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Impactos espaciais e temporais do alagamento do reservatório de uma mega hidrelétrica
no sudoeste da Amazônia brasileira sobre a diversidade taxonômica e funcional de
morcegos Phyllostomidae

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Manaus, Amazonas

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IMPACTOS ESPACIAIS E TEMPORAIS DO ALAGAMENTO DO
RESERVATÓRIO DE UMA MEGA HIDRELÉTRICA NO SUDOESTE DA
AMAZÔNIA BRASILEIRA SOBRE A DIVERSIDADE TAXONÔMICA E
FUNCIONAL DE MORCEGOS PHYLLOSTOMIDAE

Tese apresentada ao Programa de Pós-Graduação em Zoologia, da Universidade Federal do Amazonas/Instituto Nacional de Pesquisas da Amazônia, como parte dos requisitos para obtenção do título de Doutor em Zoologia.

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Sinopse:

Esta tese investigou os efeitos temporais e espaciais do enchimento do reservatório da Usina Hidrelétrica de Santo Antônio na diversidade taxonômica e funcional de morcegos da família Phyllostomidae.

Palavras-chave:

Amazônia; Avaliação de impacto ambiental; Monitoramento de longo prazo, Mega barragem; Perda de habitat.

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Antes de iniciar meus agradecimentos, eu gostaria de contar a história que me levou a fazer um doutorado em Zoologia. Para aqueles que não sabem, eu já tenho um título de doutor pelo Programa de Pós-Graduação em Genética, Conservação e Biologia Evolutiva do Instituto Nacional de Pesquisas da Amazônia, obtido em novembro de 2007. Mas porque eu gostaria de fazer um outro doutorado e passar pelos mesmos desafios duas vezes? Juro que não foi por puro masoquismo ou um preciosismo qualquer. Eu tive que fazer outro doutorado por necessidade. Meu título de doutorado em Genética não permite que eu concorra para uma vaga no magistério superior em concursos públicos na área de conhecimento em Biodiversidade da CAPES, a qual eu dediquei a minha carreira. O curso de Genética faz parte da área de conhecimento em Ciências Biológicas I. Eu sou muito grato ao curso de Genética do INPA, pois foi lá onde eu fiz o meu Doutorado. Mas eu nunca imaginei, e nem os meus orientadores na época, que isso seria um empecilho no futuro, afinal, eu havia passado por um treinamento para ser um doutor e o meu currículo seria a minha carta de apresentação. Infelizmente, os concursos públicos no Brasil não pensam assim e eu fui indeferido no momento da inscrição algumas vezes. Moral da história, fiquem de olho nas suas pretensões futuras para escolher onde fazer seu doutorado.

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Resumo

A Amazônia brasileira possui aproximadamente 90% (~ 95 MW) de potencial de energia não explorado e agências governamentais planejaram estudos para a construção de 254 novas barragens de hidrelétricas na região amazônica em um futuro próximo. Embora as usinas hidrelétricas têm sido promovidas como fontes de energia mais limpas, o barramento dos rios interrompe a continuidade do rio e causam a inundação dos ecossistemas ribeirinhos e terrestres adjacentes. A inundação das terras baixas causa perturbação direta na abundância e na composição das espécies, em particular nas espécies diretamente associadas aos gradientes inundados. A maioria dos dados disponíveis sobre os efeitos das barragens de hidrelétricas são como imagens estáticas de certos estágios pós-inundação resultantes de projetos de curto prazo, muitas vezes realizados anos após o enchimento do reservatório. Para uma melhor compreensão dos impactos ambientais das barragens hidrelétricas sobre as espécies silvestres, é aconselhável avaliar os impactos antes e depois das cheias do reservatório. Os morcegos são excelentes indicadores da saúde dos ecossistemas, particularmente os morcegos Phyllostomidae, que são altamente diversos tanto em riqueza de espécies quanto na sua ecologia. A perda de habitat por interferência humana tem sido repetidamente identificada como a principal ameaça à sobrevivência de muitas espécies de morcegos, mas os efeitos do estabelecimento e operação de usinas hidrelétricas nas assembleias de morcegos ainda são mal compreendidos. 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 morcegos 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 três capítulos que avaliam diferentes aspectos dos efeitos temporais e espaciais do enchimento da barragem na composição taxonômica e funcional dos morcegos. No capítulo 1, um total de 49 parcelas distribuídas ao longo das áreas que serão inundadas pela barragem e as que permanecerão secas foram amostradas. Como preditores da distribuição das espécies, eu testei as variáveis de estrutura da vegetação e topografia. Um total de 2306 morcegos pertencentes a 58 espécies foram capturados. A composição de espécies diferiu amplamente entre as parcelas secas e as parcelas localizadas em áreas que serão inundadas, e isso foi fortemente associado às variáveis área basal da floresta e elevação do terreno. Variáveis relacionadas à vegetação também

tiveram forte influência na distribuição das guildas dos morcegos. A inundação de áreas de elevações mais baixas irá afetar negativamente o número de espécies e a abundância de espécies frugívoras. Em contraste, é provável que os animalívoros sejam menos vulneráveis às inundações induzidas pela barragem, uma vez que foram mais abundantes nas áreas que não se espera serem inundadas. No capítulo 2, eu amostréi 12 parcelas que seriam inundadas (pré-inundado) após o estabelecimento da barragem e 34 parcelas que permaneceriam secas (pré-não inundado). Das parcelas que permaneceram secas, 25 delas foram reamostradas após o represamento do rio (pós-barragem). Um total de 3096 morcegos pertencentes a 59 espécies foram capturados. As taxas de captura e o número de espécies foram semelhantes entre as parcelas pré-inundado, pré-não inundado e pós-barragem. Por outro lado, a composição de espécies e de morcegos frugívoros diferiu entre os três tipos de parcelas, com uma clara discriminação das parcelas de várzea do período pré-inundado. A comparação entre as parcelas secas pré- e pós-barragem mostrou que 60% das parcelas diminuíram na abundância e 68% das parcelas diminuíram na abundância dos morcegos frugívoros. No capítulo 3, foram amostradas as mesmas parcelas do capítulo 2. A inundação das terras baixas aumentou significativamente a diversidade α taxonômica e funcional e a singularidade funcional das assembleias dos morcegos. Eu encontrei fortes evidências de uma mudança nas características funcionais após o represamento do rio Madeira, com um aumento na frequência de morcegos animalívoros e uma redução dos fitófagos. Os resultados da diversidade β funcional mostram que o β total resulta do β substituição funcional - substituição de caracteres ponderada pela abundância das espécies - e não pela perda ou ganho de traços funcionais. 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 morcegos 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 morcegos, mas os morcegos frugívoros responderam negativamente com uma perda geral de abundância após a inundação do reservatório. Como novos barramentos de hidrelétricas estão planejados para a Amazônia, eu recomendo 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. Essa estratégia de gestão da conservação deve ser financiada pelas empresas produtoras de energia.

Palavras-chave: Amazônia; Avaliação de impacto ambiental; Monitoramento de longo prazo, Mega barragem; Perda de habitat.

Abstract

The Brazilian Amazon has approximately 90% (~ 95 MW) of unexploited energy potential and government agencies have planned studies for the construction of 254 new hydroelectric dams in Amazon region in the near future. Although hydroelectric power stations have been promoted as cleaner sources of energy by most governmental agencies, river damming interrupts the continuity of the river and causes the flooding of adjacent riverside and terrestrial ecosystems. The flooding of the lowlands causes direct disturbance in the abundance and species composition, in particular those species directly associated to the flooded gradients. Most of the data currently available about the effects of the hydroelectric dams are like static pictures of certain post flooding stages resulting from short-term projects often conducted years after the reservoir is filled. For a better understanding of the environmental impacts of the hydroelectric dams on wild species, it is advisable to evaluate impacts before and after the reservoir floods. Bats are excellent indicators of the health of ecosystems, particularly the Phyllostomidae bats, which are highly diverse both in species richness and in ecology. Habitat loss from human interference has repeatedly been identified as the main threat to the survival of many bat species, but the effects of the establishment and operation of hydroelectric power stations on bat assemblages are still poorly understood. The general objective of this thesis was to evaluate the spatial and temporal effects of the flooding of the Santo Antônio Hydroelectric Plant reservoir, upper River Madeira, State of Rondônia, integrating bat data collected in areas that would be flooded and not flooded before of the dam construction with data collected in non-flooded areas after the river damming. The thesis is composed by three chapters that evaluate different aspects of the temporal and spatial effects of the dam filling on the taxonomic and functional composition of bats. In chapter 1, a total of 49 plots distributed along the areas going to be inundated by the dam and those remaining dry. As predictors for the species distribution, we tested the variables of vegetation structure and topography. A total of 2306 bats belonging to 58 species were captured. Species composition largely differed between the dry plots and the plots located in areas that will be flooded, and this was strongly associated with the variables of forest basal area and terrain elevation. Vegetation-related variables also had strong influence on the guild distribution. The flooding of lower elevations areas is expected to negatively affect the species number and abundance of frugivorous species. In contrast, it is likely that animalivores will be

less vulnerable to dam-induced flooding, since they were abundant in the areas not expect to be inundated. In chapter 2, I sampled 12 plots that were going to be flooded (pre-flooded) after the establishing of the dam, and 34 plots that were to remain dry (pre-unflooded). Of the plots that remained dry, 25 of them were resampled after the river damming (post-dam). A total of 3096 bats belonging to 59 species were captured. Capture rates and number of species were similar among pre-flooded, pre-unflooded, and post-dam plots. On the other hand, the composition of species and frugivorous bats differed between the three plot types, with a clear discrimination of the várzea plots of the pre-flooded period. The comparison between pre- and post-dam dry plots showed that 60% of plots decreased in the abundance and 68% of the plots decreased in abundance of frugivorous bats. In chapter 3, the same plots as in chapter 2 were sampled. The flooding of the lowlands increased significantly the taxonomic and functional α -diversity and functional uniqueness of the bat assemblages. I found strong evidence for a shift in functional traits after river damming, with an increase in the frequency of animalivorous bats and a reduction in phytophagues. The results of functional β -diversity show that β total results from functional β replacement - substitution of traits weighted by the species abundance - and not by the loss or gain of functional traits. The results of this thesis showed that the effects of the Madeira River damming by the Santo Antônio Hydroelectric Power Plant were rapid, observed in the first two years after the flooding of the reservoir. Bat assemblages of the várzea forest were the most impacted by the formation of the reservoir and they were not represented among the remnant unflooded areas. The implementation of the reservoir did not reduce the number of bat species, but frugivorous bats responded negatively with a general abundance loss after flooding of the reservoir. As new hydroelectric dams are planned for the Amazon, I recommend the adoption of legislation aimed at hydroelectric dams that incorporate the creation of conservation units with special attention to the vegetation types permanently suppressed. This conservation management strategy must be financed by energy producing companies.

Keywords: Amazon; Environmental impact assessment; Habitat loss; Long-term monitoring, Mega dam.

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Introdução geral

Expansão da demanda por energia elétrica e o papel da Amazônia

A demanda de energia elétrica no Brasil está intimamente relacionada com o crescimento econômico, desenvolvimento industrial, expansão demográfica e a sinergia entre estes três fatores. O aumento do consumo energético está exponencialmente ligado ao crescimento populacional. Entre 2004 e 2013, a população brasileira cresceu 10,7%, enquanto o aumento no consumo de energia elétrica foi de 31,1% no mesmo período, saltando de 979,5 MWh para 1285,4 MWh (IBGE, 2013). Apesar do Brasil usar diferentes fontes para geração energia elétrica, a maior fonte mais usada ainda é proveniente de usinas hidrelétricas. Em 2019, usinas hidrelétricas foram responsáveis por produzir 63,5% da energia elétrica do Brasil, seguida por gás natural (9,6%), usinas eólicas (8,9%) e biomassa (lenha, bagaço de cana e lixo: 8,3%) (ver Gráfico 2.2 na página 63 em EPE, 2020a). Embora a dependência de usinas hidrelétricas tenha sido maior há 10 anos atrás (84,2%; ver Tabela 2.3 na página 45 em EPE, 2011), houve um aumento de 35,3% da produção de energia elétrica por usinas hidrelétricas (2009: 462.976 GWh; 2019: 626.324 GWh). Esse aumento exigiu a construção de 57 novas usinas hidrelétricas (> 29 MW) nos últimos 10 anos (ver Tabela 2.8 na página 68 em EPE, 2020a). As cinco maiores geradoras de energia estão na região Norte do país e juntas produzem 21.458 MW (EPE, 2020a).

Por causa do grande volume de água que passa pela região e topografia com quedas significativas em seus rios, a Amazônia brasileira tem um grande potencial para geração de energia por usinas hidrelétricas. O Ministério de Minas e Energia (MME) estimou em 2013 que a Bacia do Rio Amazonas tinha um potencial disponível de 91% da sua capacidade energética, onde ainda poderia ser explorado 95.000 MW (EPE,

2013). O governo brasileiro vem planejando um número significativo de usinas hidrelétricas para a Amazônia. O “Plano 2010” (ELETROBRÁS, 1987) listou 79 barragens na região Amazônica com a capacidade de inundar 10 milhões de hectares, ou aproximadamente 3% Amazônia brasileira (ver mapa da Figura 3 na página 13 em Fearnside, 2015). Periodicamente o governo lança Planos Decenais de Expansão Energética com a previsão da expansão da rede energética pelo país. Por exemplo, o Plano Decenal de Expansão Energética 2023 prevê 28 novas grandes barragens com mais de 30 MW (EPE, 2014), enquanto o Plano de 2029 prevê três hidrelétricas (EPE, 2020b). Contudo, a construção de novas usinas depende das estimativas futuras de consumo energético e de recursos financeiros governamentais e privados. Em períodos de crise financeira os projetos são adiados, mas o planejamento e o local da obra permanecem inalterados. Alguns projetos do “Plano 2010” que não foram construídos, ainda continuam nos Planos Decenais do MME. Desde 1975 foram construídas na Amazônia 16 grandes usinas hidrelétricas (> 30 MW) e outras 34 barragens estão inventariadas ou em fase de construção (Tabela 1 e Figura 1). Outras 62 barragens estão inventariadas no “Plano 2010”, mas não aparecem nos Planos Decenais (Fearnside, 2015). Isso significa que 96 barragens em algum momento tiveram um estudo de viabilidade energética a pedido do governo federal que vislumbrou sua implementação futura. Por isso é possível esperar um número alto de novas hidrelétricas na Amazônia.

Tabela 1. Barragens existentes com reservatórios enchidos até 2016 ou planejadas na Amazônia Legal brasileira (> 30 MW).

Adaptado de Fearnside, 2015 (ver Tabelas 2 e 3 páginas 14-16).

N	Ano enchimento	Nome	Estado	Rio	Capacidade instalada (MW)	Área do reservatório (km ²)	Latitude	Longitude
UHEs existentes								
1	1975	Coaracy-Nunes	Amapá	Araguari	78	23	00N 54' 24"	51W 15' 31"
2	1977	Curuá-Una	Pará	Curuá-Una	100	78	02S 49' 11"	54W 17' 59"
3	1984	Tucuruí	Pará	Tocantins	8370	2850	03S 49' 54"	49W 38' 48"
4	1987	Balbina	Amazonas	Uatumã	250	2996	01S 55' 02"	59W 28' 25"
5	1987	Manso	Mato Grosso	Manso	212	427	14S 52' 16"	55W 47' 08"
6	1988	Samuel	Rondônia	Jamari	210	560	08S 45' 01"	63W 27' 20"
7	1999	Lajeado	Tocantins	Tocantins	800	630	09S 45' 26"	48W 22' 17"
8	2006	Peixe Angical	Tocantins	Tocantins	452	294	12S 15' 02"	48W 22' 54"
9	2011	Dardanelos	Mato Grosso	Aripuanã	261	0,24	10S 09' 37"	59W 26' 55"
10	2011	Rondon II	Rondônia	Comemoração	73,5	23	11S 58' 51"	60W 41' 56"
11	2011	Santo Antônio	Rondônia	Madeira	3150	350	08S 48' 04"	63W 56' 59"
12	2012	Estreito	Maranhão/Tocantins	Tocantins	1087	744,68	06S 35' 11"	47W 27' 27"
13	2013	Jirau	Rondônia	Madeira	3750	361,6	09S 15' 18"	64W 38' 40"
14	2014	São Manoel	Mato Grosso	Teles Pires	746	53	09S 11' 29"	57W 02' 60"
15	2015	Teles Pires	Mato Grosso	Teles Pires	1820	151,8	09S 20' 35"	56W 46' 35"
16	2016	Belo Monte	Pará	Xingu	11233	516	03S 06' 57"	51W 47' 45"
UHEs planejadas								
17		Água Limpa	Mato Grosso	Das Mortes	320	17,9	15S 20' 53"	53W 25' 49"
18		Babaquara	Pará	Xingu	6300	6140	03S 18' 00"	52W 12' 30"
19		Bem Querer	Roraima	Rio Branco	709	559,1	01N 52' 40"	61W 01' 57"
20		Cachoeira Caldeirão	Amapá	Araguari	219	48	00S 51' 00"	51W 12' 00"
21		Cachoeira do Caí	Pará	Jamanxim	802	420	05S 05' 05"	56W 28' 05"
22		Cachoeira dos Patos	Pará	Jamanxim	528	117	05S 54' 59"	55W 45' 36"
23		Cachoeirão	Mato Grosso	Juruena	64	2,6	12S 59' 22"	58W 57' 29"
24		Chacorão	Pará	Tapajós	3336	616	06S 30' 08"	58W 18' 53"

25	Colíder	Mato Grosso	Teles Pires	342	171,7	10S 59' 06"	55W 45' 58"
26	Couto Magalhães	Mato Grosso/Goiás	Araguaia	150	900	18S 12' 35"	53W 31' 06"
27	Ferreira Gomes	Amapá	Araguari	100	17,72	00N 51' 20"	51W 11' 41"
28	Foz do Apicás	Mato Grosso	Apicás	230	89,6	09S 12' 23"	57W 05' 11"
29	Ipueiras	Tocantins	Tocantins	480	933,5	11S 15' 11"	48W 28' 53"
30	Jamanxim	Pará	Jamanxim	881	75	05S 38' 48"	55W 52' 38"
31	Jardim de Ouro	Pará	Jamanxim	227	426	06S 15' 49"	55W 45' 53"
32	Jatobá	Pará	Tapajós	2336	646	05S 11' 48"	56W 55' 11"
33	Juruena	Mato Grosso	Juruena	46	1,9	13S 24' 05"	59W 00' 27"
34	Magessi	Mato Grosso	Teles Pires	53	NA	13S 34' 35"	55W 15' 54"
35	Marabá	Pará	Tocantins	2160	1115,4	05S 19' 00"	49W 04' 00"
36	Novo Acordo	Tocantins	Sono/Tocantins	160	NA	09S 58' 25"	47W 38' 23"
37	Ribeiro Gonçalves	Maranhão/Piauí	Paranaíba	113	238	07S 34' 31"	45W 19' 02"
38	Salto Augusto Baixo	Mato Grosso	Juruena	1464	107	08S 53' 06"	58W 33' 30"
39	Santa Isabel	Pará	Araguaia	1080	236	06S 08' 00"	48W 20' 00"
40	Santo Antonio do Jari	Pará/Amapá	Jari	167	31,7	00S 39' 00"	52W 31' 00"
41	São Luiz do Tapajós	Pará	Tapajós	6133	722	04S 34' 10"	56W 47' 06"
42	São Salvador	Tocantins/Goiás	Tocantins	243,2	99,65	12S 48' 45"	48W 15' 29"
43	Serra Quebrada	Maranhão	Tocantins	1328	420	05S 41' 52"	47W 29' 11"
44	Simão Alba	Mato Grosso	Juruena	3509	1000	08S 13' 33"	58W 19' 24"
45	Sinop	Mato Grosso	Teles Pires	461	329,6	11S 16' 10"	55W 27' 07"
46	Tabajara	Rondônia	Ji-Paraná	350	NA	08S 54' 15"	62W 10' 21"
47	Toricoejo	Mato Grosso	Das Mortes	76	48	15S 14' 05"	53W 06' 57"
48	Torixoréu	Mato Grosso/Goiás	Araguaia	408	900	16S 16' 59"	53W 37' 00"
49	Tupirantins	Tocantins	Tocantins	620	370	08S 10' 59"	48W 10' 00"
50	Uruçuí	Maranhão/Piauí	Paranaíba	164	279	07S 14' 08"	44W 34' 01"

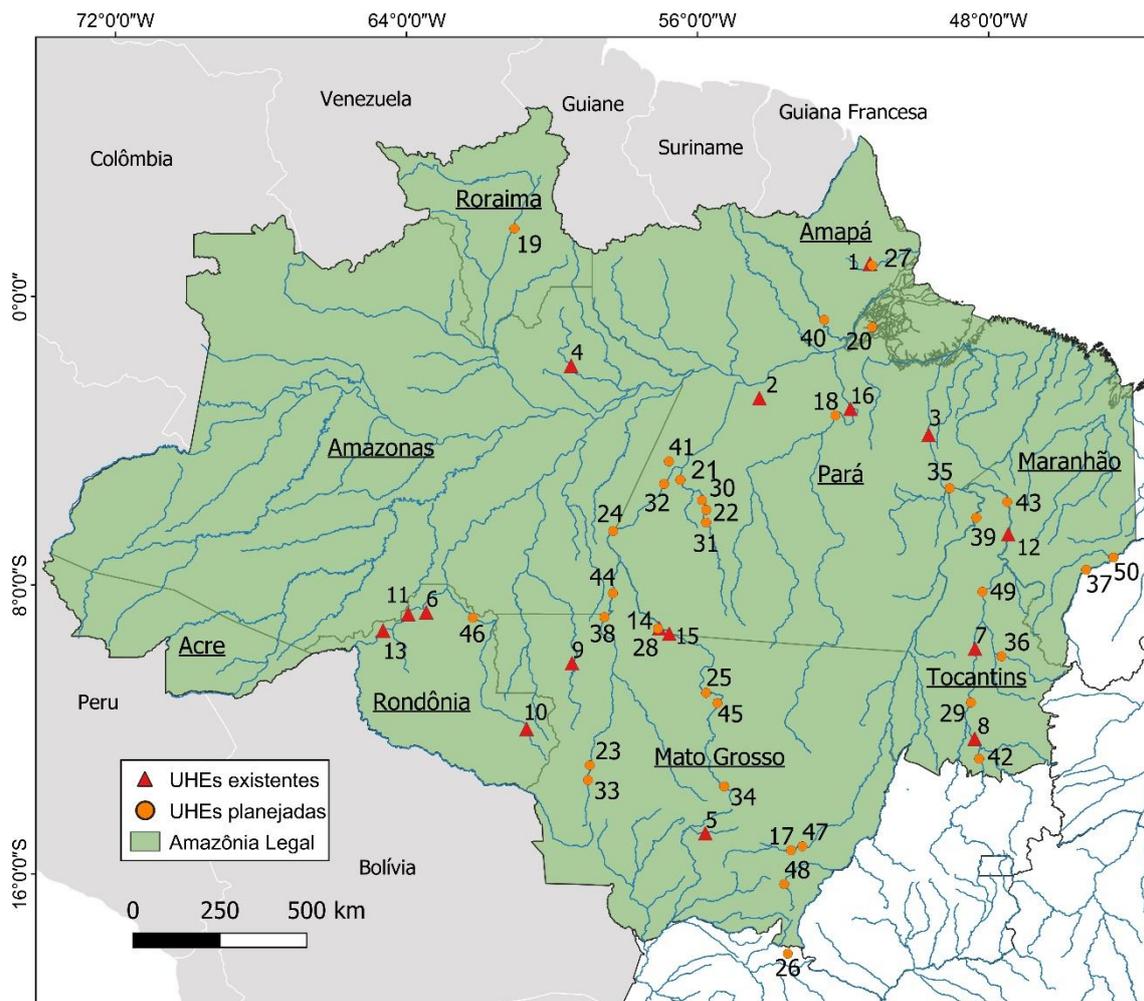


Figura 1. Barragens existentes com reservatórios enchidos até 2016 ou planejadas na Amazônia Legal brasileira (> 30 MW). Os números indicam as barragens listadas na Tabela 1.

A grande quantidade de projetos hidrelétricos na Amazônia tem consequências significativas para quem vive próximo aos empreendimentos e prejuízos no meio ambiente. No entanto, os impactos negativos são diluídos ao longo do tempo e pela grande extensão da Amazônia, uma vez que os empreendimentos não são todos construídos ao mesmo tempo e no mesmo local, com exceção das Usinas Hidrelétricas de Santo Antônio e Jirau no alto Rio Madeira, próximo a Porto Velho. Os impactos

também são subestimados e não são apresentados de forma clara para a população local que é persuadida pelos benefícios das represas com a promessa de empregos e desenvolvimento econômico da região. Os governos municipais, estaduais e federal também não planejam um modelo de desenvolvimento industrial de longo prazo para as cidades afetadas pelas barragens. No máximo o comércio local tem um estímulo econômico ao longo do período das obras. Na maioria dos casos os benefícios são destinados a populações urbanas ou indústrias sediadas a centenas de quilômetros das usinas. Não é raro observar que as populações locais não podem desfrutar ao menos da energia elétrica produzida ou terem vantagem do desgaste social e ambiental com a redução do preço da energia elétrica para as residências e comércio.

Hidrelétricas e meio ambiente

Os impactos do barramento dos rios por usinas hidrelétricas amazônicas causam perda de vegetação não só pela inundação direta do reservatório (Figura 2), mas também por causa do desalojamento das pessoas para novas áreas de assentamento, abertura de estradas e atração de pessoas em busca de trabalho nos canteiros de obras das barragens. Para as 13 grandes usinas hidrelétricas já instaladas na Amazônia, estima-se que 6772,5 km² de floresta foram inundadas pelos reservatórios (Fearnside, 2015). Essa área aumenta para 19.137,8 km² com a construção das outras 38 barragens inventariadas ou em fase de construção (Fearnside, 2015). Contudo, esses valores foram estimados somente para a área do reservatório, sem incluir desmatamentos provocados pelo deslocamento e atração de pessoas para os assentamentos.

