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# Taxonomic and functional responses of bats to habitat flooding by an Amazonian mega-dam

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## Abstract

Hydroelectric dams are among the main cause of anthropogenic impacts in tropical environments. Damming interrupts the continuity of the river and produces the flooding of adjacent terrestrial ecosystems. Despite the negative effects on terrestrial and aquatic biodiversity, studies of the impacts of hydroelectric dams on species and community functional responses to flooding are scarce. Here, we evaluated the effects of river damming on taxonomic and functional diversity of phyllostomid bats sampled before (flooded sites) and after (unflooded sites) the construction of a mega hydroelectric dam in the southwestern of the Brazilian Amazon. The flooding of the lowlands significantly increased the taxonomic and functional  $\alpha$ -diversity, as well as the species- and the community-level functional uniqueness of the bat assemblages, reflecting a reduction in the abundance of functional redundant species. Based on functional trait composition, we detected an increase in the frequency of animalivorous bats, and a reduction in phytophagous bats. Pre- and post-dam temporal differences show that functional  $\beta$ -diversity shifts were more determined by replacement of traits weighted by species abundance than by the loss or gain of traits. Functional traits linked to trophic level, body mass, and diet proved to be powerful indicators of the bat community's responses to temporal changes caused by runof-the-river dams, which degrade riparian and várzea forests. Plans to expand the electric power matrix in Brazil include the construction of several dams, potentially flooding large areas of várzea forests. We demonstrate the importance of the várzea and the riparian forests to phytophagous bats to guarantee the ecological functions they perform.

**Keywords** Functional diversity · Functional traits · Functional uniqueness · River damming · Run-of-the-river reservoir · Temporal dynamics

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## Introduction

Hydropower development is among the significant 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 a 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 to ~80% of electricity in Brazil (Zarfl et al. 2015), and 334 new hydroelectric dams are with construction planned in the Amazon Basin (Winemiller et al. 2016). Although hydropower generation is claimed to be environmentally sustainable, until 2012, approximately 1.1 million ha of forest in the Brazilian Amazon has been completely flooded (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 on the biota comes from storage reservoirs (Baumgartner et al. 2020), traditionally used worldwide (International Energy Agency 2012). This type of reservoir retains large amounts of water, causing the interruption of the natural flood level regime (Baumgartner et al. 2020) and creating several islands that may have different sizes and degrees of isolation (Benchimol & Peres 2020). Conversely, run-of-the-river reservoirs have become increasingly common in planning the expansion of the electric power matrix. Because run-of-the-river hydroelectric dams are based on the building of smaller lakes with limited water storage, they have been considered a priori less detrimental (Almeida et al. 2019), but their effects on the biota are scarcely known. New hydroelectric dams call for new perspectives of environmental impact studies, addressing multiple dimensions of diversity to better understand the river damming effects on communities.

Ecologists have traditionally attempted to estimate the effects of environmental disturbance based primarily on examining the taxonomic dimension, including analyses of species composition, richness, and relative abundance (Mackey & Currie 2001). However, these descriptors consider the species to be independent units, ignoring the functional similarities between them (Cadotte et al. 2011; Gagic et al. 2015). The different species' responses to human-made disturbances are limited by their morphology, physiology, and behavior (McGill et al. 2006; Mouillot et al. 2013; Gagic et al. 2015; Weiss & Ray 2019). Thus, studies based on functional traits offer a promising alternative approach to taxonomic diversity (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 progressively used as models to 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). In particular, Neotropical bats from the family Phyllostomidae form species-rich assemblages that are highly diverse for functional traits and promote a variety of functions in ecosystems. Ecosystem services offered by bats include functional traits associated with seed dispersal, plant pollination and insect population control (Castillo-Figueroa 2020). Additionally, certain functional traits of bats, such as trophic level and body mass, have been identified as sensitive to environmental disturbance, and larger animalivores species to have a minor chance of survival after the disturbance (Fenton et al. 1992; Farneda et al. 2015; 2018; 2020b). Frugivorous bats are associated with waterways and may be sensitive to loss of flooded and riparian forests (Bobrowiec et al. 2014; Capaverde et al. 2018). However, the knowledge about the effects of hydropower development on the functional diversity of bats comes from studies conducted in insularized landscapes generated by storage reservoirs (Cosson et al. 1999; Meyer et al. 2008; Farneda et al. 2020a; Zortéa et al. 2021).

