



**UNIVERSIDADE FEDERAL DO OESTE DO PARÁ
INSTITUTO DE CIÊNCIAS E TECNOLOGIA DAS ÁGUAS
PROGRAMA DE PÓS-GRADUAÇÃO EM
BIODIVERSIDADE**

PEDRO HENRIQUE SALOMÃO GANANÇA

**A HETEROGENEIDADE DE MACRÓFITAS AQUÁTICAS COMO PREDITOR
DA ESTRUTURA ESPACIAL DAS ASSEMBLÉIAS DE SAPOS EM UM LAGO
AMAZÔNICO**

SANTARÉM - PA

2020

PEDRO HENRIQUE SALOMÃO GANANÇA

**A HETEROGENEIDADE DE MACRÓFITAS AQUÁTICAS COMO PREDITOR
DA ESTRUTURA ESPACIAL DAS ASSEMBLÉIAS DE SAPOS EM UM LAGO
AMAZÔNICO**

Dissertação de mestrado apresentada ao Programa de Pós-Graduação em Biodiversidade, da Universidade Federal do Oeste do Pará, como parte dos requisitos para a obtenção do título de mestre.

Orientador: Alfredo Pedroso dos Santos Júnior

Co-orientador: Ricardo Alexandre Kawashita Ribeiro

SANTARÉM - PA

2020

Dados Internacionais de Catalogação-na-Publicação (CIP)
Sistema Integrado de Bibliotecas – SIBI/UFOPA

- G195h Ganança, Pedro Henrique Salomão
A heterogeneidade de macrófitas aquáticas como preditor da estrutura espacial das assembléias de sapos em um lago amazônico./ Pedro Henrique Salomão Ganança. – Santarém, 2020.
72 p. : il.
Inclui bibliografias.
- Orientador: Alfredo Pedroso dos Santos Júnior
Coorientador: Ricardo Alexandre Kawashita Ribeiro
Dissertação (Mestrado) – Universidade Federal do Oeste do Pará, Pró-Reitoria de Pesquisa, Pós-Graduação e Inovação Tecnológica, Programa de Pós-Graduação em Biodiversidade.
1. Anfíbios. 2. Anuros. 3. Ecologia de comunidades. I. Santos Júnior, Alfredo Pedroso dos, *orient.* II. Ribeiro, Ricardo Alexandre Kawashita, *coorient.* III. Título.

CDD: 23 ed. 639.3789

Bibliotecária - Documentalista: Renata Ferreira – CRB/2 1440



Universidade Federal do Oeste do Pará
PROGRAMA DE PÓS GRADUAÇÃO EM BIODIVERSIDADE

ATA Nº 8

Em acordo com o Regimento do Programa de Pós Graduação em Biodiversidade da Universidade Federal do Oeste do Pará, a dissertação de mestrado é julgada por uma Banca Avaliadora não presencial, constituída por três avaliadores titulares, sendo um deles obrigatoriamente externo ao curso, com título de doutor ou equivalente (Artigo 57 do referido regimento), e dois suplentes. O acadêmico é considerado aprovado quando ao menos dois membros avaliadores emitirem pareceres Aprovado ou Aprovado com Correções. Alternativamente, o acadêmico que comprovar o aceite ou a publicação de pelo menos um artigo resultante da sua dissertação, como primeiro autor, em co-autoria com orientador (ou orientador e co-orientador quando for o caso) em periódico avaliado pela CAPES, no sistema Periódico Qualis, nível A2 ou superior na área de biodiversidade, será dispensado da avaliação da dissertação, cabendo ao discente apenas a apresentação pública do trabalho (Artigo 59). O acadêmico que tiver sua dissertação aprovada deverá apresentá-la em sessão pública com duração entre 40 e 50 minutos, no prazo máximo de vínculo com o curso, ou seja, 24 meses desde o ingresso, a que se refere essa ata, de acordo com o Artigo 65 do Regimento do PPGBEES.

Assim, aos 3 (três) dias do mês de fevereiro do ano de 2020 (dois mil e vinte), às 15h00min, na sala 304 do Bloco Modular Tapajós, instalou-se a apresentação de seminário público da dissertação de mestrado do aluno PEDRO HENRIQUE SALOMÃO GANANÇA. Deu-se início a abertura dos trabalhos, onde o Professor Dr ALFREDO PEDROSO DOS SANTOS JUNIOR, após esclarecer as normativas de tramitação da defesa e seminário público, de imediato solicitou ao candidato que iniciasse a apresentação da dissertação, intitulada A HETEROGENEIDADE DE BANCOS DE MACRÓFITAS AQUÁTICAS COMO PREDITOR DA ESTRUTURA ESPACIAL DA ASSEMBLEIA DE SAPOS EM LAGOS AMAZÔNICOS. Concluída a exposição, o orientador comunicou ao discente que a versão final da dissertação deverá ser entregue ao programa, no prazo de 30 dias; contendo as modificações sugeridas pela banca examinadora e constante nos formulários de avaliação da banca.

A banca examinadora foi composta pelos examinadores professores doutores listados abaixo. Os pareceres assinados seguem em sequência.

ALFREDO PEDROSO DOS SANTOS JUNIOR

Orientador

PEDRO HENRIQUE SALOMÃO GANANÇA

Discente

Ao Daniel, Gustavo, João e Marcelo

AGRADECIMENTOS

À minha família por todo apoio, confiança e amor. Agradeço em especial meu pai Marcelo Ganança pelos ensinamentos da vida, confiança e ajuda.

A meu orientador Alfredo pela confiança, ideia do projeto, dicas, sugestões valiosas e por fazer o ambiente de trabalho mais alegre e descontraído. Agradeço também meu co-orientador Ricardo Kawashita pela confiança, e pela ajuda no curso e no projeto.

Agradeço muito ao Rafael de Fraga (Rato), que foi imprescindível para elaboração do projeto, por toda ajuda dentro e fora da academia, motivação e por compartilhar seu conhecimento sobre ecologia e herpetologia, valeu camarada! À minha amiga Erika (Cachita), pela amizade, pelos campos na savana e pelas risadas de sempre.

Ao amigo Neto pela parceria durante o mestrado, pela ótima companhia durante os inúmeros campos e pelos momentos de descontração fora da academia.

A todos os que ajudaram nas coletas de campo, especialmente o guia Lalico (GPS humano) que nos guiou no lago do Maicá, pelo exemplo profissional, dedicação e ensinamentos. Não poderia deixar de agradecer os amigos do seu Lalico, pelo material doado que fez o campo mais barato e confortável. Sou muito grato aos amigos Daniel e Ivan, pelo esforço dedicado e pelos momentos únicos nas macrófitas. Agradeço aos demais colegas que me ajudaram, Deivid, Tati, Francesca, Vanessa, Cauê, Greyci, Zaira, Darlisson e Iago.

A todos os professores e colegas do PPGBEES e do Laboratório de ecologia e comportamento animal – LECAN. Onde tive a sorte de fazer amigos maravilhosos.

À Albertina Lima e Bill Magnusson pelas valiosíssimas dicas e sugestões sobre o projeto e por todas as pesquisas realizadas na Amazônia, especialmente em Alter do Chão. Agradeço aos professores Amanda Mortati e Diego Zacardi pela ajuda com o material que foi usado em campo e pelas dicas na metodologia.

Aos guerreiros da Brigada de Incêndio de Alter do Chão e a todos que lutam pela floresta em pé.

À Jessica Nickel por todo o carinho, amor e apoio nos momentos difíceis, Ich liebe dich.

À Capes pela concessão da bolsa de mestrado.

Amar é um ato de coragem.

RESUMO

Investigar os efeitos de gradientes ambientais na estrutura espacial de assembleias é relevante para entender os mecanismos e processos que afetam a biodiversidade. Os gradientes ambientais podem atuar como filtros ecológicos, limitando a ocorrência e a abundância de espécies, o que gera padrões não aleatórios de ocupação do habitat. A biodiversidade mediada pela filtragem ambiental emerge das relações entre gradientes ambientais e estimativas da diversidade α e β . Tais relações foram amplamente demonstradas em assembleias de sapos que ocupam florestas na Amazônia, mas raramente são avaliadas em ecossistemas não florestais, como bancos de macrófitas em lagos. Os bancos de macrófitas podem variar espacialmente em termos de largura, altura e composição das espécies em resposta aos parâmetros físico-químicos da água. Portanto, é razoável esperar assembleias de sapos espacialmente heterogêneas quanto à variação na estratificação vertical do habitat e no formato da planta. Neste estudo, amostramos 50 parcelas cobrindo 15 km² de bancos de macrófitas contínuos, para testar os efeitos da distância da margem do lago, profundidade da água, altura e composição das macrófitas (proporções de ocupação de morfotipos), pH, oxigênio dissolvido e temperatura na diversidade α de sapos e estimativas da diversidade β . Foram encontradas 16 espécies, cuja distribuição local não foi aleatória, mas caracterizada pela diversidade α afetada positivamente pela altura das macrófitas e diversidade β afetada pela altura e composição das macrófitas e profundidade da água. Nossos resultados sugerem a filtragem ambiental como um fator importante na estruturação de assembleias de sapos, mesmo em ecossistemas relativamente pequenos e regionalmente raros. Esses achados são altamente relevantes para a ecologia e conservação, pois sugerem que os bancos de macrófitas aquáticas devem ser considerados unidades biogeográficas distintas dos habitats adjacentes.

Palavras-chave: Anfíbios. Anuros. Ecologia de comunidades. Gradientes ambientais. Vegetação aquática

ABSTRACT

Investigating the effects of environmental gradients on assemblage spatial structure is relevant to understand mechanisms and processes affecting biodiversity. Environmental gradients may act as ecological filters limiting species occurrence and abundance, which generates non-random patterns of habitat occupancy. Environmental filtering-mediated biodiversity emerges from relationships between environmental gradients and estimates of α - and β - diversity. Such relationships have been widely demonstrated in frog assemblages occupying forests in Amazonia but are rarely assessed in non-forest ecosystems such as macrophyte banks in lakes. Macrophyte banks may vary spatially in terms of width, height, and species composition, in response to physicochemical parameters of water. Therefore, it is reasonable to expect spatially heterogeneous frog assemblages in response to variation in habitat vertical stratification and perch shape. In this study we sampled 50 plots covering 15 km² of continuous macrophyte banks to test the effects of distance from the lake bank, water depth, macrophyte height and composition (proportions of morphotype occupancy), pH, dissolved oxygen and temperature on frog α -diversity and β - diversity estimates. We found 16 species, for which local distribution was not random but characterized by α -diversity positively affected by macrophyte height, and β -diversity affected by macrophyte height and composition, and water depth. Our results suggest environmental filtering as a major factor structuring frog assemblages even in relatively small and regionally rare ecosystems. These findings are highly relevant to ecology and conservation because they suggest that aquatic macrophyte banks should be considered as distinct biogeographic units from adjacent habitats.

Keywords: Amphibians. Anurans. Aquatic vegetation. Community ecology. Environmental gradients

SUMÁRIO

INTRODUÇÃO GERAL	10
CAPÍTULO 1:	15
Frogs The heterogeneity of aquatic macrophyte banks as a predictor of the frog assemblage spatial structure along Amazonian lakes	16
Abstract	17
Introduction	18
Methods	21
Results	27
Discussion	32
REFERENCES	36
SUPPLEMENTARY MATERIAL.....	34
CAPÍTULO 2:	44
Frogs and Squamata reptiles occupying aquatic macrophytes in a várzea lake in the lower Amazon River, Brazil	45
Abstract	46
Resumo	47
Introduction	40
Methods	50
Results	53
Discussion	57
CONCLUSIONS	62
REFERENCES	63
APPENDIX	70

1. INTRODUÇÃO GERAL

Como a complexidade do ambiente afeta as espécies de sapos em macrófitas aquáticas?¹

Qual o problema da pesquisa?

Lagos da várzea amazônica sofrem inundações periódicas pela natural subida e descida dos rios. Durante as cheias muitas plantas aquáticas, denominadas macrófitas, cobrem extensas áreas da superfície da água. Essas plantas são importantes para muitos animais aquáticos e não aquáticos, desde invertebrados microscópicos até grandes vertebrados como peixes-boi ou a gigantesca cobra sucuri. Esses animais podem usar as macrófitas como fonte de alimento, refúgio contra predadores, local para reprodução, berçário para filhotes e mecanismo de dispersão. Entre os animais que ocupam as macrófitas destacam-se os sapos (conhecidos cientificamente como anuros), os quais estão presentes em grandes quantidades nas macrófitas de rios e lagos amazônicos, visto que a maioria das espécies precisam de água para depositar seus ovos e para o desenvolvimento dos girinos.

As assembleias de sapos (conjunto de espécies em um determinado local e tempo) são influenciadas por muitos fatores bióticos (como competição e predação entre espécies) e abióticos (como temperatura e propriedades físico-químicas da água). As características do ambiente podem determinar quais espécies podem ocorrer em determinado local, segundo suas limitações morfológicas, fisiológicas e pela competição com outras espécies. Embora macrófitas aquáticas sejam amplamente distribuídas ao longo dos lagos amazônicos, pouco se sabe sobre padrões de ocupação de macrófitas por anuros. Macrófitas podem ser bastante heterogêneas em relação a variáveis ambientais, e por isso efeitos de filtragem ambiental sobre populações e assembleias podem ser esperados mesmo em uma localidade relativamente pequena como a de um lago.

¹ Texto de comunicação científica formatado conforme as normas do “Canal Ciência - Portal de Divulgação Científica e Tecnológica”, do Instituto Brasileiro de Informação em Ciência e Tecnologia (Ibict)

Devido a características como pele permeável e estágio larval aquático na maioria das espécies, os sapos são frequentemente considerados como bioindicadores da qualidade ambiental. Pela mesma razão, os sapos são sensíveis à degradação ambiental e são considerados os mais vulneráveis entre os grupos de vertebrados. Os sapos são organismos-modelo para investigar os efeitos da heterogeneidade ambiental nas assembleias porque respondem a gradientes ambientais nas escalas continental, regional e local. Na Amazônia, diversos estudos têm demonstrado que assembleias de anuros podem ser estruturadas pela variação ambiental em diferentes escalas, mas a maioria desses estudos é baseada em amostragens de ambientes florestais, e estudos que abordam sapos em macrófitas são raros e essencialmente descritivos, sem testar como gradientes ambientais atuam sobre essas espécies.



Figura 1. Algumas espécies de sapos encontradas nas macrófitas.

Como a pesquisa foi realizada?

Alunos de mestrado, graduação e professores da Universidade Federal do Oeste do Pará – UFOPA, estudaram a assembleia de anuros associados a macrófitas em um lago de várzea Amazônica com o objetivo de testar a hipótese geral de que os gradientes de profundidade da água, altura e composição das macrófitas, distância do banco à margem, pH e oxigênio dissolvido na água e temperatura afetam as estimativas de diversidade de sapos. O estudo foi conduzido no Lago do Maicá, próximo ao perímetro urbano da cidade de Santarém, baixo Rio Amazonas. Recentemente tal lago começou a sofrer pressões no seu ambiente, pelo crescimento urbano da cidade de Santarém e principalmente pela construção de um porto de combustíveis de combustíveis.

Os sapos foram amostrados ao longo de 15 km² em bancos de macrófitas contínuos e em contato com a margem do lago. Para isso foram amostradas 50 parcelas, cada uma com 50 m de comprimento e 6 m de largura, paralelas à margem do lago e a 500

m de distância entre as parcelas adjacentes.

Registramos sapos usando busca ativa visual e acústica, com três observadores a bordo de uma canoa de oito metros de comprimento. Coletamos os dados durante março de 2019, entre as 18:30 h e as 00:00 h. Essa abordagem foi útil na amostragem de sapos em condições ótimas de detectabilidade já que é o período de chuva e cheia dos rios, época reprodutiva para muitas espécies de anuros amazônicos.