Dentre os impactos diretos do barramento de rios, o deslocamento das pessoas que viviam na área do reservatório também contribui para o aumento do desmatamento. Isso ocorre na região para onde as pessoas foram destinadas, que geralmente se encontra

próximo de florestas intactas. Para se ter uma ideia do tamanho do problema, em Tucuruí, no Rio de Tocantins, foram deslocadas 23.871 pessoas da área inundada pelo reservatório (Fearnside, 2015). A barragem de Marabá no rio Tocantins, ainda em planejamento, pode deslocar aproximadamente 40.000 pessoas (Fearnside, 2015). Áreas indígenas também são afetadas pelo barramento de rios na amazônia, com a barragem de Tucuruí inundando parte de três reservas indígenas e sua linha de transmissão cortando outras quatro. A Hidrelétrica de Balbina inundou parte da reserva Waimiri-Atroari no Rio Uatumã. Belo Monte terá sérias consequências para as etnias localizadas no trecho do Rio Xingu conhecido como Volta Grande (Figura 2). No período de estiagem esse trecho do rio seca, inviabilizando a pesca e o deslocamento fluvial essencial para as comunidades indígenas locais. A metilação do mercúrio está ocorrendo nos reservatórios e também é uma preocupação para as pessoas que usam a água do reservatório e consomem seus peixes. Os altos níveis de mercúrio nos peixes e nos humanos atingiram níveis mais altos do que o limite de segurança ou aqueles encontrados em áreas de mineração de ouro (Leino & Lodeius, 1995).

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 (Vauchel et al., 2017; Park & Latrubesse, 2019). A redução dos sedimentos e nutrientes pode resultar em prejuízos para a biodiversidade a jusante da barragem (Park & 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). O Rio Madeira abriga uma elevada diversidade de peixes como 1.304 espécies, sendo mais de 800 delas

encontradas a montante das barragens de Santo Antônio e Jirau (Queiroz et al., 2013). 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. Na bacia do Madeira, as barragens já têm interferido na migração de muitas espécies de peixes como bagres (*Brachyplatystoma*), caracádeos (*Brycon*) e ciclídeos (*Prochilus*) (Hauser et al., 2018).

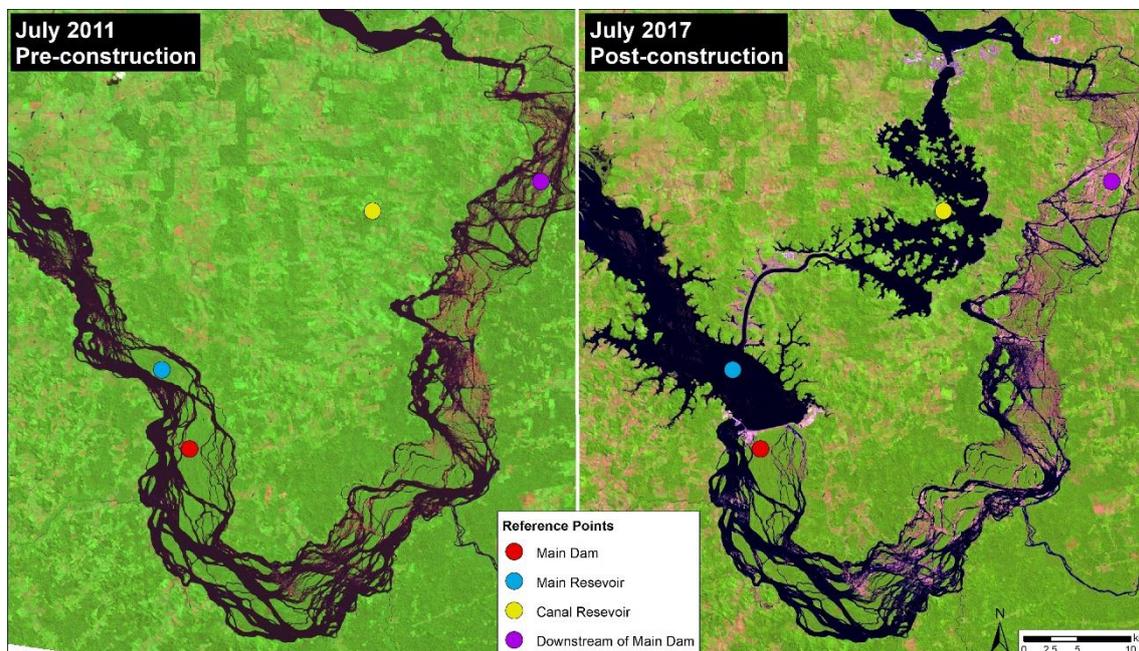


Figura 2. Comparação de antes e depois da construção e enchimento da barragem de Belo Monte no Rio Xingu, Estado do Pará. (Fonte: Finer et al., 2017 - <https://maaproject.org/2017/belo-monte/>).

As barragens também contribuem para a emissão de gases de efeito estufa na forma de dióxido de carbono (CO_2), óxido nitroso (N_2O) e metano (CH_4) ao longo da vida destes projetos. Uma importante fonte de emissões de dióxido de carbono é a decomposição das árvores mortas pela inundação. As árvores que permanecem no

reservatório e aquelas próximas nas novas margens do rio morrem pela inundação e elevação do lençol freático. Geralmente a morte das árvores ocorre nos primeiros anos da inundação do reservatório. Estima-se que 6,4 milhões de toneladas de carbono foram lançadas na atmosfera na UHE Balbina (Fearnside, 1995) e 2,5 milhões de toneladas na UHE Tucuruí (Fearnside, 2002). Quase a totalidade das emissões de óxido nitroso de barragens ocorrem na superfície do reservatório. Os reservatórios podem emitir três vezes mais óxido nitroso do que as florestas originais. O metano é formado pela decomposição da matéria orgânica sem o oxigênio no fundo do reservatório e fica retido por causa da alta pressão da coluna d'água acima. Quando as águas passam pelas turbinas, elas são lançadas para camadas mais elevadas de menor pressão e o gás é então liberado para a atmosfera rio abaixo. A emissão de metano da UHE Balbina tem o potencial de aquecimento atmosférico de 8% (Kemenes et al., 2007), assumindo que o potencial de aquecimento do metano é 21 vezes maior do que o do dióxido de carbono (Lelieveld et al., 1998).

Tipos de hidrelétricas

As hidrelétricas não são todas iguais e o tipo de barragem empregado para a operação das turbinas implica no tamanho do lago e conseqüentemente a área que será inundada. De qualquer forma, o nível do rio será alterado com a implantação da barragem e o pulso de inundação previsível e sazonal na região será extinto. A maioria das barragens e reservatórios associados são de dois tipos: barragem de armazenamento e barragem fio d'água (Baumgartner et al., 2020). A principal diferença entre as duas barragens está relacionada a capacidade de retenção-liberação de água. As barragens de armazenamento retêm grandes quantidades de água e seu fluxo depende das demandas de energia e variação na precipitação. Se a demanda de energia aumentar, as comportas

das turbinas podem ser abertas para maior fluxo de águas. O mesmo princípio ocorre nos períodos de chuvas, as comportas são abertas quando a represa atinge o nível máximo de capacidade. Barragens de armazenamento são as mais comuns em todo o mundo. Por reterem grande quantidade de água e formarem grandes lagos, as áreas de maior elevação do período pré-enchimento se transformam em ilhas. O barramento do rio Uatumã pela hidrelétrica de Balbina, Estado do Amazonas, criou um lago de 312.900 ha com 3546 ilhas (Benchimol & Peres, 2015). A hidrelétrica de Tucuruí no rio Tocantins, Estado do Pará, inundou uma área de 350.000 ha e formou mais de 1800 ilhas (Fearnside, 2015). A maioria dos estudos nesse tipo de barragem avaliam os efeitos da insularização na biodiversidade à luz da teoria de Biogeografia de Ilhas e hipótese de quantidade de habitat. Esses estudos incluem variáveis de complexidade da vegetação das ilhas e variáveis da paisagem.

Por outro lado, as barragens fio d'água com turbinas do tipo bulbo liberam quase a mesma quantidade de água que recebem rio acima. Por causa dessa equivalência de retenção-liberação, essas barragens geralmente criam reservatórios menores comparados a barragens de armazenamento com turbinas Kaplan ou Francis. Por isso, barragens fio d'água são consideradas menos prejudiciais para os ecossistemas aquáticos e terrestres e para a biodiversidade. As barragens fio d'água de Santo Antônio e Jirau inundaram 800 km² de floresta (Cochrane et al., 2017). No entanto, as mudanças no lençol freático das novas margens do rio alteram as propriedades físicas e químicas do solo (Moser et al., 2019). Esses impactos ameaçam diretamente as florestas de áreas não alagadas que não são adaptadas às inundações (Moser et al., 2019). No entanto, a extensão dos efeitos sobre a fauna associados às novas margens do rio é virtualmente desconhecida nas barragens fio d'água.

Morcegos e hidrelétricas

Os morcegos são considerados indicadores potencialmente valiosos da biodiversidade e da saúde dos ecossistemas e constituem um grupo modelo ideal para estudar os efeitos antrópicos sobre os padrões em assembleias e os processos que explicam tais padrões (Medellín et al., 2000; Bobrowiec et al., 2010). O valor dos morcegos como bioindicadores decorre de sua grande diversificação em termos de abundância, número de espécies, características morfológicas e comportamentais e papel ecológico que desempenham, como polinização, dispersão de sementes, fluxo gênico em plantas e supressão da população de insetos (Kalko, 1998).

Os efeitos do barramento de rios nos morcegos até agora têm sido pouco estudados e em sua maioria são avaliados como fenômenos estáticos. Eu preferi referir a barramento do rio no lugar de barragens de hidrelétricas porque os mais importantes exemplos a seguir não foi conduzido em reservatórios de hidrelétricas, mas na barragem do Canal do Panamá. Barragens de hidrelétricas têm os mesmos efeitos deletérios na biodiversidade e ecossistemas do que qualquer outro tipo de barragem que inunda terras baixas e cria ilhas de diferentes tamanhos e isolamento. Até o momento, onze estudos procuraram avaliar os efeitos de barragens nas assembleias de morcegos (Cosson et al. 1999a; 1999b; Henry et al., 2007; Meyer & Kalko, 2008a; 2008b; Meyer et al., 2008; Meyer et al., 2009; Rebelo & Rainho, 2009; Estrada-Villegas et al., 2010; Brändel et al., 2020; Farneda et al., 2020). Este montante de artigos só investigou dois locais da região neotropical, um no lago da barragem da hidrelétrica Petit-Saut na Guiana Francesa (Cosson et al. 1999a), e outro no lago do Canal do Panamá (Meyer & Kalko, 2008a). Em ambos locais, os morcegos foram amostrados nas ilhas formadas pelo reservatório e em áreas de terra firme adjacentes. De modo geral, a composição de espécies de

diferentes guildas diferiu entre ilhas e o continente devido aos efeitos de isolamento e tamanho das ilhas. As assembleias de morcegos Phyllostomidae das ilhas seguiram uma estrutura aninhada, com as ilhas formando subconjuntos de espécies das assembleias do continente. Ilhas de reservatório também possuem menos espécies de morcegos Phyllostomidae, mas mais espécies de morcegos insetívoros aéreos. Espécies sensíveis a bordas e os morcegos animalívoros foram os mais vulneráveis à insularização dos reservatórios.

Como constatado acima, o nosso conhecimento sobre o efeito de barragens sobre morcegos neotropicais é construído a partir de paisagens insularizadas geradas por reservatórios de armazenamento. Além disso, a maioria dos dados disponíveis sobre os efeitos das barragens em morcegos são realizados anos após o reservatório ser enchido. Apenas o estudo de Cosson et al. (1999a; 1999b) avaliou os efeitos temporais (pré- e pós-enchimento) da construção da barragem. Nenhum estudo avaliou a resposta dos morcegos a mudanças na paisagem causada por barragens fio d'água em uma perspectiva temporal, com amostragens antes e depois da inundação do reservatório. Portanto, o preenchimento dessas lacunas é muito importante, pois novas barragens hidrelétricas precisam de novas perspectivas nos estudos de impacto ambiental.

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 morcegos 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 três capítulos que avaliam diferentes aspectos dos efeitos temporais e espaciais do enchimento da barragem na composição taxonômica e funcional dos morcegos. No capítulo 1, eu avalio os efeitos da construção da barragem sobre a comunidade de morcegos

Phyllostomidae antes do enchimento do reservatório, comparando áreas que serão alagadas com áreas que permanecerão secas. Neste capítulo eu também avalio a resposta dos morcegos em relação à estrutura da vegetação e ao gradiente topográfico. No capítulo 2, eu estimo os impactos temporais do enchimento da barragem sobre a comunidade de morcegos e avalio se a composição de espécies das áreas que foram inundadas são incorporadas nas áreas que permaneceram secas. No capítulo 3, eu avalio os efeitos dos primeiros anos de inundação do reservatório sobre as diversidades funcional e taxonômica das assembleias dos morcegos.

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Capítulo 1

Establishing baseline biodiversity data prior to hydroelectric dam construction to monitoring impacts to bats in the Brazilian Amazon

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**Establishing baseline biodiversity data prior to hydroelectric dam construction to
monitoring impacts to bats in the Brazilian Amazon**

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Abstract

The modification of Amazonian rivers by the construction of megaprojects of hydroelectric dams has widely increased over the last decade. Robust monitoring programs have been rarely conducted prior to the establishment of dams to measure to what extent the fauna, and its associated habitats may be affected by upcoming impacts. Using bats as models, we performed analyses throughout the area under the influence of the Santo Antônio hydroelectric dam, Southwestern Brazilian Amazonia before its construction to estimate how the fauna and its associated habitats would be affected by the upcoming impacts. We surveyed bats in 49 plots distributed along the areas going to be inundated by the dam and those remaining dry. As predictors for the species distribution, we tested the variables of vegetation structure and topography. Species composition largely differed between the dry plots and the plots located in areas that will be flooded, and this was strongly associated with the variables of forest basal area and elevation. Vegetation-related variables also had strong influence on the guilds distribution. The flooding of lower elevations areas is expected to negatively affect the species number and abundance of frugivorous species. In contrast, it is likely that animalivores will be less vulnerable to dam-induced flooding, since they were abundant in the areas not expect to be inundated. We urge for the implementation of studies to predict impacts caused by large hydroelectric dams, including tests of the influence of the local conditions that shape diversity to avoid massive losses of the biota, and to build preventive monitoring and management actions.

Introduction

Brazilian industrial and economic development coupled with demographic expansion, contributed to >40% increase in energetic demands within a single decade, beginning in 2001 [1]. Approximately 65% of the energy currently generated for the Brazilian national grid comes from the hydroelectric power stations, which have been promoted as cleaner and less expensive sources of energy by most governmental agencies [2,3]. However, several studies have shown unequivocally that hydroelectric energy production imposes severe impacts on the regional biota [4-6]. Though many are long-term, they begin with those caused by the temporary or permanent flooding of the area of the dam and its surroundings. The construction of hydroelectric stations indeed triggers significant environmental and social impacts, but historically in Brazil, studies have underestimated the impacts of hydroelectric dams and overestimated their benefits [7,8].

Recently, Lees et al. [9] declared that the “Amazon has become synonymous with dam development”. In fact, the plan of energetic expansion 2017-2021 from the Ministry of Mines and Energy of Brazil [2] indicates that nine large hydroelectric power stations, totaling to over 30 MW of capacity, will be built on rivers in the Brazilian Amazonia. Over 80 additional hydroelectric power stations will be constructed in other neighboring Amazonian countries [10].

Modifications to natural landscapes by hydroelectric power stations interfere with the distribution and abundance of species by altering the quality of habitats [5,6,11]. It is known that different species do not use the same habitats in the same way, as they may concentrate in specific areas within ecological gradients (e.g. for frogs [12]; for large mammals [13]; for bats [14]). Anthropogenic alteration of such gradients

causes direct disturbance to relative abundance of the species, and to species composition, in particular those species directly associated to the affected gradients.

Variation in vegetation, topography, and soil properties have been considered important predictors of the structure of animal assemblages [15,16]. Topography may produce gradients of water availability [17], texture and fertility of the soil [18], light permeability through the habitats, and canopy openness [19]. Topographical features have been considered the most determinant factors affecting the species distribution of the understory shrubs and trees in the Amazonia [18,20,21]. Plant communities, in turn, shape the architecture of the forests, influence in the microclimate regulation, and in the production of feeding resources to a variety of consumers, which may become specialized and occupy different niches [22,23].

Bats are excellent indicators of the health of ecosystems, and an outstanding model group with which to evaluate anthropic effects on natural communities, particularly the Neotropical Phyllostomidae bats, which are highly diverse both in species richness and in ecology [24]. Habitat loss from human interference has repeatedly been identified as the main threat to the survival of many bat species [11,25,26], but the effects of the establishment and operation of hydroelectric power stations on bat assemblages, and to the quality of the habitats they occupy, are still poorly understood.

Most studies of bat assemblages from areas under the influence of hydroelectric power stations have been conducted after the flooding of reservoirs with the goals of evaluating the effects of the insularization of the native environments [11,27-29]. In contrast, to our knowledge only a single study has offered predictions of the effects of the establishment of the hydroelectric prior to the flooding and its real consequences [27]. Here, we analyzed the bat assemblages associated with the Santo Antônio power

station area (UHE Santo Antônio) located in the upper Madeira River, southern Amazonia, over different levels of organization (composition, richness and abundance of species and guilds) and habitat structure (vegetation and topography). We conducted our samplings prior to the construction of the power station comparing bat assemblages from areas to be submerged after the flooding, with “control areas”, which remained dry.

Specifically, we tested whether bat assemblages from areas remaining dry after the formation of the dam were different from the areas that will be underwater, and investigated how bat assemblages were associated with the vegetation structure and topography. We also analyzed how assemblage structure, gradients of the vegetation, and topography interact, how they will respond to the flooding of the original landscapes, and considered what would be the implications of such responses for the biological conservation of the bat fauna. As the formation of the dam was planned in a fashion that restricts submersion mostly to flat and low-lying areas, we predicted that bat assemblages sampled in plots in low areas to be submerged would differ from plots not affected by the UHE Santo Antonio reservoir. We also expected that variables associated to the vegetation and to the topography influence in the spatial distribution of the bats. If bat species composition differs between flooded and non-affected areas, terrain elevation may emerge as the strongest correlate of differences between these two areas.

Methods

Ethics Statement

Experienced investigators handled all captured bats. We followed the guidelines approved by the American Society of Mammalogists in our procedures [30]. Systematic

series of specimens were collected and all voucher specimens were deposited in the Mammal Collections of the Instituto Nacional de Pesquisas da Amazônia (INPA 6010-6276). Bats were euthanized humanely by sedation using ethyl ether followed by cervical dislocation. This study was undertaken under licenses for scientific purposes (capture, collection, and transport of specimens) from Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis - IBAMA (Procedure number 02001.000965/2008-83, Permit number 259/2009) and INPA (Memorandum of February 18, 2009).

Study area

The Madeira River is a major tributary of the Amazon River, and has been classified as a white and muddy water river, responsible for 15% of its overall volume [31]. The average annual precipitation in the study area is 2029 mm, with a rainy period from November to April and a dry season from June to September (1998–2007 data of the National Water Agency, ANA). The vegetation of the region was originally composed by dense tropical rainforests [32], and characterized by a mosaic of vegetation types of *terra firme* forests, lowland flooded forests on the margins of the river, and patches of campinarana and campina (sand soil vegetation typical of Amazonia).

The UHE Santo Antônio is located in the upper Madeira River, close to the city of Porto Velho, Rondônia State, in the southern Brazilian Amazonia (Fig. 1). UHE Santo Antônio is a large hydroelectric power station capable of generating 3150 MW and it is expected to cause the permanent flooding of 270 km² of primary Amazonian rainforest-surrounding the reservoir [8]. The turbines type used are Run-of-river that presumes to be less environmentally damaging than traditional dams due operate with a lower water storage using the flow within the river channel. The dam was filled in 2012.

UHE Santo Antônio is located approximately 117 km west of the Jirau dam, another large hydroelectric dam with a capacity of 3750 MW [8]. The city of Porto Velho and surroundings are areas that have suffered from historical anthropogenic disturbances mainly caused by the extensive cattle ranching. The vegetation of the riverbanks within the dam's flood quota was suppressed only after the bat captures have been conducted in all sampling plots. After the dam filling, dam floodgates controlled the water level in the quota of 70 m.

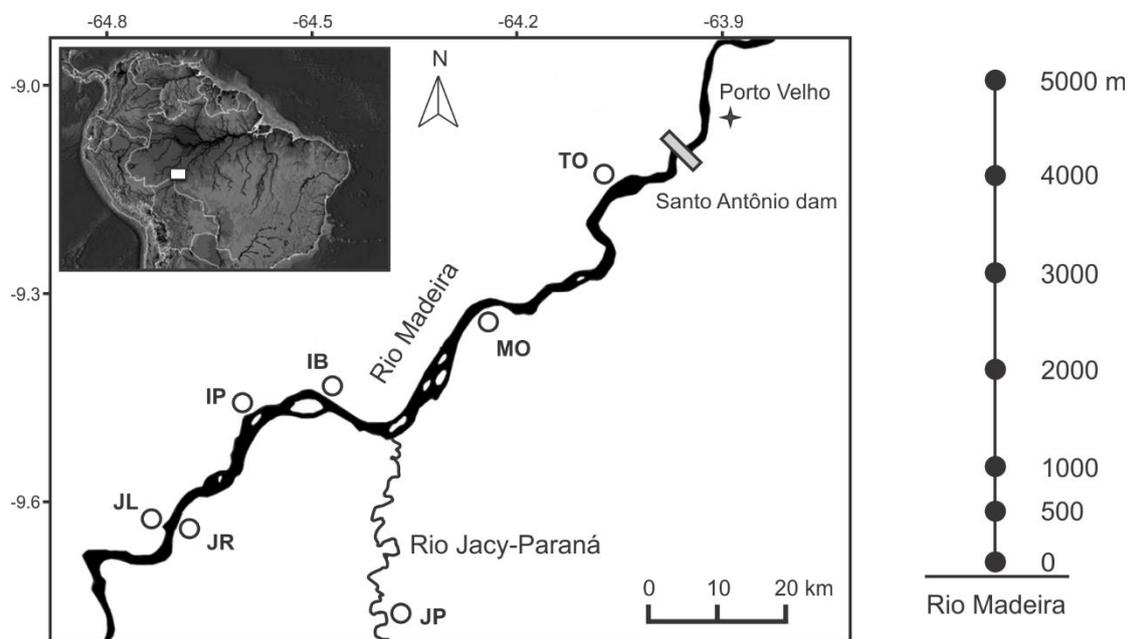


Figure 1. Map of the study area showing the seven sampling modules along the 100-km section of the River Madeira, as follows: TO = Teotônio, MO = Morrinhos, IB = Ilha dos Búfalos, IP = Ilha das Pedras, JL = Jirau Left Bank, JR = Jirau Right Bank, JC = Jaci. In detail (right), sampling design of each module of 5 km with seven plots (black circles) distributed 50, 500, 1000, 2000, 3000, 4000, and 5000 m from the Rio Madeira bank. All modules were arranged perpendicular to the river.

Bat captures

We captured bats with ground-level mist-nets distributed in standard sampling plots distributed through 100 km along the Madeira River margins close to the hydroelectric dam. Sampling plots were chosen to encompass gradients of vegetation and topography represented in the region. We obtained data on bat species composition with the support of the Program for Conservation of the Wildlife conducted by the Santo Antonio Energia, the company responsible for the building and operation of the Santo Antônio hydroelectric. We followed the RAPELD methods created to standardized inventories in the Amazonia [33].

Sampling design included seven sampling modules with seven plots each, totaling 49 sampling plots (Fig. 1). The sampling plots were distributed at 50, 500, 1000, 2000, 3000, 4000, and 5000 m distances from the Madeira River margin in trails perpendicular to the river (Fig. 1). Each plot consisted of one trail of 250 m following the contour line of the terrain, in order to minimize the topographic variations and, consequently, the variation of the vegetation inside each plot. We sampled bats in three to five nights for season (dry or rainy; S1 Appendix) between June 2010 and September 2011, totaling 217 capture nights, and 10416 mnh (1 mist-net hour, mnh, equals one 12-m net open for 1 h). To achieve this total sampling per plot we worked in three to four plots simultaneously in a same night. We gathered information on the water levels of flooding expected to be reached with the creation of the dam reservoir, and sampled 10 plots predicted to be completely submerged, and 39 predicted to remain dry (S1 Appendix).

We erected eight ground level mist-nets (12 × 3 m, 19 mm mesh, Ecotone, Poland) in each plot, arranged sequentially. The net lines started 20 m from the beginning of the centerline of each plot. The nets were left open from 18:00 h to 00:00

h, and checked at 15 minutes intervals. Bats were identified with the help of keys and descriptions found in Lim and Engstrom [34], Charles-Dominique et al. [35], and Gardner [36]. Taxonomy followed Simmons [37], with modifications found in Gardner [36] and Nogueira et al. [38]. We categorized each species within a foraging guild (frugivores, foliage-gleaning animalivores, nectarivores, omnivores, sanguinivores, and aerial insectivores), as proposed by Kalko [24]. The data and metadata of the species captured are deposited in the public repository of the PPBio (<http://ppbio.inpa.gov.br/repositorio/dados>). The data can be accessed by title "Bat species (Chiroptera) captured in 49 sampling plots in the upper River Madeira - Rondonia, Brazil" or key words "Chiroptera", "Madeira River", and "Rondônia".

Topography and vegetation structure in the plots

We used the variables forest basal area, vegetation clutter, elevation, and slope of the terrain to describe the structure of the landscapes in each plot. The forest basal area was calculated per plot as the total sum of $DBH^2\pi/4$ (DBH = circumference of the tree ≥ 1 cm at the height of its breast). We measured the CBH (circumference of the tree at the height of its breast) for each tree and transformed to DBH, using the formula $DBH = CBH/\pi$. We measured trees in each 1-ha (250 × 40 m) plot, following the hierarchical size classes of CBH [39].

The vegetation density was estimated using the intercept point sampling method, which consists in quantifying the number of direct contacts by leaves and branches to a long (1.5 m in length) stick erected at 50 cm above ground, and placed perpendicular to the terrain slope [12]. We measured the number of points that touched the stick at every 2 m along the 250 m of each transect, in each plot (n = 126 touches point), and compiled the sum of contacts for each plot.

A professional surveyor using a theodolite determined the elevations of the terrains. The terrain slope was measured perpendicular to the contour line using a clinometer placed at every 50 m along the 250 m transect of the central line of each plot (n = 5 measurements). We used the mean of the five measurements as the estimate of the slope for each plot.

Analyses

We standardized the data relative to the abundance of species and of guilds dividing raw values by the total number of individuals recorded for each plot. We included only the phyllostomid bats in our analyses, in order to minimize bias introduced by the use of ground level mist-nets, which this close to the ground are only selectively effective at capturing representatives of Phyllostomidae bat family [24].

From the original 49 plots sampled, we excluded from analyses three with less than 10 captures, because of the potential bias they may create in the analyses and as they may have been simply collection artifacts not necessarily reflecting relative abundance of bats in these plots. Other two plots lacking data for the vegetation structure and topography and were removed from the analyses. In total we conducted analyses including 44 plots, of which 10 are to be submerged by the dam, and 34 that remained dry after the nearby flooding (S1 Appendix).

