



INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Avaliação espaço-temporal dos efeitos da inundação de habitats sobre a diversidade taxonômica e funcional de anuros em uma hidrelétrica a fio d'água na Amazônia, Brasil.

JUSSARA SANTOS DAYRELL

Manaus, Amazonas

Abril, 2022

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AVALIAÇÃO ESPAÇO-TEMPORAL DOS EFEITOS DA INUNDAÇÃO DE HABITATS SOBRE A DIVERSIDADE TAXONÔMICA E FUNCIONAL DE ANUROS NA PRIMEIRA HIDRELÉTRICA A FIO D'ÁGUA NA AMAZÔNIA, BRASIL.

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Tese apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto Nacional de Pesquisas da Amazônia, como parte dos requisitos para obtenção do título de Doutor em Biologia (Ecologia).

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ATA DA DEFESA PÚBLICA DA TESE DE DOUTORADO DO PROGRAMA DE PÓS- GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 22 dias do mês de Abril do ano de 2022, às 08h30min, via videoconferência, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o Dr. **Mário Ribeiro de Moura**, da Universidade Federal da Paraíba – UFPB, a Dra. **Maíra benchimol de Souza**, da Universidade Estadual De Santa Cruz – UESC , o Dr. **Santiago Castroviejo Fisher**, da Universidade de Sevilha – US, o Dr. **Fabricio Beggiato Baccaro**, da Universidade Federal do Amazonas – UFAM e a Dra. **Ana Filipa Palmeirim**, da Universidade de East Anglia – UEA, tendo como suplentes a Dra. Camila Cherem Ribas, do Instituto Nacional de Pesquisas da Amazônia – INPA e a Dra. Fernanda de Pinho Werneck, do Instituto Nacional de Pesquisas da Amazônia – INPA, sob a presidência da orientadora, a fim de proceder a arguição pública do trabalho de **TESE DE DOUTORADO** de **JUSSARA SANTOS DAYRELL**, intitulado: “**AVALIAÇÃO ESPAÇO-TEMPORAL DOS EFEITOS DA INUNDAÇÃO DE HABITATS SOBRE A DIVERSIDADE TAXONÔMICA E FUNCIONAL DE ANUROS EM UMA HIDRELÉTRICA A FIO D'ÁGUA NA AMAZÔNIA, BRASIL**”, orientada pela Dra. Albertina Pimentel Lima e Co-orientadora pelo Dr. William Ernest Magnusson, ambos do Instituto Nacional de Pesquisas da Amazônia – INPA.

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

APROVADO (A)

REPROVADO (A)

POR UNANIMIDADE

POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

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Sinopse: Nessa tese, foram utilizados dados do Programa de Monitoramento de Herpetofauna Terrestre da Usina Hidrelétrica Santo Antônio, rio Madeira, coletados entre 2010 e 2017 para avaliar os efeitos temporais e espaciais do enchimento do primeiro reservatório a fio d'água na diversidade taxonômica e funcional de anuros.

Palavras-chave: Composição de espécies de anuros, traços funcionais; hidrelétricas; barragem a fio d'água; Monitoramento de longo prazo; Perda de habitat; Avaliação de impacto ambiental.

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Resumo

A Amazônia brasileira possui aproximadamente 90% (~ 95 MW) de potencial de energia não explorado e existem projetos futuros das agências governamentais do planejamento para a construção de mais de 200 novas barragens de hidrelétricas na região. Embora as usinas hidrelétricas tenham sido promovidas como fontes de energia mais “limpas”, o barramento dos rios interrompe a continuidade do rio e causam a inundação dos ecossistemas terrestres adjacentes. A inundação das terras baixas causa mudanças na composição das espécies, em particular nas espécies diretamente associadas aos gradientes inundados. Para uma melhor compreensão dos impactos ambientais de barragens hidrelétricas sobre as espécies silvestres, é obrigatório avaliar os impactos antes e depois das cheias do reservatório e como os animais terrestres ou aquáticos são afetados pela perda de habitat e consequente formação de reservatórios. Os levantamentos de fauna associados às avaliações de impacto ambiental da hidrelétrica de Santo Antônio em Rondônia estão entre os mais intensivos, bem planejados e de longo prazo já realizados no Brasil. Esta é uma hidrelétrica, construída em 2012, apresenta turbinas do tipo bulbo que requerem menos água e produzem um reservatório de tamanho reduzido (271 km²). O objetivo geral dessa tese foi avaliar os efeitos espaciais e temporais da inundação do reservatório da Usina Hidrelétrica de Santo Antônio integrando dados de espécies de anuros amostrados em áreas que seriam inundadas e não inundadas antes da construção da hidrelétrica com dados coletados em áreas não inundadas após o barramento do rio. Nós usamos a base de dados do Monitoramento da Herpetofauna coletados entre 2010 e 2017 em que os dados foram coletados 2 anos antes, em áreas posteriormente inundadas pela hidrelétrica (estágio pré-inundado) e não inundadas (pré-não inundado), com intervalos logo após o enchimento (pós 1) e 2 anos depois do enchimento (pós 2). A tese é composta por dois capítulos que avaliam diferentes aspectos dos efeitos temporais e espaciais do enchimento da barragem na composição taxonômica e funcional dos anuros. No total, foram registradas 120 espécies de anuros durante todo o monitoramento, incluindo registros ocasionais. No capítulo 1 o enchimento da barragem da hidrelétrica teve pouco efeito no número de espécies, mas alterou a abundância delas após a criação do reservatório. A composição de sapos nas áreas permanentemente inundadas pelo barramento do rio não se restabeleceu nas áreas remanescentes e 6% das espécies não foram mais registradas. Nas áreas não inundadas, também houve mudanças na composição de espécies ao longo do tempo, com o ganho de espécies em 82% das parcelas amostradas, principalmente naquelas localizadas próximas da nova margem do rio Madeira. Esse aumento no número de espécies nas áreas remanescentes pode ser uma resposta à inundação das áreas baixas, pois, após o enchimento do reservatório, os anuros podem ter se deslocado às áreas mais próximas, aumentando o número de espécies registradas. Isso ocorre no período de reestruturação da comunidade após uma perturbação, onde algumas populações podem diminuir enquanto outras ocupam os novos

ambientes. No capítulo 2, nós amostramos 58 parcelas antes da inundação (2010–2011), sendo 19 delas inundadas após a criação do reservatório. Para o período pré inundação categorizamos os dados em 19 parcelas inundadas e 39 parcelas não inundadas. Sendo essas amostradas novamente dois anos após o estabelecimento da barragem. Com a inundação das terras mais baixas, houve uma perda da diversidade e singularidade funcional das assembleias de anuros. A composição funcional da área inundada foi distinta da área não inundada. A inundação não resultou na eliminação completa de nenhum traço ou combinação de traços ecológicos das assembleias de anuros. As diferenças na diversidade funcional das assembleias de anuros amazônicos foram em grande parte devido a diferenças ambientais entre áreas sazonalmente inundadas e não inundadas. Traços ecológicos funcionais ligados a estratégias reprodutivas, como deposição de ovos e desenvolvimento larval, ajudam a entender as respostas de anuros em toda a comunidade às mudanças temporais causadas por barragens a fio d'água. Os resultados dessa tese mostraram que os efeitos do barramento do rio Madeira pela Usina Hidrelétrica de Santo Antônio foram rápidos, observados nos primeiros dois anos após a inundação do reservatório. As assembleias dos anuros das florestas de várzea foram as mais impactadas pela formação do reservatório e não foram incorporadas nas áreas remanescentes não inundadas depois da construção da barragem. A implantação do reservatório não reduziu o número de espécies de anuros, mas houve mudanças na composição funcional e taxonômica com uma diminuição geral na abundância após a inundação do reservatório. O entendimento dos efeitos sobre a biodiversidade requer estudos de longo prazo e, no caso dos projetos de infraestrutura de grande escala, estes estudos devem começar bem antes da construção da barragem para que flutuações naturais das espécies também possam ser documentadas. Com isso, nossos resultados mostram a necessidade de proteção das florestas naturalmente inundáveis afetadas por barramentos de hidrelétricas. Como novos barramentos de hidrelétricas estão planejados para a Amazônia, recomendamos a adoção de uma legislação voltada para hidrelétricas que incorpore a criação de unidades de conservação com especial atenção para os tipos de vegetação permanentemente suprimidos.

Palavras-chave: Composição de espécies de anuros, traços funcionais; hidrelétricas; barragem a fio d'água; Monitoramento de longo prazo; Perda de habitat; Avaliação de impacto ambiental.

Abstract

The Brazilian Amazon has approximately 90% (~ 95 MW) of untapped energy potential and there are future projects by government planning agencies to build over 200 new hydroelectric dams in the region. Although hydroelectric dams have been promoted as “cleaner” sources of energy, damming rivers interrupts river continuity and causes the flooding of adjacent riverine and terrestrial ecosystems. Flooding of the lowlands causes changes in species abundance and composition, particularly in species directly associated with the flooded gradients. For a better understanding of the environmental impacts of hydroelectric dams on wild species, it is advisable to assess impacts before and after reservoir flooding. The fauna surveys associated with the environmental impact assessments for the Santo Antônio hydroelectric dam in Rondônia are among the most intensive, well-planned, and long-term surveys ever conducted in Brazil. It is a hydroelectric plant with bulb type turbines which require less water and produce a small reservoir size (271 km²). The overall objective of this thesis was to evaluate the spatial and temporal effects of the flooding of the Santo Antônio HPP reservoir, upper Madeira River, Rondônia, integrating data on anuran species sampled in areas that would be flooded and not flooded before the construction of the hydroelectric dam with data collected in areas not flooded after the damming of the river. We used the Herpetofauna Monitoring database collected between 2010 and 2017 in which data were collected 2 years before, in areas subsequently flooded by the hydroelectric dam (pre-flooded stage) and not flooded (pre-not flooded), with intervals just after filling (post 1) and 4 years after filling (post 2). The thesis consists of two chapters that evaluate different aspects of the temporal and spatial effects of dam filling on the taxonomic and functional composition of anurans. A total of 120 species of anurans were recorded throughout the monitoring, including occasional records. In Chapter 1 the filling of the hydroelectric dam had little effect on the number of species, but altered their abundance. The frog composition in the areas permanently flooded by the damming of the river was not reestablished in the remaining areas and 6% of the species were no longer recorded. In the non-flooded areas, there were also changes in species composition over time, with a gain of species in 82% of the plots sampled, especially in those located near the new Madeira River bank. This increase in the number of species in the remaining areas may be a response to the flooding of low-lying areas, because after the reservoir was filled, the anurans may have moved to nearby areas, increasing the number of species recorded. This occurs during the period of community restructuring after a disturbance, where some populations may decrease while others occupy the new environments. In chapter 2, we sampled 58 plots before the flood (2010-2011), 19 of which were flooded after the creation of the reservoir. For the pre-flood period we categorized the data into 19 flooded and 39 non-flooded plots. These were sampled again two years after the dam was established. With the flooding of the lowlands, there was a loss of diversity and functional uniqueness of the anuran assemblages. The functional composition of the

flooded area was distinct from the non-flooded area. Flooding did not result in the complete elimination of any trait or combination of traits from the anuran assemblages. The differences in functional diversity of Amazonian anuran assemblages were largely due to baseline environmental differences between seasonally inundated and non-inundated areas. Functional traits linked to reproductive strategies, such as egg deposition and larval development, help to understand community-wide responses of anurans to temporal changes caused by run-of-the-river dams. The results of this thesis showed that the effects of the damming of the Madeira River by the Santo Antonio Hydroelectric Plant were rapid, observed in the first two years after the reservoir flooding. The anuran assemblages of the floodplain forests were the most impacted by the formation of the reservoir and were not incorporated into the remaining non-flooded areas after the dam construction. The implementation of the reservoir did not reduce the number of anuran species, but there were changes in functional and taxonomic composition with an overall decrease in abundance after the reservoir flooding. Understanding effects on biodiversity requires long-term studies, and in the case of large-scale infrastructure projects, these studies should begin well before dam construction so that natural fluctuations in species can also be documented. As new hydroelectric dams are planned for the Amazon, we recommend the adoption of legislation for hydroelectric dams that incorporates the creation of protected areas with special attention to the types of vegetation permanently suppressed. Thus, our results show the need for protection of floodplain forests affected by hydroelectric dams.

Keywords: Species composition of anurans, functional traits; hydroelectric dams; run-of-the-river dams; long-term monitoring; habitat loss; environmental impact assessment.

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INTRODUÇÃO GERAL

Um dos principais objetivos da ecologia de comunidades aplicada à conservação da biodiversidade é identificar como mudanças ambientais de origem antropogênica podem influenciar a estruturação de assembleias biológicas (Gillespie *et al.*, 2015). Para identificar as variáveis ambientais que determinam mudanças nas assembleias pode-se testar os efeitos de distúrbios ambientais sobre a composição de espécies de assembleias locais (Abreu *et al.*, 2020; Bobrowiec *et al.*, 2021; Bueno & Peres, 2020; Carneiro *et al.*, 2016). Dentre as mudanças antropogênicas em paisagens naturais que potencialmente impactam a estrutura espacial de assembleias de fauna está a construção de usinas hidrelétricas, e têm sido particularmente preocupantes nas florestas tropicais do mundo.

Apenas na Amazônia brasileira, 1.105.400 ha de florestas já foram inundadas com a implantação das hidrelétricas até 2012 (ECOA, 2012) e alguns dos maiores projetos hidrelétricos já estão funcionando, em construção ou ainda em fase de planejamento (Latrubesse *et al.*, 2017). Embora o número exato de projetos previstos esteja constantemente em mudança, foi proposto mais de 100 barragens hidrelétricas para cinco dos seis principais afluentes andinos na Bacia Amazônica a partir de 2014 (Finer & Jenkins, 2012). O Brasil já tem um histórico de grandes hidrelétricas em funcionamento na Amazônia e outras em fase de planejamento nas últimas décadas (Latrubesse *et al.*, 2017), atraindo a atenção de cientistas e de organizações não governamentais para os problemas ambientais associados (Fearnside, 2016). O Plano de Expansão Energética 2013-2022, do Ministério das Minas e Energia, indica além das hidrelétricas de Jirau e Santo Antônio já em funcionamento, outras 18 barragens com ≥ 30 MW de capacidade a serem concluídas até 2022 na Amazônia brasileira (Fearnside, 2015a). Vale ressaltar que apenas no Baixo e Médio Amazonas e seus afluentes, 34 barragens já se encontram em operação (Lees *et al.*, 2016) (mapa na figura 01).

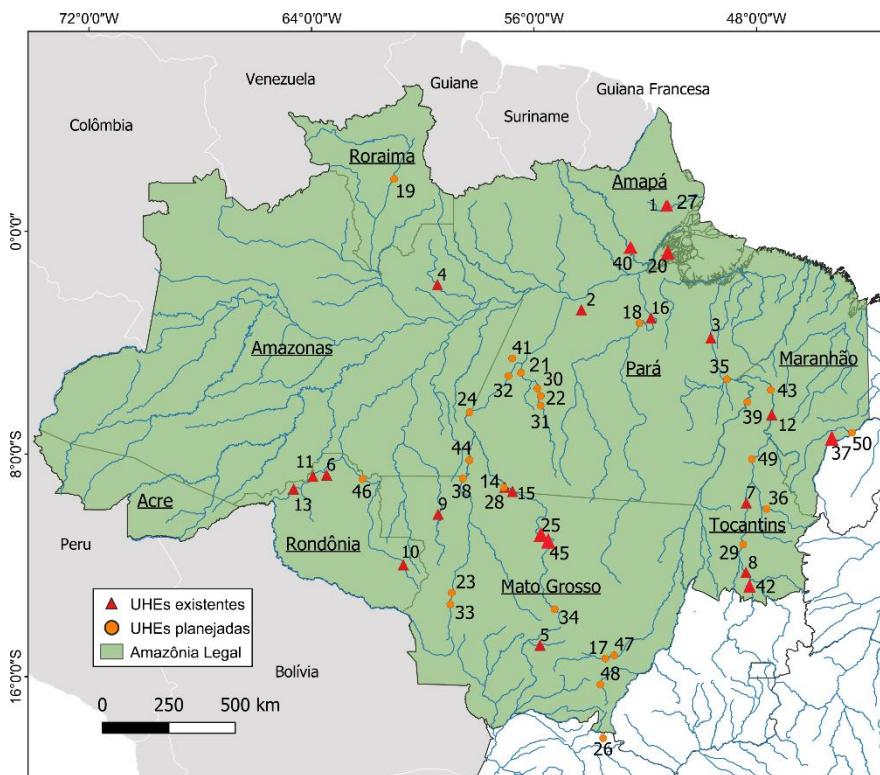


Figura 01: Usinas Hidrelétricas (UHE) já existentes até 2021 ou planejadas na Amazônia Legal brasileira (> 30 MW). *Adaptado de Fearnside (2015a) e de Bobrowiec (2021).*

O enchimento de reservatórios hidroelétricos e a consequente supressão vegetal causam alterações irreversíveis na paisagem, sendo possíveis fatores de impacto direto sobre as assembleias faunísticas, podendo afetar os modos de vida e capacidade de deslocamento de cada espécie (Fearnside, 2015a). Pode provocar modificações nas estruturas faunísticas, promovidas pela perda de habitat, interrupção de fluxo gênico, obstrução de rotas migratórias, e mudanças do regime hidrológico, especialmente nos riachos de pequeno porte que desaguam no reservatório (Eskew *et al.*, 2012; Jansson *et al.*, 2000; Junk *et al.*, 2012; Nilsson & Berggren, 2000).

Modificações oriundas do represamento dos rios na paisagem natural interferem na distribuição, diversidade e abundância de espécies de plantas (Jansson *et al.*, 2000; Nilsson & Berggren, 2000; Santos, 2015) e de organismos aquáticos como macroinvertebrados (Bredenhand & Samways, 2009), peixes (Doria *et al.*, 2018; Fearnside, 2014; Lees *et al.*, 2016; Santos *et al.*, 2018), sendo mais raros aqueles realizados com vertebrados terrestres (Benchimol & Peres, 2015; Benchimol & Venticinque, 2014; Cosson *et al.*, 1999; Dalecky *et al.*, 2002; Lima *et al.*, 2015). No entanto, esses estudos analisaram as estruturas de populações ou assembleias locais e regionais após o enchimento do reservatório hidrelétrico, principalmente com base nos

efeitos da insularização de habitats, sem incluir comparativos com a paisagem antes do enchimento ou não considerando as amplitudes do tempo e espaço.

Na Amazônia brasileira os estudos faunísticos realizados nas hidrelétricas são recentes e consideram os padrões de distribuição das espécies em escala espacial ou temporal após a implantação de grandes hidrelétricas examinando os efeitos da insularização de habitats nas assembleias de fauna devido à construção de barragens. A crescente expansão dos projetos hidrelétricos ao longo da Bacia Amazônica mostra a urgência do conhecimento acerca dos impactos sobre a biodiversidade. Essas barragens geram mudanças críticas nos fluxos de água continental, criando o risco de provocar mudanças irreversíveis nos rios e na fauna presente, embora o conhecimento ecológico acerca das dinâmicas hidrológicas seja ainda incipiente (Little, 2014).

Um dos modelos de barragem contruídos são as denominadas hidrelétricas a fio d'água que possuem reservatórios menores com potencial limitado de armazenamento de água, ao contrário das barragens de armazenamento, que formam grandes lagos (Figura 02). As usinas com reservatório de acumulação também chamadas de armazenamento alagam grandes áreas, pois necessitam de grande armazenamento de água para garantir a produção de energia. Então, toda a região do entorno do rio, tanto áreas de floresta aluvial quanto de terra firme ficam debaixo d'água e tem a criação de ilhas que são as áreas mais altas próximas ao antigo leito do rio. O isolamento dessas ilhas causa impactos sobre a fauna e flora, até mesmo podendo causar até a extinção local de algumas espécies (Benchimol & Peres, 2015; Benchimol & Venticinque, 2014). Eram as hidrelétricas mais comuns no Brasil.

As barragens a fio d'água são frequentemente consideradas como de baixo impacto ambiental devido aos menores reservatórios e baixo potencial de alteração do fluxo do rio, não sendo necessário o armazenamento de água a montante em represas adicionais (Csiki & Rhoads, 2014). Geram energia através do fluxo do rio que movimenta as turbinas do tipo bulbo e são menos dependentes da altura da queda d'água. Desta forma, o acúmulo de água no reservatório é reduzido e área alagada é menor pois acompanham o nível natural do rio. A maior parte da floresta inundada pelos reservatórios é aquela mais baixa, próxima às margens que é a floresta aluvial. Altera o pulso de inundação, que é o ciclo de subida e descida das águas de acordo com o período chuvoso. a periodicidade com que certas áreas próximas ao rio são inundadas. Essa tecnologia representa uma melhoria em relação ao reservatório de armazenamento, pois a área

alagada é reduzida, no entanto, por não ter reservatório de água para garantir a estabilidade na produção de energia, necessita de novos barramentos para conferir maior estabilidade ao sistema (Fearnside, 2014). Embora os impactos sobre ambientes de terra firme sejam reduzidos, as mudanças são ainda pouco estudadas, principalmente sobre os ambientes aluviais.

