generalist species that are typical of Caatinga environments, which are present across all sampling points. These species are adapted to explore a variety of ponds within these landscapes due to their strategies for surviving in semiarid conditions. This finding aligns with Gouveia and Faria (2015), who suggested that anurans in the Caatinga exhibit stochastic usage patterns of available water bodies.

In contrast, we observed that sampling points with a higher percentage of vegetation within the ponds and a greater diversity of marginal vegetation tended to support greater anuran abundance. Additionally, the characteristics of the ponds played a significant role in influencing anuran abundance. Other studies have similarly highlighted the impact of vegetation and pond characteristics on anuran populations (e.g., Bickford et al. 2010; Dória et al. 2015; Agostini et al. 2021). Generally, more heterogeneous areas provide greater resources (MacArthur and MacArthur 1961), which can reduce both intraspecific and interspecific competition (Morin 2011). Consequently, more heterogeneous sampling areas within the SCNP facilitate the coexistence of a higher number of individuals.

This study enhances the understanding of biodiversity in the Serra da Capivara National Park by presenting an updated anuran checklist, which may inform current and future conservation strategies. Furthermore, we found that local heterogeneity influences population sizes, emphasizing the importance of heterogeneous environments in promoting stable anuran populations. Notably, artificial drinking fountains designed to support vertebrate populations during the dry season also contribute to anuran diversity, as some species utilize these structures for reproduction and establish nearby populations. Although our study is pioneering in exploring the primary drivers of anuran diversity in the SCNP, further research is essential to deepen our understanding of the ecological processes shaping these anuran communities.

Acknowledgements

We are grateful to CNPq/CAPES/FAPEPI for financial support (Finance Code 001; 150013/2023-0), and ICMBio for the collection license (Permit: ICMBio 87498-1). NLAR thanks CAPES for granting a research grant (8888.7827305/2023-00) and Programa de Pós-graduação em Ecologia e Conservação da Biodiversidade, da Universidade Estadual de Santa Cruz (PPGECB UESC) for financial support. MS acknowledges funding by CNPq through a research scholarship (309365/2019-8). We thank the Federal Institute of Piauí for the logistical support in the field and for the use of the laboratory. This study was approved by the Ethics Committee on the Use of Animals of the Instituto Federal do Piauí (CEUA/IFPI – 02/2024).

Conflict of interest

The authors declare that there is no conflict of interest.

