UNIVERSIDADE FEDERAL DO CEARÁ
PRÓ-REITORIA DE PESQUISA E PÓS-GRADUAÇÃO
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E RECURSOS NATURAIS

CICERO RICARDO DE OLIVEIRA

INTERAÇÕES PARASITO-HOSPEDEIRO EM ANUROS DE UM ENCLAVE DE FLORESTA TROPICAL ALTITUDINAL DO SEMIÁRIDO BRASILEIRO

FORTALEZA
2023

CICERO RICARDO DE OLIVEIRA

INTERAÇÕES PARASITO-HOSPEDEIRO EM ANUROS DE UM ENCLAVE DE FLORESTA TROPICAL ALTITUDINAL DO SEMIÁRIDO BRASILEIRO

Tese apresentada a Coordenação do Programa de Pós-Graduação em Ecologia e Recursos Naturais da Universidade Federal do Ceará, como requisito parcial à obtenção do título de Doutor em Ecologia e Recursos Naturais.
Área de concentração: Ecologia e Recursos Naturais.

Orientadora: Prof.ª. Dra. Diva Maria Borges-Nojosa
Coorientador: Prof. Dr. Robson Waldemar Ávila

FORTALEZA
2023

Dados Internacionais de Catalogação na Publicação
Universidade Federal do Ceará
Sistema de Bibliotecas
Gerada automaticamente pelo módulo Catalog, mediante os dados fornecidos pelo(a) autor(a)

O46i Oliveira, Cicero Ricardo de.
Interações parasito-hospedeiro em anuros de um enclave de floresta tropical altitudinal do semiárido brasileiro / Cicero Ricardo de Oliveira. – 2023.
110 f. : il. color.

Tese (doutorado) – Universidade Federal do Ceará, Centro de Ciências, Programa de Pós-Graduação em Ecologia e Recursos Naturais , Fortaleza, 2023.
Orientação: Profa. Dra. Diva Maria Borges-Nojosa.

1. Parasitismo. 2. Anfíbios. 3. Brejos-de-altitude. 4. Semiárido Brasileiro. I. Título.
CDD 577

CICERO RICARDO DE OLIVEIRA

INTERAÇÕES PARASITO-HOSPEDEIRO EM ANUROS DE UM ENCLAVE DE FLORESTA TROPICAL ALTITUDINAL DO SEMIÁRIDO BRASILEIRO

Tese apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais da Universidade Federal do Ceará, como parte dos requisitos para obtenção do título de Doutor em Ecologia e Recursos Naturais. Área de concentração: Ecologia e Recursos Naturais.

Aprovado em 27 / 04 / 2023

BANCA EXAMINADORA

Profa. Dra. Diva Maria Borges-Nojosa (Orientadora)
Universidade Federal do Ceará (UFC)

Prof. Dr. David James Alexander Edward Harris
Universidade do Porto (CIBIO: U. Porto)

Prof. Dr. Reinaldo José da Silva
Universidade Estadual Paulista Júlio de Mesquita Filho (UNESP)

Prof. Dr. Drausio Honorio Morais
Universidade Federal de Uberlândia (UFU)

Prof. Dr. Samuel Cardozo Ribeiro
Universidade Federal do Cariri (UFCA)

Dedico aos meus pais (**Maria e Raimundo**), por todo amor e dedicação que sempre tiveram comigo.

AGRADECIMENTOS

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Código de Financiamento 001.

Esse trabalho de tese é fruto do esforço e colaboração de um grande número de pessoas, cujo não seria possível a realização sem a contribuição de todos.

Agradeço:

A **Maria Alcântara Pinho Oliveira** e **Raimundo Fernandes de Oliveira** (meus pais) por sempre estarem presentes e me apoiarem em todas as minhas escolhas.

A **Wilmara Mascarenhas** que sempre me incentivou e acreditou no meu trabalho, pelo companheirismo e apoio em todos os momentos, e pela ajuda na realização desse sonho.

A **Elvis**, **Rafael**, **Atilas** e **Mateus**, que sem as suas ajudas e auxílio em campo não seria possível a obtenção dos dados para esse trabalho.

A **Samuel Cardoso Ribeiro**, pela ajuda com material essencial para a análise dos dados em laboratório.

Aos colaboradores, **Daniel Cassiano**, **Guilherme Gonçalves-Sousa**, **Dalilange Batista** e **Kássio Araújo**, pela ajuda e contribuição na produção desse trabalho.

A minha orientadora Profa. **Dra. Diva Maria Borges-Nojosa**, pela orientação, amizade, e por apoiar e confiar nas minhas decisões, e principalmente por me ajudar a crescer pessoalmente e profissionalmente sobre sua supervisão.

Ao Prof. Dr. **Robson Waldemar Ávila**, pela coorientação, por acreditar no meu trabalho, por sempre estar disponível para me ajudar e corrigir os meus erros, e principalmente por me dedicar muito do seu tempo nessa longa jornada, sem sua orientação nada disso seria possível.

Aos amigos do **NUROF-UFC**, que sempre estiveram presentes e prontos a me ajudar.

Aos amigos, **Luana** e **Neilson**, pelo companheirismo e por tornarem os momentos difíceis durante essa jornada em divertidas lembranças, são amigos que levarei sempre comigo em meus pensamentos. Muito obrigado!

Ao Laboratório de Edição, Tradução e Revisão de Textos Acadêmicos (LETRARE), Universidade Federal do Ceará por revisar a versão em inglês.

A todos aqueles, que mesmo sem os conhecer, tiveram grande acolhimento durante os trabalhos de campo e permitiram a realização desse trabalho.

Ao **ICMBio** pela licença de coleta nas áreas (#73215-1).

A **coordenação do Programa de Pós-graduação em Ecologia e Recursos naturais**, por sempre atenderem as minhas demandas e pelo auxílio (PROAP) concedido durantes as viagens a campo.

Agradeço a **Springer Nature** pela concessão da licença de reutilização de artigo (5559440855958).

A **banca examinadora**, pelas valiosas considerações sobre este trabalho.

A **Universidade Federal do Ceará**, sem a qual nada disso seria possível.

E a todos que direta ou indiretamente contribuíram para o desenvolvimento deste trabalho, os meus mais sinceros AGRADECIMENTOS.

“*É melhor ser odiado pelo que você é, do que amado por aquilo que você não é*”

- Kurt Cobain

RESUMO

A heterogeneidade ambiental tem sido um fator bastante usado para explicar as diferentes riquezas de espécies no mundo, visto que a distribuição, diversidade e a riqueza das espécies podem ser determinadas pela estrutura do ambiente. Além disso, ambientes mais diversos abrigam maior riqueza de espécies. Outro aspecto que pode influenciar é o gradiente de altitude, um fator limitante para um conjunto de fatores bióticos e abióticos que influenciam a estrutura das comunidades. Esse tem sido o foco de muitos estudos em ecologia, principalmente de anfíbios, animais estritamente relacionados as condições ambientais, fazendo desses hospedeiros um excelente modelo para avaliar padrões na estrutura das comunidades de parasitos. Além disso, muitos processos são relatados influenciando a estrutura de comunidades de helmintos em anfíbios, dentro dos quais se incluem o tamanho do hospedeiro, o gênero, a dieta, o sítio da infecção, a espécie e o comportamento, levando a riqueza parasitária a variar dependendo das condições ambientais e devido à forma como as espécies respondem aos fatores bióticos. O domínio das Caatingas é conhecido por apresentar alto grau de endemismo da herpetofauna, principalmente nos enclaves de mata úmida, denominados por “brejos-de-altitude”. Considerando esses aspectos, utilizamos a Área de Proteção Ambiental da Serra de Maranguape para este estudo, principalmente devido a diversidade de microambientes. Distribuímos nove pontos amostrais ao longo de três gradientes de altitude e coletamos os anuros durante a estação chuvosa, através de busca ativa. Portanto, no presente estudo, tivemos como objetivos: (A) descrever a composição de endoparasitos associados a anuros de um enclave de floresta altitudinal no Nordeste do Brasil, a Serra de Maranguape; (B) testar a influência do uso de microhabitats na abundância e riqueza de endoparasitos; (C) testar a hipótese de que rãs maiores tendem a ser mais parasitadas; (D) testar a influência da heterogeneidade de habitats e do gradiente altitudinal nas relações parasito-hospedeiro em anfíbios anuros, quanto a abundância e riqueza dos endoparasitos; (E) testar a relação filogenética entre hospedeiros e parasitos; (F) testar a hipótese de que os parasitos são distribuídos seguindo seus hospedeiros, sem influência da variação ambiental; e (G) obter informações sobre a relação parasito-hospedeiro da helmintofauna da espécie criticamente em perigo *Adelophryne maranguapensis.*

Palavras-chave: parasitismo; anfíbios; brejos-de-altitude; semiárido brasileiro.

ABSTRACT

Environmental heterogeneity has been a factor often used to explain the different species richness around the world, since the distribution, diversity and richness of species can be determined by the structure of the environment. In addition, more diverse environments harbour higher species richness. Another aspect that may influence this is the altitude gradient, a limiting factor for a set of biotic and abiotic factors that influence the structure of communities. This has been the focus of many studies in ecology, especially of amphibians, animals strictly related to environmental conditions, making these hosts an excellent model to assess patterns in the structure of parasite communities. Many processes are reported to influence the structure of helminth communities in amphibians, including host size, genus, diet, site of infection, species and behaviour, leading parasite richness to vary depending on environmental conditions and the way species respond to biotic factors. The Caatinga domain is known to have a high degree of herpetofauna endemism, especially in wet forest enclaves, known as “brejos-de-altitude”. Considering these aspects, we will use the Environmental Protection Area of Serra de Maranguape due to the diversity of microenvironments, to carry out the study. Thus, we distributed nine sampling points along three altitude gradients and collected anurans during the rainy season, by active search. Therefore, in the present study, we aimed to (A) describe the composition of endoparasites associated with anurans from an altitudinal forest enclave in Northeast Brazil, the Serra de Maranguape; (B) test the influence of microhabitat use on endoparasite abundance and richness; (C) test the hypothesis that larger frogs tend to be more parasitized; (D) test the influence of habitat heterogeneity and altitudinal gradient on endoparasite abundance and richness; (E) test the phylogenetic relationship between hosts and parasites; (F) test the hypothesis that parasites are distributed following their hosts without influence of environmental variation; and (G) obtain information on the host-parasite relationship of the helminth fauna of the critically endangered species *Adelophryne maranguapensis*.

Keywords: parasitism; amphibians; “brejos-de-altitude”; brazilian semiarid.

LISTA DE FIGURAS

LISTA DE TABELAS

SUMARIO

1 INTRODUÇÃO GERAL

O Domínio morfoclimático da Caatinga é composto por um mosaico de florestas secas e vegetação arbustiva (savana-estépica), com enclaves de florestas úmidas montanhosas e áreas de Cerrados (TABARELLI; SILVA, 2003). Este domínio é marcado pelo alto grau de endemismo da herpetofauna, tanto em áreas abertas (RODRIGUES; SANTOS, 2008; ALBUQUERQUE *et al.*, 2012), quanto nos enclaves de mata úmida, conhecidos como "brejos-de-altitude" (BORGES-NOJOSA; CARAMASCHI, 2003; BORGES-NOJOSA *et al.*, 2016b). Conforme dados do Ministério do Meio Ambiente (2000) e Sousa e colaboradores (2004), a identificação de ações e áreas prioritárias para a conservação da biodiversidade tem-se mostrado importante instrumento de proteção no Brasil e no mundo. Classificadas em quatro níveis de importância biológica (Extrema importância biológica - EIB; Muito alta importância biológica - MAIB; Alta importância biológica - AIB; e Insuficientemente conhecida, mas de provável importância biológica - IC), no estado do Ceará são descritas 11 destas áreas, sendo elas: Planalto da Ibiapaba, Serra de Baturité, Serra de Maranguape/Aratanha e Chapada do Araripe (EIB); Camocim/Jericoacoara, Serra de Uruburetama, Quixadá/Estevão (MAIB); Serra da Meruoca, Foz do Acaraú, Foz do Rio Ceará e Baixo Jaguaribe (AIB).

Portanto, o complexo da Serra de Maranguape/Aratanha, área de estudo deste trabalho, desde então vem sendo classificada como uma das áreas de extrema importância biológica, por ser considerado um ambiente de enclave úmido, e de exceção no domínio das Caatingas, devido as condições climáticas locais. Como os demais brejos-de-altitude, a Serra de Maranguape forma um sistema isolado único e exclusivo, que deve ser considerado como um mantenedor de elementos vegetais e faunísticos amazônicos e atlânticos, além das espécies endêmicas (VANZOLINI, 1981; BORGES-NOJOSA; CARAMASCHI, 2003).

Sendo a estrutura do ambiente fundamental para determinar a distribuição, diversidade e a riqueza das espécies, MacArthur e MacArthur (1961) e MacArthur e colaboradores (1964) relacionaram a heterogeneidade do ambiente com riqueza de espécies, propondo que ambientes mais diversos abrigam maior riqueza de espécies. Esse tem sido um fator bastante usado para explicar as diferentes riquezas de espécies no mundo, tentando esclarecer o porquê de algumas regiões apresentarem maior riqueza de espécies do que outras. A partir dessa ideia, muitos estudos foram propostos na tentativa de explicar o porquê das diferenças entre riquezas em ambientes heterogêneos (HERRERA *et al.*, 2011; BILIA *et al.*, 2015; ALFARO *et al.*, 2016). Essa relação positiva entre o aumento da heterogeneidade ambiental e o aumento da riqueza já foi registrada para várias espécies de animais (SILVA *et* *al.*, 2010). No entanto, dependendo do grupo taxonômico e da escala espacial, a riqueza pode ter relação negativa com o aumento da heterogeneidade ambiental (TEWS *et al.*, 2004; GONZÁLEZ-MEGIAS *et al.*, 2007).

Outro aspecto observado que pode influenciar a riqueza de espécies é o gradiente de altitude. Segundo Colwell e Lees (2000) e Romdal e Grytnes (2007), os fatores ecológicos que influenciam a riqueza e a biologia das espécies variam em função dos gradientes altitudinais. De acordo com Rahbek (2005) a altitude é um fator limitante para um conjunto de fatores bióticos e abióticos que influenciam a estrutura das comunidades. Esse declínio na riqueza de espécies com o aumento da altitude é largamente aceito como um padrão (RAHBEK, 1995). Contudo, o padrão de variação na riqueza de espécies em gradientes ambientais pode diferir entre táxons, e em um mesmo táxon o padrão pode diferir entre localidades (ALMEIDA-NETO *et al.*, 2006). Esse tem sido o foco de muitos estudos em ecologia, principalmente de anfíbios (QIAN *et al.*, 2007; FLESCH *et al.*, 2010; LEMCKERT; MAHONY, 2010; HU *et al.*, 2012; SIQUEIRA; ROCHA, 2013).

Os anfíbios são considerados como um grupo dos vertebrados com alta diversidade no Planeta, sendo o Brasil atualmente o país com maior riqueza de espécies (SEGALLA *et al.*, 2021). Estes animais apresentam uma estreita ligação com as condições ambientais (DUELLMAN; TRUEB, 1994; WELLS, 2007), sendo os fatores abióticos importantes para determinar a riqueza e abundância de espécies, tanto em invertebrados (FERREIRA, 2010; AZEVEDO; KRÜGER, 2013; PETSCH *et al.*, 2013) quanto em vertebrados (MORENO-RUEDA; PIZARRO, 2007; QIAN *et al.*, 2007).

Amphibia é um dos grupos de animais que vem sendo bem estudado nas serras úmidas do Ceará (BORGES, 1991; BORGES-NOJOSA, 2007; RIBEIRO *et al.*, 2012; CASTRO *et al.*, 2019). Dentro dessa diversidade aparente há uma diversidade oculta de espécies de organismos que vivem dentro de outros animais, como é o caso de alguns helmintos parasitos de anfíbios (POULIN; MORAND, 2004; TOLEDO *et al.*, 2013; AGUIAR *et al.*, 2015; LINS *et al.*, 2017; ALCANTARA *et al.*, 2018; OLIVEIRA *et al.*, 2019; SILVA-NETA *et al.*, 2020; MASCARENHAS *et al.*, 2021). Segundo Aho (1990), a biologia desses hospedeiros os tornam excelentes modelos para avaliar padrões na estrutura das comunidades de helmintos. Porém, a última lista de helmintos associados a anfíbios aponta que somente cerca de 8% das espécies de anfíbios foi estudado quanto a sua helmintofauna (CAMPIÃO *et al.*, 2014). Estima-se que 40% dos seres vivos seja constituído por parasitos (BEGON, 1996), que é uma das estratégias de vida mais comuns do planeta. Mesmo assim, parasitos passaram por muito tempo despercebidos dentro da biodiversidade (POULIN; MORAND, 2004; DOBSON *et al.*, 2008).

Embora o número de estudos com parasitos seja crescente, a ciência ainda está muito distante de conhecer completamente a ecologia de espécies parasitos (POULIN; MORAND, 2004). Poucos são os trabalhos que se propõe a explicar os processos relacionados à ecologia de helmintos parasitos (POULIN; MORAND, 2004). Algumas destas publicações (HAMANN *et al.*, 2010; SANTOS; AMATO, 2010; CAMPIÃO *et al.*, 2014, 2015a, 2015b, 2015c; LINS *et al.*, 2017), relatam muitos processos influenciando essa estrutura de comunidades de helmintos em anfíbios, dentro os quais se incluem o tamanho do hospedeiro, o gênero, a dieta, o sítio da infecção, a espécie e o comportamento. Segundo Poulin e Krasnov (2010), a riqueza parasitária varia dependendo das condições ambientais, devido à forma como as espécies respondem a fatores bióticos. No entanto, poucos estudos mostram as relações parasito-hospedeiro em anfíbios anuros considerando a influência das variações ambientais, e menos ainda em áreas tão especiais quanto os brejos-de-altitude nordestinos.

A compreensão dos padrões de interação e dos determinantes da associação parasito-hospedeiro contribui para preencher as lacunas de conhecimento na ecologia da comunidade e da doença (CAMPIÃO *et al.*, 2015a). Esses organismos parasitos são uma parcela considerável da biomassa global, e parte importante da natureza (KURIS, 2008). Assim, o estudo da fauna parasitária é de extrema importância, pois além de contribuir para o conhecimento da biodiversidade e entendimento da relação parasito-hospedeiro, também podem ser considerados como bioindicadores e até colaborar na conservação de espécies (GALLI *et al.*, 2001; POULIN; MORAND, 2004; BRANDÃO, 2017). Além disso, os estudos parasitológicos são necessários para a compreensão do papel das espécies de parasitos nos diferentes níveis de organização ecológica (WOOD; JOHNSON, 2015).

Dessa forma, a Área de Proteção Ambiental da Serra de Maranguape, criada pelo Poder Público Municipal a partir da Lei Nº 1168, de 08 de julho de 1993, visando um melhor controle sobre o ecossistema da serra, e sendo um pico residual de embasamento cristalino com altitude máxima de 920 m, que durante muito tempo foi explorado na produção de diversas culturas como laranja, café e bananicultura (LIMA, 2005). Concentra uma diversidade de anfíbios e répteis espetacular, com vários casos de endemismos (HOOGMOED *et al.*, 1994; BORGES-NOJOSA *et al.*, 2016a; 2016b). Considerando esses aspectos, observou-se que a serra de Maranguape mantinha um ambiente ideal para a realização de um trabalho com os seguintes objetivos: (A) descrever a composição de endoparasitos associados a anuros de um enclave de floresta altitudinal no Nordeste do Brasil, a Serra de Maranguape; (B) testar a influência do uso de microhabitats nas relações parasito-hospedeiros em anfíbios anuros; (C) testar a hipótese de que rãs maiores tendem a ser mais parasitadas; (D) testar a influência da heterogeneidade de habitats e do gradiente altitudinal nas relações parasito-hospedeiros em anfíbios anuros, quanto a abundância e riqueza dos endoparasitos; (E) testar a relação filogenética entre hospedeiros e parasitos; e (F) testar a hipótese de que os parasitos são distribuídos seguindo seus hospedeiros sem influência da variação ambiental.

1.1 Organização da Tese

Os dados encontrados neste trabalho representam a continuidade das pesquisas e esforços que já vem sendo desenvolvidas pelos pesquisadores do Núcleo Regional de Ofiologia do Ceará (NUROF-UFC) ao longo dos últimos anos, nos brejos-de-altitude do Ceará.

Conforme explicitado anteriormente, teve-se como objetivos descrever a composição dos endoparasitos associados aos anuros de um enclave de floresta tropical altitudinal no nordeste do Brasil, para simultaneamente testar as seguintes hipóteses: da relação entre a heterogeneidade de habitats e o gradiente altitudinal; da influência do uso de microhabitats e dos efeitos filogenéticos e ecológicos nas relações parasito-hospedeiro em anfíbios anuros; e que as rãs maiores são mais parasitadas. Entretanto, aproveitando a oportunidade, também foi possível incluir mais um objetivo: (G) obter informações sobre a helmintofauna do sapinho *Adelophryne maranguapensis*, uma espécie endêmica do Estado do Ceará, que consta como criticamente em perigo (BRASIL, 2022), e assim entender melhor algumas características na relação parasita-hospedeiro e no uso da área deste anuro.

Os resultados, que possibilitaram atender a todos estes objetivos, são apresentados aqui, divididos em três manuscritos (dois já publicados e um submetido), que seguem as regras de formatação das revistas de publicação:

Capitulo 1: Comunidade endoparasitária de anuros de um enclave de floresta tropical altitudinal no semiárido brasileiro (*Endoparasite community of anurans from an altitudinal rainforest enclave in a Brazilian semiarid área*) - Neste capítulo, descreve-se a composição da comunidade endoparasitária associado aos anuros da Serra de Maranguape, relaciona-se a abundância e riqueza de endoparasitos com o uso de microhabitats dos hospedeiros e foi testada a hipótese de que rãs maiores são mais parasitadas, atendendo aos objetivos A, B e C. O artigo foi publicado na revista

Journal of Helminthology 96, e62, 1–17, 2022 (https://doi.org/10.1017/S0022149X22000499).

Capitulo 2: Efeito da Altitude e Heterogeneidade Espacial na Relação Parasito-Hospedeiro em Anuros de um Remanescente de Floresta Úmida no Semiárido Brasileiro (*Effect of altitude and spatial heterogeneity on the host-parasite relationship in anurans from a remnant humid forest in the Brazilian semiarid*) - No presente estudo, investigou-se os efeitos da heterogeneidade ambiental e do gradiente altitudinal na abundância e riqueza de endoparasitos, analisou-se a influência dos efeitos filogenéticos e ecológicos nos parâmetros parasitas (tais como prevalência, riqueza e abundância de espécies) e foi testada a hipótese de que os parasitos seguem a distribuição de seus hospedeiros, independentemente da variação altitudinal e/ou heterogeneidade, atendendo aos objetivos D, E e F. O artigo foi submetido a revista ***Parasitology Research***, e encontra-se em avaliação. (Link para normas: https://www.springer.com/journal/436/submission-guidelines); e

Capitulo 3: Endoparasitos de *Adelophryne maranguapensis* Hoogmoed, Borges & Cascon, 1994, (Anura, Eleutherodactylidae), uma espécie endêmica e ameaçada de um pântano de altitude no nordeste do Brasil (*Endoparasites of* Adelophryne maranguapensis *Hoogmoed, Borges & Cascon, 1994 (Anura, Eleutherodactylidae), an endemic and threatened species from an altitude swamp in northeastern Brazil*) - Neste artigo, são apresentados os dados sobre os helmintos endoparasitos, a relação da abundância parasitária com o tamanho dos indivíduos e com o sexo de *Adelophryne maranguapensis,* espécie endêmica do Estado do Ceará, considerada criticamente em perigo, para entender algumas características na relação parasito-hospedeiro e no uso da área deste anuro. Assim fornecer dados que possam servir na produção de políticas voltadas a conservação dessa espécie, atendendo ao objetivo G. O artigo foi publicado na revista ***Parasitology Research***, **121**(3), 1053-1057, 2022. (https://doi.org/10.1007/s00436-022-07458-y).

Chapter 1 –

---

2. Endoparasite community of anurans from an altitudinal rainforest enclave in a Brazilian semiarid area

Comunidade endoparasitaria de anuros de um enclave de floresta tropical altitudinal no semiárido brasileiro

Cicero Ricardo de Oliveira

Wilmara Mascarenhas

Dalilange Batista-Oliveira

Kássio de Castro Araújo

Robson Waldemar Ávila

Diva Maria Borges-Nojosa

Artigo publicado na revista ***Journal of Helminthology*** **96**, e62, 1–17, 2022

https://doi.org/10.1017/S0022149X22000499

Endoparasite community of anurans from an altitudinal rainforest enclave in a Brazilian semiarid area

Cicero Ricardo de Oliveira[1,2], Wilmara Mascarenhas[3], Dalilange Batista-Oliveira[4], Kássio de Castro Araújo[1], Robson Waldemar Ávila[1,2], Diva Maria Borges-Nojosa[1,2]

1 - Graduate Program in Ecology and Natural Resources, Block 902, Science Center, PICI Campus, Federal University of Ceará - UFC, Fortaleza - CE, Zip Code: 60455-760, Brazil.

2 - Regional Ophiology Center, Block 905, Science Center, PICI Campus, Federal University of Ceará - UFC, Fortaleza - CE, Zip Code: 60455-760, Brazil.

3 - Institute for Educators Training, Laboratory of Biology and Ecology of Wild Animals, Federal University of Cariri, Brejo Santo, Ceará, Zip Code: 63260-000, Brazil.

4 - Graduate Program in Biological Diversity and Natural Resources, Department of Biological Chemistry, Regional University of Cariri, Crato, Ceará, Zip Code: 63100-000, Brazil.

[*] **Corresponding Author:** riccicer@gmail.com

Abstract.

In the present study, we aimed to describe the composition of endoparasites associated with anurans from an altitudinal rainforest enclave in northeastern Brazil. Additionally, we tested if microhabitat use influences endoparasite abundance and richness, as well as the hypothesis that larger frogs tend to be more parasitized. We sampled 306 individuals from 25 anuran species that were necropsied and analysed using a stereomicroscope. The total endoparasite prevalence was 79.08%, with a parasitic community consisting of 46 taxa. Overall, we found the common pattern described for Neotropical amphibians, which is the predominance of generalist and direct-cycle parasites. Twenty new host records and two possible new parasite species were found, highlighting the importance of this type of inventory. We also observed that microhabitat use was associated with a significant difference in parasite richness between groups, in which arboreal and terrestrial species, and aquatic and arboreal species contributed to these differences. Moreover, larger frogs tended to be more parasitized regarding only an interspecific view. Our results suggest that parasite richness is directly related to infection cycle and how the host exploits its habitat.

Keywords: helminths; parasite; amphibians; maranguape mountain

Resumo.

No presente estudo, objetivamos descrever a composição de endoparasitas associados a anuros de um enclave de floresta tropical altitudinal no nordeste do Brasil. Além disso, testamos se o uso de microhabitat influencia a abundância e riqueza dos endoparasitas, bem como a hipótese de que os sapos maiores tendem a ser mais parasitas. Amostramos 306 indivíduos de 25 espécies de anuros que foram necropsiados e analisados usando um estereoscópio. A prevalência total de endoparasitas foi de 79,08%, com uma comunidade parasitária composta de 46 *taxa*. Em geral, encontramos o padrão comum descrito para os anfíbios neotropicais, que é a predominância de parasitas generalistas e de ciclo direto. Vinte novos registros de hospedeiros e duas possíveis novas espécies de parasitos foram encontrados, destacando a importância deste tipo de inventário. Observamos também que o uso de microhabitats foi associado a uma diferença significativa na riqueza parasitária entre grupos, nos quais espécies arbóreas e terrestres, e espécies aquáticas e arbóreas contribuíram para estas diferenças. Além disso, os sapos maiores tendiam a ser mais parasitados em relação a uma visão interespecífica. Nossos resultados sugerem que a riqueza parasitária está diretamente relacionada ao ciclo de infecção e à forma como o hospedeiro explora seu habitat.

Palavras-chave: helmintos; parasita; anfíbios; montanha de maranguape.

2.1 INTRODUCTION

Parasites are diverse organisms that are an integral part of nature, representing most of the global biodiversity and one of the most common life strategies on the planet (Windsor, 1998; Poulin & Morand, 2004; Kuris, 2008). Parasitic organisms are also ecologically important (Marcogliese, 2004; Poulin & Morand, 2004) because they are closely related to environmental conditions, and thus, might be considered potential indicators of environmental quality (Catalano *et al.,* 2013). Despite the increase of parasitological studies, the science as a whole is still far from having complete knowledge about the parasite biodiversity and ecology on Earth (Poulin & Morand, 2004). Therefore, inventories are the basis for studies, and determining which and how many species is part of an ecosystem is essential for understanding the diversity and functioning of organisms (Segalla *et al.,* 2021). In addition, these organisms are involved in various processes of nature regulation and might influence host population conditions because they interfere in crucial processes such as competition, migration, dispersal and speciation (Vitt & Caldwell, 2009; Matias *et al.,* 2018). Thus, knowledge about parasite diversity and distribution is important to understand the role of parasite-host ecological relationships on ecosystem dynamics (Poulin & Krasnov, 2010; Campião *et al.,* 2015b).

The altitudinal enclaves of humid montane forests known as ‘brejos-de-altitude’ [highland swamps] are isolated areas in the morphoclimatic domain of the Caatingas, which are marked by a high degree of endemism of their herpetofauna (Borges-Nojosa & Caramaschi, 2003; Albuquerque *et al.,* 2012; Borges-Nojosa *et al.,* 2016). As they are considered exceptional environments, due to local climatic conditions, they form isolated systems considered as unique elements (Vanzolini, 1981; Borges-Nojosa & Caramaschi, 2003). Such areas are classified as of extreme biological importance (MMA, 2000; Sousa *et al.,* 2004), and responsible for the greatest richness of anurans in Ceará state, northeastern Brazil (Roberto & Loebmann, 2016). Despite the recent increase of parasitological studies dealing with anurans from these mountains (Silva-Neta *et al.,* 2020; Mascarenhas *et al.,* 2021; Machado *et al.,* 2022), their parasite diversity is still underestimated.

According to Aho (1990), anurans show low parasite richness that is variable and isolationist when compared to other vertebrate groups. However, some amphibian species may present a higher richness of helminths (Hamann *et al.,* 2006), being currently accepted that amphibians harbour rich and diverse helminth fauna (Campião *et al.,* 2014; Oliveira *et al.,* 2019; Mascarenhas *et al.,* 2021; Machado *et al.,* 2022). Recently published studies (e.g. Campião *et al.,* 2015b; Lins *et al.,* 2017; Oliveira *et al.,* 2019; Silva-Neta *et al.,* 2020; Mascarenhas *et al.,* 2021) report processes that influence the structure of helminth communities in amphibians, including host size, genus, diet, site of infection, species and behaviour. In addition, features of host habitats are key factors in parasite colonization (Goater *et al.*, 2005), drawing attention to the composition of parasite communities, which vary widely among host populations of the same species (Poulin *et al.*, 2011; Bezerra *et al.*, 2016).

In the present study: (i) we aimed to describe the composition of endoparasites associated with anurans from an altitudinal rainforest enclave in northeastern Brazil; (ii) to test if microhabitat use influences endoparasite abundance and richness; and (iii) to test the hypothesis that larger frogs tend to be more parasitized.