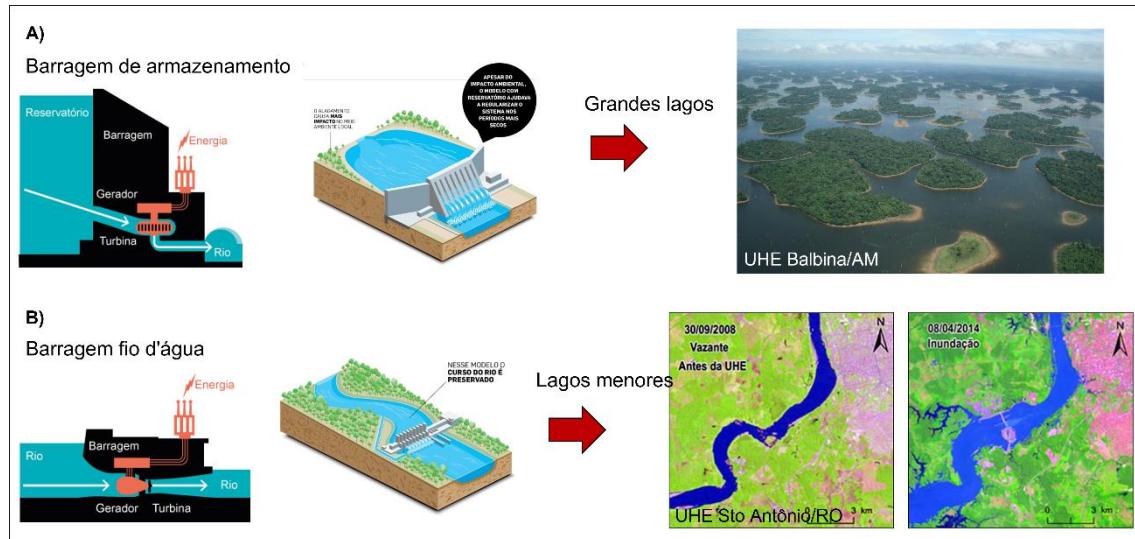


Figura 02: Modelos de barragem construídos no Brasil. A) Barragem de armazenamento; B) Barragem a fio d’água. *Retirado de* sergionobre.wordpress.com e santamarcelina.org.br.

O Baixo e Médio Amazonas e seus afluentes já têm mais de 30 barragens operacionais (Lees *et al.*, 2016), dentre elas duas das maiores barragens a fio d’água do mundo, Santo Antônio e Jirau, construídas no rio Madeira, um dos principais afluentes do rio Amazonas em termos de descarga de água e sedimentos, sendo a sub-bacia do rio Madeira considerada a mais ameaçada da Amazônia (Latrubblesse *et al.*, 2017). É um rio de águas brancas, o que significa que é turvo devido aos sedimentos suspensos derivados da erosão andina (Vauchel *et al.*, 2017) e possui planícies aluviais altamente produtivas. A bacia do Rio Madeira tem sido considerada como a mais ameaçada da Amazônia, por ser a mais habitada e comercialmente explorada da região e pela crescente expansão hidrelétrica (Latrubblesse *et al.*, 2017). As turbinas do tipo bulbo das hidrelétricas de Santo Antônio e Jirau requerem menos água do que as turbinas normais, produzindo um reservatório menor (271 km^2) do que grandes barragens hidrelétricas convencionais na Bacia Amazônica, como Tucuruí (2.086 km^2) e Balbina (2.360 km^2) (Fearnside, 2015b).

A interrupção do fluxo das águas do rio por barragens também afeta a descarga de sedimentos no Rio Amazonas. O Rio Madeira, por exemplo, fornece 40-50% da carga

total de sedimentos do Rio Amazonas (Latrubesse *et al.*, 2020). A redução dos sedimentos e nutrientes pode resultar em prejuízos para a biodiversidade a jusante da barragem (Park and Latrubesse, 2019). Uma análise das consequências esperadas pelas mais de 400 barragens já existentes ou em construção nas características hidrofísicas dos grandes rios Amazônicos indicou que a Bacia do Rio Madeira é a mais ameaçada pela construção de barragens, principalmente relacionada com a interrupção do fluxo de sedimentos (Latrubesse *et al.*, 2017). Os rios da Bacias do Rio Madeira estão em risco pela construção de 16 barragens nos Andes e na Bolívia (Latrubesse *et al.*, 2017). As barragens podem interromper a migração de peixes do canal do rio e afetar a dinâmica de inundação sazonal das florestas de várzea e igapó (Li *et al.*, 2020; Santos *et al.*, 2018).

Alguns anos após a construção das barragens de Jirau e Santo Antônio em 2010, os estudos realizados na área de influência dessas hidrelétricas a fio d'água estão começando a mostrar resultados esclarecedores sobre a alteração nos padrões de cobertura florestal, perda de ecossistemas e degradação de recursos terrestres adjacentes à nova margem (Ribas *et al.* 2020). As formações florestais mais impactadas pelo sistema hidrelétrico Jirau-Santo Antônio foram as florestas de várzea (Cochrane *et al.*, 2017). Com o aumento de 72% da área inundada (Cochrane *et al.*, 2017), as mudanças no lençol freático das novas margens do rio modificaram as florestas de terra-firme que não estavam adaptadas às inundações (Moser *et al.*, 2019). A extensão dos efeitos da perda da várzea sobre a fauna associados às margens do rio foi determinada pela mudança na composição de morcegos ao longo do tempo (Bobrowiec *et al.*, 2021), redução do número de espécies de palmeiras associadas aos ambientes de várzea e terra-firme nas margens do rio Madeira (Santos *et al.*, 2020), mortalidade de árvores na margem (Cochrane *et al.*, 2017) e redução do pescado (Santos *et al.*, 2018), além de mudança nas assembleias das aves especialistas de terras inundáveis (Melo *et al.*, 2021).

As mudanças na composição de uma assembleia de espécies em uma região impactada por um empreendimento hidroelétrico podem ocorrer por diversos fatores, pois normalmente não se tem dados coletados de forma sistematizada antes, durante e depois da implantação do empreendimento. Assim, deve-se ter cuidado com as informações obtidas através do registro de mudanças nos indicadores em um período curto sem comparativos temporais. O monitoramento dos impactos da hidrelétrica a fio d'água sobre as espécies ao longo do tempo é importante para avaliar como cada espécie se comporta com as alterações na margem do rio, pois podem ser graduais e relacionadas às mudanças mais lentas como alterações na vegetação da margem ou ao período de estabelecimento

de uma espécie em um novo local. Também podem ser drásticas e rápidas como a perda de espécies ou diminuição da abundância. São hidrelétricas relativamente recentes no Brasil, onde somente agora começam a ser publicados os dados referentes aos impactos sobre a fauna e flora (Abreu *et al.*, 2020; Bobrowiec *et al.*, 2021; Bobrowiec & Tavares, 2017; Li *et al.*, 2020; Melo *et al.*, 2021; Santos *et al.*, 2018).

No entanto, a definição de indicadores ecológicos dos efeitos de mudanças ambientais somente sobre métricas de diversidade taxonômica pode não mostrar as mudanças mais sutis. Quantificar assembleias apenas com base somente em abundâncias ou na riqueza de espécies não permite a identificação de alterações nas características morfológicas ou ecológicas (e.g. modo reprodutivo, dieta) que sejam comuns às espécies positiva ou negativamente impactadas. Alternativamente, assembleias podem ser quantificadas com base em traços funcionais, com o objetivo de identificar características específicas que possam ser mais ou menos sensíveis às alterações ambientais consequentes da barragem de rios (Weiss & Ray, 2019) e podem detectar mudanças mais sutis nas assembleias.

Traços funcionais são ferramentas para avaliar a influência de preditores ecológicos (ambientais e espaciais) em padrões de montagem de comunidades, bem como de processos de colonização e manutenção de espécies em diferentes ambientes e áreas geográficas (Tonkin *et al.*, 2016; Violle *et al.*, 2012). Respostas dos traços nos níveis de comunidade aos processos ecológicos podem ser conduzidos pela combinação de substituição e variação intraespecífica (Lepš *et al.*, 2011). Esses processos incluem filtragem ambiental, em que o ambiente age como força seletiva filtrando espécies capazes de tolerar as condições em locais específicos como ambientes de várzea, e limitação de similaridade, onde há um limite sobre quantas espécies coexistentes semelhantes morfologicamente podem ocorrer e persistir no mesmo local (Kraft *et al.*, 2015; Stubbs & Wilson, 2004).

Mudanças na estrutura do habitat frequentemente resultam em mudanças na composição das espécies (Benchimol & Peres, 2015; Benchimol & Venticinque, 2014; Bobrowiec *et al.*, 2021; Bobrowiec & Tavares, 2017; Cosson *et al.*, 1999; Lima *et al.*, 2015), mas não está claro que efeito tais mudanças terão nas características morfológicas funcionais das espécies dentro da assembleia. Algumas características das espécies podem ser selecionadas pela estrutura de habitats, por meio de dispersão limitada, competição ou incompatibilidade morfológica e fisiológica para o uso de recursos.

Uma abordagem baseada em características funcionais pode representar uma ferramenta útil para entender a estruturação das assembleias de sapos e suas relações com as mudanças ambientais naturais e antrópicas. Sapos são organismos de baixa mobilidade, abundantes nos Neotrópicos e susceptíveis a mudanças ambientais, sendo utilizados como indicadores na compreensão dos processos determinísticos nas organizações funcionais das assembleias em habitats modificados por distúrbios antrópicos (Dalmolin *et al.*, 2020; Ribeiro *et al.*, 2017). Além disso, devido ao ciclo de vida bifásico, alguns anuros dependem das mudanças ambientais, principalmente em ambientes contrastantes (Campos *et al.*, 2017; Whiles *et al.*, 2006), como áreas de várzea e terra-firme.

Dependendo da extensão das mudanças ambientais causadas por um distúrbio antropogênico, traços funcionais explicitamente associados a interações ecológicas entre espécies e habitats usualmente refletem processos ecossistêmicos que regulam a estabilidade de assembleias à alterações antropogênicas (Hooper *et al.*, 2005). Por isso, investigar os efeitos de impactos ambientais sobre métricas de estimativas de diversidade funcional e taxonômica podem ter respostas importantes para o entendimento sobre os efeitos de distúrbios antropogênicos sobre a biodiversidade (Álvarez-Grzybowska *et al.*, 2020; Berriozabal-Islas *et al.*, 2017; Farneda *et al.*, 2020) não demonstradas com o uso somente de métricas de diversidade taxonômica. Monitoramentos de longo prazo com amostragens antes e depois do alagamento do reservatório são uma oportunidade para entender os efeitos temporais e espaciais da construção de barragens de hidrelétricas sobre a fauna terrestre.

Área de Estudo

O rio Madeira é um rio de águas brancas, devido à alta carga de sedimentos suspensos derivados da erosão andina (Vauchel *et al.*, 2017), caracterizado pela presença de floresta de várzea em suas margens, alternadas com floresta de terra firme (Pires & Prance, 1985), e possui planícies aluviais produtivas para agricultura. A bacia do Rio Madeira tem sido considerada como a mais ameaçada da Amazônia, por ser a mais habitada e comercialmente explorada da região e pela crescente expansão hidrelétrica (Latrubesse *et al.*, 2017). O clima da bacia do rio Madeira é tropical úmido - Am in the Köppen classification (Cochrane *et al.*, 2017). As temperaturas médias anuais máximas e mínimas são respectivamente 32,2°C e 21,1°C, com umidade relativa anual média do ar de 79%. A precipitação média anual variou entre 1,700 e 2,200 mm.

A área inundável da bacia hidrográfica do Rio Madeira também é a maior da Amazônia, com 61% de cobertura vegetal lenhosa e 33% de cobertura herbácea (Vauchel

et al., 2017). A análise da série histórica do nível do rio (1994-2004) evidenciou que o ciclo hidrológico para a região do alto Rio Madeira está dividido em período de seca (setembro e outubro), período de enchente (novembro a fevereiro), período de cheia (março e abril) e período de vazante (maio a agosto) (Almeida *et al.*, 2019). O nível do rio Madeira não é influenciado pela época chuvosa local, uma vez que recebe muitos tributários dos Andes, então o regime de chuvas desta região é mais associado às cheias regulares do rio e às chuvas localizadas nos Andes (Park & Latrubesse, 2019).

O estudo foi realizado na área de influência da Usina Hidrelétrica Santo Antônio, que represou o Rio Madeira 10 km a montante de Porto Velho, Rondônia ($08^{\circ}48'S$; $63^{\circ}57'W$). A hidrelétrica de Santo Antônio é a quarta maior hidrelétrica em operação no Brasil, produzindo até 3.150 MW, sendo fornecida por 50 turbinas bulbo. A área oficial do reservatório de 471 km², embora o sensoriamento remoto indique uma maior área inundada (Cochrane *et al.*, 2017). A barragem tem 60 m de altura e 2,5 km de largura e o comprimento do reservatório é de 130 km (Almeida *et al.*, 2019). A hidrelétrica represou o rio Madeira em 2011 e entrou em operação 2012. O licenciamento ambiental da barragem Santo Antônio foi caracterizado por muitas controvérsias, principalmente no que diz respeito ao acúmulo de sedimentos no reservatório (Latrubesse *et al.*, 2020).

A vegetação predominantemente na região do estudo é uma associação de floresta ombrófila aberta de terras baixas com palmeiras e floresta ombrófila aberta aluvial com manchas de pastagens, formações de várzea e a transição floresta ombrófila aberta e campinarana florestada (Moser *et al.*, 2014). O Parque Nacional do Mapinguari está na margem esquerda do rio, e na margem direita do rio há formações florestais extremamente fragmentadas em consequência do uso mais intensivo da terra nas fazendas, pastagens, agricultura, estradas e rodovias (BR-364) (Ferraz *et al.*, 2005).



Figura 03: Imagem aérea do rio Madeira e da Hidrelétrica de Santo Antônio. *Retirado de rondoniagora.com.br e ultimosegundo.ig.com.br.*



Figura 04: Áreas impactadas no rio Madeira pela inundação permanente devido à criação das hidrelétricas de Santo Antônio e Jirau.

Histórico de pesquisas da herpetofauna no Alto rio Madeira

A herpetofauna do Alto rio Madeira era pouco conhecida para uma área considerada de prioridade extremamente alta para a conservação da Amazônia. A região abriga megadiversidade biológica e encontra-se sob constante pressão antrópica devido ao aumento na densidade demográfica no cinturão de desmatamento que rapidamente avança em direção norte e noroeste da Amazônia (Vogt *et al.*, 2001). Aqui apresento um breve histórico do que já foi publicado na região e, mais atualmente com base nos dados coletados do Subprograma de Monitoramento de Herpetofauna Terrestre (Anuros, Lagartos e Serpentes) da Usina Hidrelétrica (UHE) de Santo Antônio realizado entre 2009 e 2017.

O Alto rio Madeira, considerado lacuna de informações sobre padrões de diversidade biológica, passaram a ser coletados a partir da década de 70 quando (Heyer, 1977) publicou uma lista comentada das espécies de anuros nos rios Madeira e Purus. Em 1993 foi publicado uma compilação das espécies de serpentes registradas durante o resgate de fauna na hidroelétrica de Samuel, próxima à Porto Velho (RO) (Silva-Jr, 1993).

A herpetofauna do alto Rio Madeira tem sido também investigada por estudos técnicos, embora nem sempre sejam publicados. Alguns desses estudos resultaram na publicação do Guia das Espécies da Fauna Resgatada da UHE Santo Antônio (Marçal *et al.*, 2011), no qual foram listadas espécies de répteis e anfíbios resgatadas pelo Programa de Conservação e Resgate de Fauna da área de influência da UHE Santo Antônio. Alguns registros provenientes dos trabalhos de resgate das hidrelétricas de Santo Antônio e Jirau também fazem parte da lista publicada das espécies de serpentes de Rondônia (Bernarde *et al.*, 2012).

Também foram realizadas pesquisas científicas de cunho ecológico. O estudo sobre os fatores históricos e ambientais que afetam a estrutura espacial das assembleias de anuros diurnos (Dias-Terceiro *et al.*, 2015) e do uso dos modelos de distribuição espécies de anuros para auxílio na avaliação de impactos e programas de mitigação (Carneiro *et al.*, 2016). Fraga, *et al.* (2017) investigaram padrões de fluxo gênico de serpentes, determinados por distância geográfica e resistência ambiental e Nogueira *et al.* (2019) avaliaram as variáveis ambientais que influenciam na ocupação de duas espécies de serpentes próximas filogeneticamente (*Philodryas argentea* e *P. georgeboulengeri*) e sua sobreposição de nicho na região.



Figura 05: Espécies de serpentes utilizadas no estudo de (Corrêa Nogueira *et al.*, 2019).

Também houve o primeiro registro de *Allobates nidicola* para Rondônia (Kaefer *et al.*, 2012) e um estudo de hibridização entre duas espécies de *Allobates* do grupo *femoralis* (Simões *et al.*, 2012) para a região. Adicionalmente, foram descritas uma nova espécie de anuro denominada *Allobates grillisimilis*, encontrada somente na margem direita do rio Madeira, no município de Borba (RO) (Simões *et al.*, 2013), e uma espécie de salamandra (*Bolitoglossa madeira*) descrita para a margem esquerda (Brcko *et al.*, 2013). Foi onde houve o primeiro registro das espécies de anuros raros *Hamptophryne alios* (Simões *et al.*, 2011) e *Hydrolaetare caparu* (Ferrão *et al.*, 2014).

Foram registradas mais de 120 espécies de anuros em todo o monitoramento, sendo que muitas, possivelmente são novas para a ciência. Pesquisadores do Instituto de Pesquisa da Amazônia em colaboração com outros centros de pesquisa já descreveram algumas dessas espécies. (Ferrão *et al.*, 2016) mostraram que a região é uma área com alta riqueza de espécies de *Scinax*, com mais de quatro espécies novas, sendo uma importante área de conhecimento e conservação de espécies desse gênero. Também foram descritas a *Scinax onca* (Ferrão *et al.*, 2017), *Rhinella exostosica* (Ferrão *et al.*, 2020a), *Allobates caldwellae* (Lima *et al.*, 2020), *Dendropsophus bilobatus* (Ferrão *et al.*, 2020b) e *Rhinella teotonensis* (Ferrão *et al.*, 2022). Sendo que *Dendropsophus bilobatus* é encontrada somente na margem direita do Alto Madeira, até o momento.



Figura 06: Espécies de anuros registradas na região do Alto Madeira. A) *Rhinella teotonensis*, B) *Allobates* sp.1 *autazes*, C) *Pristimantis* sp.4, D) *Cochranella* sp., E) *Adelphobates quinquevittatus*, F) *Ameerega picta*, G) *Ameerega trivittata*, H) *Phyzelaphryne miriamae*.



Figura 07: Espécies de anuros registradas na região do Alto Madeira. A) *Ceratophrys cornuta*, B) *Hemiphractus scutatus*, C) *Boana cinerascens*, D) *Lysapsus limellum*, E) *Trachycephalus coriaceus*, F) *Lithodytes lineatus*, G) *Phyllomedusa vaillantii*, H) *Pipa pipa*.

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OBJETIVOS

O objetivo geral dessa tese foi avaliar os efeitos espaciais e temporais da inundação do reservatório da Usina Hidrelétrica de Santo Antônio, alto Rio Madeira, Estado de Rondônia, integrando dados de espécies de anuros amostrados em áreas que seriam inundadas e não inundadas antes da construção da hidrelétrica com dados coletados em áreas não inundadas após o barramento do rio. A tese é composta por dois capítulos que avaliam diferentes aspectos dos efeitos temporais e espaciais do enchimento da barragem na composição taxonômica e funcional dos sapos.

No capítulo 1, nós investigamos a influência do enchimento da barragem em assembleias de anuros, em particular avaliamos se a composição de espécies das áreas que foram inundadas é incorporada nas áreas que permaneceram secas. No capítulo 2, nós avaliamos os efeitos dos primeiros anos de inundação do reservatório sobre a diversidade funcional baseada em índices e prevalência de traços funcionais em assembleias de anuros.

CAPITULO 1 PUBLICADO NA PLOS ONE

CAPITULO 1: Impacts of an Amazonian hydroelectric dam on frog assemblages.

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Abstract

About 90% of the Amazon's energy potential remains unexploited, with many large hydroelectric dams yet to be built, so it is important to understand how terrestrial vertebrates are affected by reservoir formation and habitat loss. We investigated the influence of the construction of the Santo Antônio Hydroelectric dam on the Madeira River in southwestern Amazonia on the structure of frog assemblages based on samples collected in two years before the dam flooded (pre-stage) and one (post1-stage) and four years (post2-stage) after its construction. We surveyed five 500-ha plot systems three times during each stage; in the pre-stage we sampled 19 plots in low-lying areas that would be flooded by the dam, (from now called flooded pre-stage plots) and 45 plots in terra-firme forest (from now called unflooded pre-stage plots). At the post1-stage we sampled the 45 unflooded plots and in the post2-stage we sampled the remaining 39 unflooded plots. We detected frogs by active visual and acoustic searches standardized by both time and sampling area. Few species recorded in the pre-stage flooded plots were not found in the pre-stage unflooded plots or in stages after flooding, and most of these absences were probably due to the vagaries of sampling. However, the composition of frog assemblages based on relative densities in flooded pre-stage plots did not re-establish in plots on the new river margins. In unflooded areas, frog assemblages were distinct among the flooding stages with no tendency to return to the original assemblage compositions even four years after the dam was filled. For the areas that were not flooded, there was an increase in species richness in 82% of the plots between the surveys before dam construction and the first surveys after dam completion, and 65% between the pre-stage and surveys four years after dam completion. Lack of understanding by the controlling authorities of the long-term effects of landscape changes, such as water-table rises, means that studies covering appropriate periods post construction are not required in legislation, but the data from Santo Antônio indicate that changes due to dam construction are either long-term or difficult to distinguish from natural fluctuations. Future environmental-impact studies should follow strict BACI designs.

Keywords

Amazon; Environmental impact assessment; Habitat loss; Riparian habitats; Disturbance; Mega dam.

Introduction

One of the factors contributing most to deforestation and consequent biodiversity loss in the Amazon is implementation of government infrastructure programs, such as the

construction of hydroelectric dams on large rivers (Philip M. Fearnside, 2015b). Currently, 256 of the 412 large hydroelectric dams in operation, being constructed or planned for the Amazon are in Brazil (Latrubesse et al., 2017). Large hydroelectric dams in operation up to 2012 flooded 1,105,400 ha of forests in the Amazon (ECOA, 2012), and can affect aquatic and terrestrial biodiversity (Finer & Jenkins, 2012; Wu et al., 2019).