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FIGURE LEGENDS

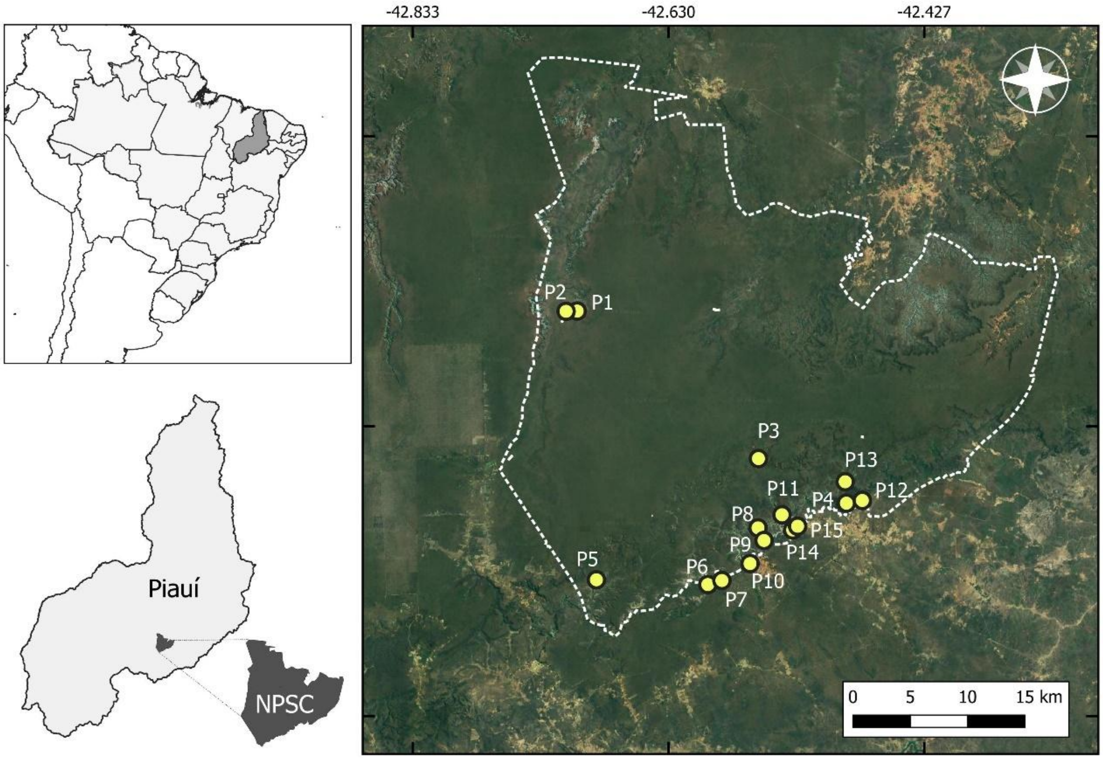

Figure 1. Geographical location of the Serra da Capivara National Park (SCNP), Piauí State, northeastern Brazil, with the distribution of the 15 sampling points

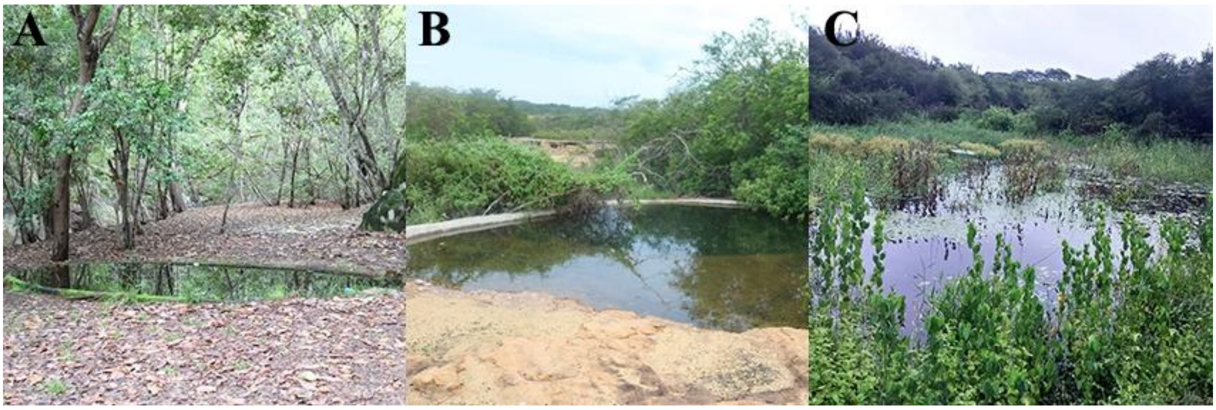

Figure 2. Sampled environments in the Serra da Capivara National Park, Piauí State, northeastern Brazil. Images **A**, **B**, and **C** represent, respectively, artificial, modified, and natural ponds