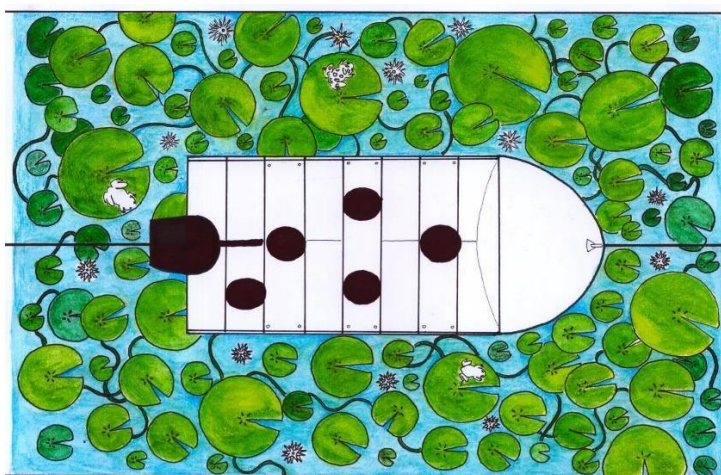


Figura 2. Representação da metodologia usada para a coleta de dados.

Qual a importância da pesquisa?

O presente estudo mostrou que a distribuição espacial de assembleias de sapos não é aleatória ao longo de um sistema de lagos Amazônicos, mas influenciada por gradientes ambientais onde macrófitas mais altas abrigam maior número de espécies de anuros. Também foi observado que ocorre substituição de espécies ao longo de gradientes de altura das macrófitas, composição das macrófitas e profundidade da água. Esses achados são relevantes para a conservação, porque mostram alta complementaridade biótica entre locais dentro de ecossistemas regionalmente raros e aparentemente homogêneos em macroescalas. Altos níveis de complementaridade biótica têm sido amplamente sugeridos como um critério eficiente para definir áreas de conservação prioritárias. Tais resultados são altamente relevantes para a ecologia e conservação, pois sugerem que os bancos de macrófitas aquáticas devem ser

considerados unidades biogeográficas distintas dos habitats adjacentes. Isso é particularmente crítico em nossa área de estudo, porque um porto para navios cargueiros está sendo construído e os estudos de impacto ambiental muitas vezes são deficientes e precários, e não levam em conta a complexidade ambiental local. Considerando a estrutura espacial local da assembléia de sapos determinada pela qualidade heterogênea do habitat, prevemos que o tráfego de navios causará a extinção local por migração ou malformação de girinos.

Autores

Pedro Henrique Salomão Ganança^{1,2*}; Rafael de Fraga^{2,3}, Ricardo Alexandre Kawashita⁴, Lourival Baía de Vasconcelos Neto^{1,2}; Ivan Alves dos Santos Junior⁵, Daniel de Sousa Guedes⁵ e Alfredo P. Santos-Jr^{1,2}

Filiações

¹ Programa de Pós-Graduação em Biodiversidade, Universidade Federal do Oeste do Pará, Santarém, PA, Brasil;

² Laboratório de Ecologia e Comportamento Animal, Universidade Federal do Oeste do Pará, Santarém, PA, Brasil

³ Programa de Pós-Graduação em Recursos Naturais da Amazônia, Universidade Federal do Oeste do Pará, Santarém, PA, Brasil.

⁴ Departamento de Ciências Biológicas, Instituto de Ciências Exatas e Experimentais, Universidade Federal de Mato Grosso, Rondonópolis, MT, Brasil.

⁵ Curso de Bacharelado em Biologia, Instituto de Ciências e Tecnologia das Águas, Universidade Federal do Oeste do Pará, Santarém, PA, Brasil.

* Autor para correspondência: psalogan@hotmail.com

Sugestão de leitura

Böning P, Wolf S, Upton K, Menin M, Venegas PJ, Lötters S. 2017. Amphibian diversity and its turnover in floating meadows along the Amazon river. *Salamandra*, 53: 379–388.

Upton K, Warren-Thomas E, Rogers I, Docherty E. 2014. Amphibian diversity on

floating meadows in flooded forests of the Peruvian Amazon. *Herpetological Review*, 45: 209–212.

Keddy PA. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*. 3,157-164.

Magnusson WE. et al. 2013. *Biodiversidade e Monitoramento Ambiental Integrado*. Ed. Áttema Editorial. Manaus, AM.

CAPÍTULO I

Pedro Henrique Salomão Ganança, Alfredo P. Santos-Jr, Ricardo A. Kawashita-Ribeiro, Lourival Baía de Vasconcelos Neto, Ivan Alves dos Santos Júnior, Daniel de Sousa Guedes, Rafael de Fraga. (2019). Frogs The heterogeneity of aquatic macrophyte banks as a predictor of the frog assemblage spatial structure along Amazonian lakes*.

* O artigo apresentado foi redigido conforme as diretrizes de submissão da revista *Austral ecology*, exceto pelas figuras inseridas no corpo do texto para facilitar a leitura. As normas indicadas para a redação de artigos pela revista estão disponíveis no link:

<https://onlinelibrary.wiley.com/page/journal/14429993/homepage/forauthors.htm>
|

The heterogeneity of aquatic macrophyte banks as a predictor of the frog assemblage spatial structure along an Amazonian lake

Pedro Henrique Salomão Ganança^{1, *}, Alfredo P. Santos-Jr¹, Ricardo A. Kawashita-Ribeiro^{1, 2}, Lourival Baía de Vasconcelos Neto¹, Ivan Alves dos Santos Júnior³, Daniel de Sousa Guedes³, Rafael de Fraga^{1, 4}

¹Laboratório de Ecologia e Comportamento Animal e Programa de Pós-graduação em Biodiversidade, Universidade Federal do Oeste do Pará, rua Vera Paz, s/n, Salé, 68040-255, Santarém, PA, Brazil; ²Departamento de Ciências Biológicas, Instituto de Ciências Exatas e Experimentais, Universidade Federal de Mato Grosso, Rodovia MT 270 Km 06, Parque Sagrada Família, 78735-901, Rondonópolis, MT, Brazil; ³Curso de Bacharelado em Biologia, Instituto de Ciências e Tecnologia das Águas, Universidade Federal do Oeste do Pará, rua Vera Paz, s/n, Salé, 68040-255 Santarém, PA, Brazil and ⁴Programa de Pós-graduação em Recursos Naturais da Amazônia, Universidade Federal do Oeste do Pará, Av. Mendonça Furtado, 2946, Fátima, 68040-050 Santarém, PA, Brazil;

*Correspondent author: psalogan@hotmail.com

The heterogeneity of aquatic macrophyte banks as a predictor of the frog assemblage spatial structure along an Amazonian lake

ABSTRACT

Investigating the effects of environmental gradients on assemblage spatial structure is relevant to understand mechanisms and processes affecting biodiversity. Environmental gradients may act as ecological filters limiting species occurrence and abundance, which generates non-random patterns of habitat occupancy. Environmental filtering-mediated biodiversity emerges from relationships between environmental gradients and estimates of α - and β -diversity. Such relationships have been widely demonstrated in frog assemblages occupying forests in Amazonia but are rarely assessed in non-forest ecosystems such as macrophyte banks in lakes. Macrophyte banks may vary spatially in terms of width, height, and species composition, in response to physicochemical parameters of water. Therefore, it is reasonable to expect spatially heterogeneous frog assemblages in response to variation in habitat vertical stratification and perch shape. In this study we sampled 50 plots covering 15 km² of continuous macrophyte banks to test the effects of distance from the lake bank, water depth, macrophyte height and composition (proportions of morphotype occupancy), pH, dissolved oxygen and temperature on frog α -diversity and β -diversity estimates. We found 16 species, for which local distribution was not random but characterized by α -diversity positively affected by macrophyte height, and β -diversity affected by macrophyte height and composition, and water depth. Our results suggest environmental filtering as a major factor structuring frog assemblages even in relatively small and regionally rare ecosystems. These

findings are highly relevant to ecology and conservation because they suggest that aquatic macrophyte banks should be considered as distinct biogeographic units from adjacent habitats.

Keywords: amphibians, Anura, aquatic vegetation, community ecology, environmental gradients

INTRODUCTION

Investigating the effects of environmental gradients on assemblage structure is relevant for understanding mechanisms and processes that affect biodiversity at multiple scales (Keddy 1992). At local scales, assemblages are expected to be composed of generalist species, which occupy relatively large portions of environmental gradients, and specialist species, which have locally restricted distribution by environmental filtering selecting phenotypes or causing competition (Kinupp & Magnusson 2005). Quantifying the local proportions of environmental gradients that are occupied by multiple species has wide application in ecology and conservation because it allows the identification of levels of biotic complementarity or redundancy among sites (Tuomisto *et al.* 2003).

Many studies in Amazonia have shown that assemblages may be spatially structured by environmental variation at different scales, but mostly based on forest sampling (e.g. Fraga 2011; Garda *et al.* 2012; Rojas-Ahumada *et al.* 2012; Dias-Terceiro *et al.* 2015). Amazonian lakes have been poorly systematically sampled, although they may contain relevant proportions of local biodiversity (Junk 1973; Parolin 2012). For instance, Amazonian lakes surrounded by

seasonally flooded forests may be rich in aquatic vegetation due to the high solar incidence and sediment-rich water and substrate (Junk 1997). Vegetation cover within lakes generates breeding, foraging, refuge, and offspring development sites for a wide variety of animals (Upton *et al.* 2014). Additionally, macrophyte banks may detach from the lake bank, carrying associated fauna when lakes are connected to rivers by seasonal rainfall, and consequently causing long-distance dispersal and gene flow, which may limit the condition of rivers as biogeographic barriers (Schiesari *et al.* 2003). Therefore, investigating local species distribution in macrophyte banks may be also relevant to understand species distribution at macroscales (e.g. Amazon Basin).

Aquatic macrophytes are important habitats for animals mainly because vegetation cover generates levels of vertical stratification that cause higher levels of environmental heterogeneity compared to vegetation-free lakes (Thomaz *et al.* 2008). While underwater roots and stems are refuge and foraging sites for fish (Sanchez-Botero & Araújo-Lima 2001; Schiesari *et al.* 2003), insects (Junk 1973) and tadpoles (Schiesari *et al.* 2003; Böning *et al.* 2017), above-water stems and leaves are perches for a wide variety of invertebrates (Junk 1973) and vertebrates (Höld 1977; Hoogmoed 1993; Upton *et al.* 2014) not strictly aquatic in at least some life stage. Therefore, aquatic macrophyte banks are ultimately interface ecosystems between terrestrial and aquatic habitats. However, macrophyte banks may contain enough structural heterogeneity for animal species to be locally filtered. For instance, the physicochemical properties of water and substrate may affect plant species or morphotype, which vary in height and shape along banks (Piedade *et al.* 2018). Additionally, the width of macrophyte banks and the water depth in which they are inserted are not spatially homogeneous,

but is expected to vary depending on topography, light intensity and microclimate. Once species distribution is often locally limited by habitat heterogeneity via ecological filtering (Moreno-Rueda & Pizarro 2007; Vasconcelos *et al.* 2009; Silva *et al.* 2011), distinct animal assemblages may be expected not only by comparing macrophyte banks and adjacent habitats, but also within macrophyte banks.

Macrophyte banks are regionally rare ecosystems in Amazonia (compared to forests), and potentially contain unique biodiversity at regional or local scales. Therefore, it is plausible to deduce that aquatic macrophytes contribute significantly to local biodiversity, even if they are arbitrarily considered as habitats independent of adjacent areas. This is particularly conspicuous in frogs, because assemblages occupying aquatic macrophytes are mainly composed of a few species adapted to open and floating habitats, which are rare conditions in adjacent forests (Ramalho *et al.* 2017). Frogs are model organisms for investigating the effects of environmental heterogeneity on assemblages because they respond to environmental gradients at continental (Duellman 1999), regional (Dias-Terceiro *et al.* 2015), and local scales (Menin *et al.* 2007; Dias-Terceiro *et al.* 2015; Jorge *et al.* 2016). Even relatively short environmental gradients associated with altitudinal variation of only 30 m may cause frog species turnover (Ribeiro-Jr. *et al.* 2012). Additionally, due to characteristics such as permeable skin and aquatic larval stage in most species (Duellman & Trueb 1994), frogs are often considered as bioindicators of environmental quality (Vitt *et al.* 1990). For the same reason, frogs may be so sensitive to environmental degradation that they are often considered to be the most vulnerable among vertebrate groups (Navas & Otani 2007). Despite levels of interspecific variation in response to habitat degradation may be expected,

habitat loss and disease introduction have ultimately been major sources of the global amphibian decline (Whittaker *et al.* 2013).

In this study we investigate the spatial structure of frog assemblages occupying aquatic macrophyte banks in a lake of the lower Amazon River. We test relationships between α and β -diversity estimates, and variables that represent the environmental heterogeneity along macrophyte banks. Specifically, we test the general hypothesis that gradients of water depth, macrophyte height and composition, bank distance, pH and dissolved oxygen in water, and temperature affect frog diversity estimates. This hypothesis is broadly based on the general assumptions of environmental filtering, which predict species tending to be filtered from suboptimal fractions of environmental gradients through physical inability to habitat occupation, physiological intolerance, interspecific competition, or a combination among factors (Keddy, 1992). The results presented here are particularly relevant for conservation because they are based on data collected in a region highly threatened by a controversial cargo-port construction.

METHODS

Study area

We sampled frogs in the Maicá Lake, located between latitudes 54°35'49"W and 54°16'93"W and longitudes 02°43'79"S and 02°26'44"S, in the municipality of Santarém, western Pará, Brazil (Figure 1). The study area covers 60 km² of an extensive floodplain lake formed at the confluence of the Amazonas, Ituqui and Paraná rivers. The Maicá Lake is formed by interconnected canals and lakes, which are strongly influenced by the seasonal flooding of the Amazonas

River that occurs from December to June (Ponte *et al.* 2019). Because water income is considerably reduced during the dry season, the Maicá Lake can dry out completely during this period (Pinheiro *et al.* 2016).

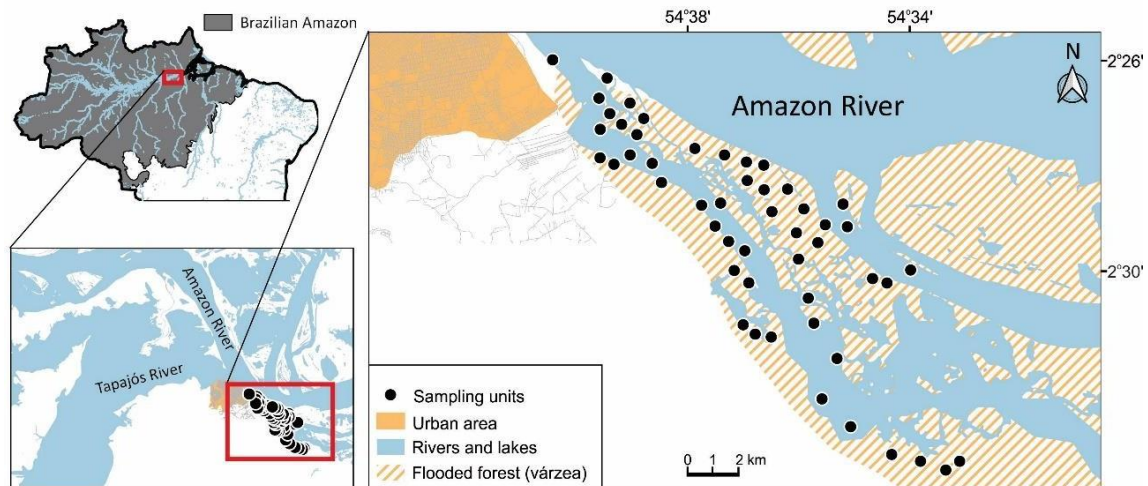


Figure 1. Study area in the Maicá Lake, lower Amazonas River, Brazil. Black circles are 50 x 6 m sampling units.

The climate of the study area is hot and humid, with average annual temperature of 25.9 °C and average annual rainfall of over 2,100 mm (data from the weather station of Santarém from 2010 to 2018). Precipitation is markedly seasonal, with a rainy season between December and June, and a dry season from July to November (Silva *et al.* 2016). Seasonality in precipitation strongly influences the level of the Amazonas River, which in turn determines the level of the Maicá Lake (Bentes *et al.* 2018).

The Maicá Lake contains extensive aquatic macrophyte banks, usually dominated by amphibious grasses such as *Paspalum repens* P.J. Bergius and *Echinochloa polystachya* (Kunth) Hitchc., and small free-floating plants such as *Eichhornia crassipes* (Mart.) Solms, *Pistia stratiotes* L. and *Salvinia* spp. (Pinheiro

et al. 2016). However, dominant species tend to be spatially replaced along the lake.