Damming rivers floods large forest areas, reduces the flood pulse and changes water-table depth (Jansson et al., 2000; Nilsson & Berggren, 2000). In addition to reducing flood pulses, damming reduces várzea forest, a type of seasonally-flooded forest with unique fauna (Alvarenga et al., 2018; Ayres, 1994; Beja et al., 2010; Paulo Estefano D. Bobrowiec, Rosa, Rosa, Gazarini, & Haugaasen, 2014; Haugaasen & Peres, 2005; May et al., 2010) and flora (E. A. Santos et al., 2020; Wittmann, Junk, & Piedade, 2004). Várzeas are flooded annually by nutrient-rich white-water rivers for 6 to 8 months and these highly-diverse areas connect habitats and play a key role in maintaining regional biodiversity due to their spatial and temporal complexities (Hamilton, Kellndorfer, Lehner, & Tobler, 2007; Junk et al., 2012). After dam construction, lowland vegetation, including várzea forest, is permanently inundated and the ground-water level in the unflooded area is raised, modifying the original vegetation (Cochrane et al., 2017). The creation of new habitats can influence the abundance and distribution of terrestrial species associated with humid lowlands, but the extent of the effects of the new habitat type on the unflooded area is unknown.

The Madeira River is the main tributary of the Amazon River (Castello & Macedo, 2016) and the fifth largest river in the world in terms of water flow (Latrubesse, 2008). The Madeira River sub-basin is one of the most endangered in the Amazon, as 40 hydroelectric dams are already operating or under construction in the sub-basin (Latrubesse et al., 2017). In 2011, two large dams on the Madeira River had their construction completed (Santo Antônio and Jirau; ~ 3500 MW each). These are run-of-the-river dams whose turbines use the river current to generate hydroelectricity and are generally considered less harmful to the environment than conventional hydroelectric dams since they flood smaller areas and generally do not form islands (Paulo Estefano D. Bobrowiec & Tavares, 2017). However, there are no published data on the impacts of run-of-the-river dams on anurans in the Amazon.

Anurans are sensitive to changes in the environment (Ribeiro et al., 2017) and climatic (Menéndez-Guerrero, Green, & Davies, 2020) variations due to permeable skin, dependence on humid environments for reproduction and biphasic life cycle (Duellmann,

1999; Skelly, 1996; Vitt, Caldwell, Wilbur, & Smith, 1990). Hydroelectric dams modify water levels and water availability, affecting terrestrial and riparian habitats and the amphibian species that occupy them (Guzy, Eskew, Halstead, & Price, 2018; Naniwadekar & Vasudevan, 2014; Nilsson & Berggren, 2000). In addition, the structure of riparian forests affects assemblages of leaf-litter frogs (Vasudevan, Kumar, Noon, & Chellam, 2008), and distance to and availability of water bodies are important for species with aquatic reproduction (Landeiro, Waldez, & Menin, 2014).

With the growing number of hydroelectric dams planned for the Brazilian Amazon (Latrubesse et al., 2017), it is important to understand how vertebrate assemblages respond to habitat modification and loss. Several studies have shown that frogs are sensitive to such changes (Cushman, 2006), and long-term monitoring with sampling before and after the dam floods is an opportunity to understand the temporal and spatial effects of dam construction.

We investigated the influence of the construction of the Santo Antônio Hydroelectric dam on the structure of frog assemblages based on samples collected in three-time intervals (two years before the dam flooded [pre-stage], and one [post1-stage] and four years [post2-stage] after its construction). The sampling regime was defined by the national environmental agency (IBAMA) and did not follow a Before-After-Control-Impact (BACI) design (Smith, Orvos, & Cairns, 1993) as it did not include a control area. Nevertheless, it permits a general evaluation of changes in the anuran assemblages in that period.

We asked the following questions: 1) Did flooding result in the loss of species in the region around the dam?; 2) Did frog assemblages from flooded areas reestablish on the new river banks after dam construction?; 3) Did frog assemblages in the unflooded plots change in ways that might suggest that they were affected by flooding of adjacent areas?; 4) If there were changes in the frog assemblages in unflooded areas, did these changes occur immediately after the construction of the dam or with a delay?; 5) Were any such changes greater in areas near the reservoir than in areas further away?

We hypothesized that the frog assemblages in periodically flooded lowland forests (*várzea*) would be eliminated and that the species composition found in this and other vegetation associations inundated by the dam might not reestablish if the habitat on the new banks of the river after dam construction did not resemble that in the areas that were inundated. We also predicted that the species composition of the unflooded areas would

change over time, especially the areas near the new banks of the Madeira River and its tributaries where the water table would be elevated.

Material and Methods

Study Area

The Madeira River is one of the main tributaries of the Amazon River, being responsible for 15% of the discharge of the Amazon into the Atlantic Ocean (Goulding, Barthem, & Ferreira, 2003). Its waters are turbid due to suspended sediments derived from the Andes (Vauchel et al., 2017); it is the most sediment-laden river in the Amazon Basin (Castello et al., 2013).

The predominant vegetation type in the upper Madeira River region was originally composed of dense tropical rainforests, with a mosaic of terra-firme forest, várzea on the river banks and patches of white-sand vegetation locally called “campinarana” (Moser et al., 2014). According to the Köppen classification, the predominant climate is Aw - Tropical Rainy. The average annual temperature varied from 25 ° to 27 ° C and the annual precipitation between 1400 and 2000 mm between 1998 and 2007 (data from the National Water Agency, ANA). The dry season generally occurs from June to September and the rainy season from November to April, with precipitation >330 mm per month in December and January. River levels can vary by more than 12 meters in some parts of the upper Madeira River (Adamy, 2016).

The Santo Antônio Hydroelectric dam (08°48'S; 63°57'W) is located 10 km upstream of the city of Porto Velho, Rondônia state, and is the fourth largest hydroelectric dam in operation in Brazil with 3,150 MW of installed capacity (Philip M. Fearnside, 2015b). It has been in operation since March 2012 with the water level at 70.2 m above the original river level. The bulb-type turbines require less water, producing a reduced reservoir size (271 km²) than conventional Amazonian hydroelectric dams, such as Tucuruí, Balbina and Samuel (Philip M. Fearnside, 2015b).

Sampling Design

Five sampling modules were installed from 10 to 100 km upstream of the dam as part of a government-mandated impact assessment. The location of each module was chosen by the environmental authority, taking into account the presence of enough vegetated area for the installation of the modules, as this region is extremely deforested. The configuration of the modules followed the method of biodiversity survey (RAPELD) developed by the Biodiversity Research Program (PPBio) (Magnusson et al., 2013). Each

module consisted of two parallel 5 km trails perpendicular to the Madeira River, separated by 1 km. Seven 250 m long plots were installed along each trail (14 plots per module). The center lines of plots followed the contours of the terrain to minimize within-plot topographic and vegetation variation. Plots were established at distances of 0, 500, 1000, 2000, 3000, 4000 and 5000 m from the original river bank (before flooding). Three modules were on the left bank of the Madeira River (Teotônio, Ilha de Búfalos, Ilha das Pedras), one was on the right bank (Morrinhos) and one was on the right bank of the Jaci-Paraná River (Jaci Margem Direita), a tributary of the right bank of the Madeira River (Fig 1).

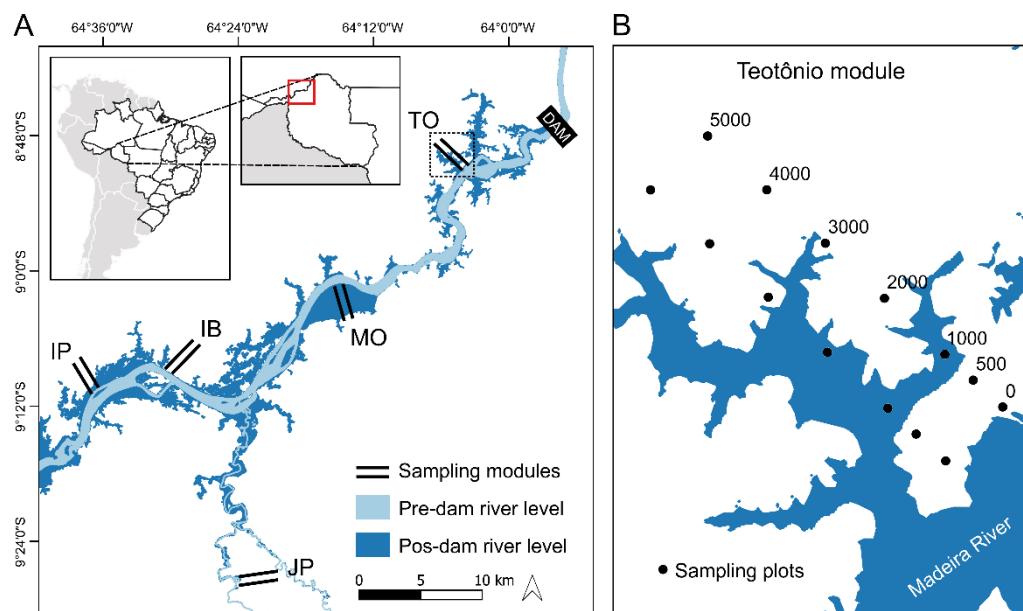


Figure 1 Location of the study area along a 100-km section of the Madeira River showing the five sampling modules. TO = Teotônio, MO = Morrinhos, IB = Ilha de Búfalos, IP = Ilha das Pedras, JP = Jaci Margem Direita. In detail (right), design of modules with two 5 km trails and seven plots (black circles) distributed 0, 500, 1000, 2000, 3000, 4000, and 5000 m from the original bank of the Madeira River.

The modules were sampled three times during each of the following stages: pre-filling (pre-stage) two years before the dam was filled in February 2010, November 2010 and February 2011; post-filling 1 (post1-stage) for surveys undertaken one year after dam filling, in February 2013, November 2013 and February 2014; post-filling 2 (post2-stage), which occurred four years after dam filling, in November 2016, January 2017 and February 2017. In the pre-stage, 64 plots were sampled. Two plots in Ilha Búfalos module, two in Morrinhos and one in Teotonio were not sampled for logistical reasons. The Jaci

Margem Direita module has 13 plots. Of the 64 plots surveyed in the pre-stage, 19 were permanently flooded after the construction of the dam, and we refer to them as pre-stage flooded. The 45 unflooded plots sampled before the construction of the dam we refer to as pre-stage unflooded. These were also sampled in the post1-stage, but in 2016 six plots were deforested and only 39 remained in the post2-stage samples (S1 Table).

Frog Sampling

We sampled the frogs by visual and acoustic survey limited by time and space along the sampling plot (250 x 10 m) with two observers per plot. To detect frog species with different activity periods (diurnal, crepuscular and nocturnal), visual and acoustic surveys were conducted between 16:30 and 18:30, and between 19:00 and 23:00.

We recorded the presence or absence of each species in each 10 m section of the 250 m long plot, resulting in a relative-abundance index that varied between 0 and 25 records per species in each plot. This standardization was necessary because some species (e.g. *Adenomera* spp., *Phyzelaphryne* spp., *Pristimantis* spp.) have high densities of calling males during the reproductive period (A. P. Lima et al., 2008), which makes it difficult to estimate the number of individuals, and some subterranean and leaf-litter species were only detected by calls and could not be counted directly.

The survey teams collected a maximum of three voucher specimens per species, per plot. These were anesthetized and euthanized with 5% xylocaine, fixed in 10% formalin, preserved in 70% ethanol and deposited in the herpetology section of the INPA Zoological Collection in Manaus, Amazonas, Brazil. All were identified in the laboratory with the help of specialized guides (e.g. (Fouquet et al., 2012; Grant et al., 2006; Jungfer et al., 2013; A. P. Lima et al., 2008; Sá et al., 2014)).

In Brazil, the collection or transport of biological material for scientific or teaching purposes requires authorization by the System for Authorization and Information on Biodiversity (Sisbio). This system is administered by the National Institute of Environment and Renewable Natural Resources (IBAMA), which is responsible for the ethical treatment of animals. Frogs were collected as part of government-mandated environmental assessment surveys, under IBAMA/SISBIO (Ministry of Environment, Government of Brazil) permit No 13777-2. This permit was subject to approval of all ethical procedures for catching and collecting species and specimens. We followed the directives of the Federal Council for Biology (CFBIO) Resolution CFBIO N° 08/12/2012,

which relates to procedures for capture, containment, release and collection of vertebrates in situ and ex situ.

Analyses

We used sample-based rarefaction (interpolation) and extrapolation curves with 95% unconditional confidence intervals (Colwell et al., 2012) to compare total frog richness between and within flooding stages. Richness and interpolation (rarefaction) and extrapolated curves of pre-stage flooded ($n = 19$ plots), pre-stage unflooded ($n = 45$), post1-stage ($n = 45$) and post2-stage ($n = 39$) were generated using the “iNEXT” package (Hsieh, Ma, & Chao, 2016).

To evaluate the effect of dam construction on the composition of frog species in a bidimensional space and represent the sampled sites in different temporal stages, we used ordinations by Principal Coordinates Analysis (PCoA) based on the Bray-Curtis dissimilarity index for relative-abundance data and the Jaccard index for occurrence data. However, distance-based analyses have been shown to confound trends in location with changes in dispersion, leading to potentially misleading results (Warton, Wright, & Wang, 2012). Therefore, we also used a latent-variable model-based ordination implemented in the boral program (Bayesian ordination and regression analysis) (Hui, Taskinen, Pledger, Foster, & Warton, 2015) which uses Another Gibbs Sampler (JAGS) (Plummer, 2003). The Bayesian model-based approach accounts for the increasing mean-variance relationship without confounding location with dispersion (Hui et al., 2015). However, the Boral did not converge for one of the analyses, and the configurations produced by Boral (S5 and S6 Fig) were similar to those produced by PCoA in all the other analyses. Therefore, we used PCoA to describe the patterns in all analyses in the main text.

To assess changes in species structure over time in the unflooded area, we grouped all data in each survey period resulting in nine points based on the same 39 plots sampled in each survey period and used the PCoA ordinations based on the Bray-Curtis dissimilarity index for relative-abundance data.

To determine if flooding resulted in changes in species composition in the region flooded by the dam we compared the pre-stage flooded ($n = 19$ plots), pre-stage unflooded ($n = 45$), post1-stage ($n = 45$) and post2-stage ($n = 39$) plot categories using the multivariate extension of generalized linear models (manyglm) function (Warton et al., 2012) in the mvabund package (Wang et al., 2020; Wang, Naumann, Wright, & Warton,

2012). This model-based approach allows for hypothesis testing, and unlike distance-based methods, does not confound location and dispersion effects due to the misspecification of the mean–variance relationship (Warton et al., 2012). The effect of flooding on the assemblages was evaluated using the `anova.manyglm` function which resampled the fitted model using ‘pit-trap’ bootstrapping to resample abundance data while accounting for correlations among species. The p-value was calculated from 999 bootstraps. Pairwise comparisons between flooding categories were assessed using the option in the `anova.manyglm` function to assess whether the assemblages in the flooded areas (pre-stage flooded) were different from the other areas. We fitted a multivariate generalized linear model with flooding categories as the predictor variable. The response variables were abundance data analyzed using a negative-binomial distribution and occurrence data analyzed using a binomial distribution for `mvabund` analyses.

These analyses were used with the complete assemblage (96 species) but rare species could represent a source of noise in multivariate analyses and thus prevent the detection of patterns of assemblage structure (Marchant, 2002) and some studies have not included them in the analyses (Sgarbi et al., 2020; Yu et al., 2017). Rarity is subjective, but we wanted to know whether patterns for species with few records in our sample were similar to those for more common species [eg. 52]. We assessed this potential effect by undertaking analyses both with the complete dataset and with only abundant species (at least 5% abundance and 4% of plots in our sample) (S3 Table) and only with species considered rare in the sampling (only records with up to 5% abundance and 4% of plots in our sample) (S4 Table). We repeated the same analyses changing using 8% abundance and 5% of plots in our sample (S5 Table). As the results were similar, we only present analyses using the whole data set in the main text.

Histograms of species distributions along environmental gradients (Dambros, 2014) constructed in R (R Development Core Team, 2018) were used to describe responses of individual species in relation to flooding stages for both abundance and occurrence data.

To quantify the temporal gains and losses of species in unflooded plots between stages, we used the Temporal Beta Index (TBI) (Legendre & Condit, 2019) in R (R Development Core Team, 2018). We used the TBI function of the `adespatial` package (Dray et al., 2019) with the Bray-Curtis distance for relative-abundance data and the Jaccard dissimilarity index for species-occurrence data in each plot. TBI is used to compare the dissimilarity values of a plot at time 1 with the dissimilarity values of the

same plot at time 2 and is composed of two parts: B = species losses (or losses in abundance per species) and C = species gains (or gains in abundance per species). We tested whether the plots were dominated by species gain or loss, and increase or decrease in species abundance, using paired t tests with 9999 permutations. As the TBI analysis compares pairs of plots, we used the same 39 plots sampled in the pre-stage unflooded, post1-stage and post2-stage categories to compare the pre-stage unflooded assemblages with those in post1 and post2-stages.

To assess the effect of distance from the bank after dam flooding on assemblage composition, we compared the species composition of the plots located between 0.35 to 2 km from the flooded areas with the plots between 2.2 and 5.0 km. As the volume of water in tributary streams increased permanently with the flooding of the dam, we used the shortest distance from the flooded area instead of the distance to the new Madeira River bank. Individuals of most frog species are unlikely to travel more than 2 km between breeding sites. We used the option of pairwise comparisons in the *anova.manyglm* function in the *mvabund* package described previously with frog-abundance data from plots sampled in all no-flood categories ($n = 39$) assuming a negative-binomial distribution of the data, and based on the same indices of similarity and standardization described previously to test the statistical significance of changes in species structure over time in the unflooded area (pre-stage unflooded, post1-stage and post2-stage) in both near (≤ 2 km) and distant (> 2 km) plots.

Analyses were conducted in R (R Development Core Team, 2018).

Results

We recorded 96 species of frogs distributed in 32 genera and 13 families (S2 Table). We recorded 62 species before flooding in plots that would be inundated, and 61 species were recorded in unflooded plots in the pre-stage. We recorded 73 species in the post1-stage and 65 species in post2-stage, of which 39 (40.6%) occurred in all flooding stages, while nine were exclusive to before flooding, seven in plots that were flooded and two in unflooded plots. Ten species were found only in post1-stage and six only in post2-stage (Figs 2 and 3).

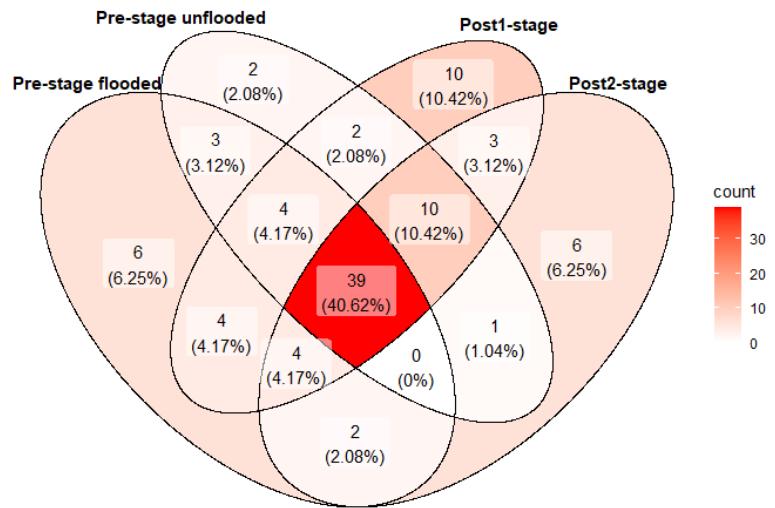


Figure 2 Venn Diagram showing the overlap in species registered in the different combinations of flooding and time since filling of the Santo Antônio dam in the Madeira River, southwestern Brazilian Amazonia.