We compared the Non-metric Multidimensional Scaling ordination (NMDS) based on a Bray-Curtis similarity matrix, for species and guild composition from the sampling plots that are going to be submerged with those remaining dry. To test for differences in species and guild composition between submerged and dry sets of plots, we used an Analysis of Similarity (ANOSIM), based on Bray-Curtis similarity distances.

We employed *t*-tests of Student to compare the total richness, total abundance, and the phyllostomid guild richness and abundance between the submerged and dry sets of plots. We compare rarefied species richness between the submerged and dry sets of plots using EstimateS v. 9.1.0 [40] with 1000 randomizations. We assessed the number of species expected to occur in both areas using the nonparametric first-order Jackknife estimator. Rarefaction curves and Jackknife 1 were based on the relative abundance of the species. We estimated the expected relative abundance changes [24] related to forest flooding as the ratio (RA) between the relative abundance of species (RA = captures/mnh) in plots that going to be submerged and in those there were going to remain dry: abundance change = $\log [(RA_{\text{submerged plots}}+0.0001)/(RA_{\text{dry plots}}+0.0001)]$.

Possible influences of the predictor variables forest basal area, vegetation clutter, elevation, and slope were tested using Generalized Linear Mixed Models (GLMM) as implemented in the lmer function in the ‘lme4’ package [41]. The models incorporated the seven modules and plot locations (including both dry and submerge sites) as random effects to account for potential spatial autocorrelations. The response variables used for the GLMM analyses were derived from the first two ordination axes of the NMDS of the species and guild composition, the number of species, the relative abundance (bats/mnh), and the relative abundance of guilds.

We estimated the Variance Inflation Factor (VIF) to test for multicollinearity among all variables for each GLMM model, as collinearity among predictor variables may lead to incorrect identifications of predictors in multivariate models [42]. Our analysis indicated low multicollinearity ($VIF < 1.7$) and consequently, no predictor variable was removed from the regression models. The total variance explained by the predictor variables in a GLMM model was calculated using r.squaredGLMM function in ‘MuMIn’ package [43]. The independent contributions of each explanatory variable

were estimated using hierarchical partitioning as implemented in the ‘hier.part’ package [44]. NMDS ordinations were estimated using the metaMDS function (arguments $k = 2$, $\text{trymax} = 5000$). The NMDS and ANOSIM analyzes were performed using the ‘vegan’ package [45], and the VIF analyzes were run with the help of the ‘car’ package [46]. Partial-regression plots were generated from multiple regression models using avPlots function in ‘car’ package [46], since it is not possible to generate partial plots from GLMM models. All analyses were undertaken with the R platform [47].

Results

Richness and relative abundance

Within the selected 44 plots (197 sampling nights, 9456 mnh), we captured 2306 bats, belonging to 58 species from six families (S2 Appendix and [48] for a complete bat inventory in the region). Species from the family Phyllostomidae represented most of the captures ($n = 2229$), and approximately 83% of the species recorded ($n = 48$).

Phyllostomid richness varied from 8 to 21 species per plot (13.0 ± 2.8 species), and number of individuals per plot varied from 26 to 161 bats (50.7 ± 26.5 individuals).

Most of the phyllostomid species (47.9%; 24 species) were rare (≤ 10 captures), and represented 3.6% of the total captures (84 individuals). Approximately 46% of the phyllostomid captures (22 species) were recorded in less than five plots, and 16.7% (8 species) were captured in a single plot. Nine species (18.8%) were broadly distributed across the plots, occurring in more than half of the total number of plots sampled ($n = 44$). No species occurred in all of the 44 sampling plots. The fruit bat *Carollia perspicillata* was the most frequently captured species, responsible for 33.2% of the total captures, and was followed by *C. brevicauda*, *Rhinophylla pumilio*, *Artibeus*

planirostris, *A. obscurus*, and *A. lituratus*, all frugivores, that together accounted for 35% of the total of individuals captured.

Topography and vegetation structure in the plots

The variables forest basal area, vegetation clutter, elevation, and slope varied widely among plots. The plots covered a forest basal area gradient ranging from 7.5 to 32 m² (17.6 ± 4.7 m²; mean \pm SD), while the vegetation clutter varied from 60 to 200 touches (116.1 ± 35.3 touches) across all plots. Slope varied from 0 to 15.3° ($2.2 \pm 2.8^\circ$), and the maximum difference of elevation among plots was 35 m, ranging from 39 to 109 m a.s.l. (84.4 ± 10.4 m). Forest basal area and vegetation clutter were variable within submerged and dry plots, and therefore no significant differences occurred between areas ($P > 0.11$). In contrast, plots that were going to be underwater had the lowest values of elevation ($t = 10.80$, $P < 0.0001$) and of slope ($t = 2.29$, $P = 0.03$).

The composition and relative abundance of the phyllostomid assemblages were related to the vegetation and to the topography variables (Table 1). Species and guild composition were responsive to forest basal area and elevation (Figs. 2 and 3), and explained from 22% to 47% of the variation, when correlated (Table 1). Variables related to the vegetation had greater independent effects ($> 38\%$) in the relative abundance of the species and guilds and in the number of species, when compared to those related to the topography (Table 1). The forest basal area was negatively correlated with the relative abundance of bats, and also of frugivores, and of nectarivores (Fig. 3). The vegetation clutter was negatively related to the number of species and to the abundance of animalivores and of nectarivores (Fig. 3). The number of bat species and the relative abundance of frugivores were negatively correlated with the elevation (Fig. 2).

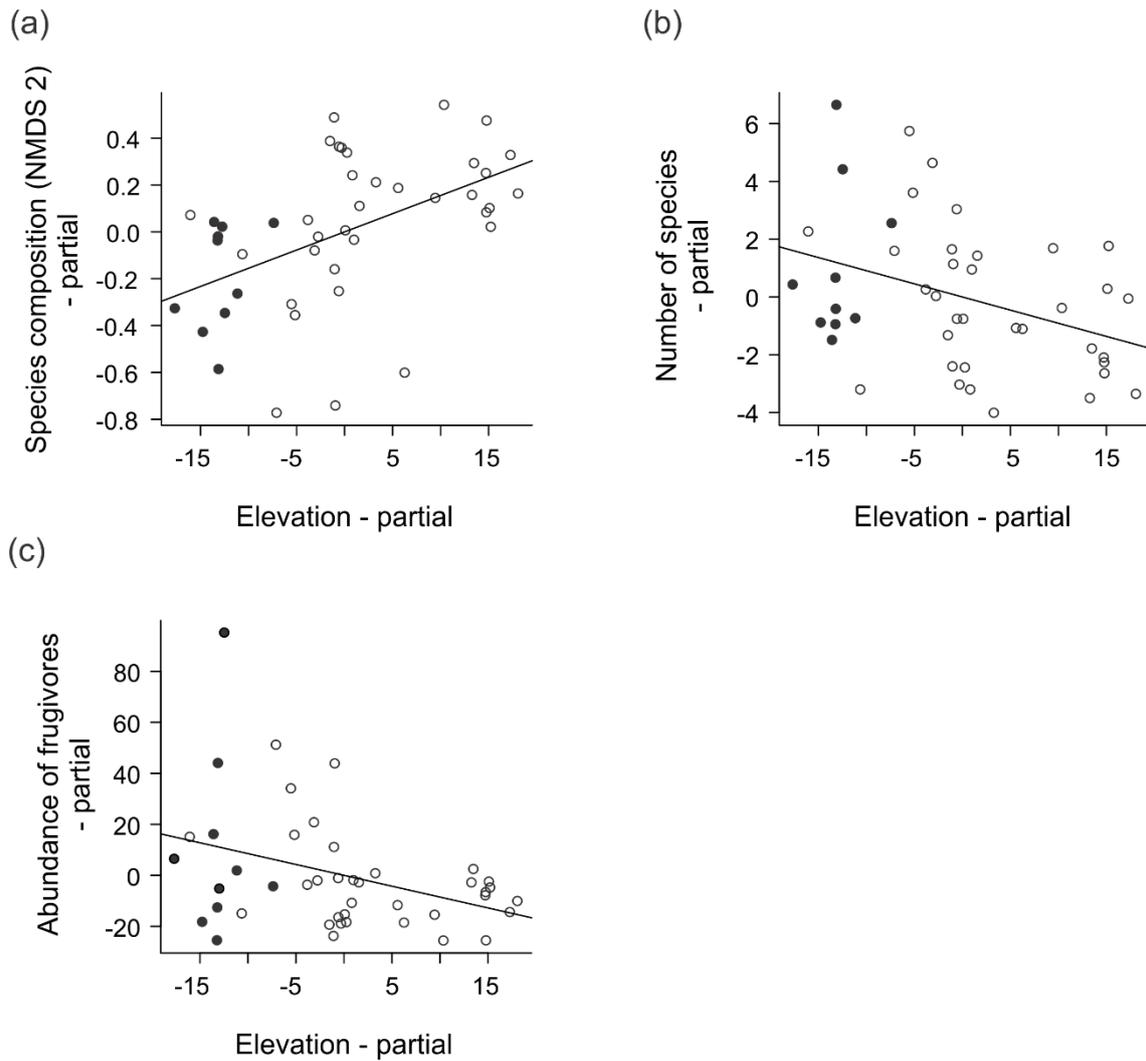


Figure 2. Relationships between different levels of bat community organization and topographic variables measured in 44 plots along the Madeira River, in Rondônia State, Brazilian Amazonia, between 2010 and 2011. Partial regression results between elevation and (a) species composition (NMDS axis 2), (b) number of species, and (c) abundance of frugivores. Black circles represent sampling plots that going to be submerged by the dam and white circles represent plots those that will remain dry.

1

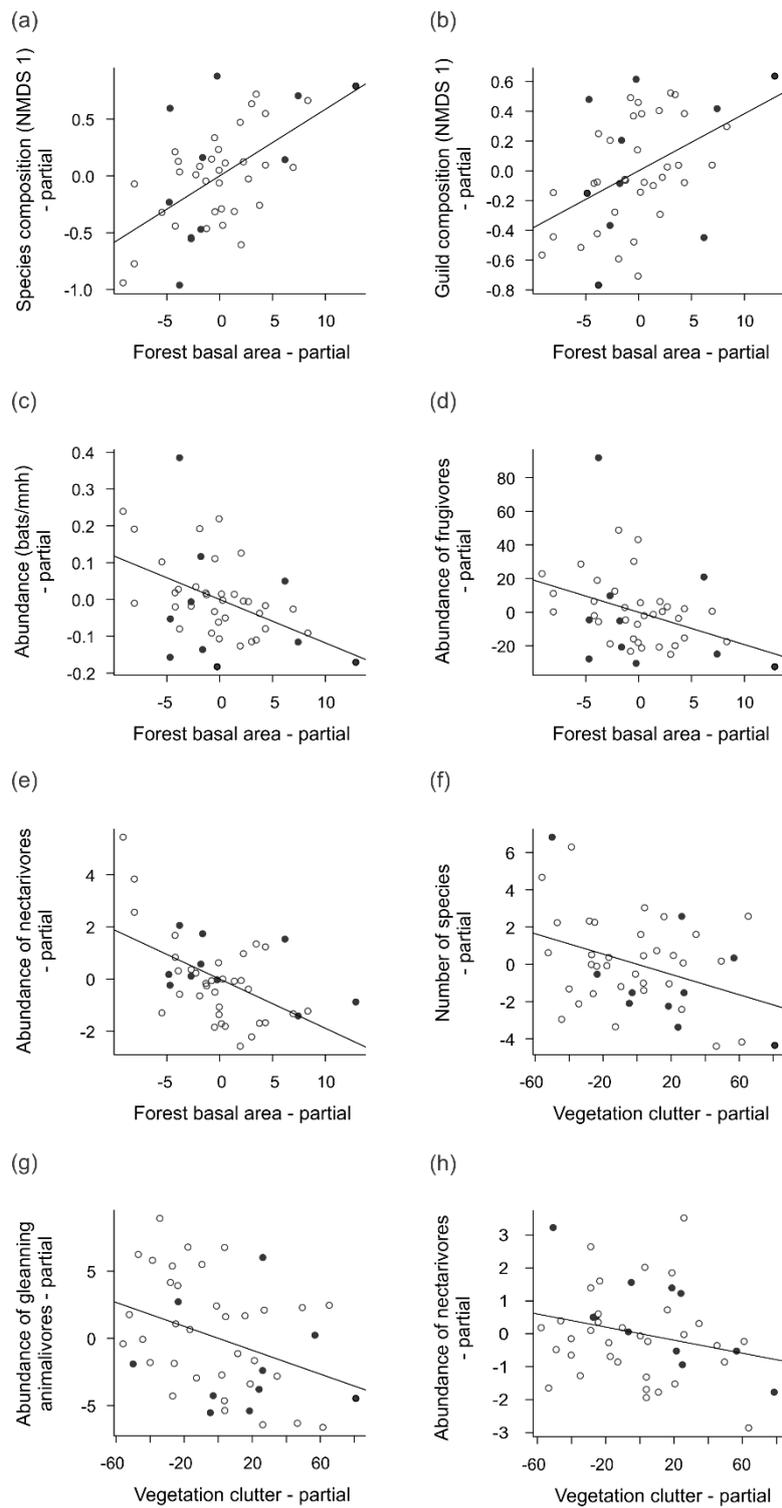
Table 1. Summary of Generalized Linear Mixed Models (GLMMs) evaluating different levels of bat community organization in relation to topographic and vegetation variables measured in 44 plots along the Madeira River, in Rondônia State, Brazilian Amazonia, between 2010 and 2011. Total explained variance of each model and independent explanatory power (HP) based on hierarchical partitioning of each significant variable are shown. Only independent power of explanatory variables with significant effect are given.

		Variance explained	Vegetation				Topography			
			Forest basal area		Vegetation clutter		Altitude		Slope	
			<i>t</i>	HP (%)	<i>t</i>	HP (%)	<i>t</i>	HP (%)	<i>t</i>	HP (%)
Species composition	NMDS axis 1	0.47	2.92 **	97.9	-0.36	0.05		0.93		
	NMDS axis 2	0.22	0.52		-0.19	3.43 **	93.5	-0.48		
Guild composition	NMDS axis 1	0.28	2.89 **	60.9	-0.18	2.09		1.11		
	NMDS axis 2	0.22	1.57		-1.83	0.28		-1.28		
Assemblage parameters	Number of species	0.53	0.50		-2.09 *	33.1	-2.98 *	36.2	-1.37	
	Relative abundance	0.25	-2.71 *	57.3	-0.51		-1.88		-1.22	
Guild abundance	Frugivores	0.22	-2.35 *	38.0	0.01		-2.39 *	49.1	-1.26	
	Animalivores	0.33	1.88		-2.12 *	32.5	0.76		-1.57	
	Nectarivores	0.67	-3.89 ***	68.0	-2.52 *	11.7	1.16		-2.12 * 20.5	
	Omnivores	0.10	-0.93		-1.73		-0.48		-1.33	
	Sanguinivores	0.14	1.38		-1.50		-0.04		1.72	

*P < 0.01, **P < 0.001, ***P < 0.0001

2

3



5

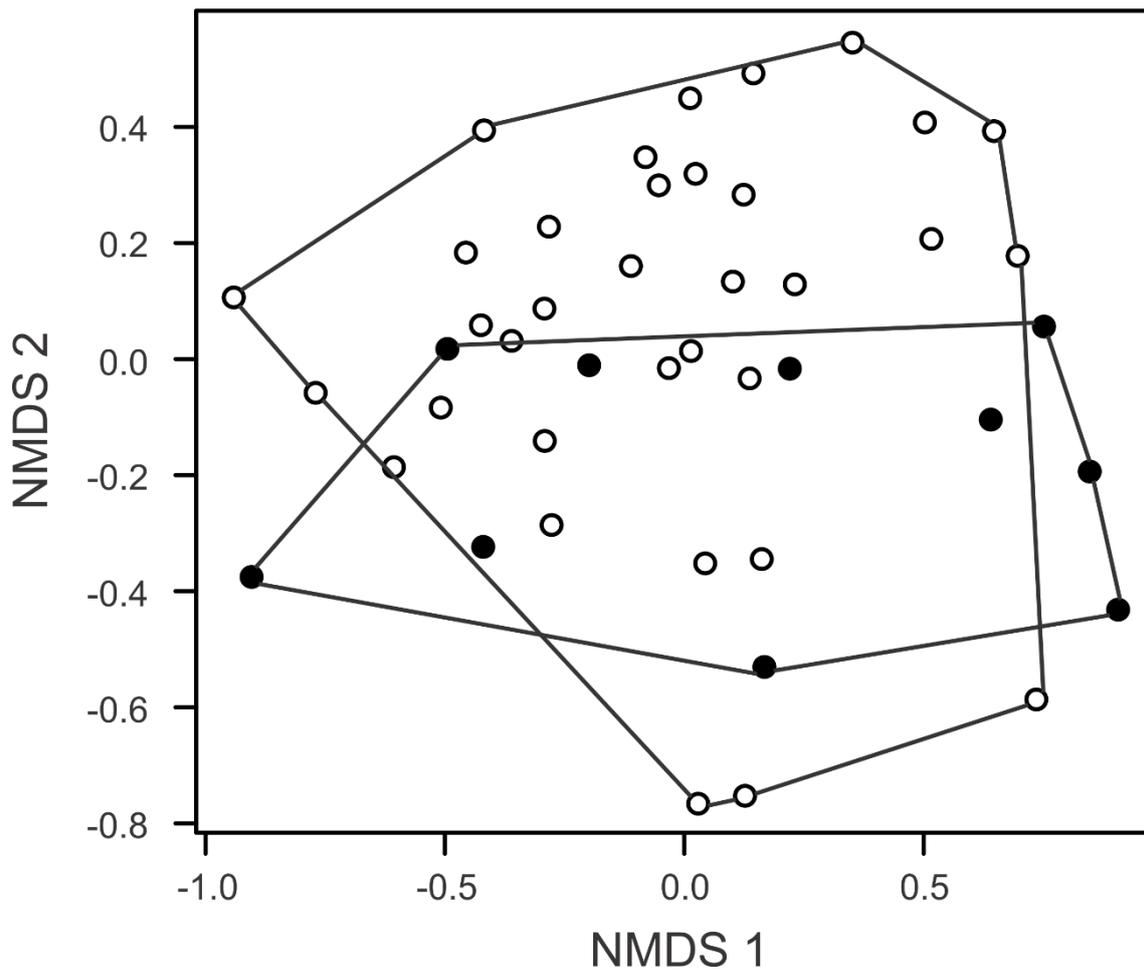
6 **Figure 3. Relationships between different levels of bat community organization**7 **and variables related to the vegetation measured in 44 plots along the Madeira**8 **River, in Rondônia State, Brazilian Amazonia, between 2010 and 2011. Partial**9 **regression results between forest basal area and (a) species composition (NMDS axis 1),**

10 (b) guild composition (NMDS axis 1), (c) relative abundance (bats/mnh), (d) abundance
11 of frugivores, (e) abundance of nectarivores, and between vegetation clutter and (f)
12 number of species, (g) abundance of gleaning animalivores, and (h) abundance of
13 nectarivores. Black circles represent sampling plots that going to be submerged by the
14 dam, and white circles represent those plots that will remain dry.

15

16 **Effects of the formation of the dam in the composition of species and guilds of bats**

17 Our level of completeness for the inventories reached 76.2% (Jackknife 1 = 62.6 ± 4.3)
18 for the submerged plots, and 76.1% (Jackknife 1 = 66.9 ± 3.1) for the dry plots (S3
19 Appendix). There were no differences in the number of species ($t = 1.08$, $P = 0.30$) and
20 capture rates of phyllostomid bats ($t = 0.35$, $P = 0.73$) between the plots remaining dry
21 and the plots going to be submerged. The rarefaction curves of the species richness
22 presented great overlap, reinforcing the similarity of the number of species between the
23 areas (S3 Appendix). On the other hand, the composition of phyllostomids (Fig. 4)
24 differed between plots remaining dry and plots to be submerged (ANOSIM, Global R =
25 0.22, $P = 0.02$) with a more obvious separation along axis 2. The ordination of the plots
26 along the two NMDS axes was responsible for 80.3% of the variation in the species
27 composition (Stress = 0.17) indicating an adequate representation of the data. The two
28 sets of plots shared 72.9% of the total of the species of phyllostomids (35 of the 48
29 species). Four species were captured only in the plots going to be submerged and nine
30 species were restricted to the dry plots (Table 1). Furthermore, 20 phyllostomid species
31 (41.7%), most of them rarely captured (≤ 10 captures) had at least one third of captures
32 in plots that going to be submerged. The relative abundance of the most widespread
33 species (*A. lituratus*, *Lonchophylla thomasi*, and *R. pumilio*) were larger in the plots to
34 be submerged ($P < 0.05$).



36

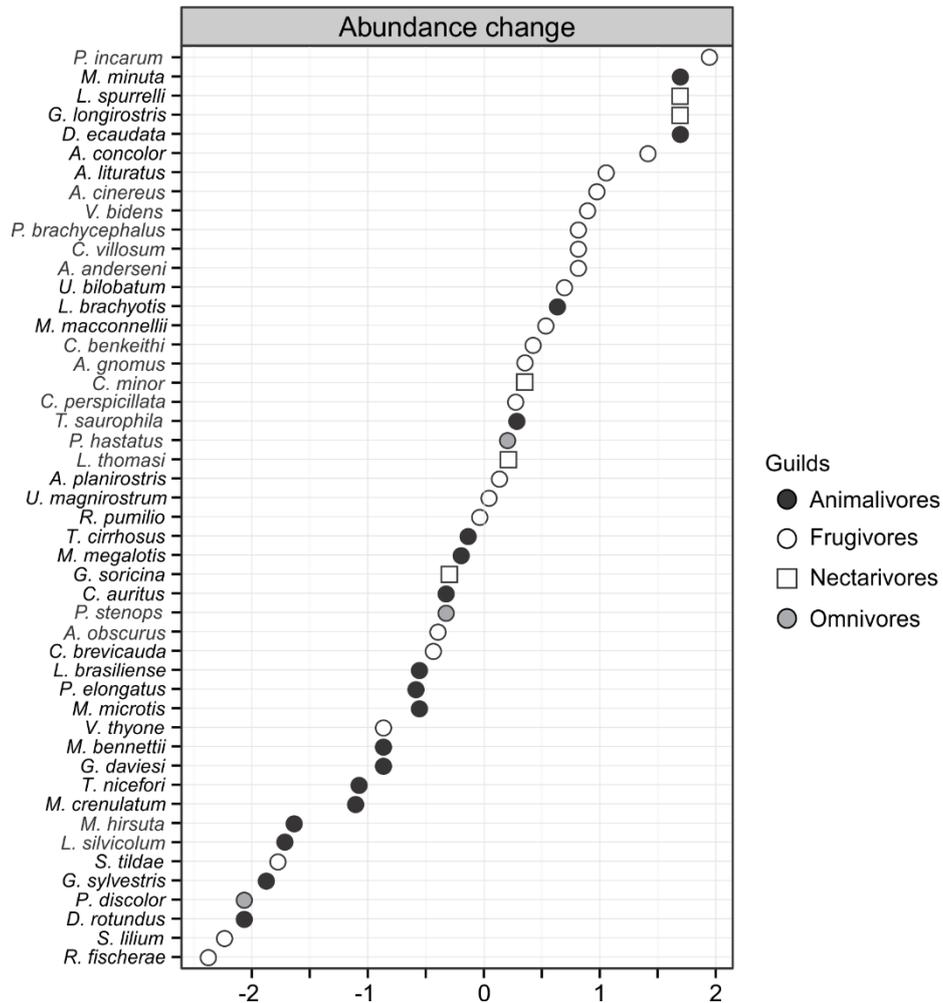
37 **Figure 4. Non-metric multidimensional scaling ordination (NMDS) of the bat**
 38 **species composition between sampling plots that were planned to be submerged by**
 39 **the dam (black circles) and those that will remain dry (open circles) at the Santo**
 40 **Antônio hydroelectric power station area, Southwestern Amazonia, Brazil.**

41

42 Overall, frugivores had more species (22) and individuals (1794 bats), followed
 43 by animalivores (16 species, 325 bats; Table 2). The ordination of the plots along the
 44 two NMDS axes was able to capture 97.8% of the guild composition variation (Stress =
 45 0.06). Guild composition was not different between the sets of plots going to be
 46 submerged by the dam and those remaining dry (ANOSIM, Global R = 0.011, $P =$
 47 0.08). Animalivores however ($t = 2.47$, $p = 0.024$) were more abundant in the plots

48 remaining dry (Fig. 5). In contrast, there were more frugivores ($t = 3.01, P = 0.007$) in
 49 the plots going to be submerged (Fig. 5).

50



51

52 **Figure 5. Expected changes in abundance of 48 bat species due to flooding of the**
 53 **Santo Antônio hydroelectric dam, Rondônia State, Brazil, quantified as abundance**
 54 **changes.** Changes of abundance greater than zero indicate species with more captures in
 55 plots that going to be submerged by the dam. Black circles: animalivores; white circles:
 56 frugivores; grey circles: omnivores; white squares: nectarivores.

57

Table 2. Species richness (S), number of captures (N), and relative abundance (%) of bat guilds at Santo Antônio hydroelectric dam area, Southwestern Amazonia, Brazil

Guilds	Plot											
	Submerse				Dry				Total			
	S	N	%	Mean±SD	S	N	%	Mean±SD	S	N	%	Mean±SD
Frugivore	19	504	82.5	50.4±37.9	22	1290	76.1	37.9±20.3	22	1794	77.8	40.8±25.4
Gleaning animalivore	12	46	7.5	4.6±3.9	15	279	16.5	8.2±4.6	16	325	14.1	7.4±4.6
Nectarivore	5	23	3.8	2.3±1.4	3	58	3.4	1.7±1.7	5	81	3.5	1.8±1.7
Aerial insectivore	9	33	5.4	3.3±3.4	7	44	2.6	2.8±3.5	10	77	3.3	1.8±2.7
Omnivore	2	4	0.7	0.4±0.7	3	19	1.1	0.6±1.0	3	23	1.0	0.5±1.0
Sanguinivore	1	1	0.2	0.1±0.3	1	5	0.3	0.2±0.4	2	6	0.3	0.1±0.3
Total	48	611	100.0	69.5±23.0	51	1695	100.0	47.4±25.9	58	2306	100.0	52.4±26.7

61 **Discussion**

62 Data collected prior to the establishment of hydroelectric power stations have rarely
63 been made available to serve as baseline for monitoring programs. Because we began
64 our sampling of the Santo Antônio areas before any deleterious effects from upcoming
65 impacts of the dam were incorporated in the system, we were able to make predictions
66 on to what extent the bat fauna and associated habitats could be affected in the upper
67 Madeira river area. The species composition of the phyllostomid assemblages at upper
68 Madeira was different between plots that were planned to be submerged and those
69 planned to remain dry. Also the distribution of bat guild compositions was
70 heterogeneous, and correlated primarily with vegetation-related environmental factors.