Sampling design

We sampled frogs along 15 km² of continuous aquatic macrophyte banks in contact with the lake bank. We sampled 50 plots, each of which 50 m long and 6 m wide, parallel to the lake bank, and 500 m apart between adjacent plots. We counted frogs using visual and acoustic active search, with three observers aboard an eight-meter-long canoe. We collected the data during March 2019, between 18:30 and 00:00. This approach was useful for sampling frogs under optimal detectability conditions, since it is the period of maximum quota of the rivers, when most known frogs in Amazonia are in reproductive activity evidenced by male choruses. We standardized sampling by space (plot area, 300 m²), because the sampling time (50–70 minutes) depended on the navigation conditions in each plot.

We collected frogs in compliance with the collection protocols authorized by the license IBAMA/ICMBio/SISBIO nº 24072-1, and by the ethics committee of the Universidade Federal do Oeste do Pará – UFOPA (process number 1120180049). We identified the species using literature (Rodríguez & Duellman, 1994; Lima *et al.* 2012), and comparisons with specimens deposited in the Herpetological collection of UFOPA, Santarém, Pará. The nomenclature of taxonomic categories follows Frost (2019).

Environmental gradients

We measured environmental gradients in order to express the environmental heterogeneity along macrophyte banks, mainly associated with vegetation cover, variation in plant stratification levels, and physicochemical

parameters of water. In each plot we measured macrophyte height above the water surface every 2 meters along the plot (25 values per plot), water depth and distance from the bank, measured every 10 meters (five values per plot). We used mean values per plot in the inferential analyses. Additionally, we quantified macrophyte morphotype composition based on the occurrence frequency of eight morphotypes, quantified every two meters along each plot. Morphotype classification was based on external morphology, mainly defined by characters associated with stem thickness, root anchorage level, and occupied height of the water column (Supplementary Material S1). We used a field guide to aquatic macrophytes (Piedade *et al.* 2018) as a reference to distinguish morphotypes, which we illustrated in Figure 2. We summarized the frequency values of morphotype occurrence in one dimension defined by Non-Metric Multidimensional Scaling (NMDS) based on Bray-Curtis pairwise dissimilarities. The dissimilarities produced by the NMDS were 89% linearly correlated with the observed dissimilarities (Stress = 0.20).

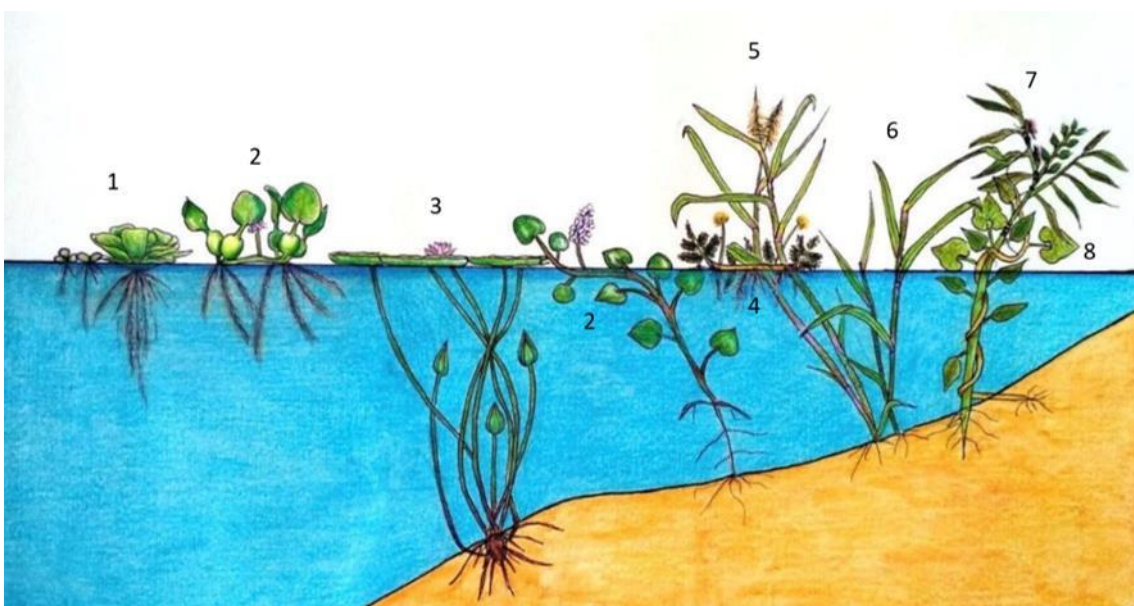


Figure 2. Illustration of the aquatic macrophytes morphotypes.

In addition to the gradients that quantify macrophyte banks structure, we measured air and water temperature, pH and dissolved oxygen in water. We measured these variables in the central region of each plot at the time of frog sampling. This approach was useful for reducing the effects of variation on water physicochemical parameters throughout the day. We collected this data using a Hanna HI 9828 multiparameter apparatus to test the environmental filtering effects generated by factors that potentially affect frog physiological, metabolic and ontogenetic processes (e.g. tadpole metamorphosis), and also plant morphotype composition. Physicochemical parameters of water have been reported in the literature as a limiting factor for frog species occurrence (Leuven *et al.* 1986; Duellman & Trueb 1994; Peltzer & Lajmanovich 2004). We summarized all environmental gradients measured in Table 1.

Table 1. Minimum (Min), maximum (Max), mean and standard deviation (SD) values of environmental gradients measured in 50 plots distributed over 60 km² of the Maicá Lake, lower Amazonas river.

Gradient	Min	Max	Mean	SD
Macrophyte height (cm)	0	127.81	54.97	26.47
Water depth (m)	0.57	3.4	2.02	0.68
Distance from the bank (m)	1.33	1542.11	180.46	321.22
Air temperature (°C)	25.1	29.79	27.19	1.15
Water temperature (°C)	27.5	31.7	28.85	0.78
pH	5.56	8.2	6.42	0.42
Dissolved oxygen (mg/ml ³)	5.9	29.9	14.82	7.52

Data analysis

To quantify frog α -diversity we used the Fisher's Index, which penalizes diversity estimates by the species abundance (Fisher et.al., 1943). We estimated β -diversity using pairwise dissimilarities in species composition among plots, which we estimated using the Bray-Curtis index applied to abundance data. We summarized the dissimilarity matrix using a Principal Coordinate Analysis (PCoA), and assumed the scores produced by the first axis as univariate representations of species composition varying among plots. The first PCoA axis captured 51% of the dissimilarities observed among plots.

To test the effects of the gradients measured on frog α and β -diversity estimates, we pre-selected environmental gradients by multicollinearity levels. We applied a Pearson correlation test and estimated variance inflation factor (VIF) using the car R-package (Fox & Weisberg, 2011). We did not include water temperature in the inferential models because this variable was 60% correlated with air temperature. High correlation was supported by a comparatively high VIF value (1.66), although acceptable for linear multiple models (we arbitrarily assumed a conservative approach). The other variables were 2–45% correlated with each other. Excluding water temperature, we obtained VIF values between 1.05–1.37.

We tested the influence of environmental gradients on frog diversity estimates using multiple linear models, separately by α and β -diversity estimates. We generated a full model given by $diversity = a + b_1 (water\ depth) + b_2 (air\ temperature) + b_3 (pH) + b_4 (dissolved\ oxygen) + b_5 (bank\ distance) + b_6 (macrophyte\ height) + b_7 (macrophyte\ morphotype\ composition)$. We applied a

stepwise regression to select the most parsimonious variable subset, so that less informative predictor variables were sequentially removed from the full model, and a final model was selected by the lowest Akaike Information Criterion (AIC) value.

We validated the most parsimonious models (lowest AIC values) by testing the normality of the residuals using Shapiro-Wilk tests. Additionally, we tested spatial autocorrelation on the residuals produced by the multiple linear models using Moran's I global test and Geary's C local test configured with ten classes of geographic distance. We defined number of distance classes to maintain as much homogeneity as possible in the number of comparisons within class. We implemented Moran's I and Geary's C tests using respectively *ape* (Paradis *et al.* 2019) and *pgirmess* (Giraudoux *et al.* 2018) R-packages.

RESULTS

We found 1,432 frogs distributed in 16 species and three families (Table 2). The most frequently sampled species was *Lysapsus limellum* (Hylidae), which occurred in 86% of the plots (798 individuals in 43 plots), and the less frequently sampled species was *Rhinella marina* (Bufonidae), which we found in only one plot (0.06 %).

The most parsimonious multiple linear model using Fisher's α -diversity as dependent variable was identified with macrophyte morphotype composition, macrophyte height and water depth as independent variables (AIC = -71.63, Δ AIC = 6.73). This model explained 21% of the variation in frog α -diversity ($P < 0.01$), although only macrophyte height contributed significantly to the model ($P = 0.003$). Morphotype composition and water depth did not significantly affect the

estimated α -diversity ($P > 0.05$ in all cases). These findings suggest that the frog assemblage is structured by plant stratification generated by macrophytes, with more species occupying higher sites (Figure 3). This model was validated by residuals not differing from a theoretical normal distribution (Shapiro-Wilk $P = 0.52$), and not spatially autocorrelated (Table 3). Independence of geographic distance was consistently defined by the Moran's I global test ($P = 0.59$), and the ten distance classes used in the local Geary's C test ($P > 0.05$ in all cases).

Table 2. Frog species sampled in 50 plots distributed in the Maicá Lake, lower Amazonas River, Brazil. Abundance (Ab) is the total number of individuals found, and frequency is relative to the number of plots.

Family / species	Ab	Frequency
Bufonidae		
<i>Rhinella marina</i> (Linnaeus, 1758)	1	2
Hylidae		
<i>Boana lanciformis</i> (Cope, 1871)	4	2
<i>Boana punctata</i> (Schneider, 1799)	56	26
<i>Boana raniceps</i> (Cope, 1862)	172	70
<i>Dendropsophus</i> gr. <i>leucophyllatus</i>	38	12
<i>Dendropsophus walfordi</i> (Bokermann, 1962)	201	50
<i>Lysapsus limellum</i> Cope, 1862	798	86
<i>Pseudis paradoxa</i> (Linnaeus, 1758)	3	4
<i>Scarthyla goinorum</i> (Bokermann, 1962)	9	12
<i>Scinax nebulosus</i> (Spix, 1824)	23	12
<i>Scinax ruber</i> (Laurenti, 1768)	2	2
<i>Scinax x-signatus</i> (Spix, 1824)	2	4
<i>Sphaenorhynchus lacteus</i> (Daudin, 1800)	15	12
<i>Trachycephalus typhonius</i> (Linnaeus, 1758)	18	10
Leptodactylidae		
<i>Leptodactylus macrosternum</i> Miranda-Ribeiro, 1926	6	12
<i>Leptodactylus wagneri</i> (Peters, 1862)	84	44

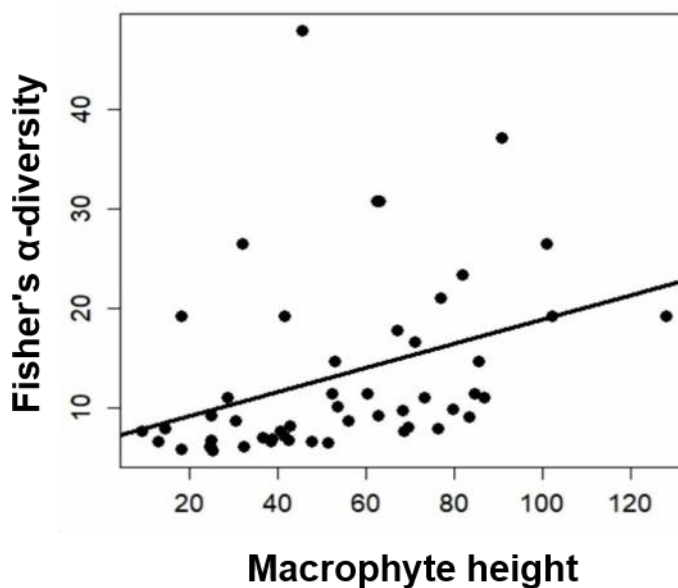


Figure 3. Relationships between frog Fisher's α -diversity and macrophyte height (partials derived from a multiple linear model). Data were collected from 50 plots distributed in the Maicá Lake, lower Amazonas River.

The most parsimonious multiple linear model using frog β -diversity as dependent variable was identified with macrophyte height, morphotype composition and water depth as independent variables (AIC = -156.29, Δ AIC = 4.84). This model explained 64% of the variation in the estimated β -diversity ($P < 0.001$), indicating non-random assemblage structure characterized by species turnover (Figure 4). The three gradients contributed significantly to the model ($P \leq 0.01$ in all cases). This model was validated by residuals not differing from a theoretical normal distribution (Shapiro-Wilk $P = 0.64$), and not spatially autocorrelated. Independence of geographical distance was consistently defined by the Moran's I global test ($P = 0.94$), and by ten distance classes used in the local Geary's C test ($P \geq 0.07$ in all cases).

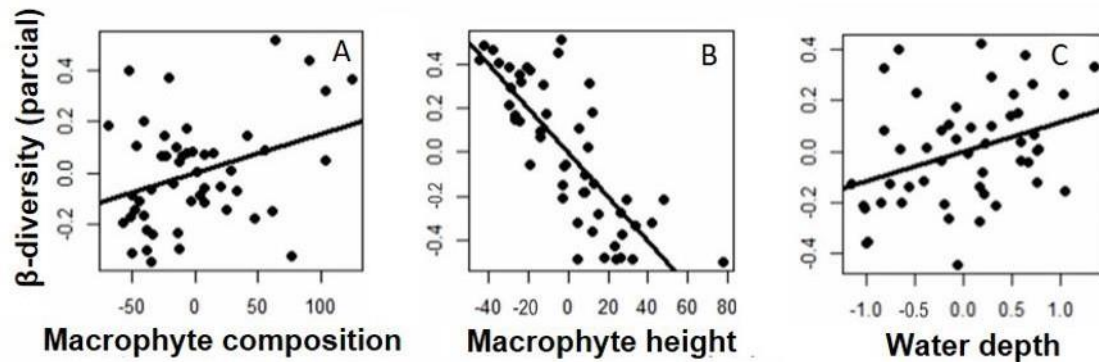


Figure 4. Relationships between frog β -diversity (Brat-Curtis dissimilarities in species abundance) and environmental gradients quantifying the overall structure of aquatic macrophyte banks (partials derived from a multiple linear model). Data were collected from 50 plots distributed in the Maicá Lake, lower Amazonas River. Trend lines are shown only in cases where the null hypothesis has been rejected at $P < 0.05$.

Table 3. Geary's local test results for spatial autocorrelation in the residuals from multiple linear models used to test the effects of environmental gradients on frog α and β -diversity estimates. The models were set up with geographic distance classes, which are shown in kilometers. N = number of pairwise comparisons within each distance class.

Fisher's α -diversity				β -diversity			
Distance	C	P	N	Distance	C	P	N
510	0.97	0.27	765	510	0.92	0.07	765
1275	0.98	0.37	808	1275	1.00	0.50	808
1785	1.01	0.57	500	1785	1.06	0.73	500
2550	0.78	0.10	246	2550	0.83	0.21	246
3315	1.04	0.57	100	3315	0.79	0.19	100
3825	1.09	0.64	32	3825	0.74	0.16	32

Species turnover along the macrophyte height gradient was characterized by the fact that species were restricted or occurred with higher abundances in relatively small fractions of the gradient, which represented plots showing low (e.g. *Boana lanciformis*, *Pseudis paradoxa*, *Dendropsopus* gr. *leucophyllatus*, *Lysapsus limellum*) or high (e.g. *Tracycephalus typhonius*) macrophytes. However, several species occurred with relatively homogeneous abundance throughout the entire gradient (e.g. *Boana punctata*, *Dendropsopus walfordii*, *Leptodactylus wagneri*). A similar finding was found for the water depth gradient, in which species occupied shallower (e.g. *Scinax x-signatus*, *Rhinella marina*, *Sphaenorhynchus lacteus*) or deeper (e.g. *Leptodactylus macrosternum*, *Boana lanciformis*, *Scinax ruber*) plots, although several species occupied the entire gradient with approximately homogeneous abundances. The distribution of each individual species along the macrophyte height and water depth gradients can be found in Figure 5.