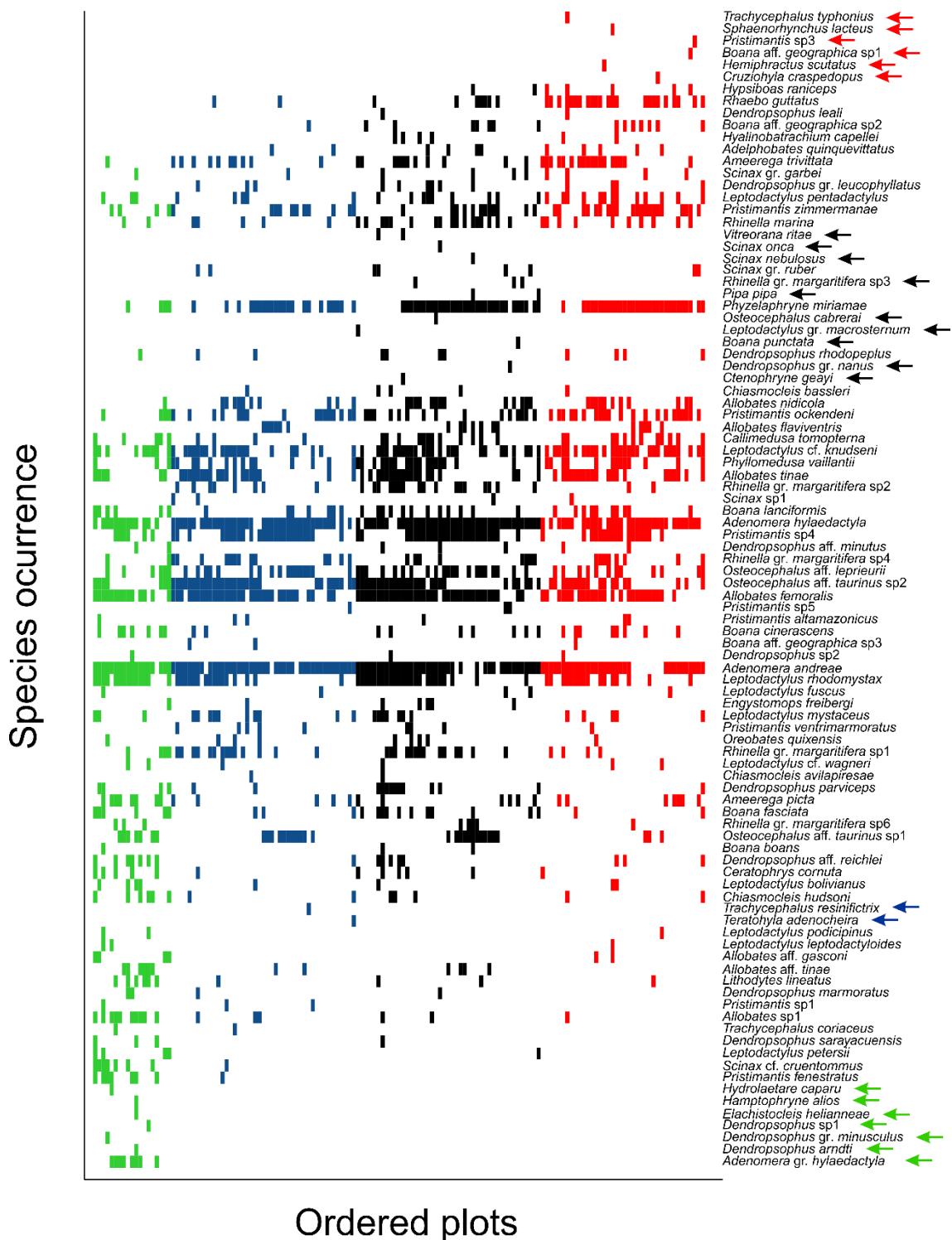


Figure 3. Plots of the occurrence of frogs in relation to flooding and time since filling of the Santo Antônio dam in the Madeira River, southwestern Brazilian Amazonia. Green = plots that were sampled pre-filling that were flooded, blue = plots that were sampled pre-filling that were not flooded, black = plots sampled 1 year after dam filling, red = plots sampled 4 years after dam filling. Arrows indicate the species registered only in one flood-by-time category (indicated by color).

Based on the sample-based rarefaction curves, numbers of species detected per plot in the pre-stage flooded and post1-stage categories were higher than the number detected in the pre-stage unflooded and post2 unflooded categories. However, extrapolation to 60 plots indicates that the 95% confidence intervals converge, so flooding stages might not differ in the total number of species they support in the whole area, even though there are differences in the mean number of species per plot (S1 Fig).

The multivariate general linear model (GLM) analyses indicated that the species compositions differed among the four categories of flooding by stage for the occurrence data (Wald= 19.14, p=0.001) and for the relative-abundance data (Wald= 20.46, p=0.001). Pairwise comparisons indicated that the species composition differed between all pairs of flooding categories (Table 1). The PCoA plots showed little difference in frog species composition of pre-stage unflooded, post1-stage and post2-stage, but pre-stage flooded plots were generally distinct (Fig 4).

Table 1. Manyglm analysis of the association between the structure of frog assemblages in flooded and unflooded plots around the Madeira River, southwestern Brazilian Amazonia in relation to inundation and time before or after dam filling.

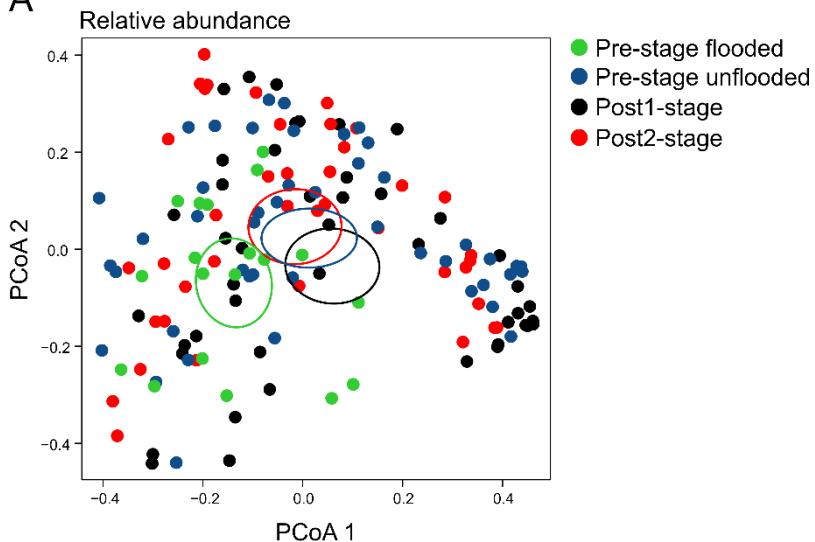
Overall effect – Abundance	Wald	P
All categories	20.46	0.001
Post hoc pairwise comparisons	Sum-of-LR statistic	P
Pre-stage flooded vs. pre-stage unflooded	269.5	0.001
Pre-stage flooded vs. post1-stage	285.4	0.001
Pre-stage flooded vs. Post2-stage	309.4	0.001
Pre-stage unflooded vs. post1-stage	151.8	0.011
Pre-stage unflooded vs. post2-stage	170.2	0.003
Post1-stage vs. post2-stage	175.9	0.002

Overall effect – Ocurrence	Wald	P
All categories	19.14	0.001
Post hoc pairwise comparisons	Sum-of-LR statistic	P
Pre-stage flooded vs. pre- stage unflooded	297.1	0.001
Pre- stage flooded vs. post1-stage	297.2	0.001

Pre- stage flooded vs. post2-stage	337.8	0.001
Pre- stage unflooded vs. post1-stage	141.8	0.013
Pre-stage unflooded vs. post2-stage	178.5	0.004
Post1-stage vs. post2-stage	166.0	0.004

Pre-stage flooded = plots that were sampled pre-filling that were flooded; pre-stage unflooded = plots that were sampled pre-filling that were not flooded; post1-stage = plots sampled 1 year after dam filling; post2-stage = plots sampled 4 years after dam filling. Results show deviance table and frequentist probabilities (p) based on 999 bootstrap iterations with PIT-trap resampling. LR means log-likelihood-ratio statistic.

A



B

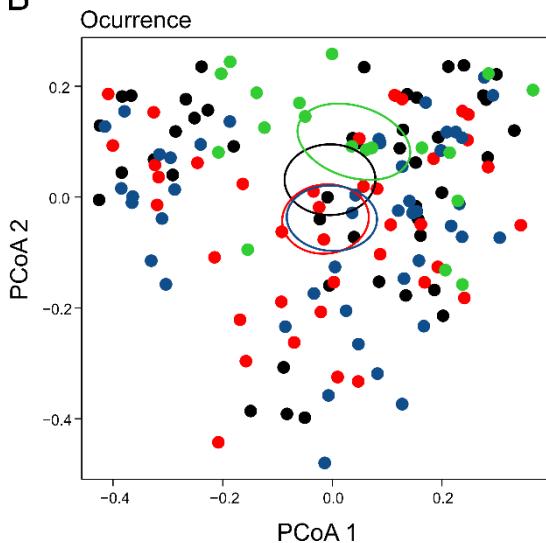


Figure 4. First two axes of a principal coordinates analysis (PCoA) based on relative abundance (A) and occurrence (B) of frog species showing the 95% confidence ellipses for the centroids of samples in plots in relation to inundation and time since filling of the Santo Antônio dam on the Madeira River, southwestern Brazilian Amazonia. green = plots that

were sampled pre-filling that were flooded; blue = plots that were sampled pre-filling that were not flooded; black = plots sampled 1 year after dam filling; red = plots sampled 4 years after dam filling.

The temporal change in assemblage structure in unflooded plots was mainly caused by gain in species per plot. About 82% of the plots had increases in the number of species from the pre-stage unflooded to post1-stage ($p < 0.001$; C-B=+) and 65% of the plots had increases in the number of species from the pre-stage unflooded to post2-stage ($p = 0.005$; C-B=+). Plots had similar abundance per species in pre-stage unflooded and the post1-stage ($p = 0.906$; C-B=0) (S6 Table).

The multivariate GLM analyses indicated that there was a temporal change in the frog assemblages of the unflooded plots within 2 km from the flooding area in all comparisons. However, this change was not detected in the assemblages in plots further than 2 km from the flooded area, which showed no statistically significant differences among stages (S7 Table) (S3 Fig).

We used the first two axes of a PCoA analysis to summarize the temporal trajectories of frog assemblages in unflooded plots over the three flooding stages (S4 Fig). Intra-annual changes were more evident along axis 1 of the PCoA, probably resulting from seasonal or weather-induced variation. Displacement along the second axis recorded changes among years, and the general trend for change in that direction was already evident in the year before flooding, indicating that the subsequent changes might not have been due to dam construction.

Discussion

Overall, our results indicate that the construction of the Santo Antônio hydroelectric had little effect on the number or identity of species in the region. Few species recorded in the pre-stage flooded plots were not found in the pre-stage unflooded plots or in stages after dam filling, and most of these absences were probably due to the vagaries of sampling. This was unexpected as many of the flooded plots were covered in várzea forest, a vegetation association often found to contain unique complements of species of other taxa (Junk et al., 2012; Parolin, Ferreira, Albernaz, & Almeida, 2004). Nevertheless, the assemblages in flooded areas based on relative abundances were distinct from upland unflooded plots and similar assemblages have not been reconstituted over time in plots near the new banks of the reservoir.

Santo Antônio and Jirau hydroelectric dams flooded 118 km² of várzea forest in the area upstream of the Santo Antônio dam (including the Jirau dam and Bolivian section of the Madeira River). In the Amazon, 83 dams are expected to be built with the potential to affect the floodplains of the Amazon River basin, with the Madeira River sub-basin considered the most threatened in the Amazon (Latrubesse et al., 2017). Run-of-the-river dams permanently impact várzea and riparian forests, and less than 1% of Amazonian floodplains in Brazil are in strictly-protected conservation areas, even though the mandatory protected area of 25% gives the impression of extensive floodplain conservation management (Albernaz et al., 2012).

Permanent inundation of the floodplains of the major Amazonian rivers could lead to irreparable losses of unique habitats (Beja et al., 2010; Haugaasen & Peres, 2006; Junk et al., 2012; Parolin et al., 2004). Assemblages of frogs in várzea and riparian forest have been shown to be distinct from unflooded terra-firme forest (Gascon, 1996; May et al., 2010; Moraes, Pavan, Barros, & Ribas, 2016). Várzea forests are periodically inundated by nutrient-rich waters (Junk et al., 2012) and tend to have more species and higher abundances of frogs than unflooded terra-firme forest. This pattern is also found in other groups of animals and plants (Alvarenga et al., 2018; Ayres, 1994; Beja et al., 2010; Paulo Estefano D. Bobrowiec et al., 2014; Haugaasen & Peres, 2005; May et al., 2010). However, our analyses did not reveal loss of species due to flooding of most of the várzea forest and this may be because most species can live in riparian areas away from the main river. However, the relative abundances of species were different in the areas that were inundated by the dam, indicating unique ecological processes maintaining assemblages. Similar assemblages may eventually be reconstituted around the edges of the reservoir, but the data up to four years after dam filling does not indicate that this is happening.

Generally, natural or anthropogenic disturbances promote changes in the composition of species (Benchimol & Peres, 2015; Lees et al., 2016). In unflooded areas around the Santo Antônio dam, frog assemblages showed constant temporal changes in species relative abundances and the number of species per plot, especially for plots within two kilometers of the new reservoir bank, and these changes had not stopped four years after dam filling. The temporal change in species composition was accompanied by a reduction in the relative abundance of frogs in most plots, but the number of species increased. The margins of a newly formed reservoir generally do not replicate the same alluvial habitats that previously existed (Abreu et al., 2020; Alho, 2011). However, there is some evidence that the frog assemblages in the unflooded area were changing even

before dam construction, so we cannot be sure whether these changes were caused by the dam filling. Extrapolation in the rarefaction analyses indicates that the total number of species (gamma diversity) might not differ among flooding stages, even though there are differences in alpha and beta diversity.

Contrary to our expectations based on data from mega dams that alter extensive areas of native vegetation (Dalecky et al., 2002; Guzy et al., 2018), the number of species increased in 65% of the plots four years after dam filling, and the changes were greatest within two kilometers of the new bank of the reservoir. The increase in number of species in areas adjacent to those flooded by the dam may be an example of the dam's extended effect (Alho, 2011; Brandão & Araújo, 2008). After reservoir filling, the animals displaced by the flooding move to the nearest remaining areas, which may have increased the number of species recorded per plot in the non-flooded areas. In the period of community restructuration after a disturbance, some populations may decrease while others can occupy the newly formed environments (Bennett & Saunders, 2011; Metzger et al., 2009). The effects of environmental impacts is almost immediate in some cases, but often it takes a considerable amount of time for declining populations to disappear following environmental perturbations (Benchimol & Peres, 2015).

Despite the changes in relative abundances of species in assemblages, dam filling did not extinguish many species, as is expected for large hydroelectric projects. Most of the species recorded in the area to be inundated before flooding were also recorded post flooding, and 40% of species were found in all flooding stages. A few species of frogs ($N = 7$) that were recorded in the pre-stage flooded plots may have disappeared from the area around the Santo Antônio hydroelectric dam. However, six of the seven species not recorded after dam filling occurred in only one plot and may have been absent from the post-filling surveys simply because of the vagaries of sampling. The only species found in more than one plot that was not captured subsequently, *Adenomera gr. marmoratus* sp1, occurred in the Morrinhos sampling module that was completely inundated. Surveys specifically for species that occurred in the Morrinhos module revealed this species to still be present on the new banks of the reservoir. This indicates that hydroelectric plants with run-of-the-river turbines may not eliminate species locally if areas with native vegetation are conserved around the new banks of the river.

The limited data collected before dam filling showed the same temporal trajectory in assemblage composition in the unflooded areas as the stages after construction of the dam. So it is possible that the changes are related to some long-term phenomenon

unrelated to the dam, and it is not possible to discount this possibility with the small number of sample dates before the dam was closed.

The faunal surveys associated with the environmental-impact evaluations for the Santo Antônio hydroelectric dam were among the most intensive, well planned and long-term ever carried out in Brazil and studies of other faunal groups have already been published, including papers on bats, fish and trees [eg. 18,21,54,55]. However, understanding long-term effects on biodiversity requires long-term studies and, in the case of large-scale infrastructure projects, future research should start well before dam construction so that natural fluctuations in species densities can be documented. The lack of understanding by the controlling authorities of the long-term effects of landscape changes, such as water-table rises, means that they also do not require studies covering appropriate periods post construction. There is evidence of long-term changes in the structure of the frog assemblages around the Santo Antônio dam, with no indication of return to the initial compositions. Long-term monitoring after project installation with less frequent sampling would allow studies over the longer periods that are often associated with relaxation of biotic communities (Abreu et al., 2020).

In summary, few, if any, species were lost from the area as a result of the Santo Antonio dam. Some assemblages with unique combinations which occurred in the areas that were flooded were not recomposed on the new banks of the reservoir during the study period. There was evidence that the dam affected the compositions of frog assemblages in unflooded areas, especially those closest to the reservoir. The mean number of species increased over time in unflooded plots, without substitution of the original species complements. However, limited evidence indicated that those changes may have been happening in unflooded areas before dam closure. Stronger conclusions about these changes in species composition would be possible using a BACI design (Fisher et al., 2019). We recommend that environmental authorities require long-term monitoring and BACI designs in future environmental-impact studies.

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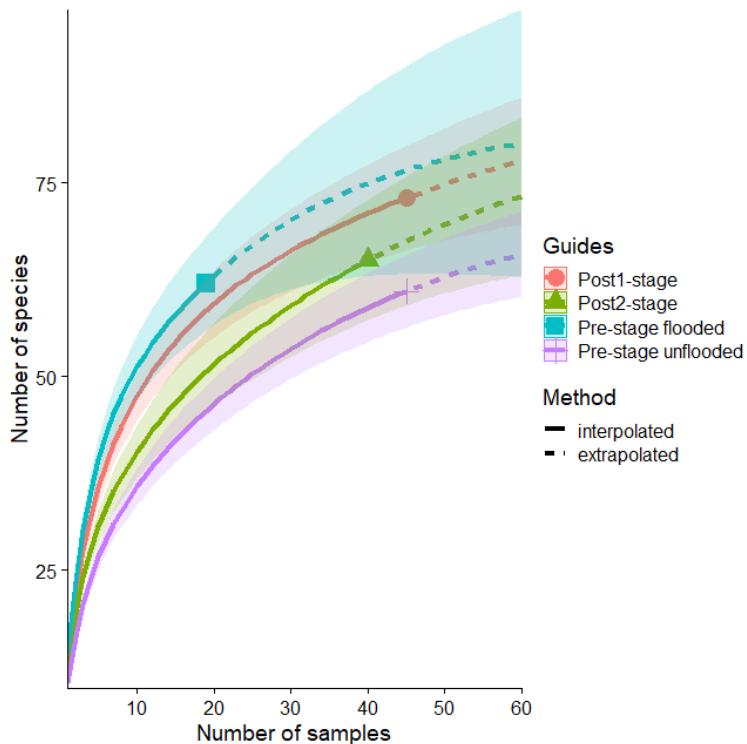
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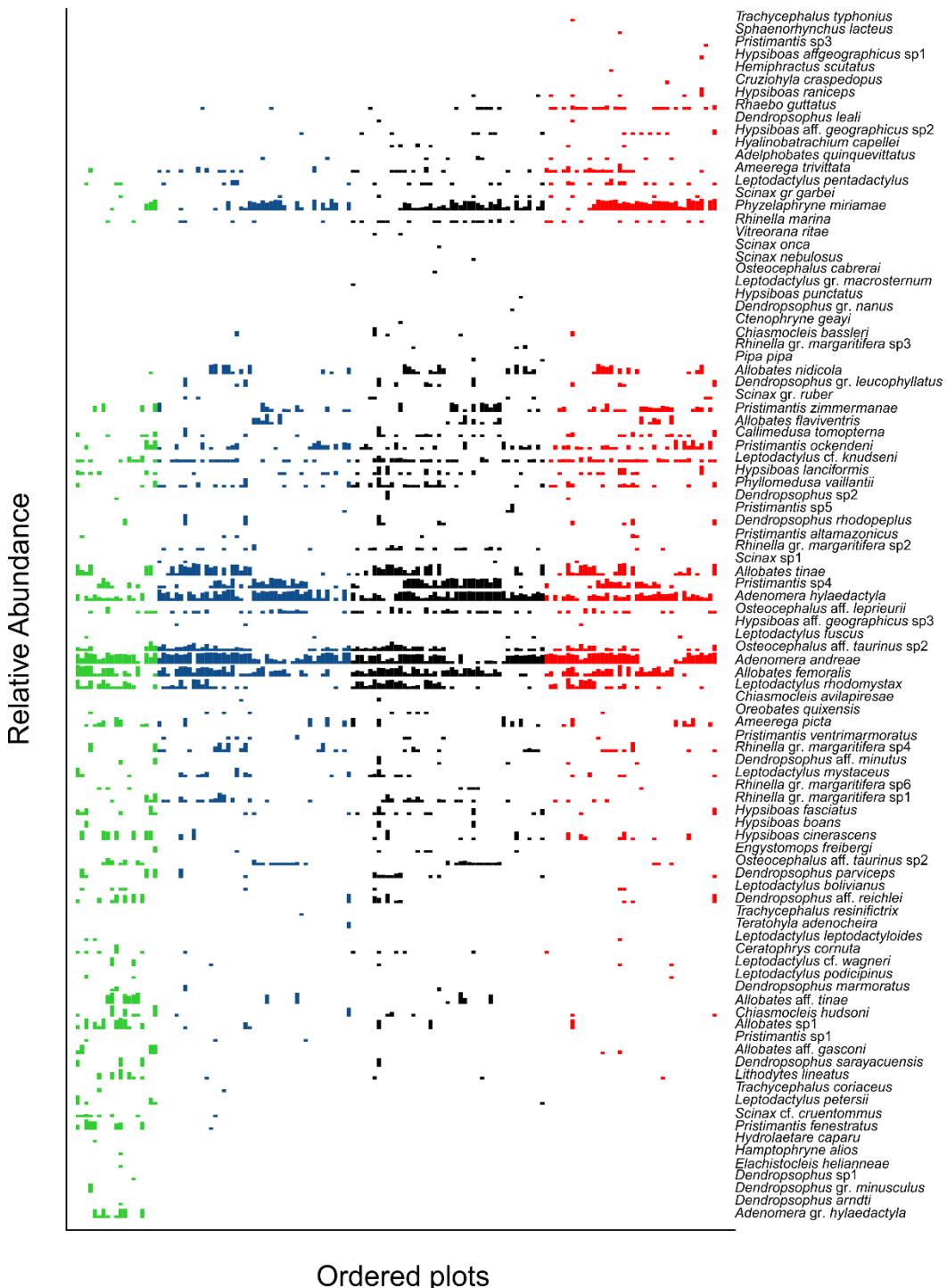
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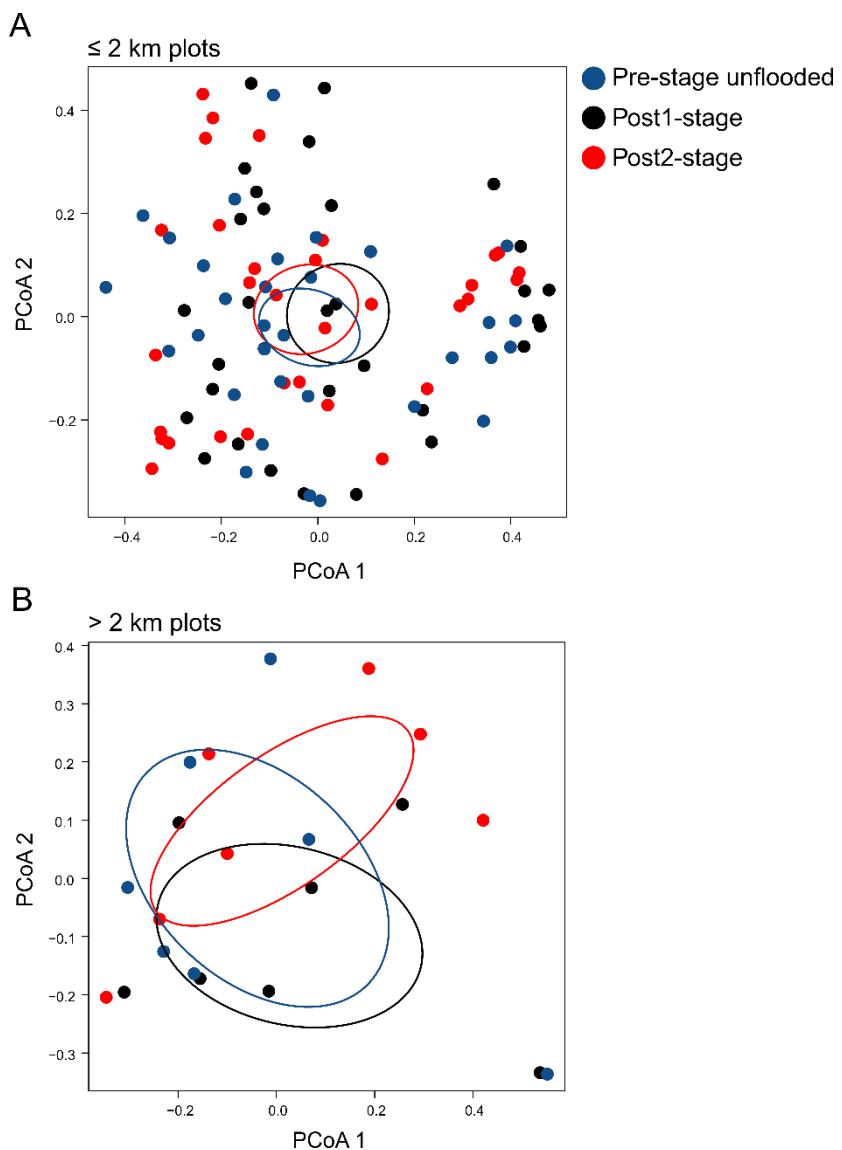
Supporting information



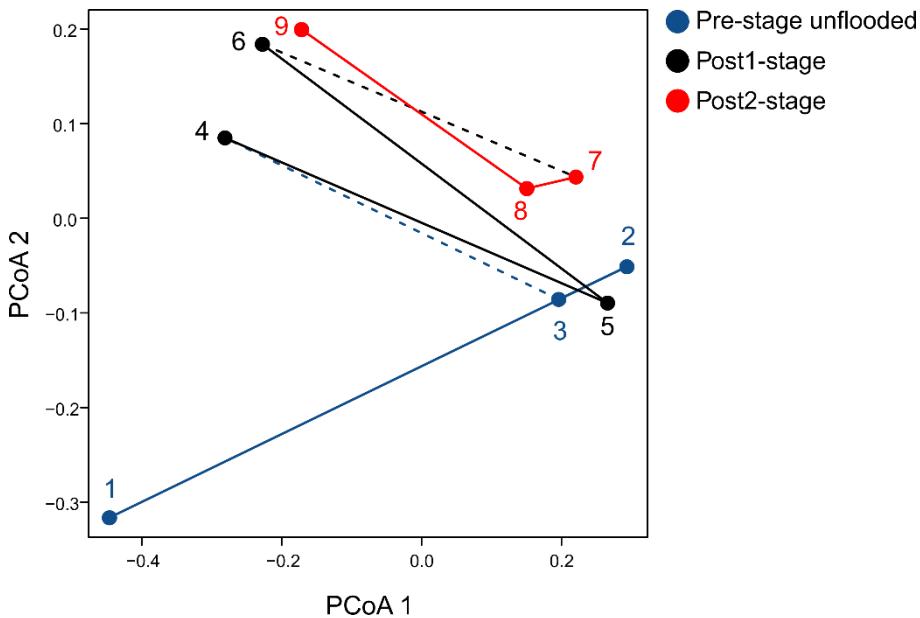
S1 Fig. Sample-based rarefaction and extrapolation for combinations of flooding and time since filling of the Santo Antônio dam on the Madeira River, southwestern Brazilian Amazonia. with 95% unconditional confidence intervals (shaded area, bootstrap with 1,000 replications). Each of the curves is extrapolated up to the maximum sample size of 60 sample units.



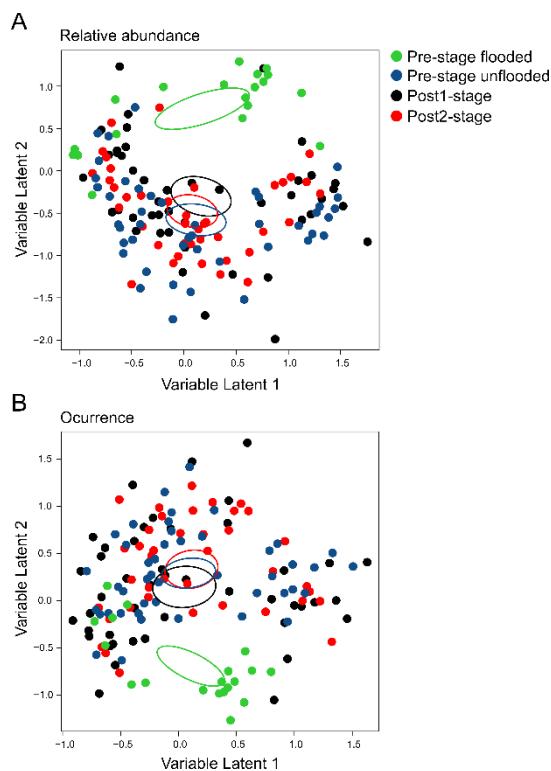
S2 Fig. Plots of relative abundance ($\log [x + 1]$ transformed relative abundance values to better visualization) of frogs in relation to flooding and time since filling of the Santo Antônio dam on the Madeira River, southwestern Brazilian Amazonia. green = plots that were sampled pre-filling that were flooded; blue = plots that were sampled pre-filling that were not flooded; black = plots sampled 1 year after dam filling; red = plots sampled 4 years after dam filling.



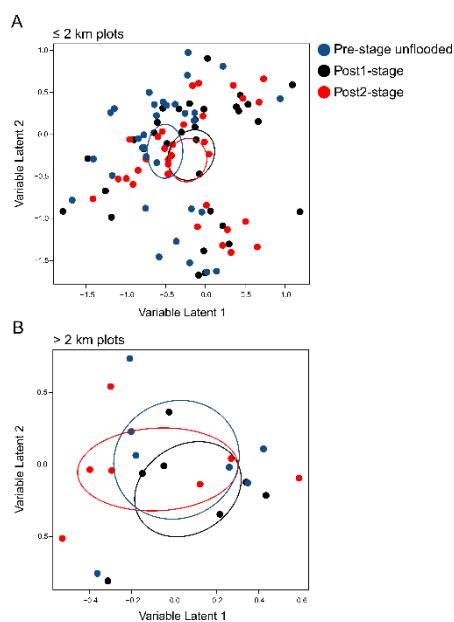
S3 Fig. First two axes of a principal coordinates analysis (PCoA) based on relative abundance in both near ($\leq 2 \text{ km}$) (A) and distant ($> 2 \text{ km}$) (B) plots showing the 95% confidence ellipses for the centroids of samples in relation to flooding and time since filling of the Santo Antônio dam on the Madeira River, southwestern Brazilian Amazonia. blue = plots that were sampled pre-filling that were not flooded; black = plots sampled 1 year after dam filling; red = plots sampled 4 years after dam filling.



S4 Fig. First two axes of a principal coordinates ordination (PCoA) of frog species composition showing the 95% confidence ellipses for the centroids of samples in plots in relation to the flooding and time since filling of the Santo Antônio dam on the Madeira River, southwestern Brazilian Amazonia. blue = plots that were sample pre-filling that were not flooded, black = plots sampled 2 years after dam filling, red = plots sampled 4 years after dam filling. Numbers indicate temporal trajectories. Dotted lines indicate change of flooding period. All data were grouped in each survey period resulting in nine points based on the same 39 plots sampled in each period.



S5 Fig. Distribution of plots in the multivariate space defined by the best-fit latent variables based on relative abundance (A) with a negative-binomial distribution and occurrence (B) with a binomial distribution of frog species showing the 95% confidence ellipses for the centroids of samples in plots in relation to the flooding and time since filling of the Santo Antônio dam on the Madeira River, southwestern Brazilian Amazonia. green = plots that were sampled pre-filling that were flooded; blue = plots that were sampled pre-filling that were not flooded; black = plots sampled 1 year after dam filling; red = plots sampled 4 years after dam filling.



S6 Fig. Distribution of plots in the multivariate space defined by the best-fit latent variables based on relative abundance with a negative-binomial distribution in both near (≤ 2 km) (A) and distant (> 2 km) (B) plots showing the 95% confidence ellipses for the centroids of samples in relation to the flooding and time since filling of the Santo Antônio dam on the Madeira River, southwestern Brazilian Amazonia. blue = plots that were sampled pre-filling that were not flooded; black = plots sampled 1 year after dam filling; red = plots sampled 4 years after dam filling.

S1 Table. Summary of flooding, time since dam filling, distance from river and coordinates of the 66 plots sampled around the Santo Antônio hydroelectric dam, Western Amazonia, Brazil. Pre-stage flooded = plots that were sampled pre-filling that were flooded; pre-stage unflooded = plots that were sample pre-filling that were not flooded; post1-stage = plots sampled 1 year after reservoir filling; post2-stage = plots sampled 4 years after reservoir filling.

S2 Table. Number of species recorded, median of abundance and number of plots with records of anuran species sampled in relation to flooding and time since filling of the Santo Antônio hydroelectric dam on the Madeira River, Western Amazonia, Brazil. n plots= number of plots with species records; total plots= total number of plots surveyed; pre-stage flooded = Plots that were sampled pre-filling that were flooded; pre-stage unflooded = plots that were sample pre-filling that were not flooded; post1 stage = plots sampled 1 year after reservoir filling; post2-stage = plots sampled 4 years after reservoir filling.

S3 Table. Manyglm analysis examining the association between the structure of frog assemblages with only abundant species (at least 5% abundance and 4% of plots in our sample) recorded in flooded and unflooded plots around the Madeira River, southwestern Brazilian Amazonia. Pre-stage flooded = plots that were sampled pre-filling that were flooded; pre-stage unflooded = plots that were sampled pre-filling that were not flooded; post1-stage = plots sampled 1 year after dam filling; post2-stage = plots sampled 4 years after dam filling. Results show deviance table and frequentist probabilities (p) based on 999 bootstrap iterations with PIT-trap resampling. LR means log-likelihood-ratio statistic.

Overall effect – Abundance	Wald	p
All treatments	20.22	0.001
Post hoc pairwise comparisons	Sum-of-LR statistic	p
Pre-stage flooded vs. pre-stage unflooded	247.2	0.001
Pre-stage flooded vs. post1-stage	253.9	0.001
Pre-stage flooded vs. post2-stage	284.2	0.001
Pre-stage unflooded vs. post1-stage	126.0	0.003
Pre-stage unflooded vs. post2-stage	152.2	0.010
Post1-stage vs. post2-stage	149.6	0.004
Overall effect – Ocurrence	Wald	p
All treatments	19.45	0.001
Post hoc pairwise comparisons	Sum-of-LR statistic	p
Pre-stage flooded vs. pre-stage unflooded	280.9	0.001

Pre-stage flooded vs. post1-stage	277.4	0.001
Pre-stage flooded vs. post2-stage	319.3	0.001
Pre-stage unflooded vs. post1-stage	129.2	0.013
Pre-stage unflooded vs. post2-stage	166.8	0.005
Post1-stage vs. post2-stage	147.9	0.011

S4 Table: Manyglm analysis examining the association between the structure of assemblages with only abundant species (at least 8% abundance and 5% of plots in our sample) recorded in flooded and unflooded plots around the Madeira River, southwestern Brazilian Amazonia. Pre-stage flooded = plots that were sampled pre-filling that were flooded; pre-stage unflooded = plots that were sampled pre-filling that were not flooded; post1-stage = plots sampled 1 year after dam filling; post2-stage = plots sampled 4 years after dam filling. Results show deviance table and frequentist probabilities (p) based on 999 bootstrap iterations with PIT-trap resampling.

Overall effect – Abundance	Wald	p
All treatments	19.38	0.001
Post hoc pairwise comparisons	Sum-of-LR statistic	p
Pre-stage flooded vs. pre-stage unflooded	203.3	0.001
Pre-stage flooded vs. post1-stage	217.4	0.001
Pre-stage flooded vs. post2-stage	250.6	0.001
Pre-stage unflooded vs. post1-stage	110.9	0.001
Pre-stage unflooded vs. post2-stage	138.8	0.011
Post1-stage vs. post2-stage	128.2	0.002

Overall effect – Ocurrence	Wald	p
All treatments	18.42	0.001
Post hoc pairwise comparisons	Sum-of-LR statistic	p
Pre-stage flooded vs. pre-stage unflooded	232.5	0.001
Pre-stage flooded vs. post1-stage	227.1	0.001
Pre-stage flooded vs. post2-stage	286.4	0.001
Pre-stage unflooded vs. post1-stage	102.8	0.001
Pre-stage unflooded vs. post2-stage	148.5	0.011

Post1-stage vs. post2-stage	119.6	0.018
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S5 Table: Manyglm analysis examining the association between the structure of assemblages of species considered rare in the sampling (only records with up to 5% abundance and 4% of plots in our sample) in flooded and unflooded plots around the Madeira River, southwestern Brazilian Amazonia. Pre-stage flooded = plots that were sampled pre-filling that were flooded; pre-stage unflooded = plots that were sampled pre-filling that were not flooded; post1-stage = plots sampled 1 year after dam filling; post2-stage = plots sampled 4 years after dam filling. Results show deviance table and frequentist probabilities (p) based on 999 bootstrap iterations with PIT-trap resampling.

Overall effect – Abundance	Wald	p
All treatments	2.264	0.185
Post hoc pairwise comparisons	Sum-of-LR statistic	p
Pre-stage flooded vs. pre-stage unflooded	22.29	0.098
Pre-stage flooded vs. post1-stage	31.49	0.022
Pre-stage flooded vs. post2-stage	25.14	0.098
Pre-stage unflooded vs. post1-stage	25.76	0.098
Pre-stage unflooded vs. post2-stage	17.95	0.098
Post1-stage vs. post2-stage	26.33	0.098
Overall effect – Ocurrence	Wald	p
All treatments	0.552	0.871
Post hoc pairwise comparisons	Sum-of-LR statistic	p
Pre-stage flooded vs. pre-stage unflooded	16.22	0.076
Pre-stage flooded vs. post1-stage	19.78	0.076
Pre-stage flooded vs. post2-stage	18.53	0.076
Pre-stage unflooded vs. post1-stage	12.58	0.122
Pre-stage unflooded vs. post2-stage	11.69	0.122
Post1-stage vs. post2-stage	18.10	0.076

S6 Table. Tests for differences in temporal beta-diversity indices (TBI) for the structure of frog assemblages between the flooding stages in unflooded plots around the Santo Antônio reservoir on the Madeira River, southwestern Brazilian Amazonia, Brazil. These analyses include only plots surveyed during all flooding stages. N_plots+ is the number of plots with gains in number of species or abundance of species; N_plots- is the number of plots with losses in number of species or abundance of species and N_plots0 is the number of plots without changes in number of species or abundance of species. Pre-stage unflooded = plots that were sample pre-filling that were not flooded; post1-stage = plots sampled 1 year after reservoir filling; post2-stage = plots sampled 4 years after reservoir filling. *p* represents the frequentist probability of a difference between the *B* and *C* statistics.

Post hoc pairwise comparisons	B (losses)	C (gains)	C-B (change)	N_plots-	N_plots+	n_plots0	p
Pre-stage unflooded vs. post1-stage – Abundance	0.22	0.22	0	23	19	3	0.906
Pre-stage unflooded vs. post2-stage – Abundance	0.27	0.23	-	25	15	0	0.198
Pre-stage unflooded vs. post1-stage – Ocurrence	0.12	0.27	+	3	37	5	< 0.001
Pre-stage unflooded vs. post2-stage – Ocurrence	0.17	0.26	+	10	26	4	0.005

S7 Table. Manyglm analysis for pairwise tests of differences in the structure of frog assemblages less than 2 km and between 2 km and 5 km distant from the flood margin between the flooding stages in unflooded plots of the Santo Antônio reservoir in the Madeira River, southwestern Brazilian Amazonia, Brazil. Pre-stage unflooded = plots that were sample pre-filling that were not flooded; post1-stage = plots sampled 1 year after reservoir filling; post2-stage = plots sampled 4 years after reservoir filling. Results show deviance table and frequentist probabilities (p) values based on 999 bootstrap iterations with PIT-trap resampling. LR means log-likelihood-ratio statistic.

Pairwise comparisons	Sum-of-LR statistic	p
until 2 km		
Pre-stage unflooded vs. post1-stage	133.3	0.036
Pre-stage unflooded vs. post2-stage	135.1	0.034
Post1-stage vs. post2-stage	132.5	0.036
Between 2 km and 5 km		
Pre-stage unflooded vs. post1-stage	63.30	0.239
Pre-stage unflooded vs. post2-stage	82.51	0.209
Post1-stage vs. post2-stage	78.56	0.209

CAPITULO 2 SUBMETIDO NA FUNCTIONAL ECOLOGY

CAPITULO 2: Functional responses of Amazonian frogs to flooding by a large hydroelectric dam

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Abstract

1. The 471-km² Santo Antônio Dam, filled in 2010, resulted in reduced forest cover, loss of riparian ecosystems, and degradation of terrestrial resources adjacent to the newly formed riverbank along the artificial reservoir. The regions most impacted by the dam were the lower-elevation alluvial plains near the margins, mainly comprised of seasonally flooded “várzea” forests, which harbour very rich animal assemblages. These impacts can be quantified based on functional traits to identify specific characteristics that may be sensitive to environmental changes resulting from a large-scale disturbance, such as river impoundment
2. We used data from eight years of monitoring the area of influence of the Santo Antônio Dam in southwestern Brazilian Amazonia to investigate the effects of forest inundation on estimates of functional diversity and functional traits in frog assemblages. We examined functional diversity estimates based on 84 frog species since before the Santo Antônio reservoir was inundated until four years thereafter.
3. Functional indices in the pre-flooding flooded forest plots diverged from unflooded plots before and after dam closure but remained similar after flooding in plots across unflooded areas. Flooding by the Santo Antônio Dam did not result in the complete elimination of any trait or trait combination characterizing frog assemblages. Differences in the functional diversity of Amazonian frog assemblages were largely due to baseline environmental differences between seasonally flooded and unflooded areas. Functional traits linked to reproductive strategies, such as egg deposition and larval development, were the most affected by the Santo Antônio Dam.
4. Longer monitoring periods before and after reservoir filling would be necessary to clearly identify the effects of major infrastructure projects.

Keywords

Amazon; Environmental-impact assessment; Functional traits; Riparian habitats; Disturbance; run-of-river dam; Tropics.

Introduction

Hydroelectric dams have generated socio-environmental concerns in the tropical forests because many are in operation or planned for construction (Castello & Macedo, 2016; Latrubblesse et al., 2017). Dams flood vast forest areas, alter the physical and chemical characteristics of the water by removing sediments, disrupting fish migrations, and detrimentally affecting human settlements by displacing them and degrading their resource base (Fearnside, 2014; Latrubblesse et al., 2020).

One option to minimize the environmental impacts of the huge lakes created by mega-dams is the construction of run-of-the-river dams, which form relatively small reservoirs, with limited potential for water storage. Run-of-the-river dams are often extolled by hydropower sector as a model of low environmental impact, due to their low potential for altering river flow (Csiki & Rhoads, 2014). Although smaller than traditional dams, run-of-river dams often require additional upstream reservoirs, and the potential impacts of this model on aquatic and terrestrial ecosystems in the Amazon are still poorly understood (Cochrane et al., 2017; Fearnside, 2014).

Two of the world's largest run-of-river dams— Santo Antônio and Jirau — are located on the upper Madeira River, the largest tributary of the Amazon River in terms of water and sediment discharge prior to those two dams (Park & Latrubblesse, 2019). The Madeira is a ‘white-water’ river due to the heavy load of suspended sediments derived from Andean erosion (Park & Latrubblesse, 2019), and the floodplains formed on its banks can be up to 1-km wide and are mainly covered by seasonally flooded “várzea” forests. Farther inland from the floodplains, there are “terra firme” forests, which do not flood on a seasonal basis but may experience sporadic, small-scale rain-fed inundation (Pires & Prance, 1985).