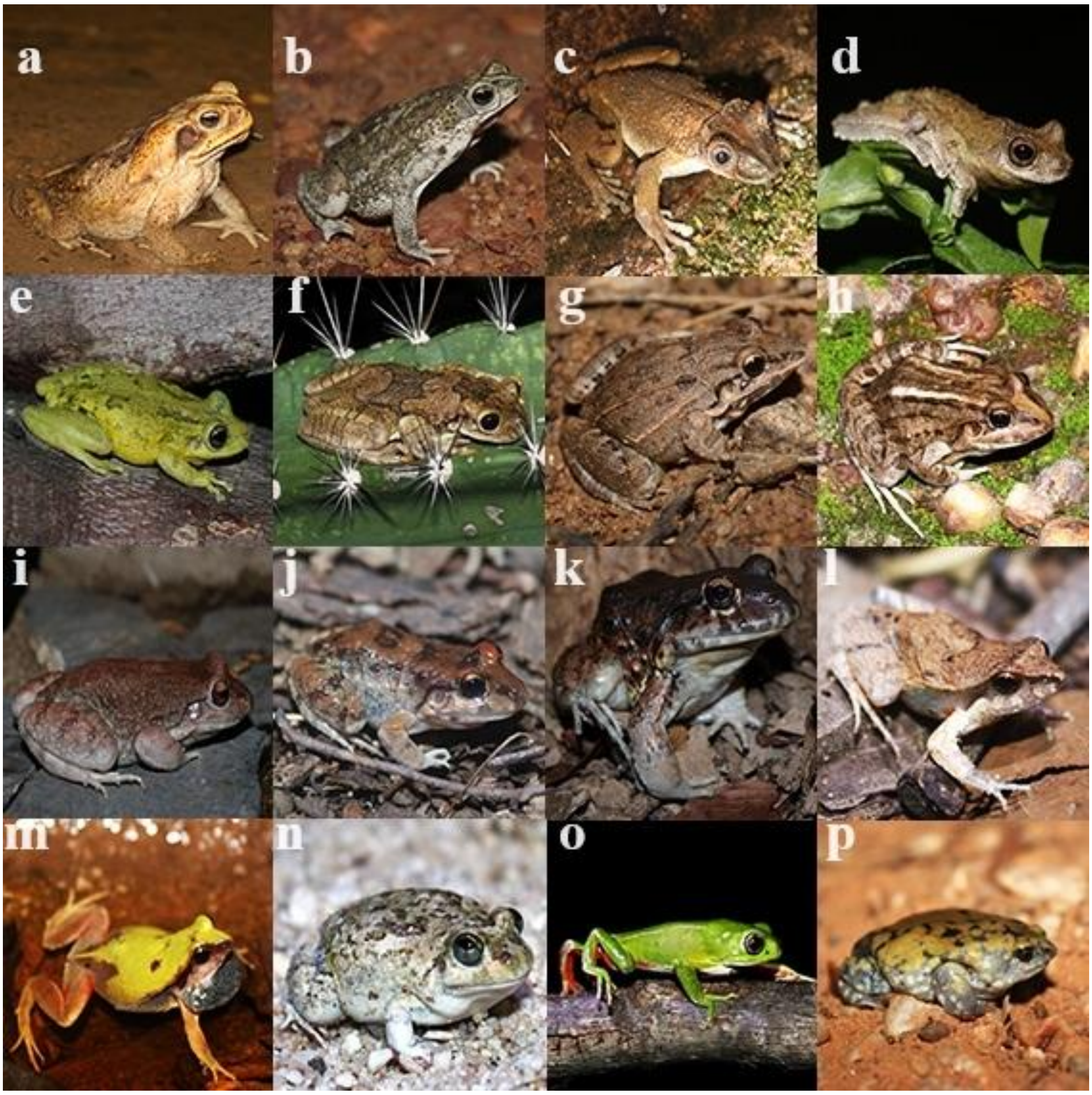

Figure 3. Anurans registered in the Serra da Capivara National Park, Piauí State, northeastern Brazil: a) *Rhinella diptycha*, b) *Rhinella granulosa*, c) *Corythomantis greeningi*, d) *Dendropsophus soaresi*, e) *Scinax x-signatus*, f) *Trachycephalus* cf. *nigromaculatus*, g) *Leptodactylus fuscus*, h) *Leptodactylus macrosternum* i) *Leptodactylus syphax*, j) *Leptodactylus troglodytes*, k) *Leptodactylus vastus*, l) *Physalaemus cicada*, m) *Physalaemus cuvieri*, n) *Pleurodema diplolister*, o) *Pithecopus gonzagai*, p) *Dermatonotus muelleri*