2.2 MATERIAL AND METHODS

2.2.1 Study area

Sampling took place in the Maranguape mountain, Ceará state, northeastern Brazil (Fig. 1), a crystalline residual massif with a maximum altitude of 920 m, vegetation composed of humid forest covering the highest points, dry forest in the intermediate points gradually replacing the humid forest, and Caatinga in the lowlands (Borges-Nojosa & Caramaschi, 2003). The climatic regime is defined by two distinct seasons: dry season from June to December, and rainy season from January to May, with average annual precipitation of 1300 mm, and temperatures ranging from 26°C to 28°C (Ceará, 2002; IPECE, 2017).

2.2.2 Sampling

Anuran sampling occurred during the rainy season, from April to May 2019 (15 days of sampling) and from February to May 2020 (17 days of sampling), through visual and auditory searches (Bernarde, 2012). The sampling period started at dusk and extended until midnight (17:00–00:00 h), which is the time period when the majority of anuran species are most active in foraging and reproduction. For each individual, we determined the microhabitat use considering the site of capture (arboreal, aquatic or terrestrial).

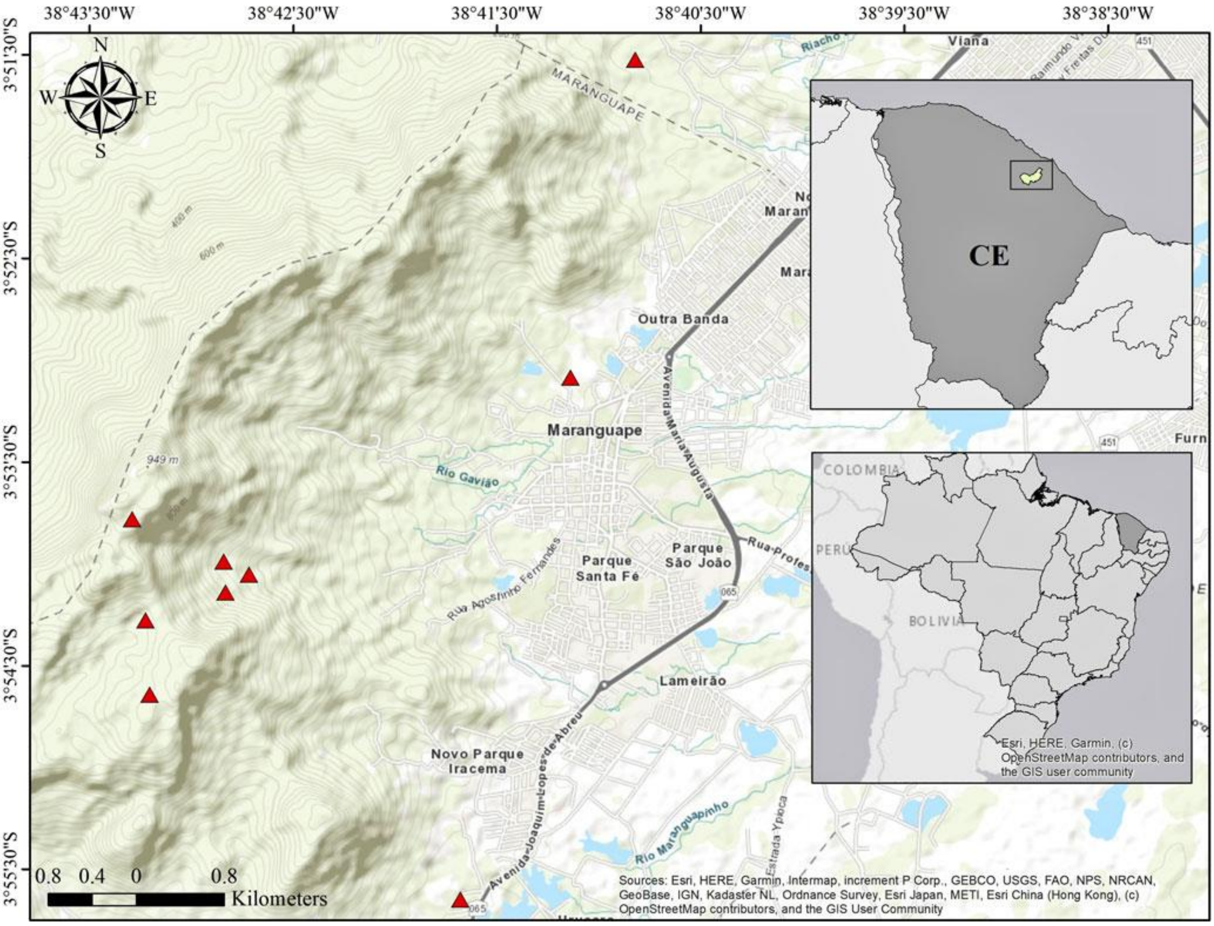

Fig. 1. Schematic map of the sampling points in Maranguape mountain, Ceará state, northeastern Brazil. Red triangles represent sampling points.

The collected specimens were euthanized with a lethal injection of sodium thiopental (Thiopentax®), following the ethical procedures of the Federal Council of Veterinary Medicine – CFMV (2013). Afterwards, we measured the mass with a Pesola scale (precision 0.1 g) and the snout–vent length (SVL) using a Mitutoyo® digital caliper (precision 0.01 mm). Voucher specimens were fixed in 10% formalin according to Calleffo (2002) and deposited in the Herpetological Collection of the Federal University of Ceará (CHUFC – A 9762 to A 9953), Fortaleza, Brazil.

2.2.3 Parasitological Procedures

We necropsied the anurans after performing a ventral incision and examined for the presence of endoparasites in the organs (gastrointestinal tract, lungs, liver and kidneys) and internal cavity using a stereomicroscope according to Amato *et al.* (1991). For species identification, we collected and prepared the endoparasites following specialized methodologies according to each taxonomic group (Yamaguti, 1971; Schmidt, 1986; Vicente *et al.*, 1991; Andrade, 2000). Temporary slides were analysed using a light microscope. Voucher specimens were deposited in the Parasitological Collection of the Universidade Federal do Ceará (CPUFC – 196 to 441), Fortaleza, Brazil.

We measured the following parasitological parameters according to Bush *et al.* (1997): prevalence (percentage of parasitized amphibians in each host species); mean intensity of infection (mean number of parasites in parasitized amphibians); and mean parasite abundance.

2.2.4 Statistical Analyses

We used the non-parametric Kruskal-Wallis test (Shapiro-Wilk < 0.05) to investigate whether parasite richness and abundance vary in response to microhabitat used by anuran species (aquatic, arboreal and terrestrial), followed by Dunn's *post-hoc* test to investigate which groups contributed most to the differences (*P*-values adjusted with the Benjamini-Hochberg method). Regarding both interspecific and intraspecific views, we tested the influence of anuran body size (SVL and mass) on the abundance and richness of parasites with a linear mixed model, using host sex as a random effect. For this test, we used only anuran species with more than five individuals parasitized. Analyses and graphs were performed using the packages ggplot2 (Wickham, 2016), nlme (Pinheiro & Bates, 2000), vegan (Oksanen *et al.*, 2016) and FSA (Ogle *et al.,* 2022) from R software (R core team, 2021).

2.2.5 Ethical standards

The authors assert that all procedures contributing to this work comply with the ethical standards of the relevant national and institutional guides on the care and use of laboratory animals. Collection permit Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio (#72384-1 and #73215-1) and Ethic Committee on Animal Use of the Federal University of Ceará (CEUA-UFC) (#CEUA 6314010321).

2.3 RESULTS

We sampled 306 individuals from 25 anuran species (Fig. 2), of which 242 individuals (75 females, 161 males and six juveniles) were parasitized with at least one parasite taxon. We found 7042 helminth specimens, with an overall prevalence of 79.08%, mean infection intensity of 29.09 and total abundance of 23.01 ± 1.58. The endoparasite community consisted of 46 taxa. The most abundant taxa were *Raillietnema spectans*, *Oswaldocruzia* *mazzai* and *Schrankiana schranki*. The highest prevalence values were observed for *Oswaldocruzia mazzai*, *Physaloptera* sp. and *Centrorhynchus* sp. Endoparasite richness ranged from two to 17 parasites taxa per host, *Oswaldocruzia mazzai* and *Physaloptera* sp. being the most prevalent parasites (Table 1).

The most parasitized anurans were *Trachycephalus typhonius* (n = 17), *Pristimantis relictus* (n = 17) and *Physalaemus cuvieri* (n = 15). *Adelophryne maranguapensis* was not parasitized, while *Leptodactylus troglodytes* (n = 2), *Rhinella granulosa* (n = 3) and *Adenomera juikitam* (n = 3) had few associated parasite taxa. In addition, we found 20 new host records and two possible new parasite species (Table 2).

Fig. 2. Anurans found in Maranguape mountain, Ceará state, northeastern Brazil: (A) *Rhinella diptycha*; (B) *Rhinella granulosa*; (C) *Adelophryne maranguapensis*; (D) *Boana raniceps*; (E) *Corythomantis greeningi*; (F) *Dendropsophus minusculus*; (G) *Dendropsophus minutus*; (H) *Dendropsophus nanus*; (I) *Dendropsophus tapacurensis*; (J) *Scinax x-signatus*; (K) *Trachycephalus typhonius*; (L) *Adenomera juikitam*; (M) *Leptodactylus fuscus*; (N) *Leptodactylus macrosternum*; (O) *Leptodactylus mystaceus*; (P) *Leptodactylus pustulatus*; (Q) *Leptodactylus syphax*; (R) *Leptodactylus troglodytes*; (S) *Leptodactylus vastus*; (T) *Physalaemus cuvieri*; (U) *Elachistocleis piauiensis*; (V) *Proceratophrys cristiceps*; (W) *Proceratophrys renalis*; (X) *Pithecopus gonzagai*; and (Y) *Pristimantis relictus*.

Table 1. The endoparasite community found in the anuran species from Maranguape mountain, Ceará state, northeastern Brazil.

PARASITES	**N**	**N.H**	**P (%)**	**M.I. + R**	**Ab. ± S.E.**	**S.I.**
Acanthocephala						
Centrorhynchus sp.	168	14	16.67	0.69 (1 – 15)	0.55 ± 0.50	S. C. SI. LV.
Oligacanthorhynchus sp.	16	3	1.96	0.07 (1 – 10)	0.05 ± 1.47	C.
Annelida						
Dero (Allodero) lutzi	4	3	0.98	0.02 (1 – 2)	0.01 ± 0.33	UD.
Nematoda						
Aplectana crucifer	7	1	0.33	0.03 (7)	0.02	LI.
Aplectana membranosa	43	6	4.58	0.18 (1 – 9)	0.14 ± 0.69	SI. LI.
Aplectana meridionalis	45	1	1.96	0.19 (3 – 21)	0.15 ± 2.81	SI. LI.
Capillaria sp.	1	1	0.33	0.004 (1)	0.003	UD.
Cosmocerca brasiliense	10	1	0.33	0.04 (10)	0.03	SI. LI.
Cosmocerca parva	265	12	13.07	1.10 (1 – 74)	0.87 ± 2.08	S. SI. LI. LG.
Cosmocerca podicipinus	46	1	1.63	0.19 (2 – 26)	0.15 ± 4.28	S. SI. LI. LG.
Cosmocerca rara	85	4	1.96	0.35 (2 – 48)	0.28 ± 7.76	SI. LI.
Cosmocerca sp.	282	10	15.36	1.17 (1 – 41)	0.92 ± 1.32	S. SI. LI.
Cosmocercoides sp.	4	1	0.52	0.02 (4)	0.01	LI.
Falcaustra mascula	23	4	1.31	0.10 (1 – 11)	0.08 ± 2.49	SI. LI.
Ochoterenella convolute	4	1	0.33	0.02 (4)	0.01	C.
Ochoterenella cf. *vellardi*	12	1	0.65	0.05 (2 – 10)	0.04 ± 4	C.
Ochoterenella sp.	4	3	0.65	0.02 (1 – 3)	0.01 ± 1	C. S.
Oswaldocruzia mazzai	980	15	27.12	4.05 (1 – 87)	3.20 ± 1.90	C. S. SI. LI.
Oxyascaris caatingae	21	3	0.98	0.09 (1 – 18)	0.07 ± 5.50	SI. LI.
Parapharyngodon cf. *duniae*	15	1	0.65	0.06 (6 – 9)	0.05 ± 1.50	SI. LI.
Physaloptera sp.	247	19	19.61	1.02 (1 – 37)	0.81 ± 0.78	C. S. LV. LG.
Physalopteroides venancioi	8	2	0.65	0.03 (2 – 6)	0.03 ± 2.0	C. S. SI.
Porrocaecum sp.	13	4	1.31	0.05 (1 – 8)	0.04 ± 1.60	C. S. LV.
Raillietnema spectans	1026	13	13.73	4.24 (1 – 253)	3.35 ± 7.79	SI. LI.
Rhabdias breviensis	276	11	11.44	1.14 (1 – 80)	0.90 ± 2.68	LG. LV.
Rhabdias cf. *stenocephala*	10	2	1.63	0.04 (1 – 4)	0.03 ± 0.54	LG.
Rhabdias pseudosphaerocephala	27	2	0.98	0.11 (9)	0.09	LG.
Rhabdias sp.	447	13	14.38	1.85 (1 – 105)	1.46 ± 2.90	LG.
Schrankiana schranki	905	4	1.96	3.74 (1 – 700)	2.96 ± 111.62	SI. LI.
Strongyloides sp.	14	6	2.61	0.06 (1 – 4)	0.05 ± 0.41	S. SI. LI.
Nematoda gen. sp.	7	2	0.65	0.03 (1 – 6)	0.02 ± 2.50	S. LI.
Unidentified Ascarididae larvae	2	2	0.52	0.008 (1)	0.007	C.
Unidentified Cosmocercidae larvae	1740	18	18.30	7.19 (1 – 247)	5.69 ± 7.36	S. SI. LI. LV.
Platyhelminthes						
Cestoda						
Cylindrotaenia americana	6	2	0.98	0.02 (2)	0.02	SI.

Monogenea						
Polystoma cf. *lopezromani*	14	2	0.98	0.06 (1 – 8)	0.05 ± 2.02	UB.
Trematoda						
Catadiscus marinholutzi	1	1	0.33	0.004 (1)	0.003	LI.
Catadiscus propinquus	76	3	2.61	0.31 (2 – 22)	0.25 ± 2.67	SI. LI.
Choledocystus simulans	37	1	0.98	0.15 (1 – 35)	0.12 ± 11.33	SI.
Choledocystus vitellinophilum	1	1	0.33	0.004 (1)	0.003	SI.
Gorgoderina parvicava	3	1	0.33	0.01 (3)	0.01	UB.
Lophosicyadiplostomum sp.	17	3	0.98	0.07 (3 – 7)	0.06 ± 1.33	K.
Mesocoelium monas	3	1	0.65	0.01 (1 – 2)	0.01 ± 0.50	SI.
Neohaematoloechus neivai	56	1	1.31	0.23 (3 – 21)	0.18 ± 4.18	G. SI.
Rauschiella linguatula	13	2	1.96	0.05 (1 – 4)	0.04 ± 0.60	S. SI.
Rudolphitrema sp.	5	1	0.33	0.02 (5)	0.02	SI.
Unidentified Metacercaria larvae	53	4	1.96	0.22 (5 – 18)	0.17 ± 2.05	K.
Total	**7042**	**242**	**79.08**	**29.09 (1 – 700)**	**23.01 ± 1.58**	

n, number of parasites; N.H, number of infected hosts; P%, prevalence; M.I., mean intensity; R, range; Ab., abundance; S.E., standard error; S.I., site of infection; C, cavity; S, stomach; SI, small intestine; LI, large intestine; LV, liver; LG, lung; G, gallbladder; PA, pancreas; K, kidney; UB, urinary bladder; and UD, urinary duct.

We observed that microhabitat use was associated with a significant difference in parasite richness between groups (H = 13.35, *P* = 0.0012), in which Dunn's *post-hoc* test evidenced that arboreal and terrestrial species (*P* = 0.001) and aquatic and arboreal species (*P* = 0.023) contributed significantly to these differences (Fig. 3). By contrast, parasite abundance did not vary significantly between groups (H = 5.2821, *P* > 0.05).

We also observed that larger frogs (SVL) tend to be more parasitized considering the parasite abundance (T = 2.148, P = 0.0328) and richness (T = 4.576, *P* = 0.0001), regardless of sex (intercept = 0.0041 and 0.1291, respectively) (Fig. 4). Mass had no significant influence on both abovementioned parasitological descriptors (*P* > 0.05). In an intraspecific view, parasite load (richness and abundance) seemed not to be influenced by the size of each anuran species (Table 3).

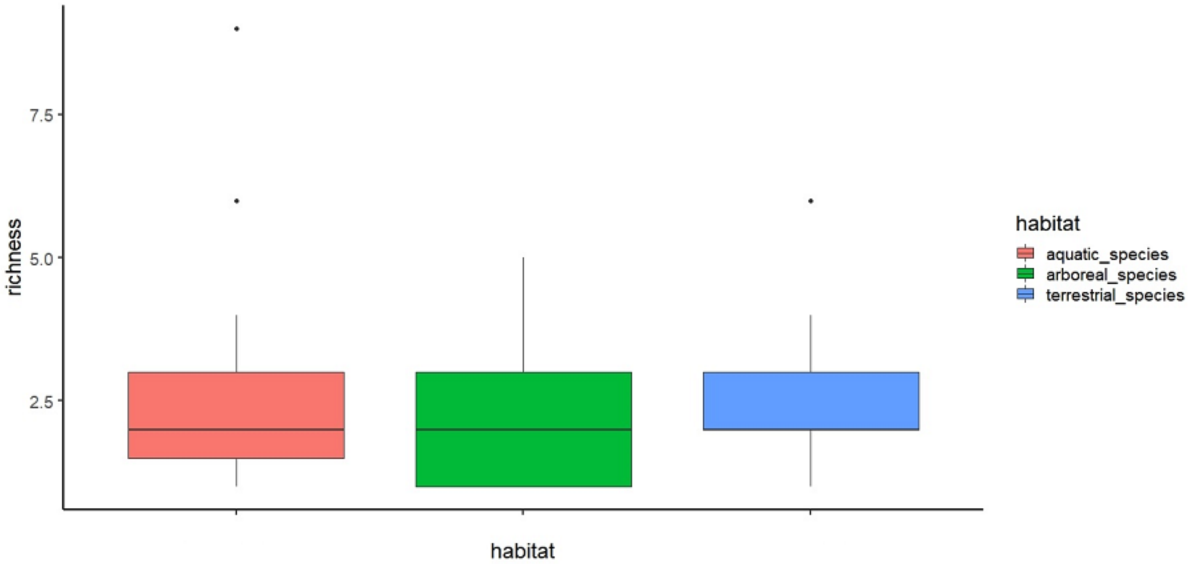

Fig. 3. Boxplot representing the parasite richness between the groups of microhabitats used by the anurans.

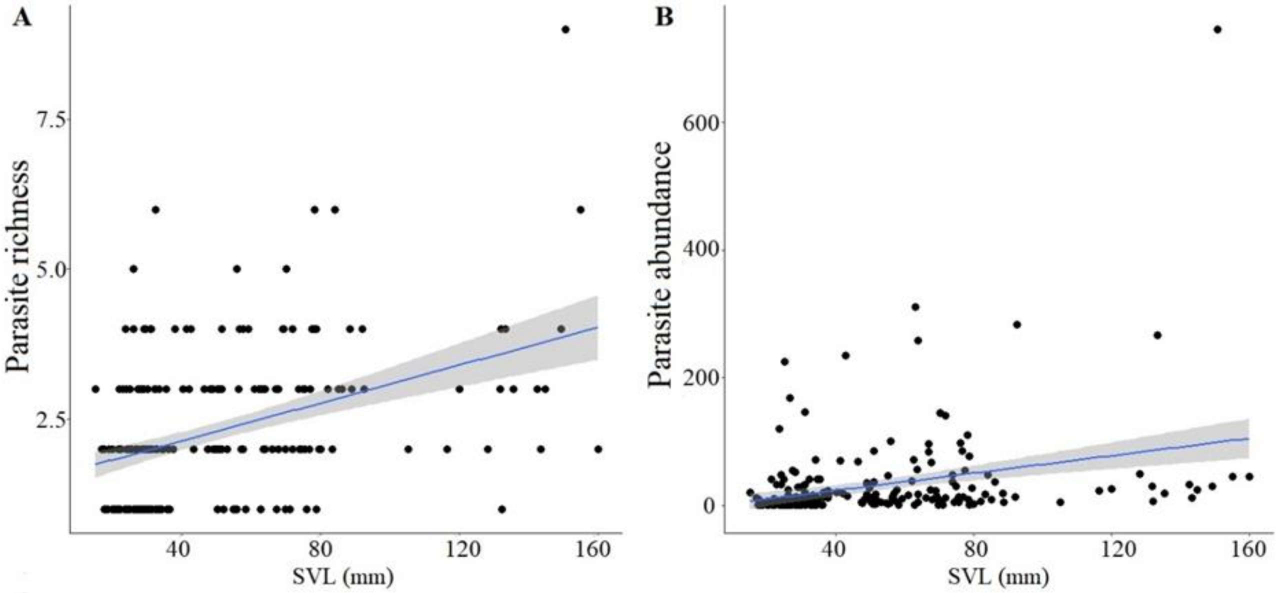

Fig. 4. Relationship of parasite richness (A) and abundance (B) with the host's body size (anuran interspecific view) from Maranguape mountain, Ceará state, northeastern Brazil.

Table 2. List of endoparasites found in the anuran species from Maranguape mountain, Ceará state, Brazil and literature review for previous records. *n*= Number of hosts; *P%*= Prevalence; A.M.= Abundance; ***** Possible new species.

Hosts (*n*= 306)	**Parasite Species**	***P (%)***	**A.M.**	**Reference**
BUFONIDAE				
Rhinella diptycha	Unidentified Cosmocercidae larvae	13.3	16.7	-
(*n*=15*; P%*=86.7)	*Cosmocerca* sp.	26.7	3.5	New record
	Ochoterenella sp.	6.7	0.2	Aguiar *et al.*, 2021
	Oswaldocruzia mazzai	53.3	8.9	Aguiar *et al.*, 2021
	Physaloptera sp.	13.3	0.4	Amorim *et al.*, 2019
	Raillietnema spectans	6.7	0.9	Amorim *et al.*, 2019
	Rhabdias pseudosphaerocephala	20	1.8	Aguiar *et al.*, 2021
	Rhabdias sp.	60	4.8	Amorim *et al.*, 2019; Aguiar *et al.*, 2021
	Schrankiana schranki	6.7	0.1	New record
	Centrorhynchus sp.	13.3	0.6	New record
	Oligacanthorhynchus sp.	6.7	0.1	New record
	Mesocoelium monas	13.3	0.2	New record
Rhinella granulosa	*Oswaldocruzia mazzai*	66.7	3.2	Silva-Neta *et al.*, 2020
(*n*=6*; P%*=83.3)	*Physaloptera* sp.	66.7	5.7	Campião *et al.*, 2014; Teles *et al.*, 2018
	Raillietnema spectans	83.3	14.8	Teles *et al.*, 2018; Silva-Neta *et al.*, 2020
STRABOMANTIDAE				
Pristimantis relictus	Unidentified Cosmocercidae larvae	15.6	7.2	-
(*n*=45*; P%*=88.9)	*Aplectana membranosa*	13.3	0.5	New record
	Aplectana meridionalis	13.3	1	New record
	Capillaria sp.	2.2	0.02	New record
	Cosmocerca parva	8.9	0.1	New record
	Cosmocerca rara	2.2	1.1	New record

	Cosmocerca sp.	33.3	1.4	New record
	Ochoterenella cf. *vellardi*	4.4	0.3	New record
	Oswaldocruzia mazzai	2.2	0.02	New record
	Physaloptera sp.	13.3	0.2	New record
	Raillietnema spectans	20	6.1	New record
	Rhabdias breviensis	15.6	0.2	New record
	Rhabdias sp.	13.3	0.7	New record
	Strongyloides sp.	2.2	0.02	New record
	Nematoda gen. sp. (females)	2.2	0.02	*
	Choledocystus simulans	6.7	0.8	New record
	Gorgoderina parvicava	2.2	0.1	New record
ELEUTHERODACTYLIDAE				
Adelophryne maranguapensis	-	-	-	Not parasitized
HYLIDAE				
Boana raniceps	Unidentified Cosmocercidae larvae	60	30.67	-
(*n*=15; *P%*=93.3)	*Aplectana membranosa*	6.7	0.53	Aguiar *et al.*, 2021; Sani *et al.*, 2021
	Cosmocerca parva	13.3	5.67	González & Hamann, 2011, 2015; Machado *et al.*, 2022
	Cosmocerca rara	6.67	1.73	New record
	Oswaldocruzia mazzai	46.67	17.2	Campião *et al.*, 2015a; Machado *et al.*, 2022
	Oxyascaris caatingae	6.67	0.07	New record
	Physaloptera sp.	13.33	1.27	Campião *et al.*, 2016a; Graça *et al.*, 2017; Sani *et al.*, 2021
	Physalopteroides venancioi	6.67	0.4	Campião *et al.*, 2016b
	Rhabdias breviensis	33.33	9.67	New record
	Rhabdias sp.	40	8.73	Graça *et al.*, 2017; Sani *et al.*, 2021; Machado *et al.*, 2022
	Strongyloides sp.	6.67	0.27	New record
	Centrorhynchus sp.	20	0.8	New record
	Choledocystus vitellinophilum	6.67	0.07	Travassos *et al.*, 1969; Aguiar *et al.*, 2021

Corythomantis greeningi	Unidentified Cosmocercidae larvae	20	11	-
(*n*=5; *P%*=100)	*Cosmocerca* sp.	20	2.2	New record
	Oswaldocruzia mazzai	60	1.2	New record
	Rhabdias sp.	20	2.6	New record
	Dero (Allodero) lutzi	20	0.2	Morais *et al.*, 2017
	Polystoma cf. *lopezromani*	20	0.2	New record
Dendropsophus minusculus	Unidentified Cosmocercidae larvae	13.3	0.8	-
(*n*=15; *P%*= 40)	*Cosmocerca parva*	6.7	0.8	New record
	Physaloptera sp.	6.7	3.4	New record
	Rhabdias breviensis	13.3	0.8	New record
	Centrorhynchus sp.	6.7	0.4	New record
	Cylindrotaenia americana	6.7	0.4	New record
	Unidentified Metacercaria larvae	6.7	2.2	-
Dendropsophus minutus	Unidentified Cosmocercidae larvae	6.3	2.5	-
(*n*=16; *P%*=75)	*Cosmocerca parva*	31.3	2.9	New record
	Cosmocerca sp.	12.5	0.1	Martins-Sobrinho *et al.*, 2017
	Ochoterenella sp.	6.3	0.06	New record
	Oswaldocruzia mazzai	6.3	0.06	New record
	Physaloptera sp.	6.3	0.06	New record
	Raillietnema spectans	6.3	0.06	New record
	Rhabdias breviensis	6.3	0.4	New record
	Rhabdias pseudosphaerocephala	6.3	0.1	New record
	Rhabdias sp.	6.3	0.06	New record
	Centrorhynchus sp.	6.3	0.9	New record
	Lophosicyadiplostomum sp.	6.3	0.4	Aguiar *et al.*, 2021
	Unidentified Metacercaria larvae	6.3	0.3	-
Dendropsophus nanus	Unidentified Cosmocercidae larvae	7.7	0.06	-

(*n*=13; *P%*=38.5)	*Centrorhynchus* sp.	23.1	0.8	Campião *et al.*, 2014
	Cylindrotaenia americana	15.4	0.3	Hamann & Kehr, 1998
	Lophosicyadiplostomum sp.	7.7	0.4	Queiroz *et al.*, 2020
Dendropsophus tapacurensis	Unidentified Cosmocercidae larvae	5.9	0.06	-
(*n*=17; *P%*= 23.5)	*Physaloptera* sp.	17.6	0.4	New record
	Rhabdias breviensis	5.9	0.06	New record
Scinax x-signatus	Unidentified Cosmocercidae larvae	17.4	2	-
(*n*=23; *P%*= 69.6)	*Aplectana membranosa*	4.3	0.04	New record
	Cosmocerca parva	8.7	0.5	New record
	Cosmocerca rara	4.3	0.2	New record
	Cosmocercoides sp.	4.3	0.2	*
	Physaloptera sp.	21.7	1.9	New record
	Rhabdias breviensis	26.1	2.9	New record
	Rhabdias sp.	13	3.2	New record
	Strongyloides sp.	4.3	0.04	New record
	Centrorhynchus sp.	8.7	1.2	Martins-Sobrinho *et al.*, 2017
	Oligacanthorhynchus sp.	4.3	0.04	New record
	Dero (Allodero) lutzi	4.3	0.04	Morais *et al.*, 2017
	Lophosicyadiplostomum sp.	4.3	0.1	New record
	Unidentified Metacercaria larvae	4.3	0.3	-
Trachycephalus typhonius	Unidentified Ascarididae larvae	5.6	0.1	-
(*n*=18; *P%*=100)	Unidentified Cosmocercidae larvae	50	13.5	-
	Aplectana crucifer	5.6	0.4	New record
	Cosmocerca parva	5.6	0.2	New record
	Cosmocerca sp.	27.8	3.3	Campião *et al.*, 2014
	Oswaldocruzia mazzai	55.6	10.4	New record
	Parapharyngodon cf. *duniae*	11.1	0.8	Bursey & Brooks, 2004

	Physaloptera sp.	5.6	0.1	Campião *et al.*, 2016a; Graça *et al.*, 2017
	Raillietnema spectans	22.2	1.1	New record
	Rhabdias breviensis	5.6	0.1	New record
	Rhabdias sp.	5.6	0.1	Graça *et al.*, 2017
	Schrankiana schranki	5.6	0.1	New record
	Strongyloides sp.	11.1	0.3	New record
	Nematoda gen. sp. (female)	5.6	0.3	*
	Centrorhynchus sp.	38.9	0.7	Aguiar *et al.*, 2021
	Dero (Allodero) lutzi	5.6	0.1	Graça *et al.*, 2017
	Polystoma cf. *lopezromani*	11.1	0.7	Campião *et al.*, 2014; Graça *et al.*, 2017
LEPTODACTYLIDAE				
Adenomera juikitam	*Cosmocerca* sp.	25	0.5	New record
(*n*=8; *P%*= 25)	*Oswaldocruzia mazzai*	12.5	0.13	New record
	Rhabdias sp.	12.5	0.13	New record
Leptodactylus fuscus	*Cosmocerca parva*	25	0.3	Morais, 2013; Campião *et al.*, 2014
(*n*=4; *P%*=100)	*Physaloptera* sp.	50	2	Morais, 2013
	Raillietnema spectans	50	29.5	Silva-Neta *et al.*, 2020
	Rhabdias sp.	50	1.3	Cañizales, 2021
	Schrankiana schranki	75	50.5	Morais, 2013
	Centrorhynchus sp.	50	1.3	Sani *et al.*, 2021
	Catadiscus propinquus	25	0.5	Aguiar *et al.*, 2021
Leptodactylus macrosternum	Unidentified Cosmocercidae larvae	14.3	0.2	-
(*n*=14; *P%*=100)	*Cosmocerca parva*	7.1	2.6	González & Hamann, 2011; Campião *et al.*, 2014
	Cosmocerca sp.	14.3	0.7	New record
	Falcaustra mascula	7.1	0.07	Morais, 2013; Graça *et al.*, 2017
	Oswaldocruzia mazzai	35.7	5.1	Silva-Neta *et al.*, 2020
	Physaloptera sp.	42.9	2.2	Campião *et al.*, 2016a; Queiroz *et al.*, 2020; Vieira *et al.*, 2021