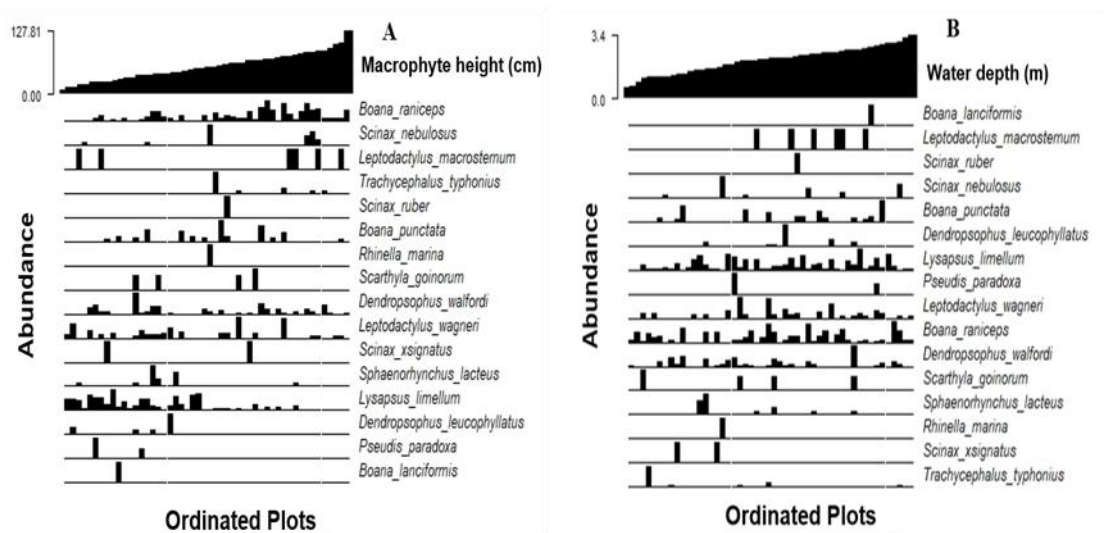


Figure 5. Sampling plots ordered along a gradient of macrophyte height (A) and water depth (B). The height of the black rectangles represents abundance per species. Blank spaces indicate absence of species from plots.

DISCUSSION

Our results showed that the local spatial structure of the sampled frog assemblages is not random along the aquatic macrophyte banks but characterized by α -diversity positively affected by macrophyte height, and β -diversity affected by macrophyte height, morphotype composition and water depth. Frog diversity determined by environmental heterogeneity is consistent with the literature, and often associated to ecological filtering causing different species subsets across heterogeneous habitats (e.g. Ribeiro-Jr. *et al.* 2012, Rojas-Ahumada *et al.* 2012, Dias-Terceiro *et al.* 2015). However, most studies in Amazonia have been based on sampling forests, from which relatively extensive environmental gradients are usually measured. We have shown that even in apparently homogeneous ecosystems, which are rarely considered to be distinct biographic units from adjacent habitats, frog assemblages respond to environmental heterogeneity through non-random spatial distribution of diversity estimates. These findings have broad application for ecology and conservation because ultimately reveal subtle biotic complementarities among sites within a regionally rare ecosystem.

All species in this study are widely distributed in Amazonia, and have been found occupying aquatic macrophytes (Upton, 2014; Böning *et al.* 2017; Ramalho *et al.* 2017). However, despite the wide distribution at macroscales, our models detected frog assemblages composed of species locally restricted to optimal fractions of environmental gradients. Specifically, the patterns of spatial structure found may be directly associated with relationships between species traits (e.g. body size, finger and toe shape) and macrophyte height and shape causing spatial segregation (Hödl, 1977). For instance, species that lack well-developed

adhesive discs (e.g. *Lysapsus limellum*, *Pseudis paradoxa*) were filtered from plots dominated by tall macrophytes, while climbing species occupied tall macrophytes (e.g. *Trachycephalus typhonius*) or showed relatively homogeneous abundance distribution along the gradient of macrophyte height (e.g. *Boana raniceps*, *Dendropsophus walfordi*). In addition, fragile and floating macrophyte morphotypes (e.g. *Pistia*, *Salvinia*) were usually occupied by small frogs (e.g. *Lysapsus limellum*, *Leptodactylus wagneri*), suggesting environmental filtering selecting species by body mass. In fact, heavy-bodied species such as *Rhinella marina* were restricted to shallow-water plots, covered by rigid and robust macrophytes. This species should be considered as a temporary visitor to macrophyte banks, especially during river floods, when unflooded habitats are scarce (Upton *et al.* 2014). Nonetheless, an overview of our results suggests environmental filtering determining assemblages through species trait selection as a major source of spatial structure.

Overall, the multiple linear models returned results that fit well with environmental filters selecting species through their ability to occupy available habitats or survive. This finding is supported by the fact that almost 70% of the sampled species are climbing hylid treefrogs, and we found a positive relationship between α -diversity and macrophyte height. Frog assemblages in aquatic macrophytes dominated by hylid treefrogs are an expected result (Upton 2014; Ramalho 2017; Böning 2017), and we have shown that this feature emerges from the habitat verticalization provided by tall macrophytes. However, we also found species turnover along a water depth gradient, which may be related to predator pressure on tadpoles. Predator fish density may change with depth, because fish assemblages are often composed of different species subsets along depth

gradients (Rodríguez & Lewis 1997; Tejerina-Garro *et al.* 1998). Therefore tadpole-predator relationships may be expected to vary spatially, suggesting that the local distribution of frogs is also determined by tadpole survival. We argue that the influence of environmental gradients on frog diversity in aquatic macrophytes may not be solely defined by the ability to climb vegetation, but is part of complex interactions among frogs, predators and habitats. However, the role of predator pressure on tadpoles is indirectly demonstrated in this study, since we have no data available on tadpole or fish densities.

We found non-random spatial structure in frog assemblages, which indicates that sites within aquatic macrophyte banks are not homogeneously suitable for all sampled species, but distinct species subsets may be expected along the plots. These finding suggests high levels of biotic complementarity within macrophyte banks, although they appear structurally homogeneous at macroscales (e.g. satellite images). However, temporal patterns of species turnover should also be expected as macrophyte banks may be changed in response to water-level fluctuations and wind moving floating macrophytes. Since the overall structure of macrophyte banks determines the quality of frog habitats, but change over time, understanding assemblage structure at temporal scales should be based on multiple sampling of frogs and environmental gradients.

Macrophyte banks are expected to contain distinct assemblages of adjacent forests because they are structurally very distinct. High levels of beta diversity in frogs have been found in Amazonia even along subtler environmental variation (Ribeiro-Jr *et al.* 2012; Rojas-Ahumada *et al.* 2012). However, we have shown that different assemblages should be expected even within macrophyte banks, since species may be filtered under suboptimal conditions. These findings

are relevant for conservation because they have ultimately revealed high biotic complementarity between sites within regionally rare and apparently homogeneous ecosystems at macroscales. High levels of biotic complementarity have been widely suggested as an efficient criterion for defining priority conservation areas. Additionally, although macrophyte banks in Amazonia are often considered to be part of várzea forests (Piedade 2010; Junk 2011), we argue that they should be considered as distinct biogeographic units from adjacent habitats, because they contain unique and spatially heterogeneous biodiversity. This is particularly critical in our study area because a cargo ship port is being built lacking any environmental-impact study based on systematically collected data. Considering frog assemblage local spatial structure determined by the heterogeneous habitat quality, we predict that ship traffic will cause local extinction through migration or tadpole malformation.

ACKNOWLEDGEMENTS

We are very thankful to the guide Lalico and Lázaro for the field support in Maicá lake. Bill Magnusson and Albertina Lima provided valuable suggestions on the sampling design. Many undergrad students at the Universidade Federal do Oeste do Pará helped in the data collection. The 1st Oficina de Publicação do Programa de Pós-Graduação em Biodiversidade, financed by Programa Nacional de Cooperação Acadêmica na Amazônia (PROCAD-AM/CAPES Nº 21/2018, process Nº 88887.200472/2018-00) provided a valuable review on the early drafts of the manuscript. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – FianceCode 001, for PHSG (master's degree scholarship), and RF (PNPD postdoc

fellowship). LBNV received a scholarship from Fundação Amazônia de Amparo e Estudos e Pesquisas (FAPESPA).

REFERENCES

- Böning P., Wolf S., Upton k., Menin M., Venegas P. J., Lötters S. (2017) Amphibian diversity and its turnover in floating meadows along the Amazon river. *Salamandra*. **53**: 379-388.
- Bentes K. L. S., Oliveira L. L., Zcardi D. M., Barreto N. J. C. (2018) The relationship between hydrologic variation and fishery resources at the lower Amazon, Santarém, Pará. *Revista Brasileira de Geografia Física*. **11(4)**: 1478–1489.
- Dias-Terceiro R. G., Kaefer I. L., Fraga R., Araujo M., Simoes P. I., Lima A. (2015) A matter of scale: Historical and environmental factors structure anuran assemblages from the upper Madeira River, Amazonia. *Biotropica*. **0**: 1-8.
- Duellman W. E & Trueb L. (1994) *Biology of amphibians*, p. 670. The Johns Hopkins University Press, Baltimore.
- Duellman WE. 1999. Distribution patterns of amphibians in South America. In *Patterns of Distribution of Amphibians* (ed. W.E. Duellman) pp. 255–327. The Johns Hopkins University Press. Baltimore and London.
- Fisher R. A., Corbet A.S., Willians C.B. (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology*. **12**:42-58.
- Fox J., S Weisberg. (2011) *An R companion to applied regression*, 2nd ed. SAGE Publications Inc, Thousand Oaks, CA.

- Fraga R., Lima A. P., Magnusson W. E. (2011) Mesoscale spatial ecology of a tropical snake assemblage: the width of riparian corridors in central Amazonia. *Herpetological Journal*. **21**: 51-57.
- Frost D.R. (2019) Amphibian species of the world: an online reference. Version 6.0. American Museum of Natural History, New York. [Cited on 28 September 2019]. Available from URL: <http://research.amnh.org/herpetology/amphibia/index.html>.
- Garda A. A., Wiederhecker H. C., Gainsbury A. M., Costa G. C., Pyron R. A., Vieira G. H. C., Werneck F. P., Colli, G. R. (2012) Microhabitat variation explains local-scale distribution of terrestrial amazonian lizards in Rondônia, Western Brazil. *Biotropica*. **0**:1-8.
- Giraudoux P., Giraudoux M. P., Mass S. (2018) pgirmess: Spatial analysis and data mining for field ecologists. R package version **1.6.9**.
- Hödl W. (1977) Call differences and calling site segregation in anuran species from Central Amazonian floating meadows. *Oecologia*. **28**:351–363.
- Hoogmoed M. S. (1993) The herpetofauna of floating meadows. In *The Freshwater Ecosystem of Suriname* (P.E. Ouboter, org) pp.199–213. Academic Publishers, **Dordrecht**.
- Junk W. J., Ohly J. J., Piedade M. T. F., Soares M. G. M. (2000) *The central Amazon floodplain actual use and options for a sustainable management*. Backhuys Publishers, Leiden.
- Junk W. J. (1973) Investigation of the ecology and production-biology of the “floating meadows” (Paspalo- Echinochloetum) on the Midler Amazon. II. The aquatic fauna in the root zone floating vegetation. *Amazon*. **4**: 9-112.
- Junk W. J. (1997). *The Central Amazon Floodplain*. Springer-Verlag: New York.

- Junk W. J., Piedade M. T. F., Schöngart J., Cohn-Haft M., Adeney J. M., Wittmann F. (2011) A classification of major naturally-occurring amazonian lowland wetlands. *Wetlands*. **31**: 623–640.
- Jorge R. F., Simões P. I., Magnusson W. E., Lima A. P. (2016) Fine-scale habitat heterogeneity explains the local distribution of two Amazonian frog species of concern for conservation. *Biotropica*. **48(5)**: 694–703
- Keddy P. A. (1992) Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*. **3**:157-164.
- Kinupp V. F., Magnusson W. E. (2005) Spatial patterns in the understory shrub genus *Psychotria* in central Amazonia: effects of distance and topography. *Journal of Tropical Ecology*. **21**: 363-374.
- Lima A. P., Magnusson W.F., Menin M., Erdtmann L. K., Rodrigues D. J., Keller C., Hödl W. (2012) *Guia de Sapos da Reserva Adolph Ducke - Amazônia Central*, p 168. Editora Attema INPA, Manaus.
- Leuven R. S. E. W., Den Hartog C., Christiaans M. M. C., Heijligers, W. H. C. (1986) Effects of water acidification on the distribution pattern and the reproductive success of amphibians. *Experientia*. **42**:495–503.
- Menin M., Lima A. L., Magnusson W. E.; Waldez F. (2007) Topographic and edaphic effects on the distribution of terrestrially reproducing anurans in the Central Amazonia: mesoscale spatial patterns. *Journal of Tropical Ecology*, **23**: 539–547.
- Moreno-Rueda G. & Pizarro M. (2007) The relative influence of climate, environmental heterogeneity, and human population on the distribution of

- vertebrate species richness in south-eastern Spain. *Acta Oecologica*. **32 (1)**: 50-58.
- Navas C. A., Otani L. (2007) Physiology, environmental change, and anuran conservation. *Phyllomedusa*. **6**: 83-103.
- Paradis E., Bolker B., Claude J. *et al.* (2019): ape. Analyses of phylogenetics and evolution. R package version 5.3.
- Parolin P. (2012) Diversity of adaptations to flooding in trees of Amazonian floodplains. *Revista Pesquisas-Botânica*. **63**: 7–28.
- Peltzer P. M. & Lajmanovich R. C. (2004) Anuran tadpole assemblages in riparian areas of the Middle Paraná River, Argentina. *Biodiv Conserv*. **13**: 1833-1842.
- Piedade M. T. F., Junk W. J., D'Angelo S. A., Wittmann F., Schöngart J., Barbosa K. M. N., Lopes A. (2010) Aquatic herbaceous plants of the Amazon floodplains: state of the art and research needed. *Acta Limnologica Brasiliensia*. **22(2)**: 165-178.
- Piedade M.T.F., Lopes A., Demarchi L. O., Junk W., Wittmann F. K., Schöngart J., Cruz J. (2018) *Guia de campo de herbáceas aquáticas: várzea Amazônica*. Editora do INPA, Manaus.
- Pinheiro D. T., Correa J. M. S., Chaves C. S., Campos D. P. F., Ponte S. C. S., Zacardi, D. M. (2016) Diversidade e distribuição da ictiofauna associada a bancos de macrófitas aquáticas de um lago de inundação amazônico, estado do Pará, Brasil. *Acta of Fisheries and Aquatic Resources*. **2**: 59–70.
- Ponte S. C. S., Oliveira L. S., Zacardi D. M. (2019) Variação temporal de larvas de peixes de um lago de inundação como subsídio à gestão ambiental. *Journal of Applied Hydro-Environment and Climate*. **1(1)**: 1–13.

- R Development Core Team (2018) *R: a language and environment for statistical computing*. R foundation for Statistical Computing. Available from URL: <http://www.R-project.org>.
- Ramalho W. P., Machado I. F., Vieira L. J. S. (2017) Do flood pulses structure amphibian communities in floodplain environments? *Biotropica*. **50**: 338-345.
- Ribeiro-Jr J. W., Lima A. P., Magnusson W. E. (2012) The effect of riparian zones on species diversity of frogs in amazonian forests. *Copeia*. **3**: 375–381.
- Rodríguez L. & Duellman W. (1994) *Guide to the frogs of the Iquitos Region, Amazonian Peru*, p. 103. Lawrence, Kansas.
- Rodríguez M. A. & Lewis J. W. M. (1997) Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. *Ecological Monographs*. **67**, 109–128.
- Rojas-Ahumada D. P., Landeiro V.L., Menin M. (2012) Role of environmental and spatial processes in structuring anuran communities across a tropical rain forest. *Austral Ecol.* **37**: 865–873.
- Sanchez-Botero J. I., Araújo-Lima A. R. M. (2001) As macrófitas aquáticas como berçário para a ictiofauna da várzea do rio Amazonas. *Acta Amazonica*, **31(3)**: 437–447.
- Schiesari L., Zuanon J., Azevedo-Ramos C., Garcia M., Gordo M., Messias M., Monteiro E. (2003) Macrophyte rafts as dispersal vectors for fishes and amphibians in the Lower Solimões River, Central Amazon. *Journal Tropical Ecology*. **19**: 333-336.