Here, we evaluate the effects of river damming on the taxonomic and functional diversity of phyllostomid bats in areas that would be flooded and not flooded before and after the construction of the Santo Antônio Hydroelectric dam, located in southwestern Brazilian Amazon. Additionally, we investigate how bat functional traits are affected by river damming and how the flooding of lowlands contributes to changes in functional  $\beta$ -diversity. Our hypothesis is that functional and taxonomic  $\alpha$ -diversity, and functional uniqueness at the communities and species-level decrease after the river damming due to assemblages functionally similar and simplified. We predicted that after dam filling:

- 1. functional and taxonomic  $\alpha$ -diversity and community-level functional uniqueness would decrease based on negative species responses to environmental changes.
- species-level functional uniqueness would increase for phytophagous species because of their positive association with the lowlands that would be flooded (Bobrowiec et al. 2014).
- 3. functional traits associated with phytophagous species would be negatively affected because these species are more abundant in lowland forests (Capaverde et al. 2018).
- 4. temporal differences in functional  $\beta$ -diversity would be mainly determined by the replacement of functional traits than by the gain of traits.

## Materials and methods

#### Study area

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



**Fig. 1** Map of the study area downstream of the Santo Antônio Hydroelectric in the upper Madeira River, Southwestern Brazilian Amazonia. (a) Light blue indicates the area occupied by the original river before dam construction, the dark blue indicates the extent of the reservoir after the full dam flooding. (b) Illustration of the plot's distribution in the one site in relation to the post-dam Madeira River level. The sampling sites are: TO=Teotônio, MO=Morrinhos, IB=Ilha dos Búfalos, IP=Ilha das Pedras, JL=Jirau Left Bank, JR=Jirau Right Bank, JP=Jaci-Paraná. Sampling sites that were sampled after the river damming are indicated by asterisk (\*)

#### Bat sampling

We captured bats in seven sampling sites with seven plots in each, totaling 46 sampling plots (Fig. 1, Table S1). Six sites were located on the Madeira River and one on the Jaci-Paraná River (Fig. 1). The plots were distributed 50, 500, 1000, 2000, 3000, 4000, and 5000 m away from the riverbank on a trail perpendicular to the river bank (Fig. 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 250 m long and 40 m wide plots that follow the topographic contour to minimize internal heterogeneity in soil properties and drainage.

We sampled the plots in two stages (Table S1): Pre-dam stage=12 plots located in areas that were going to be flooded by the reservoir (pre-flooded plots), and 34 plots that were going to remain dry (pre-unflooded plots) (June 2010 to September 2011); and Post-dam stage=25 pre-unflooded plots resampled after the flooding of the reservoir (post-dam plots) (June 2013 to June 2014).

We captured bats using eight ground-level mist-nets ( $12 \times 2.5$  m, 36 mm mesh, Ecotone Inc, Poland) per plot. 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 (13,920 mnh; 1 mist-net hour, mnh, equals one 12-m net open for 1 h; Table S2). Species were identified following Charles-Dominique et al. (2001), Lim and Engstrom (2001), and Gardner (2007). Taxonomy follows Garbino et al. (2020).

#### **Species traits**

We selected five functional traits (Table 1 and S3) related to the variability of diets and movement ability of bats. These traits have been used to predict the response of bats to anthropogenic environmental changes (Castillo-Figueroa & Pérez-Torres 2021) and may be defined as follows:

Body mass – this trait has been widely used in bat functional studies (Farneda et al. 2015; Castillo-Figueroa & Pérez-Torres 2021) and was obtained during our fieldwork using a balance with 0.5 g of precision.

Wing morphology – the shape of the wings of a bat constraint its flying mode and performance and may be described in two functional traits: relative wing loading and aspect ratio (Norberg & Rayner 1987). Wings with a high aspect ratio and relative wing loading are suitable for high-speed flights, little maneuverability in obstructed habitats, but advantageous for foraging in open spaces (Norberg & Rayner 1987; Tavares 2013; Marinello & Bernard 2014). Values of relative wing loading and aspect ratio of 41 species sampled in our study were obtained from Marinello & Bernard (2014) and Farneda et al. (2015). For the other seven species, we estimated the values of relative wing loading and aspect ratio using the equation of linear regressions of these traits with body mass (Relative wing loading: t=-1.94, P=0.06,  $r^2$ =0.088, RWL = -0.069 × (body mass)+39.5; Aspect ratio: t=1.15, P=0.26,  $r^2$ =0.034, AR=0.0035 × (body mass)+6.13) (Table S3).