	Physalopteroides venancioi	7.1	0.1	Morais, 2013; Campião *et al.*, 2016a
	Rhabdias breviensis	21.4	0.5	New record
	Rhabdias sp.	35.7	0.9	González & Hamann, 2011; Graça *et al.*, 2017; Queiroz *et al.*, 2020; Vieira *et al.*, 2021
	Centrorhynchus sp.	21.4	0.3	Campião *et al.*, 2014
	Porrocaecum sp.	7.1	0.6	González & Hamann, 2015
	Catadiscus propinquus	7.1	0.1	Queiroz *et al.*, 2020
	Rauschiella linguatula	14.3	0.4	Graça *et al.*, 2017; Aguiar *et al.*, 2021
Leptodactylus mystaceus	*Cosmocerca* sp.	66.7	0.7	New record
(*n*=3; *P%*=100)	*Oswaldocruzia mazzai*	66.7	1.7	Campião *et al.*, 2015a
	Physaloptera sp.	33.3	0.07	Queiroz *et al.*, 2020
	Raillietnema spectans	33.3	2.7	Silva-Neta *et al.*, 2020
Leptodactylus pustulatus	Unidentified Cosmocercidae larvae	9.1	0.3	-
(*n*=11; *P%*=90.9)	*Cosmocerca* sp.	9.1	0.4	New record
	Oxyascaris caatingae	9.1	0.2	New record
	Physaloptera sp.	9.1	0.5	Morais, 2013
	Rhabdias cf. *stenocephala*	36.4	0.5	New record
	Rhabdias sp.	9.1	0.2	New record
	Centrorhynchus sp.	18.2	0.5	New record
	Catadiscus propinquus	54.5	6.5	New record
	Rauschiella linguatula	36.4	0.7	New record
Leptodactylus syphax	*Falcaustra mascula*	50	4.5	Morais, 2013
(*n*=2; *P%*=100)	*Ochoterenella convoluta*	50	2	New record
	Oswaldocruzia mazzai	100	3.5	New record
	Raillietnema spectans	100	96	New record
	Rhabdias cf. *stenocephala*	50	2	New record
	Porrocaecum sp.	50	1	New record
Leptodactylus troglodytes	Unidentified Cosmocercidae larvae	100	1	-

	Raillietnema spectans	100	17	New record
Leptodactylus vastus	Unidentified Cosmocercidae larvae	22.2	0.4	-
(*n*=9; *P%*=100)	*Falcaustra mascula*	11.1	1.2	New record
	Ochoterenella sp.	11.1	0.1	New record
	Oswaldocruzia mazzai	55.6	1.6	Silva-Neta *et al.*, 2020
	Oxyascaris caatingae	11.1	2	New record
	Physaloptera sp.	55.6	3.3	New record
	Raillietnema spectans	11.1	28.1	Silva-Neta *et al.*, 2020
	Rhabdias breviensis	44.4	1.9	New record
	Rhabdias sp.	33.3	4	New record
	Schrankiana schranki	11.1	77.8	Campião *et al.*, 2014
	Centrorhynchus sp.	33.3	2.9	New record
	Oligacanthorhynchus sp.	44.4	1.6	New record
	Neohaematoloechus neivai	44.4	6.2	New record
	Porrocaecum sp.	11.1	0.2	New record
Physalaemus cuvieri	Unidentified Cosmocercidae larvae	17.2	6.7	-
(*n*=29; *P%*=96.6)	*Aplectana membranosa*	3.4	0.1	New record
	Cosmocerca parva	27.6	1	Santos & Amato, 2013
	Cosmocerca podicipinus	10.3	0.2	New record
	Cosmocerca rara	24.1	2.5	New record
	Cosmocerca sp.	20.7	0.5	Aguiar *et al.*, 2015
	Oswaldocruzia mazzai	27.6	0.4	Oliveira *et al.*, 2019
	Physaloptera sp.	17.2	0.6	Toledo *et al.*, 2017; Sani *et al.*, 2021;
	Raillietnema spectans	17.2	2.3	Oliveira *et al.*, 2019; Silva-Neta *et al.*, 2020
	Rhabdias breviensis	3.4	0.03	New record
	Rhabdias sp.	17.2	1.6	Graça *et al.*, 2017; Toledo *et al.*, 2017; Aguiar *et al.*, 2021
	Strongyloides sp.	10.3	0.2	New record

	Centrorhynchus sp.	3.4	0.03	New record
	Porrocaecum sp.	3.4	0.2	New record
	Rudolphitrema sp.	20.7	0.3	New record
MICROHYLIDAE				
Elachistocleis piauiensis	*Cosmocerca parva*	50	9.5	New record
(n=4; P%=75)	*Physaloptera* sp.	25	0.3	New record
	Raillietnema spectans	25	1	New record
ODONTOPHRINIDAE				
Proceratophrys cristiceps	Unidentified Cosmocercidae larvae	50	0.04	-
(n=2; P%=100)	*Aplectana membranosa*	50	0.04	Teles *et al.*, 2017; Silva *et al.*, 2019
	Falcaustra mascula	50	0.04	Silva *et al.*, 2019
	Physaloptera sp.	50	1	Teles *et al.*, 2017; Silva *et al.*, 2019
Proceratophrys renalis	Unidentified Ascarididae larvae	7.1	0.1	-
(n=14; P%=92.9)	Unidentified Cosmocercidae larvae	21.4	3.1	-
	Aplectana membranosa	14.3	0.4	New record
	Cosmocerca parva	42.9	1.4	New record
	Oswaldocruzia mazzai	85.7	13.8	New record
	Physaloptera sp.	21.4	0.7	New record
	Raillietnema spectans	28.6	1.5	New record
	Centrorhynchus sp.	21.4	0.6	New record
PHYLLOMEDUSIDAE				
Pithecopus gonzagai	Unidentified Cosmocercidae larvae	21.4	1.5	-
(n=14; P%= 92.9)	*Cosmocerca parva*	7.1	0.07	Martins-Sobrinho *et al.*, 2017
	Cosmocerca brasiliense	7.1	0.7	New record
	Oswaldocruzia mazzai	7.1	0.5	New record
	Physaloptera sp.	14.3	0.3	New record
	Rhabdias breviensis	14.3	0.7	New record

	Strongyloides sp.	14.3	0.1	New record
	Centrorhynchus sp.	42.9	1.1	Martins-Sobrinho *et al.*, 2017
	Catadiscus marinholutzi	7.1	0.07	New record
	Unidentified Metacercaria larvae	21.4	2.1	-

Table 3. Relationship between parasite richness and abundance with anuran body size (snout–vent length - SVL and mass), regarding an interspecific view, obtained through linear mixed models.

	Parasite richness				Parasite abundance		
TAXA	**St. D. ± S.E.**	***T***	***P***	**RE**	***T***	***P***	**RE**
Bufonidae							
Rhinella diptycha				0.000131			0.00604
Mass	141.86 ± 39.34	-0.566	0.586		-0.584	0.575	
SVL	31.09 ± 8.62	0.183	0.859		0.322	0.755	
Hylidae							
Boana raniceps				1.721969			43.6378
Mass	6.62 ± 1.76	0.0891	0.930		-0.262	0.798	
SVL	7.80 ± 2.08	0.880	0.399		-0.067	0.947	
Dendropsophus minutus				2.577e-05			0.00364
Mass	0.17 ± 0.05	-0.116	0.910		0.099	0.923	
SVL	3.13 ± 0.94	1.562	0.162		-0.294	0.776	
Scinax x-signatus				7.145e-05			0.00087
Mass	0.49 ± 0.12	0.453	0.658		-1.731	0.108	
SVL	2.60 ± 0.65	-0.537	0.600		1.964	0.073	
Trachycephalus typhonius				2.401e-05			0.00168
Mass	6.69 ± 1.57	-0.734	0.474		-1.429	0.174	
SVL	10.02 ± 2.36	0.498	0.625		1.305	0.212	
Leptodactylidae							
Leptodactylus macrosternum				2.686e-05			0.000906
Mass	25.08 ± 6.70	0.727	0.485		0.971	0.356	
SVL	15.34 ± 4.10	0.966	0.359		-1.110	0.295	
Leptodactylus pustulatus				0.4825533			13.08361
Mass	5.19 ± 1.64	-0.664	0.530		-0.743	0.485	
SVL	9.22 ± 2.91	0.754	0.479		1.190	0.278	
Leptodactylus vastus				6.832e-05			0.028361
Mass	104.23 ± 34.74	1.473	0.200		1.257	0.264	
SVL	37.15 ± 12.38	-0.352	0.738		-0.777	0.472	
Physalaemus cuvieri				2.987e-05			13.82402
Mass	0.42 ± 0.07	0.634	0.531		-0.263	0.794	
SVL	1.87 ± 0.35	-0.242	0.810		-0.427	0.672	
Odontophrynidae							
Proceratophrys renalis				3.469e-05			9.79580
Mass	3.47 ± 0.96	1.138	0.284		1.184	0.266	
SVL	3.33 ± 0.92	-0.475	0.645		-2.072	0.068	
Phyllomedusidae							
Pithecopus gonzagai				3.101e-05			0.000532
Mass	0.33 ± 0.09	1.249	0.243		0.790	0.449	
SVL	2.29 ± 0.63	-0.118	0.908		-0.093	0.927	
Strabomantidae							
Pristimantis relictus				4.676e-05			0.002645
Mass	0.48 ± 0.07	0.919	0.363		-0.196	0.864	
SVL	3.81 ± 0.60	-0.012	0.990		0.171	0.845	

St. D. ± S.E.= Standard deviation and standard error.
Significant values and percentage of variation in response that is explained by the fixed effects (mass and SVL) are represented by *P* and *T* values. Random effects were obtained through the intercept values (RE).

2.4 DISCUSSION

Communities of endoparasites associated with anurans generally show high richness and diversity (Campião *et al.,* 2014); in the present study, we found 46 parasite *taxa*, corroborating this pattern. Following the same infection pattern found in other Neotropical anurans (Lins *et al.,* 2017; Oliveira *et al.,* 2019; Silva-Neta *et al.,* 2020; Mascarenhas *et al.,* 2021), as well as in other vertebrate groups, such as reptiles (Brito *et al.,* 2014; Carvalho *et al.,* 2018), mammals (Santos *et al.,* 2015; Biolchi *et al.,* 2021) and birds (Santos *et al.,* 2015), nematodes was the helminth group with the highest representation (65.2%) of the collected specimens. Nematodes are abundant in the number of species, generalists, and well distributed in the environment. Species with direct life cycle reach their hosts by oral ingestion or active penetration of infectious larvae through the skin, not requiring an intermediate host for their development (Anderson, 2000), which facilitates the dispersion and high incidence of infection of this parasite group. Although parasitological studies dealing with anuran communities in northeastern Brazil have recently increased, there are still important gaps in our knowledge about them. For example, of the 25 host species sampled herein, six have not been surveyed for parasites yet. In addition, we present 20 new host records (see table 2), reinforcing the importance of parasite checklists.

Due to the increase in parasitological studies (Mascarenhas *et al.,* 2021), it is quite common to find records of parasites not previously reported for host species (Aguiar e*t al.,* 2014; Silva *et al.,* 2019). In the last decade, several studies on parasitism in Neotropical amphibians have been conducted (Madelaire *et al.,* 2012; Aguiar *et al.,* 2015; Chero *et al.,* 2016; Amorim *et al.,* 2019; Silva-Neta *et al.,* 2020; Sani *et al.,* 2021; Machado *et al.,* 2022), with the nematode parasites *Falcaustra mascula*, *Ochoterenella* sp., *Oswaldocruzia mazzai*, *Oxyascaris oxyascaris*, *Physaloptera* sp., *Raillietnema spectans* and *Rhabdias* sp. being the most commonly reported species. In our study, we found the same scenario, despite the low prevalence for some of the aforementioned species. This result is possibly due to the wide distribution of these parasites and their generalist habitats regarding host selection (Campião *et al.,* 2014, 2015b; Oliveira *et al.,* 2019). In addition, the lack of taxonomic studies can be a limiting factor for an accurate identification of some parasite species distributed in the studied region. However, the description of new species has been increasing as parasitological studies progress (Felix-Nascimento *et al.,* 2020).

Oswaldocruzia mazzai showed the highest prevalence (27.12%) and was present in 60% of the parasitized host species in the anuran community in our study. This result may be related to the direct life cycle of this parasite and the simple mode of transmission (Anderson, 2000). The genus *Physaloptera* had the second highest prevalence (19.61%). Parasites of this group are commonly found in all anuran parasite studies and have also been observed in several classes of terrestrial vertebrates (Ogassawara *et al.*, 1986; Tung *et al.*, 2009; Cabral *et al.*, 2018). In amphibians, they are usually found in the larval stage, suggesting that these vertebrates are used as paratenic hosts. We also collected four individuals of *Cosmocercoides* sp. (one male and three females) in the large intestine of one specimen of *Scinax x-signatus*. The species was assigned to the genus *Cosmocercoides* due to the presence of a large number of rosette-like caudal papillae surrounded by punctuations. This is the first record of *Cosmocercoides* sp. for altitudinal rainforest enclave areas within the large Caatinga phytophysiognomy, nevertheless, further studies are necessary to define the species. Additionally, we also provide the first record of infection in Brazil of the species *Parapharyngodon* cf. *duniae*.

We also found nematode larvae parasitizing the small intestine and/or large intestine of several host species. Larvae of this type are commonly found in amphibian and reptile species (Ávila & Silva, 2010; Campião *et al.,* 2014), and this larval stage may be associated with the monoxenous cycle of the parasite (Anderson, 2000), besides representing a recent infection and/or reproduction of the adult parasites in the host.

Platyhelminthes was the second most diverse phylum found in the present study, with 13 different taxa belonging to three classes (Cestoda, Monogenea and Trematoda). The most diverse class of Platyhelminthes was Trematoda with 11 *taxa* recorded. The aquatic habitat facilitates trematodes' infection, which usually have snails as intermediate hosts (Madelaire *et al.,* 2012). These parasites also use amphibians as intermediate hosts (Guillén-Hernández *et al.,* 2000), found more often in aquatic and semiaquatic frogs such as leptodactylids (Campião *et al.,* 2014; Oliveira *et al.,* 2019). *Catadiscus propinquus* was the most abundant trematode and represents a new host record for *Leptodactylus pustulatus*. Indeed, some species are new host records; however, all trematodes had low prevalence considering the species pool (see table 2). Cestodes were represented by *Cylindrotaenia americana*, a cestode commonly found in Brazil, including in altitudinal rainforest's enclaves (Oliveira *et al.,* 2019; Silva-Neta *et al.,* 2020). Herein, we provide the first record of this cestode in the treefrogs *Dendropsophus minusculus* and *Dendropsophus nanus*. Regarding monogenean parasites, we found 14 individuals of *Polystoma* cf. *lopezromani* parasitizing *Corythomantis greeningi* and *Trachycephalus typhonius*. *Polystoma* is the most diverse genus known in Polystomatidae (Sinnappah *et al.,* 2001), having a direct life cycle, which can be completed in the gills of tadpoles or urinary duct of adult anurans (Bentz *et al.,* 2006).

Acanthocephalans are extensively reported for reptiles (Matias *et al.,* 2018; Araújo *et al.,* 2020) and amphibians (Oliveira *et al.*, 2019; Silva-Neta *et al.*, 2020) as cystacanths. They are parasites with indirect life cycle, in which arthropods act as intermediate hosts, and fish, mammals or waterfowl as final hosts (Baker, 2007). The presence of these cystacanths in amphibian hosts indicates that these species are used as paratenic hosts, possibly infected through the diet. In the present study, we found two genera represented by *Centrorhynchus* and *Oligacanthorhynchus*. *Centrorhynchus* sp. is the most common genus reported in Brazil for anuran hosts (Fabio, 1982; Smales, 2007). *Oligacanthorhynchus* sp. are heteroxenous parasites and usually have mammals as final hosts (Richardson *et al.*, 2014). In South America, they are reported infecting *Odontophrynus americanus* (Silva *et al.*, 2018) and *Pleurodema diplolister* (Silva-Neta *et al.,* 2020). This study is the first record of *Oligacanthorhynchus* sp. for the anurans *Leptodactylus vastus*, *Rhinella diptycha* and *Scinax x-signatus*.

Regarding the phylum Annelida, we found four individuals of *Dero* (*Allodero*) *lutzi* in the urinary duct of *Corythomantis greeningi*, *Scinax x-signatus* and *Trachycephalus typhonius*. The genus *Dero* is known to use frogs for transport and as hosts (Oda *et al.*, 2015). This behaviour is stimulated by chemicals released by the amphibians, which are used by the parasite for dispersal (Lopez *et al.*, 2005). *Dero* (*Allodero*) *lutzi* has been found parasitizing different amphibians, mainly arboreal species (Oda *et al.*, 2015), likely because these parasites are free-living inhabitants of bromeliad ponds and tree holes (Lopez *et al.*, 1999).

The characteristics and the way the host explores its habitat can influence the composition and structure of the helminth fauna, and explain the richness and diversity of the parasites associated with it (Poulin & Morand, 2004; Chandra & Gupta, 2007; Euclydes *et al.*, 2021). Thus, anuran amphibians have a diverse parasite fauna due to their natural history (Prudhoe & Bray, 1982), which are generally associated with two types of environments, aquatic and terrestrial (Chandra & Gupta, 2007). Species of arboreal amphibians tend to have low parasite richness, due to a possible reduction in the encounter with infective parasitic larvae. On the other hand, host anurans with terrestrial or semiaquatic habitats tend to have greater contact with the terrestrial environment when searching for water bodies, increasing the odds of contact with a greater number of parasites (Pizzatto *et al.*, 2013; Euclydes *et al.*, 2021).

However, we observed that the arboreal habitat had great parasite richness. The higher number of individuals classified as arboreal (n = 163) in the present study may be an explanation for the significant relationship of arboreal habitat with parasite richness. Most species classified as arboreal were found during the reproductive period, in which anurans seek out puddles and mate for reproduction, passing through terrestrial and aquatic environments.

This provides a greater likelihood of direct contact with infectious larvae, which allows a greater variety of parasites to become established in these animals (Chandra & Gupta, 2007).

According to Todd (2007), endoparasitic helminths of amphibians require an aquatic environment for the development and transmission of their infective stages, as this promotes increased parasite transmission. However, we observed that the use of terrestrial and arboreal microhabitat contributed significantly to the abundance of parasites, showing that most helminth parasites of amphibians do not require an aquatic environment in the process of transmission and infection. Our data also indicated no relationship between host sex and parasite richness, but this result may have been influenced by the difference in the number of individuals of each sex analysed (Madeira & Sogayar, 1993). Moreover, most anuran hosts do not present differentiation in habitat use according to sex, being both subject to the same chances of infection by infective larvae available in the environment. It is also noteworthy that biotic factors such as the immune system and host age also affect parasitism, as they influence the life of both parasite and host (Pietrock & Marcogliese, 2004).

Overall, at an interspecific view, we observed that larger frogs tend to be more parasitized. Indeed, larger hosts can support a higher parasite load and even higher species richness because they offer greater microhabitat diversity favouring the development and reproduction of parasites (George-Nascimento *et al.,* 2004; Campião *et al.,* 2015b). However, this hypothesis was not supported in the present study at intraspecific views. This pattern was also found in other parasitological studies dealing with amphibians (e.g. Oliveira *et al.,* 2019; Mascarenhas *et al.,* 2021; Machado *et al.,* 2022). It seems that this hypothesis might be more evidenced concerning a species pool with anuran species of different sizes (e.g. Silva-Neta *et al.,* 2020). Therefore, for congeneric species, we believe that other aspects such as microhabitat use, physiology, behaviour and seasonality, might have a greater influence on parasite load than the anuran size.

We conclude that the endoparasite composition of anurans from Maranguape mountain follow the common pattern described for Neotropical amphibians, showing high species richness and prevalence. We also recorded the first parasitological data for six anuran species and 20 new host records, which corroborates the hypothesis that amphibians are good models for parasite studies due to their way of life, behaviour and feeding. Furthermore, we stress the importance of parasite inventories for host species in understudied regions. We also emphasize that endoparasite composition has a significant relationship with the type of habitat used by the host due to the life cycle and mode of transmission of the parasites. As for the relationship between richness and host size, we indicate here that the size factor is predictive only if it has a large variation from the average host size.

REFERENCES

Aguiar, A., Morais, D.R., Pyles, P.C. and Silva, R.J. (2014) Evaluation of helminths associated with 14 amphibian species from a neotropical island near the southeast coast of Brazil. *Herpetological Review* **45**(2), 227–236.

Aguiar, A., Toledo, G.M., Anjos, L.A. and Silva, R.J. (2015) Comunidades de helmintos parasitas de duas populações de *Physalaemus cuvieri* Fitzinger, 1826 (Anura: Leiuperidae) sob diferentes condições de integridade de habitat na Mata Atlântica do Brasil. [Communities of helminth parasites of two populations of *Physalaemus cuvieri* Fitzinger, 1826 (Anura: Leiuperidae) under different habitat integrity conditions in the Atlantic Forest of Brazil]. *Revista Brasileira de Biologia* **75**(4), 963–968. [In Portuguese]

Aguiar, A., Morais, D.H., Silva, L.A.F., Dos Anjos, L.A., Foster, O.C. and Da Silva, R.J. (2021). Biodiversity of anuran endoparasites from a transitional area between the Atlantic Forest and Cerrado biomes in Brazil: New records and remarks. *Zootaxa*, **4948**(1), 1-41.

Aho, J.M. (1990) Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and processes. pp. 157-195 in Esch, G.W., Bush, A.O. and Aho, J.M. (*Eds*) *Parasite Communities: Patterns and processes*. New York, Chapman and Hall.

Albuquerque, U.P., De Lima Araújo, E., El-Deir, A.C.A., De Lima, A.L.A., Souto, A., Bezerra, B.M. and Severi, W. (2012) Caatinga revisited: ecology and conservation of an important seasonal dry forest. *The Scientific World Journal* **2012**, 205182.

Amato, J.F.R., Boeger, W.A. and Amato, S.B. (1991) *Protocolos para laboratório – Coleta e processamento de parasitos de pescado*. Rio de Janeiro: Imprensa Universitária – FRRJ.

Amorim, D.M., Oliveira, R.H., Dyna, C.S., Sousa, D.M., Santos, M.E.P., Lima, L.S., Pinto, L.C. and Ávila, R.W. (2019) Nematodes Parasites of *Rhinella jimi* (Stevaux, 2002) (Anura: bufonidae) in areas of Caatinga, Northeastern Brazil. *Neotropical Helminthology* **13**, 265–271.

Anderson, R.C. (2000) *Nematode parasites of vertebrates, their development and transmission*. 2nd ed. 650 pp. Wallingford, Oxon, CABI Publishing.

Andrade, C. (2000) *Meios e soluções comumente empregados em laboratórios*. Seropédica, UFRRJ.

Araújo, K.C., Silva, C.D.S., Machado, H.D.S., Oliveira, C.R. and Ávila, R.W. (2020) Endoparasites of *Philodryas olfersii* (Lichtenstein, 1823) in restinga environments of the Parnaíba River Delta, Northeastern Brazil. *Neotropical Helminthology* **14**, 129–141.

Ávila, R.W. and Silva, R.J. (2010) Checklist of helminths from lizards and amphisbaenians (Reptilia, Squamata) of South America. *Journal of Venomous Animals and Toxins Including Tropical Diseases* **16**(4), 543–572.

Baker, D.G. (2007). *Flynn's Parasites of Laboratory Animals: Second Edition.* Second ed. Oxford, UK: Blackwell Publishing Ltd.

Bentz, S., Sinnappah-Kang, N.D., Lim, L.H.S., Lebedev, B., Combes, C. and Verneau, O. (2006) Historical biogeography of amphibian parasites, genus *Polystoma* (Monogenea: Polystomatidae). *Journal of Biogeography* **33**, 742–749.

Bernarde, P.S. (2012) *Anfíbios e répteis: introdução ao estudo da herpetofauna brasileira*. 1 ed. Anolis Books, Curitiba.

Bezerra, C.H., Pinheiro, L.T., Melo, G.C., Zanchi-Silva, D., Queiroz, M.S., Anjos, L.A., Harris, D.J. and Borges-Nojosa, D.M. (2016) Assessing the influence of geographic distance in parasite communities of an exotic lizard. *Acta Parasitologica* **6**, 136–143.

Biolchi, J., Pontarolo, G.H., de Cássia Karvat, D., and Pedrassani, D. (2021). Análise coproparasitológica de gambás-de-orelha-branca pertencentes a áreas urbanas e rurais do município de canoinhas, norte de Santa Catarina. *Archives of Veterinary Science* **26**, 79–89.

Borges-Nojosa, D.M. and Caramaschi, U. (2003) Composição e análise comparativa da diversidade e das afinidades biogeográficas dos lagartos e anfisbenídeos (Squamata) dos brejos nordestinus. [Composition and comparative analysis of the diversity and biogeographic affinities of lizards and amphisbaenids (Squamata) from the northeastern swamps]. pp. 489–540. In Leal IR, Tabarelli M and Silva JMC (Eds) *Ecologia e conservação da Caatinga* [Ecology and conservation of the Caatinga]. Recife, UFPE.
[In Portuguese.]

Borges-Nojosa, D.M., Lima, D.C., Bezerra, C.H. and Harris, D.J. (2016) Two new species of *Apostolepis* Cope, 1862 (Serpentes: Elapomorphini) from Brejos de altitude in northeastern Brazil. *Revista Nordestina de Zoologia* **10**(1), 74–94.

Brito, S.V., Corso, G., Almeida, A.M., Ferreira, F.S., Almeida, W.O., Anjos, L.A., Vasconcellos, A. (2014) Phylogeny and micro-habitats utilized by lizards determine the composition of their endoparasites in the semiarid Caatinga of Northeast Brazil. *Parasitology Research* **113**, 3963–3972.

Bursey, C.R. and Brooks, D.R. (2004) *Parapharyngodos Dunniae* n. sp. (Nematoda: Pharyngodonidae) in *Phrynohyas venulosa* (Anura: Hylidae) from the área conservación Guanacaste, Costa Rica. *Journal of Parasitology* **90,** 137–139.

Bush, A.O., Lafferty, K.D., Lotz, J.M. and Shostak, A.W. (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology* **83**, 575–583.

Cabral, A.N., Teles, D.A., Brito, S.V., Almeida, W.O., Dos Anjos, L.A., Guarnieri, M.C. and Ribeiro, S.C. (2018) Helminth parasites of *Mabuya arajara* Rebouças-Spieker, 1981 (Lacertilia: Mabuyidae) from Chapada do Araripe, northeastern Brazil. *Parasitology Research* **117**, 1185–1193.

Calleffo, M.E.V. (2002) Anfíbios. pp.45-73 in Auricchio, P. and Salomão, M.G. (*Eds*) *Técnicas de coleta e preparação de vertebrados para fins científicos e didáticos.* Instituto Pau Brasil de História Natural, São Paulo.

Campião, K.M., Morais, D.H., Dias, O.T., Aguiar, A., Toledo, G., Tavares, L.E.R., and Silva, R.J. (2014) Checklist of helminth parasites of amphibians from South America. *Zootaxa* **3843**, 1–93.

Campião, K.M., Ribas, A. and Tavares, L.E.R. (2015a) Diversity and patterns of interaction of an anuran-parasite network in a neotropical wetland. *Parasitology* **142**, 1751–1757.

Campião, K.M., Ribas, A.C.A., Morais, D.H, Dias, O.T, Silva, R.J. and Tavares, L.E.R. (2015b) How Many Parasites Species a Frog Might Have? Determinants of Parasite Diversity in South American Anurans. *PloSone* **10**, e0140577.

Campião, K.M., Silva, I.C.O., Dalazen, G.T., Paiva, F. and Tavares, L.E.R. (2016a) Helminth Parasites of 11 Anuran Species from the Pantanal Wetland, Brazil. *Comparative Parasitolgy* **83**, 92–100.

Campião, K.M., Ribas, A.C.A., Silva, I.C., Dalazen, G.T., Tavares, L.E.R. (2016b): Anuran helminth communities from contrasting nature reserve and pasture sites in the Pantanal wetland, Brazil. Journal of Helminthology **91**: 91–96.

Cañizales, I. (2021). Helmintos endoparásitos en anuros de Venezuela: Revisión sistemática y análisis de diversidad. *Acta Biologica Venezuelica* **40**,109–127.

Carvalho, E.D., Silva-Neta, A.F.D., Silva, C.D.S., Oliveira, C.R., Nunes, J.D.C.X., Souza, T.G., and Ávila, R.W. (2018). Helminths Infecting the Cat-eyed Snake *Leptodeira Annulata* Linnaeus 1758 (Squamata: Dipsadidae) in a Semiarid Region of Brazil. *Helminthologia* **55**, 281–285.

Catalano, S.R., Whittington, I.D., Donnellan, S.C. and Gillanders, B.M. (2013) Parasites as biological tags to assess host population structure: Guidelines, recent genetic advances and comments on a holistic approach. *International Journal for Parasitology: Parasites and Wildlife* **3**, 220–226.

Ceará (2002) *Zoneamento ambiental e plano de manejo da área de proteção ambiental (APA) da serra de Maranguape (CE).* Fortaleza: SEMACE.

CFMV – Conselho Federal de Medicina Veterinária (2013) Métodos de eutanásia. pp.28-29 in Comissão de ética, Bioética e bem-estar animal - CFMV, (*Eds*) *Guia brasileiro de boas práticas de eutanásia em animais.* ASCOM/CFMV, Brasília.

Chandra, P. and Gupta, N. (2007). Habitat Preference and Seasonal Fluctuations in the Helminthofauna of Amphibian Hosts of Rohilkhand Zone, India. *Asian Journal of Experimental Sciences* **21**, 69–78.

Chero, J., Cruces, C., Iannacone, J., Sáez, G., Alvariño, L., Luque, J. and Morales, V. (2016) Comunidad de helmintos parásitos del sapo espinoso *Rhinella spinulosa* (Wiegmann, 1834)(Anura: Bufonidae) de Perú. *Revista de Investigaciones Veterinarias del Perú* **27**, 114-129.

Euclydes, L., Dudczak, A.C. and Campião, K.M. (2021) Anuran's habitat use drives the functional diversity of nematode parasite communities. *Parasitology Research* **120**(3), 993–1001.

Fabio, S.P. (1982) Helmintos de populações simpátricas de algumas espécies de anfíbios anuros da Família Leptodactylidae. *Arquivos da Universidade Federal do Rio de Janeiro* **5**, 69–83.

Felix-Nascimento, G., Vieira, F.M., Muniz-Pereira, L.C. and De Moura, G.J.B. (2020). Two new species of Cosmocercidae (Nematoda: Cosmocercoidea) of Leptodactylus macrosternum Miranda-Ribeiro (Anura: Leptodactylidae) from Caatinga Biome, Brazil. *Zootaxa*, **4877**, 274–290.