The Jirau and Santo Antônio Dams, built on the Madeira River and filled in 2010, caused a reduction in forest cover, loss of riparian ecosystems, and degradation of terrestrial resources adjacent to the newly formed riverbank along the artificial reservoirs (Latrubblesse et al., 2017; Rivera et al., 2019; Santos et al., 2020). The regions most impacted by these dams were the lower-elevation alluvial plains near the margins, comprised mainly of seasonally flooded “várzea” forests, but also continuous strips of “terra firme” forests and “campinaranas” (stunted forests on sandy soils). The principal landscape changes included a 72% increase in permanently flooded areas (Cochrane et al., 2017; Oliveira et al., 2021), and extensive tree mortality near the newly formed margins, due to soil saturation in environments where the vegetation was flood-

intolerant (Cochrane et al., 2017; Moser et al., 2019; Santos et al., 2020). Additionally, these dams changed the composition of frog (Dayrell et al., 2021) and phyllostomid bat (Bobrowiec et al., 2021) assemblages in the areas adjacent to the reservoir, and the avifauna occupying floodplains (Melo et al., 2021).

Changes in the composition of frog assemblages near the reservoir were mainly driven by a decrease in the abundance of some species and increase in richness (Dayrell et al., 2021). Alternatively, animal assemblages can be quantified based on functional traits to identify characteristics that may be sensitive to environmental change resulting from a large-scale disturbance, such as river impoundment (Weiss & Ray, 2019). Functional Diversity metrics can pinpoint the effects of anthropogenic disturbances on biodiversity that cannot be demonstrated through traditional metrics based solely on species abundance (Álvarez-Grzybowska et al., 2020; Berriozabal-Islas et al., 2017).

In this study, we used data from eight years of monitoring the “area of influence” of the Santo Antônio Dam of southwestern Brazilian Amazonia to investigate the effects of forest inundation on functional diversity and prevalence of functional traits in frog assemblages. Changes in habitat characteristics resulting from flooding extensive forest strips may result in the occurrence of species with morpho-ecological traits that diverge from those in the original assemblage. Alternatively, species may be replaced by others with similar traits, which would result in changes in the taxonomic, but not functional composition of assemblages (Lepš et al., 2011).

Considering that the riparian forests of the upper Madeira River occupy narrow strips of alluvial soil along the river (Moser et al., 2014) and that some “terra firme” forest areas succumb to sporadic local flooding due to heavy rainfall, our goal was to determine the degree to which estimates of multivariate functional diversity (richness, equity, and divergence) and frequency of occurrence of individual traits in the flooded area are distinct from those in non-flooded areas. Additionally, as the artificial flooding of habitats altered the structure of both the soil and vegetation cover (Cochrane et al., 2017; Moser et al., 2019), we assessed the effects of flooding on the functional diversity, mediated by filtering traits less adjusted to the new environmental conditions. We used a temporal approach with sampling conducted both before (2009-2011) and four years (2016-2017) after the Santo Antônio reservoir was filled (2012). As taxonomic composition of frog assemblages changed (Dayrell et al., 2021), we hypothesized that this might have resulted in differences in the functional composition of frog assemblages. Since the size structure and behavioural or ecological

characteristics of frog assemblages (e.g. reproductive mode, use of vertical vegetation strata) can be differentially affected by environmental disturbances (Riemann et al., 2017), we sought to determine whether changes in species composition also resulted in changes in the occurrence of behavioural and ecological traits.

Material and Methods

Study Area

This study was conducted along the Madeira River, within the area of influence of the Santo Antônio hydroelectric dam, southwestern Amazon ($08^{\circ}48'S$; $63^{\circ}57'W$). Santo Antônio is a mega-dam that went into operation in March 2012, with a generation capacity of 3,150 MW, and a reservoir area of 471 km^2 (P. Fearnside, 2015). The dam is a run-of-the-river project with bulb-type turbines which serve smaller reservoirs and require less water storage than traditional hydroelectric dams. However, the reservoir reaches 70 m above the river's maximum natural flood level.

The regional climate is tropical humid hyperthermic (Cochrane et al., 2017). The vegetation is predominantly an association of lowland open tropical forest with palm trees and alluvial open forest with patches of pastures, lowland formations, and the transition between open rainforest and stunted “campinarana” forest (Moser et al., 2014). The study area on the west bank of the Madeira River is relatively well protected by the Mapinguari National Park, but forests on the east bank are fragmented by pastures, cropland, and roads (Ferraz et al., 2005).

Experimental Design

The sampling design followed the RAPELD method for standardized surveys of fauna and flora developed by the PPBio Biodiversity Research Program (Magnusson et al., 2013). RAPELD plots are 250-m long and up to 40-m wide and follow topographic contours to minimize internal heterogeneity in soil properties, drainage, and correlated variables. Each RAPELD module was composed by 14 plots, with plot pairs distributed at 50; 500; 1,000; 2,000; 3,000; 4,000; and 5,000 m from the riverbank along trails perpendicular to the riverbank. We installed four modules (Fig. 1, M1 to M4) on the Madeira River and one on the Jaci-Paraná River, a right-bank tributary of the Madeira River, totaling 69 sampling plots (Table S1).

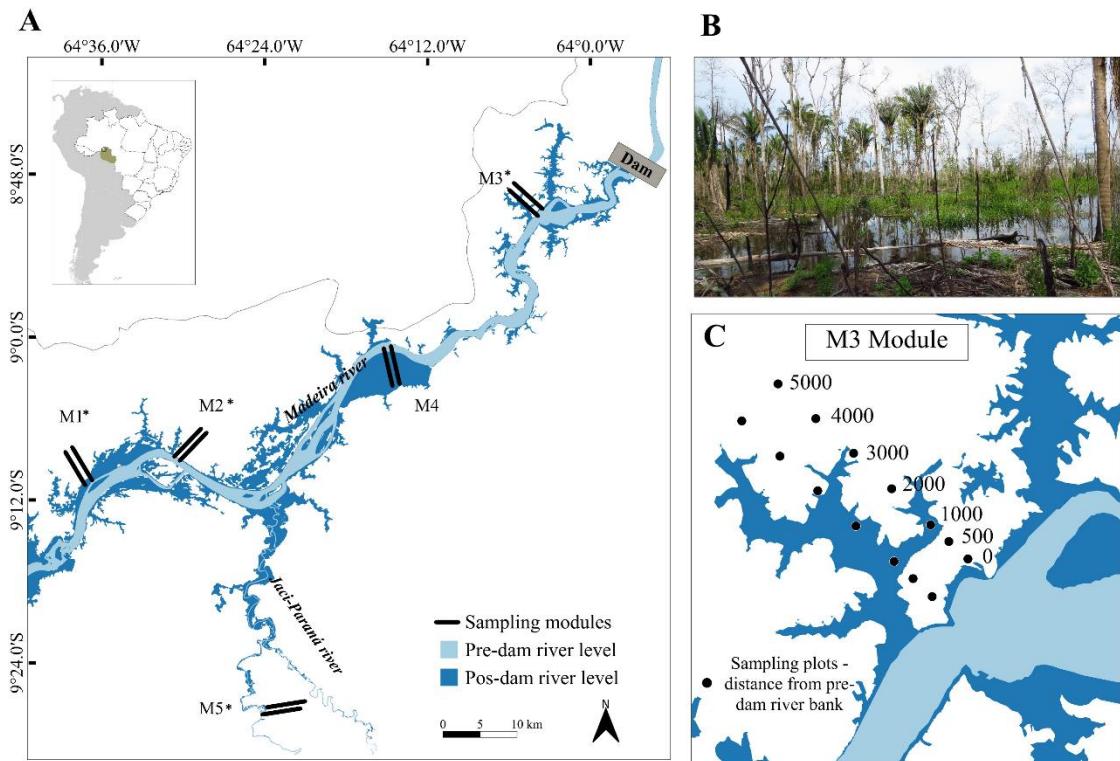


Figure 1 Location of the study area upstream of the Santo Antônio hydroelectric dam on the upper Madeira River. A) M1, M2, M3 = left-bank modules; M4, M5 = right-bank modules. B) View of M1 module in 2017, after the dam was filled (photo credit: J. Dayrell). C) Spatial distribution of sampling plots in M3 Module in relation to the post-flooding water level. Asterisks indicate sampling sites surveyed in the aftermath of river damming.

Sampling Data

We sampled the 58 plots in 2010-2011, before the flooding of the dam reservoir (2011-2012). Of the 58 sampled plots, only 19 of were completely flooded. Therefore, for the period prior to dam closure, we assigned the pre-flooding data to either 19 plots that were inundated (pre-flooded plots) and 39 that remained unflooded (pre-unflooded plots). Following the rise of floodwaters, we resampled these same 39 plots that remained unflooded four years (2016-2017) after the flooding, so we classed them as post-unflooded plots. Given the different combinations of sampling periods and degree of flooding, we assigned the data to two categories (unflooded pre-stage, unflooded post2-stage), which we used to assess the spatiotemporal variation in trait occurrence.

The anuran sampling in each plot (250 m x 10 m) took place by visual and acoustic surveys limited by space, with two simultaneous observers per plot. To detect

anuran species with different activity time (diurnal, crepuscular, and nocturnal), visual and acoustic surveys were conducted between 16:30h and 18:30h, and between 19:00h and 23:00h. We recorded adults species presences within each 10-m section of the 250-m-long plot, resulting in a relative-abundance index that varied between 0 and 25 records per species per plot. Each plot was simultaneously sampled by a lead researcher and a field assistant, but only one record per plot segment per survey was used in the analyses.

Species Traits

To estimate functional metrics, we used traits that mediate biotic and abiotic interactions that potentially affect species occurrence under different levels of environmental disturbances caused by the hydroelectric dam.

We used one continuous trait—body length (snout-vent length)—that may reflect dispersal capacity and predation pressure, and 10 binary traits to inform activity time (diurnal, nocturnal), vertical stratification (terrestrial, fossorial, arboreal), reproductive mode (eggs deposited in water, soil, or arboreal strata) and development site of larvae (water or ground). Whenever possible, we measured body length from specimens captured in the field or housed in the Herpetology Collection of the INPA. We measured five adult individuals per species and used means in the analyses. Non-continuous functional traits were extracted AmphiBIO (Oliveira et al., 2017), and complemented with pertinent literature for species with missing data (Buckley et al., 2005; Duellman & Trueb, 1994; Magnusson & Hero, 1991; Nunes-De-Almeida et al., 2021; Oliveira et al., 2017) (Table 1).

TABLE 1 Species traits and underlying ecological processes that potentially mediate relationships between anuran functional and river damming.

Trait	Data Type	Description	Relevance	Attribute	Definition
Daily activity (diurnal or nocturnal)	Binary	Period of activity when the species feed and reproduce.	The period during which a species is more active is related to the differential contribution of matter and energy in time.	Diurnal	Species are more active during the day.
				Nocturnal	Species are more active during the night.
Habitat foraging	Ordinal	The microhabitat	The environmental/vertical	Terrestrial	Species that live in the ground.

			used by adults most of the time for calling and live.	stratum with which the species is most strongly associated determines whether and with what intensity it will be affected by habitat alteration and loss.	Fossorial	Species that live underground or are buried for some period.
					Arboreal	Species are often found perched on herbaceous or arboreal vegetation.
Body length	Continuous	Snout-Vent Length (SVL) (millimeters)	Morphometric traits potentially are related to mobility, determining the ability to disperse, forage and escape predators.	SVL	Average snout-vent distance (in mm) in adult males.	
Investment in growth and development	Binary	Oviposition site	The substrate in which the species lay its eggs is associated with the life history strategy and reproductive success. During the egg and larval stage, amphibians are especially vulnerable to environmental factors such as dehydration, UV light, predation, or changes in the levels of water bodies.	Aquatic spawning Terrestrial spawning Arboreal spawning	For eggs laid directly in the flowing or still water. Species that deposit eggs in terrestrial environments as the ground, rocks, or leaf on the ground. Species that deposit eggs on leaves above the water system or in trees.	
Investment in growth and development	Binary	Ending larval development site (tadpole)	In the amphibian biphasic life cycle, the egg and larval stages are most vulnerable to environmental factors, such as habitat degradation and loss. This determines a species' vulnerability to severe changes and levels of	Aquatic tadpoles Terrestrial tadpoles	Ending larval development in the water. Completion of larval development in terrestrial environments as the ground, rocks, or leaves on the ground.	

		water bodies in the habitat.		
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Statistical analyses

We calculated functional diversity, and community-level functional uniqueness using Rao's index Q for functional metrics to takes the species dissimilarities into account for the calculation of functional diversity, as proposed by (Ricotta et al., 2016) based on species abundance. We used this approach to examine patterns of trait convergence or divergence (i.e., a decrease or increase in trait dissimilarity compared to a random expectation). We calculated the Rao's Q and U indices using the *uniqueness* function of the *adiv* package (Pavoine, 2020) based on Gower's functional dissimilarity, as well as the *gawdis* package (de Bello et al., 2021), which allows the inclusion of both categorical and quantitative traits. We also measured functional richness (FRic), which represents the amount of functional space filled by each species in each plot. To estimate FRic, we used the *dbFD* function of the *FDR*-package (Laliberte & Legendre, 2010).

We calculated community-weighted mean trait values (CWM; (Lavorel et al., 2008), which quantifies the mean of a given functional trait for species in a sample weighted by the respective relative abundance of each species (Ricotta & Moretti, 2011). The CWM reflects changes in the relative contributions of each species to the overall functional structure (Lavorel et al., 2008). We calculated CWM values using the *functcomp* function of the *FD* R-package (Laliberte & Legendre, 2010).

We tested for changes in functional composition (functional area, represented by the PCoA axes for functional structure) across flooding categories over time, using Principal Coordinates Analysis (PCoA) ordination based on the CWM matrix for individual sampling units. Plot scores from PCoA axes 1 and 2 in each category were then used as response variables in a linear mixed-effect regression analysis.

To test for differences in each multivariate functional diversity metric and individual traits across flooding categories, we applied generalized linear-mixed models (GLMMs) with normal or Tweedie distributions using the *glmmTMB* package (Brooks et al., 2017). We used flooding categories as the fixed effect and plot identity as a random effect, nested within the sample modules, to consider repeated measures over time and spatial autocorrelation (Zuur et al., 2009), before and after flooding. We

evaluated the distribution of residuals for each model to verify assumptions of normality and homogeneity of variance. The Tweedie distribution was used when residuals from GLMMs did not have a normal distribution and homogeneous residual variance. Model inferences were implemented by full null-model comparisons using a likelihood-ratio test with the ANOVA R-function (Dobson & Barnett, 2011). For those models that returned significant overall differences, we undertook post-hoc Tukey tests for multiple pairwise comparisons using the *glht* function in the multcomp R package (Hothorn et al., 2016), which were used to identify treatment-level differences.

Results

Sampling overview

We recorded 84 anuran species representing 28 genera and 12 families (Table S1 and Table S2). Prior to flooding, we recorded 62 species in pre-flooded plots and 59 in pre-unflooded plots. After the dam was flooded, we recorded a total of 64 species. We found 39 species common to all flooding and time categories, and *Adenomera andreae* was the most frequently sampled species, recorded in 94% of all pre-stage plots (both flooded and unflooded) and 80% of all post-unflooded plots. Eleven species occurred only within the pre-flooded plots (Table S3), three were exclusively found in pre-unflooded plots, and eight recorded only in post-unflooded plots (Fig. 2).

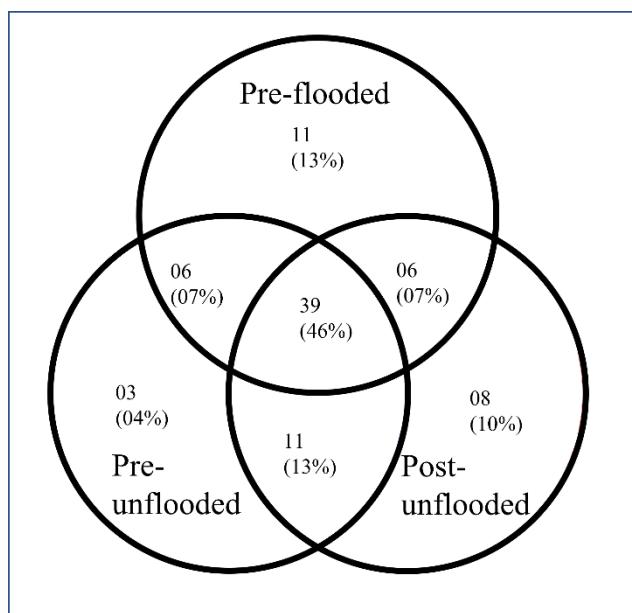


FIGURE 2 Venn Diagram shows the overlap in species recorded within plots subjected to different combinations of flooding and time since filling of the Santo Antônio Dam reservoir on the Madeira River, southwestern Brazilian Amazon.

Changes in functional diversity after flooding

The first two PCoA axes captured 82% of the variation in functional composition. We detected significant changes in the functional composition of traits among flooding categories (GLMM: $X^2= 20.54$, $p < 0.001$). The functional composition of permanently flooded plots differed from that of both unflooded forest plots sampled prior to dam construction and unflooded forest plots sampled 4 years after reservoir filling (Tukey's post-hoc test: both $p < 0.001$). There was no significant difference between upland plots that were never flooded before and after reservoir filling (Tukey's post-hoc test: $p = 0.3$) (Fig. 3, Table 2). On average, the functional composition of permanently flooded plots by dam was different from that in unflooded plots before and after dam closure, although there was an overlap in the values between the three categories (Fig. 3).

Functional diversity indices (Figure 3) were higher in pre-flooded plots in terms of FRic (Tukey's post-hoc test: $p = 0.001$), Rao's Q (Tukey's post-hoc test: $p = 0.0002$) and U (Tukey's post-hoc test: $p = 0.006$). Although FRic in unflooded forest plots after reservoir filling was higher than before filling (Tukey's post-hoc test: $p = 0.002$), Rao's Q and U did not differ between these two periods (Tukey's post-hoc test: $p > 0.13$ in both cases). Overall, considering that permanently flooded plots were installed on lowland “várzea” floodplains, our findings suggest that differences in functional diversity estimates between periods are more closely associated with natural topographic features of the landscape than with the effects of flooding per se.

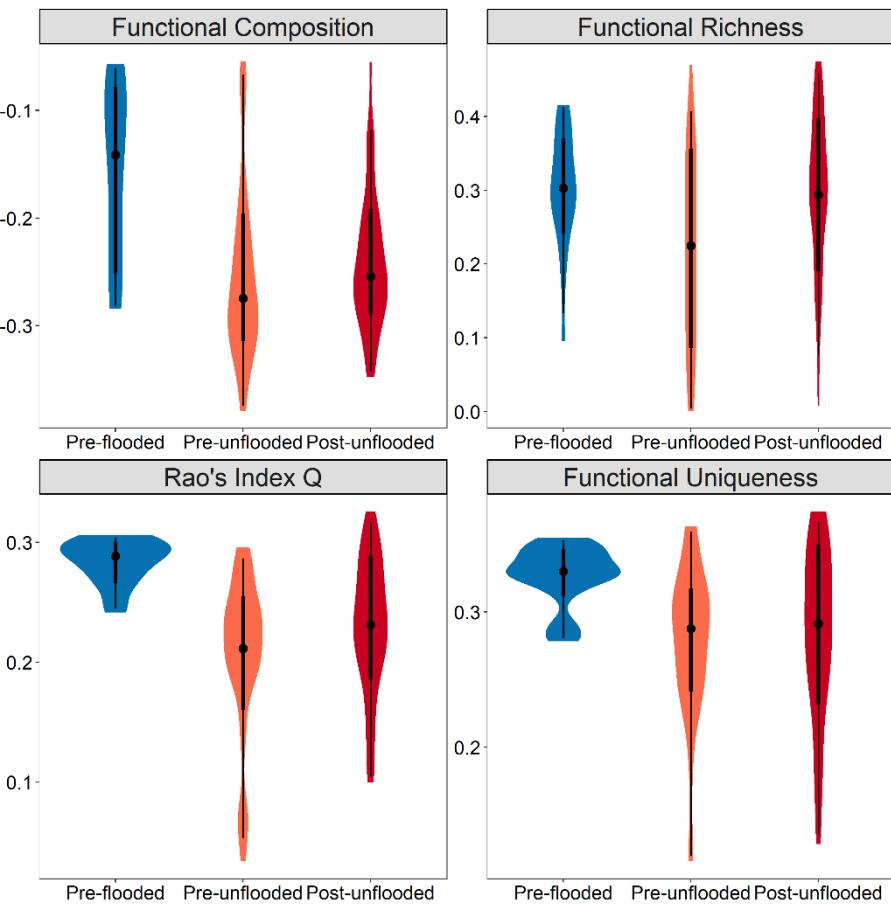


FIGURE 3. Mean differences in estimates of multivariate functional diversity of anura assemblages among plots that were flooded (pre-flooded) and plots that remained unflooded both before (pre-unflooded) and after the rise of floodwaters (post-unflooded) in the Santo Antônio dam reservoir, southwestern Brazilian Amazon. The indices were estimated based on 10 continuous and categorical species traits (Table S3). Solid dots and vertical lines represent means and 95% confidence intervals, respectively.

The mean frequencies of most individual traits diverged between permanently flooded plots and upland plots that remained unflooded both before and after reservoir flooding (GLMM: $p < 0.05$, Appendix Table S3), except for anuran exhibiting diurnal (GLMM: $X^2 = 0.54$, $p = 0.17$) or nocturnal habits (GLMM: $X^2 = , p = 0.19$, Appendix Table S3) or occupying arboreal habitats (GLMM: $X^2 = 3.23, p = 0.11$, Appendix Table S3) that did not show any divergence (Table 2, Fig. 4). Even after reservoir filling, the incidence of anuran that lay their eggs in water or tree cavities, and those that terminate larval development in water, were lower in the unflooded area (Fig. 4). The incidence of terrestrial or fossorial anuran, which lay their eggs and terminate larval development in the soil was higher in the non-flooded area. In the unflooded area during the post-filling

stage, there was an increase in the average frequency of large-bodied anuran and a decline in the abundance of fossorial anuran ($P < 0.01$ in both cases). Differences in mean functional metrics within plots in the flooded area were largely due to the higher variation around the mean in the unflooded area and, most of the trait combinations and the functional diversity of the flooded areas were also found in the unflooded areas.

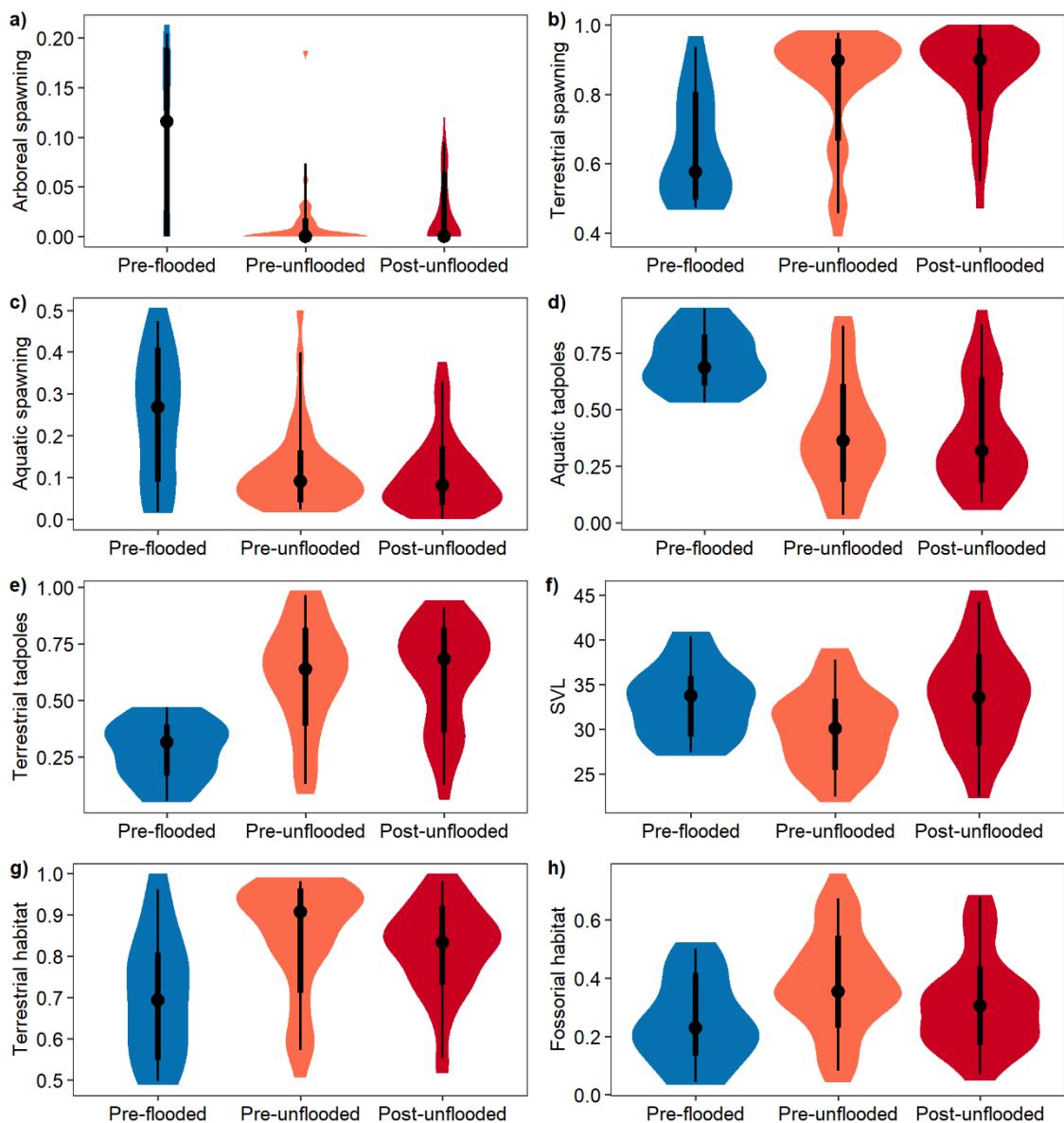


FIGURE 4 Comparisons of community-weighted mean (CWM) trait values for which the null hypothesis of no difference was rejected for plots that were flooded (pre-flooded) and plots that remained unflooded (pre-unflooded and post-unflooded) in the Santo Antônio dam reservoir. Solid dots and vertical lines represent CWM means across plots and 95% confidence regions.

TABLE 2 Summary of Tukey's post-hoc comparison of multivariate functional diversity estimates and community-weighted-mean (CWM) trait values among plots that were flooded (pre-flooded) and plots that remained unflooded both before and after reservoir filling. The overall trait matrix was based on all 84 anuran species recorded in this study.

Index	Pre-flooded × Pre-unflooded		Pre-flooded × Post-unflooded		Pre-unflooded × Post-unflooded	
	Z	P	Z	P	Z	P
Functional composition	-4.840	<1e-04	-4.18	<1e-04	1.43	0.309
Functional richness	-2.720	0.017	-0.160	0.980	3.670	0.002
Rao's Q	-4.337	<1e-04	-2.883	0.0108	1.92	0.131
Functional uniqueness	-3.240	0.001	-2.095	0.040	1.690	0.277
Traits						
Arboreal spawning	-2.370	0.040	-3.370	0.002	-1.230	0.430
Aquatic spawning	-3.25	0.003	-3.94	0.0002	-1.130	0.490
Terrestrial spawning	4.521	<0.001e	5.070	<0.001	0.780	0.710
Aquatic tadpoles	-5.08	<0.001	-5.140	<0.001	-0.080	0.990
Terrestrial tadpoles	4.720	<0.001	4.72	<0.001	0.08	0.99
SVL	-2.340	0.175	-0.631	0.810	2.740	0.012
Diurnal activity	-1.618	0.233	-1.882	0.140	-0.374	0.924
Nocturnal activity	1.618	0.233	1.882	0.140	0.374	0.924
Arboreal habitat	-1.405	0.332	-0.084	0.996	1.980	0.114
Fossorial habitat	3.053	0.006	1.413	0.323	-2.922	0.009
Terrestrial habitat	4.141	0.0001	3.181	0.004	-1.371	0.352

Discussion

Anuran assemblages in the lowland forest landscape flooded by the Santo Antônio Dam were functionally distinct from those occupying higher areas that were not flooded. The main differences were that the former was more species-rich and had a more unique functional composition than that in the latter. These results suggest a loss in functional diversity since terrestrial areas that were inundated were not functionally replaced along the newly formed margins of the hydroelectric reservoir. This distinction between seasonally-flooded and unflooded areas reflects natural differences in the composition of anuran assemblages between “várzea” and “terra firme” forests (Gascon, 1996; May et al., 2010; Waldez et al., 2013), and indicates that lowland forest assemblages subjected to a seasonal flood pulse are more sensitive to permanent inundation. From a conservation perspective, this is meaningful because ~11,800 ha of “varzea” forests (from a total of ~80,000 ha of lowland forest) were flooded by the Jirau and Santo Antônio hydroelectric complex along 245 km of the Madeira River (Cochrane et al., 2017). Therefore, even though our models did not detect significant changes in the functional diversity estimated for upland areas that were not flooded, they indicate that the ecological impacts of large hydroelectric dams on the functional diversity of anuran can vary considerably depending on the natural characteristics of the landscape.

At least part of the functional diversity that was locally purged by flooding also occurs in unflooded areas, as seen in plots with similar functional uniqueness values across different flooding categories. In floodplain “várzea” forest, there was a high level of functional diversity, presumably promoted by seasonal flooding, as hyperdynamic environments subject to periodic disturbances tend to host greater functional divergence (Cadotte, 2011). Upland terra firme forests, on the other hand, on average had lower functional diversity but greater variation in functional diversity among sampling units due to local environmental heterogeneity. Although terra firme forests can ensure year-round persistence of terrestrial and fossorial species, they also include areas with similar microhabitats to those in the floodplain, such as seasonal ponds and pools.

Functionally redundant assemblages may occur in habitats that have been impacted at different levels. The intensity of anthropogenic impacts on biotic diversity typically depends on the degree of functional redundancy because, if the regional pool contains species sharing similar functions, the loss of one of them is not as dramatic as in functionally unique assemblages (Naeem, 1998). Assemblages with higher levels of functional redundancy therefore tend to be more resilient to anthropogenic impacts

(Petchey et al., 2007), because many functionally similar species would need to be removed before an entire functional attribute is driven to local extinction (Fonseca & Ganade, 2001). Furthermore, functional redundancy generates stable assemblages with greater capacity to recover from anthropogenic impacts (Biggs et al., 2020). In such cases, the addition or loss of a given species may not change ecosystem functioning, as some species may be redundant in terms of ecosystem services they provided (Díaz & Cabido, 2001). In unflooded areas there was no change in functional diversity after flooding. An increase in functional diversity after human-induced impacts has been observed to other vertebrate groups as bird (Melo et al., 2021), fish (Stegmann et al., 2019), and bats assemblages (Farneda et al., 2020). The high variation in functional diversity of anuran species and their functional traits found in the unflooded area, most of which comprised of terra firme forest, serves as natural protection against the effects of artificial flooding, which would likely have been more severe if local assemblages contained more functionally distinct species. This may be the reason we failed to detect changes in functional and trait diversity even four years after flooding.

Dissimilarities between flooding categories were also captured by the functional diversity (Rao's Q) and uniqueness indices, which were higher in forest areas flooded by the dam. Sites with dynamic environmental disturbances, such floodplains subjected to hydrological alterations promote greater divergence and functional diversity (Cadotte, 2011) and one of the reasons is because local conditions in seasonally flooded (“várzea”) forests change according to the frequency and depth of the annual flood pulses. Different dynamic conditions at the same site promote distinct traits, which are linked to the flood conditions of the environment because these ecosystems harbour a unique set of flood-tolerant species that do not occur in the surrounding upland forests (Arias et al., 2018). Functional diversity indices are sensitive to species abundances (Bello et al., 2007) and the loss of environments with high functional diversity and uniqueness indicates that flooded areas had a different functionality in the regional structure of the anuran assemblage, based mainly on the abundance of species and their functional traits.

Our data shows that the floodplains of the Madeira River upstream of the Santo Antônio dam harboured anuran assemblages characterized by aquatic and arboreal spawning species and aquatic tadpoles. Some reproductive modes are likely to be more sensitive to hydropower impacts, as they tend to occur most frequently in habitats that are most affected by permanent artificial flooding. This has implications for biological

monitoring in areas immediately affected by dams because studies targeted to some functional groups can save time and money, especially in functionally diverse assemblages that are species-rich.

Floodplain areas that were permanently flooded by the dam had a lower incidence of terrestrial and fossorial species, which is likely associated with high levels of soil-water saturation and the frequently overflowing water table (Cochrane et al., 2017). As fossorial or soil-breeding species were primarily found in unflooded upland forests and away from the newly created reservoir margins, the impacts of artificial flooding were much lower in these functional groups. There were no changes in functional groups in upland unflooded areas, even two years after the reservoir was filled. Species that do not depend on water bodies for reproduction were less affected by flooding. The prevalence of small ponds and other suitable aquatic breeding sites is higher in seasonally-flooded environments, meeting both the adult and larval requirements of those functional groups.

Body length was the only functional trait showing differences in unflooded areas after reservoir filling. Anuran species recorded post-flooding were on average larger than those prior to reservoir filling, resulting from an increase in the abundance of some large-bodied species in unflooded areas. Although the difference on average size was not pronounced, this indicates that large-bodied species could have been favoured by the perennial flood. Large-bodied and disturbance-tolerant species, such as *Rhaebo guttatus*, *Boana raniceps* and *Leptodactylus cf. knudseni*, were more frequently found after the dam was inundated (Dayrell et al., 2021). Body size is an influential trait, usually correlated with factors such as rate of exploitation, population size, and clutch size, all of which may affect species extinction risk (Blueweiss et al., 1978). Large-bodied amphibians have proportionately smaller surface areas with respect to body volume and therefore lower rates of desiccation than smaller species (Duellman & Trueb, 1994). Large-bodied anuran are also more susceptible to habitat modification and disturbances (Lips et al., 2003), or are more tolerant to anthropogenic disturbances (Suazo-Ortuño et al., 2008; Torralvo et al., 2022). However, only four years of monitoring after reservoir flooding may not be enough time to determine with certainty whether the persistence of large-bodied anuran is related to disturbance or represents a natural phenomenon.

Conclusion

Differences in the functional diversity of anuran assemblages in the area affected by the Santo Antônio Dam were largely due to baseline environmental differences between seasonally-flooded and unflooded areas on higher ground. This is consistent with Amazonian studies showing that anuran assemblages in lowland floodplains and unflooded upland forests are naturally different, regardless of any anthropogenic impact (Gascon, 1996; May et al., 2010). We were unable to detect any significant change in the functional composition of anuran assemblages in areas that remained unflooded, even four years after river damming. However, traits linked to reproductive modes, such as spawning and larval development sites, are potentially excellent options for monitoring areas affected by hydroelectric dams, since anuran assemblages occupying the most vulnerable floodplains were usually dominated by species with aquatic spawning and tadpoles. Studies of functional traits linked to reproductive strategies, such as egg deposition and larval development, may help to understand community-wide anuran responses to temporal changes caused by run-of-river dams, which are often extolled as “low impact”, but inevitably degrade large areas of riparian and floodplain forests.

Although flooding by the Santo Antônio Dam did not result in the complete elimination of any trait or trait combination from anuran assemblages, the loss of large areas containing distinct assemblages may affect other associated taxa. Therefore, it is important to set-aside riparian areas in forest reserves within the region to effectively retain a full complement of functional diversity.

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Supplementary Material

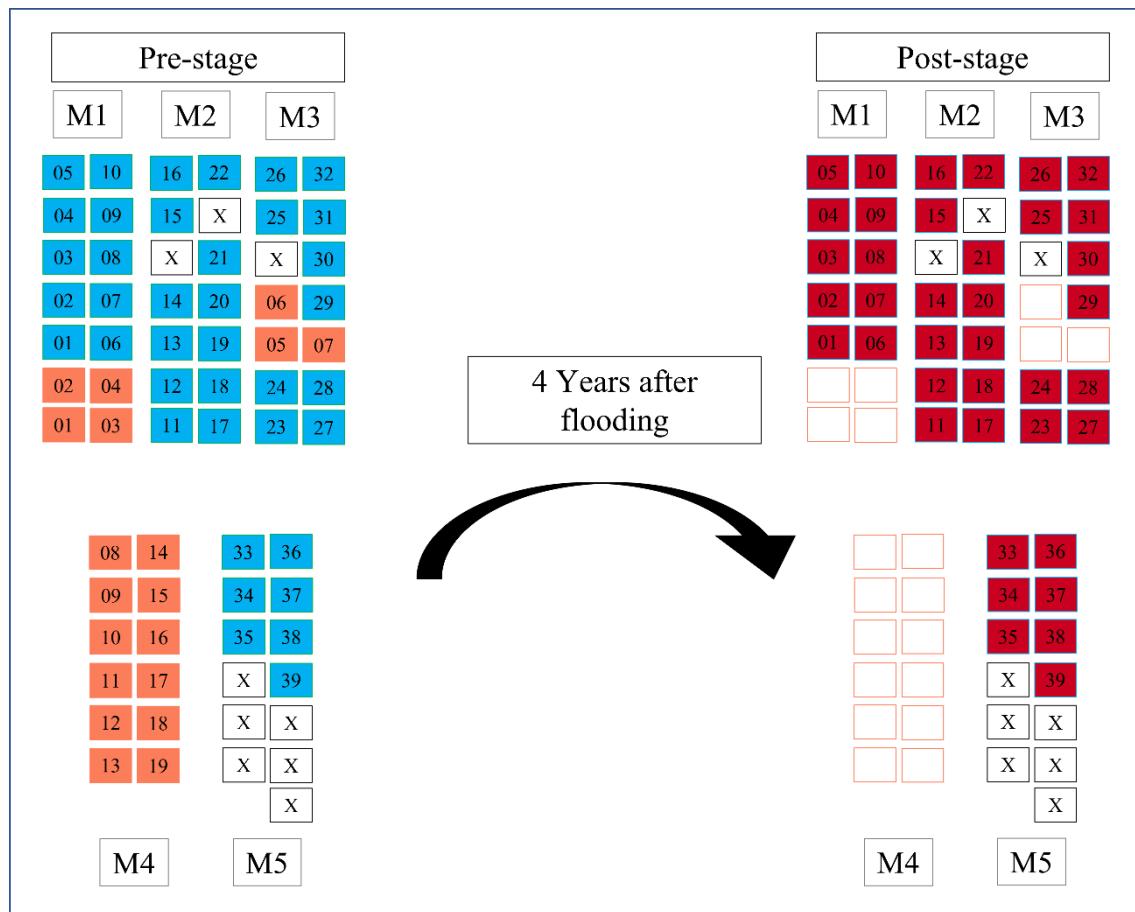


Figure S1. Sampling scheme plots around the Santo Antônio dam, Western Amazonia, Brazil. M1, M2, M3 = modules on the left bank of the Madeira River; M4, M5 = modules on the right bank of Madeira River; squares = plots of each module. Blue = pre-flooded (flooded forest plots sampled before reservoir filling); orange = pre-unflooded (unflooded forest plots sampled before reservoir filling); red = post-unflooded = the same unflooded plots sampled 4 years after reservoir filling; X = plots that were not sampled for logistical reasons.

TABLE S1 Number of species recorded, mean abundance, and percent of plots with records of frog species sampled in relation to flooding and time since the filling of the Santo Antônio hydroelectric reservoir on the Madeira River, southwestern Brazilian Amazonia. Pre-flooded = flooded forest plots sampled before the dam was filled; pre-unflooded = unflooded forest plots sampled before the dam was filled; post-unflooded = the same unflooded forest plots as in pre-stage unflooded but sampled 4 years after reservoir filling.

Taxa	Flooding Stages					
	Anura		Pre-flooded		Pre-unflooded	
			Records	% plots	Records	% plots
Aromobatidae						
<i>Allobates femoralis</i> (Boulenger, 1884)		8.37	68.42	6.33	71.79	5.15
<i>Allobates aff. gasconi</i>		4.16	21.05	0.00	0.00	0.10
<i>Allobates aff. tinae</i>		6.32	31.58	0.00	0.00	0.00
<i>Allobates flaviventris</i> Melo-Sampaio, Souza & Peloso, 2013		0.00	0.00	1.08	7.69	1.05
<i>Allobates nidicola</i> (Caldwell & Lima, 2003)		0.11	5.26	2.62	20.51	2.59
<i>Allobates</i> sp1		6.16	52.63	0.36	7.69	0.26
<i>Allobates tinae</i> Melo-Sampaio, Oliveira & Prates, 2018		5.84	31.58	8.46	46.15	5.72
Bufoidae						
<i>Rhaeboguttatus</i> (Schneider, 1799)		0.00	0.00	0.03	2.56	0.82
<i>Rhinella</i> gr. <i>margaritifera</i> sp1		2.05	21.05	1.56	30.77	0.15
<i>Rhinella</i> gr. <i>margaritifera</i> sp2		0.00	0.00	0.41	20.51	0.05
<i>Rhinella</i> gr. <i>margaritifera</i> sp4		2.37	10.53	2.97	33.33	0.85
						20.51

<i>Rhinella exostosica</i> Ferrão, Lima, Ron, Santos, and Hanken, 2020	0.21	15.79	0.00	0.00	0.03	2.56
<i>Rhinella marina</i> (Linnaeus, 1758)	0.11	10.53	0.13	12.82	0.31	25.64
Centrolenidae						
<i>Hyalinobatrachium cappellei</i> (van Lidth de Jeude, 1904)	0.00	0.00	0.00	0.00	0.05	5.13
<i>Teratohyla adenocheira</i> (Harvey & Noonan, 2005)	0.00	0.00	0.23	2.56	0.00	0.00
Ceratophryidae						
<i>Ceratophrys cornuta</i> (Linnaeus, 1758)	1.53	26.32	0.03	2.56	0.03	2.56
Craugastoridae						
<i>Oreobates quixensis</i> Jiménez de la Espada, 1872	0.05	5.26	0.10	7.69	0.03	2.56
<i>Pristimantis altamazonicus</i> (Barbour & Dunn, 1921)	0.05	5.26	0.05	5.13	0.15	5.13
<i>Pristimantis fenestratus</i> (Steindachner, 1864)	4.47	36.84	0.03	2.56	0.00	0.00
<i>Pristimantis ockendeni</i> (Boulenger, 1912)	2.95	21.05	2.82	41.03	2.85	53.85
<i>Pristimantis</i> sp1	0.05	5.26	0.03	2.56	0.00	0.00
<i>Pristimantis</i> sp4	2.26	31.58	4.41	51.28	2.87	43.59
<i>Pristimantis</i> sp5	0.00	0.00	0.03	2.56	0.00	0.00
<i>Pristimantis ventrimarmoratus</i> (Boulenger, 1912)	0.00	0.00	0.18	10.26	0.03	2.56
<i>Pristimantis zimmermanae</i> (Heyer & Hardy, 1991)	3.05	21.05	1.08	17.95	2.13	53.85
Dendrobatidae						
<i>Adelphobates quinquevittatus</i> (Steindachner, 1864)	0.00	0.00	0.08	2.56	0.13	12.82

<i>Ameerega picta</i> (Bibron in Tschudi, 1838)	1.74	36.84	1.64	12.82	1.03	17.95
<i>Ameerega trivittata</i> (Spix, 1824)	0.26	5.26	0.64	20.51	1.18	46.15
Eleutherodactylidae						
<i>Phyzelaphryne miriamae</i> Heyer, 1977	2.79	21.05	5.85	46.15	9.97	76.92
Hemiphractidae						
<i>Hemiphractus scutatus</i> (Spix, 1824)	0.00	0.00	0.00	0.00	0.03	2.56
Hylidae						
<i>Boana</i> aff. <i>geographica</i> sp1	0.00	0.00	0.00	0.00	0.10	2.56
<i>Boana</i> aff. <i>geographica</i> sp2	0.00	0.00	0.03	2.56	0.33	17.95
<i>Boana</i> aff. <i>geographica</i> sp3	0.00	0.00	0.05	5.13	0.03	2.56
<i>Boana boans</i> (Linnaeus, 1758)	0.53	5.26	0.00	0.00	0.00	0.00
<i>Boana cinerascens</i> (Spix, 1824)	8.95	36.84	0.85	5.13	1.41	20.51
<i>Boana fasciata</i> (Günther, 1858)	2.58	31.58	0.08	7.69	0.18	5.13
<i>Boana lanciformis</i> (Cope, 1871)	1.11	31.58	0.28	17.95	1.26	25.64
<i>Boana raniceps</i> (Cope, 1862)	0.00	0.00	0.00	0.00	0.77	12.82
<i>Dendropsophus</i> aff. <i>minutus</i>	0.79	10.53	0.00	0.00	0.05	5.13
<i>Dendropsophus</i> aff. <i>reichlei</i>	4.79	36.84	0.64	2.56	0.67	7.69
<i>Dendropsophus arndti</i> Caminer, Milá, Jansen, Fouquet, Venegas, Chávez, Lougheed & Ron, 2017	0.11	5.26	0.00	0.00	0.00	0.00
<i>Dendropsophus</i> gr. <i>leucophyllatus</i>	0.00	0.00	1.03	7.69	0.44	10.26

<i>Dendropsophus</i> gr. <i>minusculus</i>	1.32	5.26	0.00	0.00	0.00	0.00
<i>Dendropsophus bilobatus</i> Ferrão, Moravec, Hanken, and Lima, 2020	0.05		0.00		0.00	0.00
<i>Dendropsophus leali</i> (Bokermann, 1964)	0.00	0.00	0.00	0.00	0.03	2.56
<i>Dendropsophus marmoratus</i> (Laurenti, 1768)	0.37	10.53	0.26	2.56	0.00	0.00
<i>Dendropsophus parviceps</i> (Boulenger, 1882)	4.05	21.05	0.67	5.13	0.08	2.56
<i>Dendropsophus rhodopeplus</i> (Günther, 1858)	0.53	5.26	1.28	5.13	0.33	10.26
<i>Dendropsophus sarayacuensis</i> (Shreve, 1935)	3.16	15.79	0.00	0.00	0.00	0.00
<i>Dendropsophus</i> sp1	0.11	5.26	0.00	0.00	0.03	2.56
<i>Osteocephalus</i> aff. <i>lepturiae</i>	0.79	31.58	0.56	33.33	0.51	30.77
<i>Osteocephalus</i> aff. <i>taurinus</i> sp1	1.47	36.84	0.33	17.95	0.10	7.69
<i>Osteocephalus</i> aff. <i>taurinus</i> sp2	2.21	36.84	2.33	76.92	1.23	46.15
<i>Scinax</i> cf. <i>cruentommus</i>	0.53	31.58	0.03	2.56	0.00	0.00
<i>Scinax</i> gr. <i>garbei</i>	0.05	5.26	0.03	2.56	0.10	10.26
<i>Scinax</i> gr. <i>ruber</i>	0.00	0.00	0.08	5.13	0.05	2.56
<i>Scinax</i> aff. <i>chiquitanus</i>	0.00	0.00	0.05	5.13	0.03	2.56
<i>Sphaenorhynchus lacteus</i> (Daudin, 1800)	0.00	0.00	0.00	0.00	0.03	2.56
<i>Trachycephalus coriaceus</i> (Peters, 1867)	0.21	5.26	0.03	2.56	0.00	0.00
<i>Trachycephalus typhonius</i> (Linnaeus, 1758)	0.00	0.00	0.00	0.00	0.03	2.56
Leptodactylidae						

<i>Adenomera andreae</i> (Müller, 1923)	16.63	94.74	17.79	94.87	14.03	79.49
<i>Adenomera gridipappi</i> Carvalho, Moraes, Lima, Fouquet, Peloso, Pavan, Drummond, Rodrigues, Giaretta, Gordo. Neckel-Oliveira, Haddad, 2020	6.47		0.00		0.00	
		36.84		0.00		0.00
<i>Adenomera hylaedactyla</i> (Cope, 1868)	3.00	63.16	13.49	87.18	6.33	79.49
<i>Engystomops freibergi</i> (Donoso-Barros, 1969)	0.47	5.26	0.03	2.56	0.00	0.00
<i>Leptodactylus bolivianus</i> Boulenger, 1898	0.21	21.05	0.03	2.56	0.05	5.13
<i>Leptodactylus cf. knudseni</i>	1.11	47.37	0.69	48.72	1.36	71.79
<i>Leptodactylus cf. wagneri</i>	1.63	10.53	0.03	2.56	0.05	5.13
<i>Leptodactylus fuscus</i> (Schneider, 1799)	0.05	5.26	0.03	2.56	0.08	2.56
<i>Leptodactylus leptodactyloides</i> (Andersson, 1945)	0.16	10.53	0.00	0.00	0.03	2.56
<i>Leptodactylus mystaceus</i> (Spix, 1824)	1.53	15.79	1.44	25.64	0.21	12.82
<i>Leptodactylus pentadactylus</i> (Laurenti, 1768)	0.16	15.79	0.31	12.82	0.79	33.33
<i>Leptodactylus petersii</i> (Steindachner, 1864)	2.11	21.05	0.00	0.00	0.00	0.00
<i>Leptodactylus podicipinus</i> (Cope, 1862)	0.32	10.53	0.00	0.00	0.03	2.56
<i>Leptodactylus rhodomystax</i> Boulenger, 1884	5.16	73.68	2.69	41.03	3.10	41.03
<i>Lithodytes lineatus</i> (Schneider, 1799)	3.05	31.58	0.03	2.56	0.05	2.56
Microhylidae						
<i>Chiasmocleis avilapiresae</i> Peloso & Sturaro 2008	0.00	0.00	0.05	2.56	0.00	0.00
<i>Chiasmocleis bassleri</i> Dunn, 1949	0.00	0.00	0.15	2.56	0.15	2.56

<i>Chiasmocleis hudsoni</i> Parker, 1940	3.26	31.58	0.56	5.13	0.05	5.13
<i>Elachistocleis helianneae</i> Caramaschi, 2010	0.11	5.26	0.00	0.00	0.00	0.00
<i>Hamptophryne alios</i> (Wild, 1995)	0.05	5.26	0.00	0.00	0.00	0.00
Phyllomedusidae						
<i>Callimedusa tomopterna</i> (Cope, 1868)	0.74	26.32	0.72	7.69	0.67	30.77
<i>Cruziohyla craspedopus</i> (Funkhouser, 1957)	0.00	0.00	0.00	0.00	0.08	2.56
<i>Phyllomedusa camba</i> De la Riva, 1999	0.84	5.26	0.00	0.00	0.00	0.00
<i>Phyllomedusa vaillantii</i> Boulenger, 1882	0.79	15.79	1.31	33.33	0.85	33.33
TOTAL = 84	62		59		64	

TABLE S2 Trait matrix for 12 morphological and life-history traits for 84 anuran species from Upper Madeira River, southwestern Amazon, Brazil. Categorical trait values are expressed as either presence (1) or absence (0). Daily activity period: diurnal or nocturnal; Foraging habitat: fossorial, terrestrial and arboreal; Body size: Mean Snout-Vent Length (SVL); Oviposition site: aquatic spawning, terrestrial spawning, and arboreal spawning; Final larval development site: aquatic tadpoles or ground tadpoles.

Species	Diurnal	Nocturnal	Fossorial	Terrestrial	Arboreal	SVL (mm)	Aquatic spawning	Terrestrial spawning	Arboreal spawning	Aquatic tadpoles	Terrestrial tadpoles
<i>Adelphobates quinquevittatus</i> (Steindachner, 1864)	1	0	0	1	1	17.71	0	1	0	1	0
<i>Adenomera andreae</i> (Müller, 1923)	0	1	1	1	0	20.70	0	1	0	0	1
<i>Adenomera gridipappi</i> Carvalho, Moraes, Lima, Fouquet, Peloso, Pavan, Drummond, Rodrigues, Giaretta, Gordo. Neckel-Oliveira, Haddad, 2020	1	0	1	1	0	25.40	0	1	0	0	1
<i>Adenomera hylaedactyla</i> (Cope, 1868)	0	1	1	1	0	24.00	0	1	0	0	1
<i>Allobates aff. gasconi</i>	1	0	0	1	0	16.28	0	1	0	1	0
<i>Allobates aff. tinae</i>	1	0	0	1	0	15.56	0	1	0	1	0
<i>Allobates femoralis</i> (Boulenger, 1884)	1	0	0	1	0	26.50	0	1	0	1	0
<i>Allobates flaviventris</i> Melo-Sampaio, Souza & Peloso, 2013	1	0	0	1	0	18.80	0	1	0	1	0
<i>Allobates nidicola</i> (Caldwell & Lima, 2003)	1	0	0	1	0	21.40	0	1	0	0	1
<i>Allobates sp1 madeira</i>	1	0	0	1	0	15.32	0	1	0	1	0
<i>Allobates tinae</i> Melo-Sampaio, Oliveira & Prates, 2018	1	0	0	1	0	15.72	0	1	0	1	0
<i>Ameerega picta</i> (Bibron in Tschudi, 1838)	1	0	0	1	0	22.20	0	1	0	1	0
<i>Ameerega trivittata</i> (Spix, 1824)	1	0	0	1	0	43.50	0	1	0	1	0

<i>Callimedusa tomopterna</i> (Cope, 1868)	0	1	0	0	1	55.50	0	0	1	1	0
<i>Ceratophrys cornuta</i> (Linnaeus, 1758)	0	1	0	1	0	94.00	1	0	0	1	0
<i>Chiasmocleis avilapiresae</i> Peloso & Sturaro 2008	0	1	1	1	0	24.80	1	0	0	1	0
<i>Chiasmocleis bassleri</i> Dunn, 1949	0	1	1	1	0	20.30	1	0	0	1	0
<i>Chiasmocleis hudsoni</i> Parker, 1940	0	1	1	1	0	18.20	1	0	0	1	0
<i>Cruziohyla craspedopus</i> (Funkhouser, 1957)	0	1	0	0	1	73.00	0	0	1	1	0
<i>Dendropsophus</i> aff. <i>minutus</i>	0	1	0	0	1	21.87	1	0	1	1	0
<i>Dendropsophus</i> aff. <i>reichlei</i>	0	1	0	0	1	21.50	0	0	1	1	0
<i>Dendropsophus arndti</i> Caminer, Milá, Jansen, Fouquet, Venegas, Chávez, Lougheed & Ron, 2017	0	1	0	0	1	26.70	0	0	1	1	0
<i>Dendropsophus bilobatus</i> Ferrão, Moravec, Hanken, and Lima, 2020	0	1	0	0	1	20.80	0	0	1	1	0
<i>Dendropsophus</i> gr. <i>leucophyllatus</i>	0	1	0	0	1	29.20	0	0	1	1	0
<i>Dendropsophus</i> gr. <i>minusculus</i>	0	1	0	0	1	20.00	0	0	1	1	0
<i>Dendropsophus leali</i> (Bokermann, 1964)	0	1	0	0	1	28.00	0	0	1	1	0
<i>Dendropsophus marmoratus</i> (Laurenti, 1768)	0	1	0	0	1	35.50	1	0	0	1	0
<i>Dendropsophus parviceps</i> (Boulenger, 1882)	0	1	0	0	1	23.45	0	0	1	1	0
<i>Dendropsophus rhodopeplus</i> (Günther, 1858)	0	1	0	0	1	27.30	0	0	1	1	0
<i>Dendropsophus sarayacuensis</i> (Shreve, 1935)	0	1	0	0	1	25.60	0	0	1	1	0
<i>Dendropsophus</i> sp14	0	1	0	0	1	19.85	0	0	1	1	0

<i>Elachistocleis helianae</i> Caramaschi, 2010	0	1	1	1	0	32.55	1	0	0	1	0
<i>Engystomops freibergi</i> (Donoso-Barros, 1969)	0	1	0	1	0	27.50	1	0	0	1	0
<i>Hamptophryne alios</i> (Wild, 1995)	0	1	1	0	0	49.50	1	0	0	1	0
<i>Hemiphractus scutatus</i> (Spix, 1824)	0	1	0	1	0	48.00	0	0	0	0	0
<i>Hyalinobatrachium cappellei</i> (van Lidth de Jeude, 1904)	0	1	0	0	1	21.80	0	0	1	1	0
<i>Boana</i> aff. <i>geographica</i> sp1	0	1	0	0	1	39.87	1	0	0	1	0
<i>Boana</i> aff. <i>geographica</i> sp2	0	1	0	0	1	41.09	1	0	0	1	0
<i>Boana</i> aff. <i>geographica</i> sp3	0	1	0	0	1	52.54	1	0	0	1	0
<i>Boana boans</i> (Linnaeus, 1758)	0	1	0	0	1	105.00	1	0	0	1	0
<i>Boana cinerascens</i> (Spix, 1824)	0	1	0	0	1	36.20	1	0	0	1	0
<i>Boana fasciata</i> (Günther, 1858)	0	1	0	0	1	35.40	1	0	0	1	0
<i>Boana lanciformis</i> (Cope, 1871)	0	1	0	0	1	63.20	1	0	0	1	0
<i>Boana raniceps</i> (Cope, 1862)	0	1	0	0	1	69.00	1	0	0	1	0
<i>Leptodactylus bolivianus</i> Boulenger, 1898	0	1	0	1	0	89.30	1	0	0	1	0
<i>Leptodactylus</i> cf. <i>knudseni</i>	0	1	0	1	0	132.00	0	1	0	1	0
<i>Leptodactylus</i> cf. <i>wagneri</i>	0	1	0	1	0	65.50	1	0	0	1	0
<i>Leptodactylus fuscus</i> (Schneider, 1799)	0	1	0	1	0	43.70	1	0	0	1	0
<i>Leptodactylus leptodactyloides</i> (Andersson, 1945)	0	1	0	1	0	46.30	1	0	0	1	0
<i>Leptodactylus mystaceus</i> (Spix, 1824)	0	1	0	1	0	43.60	1	0	0	1	0
<i>Leptodactylus pentadactylus</i> (Laurenti, 1768)	0	1	0	1	0	148.10	0	1	0	0	1

<i>Leptodactylus petersii</i> (Steindachner, 1864)	0	1	0	1	0	39.10	1	0	0	1	0
<i>Leptodactylus podicipinus</i> (Cope, 1862)	0	1	0	1	0	38.80	1	0	0	1	0
<i>Leptodactylus rhodomystax</i> Boulenger, 1884	0	1	0	1	0	76.50	0	1	0	1	0
<i>Lithodytes lineatus</i> (Schneider, 1799)	0	1	1	1	0	54.00	0	1	0	1	0
<i>Oreobates quixensis</i> Jiménez de la Espada, 1872	0	1	0	1	0	58.00	0	1	0	1	0
<i>Osteocephalus aff. leprieurii</i>	0	1	0	0	1	48.25	1	0	0	1	0
<i>Osteocephalus aff. taurinus</i> sp1	0	1	0	0	1	82.50	1	0	0	1	0
<i>Osteocephalus aff. taurinus</i> sp2	0	1	0	0	1	82.50	1	0	0	1	0
<i>Phyllomedusa camba</i> De la Riva, 1999	0	1	0	0	1	81.46	0	0	1	1	0
<i>Phyllomedusa vaillantii</i> Boulenger, 1882	0	1	0	0	1	44.00	0	0	1	1	0
<i>Phyzelaphryne miriamae</i> Heyer, 1977	0	1	0	1	1	19.60	0	1	0	0	1
<i>Pristimantis altamazonicus</i> (Barbour & Dunn, 1921)	0	1	0	0	1	27.90	0	1	0	0	1
<i>Pristimantis fenestratus</i> (Steindachner, 1864)	0	1	0	1	1	41.50	0	1	0	0	1
<i>Pristimantis ockendeni</i> (Boulenger, 1912)	0	1	0	0	1	26.50	0	1	0	0	1
<i>Pristimantis</i> sp1	0	1	0	1	0	33.69	0	1	0	0	1
<i>Pristimantis</i> sp4	0	1	0	1	1	39.01	0	1	0	0	1
<i>Pristimantis</i> sp5	0	1	0	1	1	36.68	0	1	0	0	1
<i>Pristimantis ventrimarmoratus</i> (Boulenger, 1912)	0	1	0	0	1	36.90	0	1	0	0	1
<i>Pristimantis zimmermanae</i> (Heyer & Hardy, 1991)	0	1	0	0	1	19.10	0	1	0	0	1
<i>Rhaebo guttatus</i> (Schneider, 1799)	0	1	0	1	0	174.30	1	0	0	1	0

<i>Rhinella</i> gr. <i>margaritifera</i> sp1	1	0	0	1	1	38.64	1	0	0	1	0
<i>Rhinella</i> gr. <i>margaritifera</i> sp2	1	0	0	1	1	43.92	1	0	0	1	0
<i>Rhinella</i> gr. <i>margaritifera</i> sp4	0	1	0	1	0	60.63	1	0	0	1	0
<i>Rhinella exostosica</i> Ferrão, Lima, Ron, Santos, and Hanken, 2020	0	1	0	1	0	70.23	1	0	0	1	0
<i>Rhinella marina</i> (Linnaeus, 1758)	0	1	0	1	0	97.50	1	0	0	1	0
<i>Scinax</i> aff. <i>chiquitanus</i>	0	1	0	0	1	30.86	1	0	0	1	0
<i>Scinax</i> cf. <i>cruentommus</i>	0	1	0	0	1	28.00	1	0	0	1	0
<i>Scinax</i> gr. <i>garbei</i>	0	1	0	0	1	41.30	1	0	0	1	0
<i>Scinax</i> gr. <i>ruber</i>	0	1	0	0	1	40.30	1	0	0	1	0
<i>Sphaenorhynchus lacteus</i> (Daudin, 1800)	0	1	0	0	1	42.60	1	0	0	1	0
<i>Teratohyla adenocheira</i> (Harvey & Noonan, 2005)	0	1	0	0	1	23.10	0	0	1	1	0
<i>Trachycephalus coriaceus</i> (Peters, 1867)	0	1	0	0	1	55.73	1	0	0	1	0
<i>Trachycephalus typhonius</i> (Linnaeus, 1758)	0	1	0	0	1	88.60	1	0	0	1	0

TABLE S3 Generalized linear-mixed models used to explain multivariate functional-diversity estimates and community-weighted mean (CWM) trait values among plots that were flooded (pre-flooded), plots that remained unflooded (pre-unflooded and post-unflooded) in the Santo Antônio hydroelectric reservoir on the upper Rio Madeira, southwestern Amazonia. Marginal R² (R²m) represents the variance explained by the fixed effects, while conditional R² (R²c) is interpreted as a variance explained by the entire model, fixed and random effects. SVL = snout-vent length. The trait matrix was based on 84 frog species.

Index	χ^2	R ² m	R ² c	P
Functional composition	20.54	0.21	0.74	0.000
Functional richness	14.02	0.11	0.34	0.001
Rao's Q	16.46	0.22	0.26	0.000
Functional Uniqueness	10.23	0.18	0.21	0.006
Traits				
Terrestrial spawning	8.15	0.11	0.56	0.010
Aquatic spawning	7.43	0.18	0.52	0.024
Terrestrial spawning	20.23	0.25	0.73	0.010
Aquatic tadpoles	17.34	0.27	0.70	0.0001
Terrestrial tadpoles	17.32	0.28	0.71	0.0001
SVL	20.87	0.20	0.28	0.0001
Activity diurnal	0.54	0.38	0.29	0.170
Activity nocturnal	3.23	0.03	0.30	0.190
Habitat arboreal	4.35	0.03	0.34	0.110
Habitat fossorial	13.56	0.11	0.52	0.001
Habitat terrestrial	15.36	0.15	0.42	0.0001

RECOMENDAÇÕES GERAIS

Avaliação espaço-temporal dos efeitos da inundação de habitats sobre a diversidade taxonômica e funcional de anuros na primeira hidrelétrica a fio d'água na Amazônia, Brasil.

Os resultados obtidos nessa tese de doutorado demonstram que o entendimento desses efeitos sobre a biodiversidade requer estudos de longo prazo e, no caso de projetos de infraestrutura de grande escala, devem começar bem antes da construção da barragem para que flutuações naturais das espécies também possam ser documentadas.

Aqui listamos algumas recomendações gerais com base nos resultados dos capítulos e de acordo com nossa experiência no local.

- Adoção de uma legislação voltada para hidrelétricas que incorpore a criação de unidades de conservação com especial atenção para os tipos de vegetação permanentemente suprimidos. Essa estratégia de gestão da conservação deve ser financiada pelas empresas produtoras de energia;
- As diferenças aqui encontradas foram em grande parte devido às diferenças ambientais entre áreas inundadas sazonalmente e não inundadas em terrenos mais elevados. As áreas ripárias retêm um complemento importante de diversidade funcional dos anuros. O que mostra a importância da preservação das áreas ribeirinhas e ripárias em outros locais próximos à região dos empreendimentos hidrelétricos;
- Monitoramento temporal dos efeitos da inundação do reservatório. As amostragens devem ser conduzidas antes e em diferentes períodos depois da construção da barragem. Uma vez que grandes hidrelétricas alteram definitivamente o ecossistema é necessário o monitoramento dos seus impactos antes e depois da construção da barragem;
- Manutenção e preservação das áreas de amostragem ao longo dos anos de monitoramento. As áreas que serão monitoradas devem ser mantidas de alguma forma para que as influências externas sejam pequenas;
- Inclusão de métricas de diversidade funcional, indicando quais características das espécies podem ser afetadas.