- Silva R. A., Martins I. A., Rossa-Feres D. C. (2011) Environmental heterogeneity: Anuran diversity in homogeneous environments. *Zoologia*. **28(5)**: 610-618.
- Silva M. A. G., Guimarães J. M. J., Silva N. F. C., Santos F. C. V., Ucker F. E. (2016) Caracterização pluviométrica de Santarém-PA, Brasil. *Renefara*, **10**: 112–120.
- Tejerina-Garro F. L., Rejean F., Rodríguez M. A. (1998). Fish community structure in relation to environmental variation in floodplain lakes of the Araguaia River, Amazon basin. *Environmental Biology of Fishes*. **51**, 399–410.
- Thomaz S. M., Dibble E. D., Evangelista L. R., Higuti J., Bini L. M. (2008) Influence of aquatic macrophyte habitat complexity on invertebrate abundance and richness in tropical lagoons. *Freshwater Biol.* **53**:358-367.
- Tuomisto H., Ruokolainen K., Yli-Halla M. (2003). Dispersal, environment, and floristic variation of western *amazonian forests*. *Science*. **299**: 241–244.
- Upton K., Warren-Thomas E., Rogers, I. (2014) Amphibian diversity on floating meadows in flooded forests of the Peruvian Amazon. *Herpetol. Review*. **45(2)**: 209–212.
- Vasconcelos T. S., Santos T. G., Rossa-Feres D. C., Haddad C. F. B. (2009) Influence of the environmental heterogeneity of breeding ponds on anuran assemblages from southeastern Brazil. *Canad. Journal of Zool.* **87**: 699-707.
- Vitt L. J., Caldwell J. P., Wilbur H. M., Smith D.C. (1990) Amphibians as harbingers of decaly. *BioScience*. **40**: 4-18.
- Whittaker K., Koo M. S., Wake, D. B., Vredenburg V. T. (2013) Global Declines of Amphibians. In: *Encyclopedia of Biodiversity* (Ed. Levin, S.A) pp. 691-699. Academic Press, San Diego.

S1. SUPPLEMENTARY MATERIAL

Eight macrophyte morphotypes were established according to the external morphology, as detailed below.

- Morphotype 1: not necessarily rooted in the soil, thin leaves, approximately 3 cm wide, up to 1.2 m tall, predominantly green. This morphotype is mainly composed of *Paspalum repens*.
- Morphotype 2: rooted in the soil, above-water leaves, thin and erect stems, up to 1.2 meters tall, thin and alternate leaves along the stem, green to light brown. This morphotype is mainly represented by *Echinochloa polystachya*, *Paspalum* spp. and *Oryza* spp.
- Morphotype 3: rooted in the soil or free-floating macrophytes, up to 40 centimeters tall, floating stem, rounded leaves (10–15 cm in diameter), green. Mainly represented by *Eichhornia azurea*, *E. crassipes* and *Pontederia rotundilofia*.
- Morphotype 4: climbing macrophytes, green leaves alternated along the thin stem, up to 10 cm long, usually rooted in the soil, eventually epiphyte. Mainly represented mainly by *Luffa* spp. and *Ipomoea* spp.
- Morphotype 5: free, emergent-floating plants, small, floating leaves, green or purple, up to 2 cm tall, forming carpet-shaped banks. Mainly represented by *Pistia* spp. and *Salvinia* spp.
- Morphotype 6: rooted in the soil, floating green and orbicular leaves, only the leaves lay on the surface. The leaves are flat, rounded and may be more than 1.5 meters in diameter. Mainly represented by *Victoria amazonica* and *Nymphaea* sp.

- Morphotype 7: erect green plants, fixed and sparsely branched stem, oval-shaped sessile leaves, more than 1.5 m tall. Mainly represented by *Pacourina edulis*.
- Morphotype 8: rooted, floating or emerged stem, up to 20 cm in tall. Sensitive leaves, bipanate with 8–20 pairs of leaflets. Floating stem, fibrous and spongy, up to 1.5 m tall. Mainly represented by *Neptunia oleracea*.

CAPÍTULO II

Pedro Henrique Salomão Ganança, Rafael de Fraga, Ricardo A. Kawashita-Ribeiro, Lourival Baía de Vasconcelos Neto, Ivan Alves dos Santos Júnior, Daniel de Sousa Guedes, Francesca Nicole Angiolani Larrea, Alfredo P. Santos-Jr. Frogs and Squamata reptiles occupying aquatic macrophytes in a *várzea* lake in the lower Amazon River, Brazil. *Submitted to Acta Amazonica**

* O artigo apresentado foi redigido conforme as diretrizes de submissão da revista *Acta amazonica*, exceto pelas figuras inseridas no corpo do texto para facilitar a leitura. As normas indicadas para a redação de artigos pela revista estão disponíveis no link: <http://www.scielo.br/revistas/aa/iinstruc.htm>

Acta Amazonica**Frogs and Squamata reptiles occupying aquatic macrophytes in a várzea lake in the lower Amazon River, Brazil**

Pedro Henrique Salomão GANANÇA^{1, *}, Rafael de FRAGA^{1, 2}, Ricardo A. KAWASHITA-RIBEIRO^{1, 3}, Lourival Baía de Vasconcelos NETO¹, Ivan Alves dos SANTOS JÚNIOR⁴, Daniel de Sousa GUEDES⁴, Francesca Nicole ANGIOLANI LARREA¹, Alfredo P. SANTOS-JR¹

¹Laboratório de Ecologia e Comportamento Animal e Programa de Pós-graduação em Biodiversidade, Universidade Federal do Oeste do Pará, rua Vera Paz, s/n, Salé, 68040-255, Santarém, PA, Brazil.

²Programa de Pós-graduação em Recursos Naturais da Amazônia, Universidade Federal do Oeste do Pará, Av. Mendonça Furtado, 2946, Fátima, 68040-050 Santarém, PA, Brazil.

³Departamento de Ciências Biológicas, Instituto de Ciências Exatas e Experimentais, Universidade Federal de Mato Grosso, Rodovia MT 270 Km 06, Parque Sagrada Família, 78735-901, Rondonópolis, MT, Brazil.

⁴Curso de Bacharelado em Biologia, Instituto de Ciências e Tecnologia das Águas, Universidade Federal do Oeste do Pará, rua Vera Paz, s/n, Salé, 68040-255 Santarém, PA, Brazil.

*Correspondent author: psalogan@hotmail.com

Frogs and Squamata reptiles occupying aquatic macrophytes in a várzea lake in

27 **the lower Amazon River, Brazil**

28 **ABSTRACT.** *Várzeas* are aquatic and terrestrial ecosystems which usually show high
29 primary productivity associated with high nutrient availability. A combination of high
30 nutrient availability and light incidence in aquatic ecosystems such as lakes allows the
31 growth of extensive aquatic macrophyte banks, which are excellent foraging, resting,
32 sheltering and breeding sites for a wide variety of vertebrates and invertebrates. In this
33 study we sampled Squamata reptiles and frogs on aquatic macrophyte banks in a *várzea*
34 lake in eastern Amazonian Brazil. We used a canoe to survey (visual and acoustic
35 sampling) 50 plots, each of which 50 m long and 6 m wide, spaced at least 500 m apart.
36 We found 16 frog species (three families), four lizards (four families) and seven snakes
37 (two families). We discuss our results in terms of variation in habitat-specificity shown
38 by the sampled species. While some species apparently have locally restricted distribution
39 to aquatic macrophytes, others only benefit from the high quality of habitats, or even use
40 these habitats occasionally. We also discuss the importance of aquatic macrophytes for
41 the conservation of the local biodiversity. This is particularly relevant to our study area
42 since it is likely to be severely disturbed by the ongoing controversial construction of a
43 port.

44

45 **Key words:** Amazon, Floating meadows, Floodplain, Herpetofauna

46

47

48

49

50

51

52 **Sapos e répteis Squamata ocupando macrófitas aquáticas em um lago de várzea no**
53 **baixo Rio Amazonas, Brasil**

54

55 **RESUMO**

56 As várzeas abrangem ecossistemas aquáticos e terrestres, os quais geralmente têm alta
57 produtividade primária associada à alta disponibilidade de nutrientes. Uma combinação
58 de alta disponibilidade de nutrientes e incidência luminosa em ecossistemas aquáticos
59 como lagos permite o crescimento de extensos bancos de macrófitas aquáticas, que são
60 excelentes sítios de forrageamento, repouso, abrigo e reprodução para uma grande
61 variedade de vertebrados e invertebrados. Neste estudo, amostramos répteis e sapos
62 Squamata em bancos de macrófitas aquáticas em um lago de várzea no leste da Amazônia
63 brasileira. Utilizamos uma canoa para contar indivíduos (amostragem visual e acústica)
64 em 50 parcelas, cada uma com 50 m de comprimento e 6 m de largura, espaçadas com
65 pelo menos 500 m. Encontramos 16 espécies de sapos (três famílias), quatro de lagartos
66 (quatro famílias) e sete espécies de serpentes. Discutimos nossos resultados em termos de
67 variação na especificidade de habitat mostrada pelas espécies amostradas. Enquanto
68 algumas espécies aparentemente têm a distribuição localmente restrita a macrófitas
69 aquáticas, outras apenas se beneficiam da alta qualidade de habitats ou usam esses
70 habitats ocasionalmente. Nós também discutimos a importância de macrófitas aquáticas
71 para a conservação da biodiversidade local. Isso é particularmente relevante para nossa
72 área de estudo, pois ela provavelmente será gravemente perturbada pela controversa
73 construção de um porto, que já se encontra em andamento.

74 **Palavras-chave:** Amazônia, Herpetofauna, Planície de inundação, Vegetação flutuante.

75

76

77 INTRODUCTION

78 Várzeas are seasonally flooded forests, which are among the richest ecosystems in
79 Amazonia (Junk *et al.* 2000; Parolin 2012). High levels of biodiversity (e.g. species
80 richness and turnover) are mainly associated with high levels of primary productivity,
81 which is optimized by erosion sediments from the Andes, which are transported by the
82 Amazon River (Junk *et al.* 2011). Nutrient-rich sediment loads favor terrestrial and
83 aquatic biodiversity, although habitat availability and quality may be highly influenced
84 by habitat flooding caused by river-level seasonality (Junk *et al.* 1989, 2011).

85 Sediment loads carried by the Amazon River favors primary productivity in
86 terrestrial habitats in várzeas, because accumulated sediment produces rich soils (Junk *et*
87 *al.* 2011). High primary productivity can also be expected in várzea lakes because aquatic
88 plants have wide access to high amounts of nutrients, water and light (Piedade *et al.* 2010).
89 In addition to primary producers, aquatic macrophytes provide breeding, foraging and
90 refuge sites for a wide variety of aquatic, semi-aquatic and terrestrial organisms (Junk
91 1973). However, knowledge about species that occupy macrophytes is still scarce for
92 several groups of organisms, such as amphibians and especially reptiles. Sampling
93 organisms in a specific habitat type which is not widely available at regional or local
94 scales is a fundamental basis for ecological and biogeographic studies, because patches
95 of relatively rare habitats potentially contain unique local assemblages (Wintle *et al.*
96 2019). Unique biodiversity has been used as a criterion for prioritizing conservation areas
97 (Brooks *et al.* 2006), and therefore sampling locally sparse habitats is relevant for
98 conservation decision-making.

99 Aquatic macrophytes are often used by a very diverse fauna represented by
100 invertebrates (Junk 1973; Achaval *et al.* 1979; Sarli *et al.* 1992), fish (Achaval *et al.* 1979;
101 Sarli *et al.* 1992; Schiesari *et al.* 2003), birds (Achaval *et al.* 1979), mammals (Achaval

102 *et al.* 1979; Sarli *et al.* 1992), amphibians (Höld 1977; Schiesari *et al.* 2003; Böning *et al.*
103 2017) and reptiles (Achaval *et al.* 1979; Sarli *et al.* 1992; Hoogmoed 1993). Animals may
104 use macrophytes as refuge, foraging, breeding and nursery sites (Junk 1973; Sanchez-
105 Botero and Araújo-Lima 2001; Padial *et al.* 2009; Upton *et al.* 2014). In addition, floating
106 macrophyte banks act as long-distance dispersal corridors and bridges for gene flow,
107 which limits the condition of rivers as biogeographic barriers (Schiesari *et al.* 2003).
108 However, few studies have evaluated species richness and composition based on reptile
109 and amphibian data from aquatic macrophytes (*e.g.* Höld 1977; Hoogmoed 1993; Upton
110 *et al.* 2014; Böning *et al.* 2017). In South America, it has been suggested that frog
111 assemblages are dominated by Hylidae species (Upton *et al.* 2014; Böning *et al.* 2017;
112 Ramalho *et al.* 2017), while Dipsadidae snakes (Ihering 1911; Achaval *et al.* 1979) and
113 Teiidae lizards (Hoogmoed 1993; Gerrero *et al.* 2017) are most often sampled in aquatic
114 macrophytes.

115 The Amazon ecosystems are special places to study herpetofauna, because they
116 have shown the highest estimates of reptile and amphibian diversity on the Planet (Ávila-
117 Pires *et al.* 2007). Large proportions of the high species diversity have been explained by
118 the high environmental heterogeneity, which often explain high levels of alpha and beta
119 diversity estimates (Ramalho *et al.* 2017; Böning *et al.* 2017; Fraga *et al.* 2018). To date,
120 at broad spatial scales, the Brazilian Amazonia contains 355 formally described species
121 of amphibians, of which 329 are frogs (Hoogmoed and Galatti 2019), 21 caecilians
122 (Hoogmoed 2018a) and five salamanders (Hoogmoed 2018b), and 375 Squamata reptile
123 species, of which 189 are snakes (Prudente and Da Silva 2017), 140 are lizards and 18
124 are amphisbaenians (Ávila-Pires and Ramalho 2019). Estimates of species richness often
125 change, as new species and new occurrence data are constantly being described as remote
126 regions are sampled (*e.g.* Azevedo-Ramos and Galatti 2002; Ávila-Pires *et al.* 2007;

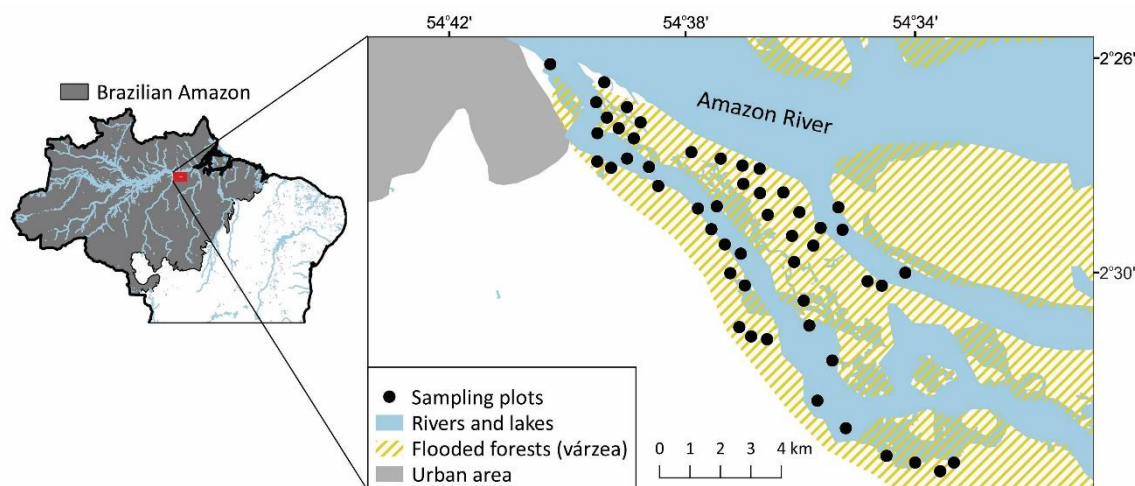
127 Fraga and Torralvo 2019). Nonetheless, it has been clear that the Amazon ecosystems are
128 important centers for amphibian and reptile diversification, and should therefore receive
129 attention for conservation. Amphibians (Whittaker *et al.* 2013) and reptiles (Gibbons *et*
130 *al.* 200) are facing global decline, and the Amazon ecosystems contain large proportions
131 of the global diversity of both groups.