71 Making predictions of the impacts caused by the implementation of a large
72 hydroelectric power station is a multifaceted task, because each species has a different
73 suite of ecological requirements and evolutionary constraints [49]. Differences in
74 species composition were also observed for lizard and bird assemblages studied in the
75 same plots [50] before dam construction suggesting a possible concurrent response of
76 different animal communities to landscape changes caused by hydroelectric dams, on a
77 regional scale.

78 Bat communities appear to take a long time to recover from the impacts caused
79 by hydroelectric power station, as in the case of the more than 100 years-old areas
80 surrounding the Lake Gatun of Panamá, which appear to have low rates of species
81 substitutions, and somewhat stabilized bat assemblages [11]. Changes in the
82 environment may also not cause immediate measurable changes in communities. Some
83 evidence points to the occurrence of time lags of up to three-years between a given
84 impact and the observation of unstable species richness and/or unstable compositions of
85 bat assemblages [27]. However, our results indicated possible severe and faster effects

86 of the UHE Santo Antônio dam because of the combination of unavoidable changes in
87 the flooded areas (as in the permanent flooding of *várzea* forests), and of the singularity
88 of the landscape of each area and their associated animal assemblages that may not be
89 replaceable. These effects can be still more intense under natural disaster scenarios
90 when additive effects to the dam can be expected as in the case of the large flooding of
91 the River Madeira that took place in 2014, partially caused by the River Beni flood in
92 Bolivia. Headwater originated floods in the regions nearby Amazonian rivers have been
93 becoming more intense and frequent in the last years, and that have been caused both by
94 the high temperatures recorded in the equatorial Pacific, and phenomena such as La
95 Niña, which tends to increase rainfall. Water level management are unlikely to mitigate
96 large flood effects, and the opening of dam gates will probably flood the municipality of
97 Porto Velho, which is located downstream of the dam.

98 The Madeira River carries large amounts of nutrient-rich sediments annually
99 deposited in the riverbanks during its annual flooding [31]. Those fertile soils may
100 support higher abundance and biomass of several species including primates [51,52],
101 and bats [16,53], because of the greater production of fruits. Overall, the areas with the
102 lowest elevations within our sampling plots had higher species richness than those at
103 higher elevations, and had greater abundance of bats, particularly of frugivores. Thus,
104 the permanent flooding of the River Madeira riverbanks can damage rich areas with
105 multiple ecological gradients associated to lower elevations, such as in the case of the
106 areas of *várzea* [16]. Frugivorous and animalivorous bats increase their abundance
107 during high-water season in the Amazonian *várzea* forests [16]. The river level will be
108 changed by the implementation of dam, and the naturally predictable and seasonal
109 flooding pulse in the region will be extinguished. In addition, the high areas that may be
110 eventually flooded are not real *várzea* forests, since the *várzea* forest was suppressed by

111 the UHE. Species associated with the flood pulse and *várzea* forests must adapt to the
112 new flood regime imposed by the dam, and that should be measured.

113 Several studies have indicated that foliage-gleaning bats are sensitive to
114 environmental disturbance, because of their specialized foraging habits that require a
115 more complex environment, and their highly selective avoidance of forest edges and
116 altered areas [11,54]. However, since animalivores were more abundant in the areas not
117 expected to be submerged by the dam, it is possible that their populations will be less
118 vulnerable to flooding. On the other hand, differences in the environmental
119 characteristics of the two sets of plots may trigger changes to the richness and to the
120 abundance of frugivores. The topographic variables (elevation and slope) varied
121 between the two sets of plots, and flooding of the areas situated in lower elevations
122 imposes losses to the vegetation gradients required for the maintenance of fruit-eating
123 bats.

124 Landscape variation of the vegetation and of the topography has been shown to
125 be fundamental in shaping the composition of bat assemblages [14,16,25,55,56].
126 Topographical variables relevant to our study influenced both the distribution and the
127 composition of bat assemblages. Notably large altitudinal variation correlates with equally
128 large environmental changes, and consequently with the shifting of the composition and
129 structure of bat assemblages [25,55]. In the UHE Santo Antônio area, although elevation
130 gradients were relatively subtle (< 100 m), they were enough to alter the composition of
131 the bat assemblages.

132 Variations of the elevation of terrains have been linked with gradients of
133 humidity and of soil type (18,20,32), and plants may show different degrees of tolerance
134 to the physicochemical properties associated to these gradients [21]. Low-lying areas
135 generally retain more humidity than do adjacent higher altitude sites, because they are

136 generally associated to watercourses and/or to shallow water tables [20,21]. Thus, even
137 subtle variations of the elevation may influence the composition and distribution of
138 plant species, also interfering in the shaping of the local vegetation structure [57], food
139 availability, air humidity, and ultimately constraining directly the habitat use by the
140 understory bats. Recent studies conducted in the Central Amazonia have further
141 demonstrated that the elevation has strong relations with the abundance and mass of
142 fruits and insects consumed by bats [58, Capaverde Jr., personal communication].
143 Vegetation tends to be more open in lower areas, allowing to easier circulation of bats,
144 in particular of frugivorous species. Moreover, some frugivores remaining closer to
145 areas that are more humid near the riverbank and the *várzea* forests.

146 Our results also allowed us to record responses in relation to the variations of the
147 vegetation structure from the perspective of guilds, as the relative abundance of the
148 frugivores, nectarivores, and animalivores responded negatively in relation to the
149 vegetation structure, as has previously been documented elsewhere [14,16,59,60].
150 Habitat use by bats is directly affected by the physical obstructions present in the
151 forested habitats [14]. Bats try to avoid navigating in extensive cluttered vegetation
152 because it hinders their flight and the reception of echolocation signals used to detect
153 the potential obstacles and prey [61-63]. The abundance of frugivores and nectarivores
154 in the UHE Santo Antônio area was associated to the forest basal area that account for
155 the occurrence of large obstacles in the vegetation. In contrast, the relative abundance of
156 animalivores was correlated with a finer component of the vegetation, which was the
157 arrangement of leaves and branches.

158 The responses of the phyllostomid guilds to diverse vegetation characteristics
159 have ultimately been related to wing morphology, foraging mode, and echolocation
160 behavior [64,65]. Frugivores and nectarivores are adapted to search for widely dispersed

161 resources since they consume fruits and nectar from patchily distributed shrubs and
162 trees, but they are constrained by their higher wing loading and lower aspect ratios [64-
163 66]. Trunks may represent major obstacles that limit movements between feeding areas,
164 and dense vegetation will require greater maneuverability, which is very expensive
165 energetically, and even more if flights are to be longer. In contrast, animalivores tend to
166 forage over lower distances in a daily basis when searching for prey, and to rely in
167 acoustic orientation by listening to the sounds generated by the arthropods on the
168 surrounding vegetation and soil [61,62]. In these cases, echolocation calls may provide
169 to the bats most of the necessary cues to locate and capture their prey. Short and broad
170 wings with rounded tips allow to a finely maneuverable and slow flight facilitating the
171 capture of prey in the substrate [64-66]. However, even the specialized abilities of the
172 animalivores to capture prey may be limited by the position of the prey on the
173 vegetation. Smaller obstacles generated by the intricate architecture formed by the
174 arrangement of the leaves and the branches in the vegetation can obstruct the reception
175 of the echolocation calls of animalivores, and decrease the efficiency to detect, classify,
176 locate, and to catch their preys.

177 The plan of energetic expansion 2017-2021 from the Ministry of Mines and
178 Energy of Brazil, which include the construction of nine large hydroelectric dams in the
179 Brazilian Amazon, show an urgent call to adjust the energetic needs of the country to a
180 scenario of lower impacts in the Amazonian natural landscapes. These large buildings
181 need to be accompanied by robust biodiversity monitoring plans conducted pre and post
182 landscape impact and in pristine and altered environments [67]. In order to be useful,
183 studies of the impact caused by the implementation of large hydroelectric power
184 stations must be conducted considering different levels of organization (composition,
185 richness and abundance of species and guilds), and to test how local conditions

186 influence and shape biodiversity. It is of paramount importance that such studies are
187 conducted prior to the initiation of any disturbances associated with the establishment of
188 the hydroelectric stations, departing from the zero from the whole communities'
189 perspective, and so increase the chances of their resilience and future long-term
190 survival. At the moment, we do not know the resilience of the bat species, how they will
191 respond to vegetation changes and the new regime of the flood pulse imposed by dam,
192 and we know nothing about their ability to migrate to drier forested areas. However, we
193 can predict that large environmental changes will bring deleterious effects to local
194 biodiversity and that proactive management strategies may improve chances of survival
195 for several species, including bats. As management strategies, we suggest the expansion
196 and/or creation of conservation units in the directly affected area of the dam, with
197 special attention to lowlands areas and to resources considered as conservation hotspots
198 for the bats of the Madeira river, such as the riverbed rocky outcrops [48]. The
199 Mapinguari National Park, with 1,776,914.18 ha, is a conservation unit in the region
200 that may perhaps play a role in the mitigation of the impacts of the dam. Another point
201 is to guarantee logistical and financial assistance for long-term biodiversity monitoring
202 in the region.

203

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S1 Appendix. Summary of sampling effort, number sampling nights, and dam effect in the 44 sampling plots that will be submerged and those that remain dry by the Santo Antônio hydroelectric dam, Western Amazonia, Brazil.

ModuleID	PlotID	lat	long	Dam effect	Sampling effort (mn*h)	Number of sampling nights
Ilha dos Búfalos	B_00	-9.14664	-64.50953	Dry	240	5
Ilha dos Búfalos	B_500	-9.14352	-64.50672	Dry	240	5
Ilha dos Búfalos	B_1000	-9.14007	-64.50364	Dry	240	5
Ilha dos Búfalos	B_2000	-9.13327	-64.49726	Dry	240	5
Ilha dos Búfalos	B_3000	-9.12680	-64.49052	Dry	240	5
Ilha dos Búfalos	B_5000	-9.11337	-64.47754	Dry	240	5
Jaci	Jaci_00	-9.45359	-64.39452	Dry	240	5
Jaci	Jaci_500	-9.45261	-64.39004	Dry	240	5
Jaci	Jaci_1000	-9.45205	-64.38508	Dry	240	5
Jaci	Jaci_2000	-9.45122	-64.37603	Dry	240	5
Jaci	Jaci_3000	-9.45022	-64.36745	Dry	240	5
Jaci	Jaci_4000	-9.44910	-64.35772	Dry	240	5
Jaci	Jaci_5000	-9.44732	-64.34945	Dry	240	5
Jirau Right Bank	JD_00	-9.33632	-64.72861	Dry	192	4
Jirau Right Bank	JD_500	-9.33769	-64.72511	Dry	192	4
Jirau Right Bank	JD_1000	-9.33952	-64.71997	Dry	192	4
Jirau Right Bank	JD_2000	-9.34257	-64.71217	Dry	192	4
Jirau Right Bank	JD_3000	-9.34596	-64.70309	Dry	192	4
Jirau Right Bank	JD_4000	-9.34875	-64.69523	Dry	192	4
Jirau Right Bank	JD_5000	-9.35181	-64.68707	Dry	192	4
Jirau Left Bank	JE_00	-9.31288	-64.71913	Dry	192	4
Jirau Left Bank	JE_500	-9.30947	-64.72231	Dry	192	4
Jirau Left Bank	JE_1000	-9.30632	-64.72544	Dry	192	4
Jirau Left Bank	JE_5000	-9.28097	-64.75053	Dry	192	4
Ilha das Pedras	I_00	-9.18178	-64.61836	Flooded	240	5
Ilha das Pedras	I_500	-9.17877	-64.62089	Flooded	240	5
Ilha das Pedras	I_1000	-9.17455	-64.62387	Dry	240	5
Ilha das Pedras	I_2000	-9.16707	-64.62911	Dry	240	5
Ilha das Pedras	I_3000	-9.15892	-64.63412	Dry	240	5
Ilha das Pedras	I_4000	-9.15165	-64.63877	Dry	240	5
Ilha das Pedras	I_5000	-9.14396	-64.64354	Dry	240	5
Teotônio	T_00	-8.84126	-64.06220	Dry	144	3
Teotônio	T_500	-8.83823	-64.06554	Dry	144	3
Teotônio	T_1000	-8.83531	-64.06874	Flooded	144	3

Teotônio	T_2000	-8.82898	-64.07556	Dry	144	3
Teotônio	T_3000	-8.82276	-64.08224	Dry	144	3
Teotônio	T_5000	-8.81064	-64.09554	Dry	144	3
Morrinhos	M_00	-9.02056	-64.24490	Flooded	240	5
Morrinhos	M_500	-9.02499	-64.24381	Flooded	240	5
Morrinhos	M_1000	-9.02858	-64.24280	Flooded	240	5
Morrinhos	M_2000	-9.03800	-64.24089	Flooded	240	5
Morrinhos	M_3000	-9.04688	-64.23905	Flooded	240	5
Morrinhos	M_4000	-9.05573	-64.23687	Flooded	240	5
Morrinhos	M_5000	-9.05573	-64.23687	Flooded	240	5

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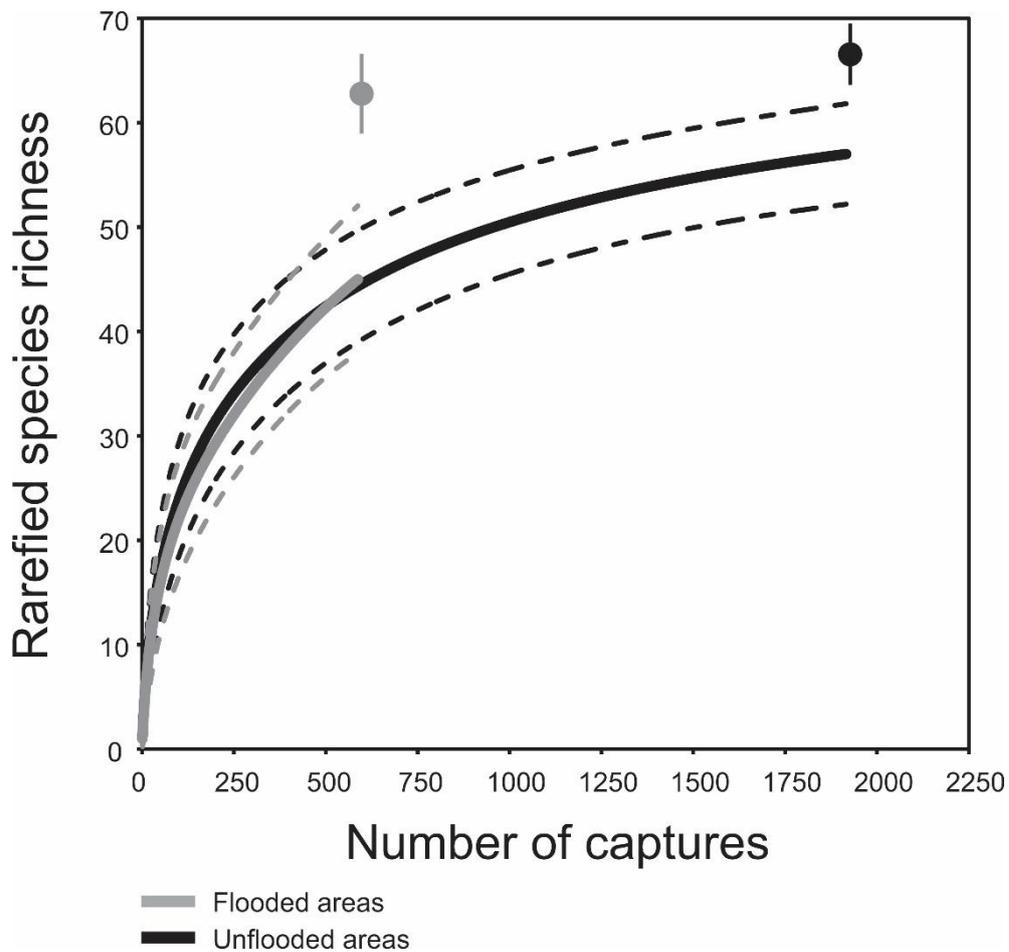
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S2 Appendix. List of bat species, guilds, occurrence per sampling plot, and sampling effort of captures in the 44 sampling plots that will be submerged and those that remain dry by the Santo Antônio hydroelectric dam, Western Amazonia, Brazil.

Taxon	Flooded plots (n = 10 plots)	Plots ocurrence	Unflooded plots (n = 34 plots)	Plots ocurrence	Total abundance	Guilds
Emballonuridae						
<i>Rhynchonycteris naso</i> (Wied-Neuwied, 1820)	2	1	0	0	2	Aerial insectivore
<i>Saccopteryx bilineata</i> (Temminck, 1838)	1	1	2	0	3	Aerial insectivore
<i>Saccopteryx leptura</i> (Schreber, 1774)	4	1	3	2	7	Aerial insectivore
Mormoopidae						
<i>Pteronotus parnellii</i> (Gray, 1843)	15	5	30	12	45	Aerial insectivore
Thyropteridae						
<i>Thyroptera discifera</i> (Lichtenstein and Peters, 1854)	1	1	0	0	1	Aerial insectivore
<i>Thyroptera tricolor</i> Spix, 1823	2	2	3	3	5	Aerial insectivore
Natalidae						
<i>Natalus macrourus</i> (Gervais, 1856)	0	0	1	1	1	Aerial insectivore
Phyllostomidae						
Desmodontinae						
<i>Desmodus rotundus</i> (Geoffroy, 1810)	0	0	5	5	5	Hematophagous
<i>Diphylla ecaudata</i> Spix, 1823	1	1	0	0	1	Hematophagous
Glossophaginae						
<i>Choeroniscus minor</i> (Peters, 1868)	1	1	2	2	3	Nectarivore
<i>Glossophaga soricina</i> Pallas, 1766	3	2	13	7	16	Nectarivore
<i>Glossophaga</i> aff. <i>longirostris</i> Miller, 1898	1	1	0	0	1	Nectarivore
<i>Lonchophylla thomasi</i> J. A. Allen, 1904	17	9	43	20	60	Nectarivore
<i>Lionycteris spurrelli</i> Thomas, 1913	1	1	0	0	1	Nectarivore
Phyllostominae						

<i>Chrotopterus auritus</i> (Peters, 1856)	2	2	9	7	11	Gleaning animalivore
<i>Glyphonycteris daviesi</i> (Hill, 1965)	0	0	1	1	1	Gleaning animalivore
<i>Glyphonycteris sylvestris</i> (Thomas, 1896)	0	0	4	3	4	Gleaning animalivore
<i>Lamproncycteris brachyotis</i> (Dobson, 1879)	2	2	3	3	5	Gleaning animalivore
<i>Lophostoma brasiliense</i> Peters, 1866	1	1	6	5	7	Gleaning animalivore
<i>Lophostoma silvicolum</i> d'Orbigny, 1836	5	5	90	26	95	Gleaning animalivore
<i>Micronycteris hirsuta</i> (Peters, 1869)	0	0	3	3	3	Gleaning animalivore
<i>Micronycteris megalotis</i> Gray, 1842	1	1	4	3	5	Gleaning animalivore
<i>Micronycteris microtis</i> Miller, 1898	1	1	6	6	7	Gleaning animalivore
<i>Micronycteris minuta</i> (Gervais, 1856)	1	1	0	0	1	Gleaning animalivore
<i>Mimon bennettii</i> (Gray, 1838)	0	0	1	1	1	Gleaning animalivore
<i>Mimon crenulatum</i> (E. Geoffroy, 1803)	1	1	11	8	12	Gleaning animalivore
<i>Phylloderma stenops</i> W. Peters, 1865	2	1	9	7	11	Omnivore
<i>Phyllostomus discolor</i> Wagner, 1843	0	0	5	1	5	Omnivore
<i>Phyllostomus elongatus</i> (E. Geoffroy, 1810)	10	5	57	21	67	Gleaning animalivore
<i>Phyllostomus hastatus</i> (Pallas, 1767)	2	2	5	4	7	Omnivore
<i>Trachops cirrhosus</i> (Spix, 1823)	8	4	29	15	37	Gleaning animalivore
<i>Trinycteris nicefori</i> Sanborn, 1949	3	2	29	11	32	Gleaning animalivore
<i>Tonatia saurophila</i> Koopman e Williams, 1951	11	3	26	18	37	Gleaning animalivore
Carolliinae						
<i>Carollia benkeithi</i> S. Solari and Baker, 2006	4	1	8	4	12	Frugivore
<i>Carollia brevicauda</i> (Schinz, 1821)	32	7	156	33	188	Frugivore
<i>Carollia perspicillata</i> (Linnaeus, 1758)	225	10	540	33	765	Frugivore
<i>Rhinophylla fischeriae</i> D. C. Carter, 1966	0	0	7	5	7	Frugivore
<i>Rhinophylla pumilio</i> Peters, 1865	42	10	137	30	179	Frugivore
Stenodermatinae						
<i>Artibeus</i> aff. <i>anderseni</i> Osgood, 1916	1	1	1	1	2	Frugivore

<i>Artibeus cinereus</i> (Gervais, 1856)	13	5	15	10	28	Frugivore
<i>Artibeus concolor</i> Peters, 1865	2	2	1	1	3	Frugivore
<i>Artibeus gnomus</i> Handley, 1987	10	6	22	11	32	Frugivore
<i>Artibeus lituratus</i> (Olfers, 1818)	56	10	61	21	117	Frugivore
<i>Artibeus obscurus</i> (Schinz, 1821)	27	7	127	26	154	Frugivore
<i>Artibeus planirostris</i> (Spix, 1823)	45	9	124	25	169	Frugivore
<i>Chiroderma villosum</i> Peters, 1860	1	1	1	1	2	Frugivore
<i>Mesophylla macconnelli</i> Thomas, 1901	12	3	22	14	34	Frugivore
<i>Platyrrhinus brachycephalus</i> Rouk & Carter, 1972	1	1	1	1	2	Frugivore
<i>Platyrrhinus incarum</i> (Thomas, 1912)	8	6	3	3	11	Frugivore
<i>Sturnira lilium</i> (Geoffroy, 1810)	0	0	6	2	6	Frugivore
<i>Sturnira tildae</i> de la Torre, 1959	1	1	22	11	23	Frugivore
<i>Uroderma bilobatum</i> Peters, 1866	11	6	17	9	28	Frugivore
<i>Uroderma magnirostrum</i> Davis, 1968	1	1	3	2	4	Frugivore
<i>Vampyressa thylene</i> Thomas, 1909	0	0	1	1	1	Frugivore
<i>Vampyriscus bidens</i> (Dobson, 1878)	12	6	15	11	27	Frugivore
Vespertilionidae						
<i>Eptesicus</i> spp	2	2	0	0	2	Aerial insectivore
<i>Myotis nigricans</i> (Schinz, 1821)	5	4	3	3	8	Aerial insectivore
<i>Myotis riparius</i> Handley, 1960	1	1	2	2	3	Aerial insectivore
Captures	611		1695		2306	
Species	48		51		58	
Nights	48		149		197	
Sampling effort (net*hour)	2304		7152		9456	



S3 Appendix. Species-accumulation curves for phyllostomid bats captured in the 44 sampling plots that will be submerged and those that remain dry by the Santo Antônio hydroelectric dam, Western Amazonia, Brazil. Dashed lines represent 95% confidence intervals, grey line and circle represent flooded plots, and dark line and circle represent dry plots. Circles indicates the estimated number of species (\pm SD) based on the Jackknife 1 estimator.

Capítulo 2

Monitoring of impacts caused by an Amazonian mega hydroelectric dam revealed immediate effect on frugivorous bat assemblages

**Monitoring of impacts caused by an Amazonian mega hydroelectric dam revealed
immediate effect on frugivorous bat assemblages**

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Abstract

A large portion of the depletion of the tropical forests is associated to flooding of terrestrial ecosystems by mega hydroelectric dams. Run-of-the-water dams have smaller reservoirs with limited water storage and are therefore commonly considered less environmentally harmful. However, our knowledge of how run-of-river dams effect biodiversity is limited. We evaluate the impacts of the Santo Antônio Hydroelectric Plant, a run-of-river dam, on the bat community during the early years of its operation. We employed a temporal sampling design that integrated data collected in areas that would be flooded and not flooded, before and after the construction of the dam. We sampled 12 plots that were going to be flooded after the establishing of the dam, and 34 plots that were to remain dry. Of the plots that remained dry, 25 of them were resampled after the river damming. We captured 3096 bats belonging to 59 species. Capture rates and number of species were similar among pre-flood, pre-unflood, and post-dam periods. On the other hand, the composition of species and frugivorous bats differed between the three periods, with a clear discrimination of the várzea plots of the pre-flooded period. The comparison between pre- and post-dam dry plots showed that 60% of plots decreased in the abundance and 68% of the plots decreased in abundance of frugivorous bats. Capture rates, number of species and species composition were not related to the distance from the new riverbanks. Our results demonstrate that run-of-river dam affect the assemblages of Phyllostomidae bats. Frugivorous bats were most vulnerable to habitat loss. The remaining areas that were not flooded did not incorporate the bat assemblages from the várzea forests that were permanently flooded by the reservoir. We suggest changes in the Brazilian environmental policy that consider the establishment of protection reserves financed by energy producing companies as an instrument for biodiversity conservation, with special attention to the floodplain forests.

Keywords: Amazon; environmental impact assessment; habitat loss; long-term monitoring, mega dam; várzea forest.

1. Introduction

Amazonian tropical forests are decreasing at alarming annual rates, and in Brazil alone we have estimates of 6.3 million ha. of deforestation over the last decade (Assis et al., 2019; Cruz et al., 2020). A large portion of the depletion of the Amazonian forest is associated to the hydroelectric dams, commonly promoted as cleaner sources of energy by most government agencies. However, hydropower dams disrupt the continuity of rivers and cause the flooding of adjacent riparian and terrestrial ecosystems (Stickler et al., 2013; Winemiller et al., 2016). Nonetheless the Brazilian Amazon still has approximately 90% (~ 95 MW) of unexploited energy potential and government agencies have planned studies for the construction of 254 new hydroelectric dams in the Amazon region in the near future (MME, 2013).