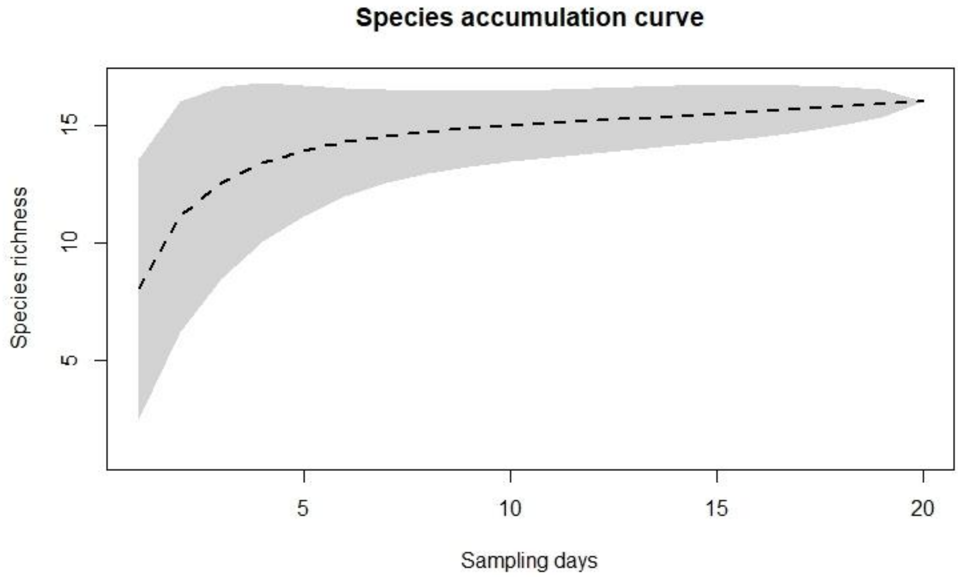

Figure 4. Accumulation curve for anurans sampled in the Serra da Capivara National Park, Piauí State, northeastern Brazil, based on the number of samples, constructed from 1000 randomizations