Trophic level – we divided this trait into two main categories: phytophagous phyllostomids (which consume fruits, seeds, nectar, leaves, and flowers), and animalivorous phyllostomids (including insects, small rodents, frogs, and blood in their diets) (Giannini & Kalko 2004).

Diet – this trait conveys a more detailed scale of trophic level and represents the main food item eaten by bats. We ranked the diet of bat species according to the classification found in the literature (Giannini & Kalko 2004), including the categories as follows: frugivores, nectarivores, gleaning insectivores, carnivores, omnivores and sanguinivores.

#### Data analysis

We calculated the taxonomic and functional  $\alpha$ -diversity, and the community-level functional uniqueness following the methodological approach proposed by Ricotta et al. (2016), which

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	Phytophagues 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

 Table 1
 List and description of the bat functional traits used in taxonomic and functional analyses at Santo

 Antonio Hydroelectric, Southwestern Amazonia, Brazil.
 Table S3 shows the values of each functional trait

consists of using Simpson index D for taxonomic diversity and Rao's index O for functional diversity. Simpson D considers all species functionally similar, but taxonomically different, and Rao's Q takes the species dissimilarities into account to calculate 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; 2020b). Both indexes consider the relative species abundance and, therefore, are good indicators of early warning of disturbances as they do not only need species extinctions to change (Mouillot et al. 2013). We also calculate the index of functional richness (Fric) that does not consider the abundance of species (Villéger et al. 2008). Fric is the total amount of functional space filled by the community and increases by adding functionally unique species to the assemblage, but remains unchanged with the addition of functionally redundant species (Villéger et al. 2008). We compared each index (D, Q, U, Fric) between the pre- (pre-unflooded+preflooded; Table S1) and post-dam plots, and also between the three categories of plots (preunflooded, pre-flooded, post-dam; Table S1) using a Generalized Linear Mixed Model (GLMM) in *lme4* package (Brooks et al. 2017). Pre-dam plots account for all plots sampled before filling the reservoir, both pre-flooded and pre-unflooded plots (Table S1). Thus, we can understand how pre-dam plots differ from post-dam plots. The models incorporated the sampling sites and plots as random effects to account for potential spatial autocorrelations. We assessed pairwise comparison among pre-unflooded, pre-flooded, and post-dam with the 'glht' function from *multcomp* package (Hothorn et al. 2008).

To evaluate the relevance of each species in a particular function about the river damming, we calculated the species-level functional uniqueness  $\overline{K_i}$ , which is also based on the relative species abundance.  $\overline{K_i}$  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  $\overline{K_i}$ values between pre- and post-dam periods for phytophagous and animalivorous bats using permutational paired *t*-tests with 9999 randomizations in the *broman* package (Broman 2020). For this, we used only the species that were recorded in both periods. We also compared the  $\overline{K_i}$  values between animalivorous and phytophagous bat species before and after the dam construction using permutational *t*-tests with 9999 randomizations (*RVAideMemoire* package, Hervé 2020). We calculated the Q, D, U and  $\overline{K_i}$  indices using the 'uniqueness' function of the *adiv* package (Pavoine 2020), based on Gower's functional dissimilarity that allows including categorical and quantitative traits (*gawdis* package, de Bello et al. 2021). We used 'functcomp' function from *FD* package (Laliberté et al. 2014) to perform the Fric index.

To understand how each functional trait respond to the river damming, we calculated the community-weighted mean trait values (CWM; Lavorel et al. 2008). The CWM employs the average value of each trait weighted by the abundance of each species (Violle et al. 2007). We calculated the CWM traits using the 'functionp' 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 GLMMs as previously described.

Temporal changes for functional structure of communities before and after disruption can be assessed by calculating the functional  $\beta$ -diversity (Mouillot et al. 2013). Total functional  $\beta$ -diversity ( $\beta$ total) is represented by replacement (turnover of species functional

traits,  $\beta$ repl) and difference in species richness (loss or gain of traits,  $\beta$ rich). We use the Cardoso et al. (2015) approach that predicts that  $\beta$ total corresponds to the sum of the replacement component with the richness difference component ( $\beta$ total= $\beta$ repl+ $\beta$ rich). The  $\beta$ total and its components were calculated using the 'beta' function of the *BAT* package (Cardoso et al. 2020), based on a site × 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 × traits, submitted to a hierarchical clustering procedure using UPGMA with Gower distance (Cardoso et al. 2015). We used a rarefaction for the same abundance as the plot with the least individuals sampled (argument raref=1). The functional  $\beta$ -diversity of bat assemblages was calculated between pre- and post-dam periods with all plots (pre-dam × post-dam), and between pre-unflooded plots and post-dam (without pre-flooded plots). All analyses were performed in R (R Core Team 2020).

## Results

We captured 2981 bats belonging to 48 species (Table S2). Post-dam plots had higher taxonomic (D) and functional diversity (Q), and higher functional uniqueness (U) than predam plots (pre-unflooded+pre-flooded), but functional richness (Fric) was similar to the pre-unflooded stage (Table 2; Fig. 2). When we contrasted post-dam with pre-flooded and pre-unflooded plots, we observed that post-dam had higher taxonomic diversity (D) and functional diversity (Q) compared to pre-unflooded plots, but were similar to pre-flooded plots for D and Q (Table 3; Fig. S1).

	Pre-dam × Post-dam		
Indices	t	Р	
Simpson D	2.29	0.031	
Functional richness FRic	-1.01	0.35	
Rao's Q	2.41	0.022	
Functional Uniqueness U	2.05	0.048	
Traits			
Body mass	0.19	0.85	
Relative wing load	1.52	0.13	
Aspect ratio	-0.06	0.96	
Trophic level:			
phytophagues	2.17	0.034	
animalivores	-2.18	0.033	
Diet:			
frugivores	3.29	0.002	
nectarivores	-1.28	0.21	
gleaning insectivores	-1.69	0.09	
carnivores	-1.14	0.26	
omnivores	-1.11	0.27	
sanguinivores	-1.67	0.09	

 Table 2
 Results of the GLMM for the taxonomic (D) and functional (FRic, Q and U) diversity indices, and for each functional trait used in community-weighted mean (CWM) analyses. Comparisons were made between pre-dam (pre-flooded and pre-unflooded combined) and post-dam plots. P<0.05 are in bold</th>



Fig. 2 Taxonomic diversity (Simpson index D), functional diversity (Functional richness and 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, Southwestern Amazonia, Brazil. Black circles represent the means of the functional indexes values. \* P<0.05 (see Table 2). Pre-dam represent pre-flooded and pre-unflooded plots combined

We recorded relevant changes for bat species-level functional uniqueness  $(\overline{K_i})$ . For example,  $\overline{K_i}$  of seven species (14.5% of all species) of animalivorous bats (e.g., *Diphylla ecaudata*, *Chrotopterus auritus*, *Micronycteris megalotis*) decreased with dam construction. In contrast,  $\overline{K_i}$  increased for 15 species (31.3%) of phytophagous bats (e.g., *Rhinophylla fischerae*, *Platyrrhinus brachycephalus*, *Uroderma bilobatum*) (Fig. 3). The mean functional uniqueness of all bat species increased following the river damming (paired t-test: t = -2.37; P=0.019) mainly for phytophagous bats (paired t-test: t = -3.13; P=0.007), and remained similar in animalivorous (paired t-test: t = -0.12; P=0.86). Species-level functional uniqueness of animalivorous bats during the periods pre- (t-test: t=8.01; P<0.0001) and post-dam (t-test: t=8.23; P<0.0001) were, in average, 1.9 and 1.7 times greater than that of phytophagous bats, respectively (Fig. S2).

Changes in functional traits composition were associated with the effects of river damming, as demonstrated by the community-weighted mean trait values (CWM). The traits that revealed significant changes in CWM after the construction of the dam were trophic level, diet, and body mass (Tables 2 and 3). The CWM trait values of animalivores increased significantly (P=0.033) after the dam construction, while for phytophagous bats (P=0.034) represented mainly by the frugivores (P=0.002) it decreased (Table 2; Fig. 4). Frugivorous bats were less frequent (P=0.003) in the post-dam plots compared to pre-unflooded and pre-flooded plots (Table 3; Fig. S3). Animalivorous bats were more frequent in pre-unflood and post-dam plots than pre-flooded plots (Table 3; Fig. S3). Body mass was higher in preflooded plots than pre-unflooded and post-dam plots (Table 3; Fig. S3).

	$\operatorname{Pre-flood} \times \operatorname{Pre-unflood}$		$\operatorname{Pre-flood} \times \operatorname{Post-dam}$		Pre-unflood × Post-dam	
Indices	t	Р	t	Р	$-\frac{1}{t}$	Р
Simpson D	-2.39	0.041	-0.84	0.67	2.66	0.020
Functional richness FRic	0.31	0.95	-0.4	0.91	-1.03	0.55
Rao's Q	-0.85	0.66	0.67	0.77	2.52	0.029
Functional Uniqueness U	-0.40	0.91	0.91	0.62	2.08	0.09
Traits						
Body mass	-2.84	0.012	2.49	0.032	-0.21	0.97
Relative wing load	-1.49	0.29	2.12	0.08	1.21	0.44
Aspect ratio	-2.15	0.08	1.59	0.25	-0.59	0.82
Trophic level:						
phytophagues	-0.82	0.68	1.77	0.17	1.62	0.23
animalivores	0.82	0.68	-1.78	0.17	-1.63	0.22
Diet:						
frugivores	-0.78	0.71	2.58	0.03	3.06	0.006
nectarivores	-1.27	0.40	0.38	0.92	-1.43	0.31
gleaning insectivores	2.07	0.09	-2.69	0.02	-1.28	0.39
carnivores	-0.95	0.61	-0.09	0.99	-1.37	0.35
omnivores	0.17	0.98	-0.81	0.69	-1.04	0.54
sanguinivores	-0.31	0.95	-0.93	0.62	-1.68	0.21

**Table 3** Results of the GLMM for the taxonomic (D) and functional (FRic, Q and U) diversity indices, and for each functional trait used in community-weighted mean (CWM) analyses. Comparisons were made between pre-flooded, pre-unflooded, and post-dam plots. P<0.05 are in bold

The differences in functional  $\beta$ total (0.089) between pre- and post-dam bat assemblages was mostly explained by the replacement of species traits ( $\beta$ repl=0.067; 75.3% of the  $\beta$ total) compared to loss or gain of traits ( $\beta$ rich=0.017; 19.1%) (Fig. 5). When we removed the pre-flooded plots from the analysis,  $\beta$ rich slightly increased (Fig. 5).

## Discussion

Hydroelectric dams have become one of the main drivers of changes in tropical biota (Winemiller et al. 2016; Jones et al. 2016). Identifying the functional traits that explain species' responses to river damming may help to choose management practices that restore ecosystem functions (Spasojevic et al. 2018). Contrary to our expectations, the flooding of lowland areas of the Madeira River increased the taxonomic and functional  $\alpha$ -diversity and functional uniqueness of the bat assemblages. We also found strong evidence for a shift in functional traits after river damming, with an increase in the frequency of animalivorous bats and a reduction of phytophagous. Our data show that total  $\beta$ -diversity results from replacing functional traits (i.e., the substitution of functional traits weighted by the species abundance) and not by the loss or gain of traits.

In scenarios of recent and extensive environmental disturbances, such as the implementation of dams, the species need to adapt to new conditions until the equilibrium is found (Dayrell et al. 2021). Indices of functional diversity and uniqueness are very sensitive to species abundance (de Bello et al. 2007). The increase in functional  $\alpha$ -diversity and functional uniqueness, as demonstrated by our data, is likely a result of the influx of individuals



Fig. 3 Species-level functional uniqueness of the bat species sampled pre-dam (blue circles) and post-dam (red circles) at Santo Antonio Hydroelectric, Southwestern Amazonia, Brazil. Species names in green represent phytophagous bats, and names in red represent animalivorous bats. Pre-dam represent pre-flooded and pre-unflooded plots combined

from the areas lost to the remaining landscape. Contrary to our prediction 1, the taxonomic diversity (D), functional diversity (Q), and functional uniqueness (U) increased in magnitude after the disturbance caused by the dam due to the reduction in the abundance of the functional redundant bat species. On the other hand, the functional richness was similar between the three categories of habitats (pre-flooded, pre-unflooded, and post-dam), indicating that the flooding of the reservoir did not affect the number of functionally unique species. An increase in functional diversity after human-induced impacts has also been observed in Amazonian and Atlantic Forest for ants (Zhao et al. 2020), birds (Ding et al. 2013), fish (Stegmann et al. 2019), and mammals (Bovendorp et al. 2019; Sancha et al. 2020), including bats (Farneda et al. 2018; Carvalho et al. 2020).

The functional uniqueness of bat species from the Madeira riverside communities  $(K_i)$  increased in the post-dam period. Following prediction 2, this increment of  $\overline{K_i}$  was driven by the input of 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, although it remained greater than phytophagous bats. So, the increase in the functional uniqueness of the post-dam assemblages resulted from the combination of the large abundance of frugivorous bats, that became less dominant, and the animalivorous bats with unique traits. Unique assemblages selected after human disturbance may be of special concern for the



Fig. 4 Community-weighted mean (CWM) trait values for statistically significant functional traits: Trophic guild: animalivores and phytophagues, and Diet: frugivores. Bat assemblages were sampled during pre-dam (blue circles) and post-dam (red circles) at Santo Antonio Hydroelectric, Southwestern Amazonia, Brazil. Black circles represent the means of the CWM trait values. \* P<0.05 (see Table 2). Pre-dam represent pre-flooded and pre-unflooded plots combined

conservation of ecosystems as they may lack essential functions and services (Biggs et al. 2020). These effects can be temporarily worsened if the abundance of fruit bats does not increase in the future.

Under prediction 3, our results from the CWM analyses revealed that phytophagous bats, most of them frugivores, and large bats were negatively affected by the construction of the dam. At the same time, animalivorous species responded positively to changes imposed by the dam. Similar results have been found in a small hydroelectric dam in the Brazilian Cerrado (Zortéa et al. 2021). 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, fruit bats are the most vulnerable to permanent loss of várzea and riparian forests, which constitute the larger part of the flooded area lost in the Santo Antonio dam (Santos et al. 2020). Terra firme upland forests, várzea and riparian forests have distinct 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, Zortéa et al. 2021). Moreover, we found assemblages with large bats in várzea, mainly due to the greater abundance of large-bodied species such as Artibeus lituratus, a pattern like those found in other Amazonian regions (Pereira et al. 2009; Bobrowiec et al. 2014). Nutrient-rich várzea forests have a high fruit production that attracts many frugivorous bats (Pereira et al. 2010). Plants of the genus *Piper* are common in the riparian forest and are exploited for food by frugivorous bats (Zortéa et al. 2021). The frequency reduction of frugivorous bats in post-dam areas compared to pre-unflooded areas



Fig. 5 Results of the rarefaction for components of bat functional  $\beta$  diversity between pre- (flooded and unflooded plots combined) 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, Southwestern Amazonia, Brazil.  $\beta$  total functional diversity (grey) was partitioned in the components  $\beta$  repl (blue; replacement of species functional traits) and  $\beta$ rich (orange; loss or gain of traits). Values represent means (horizontal lines)±95% confidence levels (colored bars) and maximum and minimum (vertical lines)

indicates that these bats may have moved to other forests with suitable food supply and thus reduced upland fruit bat populations. The Jirau/Santo Antônio hydroelectric complex flooded 800 km<sup>2</sup> of lowland forests along 245 km of the Madeira River, of which 118 km<sup>2</sup> were *várzea* forests (Cochrane et al. 2017). The loss of *várzea* forests can damage important ecological functions provided by frugivorous bats, such as the gene flow of plants via seed dispersal and pollination. As frugivores account for 77.5% of the phyllostomid bats sampled, the loss of ecosystem services may be more severe in assemblies with a lower frugivore abundance than the original.