The Brazilian Amazon drainage systems have been repeatedly disrupted by the construction and the operation of large and small hydroelectric complexes (e.g., Tucuruí in the Tocantins River, Balbina in the Uatumã River, Jirau and Santo Antônio in the Madeira River, Belo Monte in the Xingu River, see Fearnside, 2016). The damming of rivers decreases the flow of sediments, nutrients and of organic matter, affecting aquatic communities and ecosystem dynamics (Finer and Jenkins, 2012; Forsberg et al., 2017; Latrubesse et al., 2017). Concurrently, the loss of riparian forests by flooding and the insularization of landscapes negatively affects the distribution and abundance of species (Pereira et al., 2019) leaving vulnerable taxa prone to extinction (Benchimol and Peres, 2015, Palmeirim et al., 2018; Santos et al., 2018).

The Madeira River is one of the largest Amazonian rivers and one of the most important tributaries of the Amazon River, currently known to contribute with nearly 15% of the discharge of fresh water and sediments to the Atlantic Ocean (Goulding et al., 2003). The building of the Jirau and Santo Antônio hydroelectric complexes, upper

Madeira River was completed in 2013, flooding approximately an extension of 800 km² of land at a maximum level of 90 m (Cochrane et al., 2017). These are run-of-the-river dams that incorporate turbines and river currents to generate energy flooding a smaller area compared to conventional dams such as Tucuruí in the Eastern Amazon, which flooded an area of 2850 km² (Chen et al., 2015). The Madeira River hydroelectric reservoir did not contribute to forming islands potentially minimizing impacts associated to the insularization (Benchimol and Peres, 2015). However, changes in the water table of the new riverbanks were predicted to alter the humidity, physical and chemical properties of the soil (Moser et al., 2019). Although those impacts directly threaten the highland forests that are not adapted to flooding (Moser et al., 2019), the extent of the effects on the fauna associated to new riverbanks is virtually unknown.

Changes caused by human activities may vary in space and time and addressing only the spatial elements of habitat availability may introduce bias, and to the neglect of the temporal complexity that can influence the species distribution (Stouffer et al., 2011; Meyer et al. 2016; Rocha et al., 2018). Hydroelectric dams alter permanently the ecosystems, and it is therefore crucial to understand their effects in the original communities along time (Athayde et al., 2019) to subsidize monitoring and mitigation plans. However, most of the data currently available about the effects of the hydroelectric dams are like static pictures of certain post flooding stages resulting from short-term projects often conducted years after the reservoir is filled (Meyer et al., 2008; Benchimol and Peres, 2015). For a better understanding of the environmental impacts of the hydroelectric dams on wild species, it is advisable to evaluate impacts before and after the reservoir floods and in a more continuous fashion to be able to measure the temporal changes in the abiotic ecosystem and to the original communities (Bobrowiec and Tavares, 2017; Athayde et al., 2019).

Phyllostomid bats are a highly diverse bat family exhibiting complex patterns of evolutionary and ecological diversification (e.g., Rojas et al., 2011; Garbino and Tavares, 2018; Rossoni et al., 2019) and compose one of the richest bat assemblages in the world. Because of such unique complexity of interactions that phyllostomid bats are involved, and as they can easily be sampled, they are excellent model organisms for assessing impacts associated to habitat depletion (Medellín et al., 2000; Rocha et al., 2018). Indeed, phyllostomids have been identified as particularly susceptible to suffer from the implementation and functioning of hydroelectric power stations (Cosson et al., 1999a; Bobrowiec and Tavares, 2017).

We previously found that lowlands bat assemblages of the Madeira River were different from those in the unflooded uplands prior to the flooding of the Santo Antônio dam and estimated that fruit eating bats were more sensitive to the initial effects of the dam (Bobrowiec and Tavares, 2017). We herein aimed to estimate the impacts of the Santo Antônio hydroelectric dam on the phyllostomid bat community during the early years of functioning of the turbines in operation. We tested whether the bat assemblages living in the non-flooded areas changed after the installation of the dam, estimated species loss and effects on species abundance in the areas suppressed, and whether bat assemblages living close to the new banks of the Madeira River were the most affected. We expected that the flooding of the lowland forests to promote the displacement of species to non-flooded areas and alter the composition of species, mainly affecting the fruit bats (Bobrowiec and Tavares, 2017). We also anticipated the reduction in overall bat species numbers and abundance in areas closely located to the new banks of the Madeira River.

2. Materials and methods

2.1. Study area

The study was conducted in the area under direct influence of the Santo Antônio Hydroelectric Station (08°48'S; 63°57'W) in the Madeira River, located 5 km upstream from the Porto Velho city, State of Rondônia, Brazil (Fig. 1). The Santo Antônio Hydroelectric station is a large dam with capacity of generating 3150 MW of electricity. The hydroelectric started operating in March 2012 with the water level of 50 m above the pre-reservoir river level. Part of the tree vegetation in the flood zone was cut previous to the flooding the reservoir, to prevent it to be filled up with dead tree trunks, as it happened in the case of the Balbina Hydroelectric power reservoir (Benchimol and Peres, 2015; 2016).

The Madeira River basin originates in the Andes mountains with several tributaries from the right side deriving from recent cenozoic formations that drain nutrient-rich waters, and with left side tributaries that take in nutrient-poor waters from the old Proterozoic western Amazon plateau (Moser et al., 2014). Vegetation is composed by dense tropical forests formed by unflooded terra firme forests, várzea forest on the riverbanks, and by patches of typical vegetation formations of sandy soil called regionally *campinaranas* and *campinas* (Moser et al., 2014). Climate is tropical humid hyperthermic (Cochrane and Cochrane, 2010) with annual rainfall between 1700 and 2000 mm (Sombroek, 2000), rainy seasons occurring from November to April and dry seasons from June to September. The river reaches its highest water level in March and the lowest in September (Santos et al., 2020).

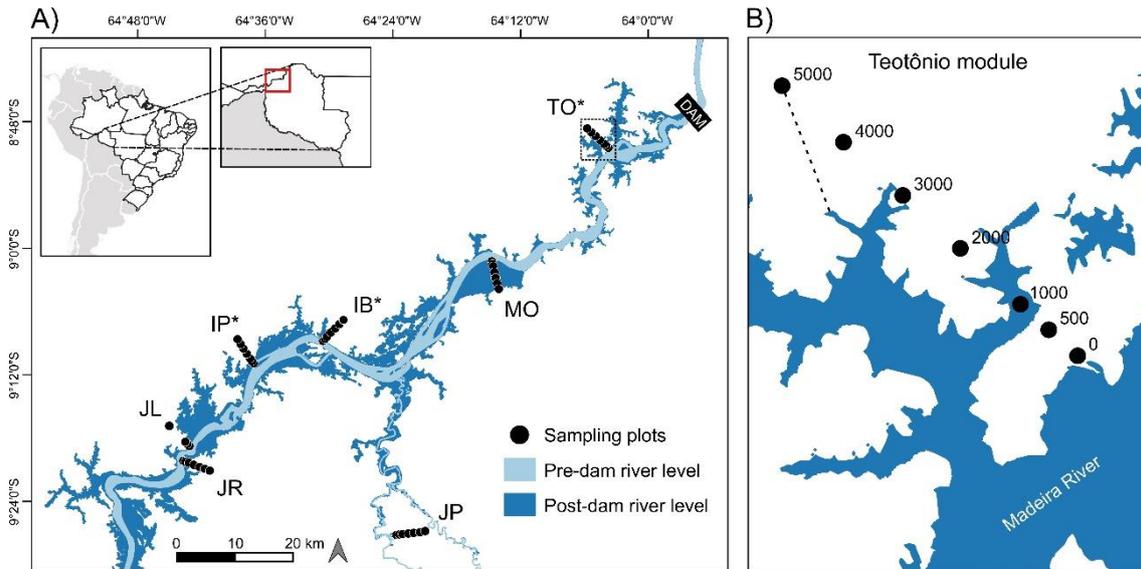


Fig. 1. Map of the study area showing the plots in the seven sampling modules downstream of the Santo Antônio Hydroelectric Station on the Madeira River, Southwestern Brazilian Amazonia. (A) Light blue indicates the area occupied by the river before the construction of the dam and the dark blue indicates the extent of the reservoir after the full dam flooding. (B) Schematic drawing of the seven plots (black circles) of the Teotônio module distributed 50, 500, 1000, 2000, 3000, 4000 and 5000 m from the new riverbank. The distance from the flooded area was considered as the shortest distance between the plot and the maximum flood limit (dashed line in B). The modules are: TO = Teotônio, MO = Morrinhos, IB = Ilha dos Búfalos, IP = Ilha das Pedras, JL = Jirau Left Bank, JR = Jirau Right Bank, JP = Jaci. * Indicates modules with plots sampled before and after the construction of the dam.

2.2. Bat captures

We captured bats using RAPELD methods (RAP = rapid survey of biological communities; PELD = long-term ecological research) for standardized surveys of fauna and flora monitoring in the Amazon (Magnusson et al., 2005). The design consisted of seven sampling modules with seven plots in each one, totaling 49 sampling plots. Of

these, six modules were located on the Madeira River and one on the Jaci-Paraná River. The plots were distributed 50, 500, 1000, 2000, 3000, 4000, and 5000 m away from the riverbank on a trail perpendicular to the Madeira River (Fig. 1). Each plot was 250 m long and 40 m wide followed the topographic contour to minimize internal heterogeneity in soil properties and drainage (Magnusson et al., 2005).

During the pre-filling period (June 2010 to September 2011) we sampled 12 plots that were going to be flooded after the establishing of the dam, and 34 plots that were to remain dry. Maps of the dam's maximum filling water level were used to identify plots that would be permanently flooded. During the post-filling period (June 2013 to June 2014) the same 25 plots of four modules from the pre-filling period were resampled (Fig. 1). Flooded plots contained várzea forests (8 plots), *terra firme* forests with terrain elevation below the reservoir flood level (3 plots), and riparian forests near the *terra firme* streams (1 plot). Unflooded plots, including those that remained unflooded after the establishment of the dam contained *terra firme* and riparian forests.

We captured bats using eight ground level mist nets (12.0 x 2.5 m, 36 mm mesh, Ecotone Inc, Poland). The nets remained open between 18:00 and 00:00 h and were checked at 15 min intervals. In both pre-flood and pos-flood periods, each plot was visited for 3-4 non-consecutive nights, totaling 270 nights (12960 mist-net hours; 1 mist-net hour is equivalent to an open mist-net for 1 hour; Table S1). Each bat was identified and categorized within a foraging guild (frugivores, gleaning animalivores, nectarivores, omnivores, sanguinivores, and aerial insectivores) as proposed by Kalko (1998). Bat identifications were based on the dichotomous keys and descriptions found in Lim and Engstrom (2001), Simmons and Voss (1998), Charles-Dominique et al. (2001), and Gardner (2007). Taxonomy follows Gardner (2007) with modifications by Garbino et al. (2020).

2.3. Statistical analysis

We performed all analyzes including only bats from the Phyllostomidae family to minimize the bias introduced by the use of mist-nets at ground level that are effective to represent this family in samplings and negatively selective to represent other bat families (Kalko, 1998). We subsumed the foliage gleaning insectivores, the omnivorous and the blood-feeding bats within the animalivorous category.

For the analysis, we set categories of plots as: “Pre-flood”, for those that were sampled before the flood and vanished under water after the establishment of the dam; “Pre-unflood”, for those that were sampled before the flood and remained dry; and “Post-unflood”, for those that were sampled after the flood and representing our sampling after the dam was completely established and operating. To compare the number of species, abundance and the number of species and abundance of the frugivorous and of the animalivorous guilds between the plot categories, we employed Analyzes of Variance (ANOVA). The composition of species and guilds of plots for each category was compared using negative binomial GLMs ‘manyglm’ function (Warton et al., 2012) in the *mvabund* package (Wang et al., 2012; 2020). This model-based approach allows testing hypotheses without confusing the location with dispersion effects, which can inflate type I and II errors (Warton et al., 2012). Pairwise comparisons between plot categories were assessed using ‘anova.manyglm’ function in *mvabund*, based in Monte-Carlo fitted model resampling and Wald test. P-values were adjusted for multiple testing and estimated using 999 bootstraps interactions. The composition of species and guilds for the plots of each category was visualized using Non-Metric Multidimensional Scaling (NMDS) ordinations based on a Bray-Curtis dissimilarity matrix of the relative abundance data. Before running NMDS, we

standardized the abundance data of species and of guilds dividing raw values by the total number of individuals recorded for each plot using 'deconstand' function in vegan package (Oksanen et al., 2020). All analyzes were performed using the R software (R Development Core Team, 2020).

To quantify the temporal gains and losses of abundance and species in unflooded plots previous and after dam construction, we used the Temporal Beta-diversity Index (Legendre and Condit, 2019) as implemented in the 'TBI' function of the package adhespatial (Dray et al., 2020). The TBI indices were computed for all species and for frugivorous and animalivorous guilds, with Bray-Curtis dissimilarity index for abundance data and Jaccard dissimilarity index for species occurrence data. We tested whether the plot was dominated by species gains or losses and increase or decrease in species abundance using a paired *t* test with 9999 random permutations. As the TBI analysis compares pairs of plots, we used the same 25 unflooded plots sampled previous and posterior to the dam, discarding the plots from the Jirau left margin and Jirau right margin because those were sampled only previously to the dam stage (Fig. 1). Differences in the abundance of the 41 bat species between the pairs of plots Pre-unflood and Post-unflood were examined using a paired *t* test with 9999 permutations ('tpaired.krandtest' function of the TBI package).

To assess whether the temporal changes in bat assemblages were related to the distances from the new riverbank formed by the flooding of the reservoir, we subtracted the number of species and the abundance of bats and guilds of the Post-unflood plots from the same Pre-unflood plots ($n = 25$ plots). For the species composition we used the Bray-Curtis dissimilarity between pairs of plots sampled before and after the establishment of the dam. Differences in the number of species, abundance and composition of species and guilds were used as the response variables in the

Generalized Linear Models with Gaussian distribution. The GLM models incorporated the linear distance from the new bank of the Madeira River and Jaci-Paraná river post flood as a predictor variable (Fig. 1B).

3. Results

We captured 3096 bats belonging 59 species from six families (Table S1). During the period preceding the filling of the dam, we captured 2156 bats from 57 species, 50 species (613 bats) of them captured in the Pre-flood plots and 48 species (1543 bats) in the Pre-unflood plots. With the establishment of the dam, we captured 940 bats from 48 species. Three species of phyllostomids were recorded exclusively in the Pre-flood plots and two other species were recorded exclusively in the Pre-unflood plots. Only one species was captured exclusively in the Post-unflood plots. Seven species were absent from the Post-unflood plots, all with less than five individuals sampled previous to the formation of the reservoir. The three categories of plots (Pre-flood, Pre-unflood, Post-unflood) shared 34 Phyllostomidae species. Data on the number of species and abundance per guild in each plot category are presented in Table S2.

Capture ($F = 0.46$, $P = 0.63$) and number of species ($F = 1.44$, $P = 0.24$) were similar between three categories of plots, but the species composition was different (Wald = 10.34, $P = 0.001$; Table 1). Pairwise comparisons test showed that the species composition of the flooded plots was different from that of the unflooded plots before and after the dam (Table 1). Temporally, unflooded plots (pre- and post-dam) also differed (Table 1). Plot ordination along the two axes of the NMDS was responsible for 61.8% of the variation in species composition (Stress = 0.2). The difference between plot categories was more evident along axis 2 of the NMDS ordination, with a clear

discrimination of some plots from Pre-flood treatment (Fig. 2). The species composition of the remaining dry plots before and after the dam overlapped (Table 1).

Table 1. Result of multivariate GLM tests (Manyglm analysis) of the bat assemblages between plots that were flooded (Pre-flood), plots that remained unflooded (Pre-unflood and Post-unflood) around the Santo Antônio Hydroelectric Station, southwestern Brazilian Amazonia. $P < 0.05$ are in bold.

Assemblage variables	Global test		Pre-flood × Pre-unflood		Pre-flood × Post-flood		Pre-unflood × Post-flood	
	<i>Wald</i>	<i>P</i>	<i>LRT</i>	<i>P</i>	<i>LRT</i>	<i>P</i>	<i>LRT</i>	<i>P</i>
All species	10.04	0.001	76.40	0.012	77.67	0.012	64.14	0.032
Frugivores	8.13	0.001	42.50	0.005	46.04	0.005	33.00	0.038
Animalivores	5.37	0.230	21.14	0.601	24.68	0.601	23.56	0.601

The number of species, and the capture rates of frugivorous and animalivorous bats were similar in the three categories of plots. Plot ordination along the two axes of the NMDS was responsible for 51% and 57% of the variation in the species composition of the frugivores (Stress = 0.17) and animalivores (Stress = 0.19), respectively. Species composition of frugivorous bats in the flooded plots differed from the Pre-unflood and Post-unflood plots in the pairwise comparisons (Table 1). Pre- and Post-dam unflooded plots also differed (Table 1). The composition of the animalivores was similar in the three categories of plots (Table 1).

Between the Pre-unflood and Post-unflood periods, the number of plots with loss of abundance was larger than the number of plots with gain for all species and for the frugivores dataset (Table 2). We observed that 60% of the plots decreased in phyllostomid abundance and 68% of the plots decreased in abundance of frugivores (Table 2). Species with significant reduction in abundance between Pre-unflood and Post-unflood periods were *Artibeus lituratus*, *Carollia perspicillata* and *Rhinophyla pumilio* (Fig. 3). These species lost 30%, 42.3% and 60% in abundance between

sampling periods, respectively. We found no difference in gains and losses of species and abundance of animalivorous bats (Table 2).

The temporal difference of the number of species, the abundance of bats and guilds and species composition between Pre-flood and Post-unflood plots were not related to the distance from the new riverbanks.

Table 2. Results of the temporal beta-diversity statistics. The sign of change indicates if gains (+ sign) or losses (– sign) dominate across all sampling plots. Number of plots with gain and losses of abundance and species, as well as number of plots with equal gain and losses are also shown. $P < 0.05$ are in bold.

Assemblage variables	TBI value	<i>P</i>	Change	N plots gain	N plots losse	N plots gain=losse
Abundance data						
All species	-2.77	0.012	-	10	15	0
Frugivores	-3.31	0.003	-	8	17	0
Animalivores	-0.02	0.98	-	13	12	0
Ocurrence data						
All species	-0.03	0.97	-	11	11	3
Frugivores	-1.07	0.29	-	8	13	4
Animalivores	0.52	0.62	+	11	8	6

4. Discussion

Land-use change studies using space-for-time approaches may incorporate both temporal and spatial changes that influence species distribution (Stouffer et al., 2011; Rocha et al., 2018). We demonstrated that the construction of the Santo Antônio hydroelectric dam affected the assemblages of Phyllostomidae bats distributed in riparian, lowland forests and especially várzea forests. As we predicted (Bobrowiec and Tavares, 2017) bat assemblages of the várzea forest were the most impacted by the formation of the reservoir, and unfortunately, they were not represented among the remnant unflooded areas. The implementation of the reservoir apparently did not reduce

the number of species in the plots, but frugivorous bats responded negatively with a general loss of abundance over time.

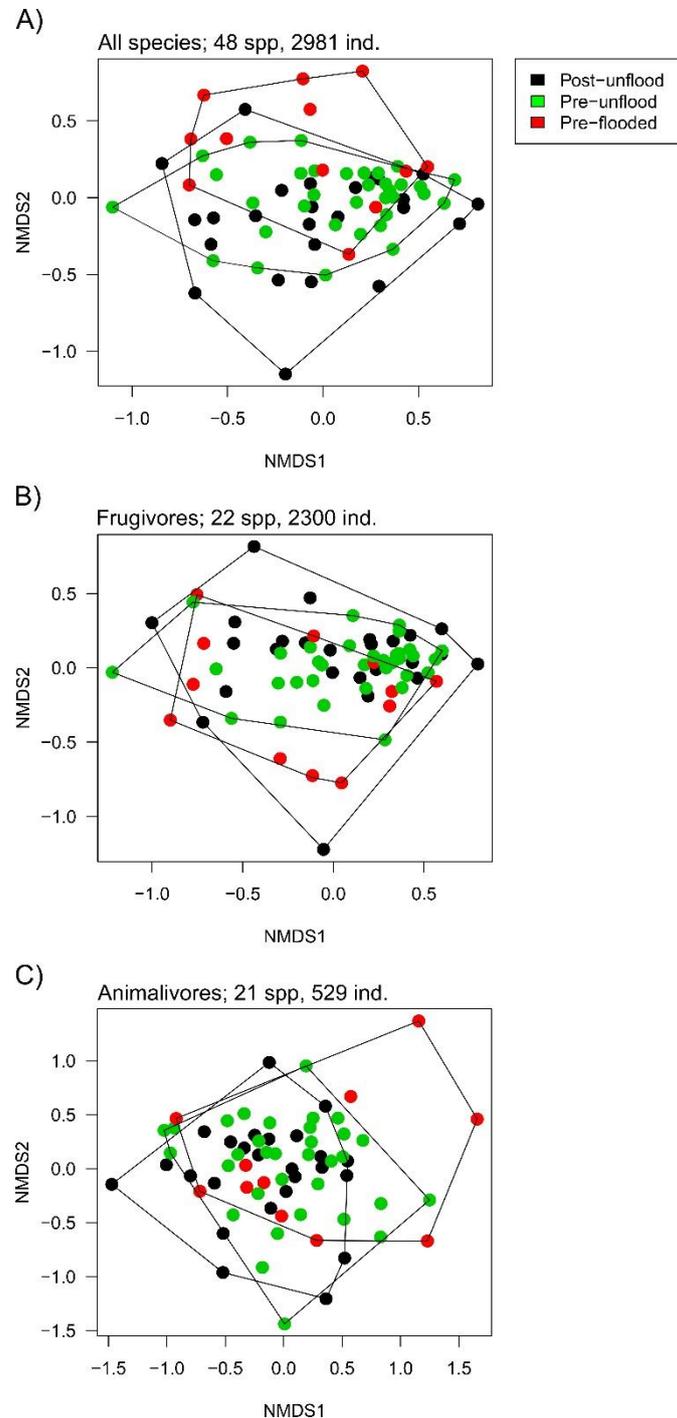


Fig. 2. First two axes of ordination by Non-Metric Multidimensional Scaling (NMDS) of the composition of (A) all species, (B) only frugivorous bats and (C) only animalivorous bats in relation to the reservoir flooding periods of the Santo Antônio

Hydroelectric Station on the Madeira River, Southwestern Brazilian Amazonia. Green are plots permanently flooded; red are unflooded plots that were sampled before to dam construction; black are unflooded plots sampled one year after the total dam filling.

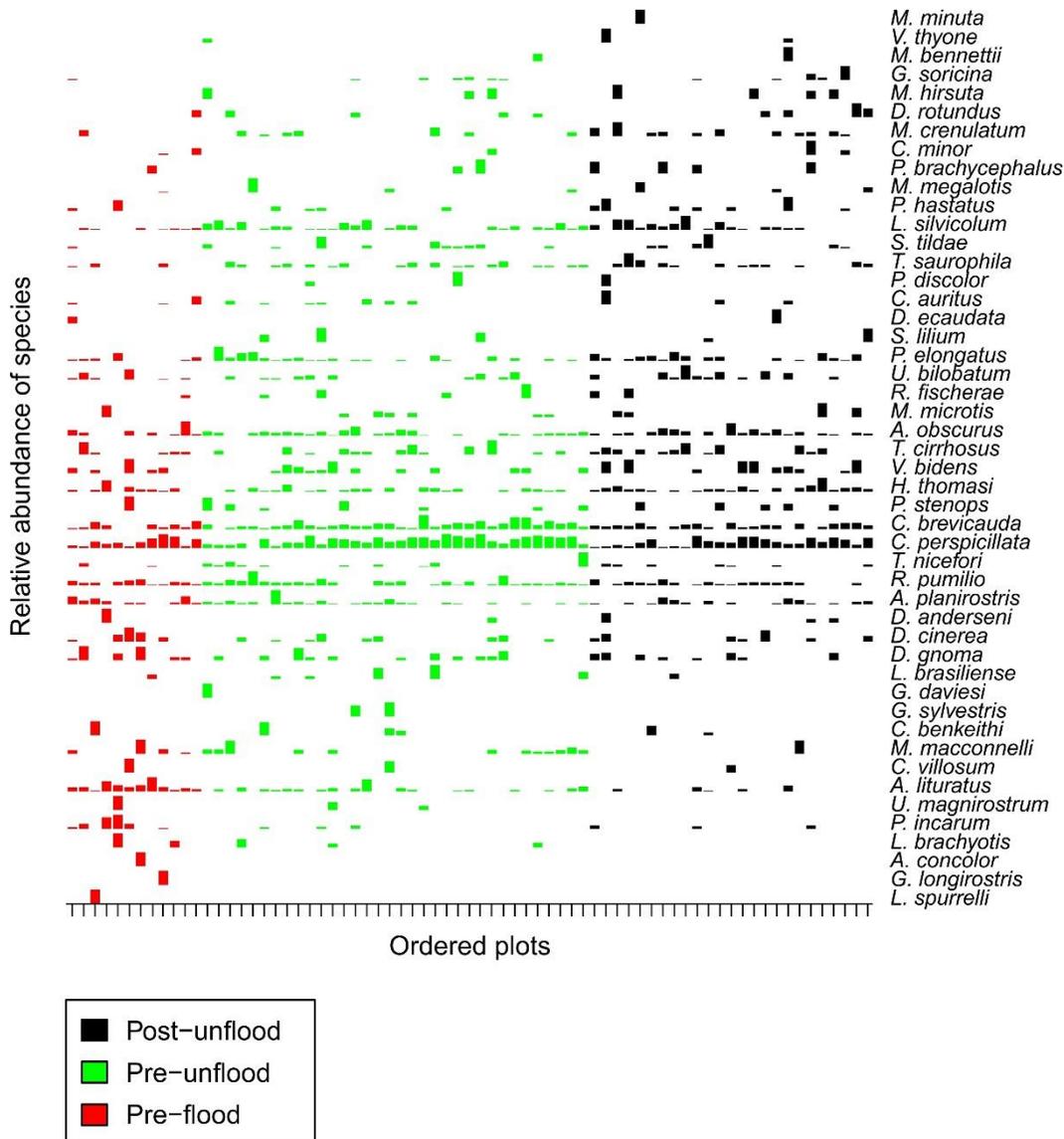


Fig. 3. Sampling plots of the relative abundance of bats ordered in relation to the flooding periods of the Santo Antônio Hydroelectric Station on the Madeira River, Southwestern Brazilian Amazonia. Green are plots that have been permanently flooded; red are unflooded plots sampled before to the filling of the dam; black are unflooded plots sampled one year after the total filling of the dam.