132 Although knowledge about Amazonian biodiversity has been considerably refined
133 in recent decades, non-forest habitats have been rarely sampled. In this study we aimed
134 to fill this gap, by sampling reptiles and frogs in aquatic macrophyte banks in a *várzea*
135 ecosystem in the lower Amazon River. We present an annotated list of species based on
136 widely distributed sampling units throughout the study area. Our findings are though as
137 an important contribution to the studies that should base the environmental licensing of a
138 cargo port, which is currently being built without any reliable environmental impact
139 study.

140

141 **MATERIAL AND METHODS**

142 Our study area (polygon edges 02°43'79" S, 54°35'49" W and 02°26'44" S, 54°16'93"
143 W) covers about 60 km² in a large *várzea* lake (Maicá) formed at the confluence of the
144 Amazon and Ituqui rivers (Figure 1), near the urban perimeter of Santarém, Pará, eastern
145 Amazonian Brazil. The Maicá Lake is formed by interconnected canals and lakes, which
146 are strongly influenced by the seasonal flooding of the Amazon River from December to
147 June (Ponte *et al.* 2019). The amount of water entering the Maicá lake is considerably
148 reduced during the dry season, when the lake can be completely dry over about six
149 months. (Pinheiro *et al.* 2016).



150

151 **Figure 1.** Amazonian várzea where we sampled Squamata reptiles and frogs in aquatic
 152 macrophyte banks. Black circles are 300 m² sampling plots, which we surveyed aboard a
 153 canoe. This figure is in color in the electronic version.

154

155 The climate of the study area is characterized by annual rainfall over 2,000 mm,
 156 with a rainy season between December and June (Silva *et al.* 2016). The average
 157 fluctuation of the lake level has been categorized (Bentes *et al.* 2018) into flood
 158 (December to March), full (April to June), ebb (July to September) and dry (October and
 159 November). The aquatic macrophyte banks covering the Maicá Lake are mainly
 160 dominated by grasses *Paspalum repens* P.J. Bergius and *Echinochloa polystachya*
 161 (Kunth) Hitchc, and by smaller floating plants such as *Eichhornia crassipes* (Mart.)
 162 Solms, *Pistia stratiotes* L. and *Salvinia* spp. (Pinheiro *et al.* 2016).

163 We sampled Squamata reptiles and frogs on continuous banks of aquatic
 164 macrophytes in contact with the lake bank. We sampled 50 plots distributed along 60 km²,
 165 50 meters long and 6 meters wide each, at least 500 m apart, which were parallel to the
 166 lake banks. We detected frogs and reptiles using visual and acoustic search, with three
 167 observers aboard an eight-meter-long canoe. We collected data at a time (March 2019)
 168 when the river flood peak causes a positive peak in reproductively active frogs. We

169 counted individuals between 6:30 PM and 12:00 AM because during this period it is
170 possible to find nocturnal species foraging or calling, and diurnal species resting on
171 macrophytes.

172 We identified species by checking diagnostic characters in the literature (*e.g.*
173 Ávila-Pires 1995; Bailey *et al.* 2005; Garda *et al.* 2010; Lima *et al.* 2012; Fraga *et al.*
174 2013), taxonomic expertise of the team, and comparing our samples with specimens
175 deposited in the Herpetological collection of the Universidade Federal do Oeste do Pará
176 (UFOPA), Santarém, Pará, Brazil. We identified the hylid treefrog *Dendropsophus gr.*
177 *leucophyllatus* at a phylogenetic clade level because there are several morphologically
178 very similar species within this clade (Caminer *et al.* 2017). The taxonomic nomenclature
179 we used follows Frost (2019) for anurans and Costa and Bérnils (2018) for reptiles.

180 We collected voucher specimens, killed them using anesthetic injection of
181 Benzocaine Hydrochloride for reptiles and 5% lidocaine hydrochloride for frogs (Sebben
182 2007), fixed them in 10% formaldehyde, and deposited in the UFOPA Herpetological
183 collection (Appendix 1). Our specimen collection protocols have been authorized by
184 IBAMA/ICMBio/SISBIO, process nº 24072-1, and the Ethics Committee of UFOPA
185 (process Nº 1120180049).

186 We constructed species accumulation curves for reptiles and frogs separately,
187 using number of sampling plots as a measure of sampling effort. We used these curves to
188 provide a quick assessment of the effects of the number and spatial distribution of
189 sampling plots on the sampled assemblages. We assumed that asymptote-stabilized
190 curves suggest little spatial structure in the species distribution, since even increasing the
191 size of the area covered by the sampling plots, the diversity of reptiles and amphibians
192 sampled would change little. We built accumulation curves in the R 3.5.1 environment
193 (R development Core Team 2018) based on raw numbers of species.

194 **RESULTS**

195 We found 27 species, which are roughly classified as 16 frogs, seven snakes and four
196 lizards species (Table 1). The frogs (Figure 2) were represented by the families Hylidae
197 (13 species), Leptodactylidae (2 species) and Bufonidae (*Rhinella marina*). The
198 frequency at which species occurred in relation to the number of plots ranged (mean
199 22.25, SD 26.16) from 2% (*Boana lanciformis*, *Rhinella marina* and *Scinax ruber*) to
200 86% (*Lysapsus limellum*). The lizards were represented by the families Mabuyidae,
201 Teiidae, Dactyloidae and Iguanidae, each of which represented by a single species (Figure
202 3). The frequency ranged (mean 9.5, SD 9.84) from 2% (*Varzea bistrata*) to 24%
203 (*Kentropyx altamazonica*). Snake sampling consisted of four Dipsadidae and two Boidae
204 species (Figure 3). The frequency ranged (mean 4, SD 3.82) from 2% (*Helicops*
205 *leopardinus*, *H. polylepis*, *Lygophis lineatus*, *Philodryas olfersii*) to 12%
206 (*Thamnodynastes lanei*).

207 Most of the sampled species are widely distributed throughout Amazonia or even
208 other ecosystems in South America (e.g. *Eunectes murinus*, *Corallus hortulanus*), and
209 have previously been found occupying aquatic macrophytes (Hoogmoed 1993). As a
210 novelty, we present the use of aquatic macrophytes by the Dipsadidae snakes
211 *Thamnodynastes lanei*, *Philodryas olfersii* and *Lygophis lineatus*, and by the lizards
212 *Varzea bistrata* (Mabuyidae) and *Iguana iguana* (Iguanidae).

213 Regarding the abundance of individuals, our sample effort resulted in the sight of
214 1,432 frogs, of which 56% correspond to the aquatic hylid *Lisapsus limellum* (n = 798).
215 Additionally, we found relatively high abundance of *Dendropsophus walfordi* (n = 201)
216 and *Boana raniceps* (n = 172), and relatively low abundance of *Rhinella marina* (n = 1),
217 *Scinax ruber* (n = 2) and *Scinax x-signatus* (n = 2). The most abundant snake was the
218 dipsadid *Thamnodynastes lanei* (n = 6), followed by *Corallus hortulanus* (n = 3), while

219 the other species were represented in our sample by a single individual. We found 24
 220 lizards, of which 54.16% are *Kentropyx altamazonica* (n = 13), 25% are *Norops auratus*
 221 (n = 6), 16.7% are *Iguana iguana* (n = 4) and 4.14% are *Varzea bistriata* (n = 1).

222

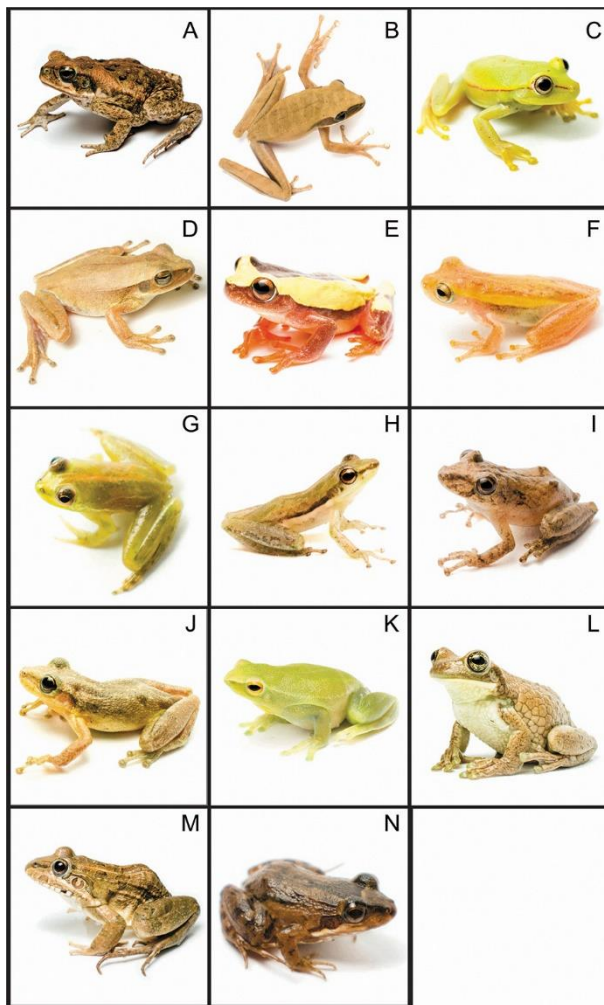
223 **Table 1.** Squamata reptiles and frogs found in aquatic macrophytes in the Maicá Lake,
 224 lower Amazon River, Brazil. Abundance is the maximum raw number of individuals per
 225 species, frequency is relative to 50 sampling plots (each of which 50 m long and 6 m
 226 wide).

Taxonomic ID	Abundance	Frequency (%)
Frogs		
Bufonidae		
<i>Rhinella marina</i> (Linnaeus, 1758)	1	2
Hylidae		
<i>Boana lanciformis</i> (Cope, 1871)	4	2
<i>Boana punctata</i> (Schneider, 1799)	56	26
<i>Boana raniceps</i> (Cope, 1862)	172	70
<i>Dendropsophus</i> gr. <i>Leucophyllatus</i>	38	12
<i>Dendropsophus walfordi</i> (Bokermann, 1962)	201	50
<i>Lysapsus limellum</i> (Parker, 1935)	798	86
<i>Pseudis paradoxa</i> (Linnaeus, 1758)	3	4
<i>Scarthyla goinorum</i> (Bokermann, 1962)	9	8
<i>Scinax nebulosus</i> (Spix, 1824)	23	12
<i>Scinax ruber</i> (Laurenti, 1768)	2	2
<i>Scinax x-signatus</i> (Spix, 1824)	2	4
<i>Sphaenorhynchus lacteus</i> (Daudin, 1800)	15	12
<i>Trachycephalus typhoni</i> (Linnaeus, 1758)	18	10
Leptodactylidae		
<i>Leptodactylus macrosternum</i> Miranda-Ribeiro, 1926	6	12
<i>Leptodactylus wagneri</i> (Peters, 1862)	84	44
Lizards		
Dactyloide		
<i>Norops auratus</i> (Daudin, 1802)	6	6
Mabuyidae		
<i>Varzea bistriata</i> (Spix, 1825)	1	2
Iguanidae		

<i>Iguana iguana</i> (Linnaeus, 1758)	4	6
Teiidae		
<i>Kentropyx altamazonica</i> (Cope, 1875)	13	24
Snakes		
Boidae		
<i>Eunectes murinus</i> (Linnaeus, 1758)	1	2
<i>Corallus hortulanus</i> (Linnaeus, 1758)	3	6
Dipsadidae		
<i>Helicops leopardinus</i> (Schlegel, 1837)	1	2
<i>Helicops polylepis</i> Günther, 1861	1	2
<i>Lygophis lineatus</i> (Linnaeus, 1758)	1	2
<i>Philodryas olfersii</i> (Liechtenstein, 1823)	1	2
<i>Thamnodynastes lanei</i> Bailey, Thomas & Silva-Jr, 2005	6	12

227

228



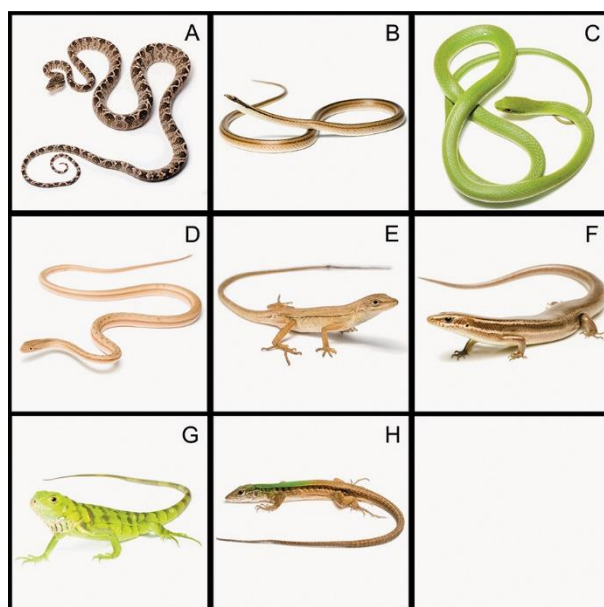
229

230

231 **Figure 2.** Some of the frogs sampled in aquatic macrophytes across the Maicá Lake, lower
 232 Amazon River, Brazil. A) *Rhinella marina*, B) *Boana lanciformis*, C) *Boana punctata* D)
 233 *Boana raniceps*, E) *Dendropsophus* gr. *leucophyllatus*, F) *Dendropsophus walfordi*, G)
 234 *Lysapsus limellum*, H) *Scarthyla goinorum*, I) *Scinax nebulosus*, J) *Scinax x-signatus*, K)
 235 *Sphaenorhynchus lacteus*, L) *Trachycephalus typhonius*, M) *Leptodactylus*
 236 *macrosternum*, N) *Leptodactylus wagneri*. Photos: Francesca N. Angiolani-Larrea. This
 237 figure is in color in the electronic version.

238

239



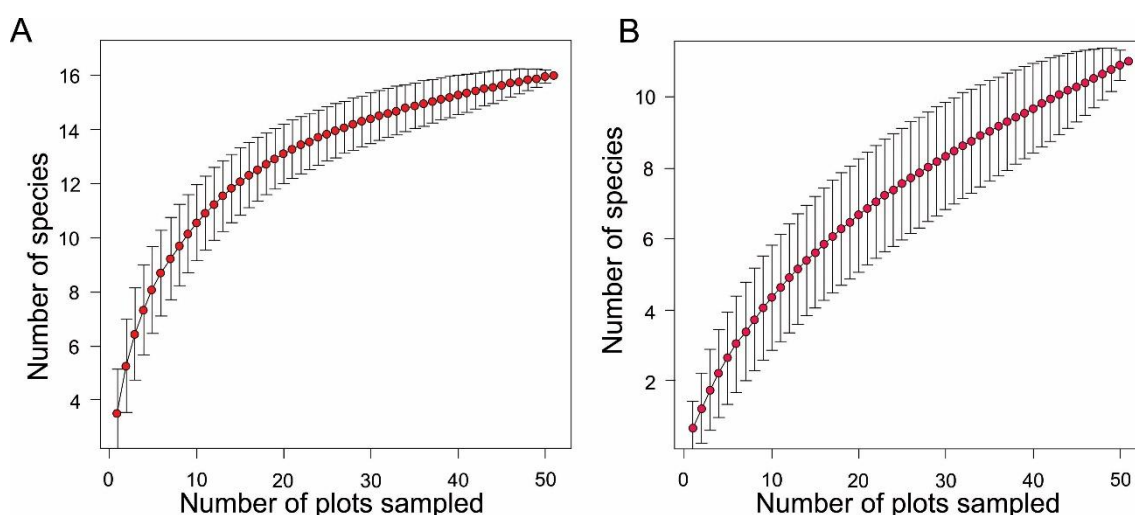
240

241 **Figure 3.** Some of the Squamata reptiles sampled in aquatic macrophytes across the
 242 Maicá Lake, lower Amazon River, Brazil. A) *Corallus hortulanus*, B) *Lygophis lineatus*,
 243 C) *Philodryas olfersii*, D) *Thamnodynastes lanei*, E) *Norops auratus*, F) *Varzea bistrriata*,
 244 G) *Iguana iguana*, H) *Kentropyx altamazonica*. Photos: Francesca N. Angiolani-Larrea.
 245 This figure is in color in the electronic version.