On the other hand, the CWM results showed that river damming positively affected animalivorous bats. The frequency increase of animalivorous bats after dam filling indicates that these bats seem to have moved from flooded to non-flooded habitat. Animalivorous phyllostomids, represented mainly by carnivores, insectivorous gleanings and omnivores are dependent on the mature forest and are overall sensitive to environmental disturbances in response to the 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 in the first two years of Santo Antônio hydroelectric dam operation. However, the integrity of the remaining forests over time is likely essential to mitigate the harmful effects of river damming (Benchimol & Peres 2020). In accordance with prediction 4, our findings regarding  $\beta$ -diversity suggest that species traits replacement is the most important component of temporal functional total  $\beta$  diversity. The prevalence of diversity components related to the replacement of functional traits is expected for forests with less severe anthropogenic disturbances (Farneda et al. 2018; Carvalho et al. 2020). At the time of our study, the remaining vegetation in the Madeira riverside close to the Santo Antônio dam has a similar structural complexity as in the pre-dam period. However, the loss of *várzea* and riparian forests increased the influence of functional diversity due to richness and inversely decreased the diversity due to the replacement of functional traits. This indicates that *várzea* and riparian forests support high taxonomic and functional diversity of ecosystems (Pereira et al. 2009; Bobrowiec et al. 2014) because they harbor species with functions that are not shared within unflooded *terra firme* forests. The loss of species signifies a loss of functions with possible implications for 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 short time, while the long-term consequences remain unknown. The two years of the Santo Antônio dam flooding may not have been long enough to change in the vegetation, affected by the rise in the water table level in the areas close to the new banks of the Madeira River and streams. The vegetation change process is not yet over and the reaction of flora and fauna to the changed conditions is probably still ongoing. The loss of várzea forest is permanent and the new margins of the reservoir will not replicate the same alluvial habitats that previously existed (Almeida et al. 2019). Evidence indicates that changes in taxonomic diversity caused by the Santo Antônio dam will continue in the region, as observed in anurans (Dayrell et al. 2021) and birds (Henriques et al. 2021). The abundance of frugivorous bat species in several plots has decreased (Bobrowiec et al. 2021), which may increase the functional uniqueness of the assemblages and the contribution of functional richness ( $\beta$ rich) if rare species are prone to local extinction over time. If declines in frugivorous bats abundance continue, a potential cascading impact on ecosystems is also expected, including a reduction in vegetation regeneration potential via seed dispersal. The main problem seems to be that ecosystems that harbor fewer functionally redundant species are less resilient to environmental changes (Díaz & Cabido 2001; Bovendorp et al. 2019; Biggs et al. 2020). Therefore, the continuous monitoring of large-scale environmental impacts, as in the case of hydroelectric dams, is required to understand the direction and magnitude of changes in functional and taxonomic diversity and to estimate when the communities may reach a new equilibrium (Dayrell et al. 2021; Souza & Fernandes 2021).

### **Conservation implications**

River damming by a run-of-the-river hydroelectric dam quickly changed the taxonomic and functional diversity of Phyllostomidae bat assemblages from Madeira riverside lowlands. Those changes were driven mainly by the replacement of traits rather than the loss or gain of traits. Due to their frequency reduction in assemblages, functional traits linked to the trophic level, diet, and body mass are powerful indicators of the responses of the bat communities to the temporal changes caused by run-of-the-river dams that putatively degrade mainly lowland, riparian and *várzea* forests in the Amazonia River systems. Therefore, studies that

consider functional diversity are promising in identifying communities that may be prone to temporal changes in the human-modified landscapes (Brandl et al. 2016; Farneda et al. 2018).

Run-of-the-river hydroelectric dams negatively affect large-body phytophagous bats by flooding *várzea* forests and riparian zones. Species with larger body sizes have been identified as a good indicator of species vulnerability (Farneda et al. 2015; 2020b). The use of bats as bioindicators is auspicious, but this property is seldom tested in the field (Russo et al. 2021). Our study provides evidence that frugivorous bats are sensitive to river damming and can be used as bioindicator. Conserving the *várzea* and riparian forests is essential to ensure ecological functions performed by phytophagous bats (frugivores and nectarivores) to ensure ecosystem functionality (Assahira et al. 2017; Forsberg et al. 2017, Santos et al. 2020; Schöngart et al. 2021). New dams are planned to be built in the Amazon with the potential to flood large 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 as standard compensation conditioning the hydroelectric dam development, including *várzea* forests. We also suggest that the energy companies should be responsible for safeguarding these reserves.

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Author contributions Paulo E. D. Bobrowiec: Conceptualization, Formal analysis, Investigation, Resources, Data Curation, Writing - Original Draft, Writing - Review & Editing. Fábio Z. Farneda: Formal analysis, 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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Availability of data and material The data and metadata of the species captured are deposited in the public repository of the Brazilian Biodiversity Research Program (PPBio): https://ppbiodata.inpa.gov.br/ metacatui/#view/PPBioAmOc.87.4. 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".

Code Availability Not applicable.

#### Declarations

**Conflicts of interest/Competing interests (include appropriate disclosures)** The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Additional declarations for articles in life science journals that report the results of studies involving humans and/or animals 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).

**Ethics approval** Experienced investigators handled all captured bats. We followed the guidelines approved by the American Society of Mammalogists in our procedures (Sikes & Gannon 2011).

**Consent to participate (include appropriate statements)** Not applicable.

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