Previous studies evaluating the effects of the hydroelectric dams in the fauna and flora assemblages were conducted in insularized environments where the loss of habitats and edge effects have been identified as the main processes that negatively affect the assemblages (Meyer and Kalko, 2008; Benchimol and Peres, 2015). On the other hand, run-of-the-river dams, such as Santo Antônio hydroelectric, take advantage of the natural current of rivers precluding the formation of deep lakes and islands which have as consequence the loss of large areas of forests located in the riverbanks. This directly affects riparian ecosystems such as the typical várzea forests (seasonally inundated forests covered with white nutrient rich waters), as well as other unique systems such as rocky outcrop communities (Tavares et al., 2017) and the campinaranas, which are located close to the river margins in the medium Madeira (Cochrane et al., 2017). The Jirau/Santo Antônio hydroelectric complex flooded approximately 800 km² of lowland vegetation along 245 km of the Madeira River, of which 118 km² were várzea forests (Cochrane et al., 2017), and nearly 200 km of which were occupied by rocky outcrops, now vanished, previously used as roosts by at least four species of bats in the area. Those rocky outcrops located in the margins and in the river Madeira previously housed unique populations of thousands of individuals of the aerial insectivorous bat species *Nyctinomops laticaudatus* (Tavares et al., 2017), and we do not know what happened to these populations.

Some plots from flooded areas had similar species compositions compared to Pre-unflood and Post-unflood plots indicating that species composition was represented in areas undisturbed by the dam. However, the effects of the dam were fast and severe in the plots located in várzea forest. Várzea forest covers approximately 400,000 km² of the Amazonia lands (Melack and Hess, 2010) and is composed by species adapted to the annual flooding pulses. Várzea forests are distinctive from *terra firme* forests in

composition and/or relative abundance of species for trees (Wittmann et al., 2004), primates (Haugaasen and Peres, 2005), medium and large size mammals (Alvarenga et al., 2018), birds (Beja et al., 2010), leaf litter frogs (Gascon, 1996), and bats (Bobrowiec et al., 2014; Pereira et al., 2009).

We found that fruit bats assemblages from the Amazonian várzeas were largely affected by the formation of the reservoir likely because assemblages of frugivores are limited by the availability of fruits, which varies with gradients as subtle as changes of elevation (Capaverde et al., 2018) and by levels of association to riparian stripes (Pereira et al., 2019). Since the vegetation close to the lowland Madeira river's margin and those associated to the várzeas were more open (Bobrowiec and Tavares, 2017) it is possible that frugivorous bats used small connecting streams and cleaner paths to travel to *terra firme* forests searching for food. This can be noted by the turnover of species composition of unflood plots between the periods preceding and posterior to the dam. Contrarily to previous studies that concluded that frugivorous bats may be less affected by anthropic changes (Bobrowiec and Gribel, 2010; Rocha et al., 2017) the várzea of Madeira river contributes uniquely to the enhancement of the regional pool of bat richness (Bobrowiec et al., 2014; Pereira et al., 2009), and the large hydroelectric of Jirau and Santo Antônio had a severe and permanent impact in these ecosystems.

The bat assemblages in Pre- and Post-dam changed in response to the construction of the dam, but these assemblages were relatively homogeneous in composition at different distances from the reservoir. This indicates that the Santo Antônio hydroelectric dam immediately changed the species compositions and guilds. Although reservoir filling affects the vegetation of the non-flooded areas near the new riverbank due to changes of the water table that increases tree mortality (Moser et al., 2019), the timing immediately after the flooding may not have accumulated sufficient

changes in the vegetation to influence many of the bats in the area. These early two years may not have been long enough for the heavier effects of habitat loss and modification upon part of the bat communities, except for the fruit bats, which have already been impacted. We believe that the flooding of the riparian zones of the *terra firme* forests may have impacted fruit bats. Species such as *C. perspicillata*, *R. pumilio* and *A. lituratus*, which correspond to 80.6% of the captured bats, decreased in abundance after the dam construction. Some taxa react immediately to these changes (Abreu et al., 2020), but some evidence points to time-lag in the response for the assemblage as a whole of more than three years to landscape modification in hydroelectric dams (Cosson et al., 1999b). A long-term monitoring study is therefore strongly recommended in this scenario.

Changes along time outside of the flooded areas did not lead to the loss of bat species in the plots. Seven species of bats (*Glossophaga longirostris*, *Lionycteris spurrelli*, *Glyphonycteris daviesi*, *G. sylvestris*, *Lampronnycteris brachyotis*, *A. concolor* and *Uroderma magnirostrum*) were not recorded in the unflooded areas after the dam, all captured in less than three plots and recorded in other parts of Amazonia (Tavares et al., 2017). On the other hand, our analyzes indicate future changes in bat assemblages because in several plots the abundance of species has been decreasing. Populations of locally rare species and those associated with várzea forests may be prone to local extinction after the continued changes in environmental conditions.

The loss of várzeas and other unique ecosystems such as the rocky outcrops without any attempt of replacement situated in the lands kept from impacts is a matter of serious concern that is replicated in other hydroelectric dams in Amazon (Fearnside, 2017; Timpe and Kaplan, 2017) and it should be planned differently for future scenarios as the Brazilian government plans to build nine large hydroelectric dams in the Amazon

(MME, 2013). Brazil has been going through a change in policy that favors dams with large reservoirs, instead of run-of-the-river dams (Fearnside, 2017). The creation of conservation units with special attention to lowland areas must be permanently incorporated as a monitoring tool and a conservation management strategy financed by energy producing companies.

Dramatic changes in the landscape as those given by large hydroelectric dams, such as the loss of várzea forests, the elevation of the water-table, and the suppression of entire ecosystems such as rocky outcrops exemplify the importance of long-term biodiversity monitoring programs. These studies need to be conducted in appropriate periods before and after the construction of the dam to assess the extent of the effects from impacts, and when equilibrium conditions are reached. Our previous study conducted prior to the filling of the dam was clear to demonstrate that frugivorous bats were vulnerable to habitat loss (Bobrowiec and Tavares, 2017), as we herein demonstrated empirically. We showed that the effects of the dam were immediate for some groups, and we can assure for the occurrence of future changes. We suggest that the Brazilian legislation should include long-term assessments in large hydroelectric dams that must include monitoring and management. Those eminent research programs need to be conducted minimally two or at least one years before the construction of the dam, one year following the flooding of the dam, and should be continued for at least 10 years. Data describing and monitoring the vegetation (composition and structure) and the variations in the water-table depth are also needed to understand how fauna responds to changes in the landscape.

Credit authorship contribution statement

Paulo E. D. Bobrowiec: Conceptualization, Formal analysis, Investigation, Resources, Data Curation, Writing - Original Draft, Writing - Review & Editing. **Carla C. Nobre:** Investigation. **Valéria C. Tavares:** Conceptualization, Investigation, Resources, Data Curation, Writing - Original Draft, Writing - Review & Editing.

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Supporting information

Table S1. List of bat species, guilds, occurrence per sampling plot and capture effort in plots that were flooded, plots that remain unflooded pre- and pos-dam construction of the Santo Antônio Hydroelectric Station, Southwest Amazon, Brazil.

Taxon	Pre-flood	Pre-unflood	Post-dam	Total	Guilds
Emballonuridae					
<i>Rhynchonycteris naso</i>	2	0	0	2	Aerial insectivore
<i>Saccopteryx bilineata</i>	1	2	1	4	Aerial insectivore
<i>Saccopteryx canescens</i>	0	0	1	1	Aerial insectivore
<i>Saccopteryx leptura</i>	4	3	16	23	Aerial insectivore
Mormoopidae					
<i>Pteronotus rubiginosus</i>	15	30	17	62	Aerial insectivore
Thyropteridae					
<i>Thyroptera discifera</i>	1	0	0	1	Aerial insectivore
<i>Thyroptera tricolor</i>	2	3	1	6	Aerial insectivore
Natalidae					
<i>Natalus macrourus</i>	0	1	0	1	Aerial insectivore
Phyllostomidae					
Desmodontinae					
<i>Desmodus rotundus</i>	1	4	4	9	Sanguinivore
<i>Diphylla ecaudata</i>	1	0	1	2	Sanguinivore
Glossophaginae					
<i>Choeroniscus minor</i>	3	0	5	8	Nectarivore
<i>Glossophaga soricina</i>	3	11	36	50	Nectarivore
<i>Glossophaga longirostris</i>	1	0	0	1	Nectarivore
<i>Hsunnycteris thomasi</i>	13	39	40	92	Nectarivore

<i>Lionycteris spurrelli</i>	1	0	0	1	Nectarivore
Phyllostominae					
<i>Chrotopterus auritus</i>	4	8	4	16	Gleaning animalivore
<i>Glyphonycteris daviesi</i>	0	1	0	1	Gleaning animalivore
<i>Glyphonycteris sylvestris</i>	0	2	0	2	Gleaning animalivore
<i>Lampronnycteris brachyotis</i>	1	4	0	5	Gleaning animalivore
<i>Lophostoma brasiliense</i>	1	6	1	8	Gleaning animalivore
<i>Lophostoma silvicolum</i>	8	78	54	140	Gleaning animalivore
<i>Micronycteris hirsuta</i>	1	2	4	7	Gleaning animalivore
<i>Micronycteris megalotis</i>	1	4	4	9	Gleaning animalivore
<i>Micronycteris microtis</i>	1	6	5	12	Gleaning animalivore
<i>Micronycteris minuta</i>	0	0	1	1	Gleaning animalivore
<i>Mimon bennettii</i>	0	1	1	2	Gleaning animalivore
<i>Gardnerycteris crenulatum</i>	1	8	13	22	Gleaning animalivore
<i>Phylloderma stenops</i>	2	9	5	16	Omnivore
<i>Phyllostomus discolor</i>	0	7	1	8	Omnivore
<i>Phyllostomus elongatus</i>	16	47	46	109	Gleaning animalivore
<i>Phyllostomus hastatus</i>	2	5	8	15	Omnivore
<i>Trachops cirrhosus</i>	12	21	18	51	Gleaning animalivore
<i>Trinycteris nicefori</i>	3	26	8	37	Gleaning animalivore
<i>Tonatia saurophila</i>	12	27	18	57	Gleaning animalivore
Carolliinae					
<i>Carollia benkeithi</i>	4	7	3	14	Frugivore
<i>Carollia brevicauda</i>	37	162	72	271	Frugivore
<i>Carollia perspicillata</i>	182	562	265	1009	Frugivore
<i>Rhinophylla fischeriae</i>	1	6	2	9	Frugivore
<i>Rhinophylla pumilio</i>	43	126	59	228	Frugivore
Stenodermatinae					
<i>Artibeus lituratus</i>	48	42	11	101	Frugivore

<i>Artibeus obscuru</i>	50	83	72	205	Frugivore
<i>Artibeus planirostris</i>	58	81	45	184	Frugivore
<i>Dermanura anderseni</i>	2	0	3	5	Frugivore
<i>Dermanura cinerea</i>	13	12	10	35	Frugivore
<i>Artibeus concolor</i>	1	0	0	1	Frugivore
<i>Dermanura gnoma</i>	11	21	12	44	Frugivore
<i>Chiroderma villosum</i>	1	1	1	3	Frugivore
<i>Mesophylla macconnelli</i>	12	15	5	32	Frugivore
<i>Platyrrhinus brachycephalus</i>	1	2	4	7	Frugivore
<i>Platyrrhinus incarum</i>	7	3	3	13	Frugivore
<i>Sturnira lilium</i>	0	6	2	8	Frugivore
<i>Sturnira tildae</i>	1	16	15	32	Frugivore
<i>Uroderma bilobatum</i>	9	18	22	49	Frugivore
<i>Uroderma magnirostrum</i>	1	3	0	4	Frugivore
<i>Vampyressa thyone</i>	0	1	3	4	Frugivore
<i>Vampyriscus bidens</i>	10	16	14	40	Frugivore
Vespertilionidae					
<i>Eptesicus</i> spp.	2	0	0	2	Aerial insectivore
<i>Myotis nigricans</i>	5	3	3	11	Aerial insectivore
<i>Myotis riparius</i>	1	2	1	4	Aerial insectivore
Captures	613	1543	940	3096	
Number of species	50	48	48	59	
Number of nights	46	130	94	270	
Samplim effort (net*hour)	2208	6240	4512	12960	

Table S2. Species richness (S), number of captures (N), and mean number of captures (\pm Standard Deviation) of bats and guilds of Phyllostomidae species at Santo Antônio hydroelectric dam area, Southwestern Amazonia, Brazil.

Assemblage variables	Pre-flood			Pre-unflood			Post-dam		
	S	N	Mean \pm SD	S	N	Mean \pm SD	S	N	Mean \pm SD
All species	41	580	48.33 \pm 37.17	42	1501	44.15 \pm 17.41	41	900	36.00 \pm 17.19
Frugivores	19	492	41.00 \pm 34.65	23	1185	34.85 \pm 16.98	21	623	24.92 \pm 15.07
Animalivores	16	67	5.58 \pm 3.70	19	266	7.82 \pm 4.63	18	196	7.84 \pm 4.60
Nectarivores	5	21	1.75 \pm 1.42	2	50	1.47 \pm 1.73	3	81	3.24 \pm 6.92

Capítulo 3

**Taxonomic and functional responses of bats to habitat flooding by a
mega hydroelectric dam in the Amazonia**

**Taxonomic and functional responses of bats to habitat flooding by a mega
hydroelectric dam in the Amazonia**

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Abstract

Hydroelectric dams are among the main anthropogenic impacts in natural environments in the tropics. Damming interrupts the continuity of the river and causes the flooding of adjacent terrestrial ecosystems. Despite the negative effects on terrestrial and aquatic biodiversity and ecosystems, studies of effects of hydroelectric dams on species response to the reservoir flooding are scarce. Here, we employed a design that integrated bat data sampled in areas that would be flooded and not flooded before the construction of a mega hydroelectric dam in the southwest of the Brazilian Amazon with data collected in non-flooded areas after the dam was filled. We evaluated the effects of river damming on the taxonomic and functional diversity of Phyllostomidae bats. We found that flooding of the lowlands increased significantly the taxonomic and functional α -diversity, as well as species- and community-level functional uniqueness of the bat assemblages, reflecting a reduction in the abundance of functional redundant species. According to functional trait composition, we found strong evidence for a shift in functional traits after river damming, with an increase in the frequency of animalivorous bats and a reduction in phytophages. Pre- and post-dam temporal differences show that functional β -diversity was determined mainly by replacement of traits weighted by species abundance than by the loss or gain of traits. Functional traits linked to the trophic level and diet proved to be powerful indicators of the bat community's responses to temporal changes caused by run-of-the-river dams that degrade mainly lowland, riparian and várzea forests. New dams are planned to be built in the Amazon with the potential to flood vast areas of várzea forests. To mitigate such losses, it is necessary that energy companies preserve the várzea and riparian forests in order to guarantee the ecological functions performed by phytophagous bats in the ecosystem.

Keywords: functional diversity, functional traits; functional uniqueness, river damming, run-of-river reservoir, temporal dynamics.

INTRODUCTION

Hydropower development is among the main anthropogenic impacts in natural environments, with well-documented negative effects on terrestrial and aquatic biodiversity and ecosystems (e.g., Gibson et al., 2013; Palmeirim et al., 2017; Anderson et al., 2018; Benchimol & Peres, 2020). These effects are associated with uniformly hostile open-water matrix that imposes a barrier to species' mobility and limits the use of resources in fragments (Farneda et al., 2020a; Benchimol & Peres, 2020).

Hydropower corresponds ~80% of electricity in the Brazil (Zarfl et al., 2015), and 334 new hydroelectric dams are planned to be built in the Amazon (Winemiller et al., 2016). Although reported by government agencies as clean energy, until 2012 has flooded 1.1 million ha of forest in Brazilian Amazon (Forsberg et al., 2017), resulting in significant impacts on ecological services and ecosystem functioning through the extinction and replacement of species.

Most of the existing knowledge about the impacts of hydroelectric dams comes from storage reservoirs (Baumgartner et al., 2020). These reservoirs type retain large amounts of water, causing an interruption of the natural flood level regime (Baumgartner et al., 2020). Storage reservoirs creates several islands of different sizes and isolation degree (Benchimol & Peres, 2020), and its operation is quite usual worldwide (International Energy Agency, 2012). Conversely, run-of-river reservoirs have smaller lakes with limited water storage (Almeida et al., 2019). However, there are few studies of how run-of-river dam can affect the biota, especially in the tropical region where this type of reservoir is increasingly common. Thus, new hydroelectric dams need new perspectives for environmental impact studies, addressing multiple dimensions of diversity to better understand the effects of the river damming on communities.

Traditionally, ecologists have assessed the effects of the environmental disturbance and its intensity on taxonomic dimension such as species composition, richness, uniformity, or population abundance (Mackey & Currie, 2001). However, these descriptors consider the species to be independent units of each other, ignoring the functional similarities between them (Cadotte et al., 2011; Gagic et al., 2015). The different responses of species to human-made disturbances depend on their morphological, physiological and behavioral characteristics (McGill et al., 2006; Mouillot et al., 2013; Gagic et al., 2015; Weiss & Ray, 2019). Thus, studies based on functional traits offer a very promising alternative approach compared to a simple species count (McGill et al., 2006; Mouillot et al., 2013; Gagic et al., 2015; Ricotta et al., 2016). Functional traits can be directly affected by the environmental disturbance, even in events where there is no change in the total number of species or composition (Flynn et al., 2009; Cadotte et al., 2011; Beiroz et al., 2018).

Bats have been a good model group in studies that assess the effects of anthropogenic landscape changes on functional diversity (e.g., García-Morales et al., 2016; Gonçalves et al., 2017; Pereira et al., 2018; Farneda et al., 2018; 2020a; Carvalho et al., 2020). Phyllostomidae bats form species-rich assemblies, highly diverse in functional traits that promote a variety of functions in ecosystems. Ecosystem services can be represented by functions related to seed dispersal, plant pollination and insect population control (Farneda et al., 2015; 2018). Certain functional characteristics of bats, such as trophic level and body mass, have been identified as good indicators of environmental disturbance by filtering characteristics that allow smaller and phytophagous species to survive post disturbance (Farneda et al., 2015; 2018; 2020b). Our knowledge of the effects of hydropower development on the functional diversity of

bats is built on insularized landscape generated by storage reservoirs (Meyer et al., 2008; Farneda et al., 2020b).

Here, we employed a design that integrated bat data collected in areas that would be flooded and not flooded before and after the construction of the Santo Antônio Hydroelectric Plant (Southwest of the Brazilian Amazon) with data collected in non-flooded areas after the dam was filled. With this design, we evaluated the effects of river damming on the taxonomic and functional diversity of Phyllostomidae bats. Additionally, we investigate how bat functional traits were affected by river damming and how the flooding of lower elevation areas contributed to changes in functional β -diversity. Our general hypothesis was that functional and taxonomic α diversity and functional uniqueness at the communities and species-level decrease after the river damming as a result of assemblages functionally similar and simplified. We predicted that after dam filling: 1) functional and taxonomic α -diversity and community-level functional uniqueness will decrease related to negative species responses to environmental change; 2) species-level functional uniqueness would increase in phytophagous species, because of its positive association with the lowlands that will be flooded (Bobrowiec et al., 2014); 3) functional traits associated to phytophagous species will be negatively affected because these species are more abundant in lowland forests (Capaverde et al., 2018); 4) temporal differences in functional β -diversity will be determined mainly by the component replacement of functional traits than the gain of traits of species.

MATERIAL AND METHODS

Study area

We captured bats in the influence area of the Santo Antônio Hydroelectric reservoir (08°48'S; 63°57'W; Figure 1), which was built on the upper Madeira River, located to ~5 km upstream from the city of Porto Velho, Rondônia State, southern Brazilian Amazonia (Figure 1). This hydroelectric started operation in March 2012, generating 3150 MW. The dam is a run-of-river project with bulb-type turbines that allow smaller reservoirs than traditional storage dams. Even so, the reservoir reached 70 m above the river's maximum natural flood level. The Madeira River originates in the Andes and while it receives nutrient-rich waters on the left margin, the tributaries on the right-side carry nutrient-poor waters from the western Amazon plateau (Moser et al., 2014). The vegetation of the region is characterized by dense tropical forest, including *terra firme* upland forests, várzea forest on the riverbanks and patches of *campinarana* and *campina* (Moser et al., 2014). The climate is classified as tropical humid hyperthermic (Cochrane & Cochrane, 2010). The average annual precipitation varies from 1700 to 2000 mm (Sombroek, 2001) with rainy season between November and April and dry season between June and September (Santos et al., 2020).

Bat sampling

We captured bats in seven sampling modules with seven plots in each, totaling 49 sample plots (Figure 1). Of these, six modules were located on the Madeira River and one on the Jaci-Paraná River (Figure 1). The plots were distributed 50, 500, 1000, 2000, 3000, 4000, and 5000 m away from the riverbank on a trail positioned perpendicular to the riverbank (Figure 1). The sample design followed the RAPELD method (RAP = rapid survey of biological communities; PELD = long-term ecological research) for standardized surveys of fauna and flora in the Amazon (Magnusson et al., 2005). The

RAPELD system consists of plots of 250 m long and 40 m wide that follow the topographic contour to minimize internal heterogeneity in soil properties and drainage.

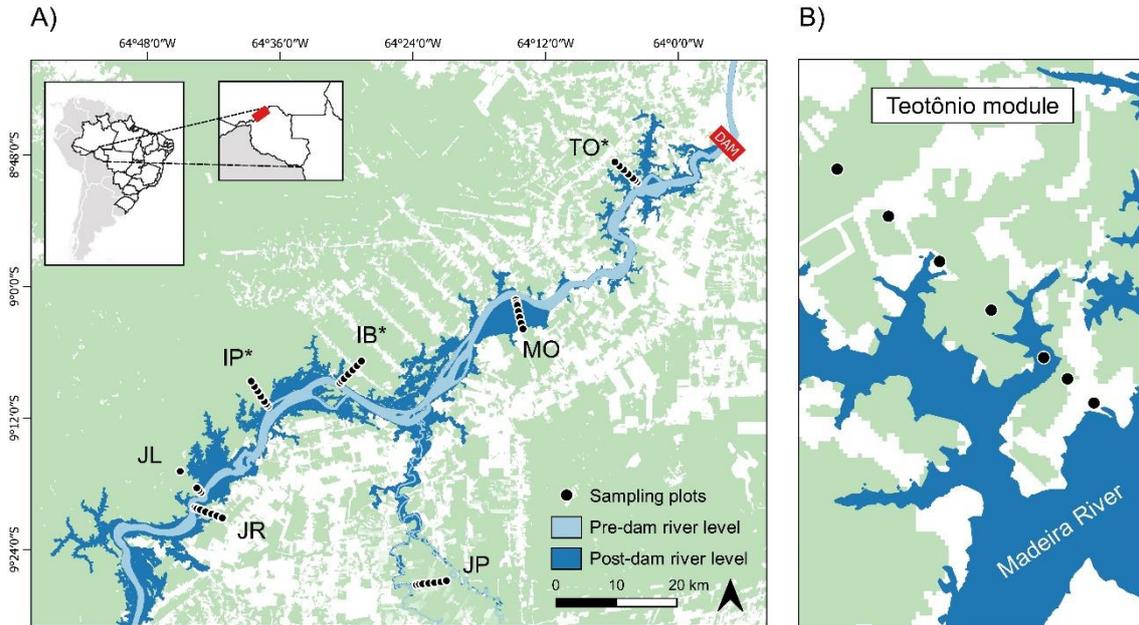


Figure 1. Map of the study area downstream of the Santo Antônio Hydroelectric Station in the upper Rio Madeira, Southwestern Brazilian Amazonia. A) Light blue indicates the area occupied by the original river before the dam construction, the dark blue indicates the extent of the reservoir after the full dam flooding, and the light green show mature forest. B) Detail of the plots distribution in the Teotônio module in relation to the post-dam Madeira river level. * indicates the modules that were sampled after the river damming. The modules are: TO = Teotônio, MO = Morrinhos, IB = Ilha dos Búfalos, IP = Ilha das Pedras, JL = Jirau Left Bank, JR = Jirau Right Bank, JC = Jaci.

We sampled the plots in two stages (Figure 1): Pre-dam stage (June 2010 to September 2011) – plots sampled before the dam construction, of which 12 plots were located in areas that would be flooded by the reservoir (named as pre-flooded plots hereinafter) and 34 plots that would remain dry (pre-unflooded plots); Post-dam stage

(June 2013 to June 2014) – 25 pre-unflooded plots resampled after flooding of the reservoir (post-dam).

We captured bats using eight ground level mist-nets (12 x 2.5 m, 36 mm mesh, Ecotone Inc, Poland). The mist-nets were opened between 18:00 and 00:00 and inspected at 15-minute intervals. Each plot was visited for 3-4 non-consecutive nights in both phases of the dam filling, totaling 290 sampling nights (13920 mnh; 1 mist-net hour, mnh, equals one 12-m net open for 1 h; Table S1). Species were identified following Gardner (2007), Charles-Dominique et al. (2001) and Lim and Engstrom (2001), and taxonomy follows Gardner (2007) with modifications by Garbino et al. (2020).

Species traits

We selected five functional traits (Table 1 and S2) of Phyllostomidae bats that reflect different foraging behaviors, diets and ecological functions that bats perform, such as seed dispersal, pollination and control of animal populations. These traits have been used to predict the response of bats to anthropic environmental changes (Castillo-Figueroa & Pérez-Torres, 2021).

Body mass – Body mass (g) has been widely used in analyzes based on functional traits of bats (Farneda et al., 2015; Castillo-Figueroa & Pérez-Torres, 2021). Species with larger body size tend to have smaller populations and have been identified as a good indicator of species vulnerability (Farneda et al., 2015; 2020a). Body mass was obtained during fieldwork.

Wing morphology – Separated into its two components: relative wing loading and aspect ratio (Norberg & Rayner, 1987). Wings with higher aspect ratio and relative wing loading values are suitable for high-speed flights, little maneuverability in obstructed habitats, but advantageous for foraging in open spaces (Marinello & Bernard,

2014; Norberg & Rayner, 1987). Relative wing loading (RWL) and aspect ratio (AR) of 41 species were obtained from Marinello & Bernard (2014) and Farneda et al. (2015). For the other seven species, we estimate the relative wing loading and the aspect ratio using the equation of linear regressions of these traits with body mass ($RWL = -0.069 \times (\text{body mass}) + 39.5$; $AR = 0.0035 \times (\text{body mass}) + 6.13$) (Table S2).

Trophic level – The trophic level was based on two main food categories: phytophagous (bats that consume fruits, seeds, nectar, leaves and flowers) and animalivores (bats that eat insects, small rodents, frogs and blood).

Diet – The diet was based on the main food item eaten by bats and represents a more detailed scale of the trophic level. The bat diet was classified as frugivore, nectarivore, gleaning insectivore, carnivore, omnivore and sanguinivore.