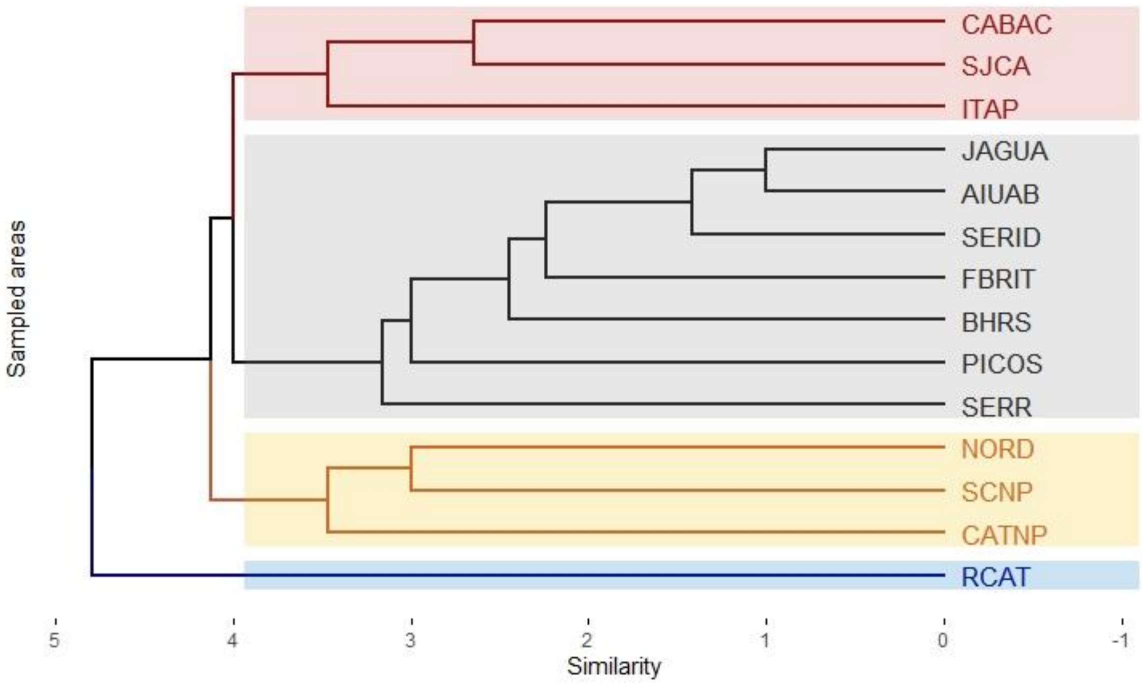

Figure 5. Similarity (Jaccard index and clustering method "UPGMA") among the anuran species composition in areas of Caatinga sensu stricto

TABLE LEGENDS

Table 1. Environmental description of the 15 sampling points in the Serra da Capivara National Park, Piauí State, northeastern Brazil

Sampling points	Geographic coordinates	Description
P1	8°38.92'S; 42°42.15'W	Artificial drinking fountain surrounded by shrubs and trees
P2	8°38.93'S; 42°42.68'W	Artificial drinking fountain surrounded by shrubs and trees
P3	8°45.97'S; 42°33.52'W	Temporary pond with shrub and tree vegetation inside and on the edge of the pond
P4	8° 48.07' S; 42° 36.55'W	Temporary pond with shrub and tree vegetation inside and on the edge of the pond
P5	8° 51.72' S; 42° 41.24' W	Rocky outcrop modified to accumulate water for longer, presence of thorny shrub and tree vegetation.
P6	8° 51.94' S; 42° 35.93' W	Artificial drinking fountain surrounded by shrubs and trees
P7	8° 51.75' S; 42° 35.26' W	Modified passage that accumulates water surrounded by shrubs and trees
P8	8° 49.24' S; 42° 33.54' W	Modified pond located inside the cave
P9	8° 49.85' S; 42° 33.25' W	Modified passage that accumulates water surrounded by shrubs and trees
P10	8° 50.94' S; 42° 33.92' W	Modified pond located inside the cave
P11	8° 48.62' S; 42° 32.40' W	Artificial drinking fountain surrounded by shrubs and trees
P12	8° 47.94' S; 42° 28.57' W	Temporary pond with shrub and tree vegetation inside and on the edge of the pond
P13	8° 47.05' S; 42° 29.39' W	Modified passage that accumulates water surrounded by shrubs and trees
P14	8° 49.34' S; 42° 31.89' W	Permanent reservoir with shrub and tree vegetation inside and on the edge of the pond
P15	8° 49.16' S; 42° 31.65' W	Temporary pond with shrub and tree vegetation inside and on the edge of the pond

Table 2. List of variables recorded at each sampling point within the Serra da Capivara National Park, Piauí State, northeastern Brazil, including unit, detailed nomenclature and method

Variable name	Definition	Unit	Method
Margin type	Pond edge characteristic	Three categories: plan (1), inclined (2) or both (3)	Visual characterization
Vegetation within the pond	Approximate percentual vegetation on pond surface	Four categories: No vegetation (0), < or = 20% (1), < or = 50% (2), > 50% (3)	Visual estimation
Types of vegetation within the pond	Characteristics of the vegetation (herbaceous, shrubby and arboreal) present in the water body	Four categories: no vegetation (0), one type of vegetation (1), two types (2), three types (3)	Visual characterization
Types of marginal vegetation	Characteristics of marginal vegetation (herbaceous, shrubby and arboreal) on the margin of the water body	Four categories: no vegetation (0), one type of vegetation (1), two types (2), three types (3)	Visual characterization
Pond localization	Characteristics of where the pond is located	Two categories: inside the cave (1), outside the cave (2)	Visual characterization
Pond number	Number of ponds present within a 200m radius of the largest pond	Three categories: one (1), two (2), more than two (3)	Visual characterization
Pond size	Surface area of the pond (m²) when full (if there is more than one pond, it will be considered the largest)	Four categories: < or = 3 m² (1), < or = 5 m² (2), < or = 10 m² (3), > 10 m² (4)	Measured using length, width and shape
Maximum pond depth	Maximum depth (m) when full (if there is more than one pond, it will be considered the largest)	Three categories: < or = 1 m (1), < or = 2 m (2), > 2 m (3)	Measured at deepest point of water body.
Pond type	Characterized based on the level of anthropic action	artificial (1), modified (2), natural (3)	Visual characterization

Table 3. Anurans registered in the Serra da Capivara National Park, Piauí State, northeastern Brazil, including voucher, occurrence in the SCNP, and distribution in the Brazilian biomes

Taxa	Voucher	Occurrence	Biome
BUFONIDAE			
Rhinella diptycha (Cope, 1862)	CBPII 534	1-3, 5-11,13-15	WD
Rhinella granulosa (Spix, 1824)	CBPII 536	2,3,5,6,8-12,14,15	WD
HYLIDAE			
Corythomantis greeningi Boulenger, 1896	CBPII 567	1,6,9,10,12	AT, CA, CE
Dendropsophus soaresi (Caramaschi & Jim, 1983)	CBPII 537	1-7,9,10	AT, CA, CE
Scinax x-signatus (Spix, 1824)	CBPII 528	1-6,9-12,14,15	WD
Trachycephalus cf. *nigromaculatus* Tschudi, 1838	CBPII 558	3	AT, CA, CE
LEPTODACTYLIDAE			
Leptodactylus fuscus (Schneider, 1799)	CBPII 590	10,12,14,15	WD
Leptodactylus macrosternum Miranda-Ribeiro, 1926	CBPII 583	10,11,13-15	WD
Leptodactylus syphax Bokermann, 1969	CBPII 569	2,6,8-11,13	WD
Leptodactylus troglodytes Lutz, 1926	CBPII 526	1 -15	WD
Leptodactylus vastus Lutz, 1930	CBPII 587	1,3-11,13-15	WD
Physalaemus cicada Bokermann, 1966	CBPII 585	11,12,15	
Physalaemus cuvieri Fitzinger, 1826	CBPII 531	1,3-9,13,14,15	WD
Pleurodema diplolister (Peters, 1870)	CBPII 769	11	AT, CA, CE
MICROHYLIDAE			
Dermatonotus muelleri (Boettger, 1885)	CBPII 555	3,4,6,7,9,11,12,15	WD
PHYLLOMEDUSIDAE			
Pithecopus gonzagai Andrade, Haga, Ferreira, Recco-Pimentel, Toledo & Bruschi, 2020	CBPII 548	1-6,9-14	CA, CE

Legends: Biome distribution: Caatinga (CA), Cerrado (CE), Atlantic Forest (AT), and widely distributed (WD). See Table 1 for sampling points characterization

4. CONCLUSÃO GERAL

Este estudo avança na compreensão da biodiversidade e dos processos ecológicos que moldam as comunidades de anuros no Parque Nacional Serra da Capivara (PNSC). Evidenciamos a importância de múltiplos fatores atuando sobre as comunidades, com destaque para os fatores filogenéticos e ecológicos que desempenham um papel significativo na estruturação das assembleias de anuros, assim a história evolutiva e as condições ambientais locais foram forças estruturantes importantes. Além disso, reforçamos o papel relevante da heterogeneidade local no estabelecimento e manutenção de populações de anfíbios. Aliada a atualização da lista da anurofauna do PNSC e aos dados sobre ecologia trófica e espacial, oferecemos uma base para a compreensão dos padrões de diversidade e estrutura da assembleia. Por fim, nosso estudo contribui para o fortalecimento das ações de conservação em ambientes semiáridos, assegurando a estabilidade ecológica e a preservação das interações fundamentais que sustentam essas comunidades.