George-Nascimento, M., Muñoz, G., Marquet, P.A. and Poulin, R. (2004) Testing the energetic equivalence rule with helminth endoparasites of vertebrates. *Ecology Letters* **7**, 527.

Goater, C.P., Baldwin, R.E. and Scrimgeour, G.J. (2005) Physicochemical determinant community structure in whitefish (*Coregonus clupeaformes*) from adjacent lakes in Northern Alberta, Canada. *Parasitology* **131**, 713–722.

Gonçalves, A.Q., Vicente, J.J. and Pinto, R.M. (2002) Nematodes of amazonian vertebrates deposited in the helminthological collection of the Oswaldo Cruz Institute with new records. *Revista Brasileira de Zoologia* **19**, 453–465.

González, C.I. and Hamann, M.I. (2011) Cosmocercid nematodes of three species of frogs (Anura: Hylidae) from Corrientes, Argentina. *Comparative Parasitology* **78**, 212–216.

Gonzalez, C.E. and Hamann. M.I. (2015). Checklist of nematode parasites of amphibians from Argentina. *Zootaxa* **3980**, 451–476.

Graça, R.J., Oda, F.H., Lima, F.S., Guerra, V., Gambale, P.G. and Takemoto, R.M. (2017) Metazoan endoparasites of 18 anuran species from the mesophytic semideciduous Atlantic Forest in southern Brazil. *Journal of Natural History* **51**, 705–729.

Guillén-Hernández, S., Salgado-Maldonado, G. and Lamothe-Argumedo, R. (2000) Digeneans (Plathelminthes: Trematoda) of seven sympatric species of anurans from Los Tuxtlas, Veracruz, Mexico. *Studies on Neotropical Fauna and Environment* **35**, 10–13.

Hamann, M.I. and Kehr, A.I. (1998) Variación espacio temporal en infrapoblaciones de helmintos y su relación con las fluctuaciones poblacionales de *Hyla nana* (Anura, Hylidae). *Cuadernos de Herpetología* **12**, 23–33.

Hamann, M.I., Kehr, A.I. and González, C.E. (2006) Species affinity and infracommunity ordination of helminths of *Leptodactylus chaquensis* (Anura: Leptodactylidae) in two contrasting environments from northeastern Argentina. *Journal of Parasitology* **92**, 1171–1179.

IPECE – Instituto de Pesquisa e Estratégia Econômica do Ceará (2017) Perfil municipal: Maranguape. Accessible at: http://www.ipece.ce.gov.br. (Last access: 21 july 2021).

Kuris, A.M. (2008) Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* **454**, 515–518.

Lins, A.G.S., Aguiar, A., Morais, D.H., Silva, L.A. F., Ávila, R.W. and Silva, R.J. (2017) Helminth fauna of *Leptodactylus syphax* (Anura: Leptodactylidae) from Caatinga biome, northeastern Brazil. *Brazilian Journal of Veterinary Parasitology* **26**, 74–80.

Lopez, L.C.S., Rodrigues, P.J.F.P. and Rios, R.I. (1999) Frogs and snakes as phoretic dispersal agents of bromeliad ostracods (*Elpidium*) and Annelids (*Dero*). *Biotropica* **31**, 705–708.

Lopez, L.C.S., Filizola, B., Deiss, I. and Rios, R.I. (2005) Phoretic behaviour of bromeliad annelids (*Dero*) and ostracods (*Elpidium*) using frogs and lizards as dispersal vectors. *Hydrobiologia* **549**, 15–22.

Machado, H.T.S., de Oliveira, S.S., Benício, R.A., Araújo, K.C. and Ávila, R.W. (2022) Helminths infecting sympatric congeneric treefrogs in northeastern Brazil. *Acta Parasitologica.* **67**(2), 658–667.

Madeira, N.G., and Sogayar, M.I.L. (1993) Prevalencia de *Demodex folliculorum* e *Demodex brevis* em uma amostra da população de Botucatu, São Paulo, Brasil. *Revista da Sociedade Brasileira de Medicina Tropical* **26**, 221–224.

Madelaire, C.B., Gomes, F.R. and Da Silva, R.J. (2012) Helmintos parasitas de *Hypsiboas prasinus* (Anura: Hylidae) de dois fragmentos de floresta atlântica, Estado de São Paulo, Brasil. *Journal of Parasitology* **98**, 560–564.

Marcogliese, D.J. (2004) Parasites: small players with crucial roles in the ecological theatre. *Ecohealth* **1**, 151–164.

Martins-Sobrinho, P.M., Silva, W.G.D.O., Santos, E.G.D., Moura, G.J.B.D. and Oliveira, J.B.D. (2017). Helminths of some tree frogs of the families Hylidae and Phyllomedusidae in an Atlantic rainforest fragment, Brazil. *Journal of Natural History* **51**, 1639–1648.

Mascarenhas, W., Oliveira, C.R., Benício, R.A., Ávila, R.W. and Ribeiro, S.C. (2021) Nematodes of *Proceratophrys ararype* (Anura: Odontophrynidae), an endemic frog from the Araripe Plateau, northeastern Brazil. *Biota Neotropica* **21**, e20201164.

Matias, C.S.L., Ferreira–Silva, C., Sousa, J.G.G. and Ávila, R.W. (2018) Helminths infecting the black false boa *Pseudoboa nigra* (Squamata: Dipsadidae) in northeastern Brazil. *Acta Herpetologica* **13**, 171–175.

Ministério do Meio Ambiente - MMA. (2000) *Avaliação e para a conservação ações prioritárias da biodiversidade da Mata Atlântica e Campos Sulinos* [Assessment and conservation priority actions for the biodiversity of the Atlantic Forest and Campos Sulinos]. Brasilia, Secretaria de Biodiversidade e Florestas (SBF), Ministério do Meio Ambiente (MMA). [In Portuguese]

Morais, D.H. (2013). *Aspectos ecológicos da helmintofauna de anfíbios Leptodactylidae (ANURA) no Estado do Mato Grosso, Brasil*. Doctorate thesis, UNESP—Campus de Botucatu, Botucatu- SP.

Morais, D.H., Aguiar, A., Campião, K.M., Tavares, L.E.R., Almeida, W.O., Ávila, R.W., and Silva, R.J. (2017) New records of *Dero* (*Allodero*) *lutzi*, an oligochaete parasite of the urinary tract of South American Anurans. *Herpetological Review* **48**, 739–743.

Oda, F.H., Petsch, D.K., Ragonha, F.H., Batista, V.G., Takeda, A.M. and Takemoto, R.M. (2015). *Dero (Allodero) lutzi* Michaelsen, 1926 (Oligochaeta: Naididae) associated with *Scinax fuscovarius* (Lutz, 1925)(Anura: Hylidae) from Semi-deciduous Atlantic Rain Forest, southern Brazil. *Brazilian Journal of Biology* **75**, 86–90.

Ogassawara, S., Benassi, S., Larsson, C.E., Leme, P.T.Z. and Hagiwara, M.K. (1986) Prevalência de infecções helmínticas em gatos na cidade de São Paulo. *Revista da Faculdade de Medicina Veterinária e Zootecnia da Universidade de São Paulo* **23**, 145–149.

Ogle, D.H., Doll, J.C., Wheeler, P. and Dinno, A. (2022). FSA: Fisheries Stock Analysis. R package version 0.9.3, https://github.com/fishR-Core-Team/FSA.

Oliveira, C.R., Ávila, R.W. and Morais, D.H. (2019) Helminths associated with three *Physalaemus* species (Anura: Leptodactylidae) from Caatinga Biome, Brazil. *Acta Parasitologica* **64**, 205–212.

Pietrock, M. and Marcogliese, D.J. (2004) Response to Morley and Lewis: Freeliving endohelminths: the influence of multiple factors. *Trends in Parasitology* **20**, 3.

Pinheiro, J.C., and Bates, D.M. (2000). Mixed-Effects Models in S and S-PLUS, Springer.

Pizzatto, L., Kelehear, C. and Shine, R. (2013) Seasonal dynamics of the lungworm, *Rhabdias pseudosphaerocephala*, in recently colonised cane toad (*Rhinella marina*) populations in tropical Australia. *International Journal for Parasitology* **43**, 753–761.

Poulin, R. and Krasnov, B.R. (2010) Similarity and variability of parasite assemblages across geographical space. pp.115-128 in Morand, S. and Krasnov, B. R. (*Eds.*) *The biogeography of hostparasite interactions.* Oxford University, New York.

Poulin, R. and Morand, S. (2004) *Parasite Biodiversity*, Smithsonian Institution Books, Washington, D.C., USA.

Poulin, R., Blanar, C.A., Thieltges, D.W. and Marcogliese, D.J. (2011) The biogeography of parasitism in sticklebacks: distance, habitat differences and the similarity in parasite occurrence and abundance. *Ecography* **34**, 540–551.

Prudhoe, S. and Bray, R.A. (1982) *Platyhelminth parasites of the Amphibia*. Oxford: British Museum (Natural History); Oxford University Press.

Queiroz, M.S., Pontes, M.R., Neto, M.C., Campião, K.M., and Anjos, L.A. (2020). Helminths of 8 anuran species from a remnant riparian forest in the Cerrado biome, Brazil. *Herpetology Notes* **13**, 463–478.

R Development Core Team. (2021). R: A language and environment for statistical computing: R Foundation for Statistical Computing version 4.1.1. (software). Austria.

Richardson, D.J., Gardner, S.L. and Allen, J.W. (2014) Redescription of *Oligacanthorhynchus microcephalus* (Oligacanthorhynchidae). *Comparative Parasitology* **81**, 53–60.

Roberto, I.J. and Loebmann, D. (2016) Composition, distribution patterns, and conservation priority areas for the Herpetofauna of the State of Ceará, Northeastern Brazil. *Salamandra* **52**(2), 134–152.

Sani, A.A., Rangel, G.T., dos Santos, L.C., and Frezza, T.F. (2021) Helmintos parasitos de répteis e anfíbios no estado de São Paulo, Brasil. *Interfaces Científicas-Saúde e Ambiente* **8**, 32–59.

Santos, V.G.T. and Amato, S.B. (2013) Species of *Cosmocerca* (Nematoda, Cosmocercidae) in Anurans from southern Santa Catarina State, Brazil. *Comparative Parasitology* **80**, 123–129.

Santos, P.M.D.S., Silva, S.G.N.D., Fonseca, C.F.D., and Oliveira, J.B.D. (2015). Parasitos de aves e mamíferos silvestres em cativeiro no estado de Pernambuco. *Pesquisa Veterinária Brasileira* **35**, 788–794.

Schmidt, G.D. (1986) *CRC Handbook of tapeworm identification*. Florida: CRC Press.

Segalla, M.V., Berneck, B., Canedo, C., Caramaschi, U., Cruz, C. A. G., Garcia, P. C. A., … and Langone, J.A. (2021) Brazilian Amphibians: List of Species. *Herpetologia Brasileira* **10**, 121–216.

Sierra, M.C., Ramírez, G.F. and Osorio, J.H. (2013). Main helminths found in a captive fauna center in Colombia. *Boletín Científico Museo de Historia Natural* **17**, 251–257.

Silva, C.D.S., Ávila, R.W. and Morais, D.H. (2018) Helminth community dynamics in a population of *Pseudopaludicola pocoto* (Leptodactylidae: Leiuperinae) from Northeast-Brazilian. *Helminthologia* **55**, 292.

Silva, C.S., Alcantara, E.P., Silva, R.J., Ávila, R.W. and Morais, D.H. (2019) Helminths parasites of the frog *Proceratophrys aridus* Cruz, Nunes, and Juncá, 2012 (Anura: Odontophrynidae) in a semiarid region, Brazil. *Neotropical Helminthology* **13**, 169–179.

Silva-Neta, A.F., Alcantara, E.P., Oliveira, C.R., Carvalho, E.F.F., Morais, D.H., Silva, R.J. and Ávila, R.W. (2020) Helminths associated with 15 species of anurans from the Ibiapaba Plateau, Northeastern Brazil. *Neotropical Helminthology* **14**, 197–206.

Sinnappah, N.D., Lim, L.H.S., Rohde, K., Tinsley, R., Combes, C. and Verneau, O. (2001) A endomorphic parasite associated with a neotenic amphibian host: phylogenetic evidence suggests a revised systematic position for Sphyranuridae within anuran and turtle polystomatoineans. *Molecular Phylogenetics and Evolution* **18**, 189–201

Smales, L.R. (2007) Acanthocephala in amphibians (Anura) and reptiles (Squamata) from Brazil and Paraguay with description of a new species. *Journal of Parasitology* **93**, 392–398.

Sousa, M.A.N., Langguth, A. and Gimenez, E.A. (2004) *Brejos de altitude em Pernambuco e Paraíba: história natural, ecologia e conservação* [Highland swamps in Pernambuco and Paraíba: Natural history, ecology and conservation]. pp. 229–254. Brasília: MMA. [In Portuguese.]

Teles, D.A., Brito, S.V., Araújo–Filho, J.A., Teixeira, A.A.M., Ribeiro, S.C., Mesquita, D.O. and Almeida, W.O. (2017) Nematode parasites of *Proceratophrys aridus* (Anura: Odontophrynidae), an endemic frog of the Caatinga domain of the neotropical region in Brazil. *Herpetological notes* **10,** 525–527.

Teles, D.A., Brito, S.V., Araujo Filho, J.A., Ribeiro, S.C., Teixeira, A.A., Mesquita, D.O. and Almeida, W.O. (2018). Nematodes of the *Rhinella granulosa* Spix, 1824 (Anura: Bufonidae) from the semiarid northeastern Caatinga Region of Brazil. *Comparative parasitology* **85**, 208–211.

Todd, B.D. (2007) Parasites lost? An overlooked hypothesis for the evolution of alternative reproductive strategies in Amphibians. *The American Naturalist* **170**, 793–799.

Toledo, G.M., Fonseca, M.G., Iannacone, J., Callirgos, J.M.C., Vidaurre, C.U.M., and da Silva, R.J. (2017) Parasitic helminths from *Rhinella marina* (Linnaeus, 1758) (Anura: Bufonidae) from Tarapoto, Peru. *The Biologist (Lima)* **15**, 459–468.

Travassos, L., Freitas, J.F. and Kohn, A. (1969). Trematódeos do Brazil. *Memórias do Instituto Oswaldo Cruz* **67**, 1–886.

Tung, K.C., Hsiao, F.C., Yang, C.H., Chou, C.C., Lee, W.M., Wang, K.S. and Lai, C.H. (2009) Surveillance of endoparasitic infections and the first report of *Physaloptera* sp. and Sarcocystis spp. in farm rodents and shrews in central Taiwan. *Journal of Veterinary Medical Science* **71**, 43–47.

Vanzolini, P.E. (1981) A quasi-historical approach to the natural history of the differentiation of reptiles in tropical geographic isolates. *Papéis Avulsos de Zoologia* **34**(19), 189–204.

Vicente, J.J., Rodrigues, H.O., Gomes, D.C. and Pinto, R.M. (1991) *Nematóides do Brasil, 2ª parte: Nematóides de anfíbios*. *Revista Brasileira de Zoologia* **7**, 549–626.

Vieira; E.F., Lima, V.D., Félix, A.J.S., Costa, M.A.T., Moura Pires, S., Santos, B.M.R., ... and de Andrade, E.B. (2021). Fauna parasitária de *Leptodactylus macrosternum* (Anura: Leptodactylidae) no município de União–PI. *Brazilian Journal of Development* **7**, 49679–49692.

Vitt, L.J. and Caldwell, J.P. (2009) *Herpetology, an introductory biology of amphibians and reptiles*. 3 ed. Elsevier, Amsterdam.

Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. Retrieved from https://ggplot2.tidyverse.org

Windsor, D.A. (1998) Controversies in parasitology, most of the species on Earth are parasites. *International journal for parasitology* **28**, 1939–1941.

Yamaguti, S. (1971) *Systema Helminthum - Trematodes*. Vol. I. Interscience Publishers, London.

Chapter 2 –

---

3 Effect of Altitude and Spatial Heterogeneity on the Host-Parasite Relationship in Anurans from a Remnant Humid Forest in the Brazilian Semiarid

Efeito da Altitude e Heterogeneidade Espacial na Relação Parasito-Hospedeiro em Anuros de um Remanescente de Floresta Úmida no Semiárido Brasileiro

Cicero Ricardo de Oliveira

José Guilherme Gonçalves-Sousa

Elvis Franklin Fernandes de Carvalho

Robson Waldemar Ávila

Diva Maria Borges-Nojosa

Artigo Submetido a revista ***Parasitology Research***

https://www.springer.com/journal/436/submission-guidelines

Effect of Altitude and Spatial Heterogeneity on the Host-Parasite Relationship in Anurans from a Remnant Humid Forest in the Brazilian Semiarid

Cicero Ricardo de Oliveira[1,2,*], José Guilherme Gonçalves-Sousa[2,3], Elvis Franklin Fernandes de Carvalho[1,2], Robson Waldemar Ávila[1,2], Diva Maria Borges-Nojosa[1,2].

1- Graduate Program in Ecology and Natural Resources, Block 902, Science Center, PICI Campus, Federal University of Ceará - UFC, Fortaleza - CE, Zip Code: 60455-760, Brazil.

2- Regional Ophiology Center, Block 905, Science Center, PICI Campus, Federal University of Ceará - UFC, Fortaleza - CE, Zip Code: 60455-760, Brazil.

3- Department of Biology, Regional University of Cariri, Campos Sales Campus, Ceará, Brazil.

[*] **Corresponding Author:** riccicer@gmail.com

Abstract

In the present study, we investigated the effect of habitat heterogeneity, altitudinal gradient, and phylogeny on the abundance and richness of anuran endoparasites, assuming that parasites follow the distribution of their hosts independently of environmental variation. We collected 192 anurans, representing 23 host species, distributed in three altitude ranges. We performed discriminant principal component analysis to verify if there is a formation of species groups in each altitude range. We estimated the niche width and overlap of the parasites and assessed whether parasite abundance is more influenced by historical or ecological effects in each altitude category and overall. Finally, we use network analyses to understand how the interaction between parasites and hosts are formed. We found 22 parasite species and the overall prevalence of infection was 74%. We did not detect abiotic (altitude and heterogeneity gradients) or phylogenetic effects acting on the parasite species. Overall, our results suggest that the parasites are distributed following the dispersal of their hosts, and are dispersed to most anuran species.

Keywords: Ecology, Phylogeny, Interaction networks, Species distribution, Helminth, Amphibians.

Resumo

No presente estudo, investigamos o efeito da heterogeneidade do habitat, gradiente altitudinal e filogenia sobre a abundância e riqueza dos endoparasitas em anuros, assumindo que os parasitos seguem a distribuição de seus hospedeiros independentemente da variação ambiental. Coletamos 192 anuros, representando 23 espécies hospedeiras, distribuídas em três faixas de altitude. Realizamos análise discriminante dos componentes principais para verificar se há formação de grupos de espécies em cada faixa de altitude. Estimamos a largura do nicho e a sobreposição dos parasitas, avaliamos se a abundância de parasitas é mais influenciada por efeitos históricos ou ecológicos em cada categoria de altitude e no geral. Finalmente, usamos análises de rede para entender como se forma a interação entre os parasitas e os hospedeiros. Encontramos 22 espécies de parasitas e a prevalência geral de infecção foi de 74%. Não detectamos efeitos abióticos (gradientes de altitude e heterogeneidade) ou filogenéticos agindo sobre as espécies parasitárias. Em geral, nossos resultados sugerem que os parasitas são distribuídos após a dispersão de seus hospedeiros, e estão dispersos para a maioria das espécies de anuros.

Palavras-chave: Ecologia, Filogenia, Redes de interação, Distribuição das espécies, Helmintos, Anfíbios.

3.1 INTRODUCTION

One of the main objectives of ecology is to determine the causes of the distribution and abundance of organisms (Krebs 2001). In this sense, ecologists have sought to identify the characteristics of populations and communities along geographical or environmental gradients that influence the species distribution (Kessler 2009; Junior and Gomes 2012; Silva and Rossa-Feres 2017). As a result, diverse ecological hypotheses and theories have been formulated to explain the patterns of distribution and species richness on the planet.

Environmental heterogeneity (MacArthur and MacArthur 1961) and latitudinal gradient (Pianka 1966; Rohde 1992), widely accepted as predictors of distribution patterns and species richness (Oliveira and Oliveira 2014), are some of the hypotheses and theories postulated to try to explain the distribution and species richness of individuals in certain habitats. In northeastern Brazil, some studies have shown that among environmental factors, temperature, humidity, and precipitation represent the main predictors of species diversity, especially of amphibians (Andrade et al. 2012; Araújo et al. 2018) and lizards (Gonçalves-Sousa et al. 2022).

Species richness is the first and oldest concept of species diversity (Krebs 2001) and the search for general patterns along environmental gradients has been investigated in different geographic areas and with different taxa, such as: amphibians (Pombal 1997; Dias-Terceiro et al. 2015; Araújo et al. 2018), birds (Kattan and Franco 2004), lizards (Gonçalves-Sousa et al. 2022), snakes (Fraga et al. 2018), mammals (Geise et al. 2004; Remonti et al. 2009); and plants (Bhattarai and Vetaas 2006; Lovett et al. 2006). Environmental heterogeneity is one of the best predictors of species diversity (Huston 1994) since the greater number of microenvironments found in more complex environments allows a greater number of species to coexist (Santos et al. 2007, 2012; Araújo et al. 2018).

Another aspect that can influence species richness is altitude (Rahbek 1995; Nunes and Santos 2011; Arita et al. 2014), which may be a limiting factor of several biotic factors and structuring the biological communities along altitudinal gradients (Colwell and Lees 2000; Rahbek 2005; Romdal and Grytnes 2007). Species richness tends to decrease with increasing altitude, with richer communities at intermediate altitudes (Rahbek 1995; Nunes and Santos 2011). However, variation in species richness across environmental gradients may differ between taxa, and the pattern found within the same taxon may differ between localities (Bernal and Lynch 2008; Hu et al. 2012; Siqueira and Rocha 2013).

According to Campião et al. (2014), anurans have parasitic communities composed of generalist helminths, which are species with wide distribution, high diversity, and low host specificity. These communities are mainly composed of direct transmission species, favoring parasites with an infectious stage in the soil, such as nematodes (Barton 1999; Bursey et al. 2001). Where, the characteristics of the habitats that hosts inhabit may be critical to parasite colonization (Goater et al. 2005). Because of the way hosts respond to biotic factors, parasite richness can vary depending on environmental conditions (Poulin and Krasnov 2010). However, few studies show the influence of environmental variations on parasite-host relationships (Azevedo et al. 2006; Vasconcelos and Dias 2014), and even fewer in areas as specific as altitudinal rainforest enclaves.

Many species distribution models using the ecological niche are useful for solving questions in ecology, conservation, and biogeography, which can be used to understand the potential distribution of these parasites (Peterson et al. 2004; Guisan and Thuiller 2005; Haverkost et al. 2010). Analyzing communities across complex networks also allows us to highlight and analyze ecological patterns (Brito et al. 2014; D'Bastiani et al. 2020), due to the importance of considering the community context to understand the ecological implications of host-parasite interactions (Poisot et al. 2015; Gonzalez and Inés 2015). Likewise, studies of biological or macro ecological interactions, including patterns of ecological networks, are important for understanding the structure of the relationships between living organisms across wide geographic spaces (Gaston 2000; Vázquez et al. 2005; Guilhaumon et al. 2012). Studies emphasizing the structure of parasite-host networks have been increasing in the last decade (Krasnov et al. 2012; Brito et al. 2014; Poisot et al. 2015; D'Bastiani et al. 2020). These studies have found that phylogeny (Cattin et al. 2004), habitat constraints (Tylianakis et al. 2007), interspecific interactions (Ings et al. 2009), and morphology (Woodward et al. 2005) are key features of the architecture of an interaction network.

In the present study we investigated (i) the effects of environmental heterogeneity and an altitudinal gradient on the abundance and richness of endoparasites; (ii) the influence of phylogenetic and ecological effects on parasite parameters (such as prevalence, species richness and abundance); (iii) and tested the hypothesis that parasites follow the distribution of their hosts, independently of variation across several environmental gradients, heterogeneity and altitudinal gradients.

3.2 MATERIAL AND METHODS

3.2.1 Study area

The study area consists of the Maranguape mountain, state of Ceará, Brazil, an enclave of the altitudinal rainforest with maximum altitude of 920m, usually known as "Brejo de altitude" (Andrade-Lima 1982; Tabarelli and Santos 2004). With a climatic regime is defined in two distinct seasons, a dry one from June to December and a rainy one concentrated between January to May, with average annual precipitation of 1300 mm, and temperatures ranging between 26ºC and 28ºC (Ceará 2002; Ipece 2017). Where, the humid vegetation is preserved, mainly in the part facing the coast, due to the altitude and location near the sea (Moro et al. 2015; Oliveira and Araújo 2007). This retained moisture helps to preserve the upper part of the mountain vegetation quite different from that found in the lower part and surroundings (Borges-Nojosa and Caramaschi 2003).

All these factors provide great variation along the vegetation gradient found on Maranguape mountain, where the open formation landscape corresponding to Caatinga (in the lower part) is being replaced by humid forest towards the top of the elevation. There is also a reduction in the total area that is covered by humid vegetation. Three basic vegetation types are found in the region, in the higher altitude range: Subperennial Cloudy Tropical Forest (Humid Forest); in the intermediate altitude range: Subcaducifolic Tropical Forest (Dry Forest); and in the lower altitude range: Thorny Caducifolic (Arboreal Caatinga), both marked by high woody components, interspersed with shrubs and vines (Figueiredo 1997; Moro et al. 2015). These vegetation variations by altitude observed in the Maranguape mountain make possible a huge environmental and climatic heterogeneity that allows different species to coexist (Borges-Nojosa and Caramaschi 2003; Diogo et al. 2021). It is also worth noting that the high and intermediate altitude ranges have long been exploited in the production of various crops, such as orange, coffee, and banana cultivation (Lima and Cascon 2008). This may have a great influence on the reduction of local species richness and diversity.

3.2.2 Data collection

We used the active search method (visual and auditory; Bernarde 2012) and manually collected, during 17 days in the rainy season from February to May 2020, 192 anurans at nine sampling points distributed over three altitude ranges in the Maranguape mountain (Fig. 1). To gauge the heterogeneity of each sampling point, we cataloged local and historical environmental descriptors according to Santos et al. (2007, 2012), and through the National Institute for Space Research - INPE. To test the altitudinal gradient, we divided the nine sample points (SP) into three altitude ranges: low (100 - 200m), intermediate (400 - 500m) and high (700 - 800m), to sample the three basic vegetation types with altitudinal variation (see Fig. 1).

In the laboratory, with lethal injection of lidocaine hydrochloride (CFMV, 2013), and then necropsied the anurans with a ventral incision and examined the presence of endoparasites in the organs (gastrointestinal tract, lungs, liver and kidneys) and internal cavity using a stereoscope according to Amato et al. (1991). We analyzed the infection parameters according to Bush et al. (1997). All identified endoparasites were deposited in the Parasitological Collection of the Federal University of Ceará (CPUFC - 196 to 441), Fortaleza, Brazil, and their hosts in the Herpetological Collection of the Federal University of Ceará (CHUFC - A 9762 to A 9953), Fortaleza, Brazil.

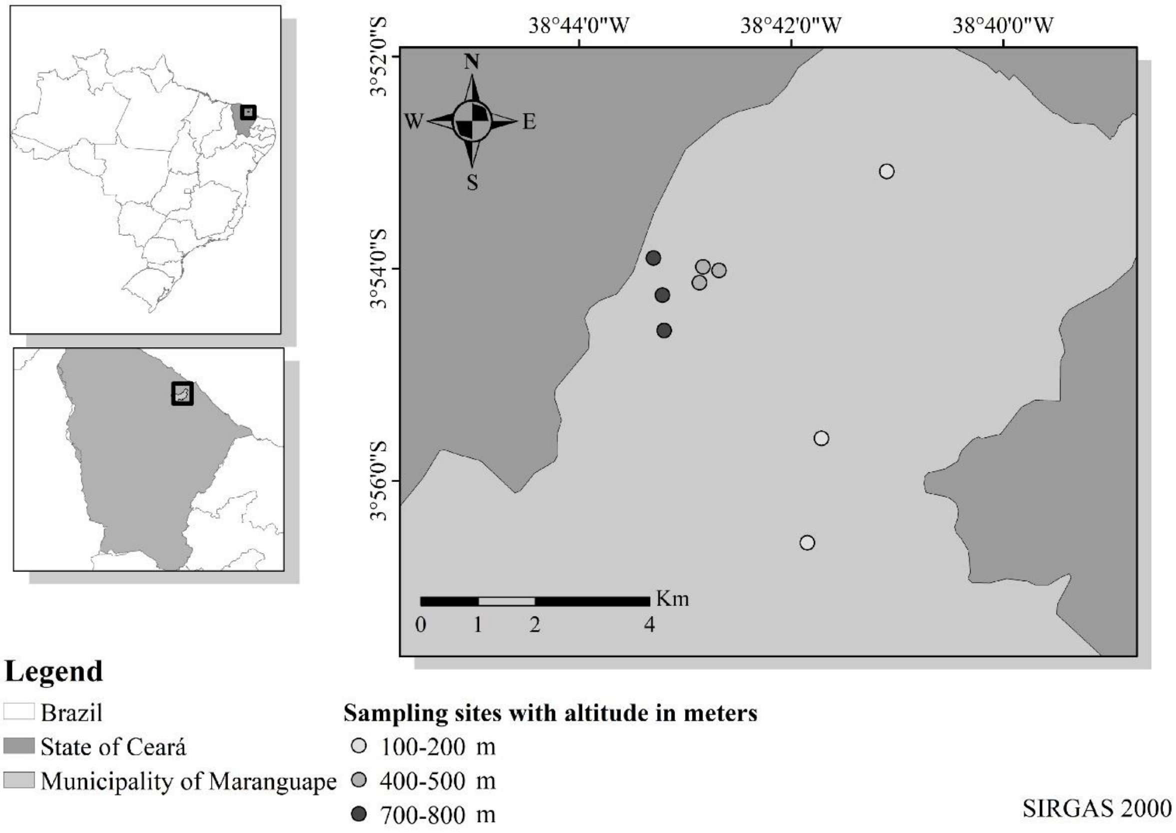

Figure 1. Schematic map of the sampling points in Maranguape mountain, Ceará state, Brazil.

3.2.3 Data Analysis

To verify if there is group formation in the occurrence of parasites and their hosts along the altitudinal ranges of the Maranguape mountain, we performed a principal component discriminant analysis (DAPC) on Jaccard dissimilarity matrices, calculated based on binary data (presence and absence), using the adegenet R-package (Jombart 2008). Then, we developed poncho plots to visualize which species occur in each altitudinal range. To verify how altitude interfere with local diversity, we calculated Shannon's diversity index (H') and

Jaccard's similarity (S) for host species and their endoparasites, and estimated niche width and overlap of parasites considering each host species as a "microhabitat" category, using the spaa R-package (Jinlong Zhang 2016). We considered values above 0.8 as a high niche overlap between pairs of species.

To understand how parasite-host interaction is formed in our dataset, we used complex network analysis with help of the bipartite R-package (Dormann et al. 2009). To check how connected are parasites and hosts in our sample community (connection is understood as the presence of interaction between at least one individual of a given parasite species and at least one individual of a given host species), we used the connectance metric (Dunne et al. 2002), and graphs were generated with the igraph R-package (Csardi and Nepusz 2006). This metric reveals the value of connections made amidst all possible connections in our dataset. To identify where the clustering density of interactions is most concentrated, i.e., where parasites or hosts would be most clustered, or, where most connections are, we used the clustering coefficient (Watts and Strogatz 1998). To verify the formation of clusters of interactions between parasites and hosts, we used the DIRTLPAwb+ algorithm (Beckett 2016), which uses the weighted data from the data matrix. This method considers the abundance of parasites in each host as the weight of the interaction and clusters will be detected around stronger interactions following this criterion. Graphs were generated with the igraph R-package (Csardi and Nepusz 2006).

We constructed a phylogenetic subtree, for the anuran community, total and for each of the altitudinal ranges, adapted from the most recent amphibian phylogenetic hypothesis (Jetz and Pyron 2018) using the ape R-package (Paradis et al. 2004). This phylogenetic hypothesis references 7238 species, and uses a Phylogenetic Set with Taxonomic Approaches and Inferences that includes all available sequence data for 15 genes (5 mitochondrial and 10 nuclear) and identifies 174 subclusters. To test whether historical effects (host phylogeny) are better predictors of parasite abundance than ecological factors, we performed phylogenetic principal component analyses (pPCA) for each altitudinal profile. To test whether phylogeny explains abundance within clades, we performed canonical phylogenetic ordering (CPO) analyses. In both cases, we used the same matrix as in the niche width analyses.

To evaluate beta diversity of parasite communities of Maranguape mountain, we used the following environmental gradients: vertical height relative to drainage-HAND, temperature, altitude, precipitation, and drainage density. We obtained altitude during field expeditions, using a Garmin eTrex 10 handheld GPS, Datum SIRGAS-2000. Data on HAND, drainage density, mean annual temperature and annual precipitation were obtained from the National Institute for Space Research (http://www.dpi.inpe.br/Ambdata/index.php).

We executed a PERMANOVA (999 randomizations) to test whether there are significant differences in parasite dispersal along different environmental gradients in the vegan R-package (Oksanen et al. 2016). Temperature and altitude showed a high positive correlation with precipitation and HAND, respectively. Considering the habits of the hosts in the study, which are strongly influenced by water-related variables, we removed the temperature and altitude from our models to avoid spatial autocorrelation effects. Then, we executed a PERMANOVA with the occurrence and abundance of parasite species per point and also per independent variable. In this analysis, we used the square root of abundance to decrease the chance of bias caused by the presence of very abundant species. Finally, we executed a PERMIDISP to check for possible dispersal effects and performed an ANOVA to test the significance of the PERMIDISP.

3.3 RESULTS

We analyzed 192 individuals distributed in 23 species of anurans (Table 1). The species *Pristimantis relictus*, *Physalaemus cuvieri*, *Scinax x-signatus* and *Rhinella diptycha* were the most abundant, while *Adelophryne maranguapensis*, *Adenomera juikitam*, *Corythomantis greeningi*, *Leptodactylus mystaceus* and *Proceratophrys cristiceps* were the rarest species.

Of the 192 specimens examined, 142 individuals (42 females, 94 males and 6 juveniles) were parasitized with at least one parasitic species (overall prevalence = 74%), mean infection intensity of 26.3 ± 4.16 and total abundance of 19.5. The endoparasite community consisted of 22 *taxa* (Table 2), of which *Raillietnema spectans*, *Oswaldocruzia mazzai* and *Rhabdias* sp. were the most abundant in the community, and *Oligacanthorhynchus* sp., *Falcaustra mascula*, *Cosmocercoides* sp., *Oxyascaris caatingae* and *Rauschiella linguatula* the rarest species observed.

Table 1. List of anuran hosts of the Maranguape mountain, Ceará state, Brazil.

Anurans Hosts	**Site (Altitudinal ranges)**			**Number of specimens**
	Low	**Middle**	**High**	
Bufonidae				
Rhinella diptycha (Cope, 1862)	7	4	1	12
Rhinella granulosa (Spix, 1824)	5	-	-	5
Eleutherodactylidae				
Adelophryne maranguapensis Hoogmoed, Borges and Cascon, 1994	-	-	3	3
Hylidae				
Boana raniceps (Cope, 1862)	5	4	-	9
Corythomantis greeningi Boulenger, 1896	-	1	1	2
Dendropsophus minusculus (Rivero, 1971)	-	5	1	6
Dendropsophus minutus (Peters, 1872)	3	-	7	10
Dendropsophus nanus (Boulenger, 1889)	8	-	-	8
Dendropsophus tapacurensis Oliveira, Magalhães, Teixeira, Moura, Porto, Guimarães, Giaretta and Tinôco, 2021	-	4	7	11
Scinax x-signatus (Spix, 1824)	12	2	-	14
Trachycephalus typhonius (Linnaeus, 1758)	-	2	6	8
Leptodactylidae				
Adenomera juikitam Carvalho and Giaretta, 2013	-	1	-	1
Leptodactylus fuscus (Schneider, 1799)	4	-	-	4
Leptodactylus macrosternum Miranda-Ribeiro, 1926	4	1	2	7
Leptodactylus mystaceus (Spix, 1824)	-	-	2	2
Leptodactylus pustulatus (Peters, 1870)	7	-	-	7
Leptodactylus vastus Lutz, 1930	2	1	1	4
Physalaemus cuvieri Fitzinger, 1826	9	9	5	23
Microhylidae				
Elachistocleis piauiensis Caramaschi and Jim, 1983	4	-	-	4
Odontophrynidae				

Proceratophrys cristiceps (Müller, 1884)	-	1	-	1
Proceratophrys renalis (Miranda-Ribeiro, 1920)	-	2	8	10
Phyllomedusidae				
Pithecopus gonzagai Andrade, Haga, Ferreira, Recco-Pimentel, Toledo and Bruschi, 2020	8	-	-	8
Strabomantidae				
Pristimantis relictus Roberto, Loebmann, Lyra, Haddad and Ávila, 2022	-	16	17	33

The DAPC indicated the formation of three species occurrence groups for both parasites and hosts, corresponding to the altitude categories of the sampled points (Fig. 2A, B). With a small overlap being observed between the intermediate and high group. Poncho plots shown host and parasites species turnover and parasitic species but indicated that parasitic species are more dispersed along the entire gradient compared to their hosts (Fig. 3A, B).

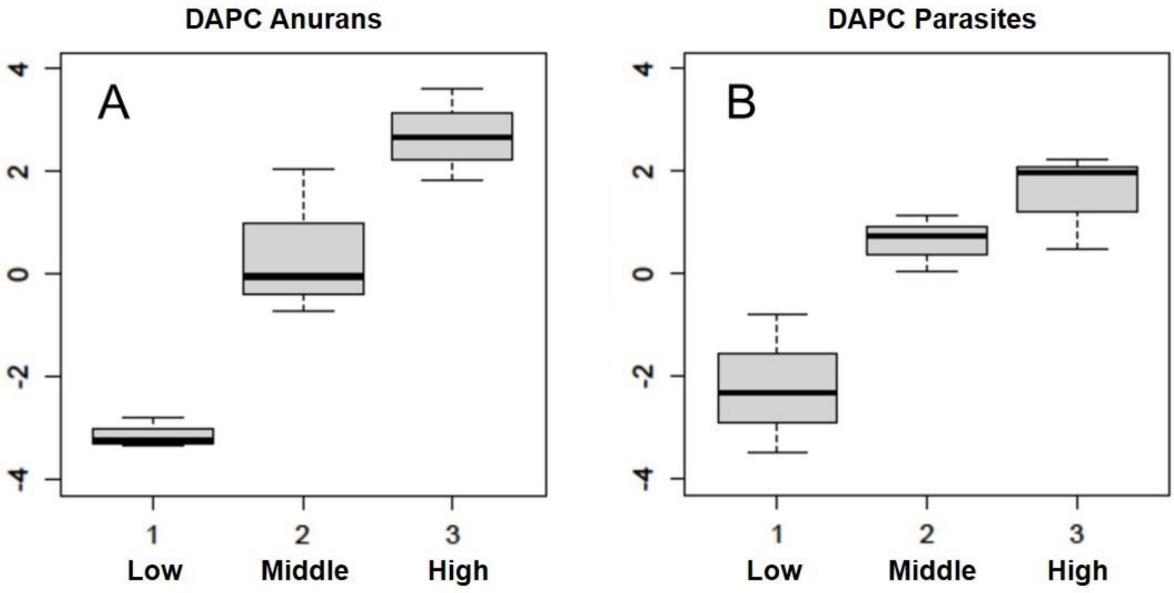

Figure 2. Discriminant Analysis of Principal Components - DAPC of the altitudinal ranges of the Maranguape Mountains, Ceará state, Brazil. A= DAPC for Anuran Hosts; B= DAPC for Parasitic Helminths.

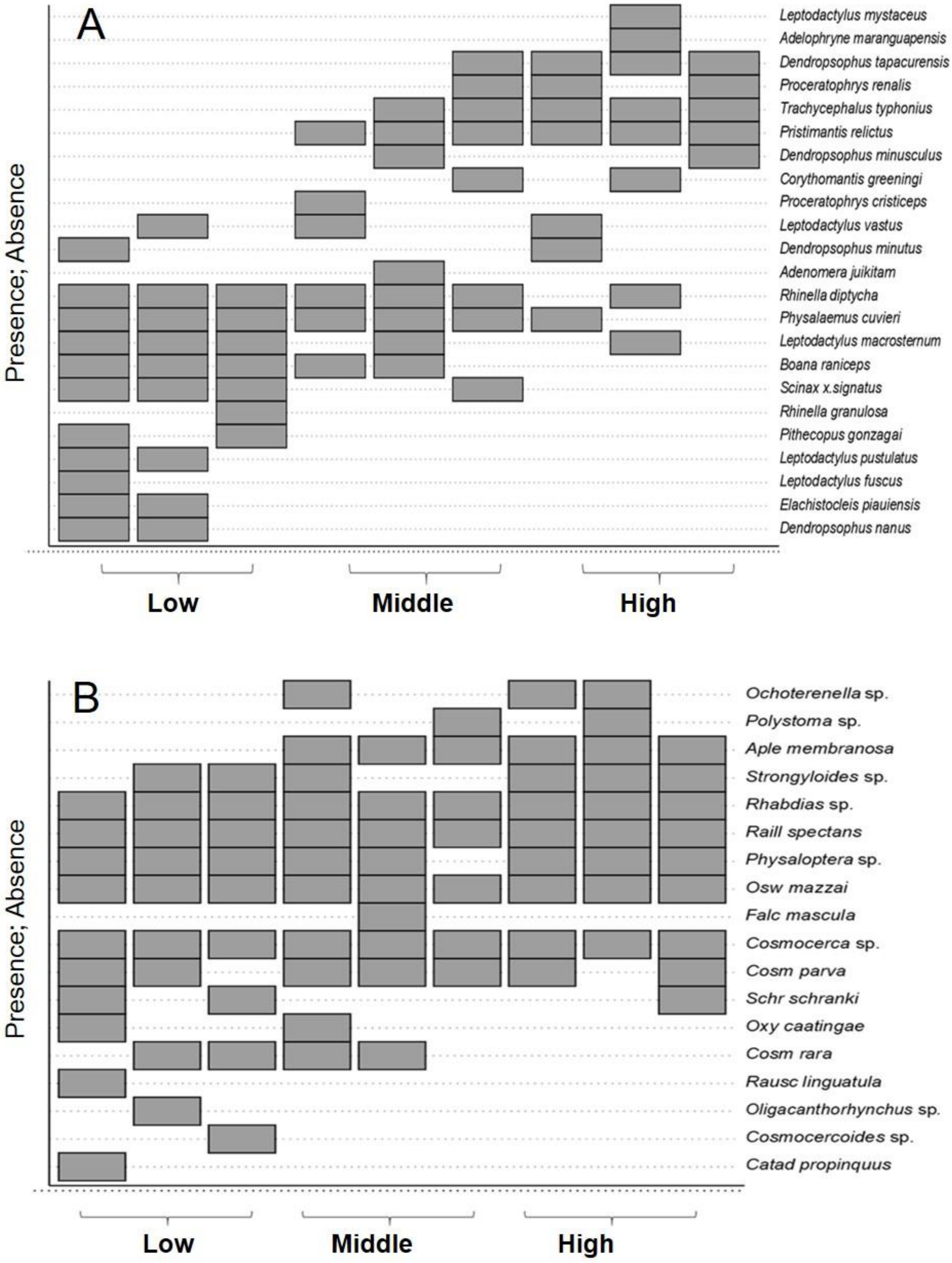

Figure 3. Distribution of species in the altitudinal ranges of the Maranguape Mountains, Ceará state, Brazil. Graphs showing: A= Anuran hosts; B= Parasites.

Table 2. Endoparasites of anuran hosts from Maranguape Mountain, Ceará state - Brazil. N= Number of parasites; P%= Prevalence; M.I.= Mean intensity of infection; S.E.= Standard error; A.M.= abundance.

ENDOPARASITE	**N**	**P (%)**	**M.I. ± S.E.**	**A.M.**	**ANURAN HOSTS**
Acanthocephala					
Centrorhynchus sp.	57	11.98	2.47 ± 0.73	0.30	*Boana raniceps*; *Dendropsophus nanus*; *Leptodactylus fuscus*; *L. macrosternum*; *L. pustulatus*; *Physalaemus cuvieri*; *Pithecopus gonzagai*; *Proceratophrys renalis*; *Scinax x-signatus*.
Oligacanthorhynchus sp.	1	0.52	1	0.01	*Leptodactylus vastus*
Nematoda					
Aplectana membranosa (Schneider, 1866)	43	7.29	3.07 ± 0.69	0.22	*Boana raniceps*; *Physalaemus cuvieri*; *Pristimantis relictus*; *Proceratophrys cristiceps*; *P. renalis*; *Scinax x-signatus.*
Cosmocerca parva Travassos 1925	200	14.06	7.40 ± 2.93	1.04	*Boana raniceps*; *Elachistocleis piauiensis*; *Leptodactylus fuscus*; *L. macrosternum*; *Physalaemus cuvieri*; *Pithecopus gonzagai*; *Pristimantis relictus*; *Proceratophrys renalis*.
Cosmocerca rara Freitas and Vicente, 1966	85	3.13	14.16 ± 7.76	0.44	*Boana raniceps*; *Physalaemus cuvieri*; *Pristimantis relictus*; *Scinax x-signatus.*
Cosmocerca sp.	282	24.48	6 ± 1.32	1.47	*Adenomera juikitam*; *Corythomantis greeningi*; *Dendropsophus minutus*; *Leptodactylus macrosternum*; *L. mystaceus*; *L. pustulatus*; *Physalaemus cuvieri*; *Pristimantis relictus*; *Trachycephalus typhonius*.
Cosmocercoides sp.	4	0.52	4	0.02	*Scinax x-signatus*
Falcaustra mascula (Rudolphi, 1819)	1	0.52	1	0.01	*Leptodactylus macrosternum*
Ochoterenella sp.	6	1.56	2 ± 0.57	0.03	*Dendropsophus minutus*; *Pristimantis relictus*; *Rhinella diptycha*.

Oswaldocruzia mazzai Travassos, 1935	497	27.60	9.37 ± 2.27	2.59	*Boana raniceps*; *Corythomantis greeningi*; *Dendropsophus minutus*; *Leptodactylus macrosternum*; *L. mystaceus*; *L. vastus*; *Physalaemus cuvieri*; *Pithecopus gonzagai*; *Pristimantis relictus*; *Proceratophrys renalis*; *Rhinella diptycha*; *R. granulosa*; *Trachycephalus typhonius*.
Oxyascaris caatingae Felix-Nascimento, Vieira, Muniz-Pereira, Moura, Ribeiro and Oliveira, 2020	3	1.04	1.50 ± 0.5	0.02	*Boana raniceps*; *Leptodactylus pustulatus*.
Physaloptera sp.	175	20.83	4.37 ± 1.09	0.91	*Boana raniceps; Elachistocleis piauiensis; Leptodactylus fuscus*; *Leptodactylus macrosternum*; *Leptodactylus pustulatus*; *Leptodactylus vastus; Physalaemus cuvieri*; *Pithecopus gonzagai*; *Pristimantis relictus*; *Proceratophrys renalis; Rhinella diptycha; Rhinella granulosa; Scinax x-signatus; Trachycephalus typhonius*.
Raillietnema spectans Gomes, 1964	558	6.77	42.92 ± 8.94	2.91	*Dendropsophus minutus*; *Elachistocleis piauiensis*; *Leptodactylus fuscus*; *L. mystaceus*; *Physalaemus cuvieri*; *Pristimantis relictus*; *Proceratophrys renalis*; *Rhinella diptycha*; *Rhinella granulosa*; *Trachycephalus typhonius*.
Rhabdias sp.	447	10.94	21.28 ± 4.20	2.33	*Adenomera juikitam*; *Boana raniceps*; *Corythomantis greeningi*; *Dendropsophus minutus*; *Leptodactylus fuscus*; *L. macrosternum*; *L. pustulatus*; *L. vastus*; *Physalaemus cuvieri*; *Pristimantis relictus*; *Scinax x-signatus*; *Trachycephalus typhonius*.
Schrankiana schranki (Travassos, 1925)	205	2.60	41 ± 24.36	1.07	*Leptodactylus fuscus*; *Rhinella diptycha; Trachycephalus typhonius*.
Strongyloides sp.	13	3.65	1.85 ± 0.45	0.07	*Boana raniceps*; *Physalaemus cuvieri*; *Pithecopus gonzagai*; *Pristimantis relictus*; *Scinax x-signatus*; *Trachycephalus typhonius*.
Nematoda gen. sp.	7	1.04	3.50 ± 2.5	0.04	*Pristimantis relictus*; *Trachycephalus typhonius*.
Unidentified Ascarididae	1	0.52	1	0.01	*Proceratophrys renalis*

Unidentified Cosmocercidae	1115	8.85	65.58 ± 16.75	5.81	*Boana raniceps*; *Dendropsophus minutus*; *Leptodactylus vastus*; *Physalaemus cuvieri*; *Pristimantis relictus*; *Scinax x-signatus*; *Trachycephalus typhonius*.
Platyhelminthes					
Monogenea					
Polystoma sp.	6	1.04	3 ± 2	0.03	*Corythomantis greeningi*; *Trachycephalus typhonius*.
Digenea					
Catadiscus propinquus Freitas and Dobbin Jr, 1956	22	1.56	7.33 ± 2.90	0.11	*Leptodactylus fuscus*; *Leptodactylus pustulatus.*
Rauschiella linguatula (Rudolphi, 1819)	3	1.04	1.5 ± 0.5	0.02	*Leptodactylus pustulatus*
Total	**3731**	**74**	**26.3 ± 4.16**	**19.5**	

Parasite and host diversity declined with increasing elevation (Fig. 4). The similarity of endoparasite species was highest among altitudinal ranges (Parasites: low vs intermediate= 0.52; low vs high= 0.44; intermediate vs high= 0.78), compared to host species (Hosts: low vs intermediate= 0.31; low vs high= 0.27; intermediate vs high= 0.57).

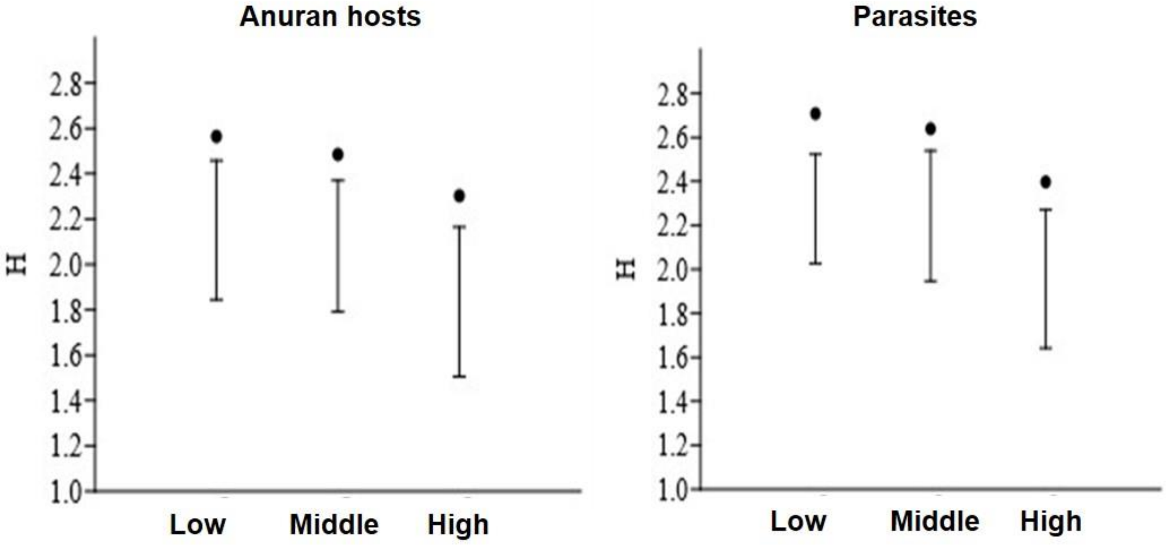

Figure 4. Diversity index of parasite and host species as a function of altitudinal ranges in the Maranguape Mountains, Ceará state, Brazil.

Overall, *R. spectans vs A. membranosa* (0.82); *O. mazzai vs C. parva* (0.83); *O. caatingae vs C. propinquus* (0.89); *R. linguatula vs O. caatingae* (0. 89); *Cosmocercoides* sp. *vs Centrorhynchus* sp. (0.9); *C. rara vs A. membranosa* (0.96) and *R. linguatula vs C. propinquus* (1.0) showed high niche overlap.

We analyzed the altitudinal quotas individually, for the highest stratum, the species: *O. mazzai vs C. parva* (0.72); *Strongyloides* sp. *vs Polystoma* sp. (0.79); *Strongyloides* sp. *vs S. schranki* (0.79) showed a high niche overlap, but we did not find niche overlap above 0.8 between pairwise species in the highest stratum of Maranguape mountain. In the intermediate range, *Falcaustra mascula vs Physaloptera* sp. (0.82); *C. parva vs Centrorhynchus* sp. (0.90) and *C. rara vs Strongyloides* sp. (0.97) showed the highest niche overlap. The lowest altitude range was the only with total species overlap (1.0): *Catadiscus propinquus vs Rauschiella linguatula*; *Catadiscus propinquus vs Oxyascaris caatingae*; *Rauschiella linguatula vs Oxyascaris caatingae* and *Rhabdias* sp. *vs C. rara* with overlap of 0.85.

When analyzing the dataset under the metrics of complex network analysis, we found that only 29% of the possible interactions occurred given the possibilities of the dataset

(C= 0.29). Looking at the clustering coefficient values, we found that there is more clustering, meaning that there is more interaction between parasites than between hosts (0.51 and 0.40, respectively). We observed the formation of six clusters in the endoparasite anuran community of Maranguape mountain (Fig. 5). These clusters were detected due to the greater interaction between the cluster components relative to all other components of the dataset.

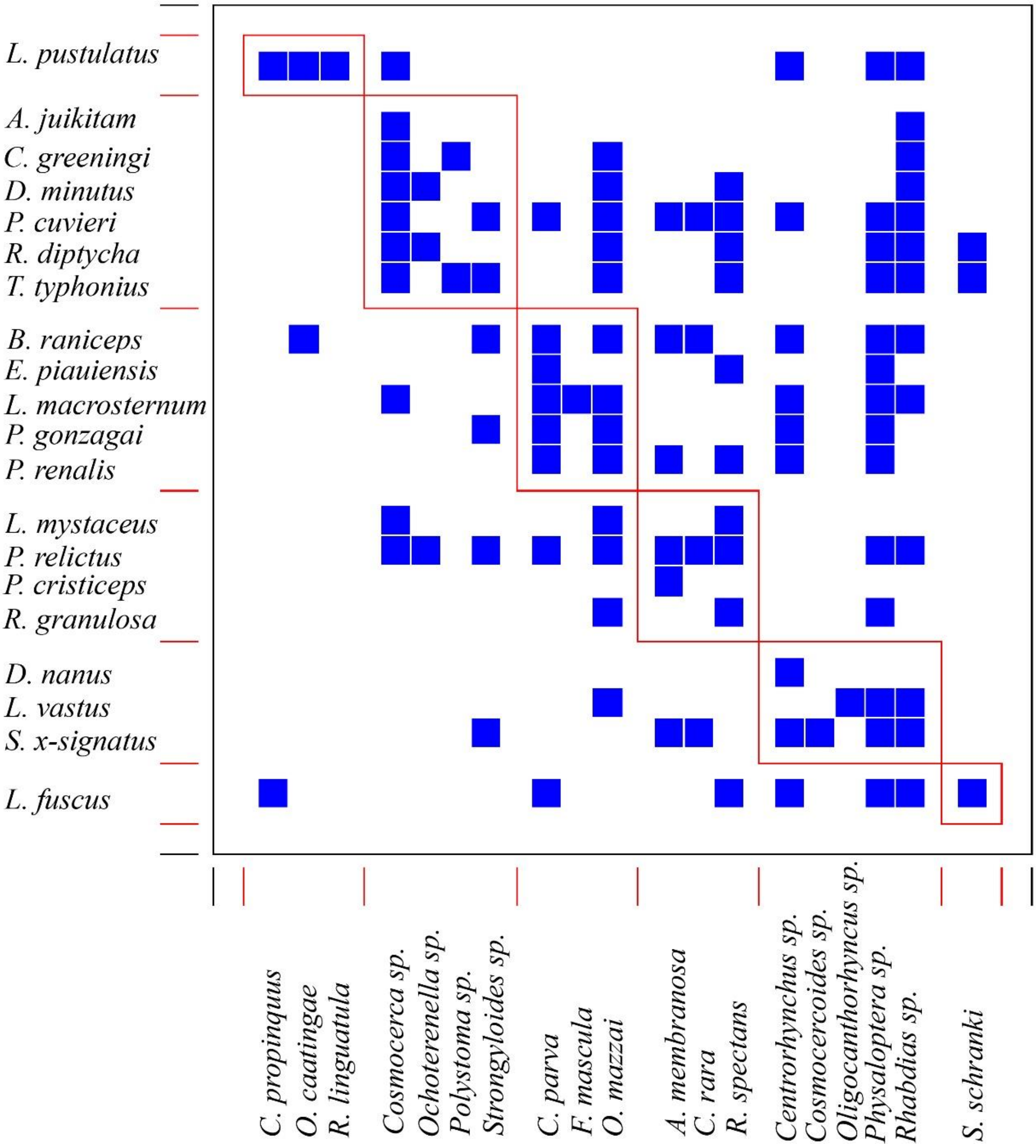

Figure 5. Clusters of parasite-host relationships in anurans of the Maranguape Mountains, Ceará state, Brazil. Legends: X axis - parasite species; Y axis - anuran species; red lines represent the clusters of interactions.

In general, phylogenetic principal component analyses (pPCA) suggest that ecological factors are better predictors than historical factors on parasite abundance at Maranguape mountain (Fig. 6), but this pattern was not followed when analyzing each altitudinal range separately. Ecological factors are stronger in the intermediate range community (Fig. 7B); historical factors were stronger in the lower range community (Fig. 7A); and both factors were influential in the higher range (Fig. 7C). The canonical phylogenetic ordering (CPO) analyses showed no significance values for any of the clades analyzed, corroborating that ecological factors are better predictors than historical factors.

We found no position effects of environmental variables on parasite occurrence (PERMANOVA, F= 1.4942; *p*= 0.215). Analyzing variables individually, results were significant for tree cover (F= 2.8657; *p*= 0.049). The PERMDISP showed that there is no dispersion effect (heterogeneity) along the tree cover gradient (F= 1.2378; *p*= 0.511), showing that there are no effects of environmental variables on the occurrence of parasites. Using the square root values of abundance (F= 1.0578; *p*= 0.401) and absolute abundance (F= 1.4942; *p*= 0.228) the results for PERMDISP were similar.

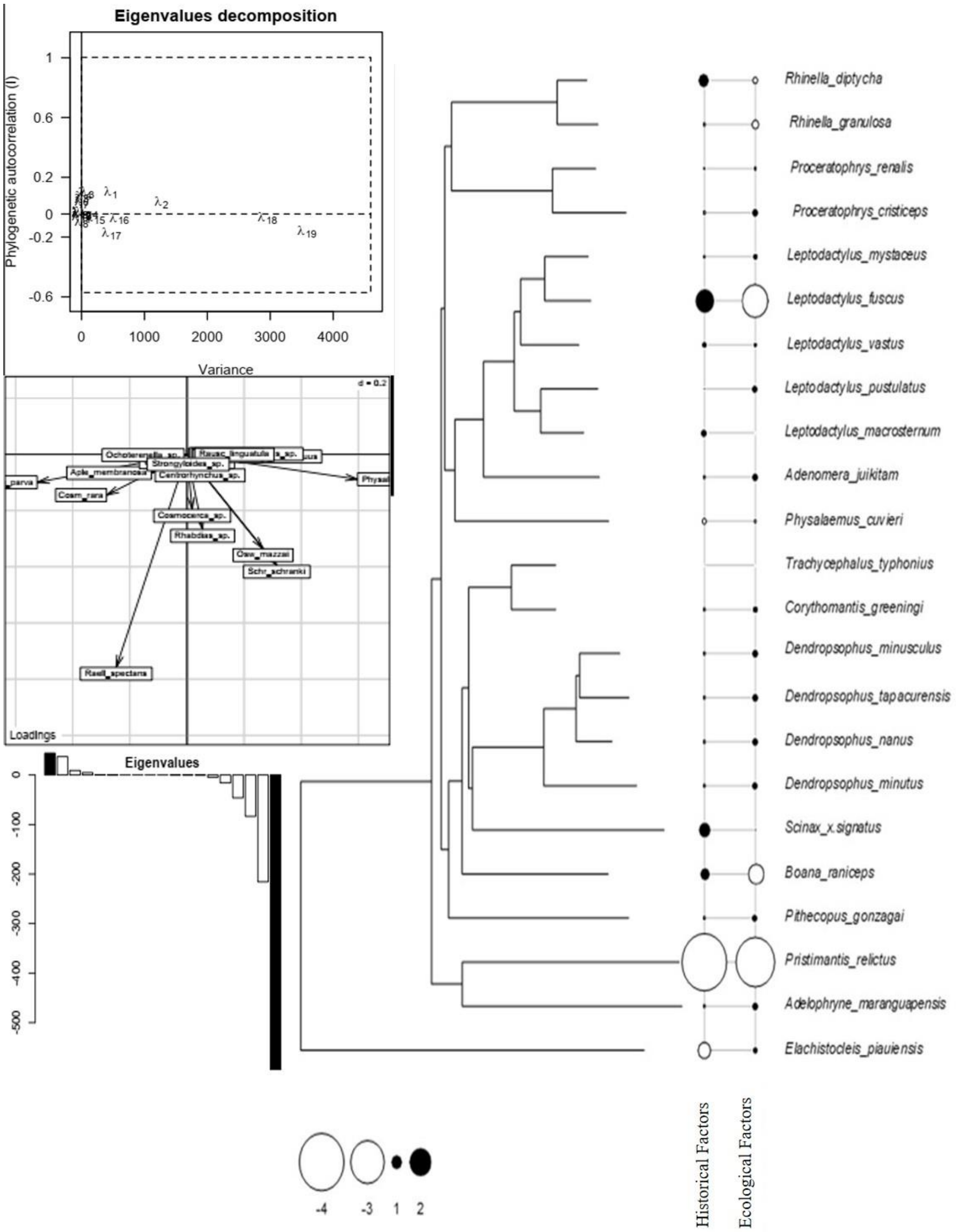

Figure 6. pPCA of parasite data in anurans from the Maranguape Mountains, Ceará State, Brazil.

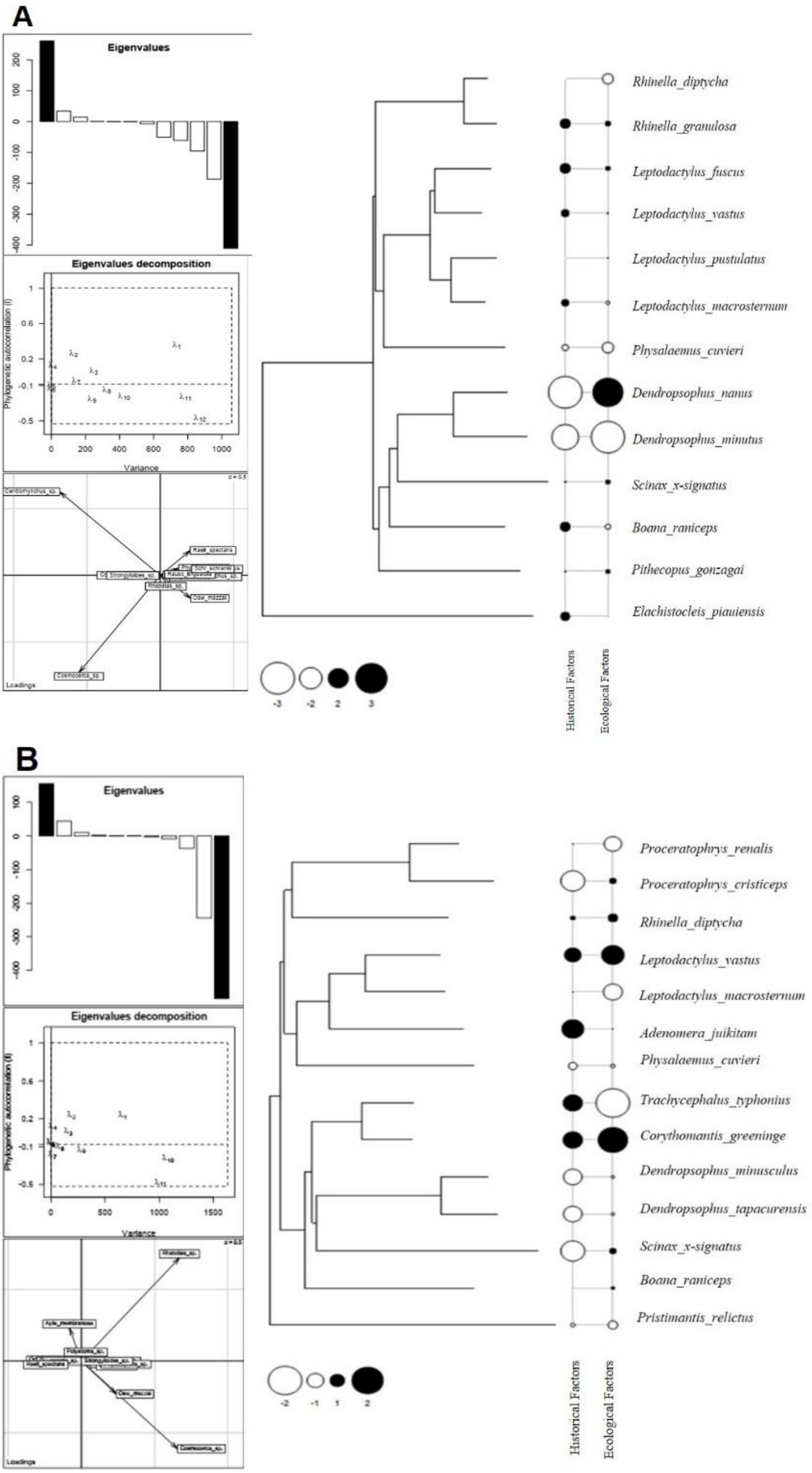

Figure 7. pPCA of parasite data in anurans relative to each altitudinal range of the Maranguape Mountains, Ceará State, Brazil. **A** = Low range (200m altitude); **B** = Intermediary range (500m altitude); **C** = High range (800m altitude).

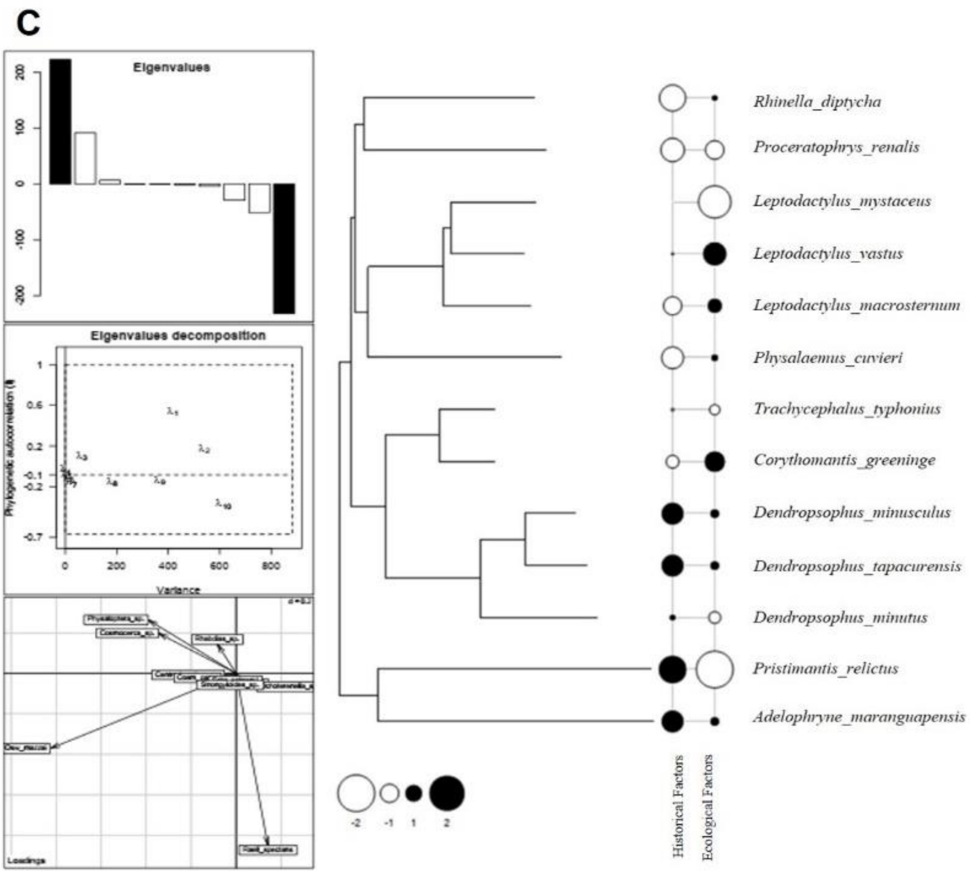

Figure 7 (continued). pPCA of parasite data in anurans relative to each altitudinal range of the Maranguape Mountains, Ceará State, Brazil. **A** = Low range (200m altitude); **B** = Intermediary range (500m altitude); **C** = High range (800m altitude).

3.4 DISCUSSION

Anurans are usually parasitized by generalist helminths, which have low host specificity and wide distribution (Campião et al. 2014). Nematodes usually represent a significant portion of the parasitic community because they are mostly direct-cycle parasites, transmitted through oral ingestion or active penetration of infective larvae in the skin (Anderson 2000). The high prevalence of nematode infection (70.3%) found in the present study reinforces these statements. We also observed that most parasite species, even those less abundant, are well distributed throughout Brazil and are often found in a large number of hosts (Campião et al. 2014), suggesting that parasitic species have a broad local and geographic distribution, especially those of direct cycle and low host-specificity.

Environmental heterogeneity in altitudinal gradients favors species variation along the gradient (e.g. Araújo et al. 2018; Caglioni et al. 2018; Gonçalves-Sousa et al. 2022). In our study, we detected the formation of three distinct groups of hosts and parasites along altitudinal gradients, where, the increase in altitudinal gradient negatively influenced the diversity of parasite and host species for the community in Maranguape mountain. This finding indicates species substitution along the gradient, however, the parasite species had lower species diversity across gradients than observed for their anuran hosts. This is corroborated by the fact that only 17% of the host species are distributed in all the areas sampled on the Maranguape mountain. Although lower than the hosts, the beta diversity of parasites is also high, with only 39% of species occurring in all sampled areas. Showing a greater similarity between altitude ranges compared to their hosts, demonstrating a greater distribution along the mountain.

The distribution of organisms may be influenced by environmental conditions of different levels, including temperature, humidity, precipitation, and environmental heterogeneity (e.g. Vasconcelos et al. 2010; Siqueira and Rocha 2013; Araújo et al. 2018). Parasite species diversity depends on how their hosts exploit the habitat (Poulin and Morand 2004; Hamann et al. 2006; Oliveira et al. 2022). On a regional scale, beta diversity tends to be lower at sites that are closer together or have similar environmental conditions (Koleff et al. 2003; Bishop et al. 2015; Caglioni et al. 2018). It is quite likely that endoparasites are not as impacted by these conditions to the same degree as their hosts. Because of this, endoparasite species can colonize any environment in our studied area as long as a host is available for colonization. The presence of anurans with a wide distribution throughout the Maranguape mountain makes them excellent parasite dispersers, allowing them to colonize several different areas, regardless of altitude gradient or heterogeneity. This characteristic, along with the direct life cycle of most parasites (Anderson 2000), explains the observed greater distribution of parasites compared to hosts in the present study along environmental gradients. This finding is supported by the fact that the majority of the found parasites are hosted by *Leptodactylus vastus*, *Leptodactylus macrosternum*, *Physalaemus cuvieri* and *Rhinella diptycha*, which are species with generalist habits and they are dispersed along the entire studied gradient. In addition, parasite species that were more abundant and distributed in the altitudinal gradient studied were species commonly found in hosts with greater phenotypic plasticity and greater distribution along the Maranguape mountain, which could justify the high rates of overlap in some species.

Overall, we recorded several parasite species with high niche overlap (based on host species) in the Maranguape mountain. Parasite aggregation may increase with host age as they are exposed to infection for a longer period of time (Pacala and Dobson 1988; Pietrock and

Marcogliese 2004). Furthermore, additional factors, such as more host species available, higher parasite abundance in particular hosts and rare parasite species, may have contributed to increasing niche overlap between parasite species (Crofton 1971; Anderson and Gordon 1982; Poulin 1993). Considering altitudinal ranges, in the lowest stratum there was total overlap between some species sharing the same host (*Leptodactylus pustulatus*). These parasite species were most trematodes. Possibly, this high niche overlap is related to the life cycle of the parasite and the type of host habitat use, which inhabits mainly aquatic environments (Anderson 2000). Becoming more visible due to the parental care behavior with the offspring exercised by species of the genus *Leptodactylus* (Santos and Amorim 2006; de Castro et al. 2013), which remain longer in aquatic environments providing greater probability of contact with this type of parasite.

The parasite-host interaction network analyses showed a higher interaction between parasites than between their hosts. According to Brito et al. (2014), the clustered structure observed for parasites may occur due to a high degree of specialization. In this case, it is expected that interaction networks between endoparasites and hosts show a compartmentalized structural pattern (Brito et al. 2014). Such interactions can also be influenced by the microhabitat in which the hosts inhabit (Krause et al. 2003; Oliveira et al. 2022). It is expected that species coexisting in the same habitats will be grouped together in the same clusters of interactions. However, there are few studies on interaction networks investigating the role of host microhabitat use on parasites (Brito et al. 2014; Sampaio et al. 2022).

In the present study, we detected six distinct groups made by the network interaction between parasites and their anuran hosts in the Maranguape mountain. The formation of three of these groups suggests that the structure of the interaction network is more related to host species than to altitude. This finding is similar to that observed for anurans in the Pantanal and Atlantic Forest (D'Bastiani et al. 2020). Herein, the formation of the groups mostly clustered different host species that were infected by the same parasite species along the altitudinal gradient. Thus, host abundance and parasite generalist may have contributed to the formation of these groups, as parasites can infect different hosts (Weaver et al. 2016), and/or expand the width of their niches in response to the availability of new resources (MacArthur et al. 1972; Wright 1980; Malcicka et al. 2015).

The heteroxenic cycle of some species was also a determining factor in the formation of two groups. The first was formed by the frog *Leptodactylus pustulatus* and the parasites *Catadiscus propinquus*, *Rauschiella linguatula*, and *Oxyascaris caatingae*. In this group, most parasitic species are trematodes that require aquatic intermediate hosts such as gastropods (Anderson 2000). These organisms facilitate the transmission of trematodes and anurans inhabiting this type of environment are more easily infected (Guillén-Hernández et al. 2000; Madelaire et al. 2012). The second group was formed by the anurans *Dendropsophus nanus*, *Leptodactylus vastus* and *Scinax x-signatus*, and the parasites *Centrorhynchus* sp., *Oligacanthorhynchus* sp., and *Physaloptera* sp., most of these parasites have an indirect life cycle, with arthropods as intermediate hosts and some species of anurans, waterfowl, mammals and fishes as final hosts (Baker 2007).

Host phylogeny may influence the parasitic fauna and is a determining factor in structuring webs between parasites and hosts, since phylogenetically close species tend to be phenotypically similar, which contributes to the relative similarity of parasite species infecting congeneric hosts (Krasnov et al. 2012; Brito et al. 2014; Oliveira et al. 2019). Seven out of eight anuran families found in Maranguape mountain were infected by at least one parasite species. Anurans of the families Bufonidae, Hylidae and Leptodactylidae were the most abundant throughout Maranguape mountain (66%) as well as in the entire Neotropical region. Studies on the distribution of parasites show that they can disperse together with ancestral species and maintain a close evolutionary relationship with these species (Rausch 1994). However, other factors such as the trophic position in the food chain of the host can also influence parasite richness (Chen et al. 2008), the higher the host is in the trophic chain, the more parasites it can potentially harbor (Marcogliese 2002).

Ecological factors exerted greater influence than phylogeny on the abundance of anuran parasites from the entire Maranguape mountain. This result suggests that most parasitic species found are not influenced by phylogenetic relationships with their hosts, similarly to the results found by D'Bastiani and Campião (2021), where the composition of parasite communities was not related to host phylogeny, species variability or functional diversity. Overall, the host-parasite relationship may be mediated by random behaviors, such as the opportunistic contact between individuals, where species that share the same habitat is supposed to have similar parasite communities (D'Bastiani and Campião 2021).

In our study, we detected an overall substitution of parasitic species along the environmental gradients tested. Where the tree cover gradient showed significance in the occurrence of parasites, but we did not detect a dispersal effect (heterogeneity) for this gradient. Thus, we can conclude that in the parasite-host relationship in anuran amphibians, ecological effects are stronger than phylogenetic effects, and parasites tend to follow their hosts independent of external factors. Not being influenced by the heterogeneity and altitude of environmental gradients, because they are protected in their hosts from environmental variations. Thus, the distribution of hosts in the environment and their niche overlap in resource use represents a key factor in structuring the interactions observed in this study.

STATEMENTS AND DECLARATIONS

Funding: This work was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) for the scholarship granted to C.R.O. [grant numbers: 88882.454307/2019-01]; and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for granting research grants R.W.A. and D.M.B.N. [grant number: 305988/2018-2 and 307722/2021-0; 309617/2012-0 and 311961/2016-9].

Conflict of interest: The authors declare that they have no conflict of interest related to the publication of this manuscript.

Availability of data and material: Authors declare the availability of the data upon personal request.

Authors' contributions: Cicero Ricardo de Oliveira and Elvis Franklin Fernandes de Carvalho collected and analyzed the data and material; Elvis Franklin Fernandes de Carvalho and José Guilherme Gonçalves-Sousa performed the statistics; Cicero Ricardo de Oliveira prepared the figures; Robson Waldemar Ávila and Diva Maria Borges-Nojosa revised the manuscript text. All authors participated in the writing of the main text.

Ethics approval: All procedures used in this work follow the ethical standards of the relevant national and institutional guides on the care and use of laboratory animals. Collection permit Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio (#73215-1) and the Ethics Committee on Animal Use of the Federal University of Ceará (CEUA-UFC) (#CEUA 6314010321).

Consent to participate: Not applicable

Consent for publication: Not applicable

Acknowledgements: We would like to acknowledge Samuel Cardozo Ribeiro, Matheus Calixto, Rafael Ramos and Átilas Rodrigues for help in the process of the analyzed material.

REFERENCES

Amato JFR, Boeger WA, Amato SB (1991). Protocolos para laboratório – Coleta e processamento de parasitos de pescado. Imprensa Universitária – FRRJ, Rio de Janeiro.

Anderson RC (2000) Nematode parasites of vertebrates, their development and transmission. 2nd ed. CABI Publishing, Wallingford, Oxon.

Anderson RM, Gordon DM (1982) Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortalities. Parasitology 85:373-98. https://doi.org/10.1017/S0031182000055347

Andrade EB, Leite JRSA., Andrade GV, Macedo RG (2012) Diversidade de Anfíbios do Delta do Parnaíba. In: Guzzi A (Org.). Biodiversidade do Delta do Parnaíba. EDUFPI, Parnaíba, pp. 209-269.

Andrade-Lima D (1982) Present day forest refuges in Northeastern Brazil. In: Prance GT (ed.) Biological Diversification in the Tropics. Columbia University Press, New York, pp. 245-254.

Araújo KC, Guzzi A, Ávila RW (2018) Influence of habitat heterogeneity on anuran diversity in Restinga landscapes of the Parnaíba River delta, northeastern Brazil. Zoo Keys 757:69-83. https://doi.org/10.3897/zookeys.757.21900

Arita HT, Vargas-Barón J, Villalobos F (2014) Latitudinal gradients of genus richness and endemism and the diversification of New Word bats. Ecography 37:1024-1033. https://doi.org/10.1111/ecog.00720

Azevedo RK, Abdallah VD, Luque JL (2006) Ecologia da comunidade de metazoários parasitos do acará *Geophagus brasiliensis* (Quoy e Gaimard, 1824)(Perciformes: Cichlidae) do rio Guandu, Estado do Rio de Janeiro, Brasil. Acta Sci. Biol. Sci. 28:403-411. https://doi.org/10.4025/actascibiolsci.v28i4.406

Baker DG (2007) Flynn's Parasites of Laboratory Animals: Second Edition. Second ed. Oxford, UK: Blackwell Publishing Ltd.

Barton DP (1999) Ecology of helminth communities in tropical Australian amphibians. Int. J. Parasitol. 29:921-926. https://doi.org/10.1016/S0020-7519(99)00057-0

Beckett SJ (2016) Improved community detection in weighted bipartite networks. R. Soc. open Sci. 3:140536. https://doi.org/10.1098/rsos.140536

Bernal MH, Lynch JD (2008) Review and analysis of altitudinal distribution of the Andean anurans in Colombia. Zootaxa 1826:1-25.

Bernarde OS (2012) Anfíbios e répteis: introdução ao estudo da herpetofauna brasileira. 1 ed. Anolis Books, Curitiba.

Bhattarai KR, Vetaas OR (2006) Can Rapoport's rule explain trees species richness along the Himalayan elevation gradient, Nepal? Divers. Distrib. 12:373-378. https://doi.org/10.1111/j.1366-9516.2006.00244.x

Bishop TR, Robertson MP, van Rensburg BJ, Parr CL (2015) Contrasting species and functional beta diversity in montane ant assemblages. J. Biogeogr. 42:1776-1786. https://doi.org/10.1111/jbi.12537

Borges-Nojosa DM, Caramaschi U **(**2003) Composição e análise comparativa da diversidade e das afinidades biogeográficas dos lagartos e anfisbenídeos (Squamata) dos brejos nordestinus. In. Leal IR, Tabarelli M, Silva JMC (eds) Ecologia e conservação da Caatinga. UFPE, Recife, pp 489-540.

Brito SV, Corso G, Almeida AM, Ferreira FS, Almeida WO, Anjos LA, Vasconcellos A (2014) Phylogeny and microhabitats utilized by lizards determine the composition of their endoparasites in the semiarid Caatinga of Northeast Brazil. Parasitol. Res. 113:3963-3972. https://doi.org/10.1007/s00436-014-4061-z

Bursey CR, Goldberg SR, Parmelee JR (2001) Gastrointestinal helminths of 51 species of Anurans from Reserva Cuzco Amazónico, Peru. Comp. Parasitol. 68:21-35.

Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. J. Parasitol. 83:575-583. https://doi.org/10.2307/3284227

Caglioni E, Uhlmann A, Curcio GR, Ramos MR, Bonnet A, Junckes AR (2018) Altitude and soils determines abrupt variation of vegetation in altitudinal gradient in Atlantic Rain Forest. Rodriguésia 69:2055-2068. https://doi.org/10.1590/2175-7860201869436

Campião KM, Morais DH, Dias OT, Aguiar A, Toledo G, Tavares LER, Silva RJ (2014) Checklist of helminth parasites of amphibians from South America. Zootaxa 3843:1-93. https://doi.org/10.11646/zootaxa.3843.1.1

Cattin MF, Bersier LF, Banašek-Richter C, Baltensperger R, Gabriel JP (2004) Phylogenetic constraints and adaptation explain food-web structure. Nature 427:835-839. https://doi.org/10.1038/nature02327

Ceará (2002) Zoneamento ambiental e plano de manejo da área de proteção ambiental (APA) da serra de Maranguape (CE). SEMACE, Fortaleza, Ceará.

Chen HW, Liu HC, Davis AJ, Jordán F, Hwang MJ, Shao KT (2008) Network position of hosts in food webs and their parasite diversity. Oikos 117:1847-1855. https://doi.org/10.1111/j.1600-0706.2008.16607.x

Colwell RK, Lees DC (2000) The mid-domain effect: geometric constraints on the geography of species richness. Trends Ecol. Evol. 15:70-76. https://doi.org/10.1016/S0169-5347(99)01767-X

Crofton HD (1971) A model of host-parasite relationships. Parasitology 63:343-64. https://doi.org/10.1017/S0031182000079890

Csardi G, Nepusz T (2006) The igraph software package for complex network research. In: https://igraph.org. (accessed 23 September 2022).

D'Bastiani E, Campião KM (2021) Disentangling the beta-diversity in anuran parasite communities. Parasitology 148:327-332. https://doi.org/10.1017/S0031182020002061

D'Bastiani E, Campião KM, Boeger WA, Araújo SB (2020) The role of ecological opportunity in shaping host–parasite networks. Parasitology 147:1452-1460. https://doi.org/10.1017/S003118202000133X

De Castro DP, Borges-Leite MJ, Lima DC, Borges-Nojosa DM (2013) Parental care in two species of *Leptodactylus* Fitzinger, 1826 (Anura, Leptodactylidae) in north-eastern Brazil. Herpetology Notes 6:267-269.

Dias-Terceiro RG, Kaefer IL, Fraga R, de Araújo MC, Simões PI, Lima AP (2015) A matter of scale: Historical and environmental factors structure anuran assemblages from the upper Madeira River, Amazonia. Biotropica 47:259-266. https://doi.org/10.1111/btp.12197

Diogo IJS, dos Santos K, da Costa IR, dos Santos FAM (2021) Effects of topography and climate on Neotropical mountain forests structure in the semiarid region. Appl. Veg. Sci. 24:e12527. https://doi.org/10.1111/avsc.12527

Dormann CF, Frueund J, Bluethgen N, Gruber B (2009) Indices, graphs and null models: analyzing bipartite ecological networks. Open Ecol. J. 2:7-24.

Dunne JA, Williams RJ, Martinez ND (2002) Food-web structure and network theory: The role of connectance and size. Proc. Natl. Acad. Sci. 99:12917-12922. https://doi.org/10.1073/pnas.192407699

Figueiredo MA (1997) A cobertura vegetal do Ceará (Unidades Fitoecológicas). In: Atlas do Ceará. Governo do Estado do Ceará; IPLANCE, Fortaleza. 65p.

Fraga R, Ferrão M, Stow AJ, Magnusson WE, Lima AP (2018) Different environmental gradients affect different measures of snake β-diversity in the Amazon rainforests. PeerJ 6:e5628.

Gaston KJ (2000) Global patterns in biodiversity. Nature 405:220-227. https://doi.org/10.1038/35012228

Geise L, Pereira LG, Bossi DEP, Bergallo HG (2004) Pattern of elevational distribution and richness of non volant mammals in Itatiaia national park and its surroundings, in southeastern Brazil. Braz. J. Biol. 64:599-612. https://doi.org/10.1590/S1519-69842004000400007

Goater CP, Baldwin RE, Scrimgeour GJ (2005) Physico-chemical determinant community structure in whitefish (*Coregonus clupeaformes*) from adjacent lakes in Northern Alberta, Canada. Parasitology 131:713-722. https://doi.org/10.1017/S0031182005008371

Gonçalves-Sousa JG, de Fraga R, Menezes BS, Mesquita DO, Ávila RW (2022) Riverine barrier and aridity effects on taxonomic, phylogenetic and functional diversities of lizard assemblages from a semi-arid region. J. Biogeogr. 49:1021-1033. https://doi.org/10.1111/jbi.14356

Gonzalez CE, Inés HM (2015) Checklist of nematode parasites of amphibians from Argentina. Zootaxa 3980:451-476. https://doi.org/10.11646/zootaxa.3980.4.1

Guilhaumon F, Krasnov BR, Poulin R, Shenbrot GI, Mouillot D (2012) Latitudinal mismatches between the components of mammal–flea interaction networks. Glob. Ecol. Biogeogr. 21:725-731. https://doi.org/10.1111/j.1466-8238.2011.00714.x

Guillén-Hernández S, Salgado-Maldonado G, Lamothe-Argumedo R (2000) Digeneans (Plathelminthes: Trematoda) of seven sympatric species of anurans from Los Tuxtlas, Veracruz, Mexico. Stud. Neotrop. Fauna Environ. 35:10-13. 10.1076/0165-0521(200004)35:1;1-M;FT010

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8:993-1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Hamann MI, Kehr AI, González CE (2006) Species affinity and infracommunity ordination of helminths of *Leptodactylus chaquensis* (Anura: Leptodactylidae) in two contrasting environments from northeastern Argentina. J. Parasitol. 92:1171-1179. https://doi.org/10.1645/GE-862R1.1

Haverkost TR, Gardner SL, Peterson AT (2010) Predicting the distribution of a parasite using the ecological niche model, GARP. Rev. Mex. Biodiv. 81:895-902.

Hu J, Li C, Xie F, Jiang J (2012) Endemic amphibians and their distribution in China. Asian Herpetol. Res. 3:163-171.

Huston MA (1994) Biological diversity: the coexistence of species on changing landscapes. Cambridge University, Cambridge.

Ings TC, Montoya JM, Bascompte J, Blüthgen N, Brown L, Dormann CF, ... Woodward G (2009) Ecological networks–beyond food webs. J. Anim. Ecol. 78:253-269. https://doi.org/10.1111/j.1365-2656.2008.01460.x

IPECE – Instituto de Pesquisa e Estratégia Econômica do Ceará (2017) Perfil municipal: Maranguape. Accessible at: http://www.ipece.ce.gov.br. (accessed 21 July 2022).

Jetz W, Pyron RA (2018) The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. Nat. Ecol. Evol. 2:850-858. https://doi.org/10.1038/s41559-018-0515-5

Jinlong Zhang (2016) spaa: SPecies Association Analysis. R package version 0.2.2. In: https://CRAN.R-project.org/package=spaa. (accessed 12 July 2021).

Jombart T (2008) adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24:1403-1405. https://doi.org/10.1093/bioinformatics/btn129

Junior BT, Gomes FR (2012) Water balance and geographical distribution of amphibians. Rev. Biol. 8:49-57. https://doi.org/10.7594/revbio.08.09

Kattan GH, Franco P (2004) Bird diversity along elevational gradients in the Andes of Colombia: area and mass effects. Glob. Ecol. Biogeogr. 13:451-458. https://doi.org/10.1111/j.1466-822X.2004.00117.x

Kessler M (2009) The impact of population processes on patterns of lessons from elevational gradients. Bas. Appl. Ecol. 10:295-299. https://doi.org/10.1016/j.baae.2008.10.006

Koleff P, Gaston KJ, Lennon JJ (2003) Measuring beta diversity for presence–absence data. J. Anim. Ecol. 72:367-382. https://doi.org/10.1046/j.1365-2656.2003.00710.x

Krasnov BR, Fortuna MA, Mouillot D, Khokhlova IS, Shenbrot GI, Poulin R (2012) Phylogenetic signal in module composition and species connectivity in compartmentalized host-parasite networks. Am. Nat. 179:501-511.

Krause AE, Frank KA, Mason DM, Ulanowicz RE, Taylor WW (2003) Compartments revealed in food-web structure. Nature 426:282-285. https://doi.org/10.1038/nature02115

Krebs CJ (2001) Ecology: the experimental analysis of distribution and abundance. Fifty Edition. Benjamin Cummings, San Francisco, CA. 695p.

Lima DC, Cascon P (2008) Aspectos socioambientais e legais da bananicultura na APA da Serra de Maranguape, Estado do Ceará. REDE – Revista Eletrônica do Prodema 2:64-79.

Lovett JC, Marshall AR, Carr J (2006) Changes in tropical forest vegetation along an altitudinal gradient in the Udzungwa Mountains National Park, Tanzania. Afr. J. Ecol. 44:478-90. https://doi.org/10.1111/j.1365-2028.2006.00660.x

MacArthur RH, Diamond JM, Karr JR (1972) Density compensation in island faunas. Ecology 53:330-342. https://doi.org/10.2307/1934090

MacArthur RH, Macarthur JW (1961) On bird species diversity. Ecology 42:594-598. https://doi.org/10.2307/1932254

Madelaire CB, Gomes FR, Da Silva RJ (2012) Helminth Parasites of *Hypsiboas prasinus* (Anura: Hylidae) from Two Atlantic Forest Fragments, São Paulo State, Brazil. J. Parasitol. 98:560-564. https://doi.org/10.1645/JP-GE-2665.1

Malcicka M, Agosta SJ, Harvey JA (2015) Multi-level ecological fitting: indirect life cycles are not a barrier to host switching and invasion. Glob. Chang. Biol. 21:3210-3218. https://doi.org/10.1111/gcb.12928

Marcogliese DJ (2002) Food webs and the transmission of parasites to marine fish. Parasitology 124:83-99. https://doi.org/10.1017/S003118200200149X

Moro MF, Macedo MB, Moura-Fé MMD, Castro ASF, Costa RCD (2015) Vegetação, unidades fitoecológicas e diversidade paisagística do estado do Ceará. Rodriguésia 66:717-743. https://doi.org/10.1590/2175-7860201566305

Nunes GM, Santos SB (2011) Gradiente de altitude e riqueza de espécies: como o estudo dos moluscos terrestres contribui com esta questão?. Oecol. Aust. 15:854-868. http://dx.doi.org/10.4257/oeco.2011.1504.06

Oksanen J, Blanchet FG, Kindt R et al. (2016) Vegan: Community Eecology Ppackage. R package version 2.3–3. Available at https://CRAN.R-project. org/package=vegan (accessed 26 May 2021).

Oliveira AKC, Oliveira IS (2014) A influência da temperatura nas histórias de vida de vertebrados. Rev. Biol. 12:8-15. http://doi.org/10.7594/revbio.12.02.02

Oliveira CR, Ávila RW, Morais DH (2019) Helminths Associated with Three *Physalaemus* Species (Anura: Leptodactylidae) from Caatinga Biome, Brazil. Acta Parasitol. 64:205-212. https://doi.org/10.2478/s11686-018-00022-8

Oliveira CR, Mascarenhas W, Batista-Oliveira D, de Castro Araújo K, Ávila RW, Borges-Nojosa DM (2022) Endoparasite community of anurans from an altitudinal rainforest enclave in a Brazilian semiarid area. J. Helminthol. 96:e62. https://doi.org/10.1017/S0022149X22000499

Oliveira TS, Araújo FS (2007) Diversidade e conservação da biota na serra de Baturité, Ceará. Fortaleza: COELCE.

Pacala SW, Dobson AP (1988) The relation between the number of parasites/host and host age: population dynamic causes and maximum likelihood estimation. Parasitology 96:197-210. https://doi.org/10.1017/S0031182000081762

Paradis E, Claude J, Strimmer K (2004) ape: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289-290. https://doi.org/10.1093/bioinformatics/btg412

Peterson AT, Bauer JT, Mills JN (2004) Ecological and geographic distribution of filovirus disease. Emerg. Infec. Dis. 10:40-47. https://doi.org/10.3201/eid1001.030125

Pianka ER (1966) Latitudinal Gradients in Species Diversity: A Review of Concepts. Amer. Nat. 100:33-46.

Pietrock M, Marcogliese DJ (2004) Response to Morley and Lewis: Freeliving endohelminths: the influence of multiple factors. Trends Parasitol. 20:115-116. https://doi.org/10.1016/j.pt.2003.12.001

Poisot T, Stouffer DB, Gravel D (2015) Beyond species: why ecological interaction networks vary through space and time. Oikos 124:243-251. https://doi.org/10.1111/oik.01719

Pombal JP (1997) Distribuição espacial e temporal de anuros (Amphibia) em uma poça permanente na Serra de Paranapiacaba, sudeste do Brasil. Rev. Bras. Zool. 57:583-594.

Poulin R (1993) The disparity between observed and uniform distributions: a new look at parasite aggregation. Int. J. Parasitol. 23:937-44. https://doi.org/10.1016/0020-7519(93)90060-C

Poulin R, Krasnov BR (2010) Similarity and variability of parasite assemblages across geographical space. In: Morand S, Krasnov BR (eds) The biogeography of host-parasite interactions. Oxford University, New York, pp 115-128.

Poulin R, Morand S (2004) Parasite Biodiversity, Smithsonian Institution Books, Washington, D.C., USA.

Rahbek C (1995) The elevational gradient of species richness: a uniform pattern?. Ecography 18:200-205. https://www.jstor.org/stable/3682769

Rahbek C (2005) The role of spatial scale and the perception of large-scale species-richness patterns. Ecol. lett. 8:224-239. https://doi.org/10.1111/j.1461-0248.2004.00701.x

Rausch RL (1994) Transberingian dispersal of cestodes in mammals. Int. J. Parasitol. 24:1203-1212. https://doi.org/10.1016/0020-7519(94)90191-0

Remonti L, Balestrieri A, Prigioni C (2009) Altitudinal gradient of Eurasian otter (Lutra lutra) food niche in Mediterranean habitats. Can. J. Zool. 87:285-291. https://doi.org/10.1139/Z09-011

Rohde K (1992) Latitudinal Gradients in Species Diversity: The Search for the Primary Cause. Oikos 65:514-527. https://doi.org/10.2307/3545569

Romdal TS, Grytnes JA (2007) An indirect area effect on elevational species richness patterns. Ecography 30:440-448.

Sampaio NKS, Teixeira AAM, Do Nascimento JM, Ribeiro SC, Almeida WO, Brito SV (2022) Endoparasite community structure of an anuran assemblage in the Caatinga, Northeastern Neotropical Region. J. Helminthol. 96:e78. https://doi.org/10.1017/S0022149X22000682

Santos EMD, Amorim FOD (2006) Parental care behaviour in *Leptodactylus natalensis* (Amphibia, Anura, Leptodactylidae). Iheringia 96:491-494. https://doi.org/10.1590/S0073-47212006000400015

Santos TG, Rossa-Feres DC, Casatti L (2007) Diversidade e distribuição espaço-temporal de anuros em região com pronunciada estação seca no sudeste do Brasil. Iheringia 97:37-49. https://doi.org/10.1590/S0073-47212007000100007

Santos TG, Vasconcelos TS, Haddad CFB (2012) The role of environmental heterogeneity in maintenance of anuran amphibian diversity of the Brazilian Mesophytic Semideciduous Forest. In. Sudarshana P, Nageswara-Rao M, Soneji J (Eds). Tropical Forests, IntechOpen, pp. 119-138.

Silva FR, Rossa-Feres DDC (2017) Fragmentation gradients differentially affect the species range distributions of four taxonomic groups in semi-deciduous Atlantic forest. Biotropica 49:283-292. https://doi.org/10.1111/btp.12362

Siqueira CC, Rocha CFD (2013) Gradientes altitudinais: conceitos e implicações sobre a biologia, a distribuição e a conservação dos anfíbios anuros. Oecol. Aust. 17:282-302. http://dx.doi.org/10.4257/oeco.2013.1702.09

Tabarelli M, Santos AMM (2004) Uma breve descrição sobre a história natural dos brejos nordestinos. In: Pôrto KC, Cabral JJP, Tabarelli M (Eds) Brejos de altitude em Pernambuco e Paraíba – História natural, ecologia e conservação. Brasília: Ministério do Meio Ambiente, pp. 17-24.

Tylianakis JM, Tscharntke T, Lewis OT (2007) Habitat modification alters the structure of tropical host–parasitoid food webs. Nature 445:202-205. https://doi.org/10.1038/nature05429

Vasconcelos HCG, Dias MT (2014) Influência da sazonalidade na infestação de *Ergasilus turucuyus* (Copepoda: Ergasilidae) em *Acestrorhynchus falcirostris* e *Hemiodus unimaculatus*

(Osteichthyes: Characiformes) do Reservatório Coaracy Nunes, estado do Amapá, Brasil. Biota Amazônia 4:106-110. http://dx.doi.org/10.18561/2179-5746/biotaamazonia.v4n1p106-110

Vasconcelos TS, Santos TG, Haddad CFB, Rossa-Feres DC (2010) Climatic variables and altitude as predictors of anuran species richness and number of reproductive modes in Brazil. J. Trop. Ecol. 26:423-432. https://doi.org/10.1017/S0266467410000167

Vázquez DP, Poulin R, Krasnov BR, Shenbrot GI (2005) Species abundance and the distribution of specialization in host-parasite interaction networks. J. Anim. Ecol. 74:946-955. https://www.jstor.org/stable/3505510

Watts DJ, Strogatz SH (1998) Collective dynamics of ‘small-world’networks. Nature 393:440-442. https://doi.org/10.1038/30918

Weaver HJ, Monks S, Gardner SL (2016) Phylogeny and biogeography of species of Syphacia Seurat, 1916 (Nemata: Oxyurida: Oxyuridae) from the Australian bioregion. Aust. J. Zool. 64:81-90. https://doi.org/10.1071/ZO15080

Woodward G, Ebenman B, Emmerson M, Montoya JM, Olesen JM, Valido A, Warren PH (2005) Body size in ecological networks. Trends Ecol. Evol. 20:402-409. https://doi.org/10.1016/j.tree.2005.04.005

Wright SJ (1980) Density compensation in island avifaunas. Oecologia 45:385-389. https://doi.org/10.1007/BF00540211

Chapter 3 –

4 Endoparasites of *Adelophryne maranguapensis* Hoogmoed, Borges & Cascon, 1994 (Anura, Eleutherodactylidae), an endemic and threatened species from an altitude swamp in northeastern Brazil

Endoparasitas de Adelophryne maranguapensis *Hoogmoed, Borges & Cascon, 1994, (Anura, Eleutherodactylidae), uma espécie endêmica e ameaçada de um pântano de altitude no nordeste do Brasil*

Cicero Ricardo de Oliveira

Daniel Cassiano Lima

Robson Waldemar Ávila

Diva Maria Borges-Nojosa

Artigo publicado na revista ***Parasitology Research***, **121**(3), 1053-1057, 2022.

https://doi.org/10.1007/s00436-022-07458-y

Endoparasites of *Adelophryne maranguapensis* Hoogmoed, Borges & Cascon, 1994 (Anura, Eleutherodactylidae), an endemic and threatened species from an altitude swamp in northeastern Brazil

Cicero Ricardo de Oliveira[1,3,*], Daniel Cassiano Lima[2,3], Robson Waldemar Ávila[1,3], Diva Maria Borges-Nojosa[1,3]

1 Programa de Pós-Graduação em Ecologia e Recursos Naturais, Bloco 902, Centro de Ciências, Universidade Federal do Ceará – UFC, Campus do PICI, Av. Humberto Monte, s/n, 60455-760 Fortaleza, Ceará, Brasil
2 Museu de História Natural do Ceará Professor Dias da Rocha, Universidade Estadual do Ceará. Rua Divino Salvador, 225, Pacoti, Ceará, Brasil. CEP 62770-000
3 Núcleo Regional de Ofiologia, Bloco 905, Universidade Federal do Ceará, Campus do PICI, Avenida Humberto Monte, s/n, Fortaleza, Ceará 60455-760, Brasil.
***Corresponding Author:** riccicer@gmail.com

Abstract

Adelophryne maranguapensis is an endangered anuran species endemic to the Maranguape residual mountain, Ceará State, northeaster Brazil, which is under strong anthropogenic pressure. There are still few studies on the natural history of this species that allow a better understanding of its biology and can provide the basis for conservation actions. Studies on endoparasitism are an important source for the comprehension of ecological relationships, as well as for providing information on host biology and its relevance to ecosystems. Thus, we present information about the endoparasites helminths, the relationship of parasite abundance with the size of individuals and the parasite difference between the sexes in *A. maranguapensis*, to elucidate some characteristics in the host-parasite relationship and the use of the area of this anuran. We analysed 107 specimens deposited in the Herpetological Collection of the Federal University of Ceará, sampled from 2010 to 2012. Total prevalence of 24.30% was recorded, and four parasitic taxa were identified, *Aplectana* sp., *Physaloptera* sp., *Parapharyngodon* sp. and an unidentified Ascarid. No relationship between the abundance of parasites and snout-vent length was found and the parasite difference between the sexes. Even though identification of the parasites at species level was not possible, *A. maranguapensis* follows a common pattern in parasitism of Neotropical species.

Key words: Helminth, Parasite, Frog, Threatened.

Resumo

Adelophryne maranguapensis é uma espécie anura endêmica e em perigo de extinção da montanha residual de Maranguape, Estado do Ceará, nordeste do Brasil, que se encontra sob forte pressão antropogênica. Ainda há poucos estudos sobre a história natural desta espécie que permitam um melhor entendimento de sua biologia e possam fornecer a base para ações de conservação. Os estudos sobre endoparasitismo são uma fonte importante para a compreensão das relações ecológicas, assim como para fornecer informações sobre a biologia do hospedeiro e sua relevância para os ecossistemas. Assim, apresentamos informações sobre os helmintos endoparasitas, a relação da abundância parasitária com o tamanho dos indivíduos e a diferença parasitária entre os sexos em *A. maranguapensis*, para elucidar algumas características na relação hospedeiro-parasita e o uso da área deste anuro. Analisamos 107 espécimes depositados na Coleção Herpetológica da Universidade Federal do Ceará, amostrados de 2010 a 2012. Registramos uma prevalência total de 24,30%, e foram identificadas quatro taxas parasitas, *Aplectana* sp., *Physaloptera* sp., *Parapharyngodon* sp. e um Ascarídeo não identificado. Não foi encontrada nenhuma relação entre a abundância de parasitas e o comprimento total ou diferença de parasitas entre os sexos. Embora não tenha sido possível identificar os parasitas em nível de espécie, *A. maranguapensis* segue um padrão comum no parasitismo das espécies Neotropicais.

Palavras Chave: Helmintos, Parasitas, Sapo, Ameaçado.

4.1 INTRODUCTION

Belonging to the family Eleutherodactylidae, the genus *Adelophryne* Hoogmoed and Lescure, 1984 currently comprises 12 species distributed in South America (Frost 2021). *Adelophryne maranguapensis* Hoogmoed, Borges and Cascon 1994 is a threatened species endemic to Maranguape residual mountain, Ceará, northeaster Brazil (IUCN 2020), which is under strong pressure from anthropic degradation. In general, threatened species are more vulnerable due to certain characteristics, including low population densities and restricted distribution, making them more fragile and susceptible to changes in the environment (Abrahão and Escarlate-Tavares 2019).

Studies on natural history are important for understanding the biology of a species, providing basis for conservation actions (Ramírez-Bautista et al. 2000), specially for species inhabiting threatened areas (Tabarelli et al. 2005). In the available literature, there are limited results on the ecology of *A. maranguapensis*, with studies reporting on reproductive biology (Cassiano-Lima et al. 2020), annunciation song (Cassiano-Lima et al. 2014) and conservation status (Silvano and Segalla 2005). However, there are still gaps on the knowledge about the life history of this species, such as diet and parasitism.

Many parasitic studies with amphibians have been conducted in the high altitude swamp or surrounding Caatinga areas; these report a high species richness, with the predominance of nematodes being a common feature of these inventories (Lins et al. 2017; Oliveira et al. 2019; Silva-Neta et al. 2020; Mascarenhas et al. 2021). These studies also share some species in common, such as *Aplectana membranosa* (Schneider, 1866), *Oswaldocruzia mazzai* Travassos, 1935, *Physaloptera* sp. Rudolphi, 1819, *Raillietnema spectans* Gomes, 1964 and *Rhabdias* sp. Stiles and Hassall, 1905 which suggests that these species are well distributed throughout the environment. Therefore, parasitism studies can reveal information on host biology, the parasite/host relationship and its relevance to ecosystems, contributing substantially to a better understanding of species conservation (Marcogliese 2004). Thus, their knowledge is of fundamental importance for the preservation of these species, which is particularly significant for hosts with restricted distribution. Since the composition of parasite communities is often significantly variable between populations of the same species (Poulin et al. 2011; Bezerra et al. 2016), and influenced by various factors such as host size, sex, diet, location and behaviour (Campião et al. 2015).

In this context, in the present study, we provide data on the endoparasites helminths, the relationship of parasite abundance with the size of individuals and the parasite difference between the sexes of the frog *Adelophryne maranguapensis*, a threatened species endemic to Ceará State, northeastern Brazil, in order to understand some characteristics in the host-parasite relationship and the use of the area of this anuran.

4.2 MATERIAL AND METHODS

Located 25 km off the coast of Ceará State, Brazil, the Maranguape residual mountain (03° 53′ 40.6″ S, 38° 43′ 21.2″ W, 920-m elevation) has annual precipitation of 1,300 mm, and the average temperature is between 23 and 26°C (Cassiano-Lima et al. 2020). Given these particular characteristics and the number of endemic species recorded, Maranguape residual mountain is considered one of the highest priority areas for amphibian conservation in northeaster Brazil (Camardelli and Napoli 2012).

Since it is an endangered species (IUCN 2020), this study was conducted using deposited host specimens. A total of 107 specimens of *A. maranguapensis* (56 males, 45 females and six juveniles), deposited in the Herpetological Collection of the Federal University of Ceará (CHUFC), Ceará State, Brazil, were surveyed for parasites. The host sampling was conducted each month from April 2010 to June 2012.

In the laboratory, we performed necropsy on all samples, and the contents of the gastrointestinal tract were analysed under a stereoscopic microscope to investigate the presence of endoparasites in the following organs: digestive tract, lungs, heart, liver and kidneys analysed according to Amato et al. (1991). For identification of parasite species, we used the following literature: Vicente et al. (1991) and Gibbons (2010). All parasites were prepared according to Amato et al. (1991).

The infection parameters analysed were prevalence, mean intensity of infection and mean abundance, according to Bush et al. (1997). We also checked whether there was a correlation between endoparasite abundance and body size (snout-vent length - SVL) of the hosts and between males and females, using Pearson’s coefficient. To check the parasite abundance difference with respect to sex, we performed a t-test.

4.3 RESULTS AND DISCUSSION

Amphibians are an excellent model for assessing patterns in helminth community structure (Aho 1990) because they occupy a variety of habitats and different positions in food webs (Koprivnikar et al. 2012). Thus, we analysed 107 specimens of *A. maranguapensis*, from which 26 individuals were infected with at least one endoparasite species (prevalence 24.30%).

We recorded a total of 56 helminth specimens, identified as four parasite taxa: *Aplectana* sp. Railliet and Henry 1916, *Physaloptera* sp., *Parapharyngodon* sp. Chatterji 1933 and unidentified specimens of Ascarididae (Table 1). In the present study, *Adelophryne maranguapensis* presented helminth fauna composed of nematodes. This infection pattern is common to other anuran species, such as *Physalaemus* spp. (Oliveira et al. 2019) and *Proceratophrys ararype* Mângia et al. 2018 (Mascarenhas et al. 2021).

Nematodes usually infect hosts by ingestion of prey infected with their larvae or skin penetration (Anderson 2000). Meanwhile, trematodes generally require aquatic intermediate hosts in addition to snails. Thus, anurans living in aquatic habitats are more easily infected than terrestrial species (Guillén-Hernández et al. 2000). Therefore, endoparasitic infections composed of nematodes in *A. maranguapensis* may be related to the direct life cycle of the host, which is associated with burlap and the use of bromeliads for egg laying and tadpole development (Cassiano-Lima et al. 2020).

Table 1 – Endoparasites of *Adelophryne maranguapensis* in Maranguape residual mountain, Ceará State, Brazil. *NS* number of parasite specimens, *P%* prevalence, *MII* mean intensity of infection, *R* range, *MA* ± *SE* mean abundance and standard error, *SI* site of infection.

ENDOPARASITES	NS	P%	MII	R	MA ± SE	SI
Aplectana sp.	38	20.56	1.73	1 – 6	0.36 ± 0.26	Id; Ig
Physaloptera sp.	3	2.80	1	1	0.03	Sto
Parapharyngodon sp.	1	0.93	1	1	0.01	Ig
Ascarididae gen. sp.	14	0.93	14	14	0.13	Id
Total	56	24.30	2.15	1 – 14	0.52 ± 0.50	

Sto stomach, *Lgi* large intestine, *Smi* small intestine.

Host body size (SVL) is widely suggested as a determinant in predicting species richness, affecting the composition of parasite communities (Campião et al. 2015). However, we found no correlation between SVL values and parasite abundance in the present study (*r*=0.15; *p*=0.11) nor between males (*r*=0.01; *p*=0.92) or females (*r*=0.10; *p*=0.48). This result may be related to the variation in the mean size (14.0±2.63) of the analysed individuals. Thus, low variation in size seems to not influence the success of parasitism (Oliveira et al. 2022). Furthermore, the heteroxenous life cycle of the parasitic nematodes observed in *A. maranguapensis* suggests that diet may be a strong factor influencing the parasite composition of this host species (Klaion et al. 2011). Additionally, we found no significant difference in parasitism between sexes in *A. maranguapensis* (p= 0.36).

The nematode *Aplectana* spp. are commonly found infecting the large intestine of reptiles and amphibians, have a direct life cycle and actively infect their hosts (Anderson 2000). Species of this genus have been observed in a variety of anurans in northeaster Brazil (Silva-Neta et al. 2020; Mascarenhas et al. 2021). These nematodes have a mouth with three lips each with two papillae, a small pharynx, a pyriform bulb posterior to oesophagus, an excretory pore located at bulb level and the nerve ring located in the middle of oesophagus (Miranda 1924). In our study, the morphometry of the total body length, distance from the excretory pore to the anterior end, distance from the vulva to the posterior and anterior end, eggs and the shape of the papillae along with the known distribution and records for anuran species matches the species of *Aplectana membranosa*. However, we did not identify the parasite to the species level due to the existence of only females in the sample, which does not allow the observation of concise identification characters. *Aplectana* spp. had the highest prevalence (18.8%) of infection in *A. maranguapensis*, which may be associated with the high number of infectious larvae in the environment produced by *Aplectana* spp. (Lins et al. 2017).

The genus *Physaloptera* is composed of approximately 100 species parasitizing amphibians, reptiles, birds and mammals throughout the world (Pereira et al. 2012). These are worms with cuticles forming a cephalic collar around the anterior end, which have a mouth with large and triangular lips, each with teeth. The oesophagus is divided into a short anterior muscular portion and long posterior glandular portion (Vicente et al. 1991). In amphibians, the acquisition of *Physaloptera* occurs through the ingestion of infected insects, mainly Orthoptera (Klaion et al. 2011). This parasite is usually found in the larval stage, which makes its identification at the species level impossible, and also suggests that amphibians are not definitive hosts (Boquimpani-Freitas et al. 2001) and could be acting as intermediate or paratenic hosts.

The genus *Parapharyngodon* currently includes 55 valid species distributed globally, eight of which have been recorded in Brazilian hosts (Bursey and Goldberg 2015; Ferreira et al. 2021). They are parasites with a mouth with three lips, with lips usually bilobed and papillae present, oesophagus with posterior bulb and presence of lateral wings, they have a truncated tail with a dorsal appendix and with lateral papillae, and the larvae usually have a fusiform body with a transversely striated cuticle with small spines (Freitas 1957). In the Caatinga biome, only the species *Parapharyngodon alvarengai* Freitas 1957 found in both lizards and amphibians (Luque et al. 2005), *Parapharyngodon sceleratus* Travassos, 1923 parasitizing lizards (Ávila et al. 2012), the species taxonomically described on hosts of the Caatinga biome, *Parapharyngodon verrucosus* on the lizard *Diploglossus lessonae* Peracca, 1890 (Freitas and Dobbin, 1959), *Parapharyngodon silvoi* described from the anuran *Dermatonotus muelleri* Boettger, 1885 (Araújo-Filho et al. 2015) and *Parapharyngodon hispidus* described for the lizard *Tropidurus hispidus* Spix, 1825 (Ferreira et al. 2021) are known. In the present study, we did not identify the parasite at the species level due to its larval stage. However, possibly this is one of the species previously mentioned, due to the distribution and record in anuran hosts in this type of environment. Although the life cycle of members of this genus remains unknown (Campião et al. 2016), we believe it is related to the feeding behaviour of the hosts, being acquired through the ingestion of arthropods.

We found 14 parasitic individuals in the gastrointestinal tract of *A. maranguapensis* belonging to the Ascarididae family, due to the larval stage at which they were found, and because they were individuals from the zoological collection, it was not possible to observe the morphological attributes (Hartwich 2009) and identify the genus. González and Hamann (2013) reported the occurrence of larvae of *Brevimulticaecum* sp. Mozgovoi, 1951 parasitizing the anurans *Lepidobatrachus laevis* Budgett, 1899, *Physalaemus albonotatus* Steindachner, 1864 and *Pseudis paradoxa* Linnaeus, 1758. Campião et al. (2016) recorded the same parasite taxon for the species *Dendropsophus nanus* Boulenger, 1889, *Boana raniceps* Cope, 1862, *Scinax nasicus* Cope, 1862, *Pseudis platensis* Gallardo, 1961, *Trachycephalus typhonius* Linnaeus, 1758 and *Pithecopus azureus* Cope, 1862, as well as a record of *Porrocaecum* Railliet and Henry, 1912 for the species *B. raniceps* and *P. azureus*. These parasites use trophic interactions to migrate hosts, with infected invertebrates being the source of infection for anurans (Campião et al. 2016), crocodilians, freshwater rays and teleosts which are considered the main definitive hosts in the life cycle of these parasites (Reyda 2008). The occurrence of these larvae in amphibian hosts indicates that they may play a role in the transmission of these nematodes, serving as intermediate or paratenic hosts (Moravec and Kaiser 1994), and based on the above records, we believe that the larvae found possibly belong to one of those genera already reported for anurans.

The parasite composition of *A. maranguapensis* follows a common pattern in neotropical species. These parasites can affect host immunity and population dynamics. Thus, the low parasite prevalence indicates that *A. maranguapensis*, despite anthropic effects on its habitat, presents a stable relationship without negative population effects, demonstrating a high resilience and a good immunological health of the species. The negative relationship between parasitism and body size of the individuals analysed and the similarity in parasitism between the sexes indicates that the species probably shares the same home range over time and presents an overlap in habitat use, and considering the life cycle of the parasites, we believe that *A. maranguapensis* present a feeding overlap, and consequently they are exposed to the same probabilities of infection. Although a more precise identification of these parasites was not possible in this study, we present relevant information for the knowledge of the natural history of this endangered anuran, thus contributing to its conservation.

REFERENCES

Abrahão, C.R. & Escarlate-Tavares, F. 2019. Ameaças à Herpetofauna da Mata Atlântica nordestina, pp. 162-174. In: Plano de ação nacional para a conservação da herpetofauna ameaçada da Mata Atlântica nordestina (C.R. Abrahão; G.J.B. Moura; M.A. Freitas; F. Escarlate-Tavares, Org.). Instituto Chico Mendes de Conservação da Biodiversidade, ICMBio, Brasília.

Aho, J.M. 1990. Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and processes. In: Parasite Communities: Patterns and Processes (G.W. Esch, A.O. Bush, J.M. Aho, eds.). New York, Chapman & Hall.

Alcântara, E.P., Ferreira-Silva, C., Silva, L.A.F., Lins, A.G.S., Ávila, R.W., Morais, D.H. & Silva, R.J. 2018. Helminths of *Dermatonotus muelleri* (Anura: Microhylidae) from Northeastern Brazil. **Journal of Parasitology** 104: 550-556.

Amato, J.F.R., Boeger, W.A. & Amato, S.B. 1991. Protocolos para Laboratório–Coleta e Processamento de Parasitos de Pescado. Seropédica, Imprensa Universitária, Universidade Federal do Rio de Janeiro, 81 pp.

Amorim, D.M., Oliveira, R.H., Dyna, C.S., Sousa, D.M., Santos, M.E.P., Lima, L.S., Pinto, L.C. & Ávila, R.W. 2019. Nematodes Parasites of *Rhinella jimi* (Stevaux, 2002) (Anura: bufonidae) in areas of Caatinga, Northeastern Brazil. **Neotropical Helminthology** 13: 265-271.

Anderson, R.C. 2000. Nematode parasites of vertebrates, their development and transmission, 2nd ed. Wallingford, Oxon, CABI Publishing, 650 pp.

Araújo-Filho, J.A., Brito, S.V., Almeida, W.O., Morais, D.H., & Ávila, R.W. 2015. A new species of *Parapharyngodon* (Nematoda: Pharyngodonidae) infecting *Dermatonotus muelleri* (Anura: Microhylidae) from Caatinga, Northeastern Brazil. **Zootaxa** 4012: 386-390.

Ávila, R.W., Anjos, L.A., Ribeiro, S.C., Morais, D.H., Silva, R.J. & Almeida, W.O. 2012. Nematodes of Lizards (Reptilia: Squamata) from Caatinga Biome, Northeastern Brazil. **Comparative Parasitology** 79: 56-63.

Bittencourt, E.B. & Rocha, C.F.D. 2003. Hostectoparasite Specificity in a Small Mammal Community in an Area of Atlantic Rain Forest (Ilha Grande, State of Rio de Janeiro), Southeastern Brazil. **Memórias do Instituto Oswaldo Cruz** 98: 793-798.

Boquimpani-Freitas, I.D., Vrcibradic, D., Vicente, J.J., Bursey, C.R., Rocha, C.F.D. & Sluys, M.V. 2001. Helminths of the horned leaf frog, *Procetatophrys appendiculata*, from southeastern Brazil. **Journal of Helminthology** 75: 233-236.

Brito, S.V., Ferreira, F.S., Ribeiro, S.C., Anjos, L.A., Almeida, W.O., Mesquita, D.O. & Vasconcellos, A. 2014. Spatialtemporal variation of parasites in *Cnemidophorus ocellifer* (Teiidae) and *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Tropiduridae) from Caatinga áreas in northeastern Brazil. **Parasitology Research** 113: 1163-1169.

Bursey, C.R. & Goldberg, S.R. 2015. Description of a new species of *Parapharyngodon* (Nematoda: Pharyngodonidae) from Mexico with a list of current species and key to species from the Panamanian region. **Journal of Parasitology** 101: 374-381.

Bush, A.O., Lafferty, K.D., Lotz, J.M. & Shostak, A.W. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. **Journal of Parasitology** 83: 575-583.

Camardelli, M. & Napoli, M. 2012. Amphibian conservation in the Caatinga Biome and semiarid region of Brazil. **Herpetologica** 68: 31-47.

Campião, K.M, Ribas, A.C.A., Morais, D.H, Dias, O.T, Silva, R.J. & Tavares, L.E.R. 2015. How Many Parasites Species a Frog Might Have? Determinants of Parasite Diversity in South American Anurans. **PloSone** 10: e0140577.

Campião, K.M., da Silva, I.C., Dalazen, G.T., Paiva, F. & Tavares, L.E. 2016a. Helminth parasites of 11 anuran species from the Pantanal Wetland, Brazil. **Comparative parasitology** 83: 92-100.

Campião, K.M., Dias, O.T., Silva, R.J., Ferreira, V.L. & Tavares, L.E.R. 2016b. Living apart and having similar trouble: are frog helminth parasites determined by the host or by the habitat? **Canadian Journal of Zoology** 94: 761-765.

Campião, K.M., Morais, D.H, Dias, O.T., Aguiar, A., Toledo, G., Tavares, L.E.R. & Da Silva, R.J. 2014. Checklist of Helminth parasites of Amphibians from South America. **Zootaxa** 3843: 1-93.

Cassiano-Lima, D., Ávila, R.W., Castro, D.P., Roberto, I.J., Borges-Nojosa, D.M. 2021. Lista de Anfíbios do Ceará. Fortaleza: Secretaria do Meio Ambiente do Ceará. Disponível em: https://www.sema.ce.gov.br/fauna-do-ceara/anfibios/. (Acessado em 24/novembro/ 2021).

Cassiano-Lima, D., Borges-Nojosa, D.M., Cascon, P. & Cechin, S.Z. 2011. The reproductive mode of *Adelophryne maranguapensis* Hoogmoed, Borges & Cascon, 1994 (Anura, Eleutherodactylidae) an endemic and threatened species from the remnants in northern Brazil. **North-Western Journal of Zoology** 7: 92-97.

Cassiano-Lima, D., Borges-Nojosa, D.M. & Cechin, S.Z. 2014. The advertisement call of *Adelophryne maranguapensis* (Anura, Eleutherodactylidae). ***Zootaxa*** 3835: 299-300.

Cassiano-Lima, D., Lima, A.V., Fortunato, M.E., de Sousa, T.A., de Castro, D.P., Borges-Nojosa, D.M. & Cechin, S.Z. 2020. Reproductive biology of direct developing and threatened frog *Adelophryne maranguapensis* (Anura, Eleutherodactylidae) reveals a cryptic reproductive mode for anurans and the first record of parental care for the genus. **Journal of Natural History** 54: 1721-1733.

Duellman, W.E. & Trueb, L. 1986. Biology of Amphibians. McGraw Hill, New York.

Frost, D.R. 2021. Amphibian Species of the World: an Online Reference. Version 6.1. Electronic Database. Accessible at: https://amphibiansoftheworld.amnh.org/index.php. Last access: 12 April 2021. American Museum of Natural History, New York, USA.

Gibbons, L. 2010. Keys to the Nematode Parasites of Vertebrates. Supplementary Volume. CABI International, Wallingford.

George-Nascimento, M., Muñoz, G., Marquet, P.A. & Poulin, R. 2004. Testing the energetic equivalence rule with helminth endoparasites of vertebrates. **Ecology Letters** 7: 527-531.

Goldberg, S.R. & Bursey, C.R. 2007. Helminths of two species of frogs. *Lithobates taylori* and *Lithobates vaillanti* (Ranidae), from Costa Rica. **Caribbean Journal of Science** 43: 65-72.

González, C.E. & Hamann, M.I. 2010. First report of nematode parasites of *Physalaemus santafecinus* (Anura: leiuperidae) from corrientes, Argentina. **Revista Mexicana de Biodiversidad** 81: 677-687.

González, C.E. & Hamann, M.I. 2013. First record of *Brevimulticaecum* larvae (Nematoda, Heterocheilidae) in amphibians from northern Argentina. **Brazilian Journal of Biology** 73: 451-452.

Guillén-Hernández, S., Salgado-Maldonado, G. & Lamothe-Argumedo, R. 2000. Digeneans (Plathelminthes: Trematoda) of seven sympatric species of anurans from Los Tuxtlas, Veracruz, Mexico. **Studies on Neotropical Fauna and Environment** 35:10-13.

Hoogmoed, M.S., Borges D.M. & Cascon P. 1994. Three new species of the genus *Adelophryne* (Amphibia: Anura: Leptodactylidae) from northeastern Brazil, with remarks on the other species of the genus. **Zoologische Mededelingen Leiden** 68: 271-300.

Hudson, P. 2005. Parasites, diversity, and the ecosystem. In: Parasitism and Ecosystems (F. Thomas, T.F. Reanud, J.F. Guegan, eds.). Oxford University Press, New York.

IUCN. 2020. The IUCN Red List of Threatened Species. Version 2020-1. Available in: https://www.iucnredlist.org (last access on: 14/04/2021).

Johnston, T.H. & Mawson, P.M. 1941. Some nematodes from Kangaroo Island, South Australia. **Records of the South Australian Museum** 7: 145-148.

Klaion, T., Gomes, M.A., Tavares, L.E.R., Rocha, C.F.D. & Sluys, M.V. 2011. Diet and nematode infection in *Proceratoprhys boiei* (Anura: Cycloramphidae) from two Atlantic Rainforest remnants in southeastern Brazil. **Anais da Academia Brasileira de Ciências** 83: 1303-1312.

Koprivnikar, J., Marcogliese, D.J., Rohr, J.R., Orlofske, S.A., Raffel, T.R. & Johnson, P.T.J. 2012. Macroparasite infections of amphibians: what can they tell us?. **EcoHealth** 9: 342-360.

Lima, A.V., Reis, A.H., Amado, N.G., Cassiano-Lima, D., Borges-Nojosa, D.M., Oriá, R.B. & Abreu, J.G. 2016. Developmental aspects of the direct-developing frog *Adelophryne maranguapensis*. ***genesis*** 54: 257-271.

Lins, A.G.S., Aguiar, A., Morais, D.H., Silva, L.A.F., Ávila, R.W. & Silva, R.J. 2017. Helmintofauna de *Leptodactylus syphax* (Anura: Leptodactylidae) do bioma da Caatinga, Nordeste do Brasil. Braz. **The journal Veterinary Parasitology** 26: 74-80.

Luque, J.L., Martins, A.N. & Tavares, L.E.R. 2005. Community structure of metazoan parasites of the yellow Cururu toad, *Bufo ictericus* (Anura, Bufonidae) from Rio de Janeiro, Brazil. **Acta Parasitologica** 50: 215-220.

Mascarenhas, W., Oliveira, C.R., Benício, R.A., Ávila, R.W. & Ribeiro, S.C. 2021. Nematodes of *Proceratophrys ararype* (Anura: Odontophrynidae), an endemic frog from the Araripe Plateau, Northeastern Brazil. **Biota Neotropica** 21: e20201164. https://doi.org/10.1590/1676-0611-BN-2020-1164).

Marcogliese, D.J. 2004. Parasites: small players with crucial roles in the ecological theatre. **Ecohealth** 1: 151-164.

Martínez-Coronel, M. & Pérez-Gutiérrez, M. 2011. Composición de la dieta de *Craugastor lineatus* (Anura: Craugastoridae) de Chiapas, México. **Acta Zoológica Mexicana** 27: 215-230.

Matias, C.S.L., Ferreira-Silva, C., Sousa, J.G.G. & Ávila, R.W. 2018. Helminths infecting the black false boa *Pseudoboa nigra* (Squamata Dipsadidae) in northeastern Brazil. **Acta Herpetologica** 13: 171-175.

Moravec, F. & Kaiser, H., 1994. *Brevimulticaecum* sp. larvae (Nematoda: Anisakidae) from the frog *Hyla minuta* Peters in Trinidad. **Journal of Parasitology** 80: 154-156.

Oliveira, C.R., Ávila, R.W. & Morais, D.H. 2019. Helminths Associated with Three *Physalaemus* Species (Anura: Leptodactylidae) from Caatinga Biome, Brazil. **Acta Parasitologica** 64: 205-212.

Oliveira, C.R., Mascarenhas, W., Batista-Oliveira, D., de Castro Araújo, K., Ávila, R.W. & Borges-Nojosa, D.M. 2022. Endoparasite community of anurans from an altitudinal rainforest enclave in a Brazilian semiarid area. **Journal of Helminthology** 96: e62.

Pereira, B.P., Sousa, B.M. & Lima, S.S. 2011. A new species of Pharyngodonidae (Nematoda) of *Tropidurus torquatus* (Squamata: Tropiduridae) from Brazil. **The Journal of Parasitology** 97: 311-317.

Pereira, F.B., Alves, P.V., Rocha, B.M., Souza Lima, S. & Luque, J.L. 2012. A new *Physaloptera* (Nematoda: Physalopteridae) parasite of *Tupinambis merianae* (Squamata: Teiidae) from south eastern Brazil. **Journal of Parasitology** 98: 1227-1235.

Pinhão, R., Wunderlich, A., Anjos, L.A. & da Silva, R.J. 2009. Helminths of toad *Rhinella icterica* (bufonidae), from the municipality of Botucatu, São Paulo State, Brazil. **Neotropical Helminthology** 3: 35-40.

Ramallo, G., Bursey, C.R. & Goldberg, S.R. 2002. *Parapharyngodon riojensis* n. sp. (Nematoda: Pharyngodonidae) from the lizard *Phymaturus punae* (Squamata: Iguania: Liolaemidae) from Northwestern Argentina. **Journal of Parasitology** 88: 979-982.

Ramírez-Bautista, A., Balderas-Valdivia, C. & Vitt, L.J. 2000. Reproductive ecology of the whiptail lizard *Cnemidophorus lineatissimus* (Squamata: Teiidae) in a tropical dry forest. **Copeia** 2000: 712-722.

Reyda, F.B. 2008. Intestinal helminthsof freshwater stingrays in Southeastern Peru, and a new genus and two new species of cestode. **Journal of Parasitology** 94: 684-699.

Sampaio, N.K.S, Silva, E.G., Pinto, C.L.M., Duarte, R.G., Teixeira, A.A.M., Almeida, W.O. & Brito, S.V. 2020. *Proceratophrys aridus* Endoparasites; **Herpetology Review** 51: 302.

Sena P.A., Conceição B.M., Silva P.F., Silva W.G., Ferreira W.B., Júnior V.A.S. & Oliveira J.B. 2018. Helminth communities of *Pithecopus nordestinus* (Anura: Phyllomedusidae) in forest remnants, Brazil. **Herpetology Notes** 11: 565-572.

Silva, C.S., Alcântara, E.P., Silva, R.J., Ávila, R.W. & Morais, D.H. 2019. Helminths parasites of the frog *Proceratophrys aridus* Cruz, Nunes, and Juncá, 2012 (Anura: Odontophrynidae) in a semiarid region, Brazil. **Neotropical Helminthology** 13: 169-179.

Silva-Neta, A.D., de Alcântara, E.P., de Oliveira, C.R., de Carvalhoł, E.F.F., Morais, D.H., da Silva, R.J. & Ávila, R.W. 2020. Helminths associated with 15 species of anurans from the Ibiapaba Plateau, northeastern Brazil. **Neotropical Helminthology** 14: 207-216.

Silvano, D.L. & Segalla, M.V. 2005. Conservation of Brazilian amphibians. **Conservation Biology** 19: 653-658.

Souza, M.J.N. 2002. Zoneamento ambiental e plano de gestão da APA da Serra de Maranguape-CE. Fortaleza: SEMACE.

Tabarelli, M., Pinto, L.P., Silva, J.M.C., Hirota, M.M. & Bedê, L.C. 2005. Desafios e oportunidades para a conservação da biodiversidade na Mata Atlântica brasileira. **Megadiversidade** 1: 132-138.

Teles, D.A., Brito, S.V., Araújo-Filho, J.A., Teixeira, A.A.M., Ribeiro, S.C., Mesquita, D.O. & Almeida, W.O. 2017. Nematode parasites of *Proceratophrys aridus* (Anura: Odontophrynidae), an endemic frog of the Caatinga domain of the Neotropical region in Brazil. **Herpetology Notes** 10: 525-527.

Velarde-Aguilar, M.G., Mata-López, R., Guillén-Hernández, S. & León-Règagnon V. 2015. *Parapharyngodon* n. spp. (Nematoda: Pharyngodonidae) parasites of hylid frogs from Mexico and review of species included in the genus. **Journal of Parasitology** 101: 212-230.

Vicente, J.J., Rodrigues, H.O., Gomes, D.C. & Pinto, R.M. 1991. Nematóides do Brasil, 2º parte: Nematóides de anfíbios. **Revista Brasileira de Zoologia** 7: 549-626.

Vieira, K.R.I., Vicentin, W., Paiva, F., Pozo, C.F., Borges, F.A., Adriano, E.A., Costa, F.E.S. & Tavares, L.E.R. 2010. *Brevimulticaecum* sp. (Nematoda: Heterocheilidae) larvae parasitic in freshwater fish in the Pantanal wetland, Brazil. **Veterinary Parasitology** 172: 350-354.

Vieira, W.L.S., Bezerra, D.M.M., Vieira, K.S., Gomes, G., Santana, P.F.G.P.M. & Alves, R.R.N. 2015. *Megascops choliba* (Strigiformes: Strigidae) predation on *Scinax x-signatus* (Anura: Hylidae) in the semiarid, Northeastern Brazil. **Herpetology Notes** 8: 275-276.

Vitt, L.J. & Caldwell, J.P. 2009. Herpetology, an Introductory Biology of Amphibians and Reptiles. Elsevier, Amsterdam.

Wallace, K.M. & Leslie, A.J. 2008. Diet of the Nile crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana. **Journal of Herpetology** 42: 361-368.

Werneck, F.P., Colli, G.R. & Vitt, L.J. 2009. Determinants of assemblage structure in Neotropical dry forest lizards. **Austral Ecology** 34: 97-115.

5 CONSIDERAÇÕES FINAIS

Os resultados obtidos neste trabalho corroboraram que os anfíbios são bons modelos para estudos com parasitos, devido ao seu modo de vida e comportamento. Também mostraram que os anfíbios da Montanha de Maranguape apresentam grande riqueza e prevalência na composição de espécies parasitos, e seguem o padrão comum descrito para os anfíbios neotropicais. Além disso, ainda permitiram o registo dos primeiros dados parasitológicos para seis espécies de anuros, 20 novos registos de hospedeiros e a indicação de duas possíveis novas espécies de parasitas, salientando a importância de inventários parasitológicos para espécies hospedeiras em regiões sub estudadas.

Não observamos indícios da influência dos gradientes ambientais na relação parasito-hospedeiro, possivelmente por serem endoparasitas, protegidos por seus hospedeiros. Quanto à relação entre riqueza e tamanho do hospedeiro, o fator tamanho só foi preditivo se existisse uma grande variação em relação ao tamanho médio. Ainda ressaltamos que a filogenia foi pouco relevante para a maioria das espécies parasitas, sendo a forma como o hospedeiro explora o ambiente o fator determinante na riqueza e abundância parasitária. Assim a composição endoparasitária tem uma relação significativa com o tipo de habitat utilizado pelo hospedeiro. Isto ocorre devido ao ciclo de vida direto da maioria dos parasitos e por serem generalistas na escolha de seus hospedeiros. Dessa forma, concluímos que os parasitos se distribuem seguindo a dispersão de seus hospedeiros, e uma vez instalados no ambiente, se dispersam para a maioria das espécies de anuros, independente dos fatores ambientais.

Quanto a composição parasitária de *Adelophryne maranguapensis*, espécie endêmica e em perigo de extinção, consideramos que a mesma seguiu o padrão comum em espécies neotropicais, com predominância de nematódeos. E a baixa prevalência de parasitas indica que *A. maranguapensis* apresenta uma relação estável com o parasitismo sem efeitos populacionais negativos e uma boa saúde imunológica. Já a relação negativa entre o parasitismo e o tamanho do corpo e a similaridade entre os sexos, considerando o ciclo de vida dos parasitos, indica que a espécie compartilha o mesmo nicho ao longo do tempo e apresenta uma sobreposição na utilização do habitat.

Por fim concluímos, com as observações morfológicas dos anuros coletados que não apresentaram indícios de perda de peso, redução de tamanho ou qualquer outra característica anormal ao padrão conhecido para as espécies em estudo, que a relação Parasito-Hospedeiro dos anuros da montanha de Maranguape, apesar dos efeitos antrópicos ao longo dos anos, se mantem estável sem efeitos negativos às populações de anuros. Dessa forma, a relação parasitaria não parece ser uma ameça a conservação das espécies locais, principalmente para aquelas criticamente ameaçadas.

REFERÊNCIAS

AGUIAR, A.; TOLEDO, G.M.; ANJOS, L.A.; SILVA, R.J. Helminth parasite communities of two *Physalaemus cuvieri* Fitzinger, 1826 (Anura: Leiuperidae) populations under different conditions of habitat integrity in the Atlantic Rain Forest of Brazil. **Brazilian Journal of Biology**, vol. 75, n. 4, p. 963–968, 2015.

AHO, J.M. Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and processes. *In*: ESCH, G.W., BUSH, A.O., AHO, J.M. (Eds.). **Parasite Communities: Patterns and Processes.** Dordrecht, Springer Netherlands, pp. 157–195, 1990.

ALBUQUERQUE, U.P.; DE LIMA ARAÚJO, E.; EL-DEIR, A.C.A.; DE LIMA, A.L.A.; SOUTO, A.; BEZERRA, B.M.; … SEVERI, W. Caatinga Revisited: Ecology and Conservation of an Important Seasonal Dry Forest. **The Scientific World Journal**, vol. 2012, no. 205182, 2012.

ALCANTARA, E.P.; FERREIRA-SILVA, C.; SILVA, L.A.F.; LINS, A.G.S., ÁVILA, R.W.; MORAIS, D.H.; DA SILVA, R.J. Helminths of *Dermatonotus muelleri* (Anura:Microhylidae) from Northeastern Brazil. **Journal of Parasitology**, vol. 104, n. 5, pp. 550–557, 2018.

ALFARO, B.J.; CHYTRÝ, M.; MUCINA, L.; GRACE, J.B.; REJMÁNEK, M. Disentangling vegetation diversity from climate-energy and habitat heterogeneity for explaining animal geographic patterns. **Ecology and Evolution**, vol. 6, n. 5, pp. 1515–1526, 2016.

ALMEIDA-NETO, M.; MACHADO, G.; PINTO-DA-ROCHA, R.; GIARETTA, A.A. Harvestman (Arachnida: Opiliones) species distribution along three Neotropical elevational gradients: an alternative rescue effect to explain Rapoport's rule? **Journal of Biogeography**, vol. 33, pp. 361–375, 2006.

AZEVEDO, R.R.; KRUGER, R.F. The influence of temperature and humidity on abundance and richness of Calliphoridae (Diptera). **Iheringia, Série Zoologia**, Porto Alegre, vol. 103, n. 2, pp. 145–152, 2013.

BEGON, M. Part 1: Single-Species Populations. *In*: BEGON, M., MORTIMER, M., & THOMPSON, D. J. (Eds.) **Population ecology: a unified study of plants and animals. -** 3rd ed. cap. 5. p. 117, 1996.

BILIA, C.G.; PINHA, G.D.; PETSCH, D.K.; TAKEDA, A.M. Influência da heterogeneidade ambiental sobre os atributos da comunidade de Chironomidae em lagoas de inundação neotropicais. **Iheringia, Série Zoologia**, Porto Alegre, vol. 105, n. 1, pp. 20–27, 2015.

BORGES, D.M. **Herpetofauna do Maciço de Baturité, estado do Ceará: composição, ecologia e considerações zoogeógraficas.** Dissertação (Mestrado em Ciências Biológicas – Zoologia), Departamento de Sistemática e Ecologia–Universidade Federal da Paraíba, Joao Pessoa, Brasil, 1991.

BORGES-NOJOSA, D.M. Diversidade de anfíbios e répteis na serra de Baturité, Ceará. *In*: OLIVEIRA T.S.; ARAÚJO, F.S. (Eds.) **Diversidade e Conservação da Biota da Serra de Baturité, Ceará.** Fortaleza: Edições UFC/COELCE, p. 225–247, 2007.

BORGES-NOJOSA, D.M.; CARAMASCHI, U. Composição e análise comparativa da diversidade e das afinidades biogeográficas dos lagartos e anfisbenídeos (Squamata) dos brejos nordestinos. *In*: LEAL, I.; SILVA, J.M.C.; TABARELLE, M. (Org.) **Ecologia e conservação da Caatinga**. 1a ed. Recife: UFPE, p. 489-540, 2003.

BORGES-NOJOSA, D.M.; CARAMASCHI, U.; RODRIGUES, M.T. A new species of lizard *Placosoma* Tschudi, 1847 (Squamata: Gymnophthalmidae) from the relictual forest mountains of the State of Ceará, Brazil. **Zootaxa**, vol. 4169, n. 1, pp. 160–170, 2016a.

BORGES-NOJOSA, D.M.; LIMA, D.C.; BEZERRA, C.H.; HARRIS, D.J. Two new species of *Apostolepis* Cope, 1862 (Serpentes: Elapomorphini) from brejos de altitude in northeastern Brazil. **Revista Nordestina de Zoologia**, vol. 10, n. 2, pp. 74–94, 2016b.

BRANDÃO, G.M.T. **Biodiversidade de helmintos parasitas de anuros procedentes de diferentes fitofisionomias no Peru.** Tese de doutorado apresentada ao programa de pós-graduação em Ciências Biológicas (Zoologia) do Instituto de Biociências da Universidade Estadual Paulista-UNESP, Campus Botucatu-SP, 2017.

CAMPIÃO, K.M.; MORAIS, D.H; DIAS, O.T.; AGUIAR, A.; TOLEDO, G.; TAVARES, L.E.R.; DA SILVA, R.J. Checklist of Helminth parasites of Amphibians from South America. **Zootaxa**, vol. 3843, n. 1, pp. 1–93, 2014.

CAMPIÃO, K.M.; RIBAS, A.; TAVARES, L.E.R. Diversity and patterns of interaction of an anuran-parasite network in a neotropical wetland. **Parasitology**, vol. 142, pp. 1751–1757, 2015b.

CAMPIÃO, K.M.; RIBAS, A.C.A.; CORNELL, S.J.; BEGON, M.; TAVARES, L.E.R. Estimates of coextinction risk: how anuran parasites respond to the extinction of their *hosts*?. **International Journal for Parasitology**, vol. 45, n. 14, pp. 885–889, 2015c.

CAMPIÃO, K.M.; RIBAS, A.C.A.; MORAIS, D.H; DIAS, O.T; SILVA, R.J.; TAVARES, L.E.R. How Many Parasites Species a Frog Might Have? Determinants of Parasite Diversity in South American Anurans. **Plos One**, vol. 10, n. 10, Artigo ID. e0140577, 2015a.

CASTRO, D.P.; RODRIGUES, J.F.M.; BORGES-LEITE, M.J.; LIMA, D.C.; BORGES-NOJOSA, D.M. Anuran diversity indicates that Caatinga relictual Neotropical forests are more related to the Atlantic Forest than to the Amazon. **PeerJ**, vol. 6, Artigo ID. e6208, 2019.

COLWELL, R.K.; LEES, D.C. The mid-domain effect: geometric constraints on the geography of species richness. **Trends in ecology & evolution**, vol. 15, n. 2, pp. 70–76, 2000.

DOBSON, A.; LAFFERTY, K.D.; KURIS, A.M.; HECHINGER, R.F.; JETZ, W. Homage to Linnaeus: How many parasites? How many hosts?. **Proceedings of the National Academy of Sciences**, vol. 105, n. 1, pp. 11482–11489, 2008.

DUELLMAN, W.E.; TRUEB, L. **Biology of Amphibians**. Baltimore, The Johns Hopkins University Press, 670p, 1994.

FERREIRA, R.M.A. **Influência de variáveis meteorológicas na riqueza, abundância e diversidade de espécies anofélicas em área rural do Município de Macapá, Amapá,**

Brasil. 109 f. Dissertação (Mestrado em Biodiversidade tropical) – Programa de Pós-graduação em Biodiversidade Tropical da Universidade Federal do Amapá, Macapá, 2010.

FLESCH, A.D.; SWANN, D.E.; TURNER, D.S.; POWELL, B.F. Herpetofauna of the Rincon Mountains, Arizona. **The Southwestern Naturalist**, vol. 55, pp. 240–253, 2010.

GALLI, P.; CROSA, G.; MARINIELLO, L.; ORTIS, M.; D'AMELIO, S. Water quality as a determinant of the composition of fish parasites communities. **Hydrobiologia**, vol. 452, pp. 173–179, 2001.

GONZÁLEZ-MEGIAS, A.; GÓMES, J.G.; SÁNCHEZ-PIÑERO, F. Diversity-habitat heterogeneity relationship at different spatial and temporal scales. **Ecography**, vol. 30, pp. 31–41, 2007.

HAMANN, M.I.; KEHR, A.I.; GONZÁLEZ, C.E. Helminth community structure of *Scinax nasicus* (Anura: Hylidae) from a South American subtropical area. **Diseases of aquatic organisms**, vol. 93, n. 1, pp. 71–82, 2010.

HERRERA, J.B. **Efeitos da heterogeneidade do ambiente, área e variáveis ambientais sobre anfíbios anuros em paisagem fragmentada de Floresta Atlântica**. 84 f. Dissertação (Mestrado em Ecologia e Biomonitoramento) – Instituto de Biologia da Universidade Federal da Bahia, Salvador, 2011.

HOOGMOED, M.S.; BORGES, D.M.; CASCON, P. Three new species of the genus *Adelophryne* (Amphibia: Anura: Leptodactylidae) from northeastern Brazil, with remarks on the other species of the genus. **Zoologische Mededelingen**, vol. 68, n. 24, pp. 271–300, 1994.

HU, J.; LI, C.; XIE, F.; JIANG, J. Endemic amphibians and their distribution in China. **Asian Herpetological Research,** vol. 3, pp. 163–171, 2012.

KURIS, A.M. Ecosystem energetic implications of parasite and free-living biomass in three estuaries. **Nature,** vol. 454, n. 7203, pp. 515–518, 2008.

LEMCKERT, F.; MAHONY, M.J. The relationship among multiple-scale habitat variables and pond use by anurans in northern New South Wales, Australia. **Herpetological Conservation Biology**, vol. 5, pp. 537–547, 2010.

LIMA, D.C. **A Bananicultura na Área de Proteção da Serra de Maranguape-CE e suas Implicações no Ambiente Físico, Humano e na Biodiversidade**. 109 f. Dissertação apresentada ao Mestrado em Desenvolvimento e Meio Ambiente (PRODEMA) - UFC, Fortaleza - CE, 2005.

LINS, A.G.S.; AGUIAR, A.; MORAIS, D.H.; DA SILVA, L.A.F.; ÁVILA, R.W.; SILVA, R.J. Helmintofauna de *Leptodactylus syphax* (Anura: Leptodactylidae) do bioma da Caatinga, Nordeste do Brasil. **Brazilian Journal of Veterinary Parasitology**, vol. 26, pp. 74–80, 2017.

M.M.A. **Avaliação e ações prioritárias para a conservação da biodiversidade da Mata Atlântica e Campos Sulinos**. Secretaria de Biodiversidade e Florestas (SBF), Ministério do Meio Ambiente (MMA). Brasilia, 2000.

MACARTHUR, R.H. Environmental Factors Affecting Bird Species Diversity. **The American Naturalist**, vol. 98, n. 903, pp. 387–389, 1964.

MACARTHUR, R.H.; MACARTHUR, J.W. On bird species diversity. **Ecology**, vol. 42, pp. 594–598, 1961.

MASCARENHAS, W.; OLIVEIRA, C.R.; BENÍCIO, R.A.; ÁVILA, R.W.; RIBEIRO, S.C. Nematodes of *Proceratophrys ararype* (Anura: Odontophrynidae), an endemic frog from the Araripe Plateau, northeastern Brazil. **Biota Neotropica**, vol. 21, Artigo ID. e20201164, 2021.

MORENO-RUEDA, G.; PIZARRO, M. The relative influence of climate, environmental heterogeneity, and human population on the distribution of vertebrate species richness in south-eastern Spain. **Acta oecologica**, vol. 32, pp. 50–58, 2007.

OLIVEIRA, C.R.; ÁVILA, R.W.; MORAIS, D.H. Helminths Associated with Three *Physalaemus* Species (Anura: Leptodactylidae) from Caatinga Biome, Brazil. **Acta Parasitológica**, vol. 64, n. 1, pp. 205–212, 2019.

PETSCH, D.K.; PINHA, G.D.; RAGONHA, F.H.; TAKEDA, A.M. Influência dos fatores ambientais sobre a distribuição da comunidade de invertebrados bentônicos em canais de uma planície de inundação neotropical. **Biotemas**, vol. 26, n. 3, pp. 127–138, 2013.

POULIN, R.; KRASNOV, B.R. **Similarity and variability of parasite assemblages across geographical space.** In: MORAND S, KRASNOV BR. (Eds.) The biogeography of host-parasite interactions. New York: Oxford University. pp. 115–128, 2010.

POULIN, R.; MORAND, S. **Parasite Biodiversity**, Smithsonian Institution Books, Washington, D.C., USA, 2004.

QIAN, H.; WANG, X.; WANG, S.; LI, Y. Environmental determinants of amphibian and reptile species richness in China. **Ecography**, vol. 30, pp. 471–482, 2007.

RAHBEK, C. The elevational gradient of species richness: a uniform pattern? **Ecography**, vol. 18, pp. 200–205, 1995.

RAHBEK, C. The role of spatial scale and the perception of large-scale species-richness patterns. **Ecology letters**, vol. 8, n. 2, pp. 224–239, 2005.

RIBEIRO, S. C.; ROBERTO, I. J.; SALES, D.L.; ÁVILA, R. W.; ALMEIDA, W. D. O. Amphibians and reptiles from the Araripe bioregion, northeastern Brazil. **Salamandra**, vol. 48, n. 3, pp. 133–146, 2012.

RODRIGUES, M.T.; SANTOS, E.M. A new genus and species of eyelid-less and limb reduced gymnophthalmid lizard from northeastern Brazil (Squamata, Gymnophthalmidae). **Zootaxa**, vol. 1873, pp. 50–60, 2008.

ROMDAL, T.S.; GRYTNES, J.A. An indirect area effect on elevational species richness patterns. **Ecography**, vol. 30, pp. 440–448, 2007.

SANTOS, V.G.T.; AMATO, S.B. Helminth fauna of *Rhinella fernandezae* (Anura: Bufonidae) from the Rio Grande do Sul coastland, Brazil: analysis of the parasite community. **Journal of Parasitology**, vol. 96, n. 4, pp. 823–826, 2010.

SEGALLA, M.V., BERNECK, B., CANEDO, C., CARAMASCHI, U., CRUZ, C. A. G., GARCIA, P. C. A., … & LANGONE, J.A. Brazilian Amphibians: List of Species. **Herpetologia Brasileira** vol. 10, pp. 121–216, 2021.

SILVA-NETA, A.F.; ALCANTARA, E.P.; OLIVEIRA, C.R.; CARVALHO, E.F.F.; MORAIS, D.H.; SILVA, R.J.; ÁVILA, R.W. Helminths associated with 15 species of anurans from the Ibiapaba Plateau, Northeastern Brazil. **Neotropical Helminthology**, vol. 14, pp. 197–206, 2020.

SILVA, R.J.D.; DINIZ, S.U.; VAZ-DE-MELLO, F.Z. Heterogeneidade do habitat, riqueza e estrutura da assembléia de besouros rola-bostas (Scarabaeidae: Scarabaeinae) em áreas de cerrado na Chapada dos Parecis, MT. **Neotropical Entomology**, vol. 39, n. 6, pp. 934–940, 2010.

SIQUEIRA, C.C.; ROCHA, C.F.D. Gradientes altitudinais: conceitos e implicações sobre a biologia, a distribuição e a conservação dos anfíbios anuros. **Oecologia Australis**, vol. 17, n. 2, pp. 92–112, 2013.

SOUSA, M.A.N.; LANGGUTH, A.; GIMENEZ, E.A. **Brejos de altitude em Pernambuco e Paraíba: História natural, ecologia e conservação**. Brasília: MMA, pp. 229–254, 2004.

TABARELLI, T.; SILVA, J.M.C. Áreas e ações prioritárias para a conservação da biodiversidade da caatinga. *In*: LEAL, I.R.; TABARELLI, M.; SILVA, J.M.C. (Orgs.). **Ecologia e conservação da caatinga**. Recife: UFPE, pp. 777–796, 2003.

TEWS, J.; BROSE, U.; GRIMM, V.; TIELBORGER, K.; WICHMANN, M.C.; SCHWAGER, M.; JELTSCH, F. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. **Journal of Biogeography**, vol. 31, pp. 79–92, 2004.

TOLEDO, G.M.; AGUIAR, A.; SILVA, R.J.; ANJOS, L.A. Helminth fauna of two species of *Physalaemus* (Anura: Leiuperidae) from an undisturbed fragment of the Atlantic Rainforest, Southeastern Brazil. **The Journal of parasitology**, vol. 99, n. 5, pp. 919–922, 2013.

VANZOLINI, P.E. A quasi-historical approach to the natural history of the differentiation of reptiles in tropical geographic isolates. **Papéis Avulsos de Zoologia**, vol. 34, n. 19, pp. 189–204, 1981.

WELLS, K.D. **The ecology and behavior of amphibians**. Chicago: The University of Chicago Press, 1400p, 2007.

WOOD, C.L.; JOHNSON, P.T.J. A world without parasites: exploring the hidden ecology of infection. **Frontiers in Ecology and the Environment**, vol. 13, pp. 425–434, 2015.