Table 1. List and description of the functional traits used in taxonomic and functional analyses. Table S2 shows the values of each functional trait.

Trait	Scale	Description	Source
Body mass	Continuous	Average body mass of each species (excluding pregnant females and juveniles)	Our capture data
Wing morphology	Continuous	Relative wing loading and aspect ratio	Marinello & Bernard (2014); Farneda et al. (2015)
Trophic level	Categorical	Phytophagous and animalivores	Our capture data
Diet	Categorical	Based on the main food item consumed by each species (i.e., frugivores, nectarivores, gleaning insectivores, carnivores, omnivores and sanguinivores)	Our capture data

Data analysis

We calculated the taxonomic and functional α -diversity and the community-level functional uniqueness following the methodological approach proposed by Ricotta et al. (2016), which consists of using Simpson index D for taxonomic diversity and Rao's

index Q for functional diversity. Simpson D considers all species functionally similar, but taxonomically different, and the Rao's Q takes the species dissimilarities into account for the calculation of functional diversity. Based on these two indices, we were further able to estimate the functional uniqueness U, which consists of the ratio between the two diversity indices: $U = Q / D$. This approach has been widely applied to compare taxonomic and functional diversity in recent ecological studies on a variety of taxa (e.g., Doxa et al., 2020; Farneda et al., 2018; 2020). Both indexes take into account the relative species abundance and are therefore good indicators of early warning of disturbances as they do not only need species extinctions to change (Mouillot et al., 2013). We compared each index (D, Q, U) between the pre- and post-dam plots and also between the three categories of plots (pre-unflooded, pre-flooded, post-dam) using a Permutational Analysis of Variance (PERMANOVA) from package *vegan* ('adonis' function, Oksanen et al., 2020) with Euclidian distance and 999 permutations. We assessed pairwise comparison among pre-unflooded, pre-flooded, and post-dam with the 'pairwise.adonis' function from *pairwiseAdonis* package (Arbizu, 2017). P-values were adjusted with a Bonferroni correction.

To evaluate the relevance of each species in a certain function in relation to the river damming, we calculated the species-level functional uniqueness \bar{K}_i , which is also based on the relative abundance of the species. \bar{K}_i varies between 0 and 1 and high values are associated with rare species linked to less common functional traits in the community. We compared the \bar{K}_i values between animalivorous and phytophagous species before and after the dam using permutational *t* tests with 999 randomizations in the *RVAideMemoire* package (Hervé, 2020). We also compared the \bar{K}_i values between pre- and post-dam periods for phytophagous and animalivorous bats using a permutational paired *t*-tests with 9999 randomizations in the *broman* package (Broman,

2020). We calculated the Q, D, U and \bar{K}_1 indices using the 'uniqueness' function of the *adiv* package (Pavoine, 2020), based on Gower's functional dissimilarity that works with categorical and quantitative traits in the *gawdis* package (de Bello et al., 2021).

To understand how each functional trait of the assemblages responded to the river damming, we calculated the community-weighted mean trait values (CWM; Lavorel et al., 2008). The CWM uses the average value of each trait weighted by the abundance of each species (Violle et al., 2007). We calculated the CWM traits using the 'functcomp' function of the *FD* package (Laliberté et al., 2014). For each functional trait, comparisons between plots of the three categories (pre-flooded, pre-unflooded and post-dam) and two categories (pre- and post-dam) were performed using (PERMANOVA tests, 'adonis' and 'pairwise.adonis' functions) based on Euclidean dissimilarity and 999 permutations as previously described.

Temporal changes in the functional structure of communities before and after the disturbance can be assessed by functional β -diversity (Mouillot et al., 2013). Total functional β -diversity (β_{total}) is represented by components replacement (turnover of species functional traits, β_{repl}) and difference in species richness (loss or gain of traits, β_{rich}). We use the Cardoso et al. (2015) approach that predicts that β_{total} corresponds to the sum of the replacement component with the richness difference component ($\beta_{total} = \beta_{repl} + \beta_{rich}$). The β_{total} and its components were calculated using the 'beta' function of the *BAT* package (Cardoso et al., 2020), based on a site \times species matrix with species occurrence data and Jaccard dissimilarity, a tree of the functional traits and rarefaction of species with 1000 runs. The functional tree was based on a matrix of species \times traits, submitted to a hierarchical clustering procedure using UPGMA with Gower distance (Cardoso et al., 2015). We used a rarefaction for 900 individuals that corresponds to the lowest abundance of bats sampled in the post-dam period. The

functional β -diversity of bat assemblages was calculated between the pre- and post-dam periods with all plots (pre-dam \times post-dam) and also between pre-unflooded plots and post-dam (without pre-flooded plots).

RESULTS

We captured 2981 bats belonging to 48 species (Table S1). Post-dam plots had higher taxonomic diversity (D), functional diversity (Q) and functional uniqueness (U) than pre-dam plots (pre-unflooded + pre-flooded) (Table 2; Figure 2). When we evaluate the contribution of the pre-flooded and pre-unflooded plots separately, post-dam plots had higher taxonomic diversity (D) and functional diversity (Q) than pre-unflooded plots, but not in relation to pre-flooded plots (Table S3; Figure S1).

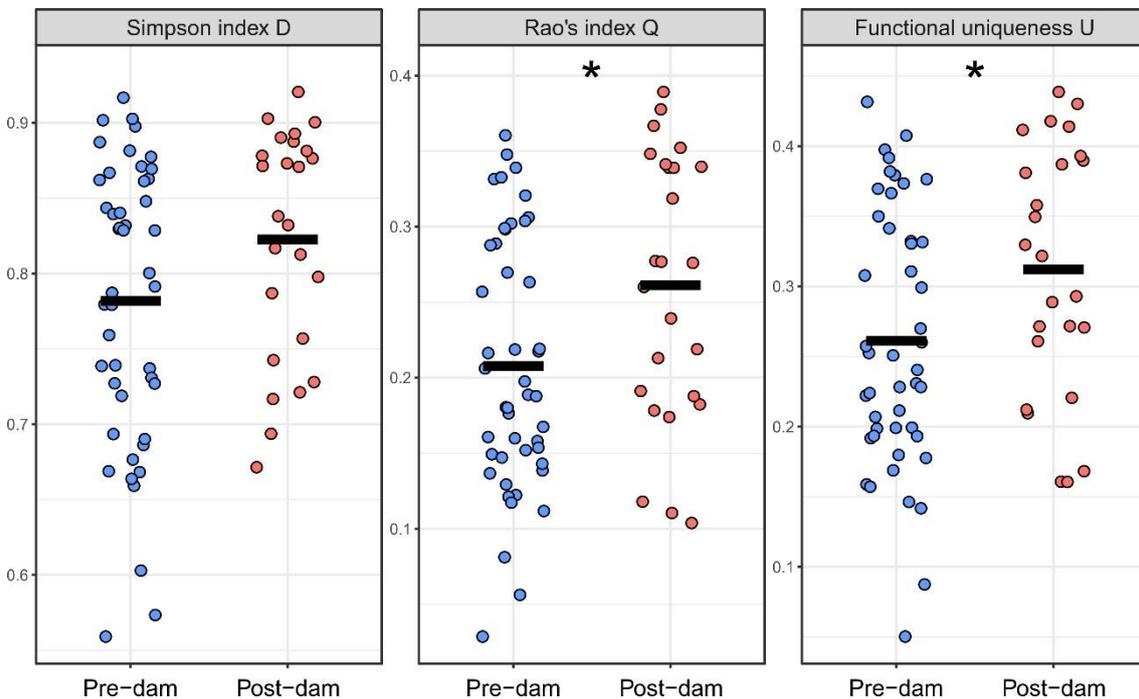


Figure 2. Taxonomic diversity (Simpson index D), functional diversity (Rao's index Q), and functional uniqueness U of the bat assemblages sampled pre-dam (blue circles) and post-dam (red circles) at Santo Antonio Hydroelectric Station, Southwestern Amazonia, Brazil. Vertical bars represent indices means. * $P < 0.06$.

Table 2. Results of the PERMANOVA tests for taxonomic (D) and functional (Q e U) diversity and for functional traits of the community-weighted mean (CWM) analysis. Comparisons were made between pre- and post-dam with all data set, and between pre-unflooded and post-dam data set (excluding pre-flooded data). Significant differences are in bold ($P < 0.06$).

Indices	Pre-dam × Post-dam		Pre-flooded × Pre-unflooded × Post-dam	
	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Simpson D	1.91	0.050	3.83	0.025
Rao's Q	2.37	0.021	2.89	0.056
Functional Uniqueness U	2.14	0.035	2.25	0.110
Traits	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Body mass	0.16	0.86	1.17	0.31
Relative wing load	-1.64	0.11	2.51	0.085
Aspect ratio	-0.09	0.98	2.27	0.11
Trophic level:				
phytophagae	-1.99	0.053	-2.42	0.11
animalivore	1.99	0.050	2.42	0.97
Diet:				
frugivore	-3.22	0.003	-5.39	0.005
nectarivore	0.71	0.35	0.88	0.43
gleaning insectivore	1.81	0.083	3.36	0.044
carnivore	0.94	0.35	0.88	0.42
omnivore	1.20	0.24	0.72	0.49
sanguinivore	1.57	0.14	1.26	0.29

Some bat species showed relevant changes in species-level functional uniqueness (\bar{K}_i). For example, while \bar{K}_i of seven species (14.5% of all species) of animalivorous bats (e.g., *Diphylla ecaudata*, *Chrotopterus auritus*, *Micronycteris megalotis*) decreased with dam construction, for 15 species (31.3%) of phytophagous bats (e.g., *Rhinophylla fischeriae*, *Platyrrhinus brachycephalus*, *Uroderma bilobatum*) \bar{K}_i increased (Figure 3). Mean functional singularity of all bat species increase following river damming ($t = -2.37$; $P = 0.019$), mainly for phytophagous bats ($t = -3.13$; $P = 0.007$), but not in animalivorous ($t = -0.12$; $P = 0.86$). Species-level functional

singularity of animalivorous bats during pre- ($t = 8.01$; $P < 0.0001$) and post-dam ($t = 8.23$; $P < 0.0001$) were on average 1.9 and 1.7 times greater than that of phytophagous bats, respectively (Figure S2).

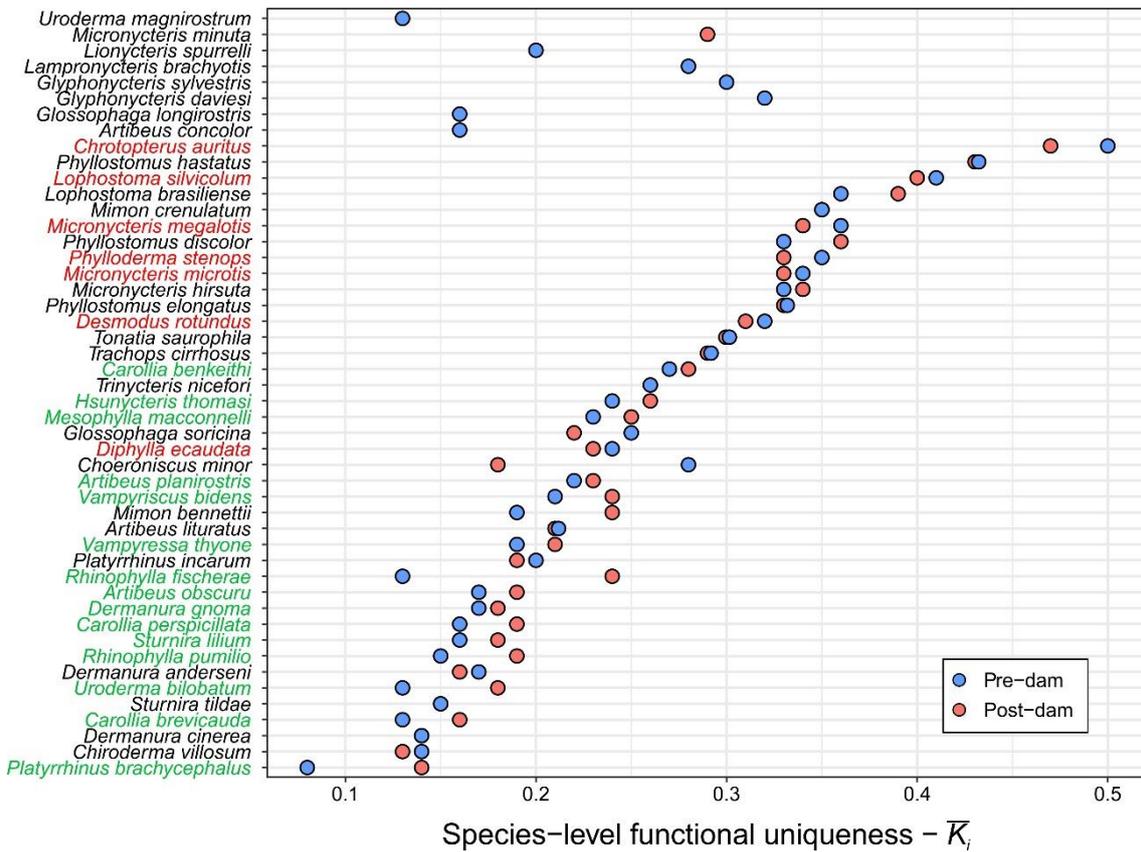


Figure 3. Species-level functional uniqueness of the bat species sampled pre-dam (blue circles) and post-dam (red circles) at Santo Antonio Hydroelectric Station, Southwestern Amazonia, Brazil. Species names in green represent phytophagous species with increased functional uniqueness during post-dam, names in red represent animalivorous species with decreased functional uniqueness post-dam, and names in black represent species with no expressive change in functional uniqueness.

Changes in functional trait composition were associated to the effects of river damming. The traits that revealed significant changes in CWM trait values after dam

construction were trophic level and diet (Table 2 and S3). The CWM trait values of the animalivorous species increased significantly ($P = 0.05$) after dam construction, while phytophagous bats ($P = 0.053$), represented mainly by the frugivores ($P = 0.003$), decreased (Table 2; Figure 4). Frugivorous bats were less frequent ($P = 0.003$) in the post-dam plots compared to pre-unflooded and flooded plots (Table S3; Figure S3). Animalivorous bats were more frequent in dry pre- and post-dam plots compared to pre-flooded plots (Table S3; Figure S3).

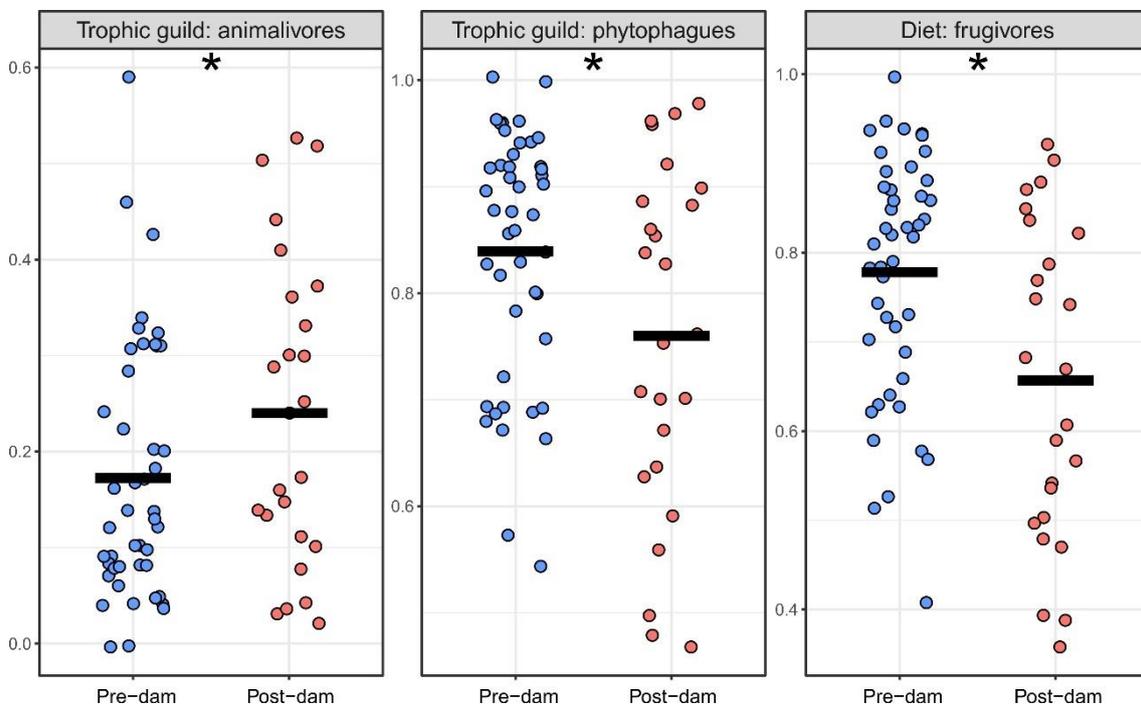


Figure 4. Community-weighted mean (CWM) trait values for statistically significant functional traits: Trophic guild: animalivores and phytophagous, and Diet: frugivores. Bat assemblages were sampled during pre-dam (blue circles) and post-dam (red circles) at Santo Antonio Hydroelectric Station, Southwestern Amazonia, Brazil. Vertical bars represent means CWM trait values. * $P < 0.06$.

The differences in functional β_{total} (0.089) between pre- and post-dam bat assemblages was more explained by the replacement of species traits ($\beta_{repl} = 0.067$;

75.3% of the β_{total}) than by the loss or gain of traits ($\beta_{rich} = 0.017$; 19.1%) (Figure 5).

When the pre-flooded plots were removed from the analysis, β_{rich} presented a slight increase (Figure 5).

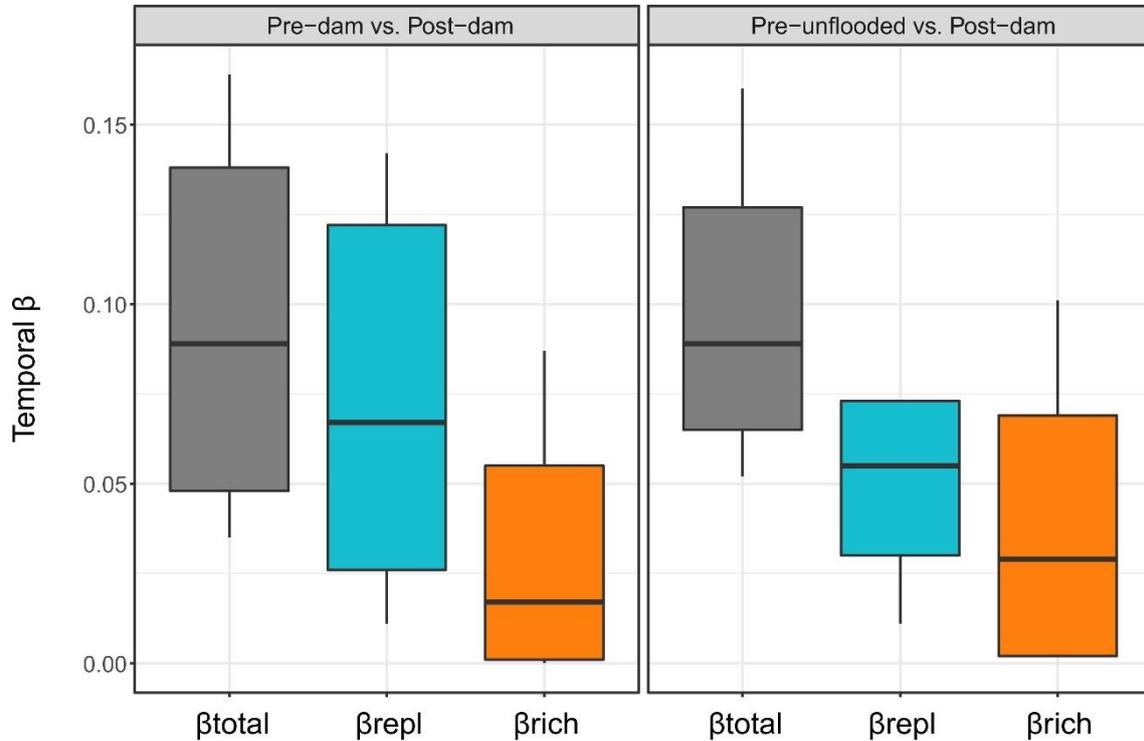


Figure 5. Results of the rarefaction procedure for components of bat functional β diversity between pre- and post-dam with all data set (left boxplots) and between pre-unflooded and post-dam data set (excluding pre-flooded data; right boxplots) at Santo Antonio Hydroelectric Station, Southwestern Amazonia, Brazil. β_{total} functional diversity (grey) was partitioned in the components β_{repl} (β diversity due to replacement of species functional traits; blue) and β_{rich} (β diversity due to loss or gain of traits; orange). Values represent means (horizontal lines) \pm 95% confidence levels (colored bars) and maximum and minimum (vertical lines).

DISCUSSION

Hydroelectric dams have become one of main drivers of changes in tropical biota (Winemiller et al., 2016; Jones et al., 2016). Identifying the functional traits that explain the species' responses to river damming is important to choose management practices that restore ecosystem functions (Spasojevic et al., 2018). Contrary our expectations, flooding of the lowlands increased significantly the taxonomic and functional α -diversity and functional uniqueness of the bat assemblages. We found strong evidence for a shift in functional traits after river damming, with an increase in the frequency of animalivorous bats and a reduction in phytophagues. Our results of functional β -diversity show that β_{total} results from functional β_{repl} - substitution of traits weighted by the species abundance - and not by the loss or gain of traits.

In recent and extensive environmental disturbances, the species need to adapt to new conditions until the equilibrium is found (Rocha et al., 2017, Dayrell et al., 2021). The increase functional α -diversity and functional uniqueness is possibly a result of the dispersion of different species across the remaining landscape after loss of lowland areas by river damming that altered the relative abundance of assemblages. Indices of functional diversity and uniqueness are sensitive to species abundance (de Bello et al., 2007). Changes in species abundance reflects the weight that a functional trait incorporates or removes into the community compared to the original community (Ricotta et al., 2016). In our study area, D, Q and U increased in magnitude due to the reduction in the abundance of functional redundant species. An increase in functional diversity after human-induced disorders has also been observed for ants (Zhao et al., 2019), birds (Ding et al., 2013), fish (Stegmann et al., 2019), and mammals (Bovendorp et al., 2018; Sancha et al., 2019), including bats (Farneda et al., 2018; Carvalho et al., 2020).

At the Santo Antônio dam, the functional uniqueness of the species (\bar{K}_l) increased in the post-dam, which may have contributed to the increase in functional uniqueness U . Increase in \bar{K}_l was driven by several species of phytophagous bats, mainly frugivores, that declined in abundance (e.g., *Rhinophylla pumilio*, *Vampyriscus bidens*, *Carollia perspicillata*, *Uroderma bilobatum*). Functional uniqueness in animalivorous bats did not change, but remained greater than in phytophagous. Assemblages of the post-dam period composed with a greater abundance of frugivorous species less redundant and animalivorous bats may have generated a particular combination of unique traits that increase functional uniqueness. More unique assemblages after human disturbance are worrying as ecosystems can lose essential functions if other species with similar traits are not incorporated in the future (Biggs et al., 2020).

Our results from the CWM analyzes revealed that phytophagous bats, mainly frugivores, were negatively affected by the construction of the dam, while species of animalivores responded positively. Several studies have shown that frugivorous bats benefit from converting the original undisturbed forest to secondary vegetation (Bobrowiec & Gribel, 2010; Rocha et al., 2017). However, in the context of permanent loss of várzea and riparian forests, without replacement by other vegetation type, frugivorous bats are the most vulnerable. The areas flooded by the dam were mainly várzea and riparian forests (Santos et al., 2020). *Terra firme* upland forests, várzea and riparian forests exhibit different bat assemblages, influenced mainly by the seasonal flooding of the várzea and water-table level (Pereira et al., 2009; Bobrowiec et al., 2014; Pereira et al., 2019). Frugivorous bats are more abundant in várzea and riparian zones (Pereira et al., 2009; Bobrowiec et al., 2014, Capaverde et al., 2018). The Jirau/Santo Antônio hydroelectric complex flooded 800 km² of lowland forests along 245 km of the

Madeira River, of which 118 km² were várzea forests (Cochrane et al., 2017). With the construction of the dam, lowland frugivorous species may have dispersed following the Madeira River channel or smaller streams (Zarazúa-Carbajal et al., 2017; Pereira et al., 2019). The role of seasonally flooded forests (*várzea* and *igapó*) in the functional diversity of bat assemblages is still poorly understood. The loss of várzea forests can damage important ecological functions that frugivorous bats play, such as the gene flow of plants via seed dispersal and pollination.

On the other hand, the CWM results showed that animalivorous bats were positively affected by the river damming. Animalivorous bats, represented mainly by carnivores, insectivorous gleanings and omnivores, are dependent on mature forest and are sensitive to environmental disturbances in response to scarcity of food and roost (Klingbeil & Willig, 2009; Farneda et al., 2015; Gonçalves et al., 2017). Areas that remained unflooded did not change the environmental conditions required by bats with these traits, at least until the two years after the dam was completed. Therefore, the integrity of the remaining forests over time is essential to mitigate the harmful effects of the river damming (Benchimol & Peres, 2020).

Our findings regarding β -diversity suggest that species replacement with similar function is the most important component of temporal functional β_{total} . The dominance of functional β_{repl} is expected for forests with less several anthropogenic disturbances (Farneda et al., 2018; Carvalho et al., 2020). At the Santo Antônio dam, the remaining vegetation still has the similar structural complexity as the pre-dam period. However, the loss of várzea and riparian forests increased the influence of functional β_{rich} (and inversely decreased β_{repl}). This indicates that várzea and riparian forests increase the taxonomic and functional diversity of ecosystems (Pereira et al., 2009; Bobrowiec et al., 2014) because they harbor species with functions that are not common in unflooded

terra firme forests. The loss of species with certain functions could have important implications for the ecosystem preservation (Leitão et al., 2016).

The Santo Antônio dam changed the taxonomic and functional α -diversity and the functional uniqueness of bat assemblages in a very short time. The two years of dam reservoir flooding may not have been long enough to accumulate changes in vegetation, affected by the rise in the water table level in the areas close to the new banks of the Madeira River and streams. Evidence indicates that changes in taxonomic diversity have not yet stopped in the region, as observed in anurans (Dayrell et al., 2021). The abundance of frugivorous species in several plots has decreased (Bobrowiec et al. in press). This can increase the functional uniqueness of the assemblages and increase the contribution of functional β rich if rare species are prone to local extinction over time. Functionally unique ecosystems are less resilient to environmental changes (Díaz & Cabido, 2001; Bovendorp et al., 2018; Biggs et al., 2020). Continuous monitoring of projects with large environmental impacts such as hydroelectric dams is desired to understand the direction of changes in functional and taxonomic diversity and to estimate when the assemblies reach equilibrium (Souza & Fernandes, 2021; Dayrell et al., 2021).

Conservation implications

Our results showed that the river damming by a run-of-river hydroelectric quickly changed the taxonomic and functional diversity of the Phyllostomidae bat assemblages. This change was driven by the replacement of traits than by the loss or gain of traits. Functional traits linked to the trophic level and diet proved to be powerful indicators of the bat community's responses to temporal changes caused by run-of-the-river dams that degrade mainly lowland, riparian and várzea forests. Therefore, studies that consider

functional diversity can be promising in identifying ecological characteristics of communities that may be more prone to temporal changes in the human-modified landscapes (Brandl et al., 2016; Farneda et al., 2018).

Run-of-river hydroelectrics, as assessed here, negatively affect phytophagous bats by flooding várzea forests and riparian zones. To mitigate such losses is necessary to prevent loss of várzea forests by river damming (Assahira et al., 2017; Forsberg et al. 2017, Santos et al., 2020; Schöngart et al., 2021). Preserving várzea and riparian forests is essential to ensure ecological functions performed by phytophagous bats (frugivores and nectarivores) in the ecosystem. New dams are planned to be built in the Amazon with the potential to flood vast areas of várzea forests (Lees et al., 2016; Forsberg et al., 2017). For these reasons, we emphasize the importance of creating a category of protected area for hydroelectric development, including várzea forests, and that the energy companies are responsible for the protection of these reserves.

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Supplementary information

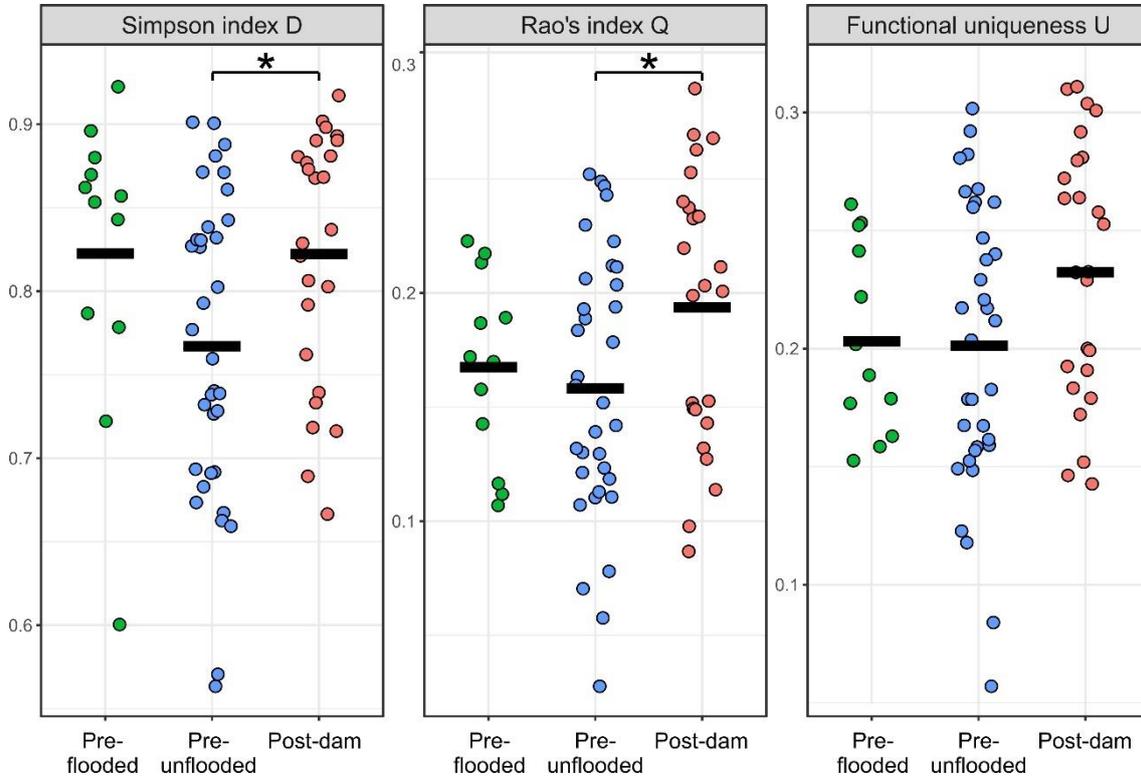


Figure S1. Taxonomic diversity (Simpson index D), functional diversity (Rao's index Q), and functional uniqueness U of the bat assemblages sampled in the pre-flooded plots (green circles), pre-unflooded plots (blue circles), and post-dam plots (red circles) at Santo Antonio Hydroelectric Station, Southwestern Amazonia, Brazil. Vertical bars represent indices means. * $P < 0.06$.

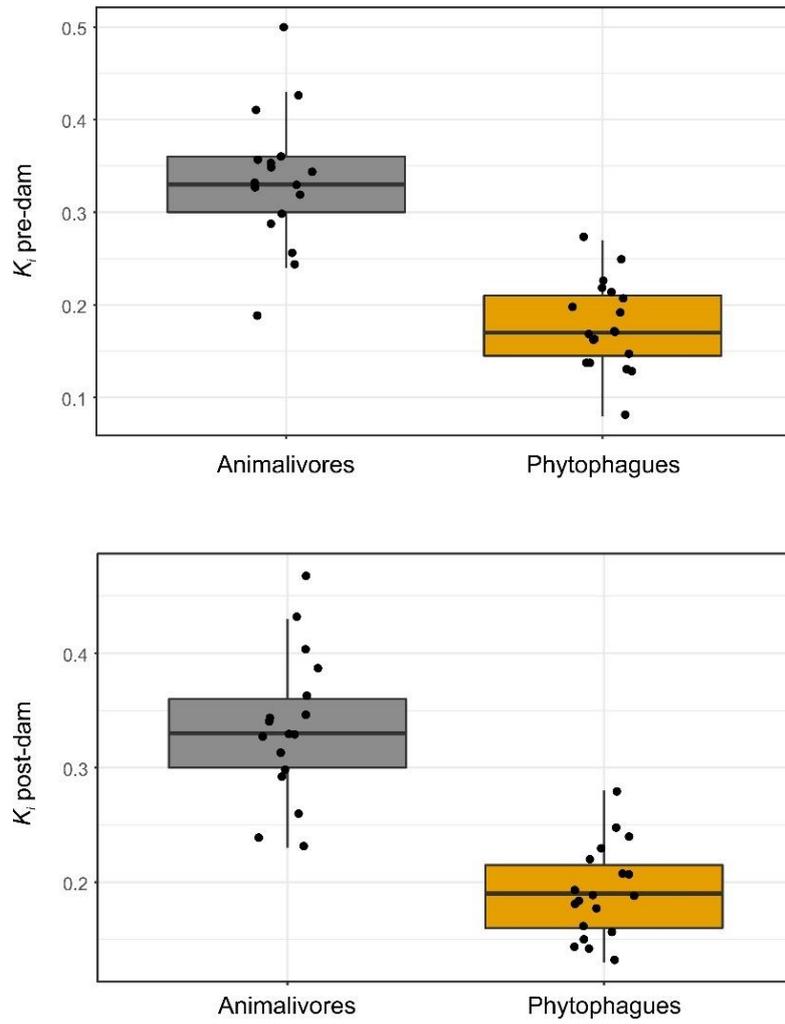


Figure S2. Comparing boxplot of the species-level functional uniqueness between animalivorous and phytophagous bat species sampled pre-dam and post-dam at Santo Antonio Hydroelectric Station.

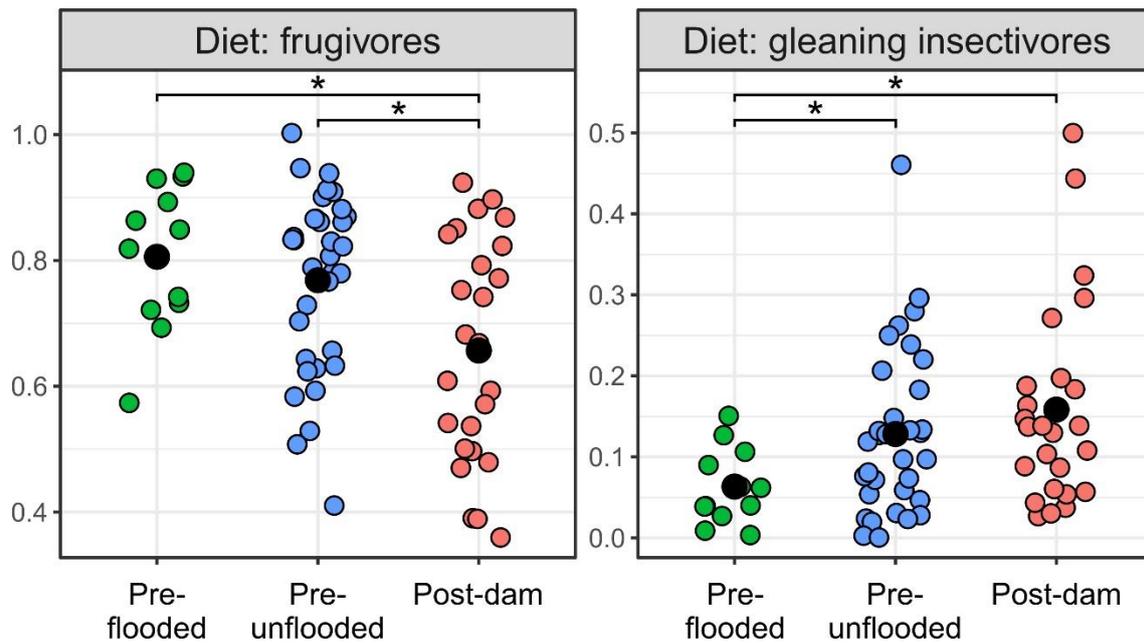


Figure S3. Community-weighted mean (CWM) trait values for statistically significant functional traits: Diet: frugivores and Diet: gleaning insectivores. Bat assemblages were sampled in the pre-flooded plots (green circles), pre-unflooded plots (blue circles), and post-dam plots (red circles) at Santo Antonio Hydroelectric Station, Southwestern Amazonia, Brazil. Vertical bars represent means CWM trait values. * $P < 0.06$.

Table S1. List of bat species captured in plots that were flooded (pre-flooded), plots that remain unflooded pre- and pos-dam construction of the Santo Antônio Hydroelectric Station, Southwest Amazon, Brazil.

Taxon	Pre-flooded	Pre-unflooded	Post-dam	Total
Desmodontinae				
<i>Desmodus rotundus</i>	0	5	4	9
<i>Diphylla ecaudata</i>	1	0	1	2
Glossophaginae				
<i>Choeroniscus minor</i>	1	2	5	8
<i>Glossophaga soricina</i>	3	13	36	52
<i>Glossophaga longirostris</i>	1	0	0	1
<i>Lonchophylla thomasi</i>	17	43	40	100
<i>Lionycteris spurrelli</i>	1	0	0	1
Phyllostominae				
<i>Chrotopterus auritus</i>	2	9	4	15
<i>Glyphonycteris daviesi</i>	0	1	0	1
<i>Glyphonycteris sylvestris</i>	0	4	0	4
<i>Lampronnycteris brachyotis</i>	2	3	0	5
<i>Lophostoma brasiliense</i>	1	6	1	8
<i>Lophostoma silvicolum</i>	5	90	54	149
<i>Micronycteris hirsuta</i>	0	3	4	7
<i>Micronycteris megalotis</i>	1	4	4	9
<i>Micronycteris microtis</i>	1	6	5	12
<i>Micronycteris minuta</i>	1	0	1	2
<i>Mimon bennettii</i>	0	1	1	2
<i>Mimon crenulatum</i>	1	11	13	25
<i>Phylloderma stenops</i>	2	9	5	16
<i>Phyllostomus discolor</i>	0	5	1	6
<i>Phyllostomus elongatus</i>	10	57	46	113
<i>Phyllostomus hastatus</i>	2	5	8	15
<i>Trachops cirrhosus</i>	8	29	18	55
<i>Trinycteris nicefori</i>	3	29	8	40
<i>Tonatia saurophila</i>	11	26	18	55
Carolliinae				
<i>Carollia benkeithi</i>	4	8	3	15
<i>Carollia brevicauda</i>	32	156	72	260
<i>Carollia perspicillata</i>	225	540	265	1030
<i>Rhinophylla fischeriae</i>	0	7	2	9
<i>Rhinophylla pumilio</i>	42	137	59	238
Stenodermatinae				
<i>Artibeus lituratus</i>	56	61	11	128
<i>Artibeus obscurus</i>	27	127	72	226
<i>Artibeus planirostris</i>	45	124	45	214
<i>Dermanura anderseni</i>	1	1	3	5
<i>Dermanura cinerea</i>	13	15	10	38

<i>Artibeus concolor</i>	2	1	0	3
<i>Dermanura gnoma</i>	10	22	12	44
<i>Chiroderma villosum</i>	1	1	1	3
<i>Mesophylla macconnelli</i>	12	22	5	39
<i>Platyrrhinus brachycephalus</i>	1	1	4	6
<i>Platyrrhinus incarum</i>	8	3	3	14
<i>Sturnira lilium</i>	0	6	2	8
<i>Sturnira tildae</i>	1	22	15	38
<i>Uroderma bilobatum</i>	11	17	22	50
<i>Uroderma magnirostrum</i>	1	3	0	4
<i>Vampyressa thylene</i>	0	1	3	4
<i>Vampyriscus bidens</i>	12	15	14	41
Captures	578	1651	900	3129
Number of species	39	44	41	48
Number of nights	48	148	94	290
Sampling effort (mnh)	2304	7104	4512	13920

Table S2. Values of the functional traits of the bat species used in functional and taxonomic analysis. Species names with an asterisk had relative wing loading and aspect ratio estimated by the linear regression equation of these traits with body mass - see material and methods for more details.

Taxon	Body mass (g)	Aspect ratio	Relative wing load	Trophic level	Diet
Desmodontinae					
<i>Desmodus rotundus</i>	30.8	6.73	41.78	Animalivore	Sanguinivore
<i>Diphylla ecaudata</i> *	23.5	6.21	37.88	Animalivore	Sanguinivore
Glossophaginae					
<i>Choeroniscus minor</i>	8.6	6.75	39.71	Phytophagae	Nectarivore
<i>Glossophaga longirostris</i> *	9.0	6.16	38.94	Phytophagae	Nectarivore
<i>Glossophaga soricina</i>	8.7	6.47	42.5	Phytophagae	Nectarivore
<i>Lionycteris spurrelli</i> *	8.5	6.16	38.88	Phytophagae	Nectarivore
<i>Lonchophylla thomasi</i>	7.4	6.35	41.08	Phytophagae	Nectarivore
Phyllostominae					
<i>Chrotopterus auritus</i>	84.1	5.68	27.35	Animalivore	Carnivore
<i>Glyphonycteris daviesi</i>	20.5	6.24	27.58	Animalivore	Insectivore
<i>Glyphonycteris sylvestris</i>	9.1	6.50	35.1	Animalivore	Insectivore
<i>Lamproncycteris brachyotis</i>	12.8	5.76	41.41	Animalivore	Insectivore
<i>Lophostoma brasiliense</i>	10.8	5.09	38.44	Animalivore	Insectivore
<i>Lophostoma silvicolum</i>	37.3	5.28	33.56	Animalivore	Insectivore
<i>Micronycteris hirsuta</i>	15.1	5.39	33.76	Animalivore	Insectivore
<i>Micronycteris megalotis</i>	6.5	5.75	33.82	Animalivore	Insectivore
<i>Micronycteris microtis</i>	7.7	5.97	31.43	Animalivore	Insectivore
<i>Micronycteris minuta</i>	7.0	5.81	40.77	Animalivore	Insectivore
<i>Mimon bennettii</i> *	22.8	6.21	37.93	Animalivore	Insectivore
<i>Mimon crenulatum</i>	15.0	6.45	27.38	Animalivore	Insectivore
<i>Phylloderma stenops</i>	49.7	6.23	30.43	Animalivore	Omnivore
<i>Phyllostomus discolor</i>	34.5	6.93	40.35	Animalivore	Omnivore
<i>Phyllostomus elongatus</i>	39.7	6.61	34.03	Animalivore	Omnivore
<i>Phyllostomus hastatus</i>	96.9	7.12	36.68	Animalivore	Insectivore
<i>Tonatia saurophila</i>	26.4	5.91	30.42	Phytophagae	Insectivore
<i>Trachops cirrhosus</i>	34.8	5.83	36.15	Animalivore	Carnivore
<i>Trinycteris nicefori</i>	8.9	6.28	36.87	Animalivore	Insectivore
Carollinae					
<i>Carollia benkeithi</i>	11.5	6.31	49.15	Phytophagae	Frugivore
<i>Carollia breviceauda</i>	15.7	6.13	38.68	Phytophagae	Frugivore
<i>Carollia perspicillata</i>	16.2	6.22	38.8	Phytophagae	Frugivore
<i>Rhinophylla fischeriae</i>	8.3	6.23	39.57	Phytophagae	Frugivore
<i>Rhinophylla pumilio</i>	9.7	6.21	38.86	Phytophagae	Frugivore
Stenodermatinae					
<i>Artibeus concolor</i>	18.0	6.46	35.78	Phytophagae	Frugivore
<i>Artibeus lituratus</i>	70.6	6.25	38.1	Phytophagae	Frugivore
<i>Artibeus obscuru</i>	38.9	6.45	38.69	Phytophagae	Frugivore
<i>Artibeus planirostris</i>	58.0	6.39	40.18	Phytophagae	Frugivore

<i>Chiroderma villosum</i>	21.8	6.37	40.35	Phytophagae	Frugivore
<i>Dermanura anderseni</i> *	9.8	6.16	38.83	Phytophagae	Frugivore
<i>Dermanura cinerea</i>	10.6	6.19	39.04	Phytophagae	Frugivore
<i>Dermanura gnoma</i>	10.6	6.05	36.54	Phytophagae	Frugivore
<i>Mesophylla macconnelli</i>	7.2	6.19	43.91	Phytophagae	Frugivore
<i>Platyrrhinus brachycephalus</i> *	12.0	6.17	38.67	Phytophagae	Frugivore
<i>Platyrrhinus incarum</i>	12.4	6.47	43.86	Phytophagae	Frugivore
<i>Sturnira lilium</i>	20.7	6.27	45.05	Phytophagae	Frugivore
<i>Sturnira tildae</i>	27.3	6.47	39.43	Phytophagae	Frugivore
<i>Uroderma bilobatum</i>	16.9	6.3	41.46	Phytophagae	Frugivore
<i>Uroderma magnirostrum</i>	17.7	6.42	40.79	Phytophagae	Frugivore
<i>Vampyressa thyoene</i> *	8.1	6.16	38.77	Phytophagae	Frugivore
<i>Vampyriscus bidens</i>	12.9	6.38	43.81	Phytophagae	Frugivore

Table S3. Results of the pairwise comparisons of the PERMANOVA tests for the indices and functional traits that were significant in the global PERMANOVA test (see Table 1). Significant differences are in bold ($P < 0.06$).

Indices	Pre-flooded × Pre-unflood		Pre-flooded × Post-dam		Pre-unflood × Post-dam	
	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Simpson D	3.40	0.083	3.76	0.994	6.31	0.021
Rao's Q	0.22	0.637	1.970	0.197	5.220	0.032
Traits						
Diet:						
frugivore	0.64	0.444	6.87	0.016	7.17	0.009
gleaning insectivore	4.32	0.042	6.41	0.014	1.11	0.319

Conclusões

Impactos espaciais e temporais do alagamento do reservatório de uma mega hidrelétrica no sudoeste da Amazônia brasileira sobre a diversidade taxonômica e funcional de morcegos Phyllostomidae

Capítulo 1.

Establishing baseline biodiversity data prior to hydroelectric dam construction to monitoring impacts to bats in the Brazilian Amazon

- A partir de dados do período do pré-enchimento da barragem da UHE Santo Antônio foi possível constatar que a composição de espécies de morcegos da família Phyllostomidae diferiu entre áreas que seriam submersas daquelas que permaneceriam secas.
- O presente estudo mostrou que os morcegos frugívoros foram mais abundantes nas áreas que seriam inundadas. O alagamento das áreas situadas em cotas mais baixas do terreno impõe perdas nos gradientes de vegetação necessários à manutenção dos morcegos frugívoros. Por outro lado, os morcegos animalívoros foram mais abundantes nas áreas que não seriam submersos pelo reservatório. Possivelmente suas populações estejam menos vulneráveis a inundações do reservatório da UHE Santo Antônio.
- Amostragem prévias, conduzidas antes dos efeitos deletérios da barragem, podem ser usados como uma ferramenta eficaz para fazer previsões sobre até que ponto a fauna de morcegos pode ser afetada.

- A variação da topografia e da estrutura da vegetação na paisagem da UHE Santo Antônio foram fundamentais para a estruturação das assembleias de morcegos. Embora os gradientes de elevação tenham sido relativamente sutis (< 100 m), eles foram suficientes para alterar a composição das assembleias de morcegos, principalmente dos frugívoros que foram mais abundantes nas cotas mais baixas. Os resultados também me permitiram registrar respostas em relação às variações da estrutura da vegetação do ponto de vista das guildas, uma vez que a abundância relativa de frugívoros, nectarívoros e animalívoros respondeu negativamente à diferentes componentes da estrutura da vegetação. A abundância dos frugívoros e nectarívoros foi negativamente associada à área basal da floresta que explica a ocorrência de grandes obstáculos na vegetação. Em contraste, a abundância dos animalívoros foi negativamente correlacionada com um componente mais fino da vegetação, formado pela densidade de folhas e galhos.

Capítulo 2.

Monitoring of impacts caused by an Amazonian mega hydroelectric dam revealed immediate effect on frugivorous bat assemblages

- A construção da hidrelétrica de Santo Antônio afetou as assembleias de morcegos Phyllostomidae. Os efeitos da barragem foram rápidos e severos nas assembleias de morcegos distribuídas nas matas ciliares e florestas de várzea.
- As assembleias de morcegos 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 morcegos, mas os morcegos frugívoros responderam negativamente com uma perda geral de abundância após a inundação do reservatório.
- As assembleias dos morcegos foram relativamente homogêneas em composição em diferentes distâncias da nova margem do reservatório. Isso indica que os primeiros dois anos após a inundação do reservatório pode não ter sido tempo suficiente para acumular mudanças suficientes na vegetação que influencia os morcegos próximos das novas margens dos riachos de terra firme e do Rio Madeira.
- Os resultados deste estudo foram provenientes de uma barragem do tipo fio d'água que aproveita a corrente natural dos rios para o funcionamento das turbinas. Esse tipo de barragem inunda grandes áreas de florestas localizadas nas margens do rio, mas impede a criação de lagos profundos, típicos de reservatórios de armazenamento. Estudos anteriores que avaliaram os efeitos das barragens de hidrelétricas nas assembleias da fauna foram realizados em reservatórios de armazenamento que geraram uma paisagem insularizada. Este tipo de hidrelétrica é a mais comum no mundo e os dados que avaliam os efeitos do barramento do rio provem das ilhas e áreas adjacentes não alagadas. Embora comumente considerados menos prejudiciais à diversidade de espécies e ao ecossistema do que os reservatórios de armazenamento, a barragem fio d'água da UHE Santo Antônio afetou negativamente os morcegos frugívoros. Diversos estudos tem mostrado que estes morcegos se beneficiam da conversão da floresta original não perturbada em áreas de vegetação secundária. Contudo, no cenário de perda permanente das florestas ciliares e das várzeas, sem substituição por outro tipo de vegetação, esses morcegos foram os mais vulneráveis.

- Os efeitos do barramento do Rio Madeira pela UHE Santo Antônio foram rápidos, observados nos primeiros dois anos após a inundação do reservatório. Contudo, não é possível determinar se a estrutura da comunidade dos morcegos e o ecossistema usado por eles já alcançaram uma condição de equilíbrio, no qual não serão encontradas mudanças. Contudo, mudanças drásticas na paisagem, como as causadas por grandes barragens de hidrelétricas, possivelmente não cessam no período de tempo de dois anos. Por isso, um monitoramento de longo prazo é fortemente recomendado para empreendimentos que causam mudanças ambientais extensas como as observadas em barragens de hidrelétricas. Esses estudos precisam ser conduzidos em períodos antes e depois da construção da barragem, a fim de avaliar a extensão dos impactos e quando as condições de equilíbrio serão alcançadas.
- Por causa da inundação permanente das florestas de várzea, este estudo recomenda 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. Essa estratégia de gestão da conservação deve ser financiada pelas empresas produtoras de energia.
- Nosso estudo anterior, realizado antes do enchimento da barragem, foi claro em demonstrar que os morcegos frugívoros são vulneráveis à perda de habitat. No presente estudo, com dados coletados depois da inundação do reservatório, essas conclusões foram demonstradas empiricamente. Isso reforça que amostragem conduzidas antes dos efeitos da barragem são uma ferramenta eficaz para fazer previsões sobre até que ponto a fauna de morcegos pode ser afetada.

Capítulo 3.

Taxonomic and functional responses of bats to habitat flooding by a mega hydroelectric dam in the Amazonia

- A inundação do reservatório aumentou a diversidade α taxonômica e α funcional e a singularidade funcional das assembleias de morcegos, possivelmente como resultado da dispersão de diferentes espécies na paisagem remanescente.
- Métricas de diversidade funcional são uma ferramenta importante para avaliar os efeitos temporais da construção de hidrelétricas.
- A redução da abundância de algumas espécies de morcegos frugívoros (por exemplo, *Rhinophylla pumilio*, *Vampyriscus bidens*, *Carollia perspicillata*, *Uroderma bilobatum*) resultou no aumento a singularidade funcional dessas espécies. As assembleias do período pós-barragem compostas por espécies frugívoras menos redundantes e morcegos animalívoros, que em geral foram mais singulares antes e depois da construção da barragem, podem ter gerado uma combinação particular de características únicas que aumentou a singularidade funcional das assembleias pós-barragem.
- O represamento do Rio Madeira aumentou frequência dos morcegos animalívoros, indicando que as florestas que permaneceram sem inundação não alteraram as condições ambientais exigidas pelos morcegos com essas características, pelo menos até dois anos após a conclusão da barragem. Por outro lado, a frequência dos morcegos frugívoros reduziu, possivelmente associado a inundação das florestas de várzea e matas ciliares.

- A diversidade β funcional entre as assembleias pré e pós-barragem foi mais explicada pela substituição de espécies com função semelhante do que pela perda ou ganho de espécies com traços únicos.