246

247

248 The species accumulation curves did not reach the asymptote for frogs (Figure
249 4A) and Squamata reptiles (Figure 4B). These findings may be associated to high
250 probabilities of adding new species as new plots were added to the sampling effort. This
251 is a particularly expected scenario in the case of the spatial distribution of plots was wide
252 enough to detect heterogeneity in species composition (*e.g.* high levels of beta diversity)
253 throughout the study area, which seems more pronounced in reptiles. However, we did
254 not evaluate patterns of spatial assemblage structure in this study, or the effects of
255 detection probabilities on our abundance data, which would depend on explicitly defined
256 hypotheses and appropriate statistical approaches.



257

258 **Figure 4.** Species accumulation curves based on abundance data of frogs (A) and
259 Squamata reptiles (B). Species were sampled in 50 plots (50 m long, 6 m wide each)
260 distributed across the Maicá Lake, lower Amazon River, Brazil. Vertical lines represent
261 95% confidence intervals. This figure is in color in the electronic version.

262

263

264 DISCUSSION

265 Our results showed that the sampled aquatic macrophyte banks contain a wide variety of
266 species with very different body sizes and life habits. Overall, the sampled species seem

267 to occupy the macrophyte banks through distinct ways. For instance, (i) Although some
268 of the sampled frogs (e.g. *Dendropsophus walfordi*, *Lysapsus limellum*, *Boana raniceps*,
269 *Sphaenorhynchus lacteus*) and reptiles (e.g. *Lygophis lineatus*, *Thamnodynastes lanei*) are
270 widely distributed in Amazonia or even other ecosystems in South America, they have
271 been absent in intensive sampling of forest habitats (e.g. Lima *et al.* 2012; Fraga *et al.*
272 2013; Moraes *et al.* 2017; Ferreira *et al.* 2017). This condition suggests that the local
273 distribution of these species is limited by the availability of aquatic vegetation, and that
274 aquatic macrophyte banks are ecologically complementary to adjacent forests. (ii)
275 Aquatic or semi-aquatic species that are not locally restricted to aquatic macrophyte banks
276 benefit from extensive water dispersal corridors to colonize macrophyte-covered areas or
277 use them as connecting bridges to adjacent habitats. This particular case involves a wide
278 variety of body sizes, such as the tiny frog *Leptodactylus wagneri* and the gigantic Green
279 Anaconda *Eunectes murinus*. (iii) Species that use grass vegetation to forage and disperse
280 (e.g. *Boana punctata*, *Norops auratus*) generally have morphological adaptations to
281 easily disperse across macrophyte banks without necessarily having to swim. However,
282 our data showed that specific swimming or climbing adaptations are not an exclusive
283 condition of species occupying aquatic macrophytes, since we found terrestrial and
284 arboreal species whose bodies do not appear to be adapted to arboreality (e.g. *Rhinella*
285 *marina*), or appear too heavy to disperse over the fragile aquatic vegetation (e.g. *Iguana*
286 *iguana*). (iv) The relatively low abundance of these species seems contradictory to the
287 fact that they are very common in forest edges and urban areas. Such comparison suggests
288 that these species eventually occupy aquatic macrophytes as habitat-opportunists.
289 Therefore, macrophyte banks are relevant habitats for habitat-specific, temporary visitors
290 and generalist species, and should not be neglected in ecology and conservation
291 assessments.

292 All the frog and Squamata reptile species we found are widely distributed along
293 Amazonia, although their local distribution may be limited by the availability of specific
294 habitat conditions (Menin *et al.* 2007; Keller *et al.* 2009; Fraga *et al.* 2011). Species that
295 occupy relatively small regions of environmental gradients depend on high levels of
296 connectivity among habitat patches to occupy wide and highly heterogeneous regions
297 such as Amazonia. Connectivity is highly expected along large rivers such as the Amazon,
298 because there are extensive continuous banks of macrophytes near the riverbanks (Junk,
299 1973). Additionally, proportions of macrophyte banks are fluctuating, and tend to
300 disperse downstream carrying associated animals (Schiesari *et al.* 2003). Therefore, we
301 hypothesized that the sampled aquatic macrophytes have played an important role in
302 defining wide geographic ranges of at least part of the sampled species, as they provide
303 conditions for long-range dispersal, both voluntary and involuntary. This is particularly
304 evident for species that are widely distributed in Amazonia, which have been found in
305 most studies based on data from aquatic macrophytes, such as the treefrogs *Boana*
306 *raniceps*, *Boana punctata*, *Sphaenorhynchus lacteus*, and *Dendropsophus* gr.
307 *leucophyllatus* (Hödl 1977; Hoogmoed 1993; Schiesari *et al.* 2003; Upton *et al.* 2014;
308 Ramalho *et al.* 2017; Böning *et al.* 2017). Species abundance and levels of gene flow
309 should be quantified in different stretches of large rivers (e.g. Amazon) and associated
310 lakes to explicitly test such hypothesis.

311 Although we have sampled typical species of aquatic ecosystems and grassy
312 vegetation, we have also found terrestrial (e.g. *Rhinella marina*, *Leptodactylus*
313 *macrosternum*) and arboreal species (e.g. *Corallus hortulanus*, *Iguana iguana*) apparently
314 poorly adapted to the fragile aquatic vegetation on a flooded substrate. This finding may
315 be associated with the fact that we collected data during the season when the regional
316 rivers reached their maximum level. Large proportions of terrestrial habitats become

317 unavailable at this time, and non-aquatic species tend to be isolated on islands of
318 unflooded habitats or disperse away to adjacent habitats (Upton *et al.* 2014). Therefore,
319 aquatic macrophyte banks primarily act as habitat flood refuges for terrestrial and arboreal
320 species. However, we have observed several individuals of *Leptodactylus macrosternum*
321 in reproductive activity (male calling, amplexus), suggesting that aquatic macrophytes
322 are not only opportunistically occupied hiding sites, but also act as reproductive sites even
323 for non-specialized species. Macrophytes are advantageous breeding and recruiting sites
324 for frogs (Hödl 1977; Upton 2013; Böning *et al.* 2017) because of the high availability of
325 shelter to tadpoles in the root zone of the floating vegetation, and the high nutritional
326 quality provided by the primary productivity and plant decomposition (Böning *et al.*
327 2017).

328 The lizard diversity we found is relatively low compared to most of forests, which
329 is consistent with the literature (Hoogmoed 1993). The most abundant species in our
330 sample, *Kentropyx altamazonica* (Teiidae), has finger lamellae that facilitate water
331 dispersal (Luke 1986), and therefore its occurrence is widely expected in macrophyte
332 banks within its geographical range (Ávila-Pires 1995; Martins 1996; Vitt *et al.* 2001).
333 However, even non-aquatic species have occupied aquatic macrophytes because of food
334 availability, thermoregulation and refuge sites in these habitats. Aquatic macrophytes
335 provide suitable habitats for a wide variety of invertebrates (Junk 1973), which are rich
336 sources of nutrients for most species we found in this study (Ávila-Pires 1995; Martins
337 1996; Vitt *et al.* 2001). Additionally, a combination of plant stratification and high solar
338 incidence generates two-way thermoregulation sites, because the perch height and
339 orientation angle relative to the sun allows heat gain or loss (Maia-Carneiro 2018).
340 Finally, plant stratification also generates levels of predatory refuge sites, as water may
341 be a barrier to terrestrial predators, and grassy vegetation can provide good conditions for

342 efficient camouflage of some species (e.g. *Norops auratus*), which should be especially
343 effective against flying predators. Therefore, although lizard diversity is relatively low in
344 aquatic macrophyte banks, and macrophytes are unlikely to act as exclusive habitats for
345 the species we found, these particular habitats should not be neglected as important
346 components of the spatial structure of lizard populations and assemblages.

347 Our snake sampling should be considered as incomplete, considering that low
348 detection probabilities often cause the need for additional surveys per sampling plot
349 (Steen 2010; Fraga *et al.* 2014). Overall, our data suggest that most species that occupy
350 the sampled macrophyte banks use these habitats occasionally as temporary foraging sites
351 and dispersal corridors. Exceptions are marked by aquatic species (e.g. *Helicops* spp.),
352 which should spend long periods among macrophytes, as there is high availability of prey
353 (i.e. fish, anurans and tadpoles), and refuge sites (Ávila *et al.* 2006). Additionally, we
354 highlight *Thamnodynastes lanei* (Dipsadidae) as a special case in which aquatic
355 macrophytes apparently favor high population densities. This finding is based on the fact
356 that the species has rarely been found in snake sampling in eastern Amazonia (e.g. Moraes
357 *et al.* 2017; Morato *et al.* 2018, Fraga unpublished data), and in our study it was the most
358 abundant species. High abundance of *Thamnodynastes* snakes has been attributed to the
359 high availability of prey frogs (Bellini 2013). Additionally, all *T. lanei* individuals we
360 found were on the floating grass *Paspalum repens*, whose dried leaves are very similar
361 in color and diameter to the body of *T. lanei*. We hypothesized that *T. lanei* populations
362 should be positively affected in aquatic macrophyte banks by a combination of high prey
363 availability and efficient camouflage. Ecological models based on multiple surveys per
364 plot are required to explicitly test such hypothesis.

365

366

367 **CONCLUSIONS**

368 Our study showed that aquatic macrophytes are important habitats for a diverse
369 fauna of reptiles and frogs with varying body sizes, shapes and life habits. Our data
370 suggest that few species have local distribution restricted to macrophyte banks, but many
371 species benefit from the environmental suitability provided by macrophytes. Although
372 apparently homogeneous, aquatic macrophytes concentrate large proportions of local
373 biodiversity, and therefore should not be neglected in environmental impact assessments.
374 This is particularly critical in our study area (Maicá Lake), because the construction of a
375 port has been started without any study of potential environmental impacts based on
376 properly collected data. We expect that our sampling design and species list may be useful
377 as a basis for decision making on environmental compensation or mitigation, or at least
378 as a benchmark for measuring future disturbances in reptile and frog assemblages. We
379 expect ship traffic across Maicá Lake to change the frog and Squamata species
380 composition and density by changing the physicochemical properties of the water and the
381 physical structure of the macrophyte banks (e.g. vegetation height and bank position
382 stability). Additionally, considering that no environmental impact assessment has been
383 officially conducted in the Maicá Lake, we expect that our study will be an incentive for
384 sampling other groups of organisms.

385

386 **ACKNOWLEDGMENTS**

387 We are very thankful to the guide Lalico and Lázaro for the field support in Maicá lake.
388 Bill Magnusson and Albertina Lima provided valuable suggestions on the sampling
389 design. Many undergrad students at the Universidade Federal do Oeste do Pará helped in
390 the data collection. This study was financed in part by the Coordenação de
391 Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Fiance Code 001, for

392 PHSG (master's degree scholarship), FNAL (master's degree scholarship through OEA
393 PAEC-GCUB agreement) and RF (PNPD postdoc fellowship). LBN received a
394 scholarship from Fundação Amazônia de Amparo e Estudos e Pesquisas (FAPESPA).

395

396 REFERENCES

397 Achaval, F.; González, J.G.; Meneghel, M.; Melgarejo, A.R. 1979. Lista comentada del
398 material recogido em Costas Uruguayas, transportado por camalotes desde el Rio
399 Paraná. *Acta Zoologica Lilloana*, 35: 195–200.

400 Ávila, R.W.; Ferreira, V.L.; Arruda, J.A. 2006. Natural history of the South American
401 water snake *Helicops leopardinus* (Colubridae: Hydropsini) in the Pantanal, Central
402 Brazil. *Journal of Herpetology*, 40(2): 274–279.

403 Ávila-Pires, T.C.S. 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata).
404 *Zoologische Verhandelingen*, 299: 1–706.

405 Ávila-Peres, T.C.S.; Ramalho, W.P. 2019. Censo da Biodiversidade da Amazônia
406 Brasileira. Grupo: Lagartos. (www.museu-goeldi.br/censo). Accessed on 30/08/2018.

407 Ávila-Pires, T.C.S.; Hoogmoed, M.S.; Vitt, L.J. 2007. Herpetofauna da Amazônia. In:
408 Nascimento, L.B.; Oliveira, M.E. (Eds). *Herpetologia no Brasil II*. Sociedade
409 Brasileira de Herpetologia, p. 13–43.

410 Azevedo-Ramos, C.; Galatti, U. 2002. Patterns of amphibian diversity in Brazilian
411 Amazonia: conservation implications. *Biological Conservation*, 103: 103–111.

412 Bailey, J.R.; Thomas, R.A.; Silva Jr., N.J. 2005. A revision of the South American snake
413 genus *Thamnodynastes* Wagler, 1830 (Serpentes, Colubridae, Tachymenini). I. Two
414 new species of *Thamnodynastes* from Central Brazil and adjacent areas, with a
415 redefinition of and neotype designation for *Thamnodynastes pallidus* (Linnaeus,
416 1758). *Phyllomedusa*, 4(2): 83–101.

- 417 Bellini, G.P.; Arzamendia, V.; Giraud, A.R. 2013. Ecology of *Thamnodynastes*
418 *hypoconia* in subtropical–temperate South America. *Herpetologica*, 69: 67-79.
- 419 Bentes, K.L.S.; Oliveira, L.L.; Zacardi, D.M.; Barreto, N.J.C. 2018. The relationship
420 between hydrologic variation and fishery resources at the lower Amazon, Santarém,
421 Pará. *Revista Brasileira de Geografia Física*, 11(4): 1478–1489.
- 422 Böning, P.; Wolf, S.; Upton, K.; Menin, M.; Venegas, P.J.; Lötters, S. 2017. Amphibian
423 diversity and its turnover in floating meadows along the Amazon river. *Salamandra*,
424 53: 379–388.
- 425 Brooks, T.M.; Mittermeier, R.A.; Fonseca, G.A.B.; Gerlach, J.; Hoffmann, M.;
426 Lamoreux, J.F.; *et al.* 2006. Global biodiversity conservation priorities. *Science*, 313:
427 58–61.
- 428 Caminer, M.A.; Milá, B.; Jansen, M.; Fouquet, A.; Venegas, P.J.; Chávez, G.; *et al.* 2017.
429 Systematics of the *Dendropsophus leucophyllatus* species complex (Anura: Hylidae):
430 Cryptic diversity and the description of two new species. *PLoS ONE* 12(3): e0171785.
- 431 Costa, H.C.; Bérnils, R.S. 2018. Répteis do Brasil e suas Unidades Federativas: Lista de
432 espécies. *Herpetologia Brasileira*, 7(1): 11–57.
- 433 Ferreira, G.C.; Sturaro, M.J.; Peloso, P.L.V. 2017. Amphibians and reptiles from Floresta
434 Nacional de Pau-Rosa, Amazonas, Brazil: an important protected area at the heart of
435 Amazonia. *Acta Amazônica*, 47(3): 259–268.
- 436 Fraga, R.; Lima, A.P.; Magnusson, E.W. 2011. Mesoscale spatial ecology of a tropical
437 snake assemblage the width of riparian corridors in central Amazonia. *Herpetological*
438 *Journal*, 21: 51–57.
- 439 Fraga, R.; Lima, A.P.; Prudente, A.L.C.; Magnusson, W.E. 2013. *Guia de cobras da*
440 *região de Manaus – Amazônia Central*. Editora INPA, Manaus, 303 p.
- 441 Fraga, R.; Stow, A.J.; Magnusson, W.E.; Lima, A.P. 2014. The costs of evaluating species

- 442 densities and composition of snakes to assess development impacts in Amazonia. *PLoS*
443 *ONE* 9: e105453.
- 444 Fraga, R.; Ferrão, M.; Stow, A.J.; Magnusson, W.E.; Lima, A.P. 2018. Different
445 environmental gradients affect different measures of snake β -diversity in the Amazon
446 rainforests. *PeerJ Preprints*, 6(1): 27146.
- 447 Fraga, R.; Torralvo, K. 2019. New record of the fringed leaf frog, *Cruziohyla craspedopus*
448 (Anura: Phyllomedusidae) extends its eastern range limit. *Acta Amazonica*, 49(3):
449 208–212.
- 450 Frost, D.R. 2019. Amphibian species of the world: an online reference. Version 6.0.
451 American Museum of Natural History, New York, USA
452 (<http://research.amnh.org/herpetology/amphibia/index.html>). Accessed on
453 28/09/2019.
- 454 Garda, A.A.; Santana, D.J.; São-Pedro, V.A. 2010. Taxonomic characterization of
455 Paradoxical frogs (Anura, Hylidae, Pseudae): geographic distribution, external
456 morphology, and morphometry. *Zootaxa*, 2666: 1-28.
- 457 Gibbons, J.; Scott, D.E.; Ryan, T.J.; Buhlmann, K.A.; Tuberville, T.D.; Metts, B.S.; *et al.*
458 2000. The Global Decline of Reptiles, *Déjà Vu* Amphibians. *BioScience*, 50: 653-666.
- 459 Guerrero, E.L.; Agnolin, F.L.; Grilli, P.; Suazo, L.F.A.; Boné, E.; Tenorio, A.B.; *et al.*
460 2017. Inventario de la fauna transportada por balsas de vegetación flotante en el
461 Sistema fluvial del Río de La Plata. *Revista del Museo Argentino de Ciencias*
462 *Naturales*, 19(2): 177–183.
- 463 Hödl, W. 1977. Call differences and calling site segregation in anuran species from
464 Central Amazonian floating meadows. *Oecologia*, 28:351–363.
- 465 Hoogmoed, M.S. 1993. The herpetofauna of floating meadows. In: Ouboter, P.E. (org.).
466 *The freshwater ecosystem of Suriname*. Academic Publishers, Dordrecht, p.199–213.

- 467 Hoogmoed, M.S.; Galatti, U. 2018a. Censo da biodiversidade da Amazônia brasileira.
468 Grupo: Gymnophiona. (<http://www.museu-goeldi.br/censo/>). Accessed on
469 13/08/2019.
- 470 Hoogmoed, M.S.; Galatti, U. 2018b. Censo da Biodiversidade da Amazônia Brasileira.
471 Grupo: Caudata. (<http://www.museu-goeldi.br/censo/>). Accessed on 13/08/2019.
- 472 Hoogmoed, M.S.; Galatti, U. 2019. Censo da Biodiversidade da Amazônia Brasileira.
473 Grupo: Anura. (<http://www.museu-goeldi.br/censo/>). Accessed on 30/08/2019.
- 474 Ihering, V.R. 1911. Cobras e amphibios das ilhotas de “Aguapé”. *Revista do Museu*
475 *Paulista* 8: 454–461.
- 476 Junk, W.J. 1973. Investigation of the ecology and production-biology of the “floating
477 meadows” (Paspalo- Echinochloetum) on the Midler Amazon. II. The aquatic fauna in
478 the root zone floating vegetation. *Amazon*, 4: 9-112.
- 479 Junk, W.J.; Bayley, P.B.; Sparks, R.E. 1989. The flood pulse concept in river-floodplains
480 systems. *Canadian Special Publication of Fisheries and Aquatic Science*, 106: 110–
481 127
- 482 Junk, W.J.; Ohly, J.J.; Piedade, M.T.F.; Soares, M.G.M. 2000. *The central Amazon*
483 *floodplain actual use and options for a sustainable management*. Backhuys Publishers,
484 Leiden, 584p.
- 485 Junk, W.J.; Piedade, M.T.F.; Schöngart, J.; Cohn-Haft, M.; Adeney, J.M.; Wittmann, F.
486 2011. A classification of major naturally-occurring amazonian lowland wetlands.
487 *Wetlands*, 31: 623–640.
- 488 Keller, A.; Rödel, M.O.; Linsenmair, E.; Grafe, U. 2009. The importance of
489 environmental heterogeneity for species diversity and assemblage structure in Bornean
490 stream frogs. *Journal of Animal Ecology*, 78: 305–314.
- 491 Lima, A.P.; Magnusson, W.F.; Menin, M.; Erdtmann, L.K.; Rodrigues, D.J.; Keller, C.;

- 492 Hodl, W. 2012. *Guia de sapos da Reserva Adolph Ducke – Amazônia Central*. Second
493 Edition. Attema, Manaus, 168p.
- 494 Luke, C. 1986. Convergent evolution of lizard toe fringes. *Biological Journal of the*
495 *Linnean Society*, 27: 1–16.
- 496 Maia-Carneiro, T.; Winck, G.R.; Pereira, M.R.; Rocha, C.F. 2018. Body orientation for
497 termo thermoregulation and daily activity cycle of *Mabuya macrorhyncha* (Squamata:
498 Scincidae). *Zoologia*, 35: e24575.
- 499 Martins, M. 1996. Defensive tactics in lizards and snakes: the potential contribution of
500 the neotropical fauna. In: Del Claro, K. (Ed.). *Anais do XIV Encontro Anual de*
501 *Etologia*. Sociedade Brasileira de Etologia, Universidade Federal de Uberlândia,
502 Uberlândia, p.185–199.
- 503 Menin, M; Lima, A.L; Magnusson, W.E.; Waldez, F. 2007. Topographic and edaphic
504 effects on the distribution of terrestrially reproducing anurans in the Central
505 Amazonia: mesoscale spatial patterns. *Journal of Tropical Ecology*, 23: 539–547.
- 506 Moraes, L.J.; Almeida, A.P.; Fraga, R.; Rojas, R.R.; Pirani, R.M.; Silva, A.A.; Carvalho,
507 V.T.; Gordo, M.; Werneck, F.P. 2017. Integrative overview of the herpetofauna from
508 Serra da Mocidade, a granitic mountain range in northern Brazil. *ZooKeys*, 715: 103–
509 159.
- 510 Morato, S.A.A.; Ferreira, G.N.; Scupino, M.R.C. 2018. *Herpetofauna da Amazônia*
511 *Central: Estudos da Flona de Saracá-Taquera*. STCP Engenharia de Projetos Ltda,
512 Curitiba; MRN -Mineração Rio do Norte S. A, Porto Trombetas, 210p.
- 513 Padial, A.A.; Thomaz, S.M.; Agostinho, A.A. 2009. Effects of structural heterogeneity
514 provided by the floating macrophyte *Eichhornia azurea* on the predation efficiency
515 and habitat use of the small Neotropical fish *Moenkhausia sanctaefilomenae*.
516 *Hidrobiologia*, 624: 161–170.

- 517 Parolin, P. 2012. Diversity of adaptations to flooding in trees of Amazonian floodplains.
518 *Revista Pesquisas-Botânica*, 63: 7–28.
- 519 Piedade, M.T.F.; Junk, W.J.; D'Angelo, S.A.; Wittmann, F.; Schoengart, J.; Lopes, A.
520 2010. Aquatic herbaceous plants of the Amazon floodplains: state of the art and
521 research needed. *Acta Limnologica Brasiliensia*, 2: 165–17.
- 522 Pinheiro, D.T.; Correa, J.M.S.; Chaves, C.S.; Campos, D.P.F.; Ponte, S.C.S.; Zacardi,
523 D.M. 2016. Diversidade e distribuição da ictiofauna associada a bancos de macrófitas
524 aquáticas de um lago de inundação amazônico, estado do Pará, Brasil. *Acta of*
525 *Fisheries and Aquatic Resources*, 2: 59–70.
- 526 Ponte, S.C.S.; Oliveira, L.S.; Zacardi, D.M. 2019. Variação temporal de larvas de peixes
527 de um lago de inundação como subsídio à gestão ambiental. *Journal of Applied Hydro-*
528 *Environment and Climate*, 1(1): 1–13.
- 529 Prudente, A.L.C.; Da Silva, F.M. 2017. Censo da Biodiversidade da Amazônia Brasileira.
530 Grupo: Serpentes. (<http://www.museu-goeldi.br/censo/>>). Accessed on 13/08/2019.
- 531 Ramalho, W.P.; Machado, I.F.; Vieira, L.J.S. 2017. Do flood pulses structure amphibian
532 communities in floodplain environments? *Biotropica*, 50: 338–345.
- 533 Sanchez-Botero, J.I.; Araújo-Lima, A.R.M. 2001. As macrófitas aquáticas como berçário
534 para a ictiofauna da várzea do rio Amazonas. *Acta Amazonica*, 31(3): 437–447.
- 535 Sarli, V.; Santos, M.; Maneyro, R.; Achaval, F. 1992. *Nuevos aportes sobre la fauna*
536 *arribada a las costas uruguayas en balsas de camalotes*. *Boletín de la Sociedad*
537 *Zoológica del Uruguay*, 7: 77–78.
- 538 Schiesari, L.; Zuanon, J.; Azevedo-Ramos, C.; Garcia, M.; Gordo, M.; Messias M.;
539 Monteiro, E. 2003. Macrophyte rafts as dispersal vectors for fishes and amphibians in
540 the lower Solimões River, Central Amazon. *Journal of Tropical Ecology*, 19: 333–
541 336.

- 542 Sebben, A. 2007. Microdissecação fisiológica a fresco: uma nova visão sobre a anatomia
543 de anfíbios e répteis. In: Nascimento, L.B.; Oliveira, M.E. (Eds). *Herpetologia no*
544 *Brasil II*. Sociedade Brasileira de Herpetologia, p.311–325.
- 545 Silva, M.A.G.; Guimarães.; J.M.J.; Silva, N.F.C.; Santos, F.C.V.; Ucker, F.E. 2016.
546 Caracterização pluviométrica de Santarém-PA, Brasil. *Renefara*, 10: 112–120.
- 547 Steen, D.A. 2010. Snakes in the grass: secretive natural histories defy both conventional
548 and progressive statistics. *Herpetological Conservation and Biology*, 5(2): 183–188.
- 549 Upton, K. 2013. The importance of floating meadows for amphibians in a flooded forest.
550 *Froglog*, 21: 62–64.
- 551 Upton, K.; Warren-Thomas, E.; Rogers, I.; Docherty, E. 2014. Amphibian diversity on
552 floating meadows in flooded forests of the Peruvian Amazon. *Herpetological Review*,
553 45: 209–212.
- 554 Vitt, L.J.; Sartorius, S.S.; Ávila-Pires, T.C.S.; Espósito, M.C. 2001. Life at river's edge:
555 Ecology of *Kentropyx altamazonica* in the Brazilian Amazon. *Canadian Journal of*
556 *Zoology*, 79: 1855–1865.
- 557 Whittaker, K.; Koo, M.S.; Wake, D.B.; Vredenburg, V.T. 2013. Global Declines of
558 Amphibians. In: Levin, S.A. (Ed.). *Encyclopedia of Biodiversity*. Waltham, MA:
559 Academic Press, San Diego, USA, p. 691-699.
- 560 Wintle, B.A.; Kujala, H.; Whitehead, A.; Cameron, A.; Veloz, S.; Kukkala, A.; *et al.*
561 2019. Global synthesis of conservation studies reveals the importance of small habitat
562 patches for biodiversity. *Proceedings of the National Academy of Sciences*, 116(3):
563 909–914.

564 **APPENDIX 1.** List of voucher specimens collected in 50 plots (300 m² each) on the
565 Maicá Lake, lower Amazon River. The specimens were deposited in the herpetological
566 collection of the Universidade Federal do Oeste do Pará, Santarém, Brazil (UFOPA-H).

567

568 **Frogs:** *Boana lanciformis* (UFOPA-H 1910), *Boana punctata* (UFOPA-H
569 H1911–1916), *Boana raniceps* (UFOPA-H 1917–1927), *Dendropsophus* gr.
570 *leocophyllatus* (1931–1938), *Dendropsophus walfordi* (1939–1949), *Leptodactylus*
571 *macrosternum* (UFOPA-H 1953, 1960), *Leptodactylus wagneri* (UFOPA-H 1954–1959),
572 *Lysapsus limellum* (UFOPA-H 1962), *Scarthyla goirorum* (UFOPA-H 1965–1967),
573 *Scinax nebulosus* (UFOPA-H 1968–1971), *Scinax x-signatus* (UFOPA-H 1972, 1973),
574 *Sphaenorhynchus lacteus* (UFOPA-H 1974–1977), *Trachycephalus typhonius* (UFOPA-
575 H 1984–1987).

576 **Lizards:** *Iguana iguana* (UFOPA-H 1951), *Kentropyx altamazonica* (UFOPA-H
577 1905–1909), *Norops auratus* (UFOPA-H 1963), *Varzea bistriata* (UFOPA-H 1928).

578 **Snakes:** *Corallus hortulanus* (UFOPA-H 1929, 1930), *Helicops polylepis*
579 (UFOPA-H 1951), *Lygophis lineatus* (UFOPA-H 1961), *Philodryas olfersii* (UFOPA-H
580 1964), *Thamnodynastes lanei* (UFOPA-H 1978–1983).

581

Comentários à coordenação do PPGBEES:

Pesquisa bem planejada e desenvolvida, com resultados alcançados analisados e apresentados de forma adequada e bem discutidos, que serão referências sobre a herpetofauna amazônica.

Avaliação final do projeto de dissertação de mestrado**I - Aprovado (X)**

indica que o revisor aprova a dissertações em correções ou com correções mínimas

II - Aprovado com Correções ()

indica que o avaliador aprova o projeto com correção extensas, mas que a dissertação não precisa retornar ao avaliador para reavaliação

III - Necessita Revisão ()

indica que há necessidade de reformulação do trabalho e que avaliador quer reavaliar a nova versão da dissertação antes de emitir uma decisão final

IV - Reprovado ()

indica que a dissertação não é adequada, nem com modificações substanciais

Identificação do membro da banca:

CPF: 095.451.098-40

Data: 07/Janeiro/2020

Assinatura:



I - Aprovado (X)

indica que o revisor aprova a dissertações em correções ou com correções mínimas

II - Aprovado com Correções ()

indica que o avaliador aprova o projeto com correção extensas,mas que a dissertação não precisa retornar ao avaliador para reavaliação

III - Necessita Revisão ()

indica que há necessidade de reformulação do trabalho e que avaliadorquer reavaliar a nova versão da dissertação antes de emitir uma decisão final

IV - Reprovado ()

indica que a dissertação não é adequada, nem com modificações substanciais

Identificação do membro da banca: Igor Luis Kaefer

Deseja identificar-se ao candidato e orientador(es): (X) Sim () Não

Data: 31/01/2020

Assinatura:



Comentários à coordenação do PPGBEES:

A dissertação está muito bem escrita e estruturada. Os resultados trazem dados novos e relevantes, e certamente é um trabalho com uma grande contribuição ao conhecimento da fauna neotropical. O trabalho também tem grande relevância social, uma vez que discute um tema complexo que são os efeitos da construção de portos na região de Santarém.

A quantidade e a qualidade das figuras são adequadas. A metodologia deve ser mais clara, permitindo ao leitor se situar melhor sobre a execução do projeto, e permitir a outros pesquisadores a replicação do estudo. Os resultados e a discussão estão coerentes e claros. Entretanto, nos dois capítulos, algumas informações devem ser movidas dos resultados para a discussão.

As referências devem ser padronizadas de acordo com as normas da revista.

Recomendo a aprovação da dissertação com apenas algumas sugestões de correções que podem ser acatadas ou não pelos autores. Nada que comprometa a qualidade final do trabalho.

Algumas dúvidas que tive e poderiam ser facilmente contornadas através de uma conversa com os autores eu incluí no pdf da dissertação.

As minhas sugestões ao texto estão inclusas no pdf em anexo.

Sugiro ao PGBEES enviar aos revisores uma versão em formato Word para facilitar a correção do texto e inclusão de sugestões.

Avaliação final do projeto de dissertação de mestrado**I - Aprovado (X)**

indica que o revisor aprova a dissertações em correções ou com correções mínimas

II - Aprovado com Correções ()

indica que o avaliador aprova o projeto com correção extensas, mas que a dissertação não precisa retornar ao avaliador para reavaliação

III - Necessita Revisão ()

indica que há necessidade de reformulação do trabalho e que avaliador quer reavaliar a nova versão da dissertação antes de emitir uma decisão final

IV - Reprovado ()

indica que a dissertação não é adequada, nem com modificações substanciais

Identificação do membro da banca: Samuel Campos Gomides

CPF: 079.715.736-00

Data: 24 de janeiro de 2020

Assinatura: