


Ecological correlates of mammal β -diversity in Amazonian land-bridge islands: from small- to large-bodied species

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Abstract

Aim: Mega hydroelectric dams have become one of the main drivers of biodiversity loss in the lowland tropics. In these reservoirs, vertebrate studies have focused on local (α) diversity measures, whereas between-site (β) diversity remains poorly assessed despite its pivotal importance in understanding how species diversity is structured and maintained. Here, we unravel the patterns and ecological correlates of mammal β -diversity, including both small (SM) and mid-sized to large mammal species (LM) across 23 islands and two continuous forest sites within a mega hydroelectric reservoir.

Location: Balbina Hydroelectric Dam, Central Brazilian Amazonia.

Methods: Small mammals were sampled using live and pitfall traps (48,350 trap-nights), and larger mammals using camera traps (8,160 trap-nights). β -diversity was examined for each group using multiplicative diversity decomposition of Hill numbers, which considers the importance of rare, common and dominant species, and tested to what extent those were related to a set of environmental characteristics measured at different spatial scales.

Results: β -diversity for both mammal groups was higher when considering species presence-absence. When considering species abundance, β -diversity was significantly higher for SM than for LM assemblages. Habitat variables, such as differences in tree species richness and percentage of old-growth trees, were strong correlates of β -diversity for both SMs and LMs. Conversely, β -diversity was weakly related to patch and landscape characteristics, except for LMs, for which β -diversity was correlated with differences in island sizes.

Main conclusions: The lower β -diversity of LMs between smaller islands suggests subtractive homogenization of this group. Although island size plays a major role in structuring mammal α -diversity in several land-bridge islands, local vegetation characteristics were additional key factors determining β -diversity for both mammal groups. Maintaining the integrity of vegetation characteristics and preventing the formation of a large set of small islands within reservoirs should be considered in long-term management plans in both existing and planned hydropower development in lowland tropical forests.

KEYWORDS

biotic homogenization, habitat fragmentation, habitat quality, hydroelectric dams, species turnover, tropical forest

1 | INTRODUCTION

Mega hydroelectric dams have become one of the main drivers of habitat loss and fragmentation worldwide (Gibson, Wilman, & Laurance, 2017; Jones, Bunnefeld, Jump, Peres, & Dent, 2016; Winemiller et al., 2016). In the aftermath of damming, lower elevation areas are flooded and the previous hilltops are converted into land-bridge forest islands, creating a complex archipelagic landscape within hydroelectric reservoirs. Despite their relatively flat terrain, rivers at hyper-diverse tropical developing countries are often targets for hydropower expansion (Zarfl, Lumsdon, Berlekamp, Tydecks, & Tockner, 2015). As such, the hydropower sector has greatly expanded in the Amazon Basin (Lees, Peres, Fearnside, Schneider, & Zuanon, 2016), with 145 existing or under-construction dams that are expected to flood ~1.5 Mha of pristine forests, and 263 additional dams earmarked for construction by current government plans (ECO, 2016). Therefore, understanding how the biota responds to the insularization created by dams poses as pivotal for long-term conservation actions in these novel landscapes.

The vast majority of studies in land-bridge island systems have assessed changes in local (α) diversity (reviewed by Jones et al., 2016; see also Si, Baselga, & Ding, 2015; Si, Baselga, Leprieur, Song, & Ding, 2016), showing that biological communities isolated within land-bridge islands are prone to experience high local extinction rates (Jones et al., 2016). However, local diversity typically represents only a small fraction of the regional species pool (MacArthur, 1972), restricting the effectiveness of conservation management efforts (Socolar, Gilroy, Kunin, & Edwards, 2016). To understand how the total number of species is organized and maintained in human-modified landscapes, or under alternative scenarios of anthropogenic disturbance, it is necessary to consider the variation in community composition among habitat patches (β -diversity; Whittaker, 1972), which is an important component of regional diversity (γ -diversity; Kadmon & Pulliam, 1993; Cottenie, 2005). Moreover, mechanisms generating species turnover between sites are not necessarily the same as those operating on local species diversity, but are equally important to be considered in effective management strategies (Bergamin et al., 2017; Edge et al., 2017). Yet studies assessing patterns of β -diversity within reservoir islands are restricted to birds and lizards in a Chinese dam (Si et al., 2015, 2016), demonstrating the importance of further studies focused on other taxonomic groups.

Mammals are widely hailed as regional conservation icons and critical components of tropical forest dynamics through their ecological roles as hyper-consumers, large predators, seed dispersal vectors and structural habitat modifiers (Dirzo et al., 2014; Mangan & Adler, 2000; Terborgh et al., 2001). Mammals can be extremely

diverse, particularly in the Amazon, ranging in body mass from <15 g to >150 kg (Paglia et al., 2012). As different components of the mammal fauna require different survey methods, ecological studies typically focus on surveying either small non-volant mammals (i.e., those usually sampled using live or pitfall trapping; hereafter, SMs) or mid-sized to large mammals (i.e., those sampled using direct or indirect observation, such as camera traps; hereafter, LMs).

Small and large mammals may differ not only in their sampling methods, but also may show contrasting responses to insularization created by dams due to the intrinsic characteristics of these two mammal groups. In fact, body size is known to interact with species dispersal ability and trophic position, differently affecting β -diversity patterns (Soininen, Heino, & Wang, 2017). Because of lower vagility, including flotation and swimming endurance (Cosson et al., 1999; Schoener & Schoener, 1984), SM assemblages should be mainly related to local habitat characteristics (Delciellos, Vieira, Grelle, Cobra, & Cerqueira, 2015; Olifiers, 2002; Pardini, de Souza, Braga-Neto, & Metzger, 2005) and present a higher species turnover among islands. Conversely, the higher vagility, larger spatial requirements and smaller population sizes of LMs (Chiarello, 1999) should result in assemblages with low β -diversity among islands, mainly related to environmental factors at the patch or landscape scales. These two hypotheses, related to small and large body sizes, have not yet been tested comparing species turnover of SMs and LMs at the same set of sites. In addition, the effect of major environmental factors correlated with compositional shifts across space remains poorly understood for both groups.

Here, we provide the first quantitative assessment of the habitat insularization effects on β -diversity of SM and LM species, conducted at one of the largest man-made archipelago in South America—the 28-year-old Balbina Hydroelectric Reservoir. Previous studies carried out in Balbina showed that island area and isolation were the strongest predictors of SM α -diversity (Palmeirim, Benchimol, Vieira, & Peres, 2018), whereas island area was the single best predictor for LM α -diversity (Benchimol & Peres, 2015a,b). We test the hypothesis that the low and high vagilities of SM and LM, respectively, generate different patterns of β -diversity for these two groups. We used multiplicative diversity decomposition of Hill numbers, an approach that considers the importance of rare, common and dominant species in generating β -diversity patterns (Jost, 2007; Tuomisto, 2010). We further examine how patterns of β -diversity are correlated to a set of environmental characteristics related to the local habitat structure, forest patch and landscape scales, which are widely recognized as important in enhancing mammal diversity (Chiarello, 1999; Delciellos et al., 2015; Pardini et al., 2005). Specifically, we predict that (1) β -diversity of both mammal groups should be higher for rare species, compared to dominant species; (2) between-island β -diversity of

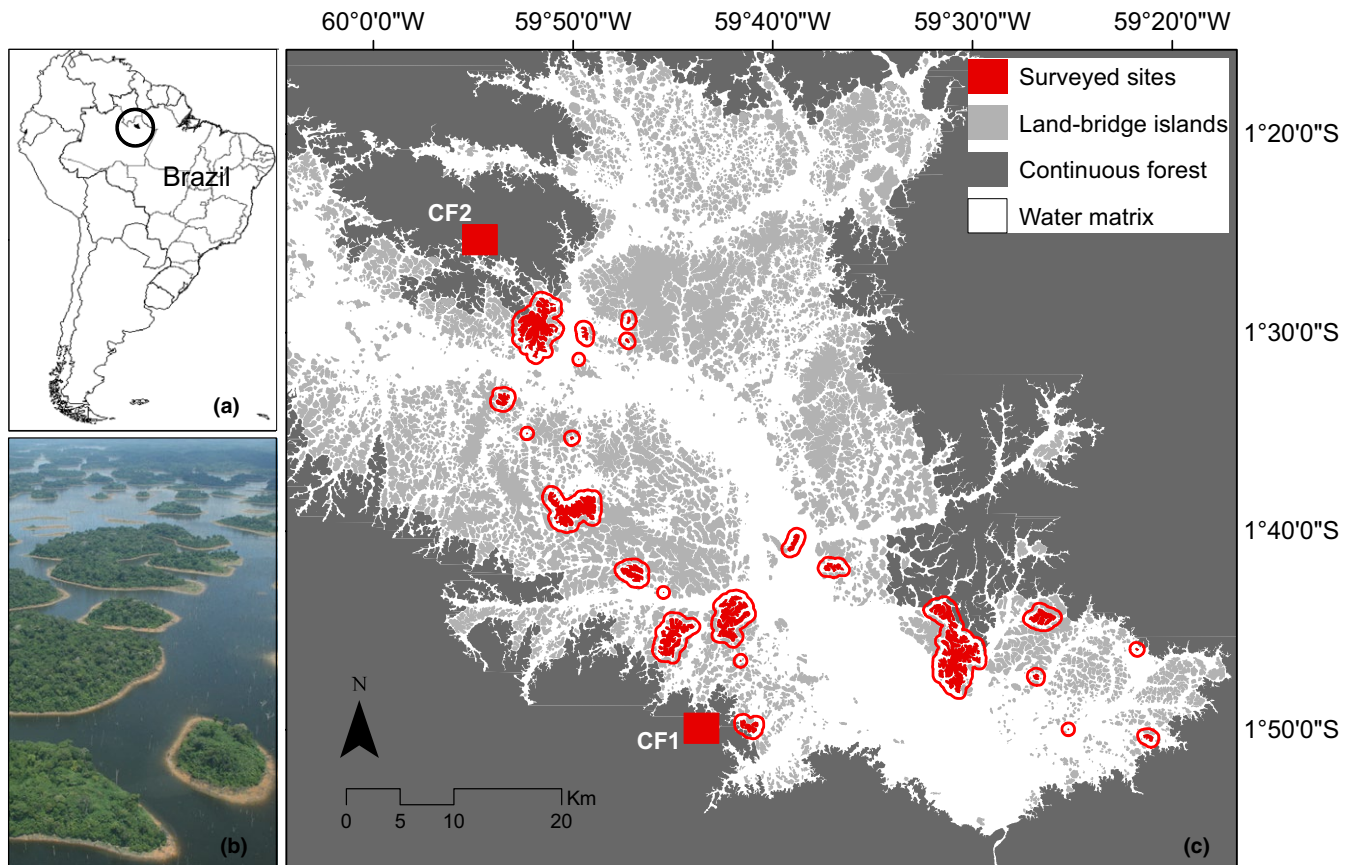


FIGURE 1 (a) Overview of the Balbina Hydroelectric Reservoir location in the Central Brazilian Amazon; (b) aerial photograph illustrating the archipelagic landscape (photo credit: E. M. Venticinque); and (c) spatial distribution of the 23 land-bridge islands (in red and highlighting the 500-m buffer polygons) and two continuous forest sites surveyed in the mainland (CF₁ and CF₂; red rectangles) [Colour figure can be viewed at wileyonlinelibrary.com]

SMs should be higher than that of LMs; and, (3) local habitat features should be a key factor of SM β -diversity, whereas LM β -diversity should be most correlated to patch or landscape metrics, such as island size and degree of isolation.

2 | METHODS

2.1 | Study area

This study was carried out at 23 islands and two continuous forest sites (hereafter, CFs) in the forest archipelago of the Balbina Hydroelectric Reservoir (1°48'S, 59°29'W; Figure 1) located in the Brazilian Amazonia. This dam was created in 1986 following the permanent closure of the Uatumã River, a left bank tributary of the Amazon River. Given the typically flat to undulating topography of the study region, a vast area of 312,900 ha of primary forest was flooded within the 443,772-ha hydroelectric reservoir (FUNCATE/INPE/ANEEL, 2000). The former hilltops of the pre-inundation forest area were converted into 3,546 land-bridge islands that are widely distributed throughout the reservoir lake. Islands and the neighbouring continuous forest sites consist of dense closed-canopy *terra firme* forest (Benchimol & Peres, 2015a). Forest islands within the reservoir have not been subject to logging nor hunting, but many

islands experienced understorey fires during the El Niño drought of late-1997 to early-1998 (Benchimol & Peres, 2015c). The mean annual temperature and rainfall in this region are 28°C and 2,376 mm, respectively (IBAMA, 1997). Part of the reservoir and a vast area of continuous forest on the left bank of the Uatumã River have been legally protected since this dam was built by the 942,786-hectare Uatumã Biological Reserve, the largest Brazilian protected area in this category.

We pre-selected 23 forest islands according to their size, degree of isolation and spatial distribution, so that a wide spectrum of island configurations could be sampled within the reservoir. Surveyed islands were at least 1-km apart from one another, with island size ranging from 0.83 to 1,466 ha (mean \pm SD: 213.47 \pm 352.31 ha; Table S1) and isolation distances to the nearest mainland varying from 44 to 11,872 m (4,503 \pm 3,352 m); CF sites were widely distributed around the reservoir and placed between 200 and 1500 m from the nearest lake margin (Figure 1).

2.2 | Mammal surveys

Small and mid-sized to large mammal assemblages were sampled twice at each forest site, during two field seasons. In 2014 and 2015, SMs were sampled along two continuous periods of 16 consecutive

nights, using linear trapping plots. Each plot consisted of a set of nine live trap stations (hereafter, LTs), followed by an array of three pitfall-trap units. Each LT station was placed 20 m apart from each other and included two Sherman traps (23 × 9 × 8 cm, H. B. Sherman Traps, Inc., Tallahassee, Florida) and one wire mesh trap (30 × 17.5 × 15 cm, Metal Miranda, Curitiba, Paraná). At each LT station, one trap was set on the ground, one in the understorey (~1.5 m high) and one in the (sub)canopy (>10 m high). Traps of different types were placed alternatively on the ground and in the understorey across consecutive stations, but only Sherman traps were placed in the canopy due to logistic limitations. At the forest canopy stratum, small mammals were sampled using an adaptation of the method described by Lambert, Malcolm, and Zimmerman (2005). LTs were baited with a mix of bananas, peanut powder, sardines and oak flocons. Pitfall traps (100 L) were also spaced apart by 20-m intervals and connected by a 50-cm high plastic fence that was buried 10 cm underground, and included 10 m of overhanging fence farther extended beyond the two external pitfalls. Due to spatial restrictions in small islands, alternative smaller trapping plots were established therein. Thus, all islands smaller than 2 ha and those between 2 and 10 ha were sampled by trapping plots containing only three LT stations followed by an array of one pitfall, and six LT stations followed by an array of two pitfalls, respectively. All traps were inspected daily and whenever live captures could not be identified in the field, a maximum of five voucher specimens per species per survey site were collected during the first trapping season and deposited at the Mammal Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), in Manaus, Brazil. All other individuals recorded were weighted and tagged (Fish and Small Animal Tag, size 1; National Band and Tag Co., Newport, Kentucky), so that any subsequent recaptures could be distinguished. Additionally, tissue samples were collected from all individuals recorded and deposited at the INPA Mammal Collection. However, we were not always able to identify at the species-level records of sympatric congeners of *Proechimys* spp. (*P. cuvieri* and *P. guyanensis*) and *Oecomys* spp. 1 (*O. roberti* and *O. bicolor*). Because these congeners are ecologically very similar (Jones et al., 2009), we further refer to those taxa as “ecospecies.” To streamline, we use hereafter “species” to refer to both species and ecospecies. Data collection followed ASM guidelines (Sikes, 2016) and was approved by an institutional animal care and use Brazilian committee (SISBIO License No. 39187-4).

In 2011 and 2012, LMs were sampled for two continuous periods of 30 days each using camera trapping. Each camera trap station (hereafter, CT) consisted of one digital camera (Reconyx HC 500 Hyperfire), unbaited and placed at 30–40 cm above ground. At each surveyed site, consecutive CT stations were established along linear transects, spaced by at least 500 m (except for small islands). We configured all CTs to obtain a sequence of five photos for each animal recorded, using 15-s intervals between records. However, we only considered conspecific records at the same CT site as independent if either intervals between photos exceeded 30 min or conspecifics of different groups could be recognized on the basis of natural marks.

To maximize the heterogeneity of environments sampled at each site and minimize variation in trap density, sampling effort was proportional to forest patch size for both mammal groups. As such, depending on their size, islands were sampled by one to four trapping plots and two to ten CT stations; whereas both CF sites were sampled by six trapping plots and 15 CT stations. This amounted to a total sampling effort of 48,350 trap-nights for SMs, and 8,160 trap-nights for LMs.

2.3 | Local habitat, patch and landscape variables

In 2012, we obtained local habitat variables to describe vegetation structure and habitat quality for each forest site surveyed using floristic surveys within 0.25-ha (250 m × 10 m) plots established in each focal island and CF site, in which all trees ≥10 cm diameter at breast height (DBH) were measured and identified at species-level. The number of plots surveyed per site was proportional to the area of each site, ranging from one to four (for details on floristic surveys, see Benchimol & Peres, 2015c). These floristic plots provided data on tree species richness (S.TREE), number of trees (N.TREE), percentage of old-growth live trees (OGT) that persisted from the pre-flooding period, aggregated basal area of live trees bearing fleshy fruits (BA_{FF}), number of woody lianas (LIANA) and a measure of ground fire severity (FIRE; see Table 1 for a description of these variables). Additionally, we conducted a semi-supervised classification to obtain four land cover classes (closed-canopy forest, open-canopy forest, bare ground and water) using ArcMap 10.1 (ESRI, 2012) and obtained the percentage of closed-canopy forest (CC) within each island and CF site based on high-resolution multi-spectral RapidEye imagery (5-m resolution with 5-band colour imagery) of the entire study region (Table 1).

Patch and landscape variables were also calculated from RapidEye imagery, using ArcMap 10.1. At the patch scale, we measured island AREA, island SHAPE (total perimeter length of each focal island divided by AREA), and its distance to the nearest lake margin (DIST.C). At the landscape scale, we obtained for each surveyed island, the total amount of land mass area within a buffer threshold (COVER), and a proximity index that considers both area and isolation of each land mass within that buffer (PROX). Because previous studies used a 500-m radial buffer to predict both small (Palmeirim, A. F., Benchimol, M., Vieira, M. V., & Peres, C. A., 2018) and mid-sized to large mammal richness (Benchimol & Peres, 2015a) at the same islands, our COVER and PROX metrics considered this radius threshold for analyses (see Table 1 and Benchimol & Peres, 2015a for further details on imagery processing, and patch and landscape metrics). Additionally, this buffer size minimizes or eliminates overlap between neighbouring landscapes, conferring greater spatial independence. Because patch and landscapes variables could not be obtained for CF sites, we assigned their metrics to closely approximate “real-world” values. Thus, for AREA, we considered an area one order of magnitude larger than our largest island; for SHAPE, we divided the total perimeter length (considered to be 1×10^8 , i.e., four orders of magnitude larger than the highest island perimeter) of each

TABLE 1 Local habitat quality, patch and landscape variables measured, potentially affecting mammal β -diversity among 25 forest sites within the Balbina Hydroelectric Reservoir archipelagic landscape. The overall range, mean and standard deviation (SD) are provided for each variable. Because patch and landscapes variables could not be obtained for continuous forest sites (CF), we assigned values to closely approximate each real value, as indicated below

Name (code name)	Variable description	Range (mean \pm SD)
Local habitat scale		
Tree species richness (S.TREES)	Number of tree species ≥ 10 cm DBH per 0.25-ha forest plots within each focal island and mainland site.	14–70.5 (54.6 \pm 11.5)
Number of trees (N.TREES)	Density of trees ≥ 10 cm DBH obtained from floristic surveys in 0.25-ha forest plots within each focal island and mainland site.	84–176 (123.4 \pm 22.8)
Closed-canopy forest (CC)	Percentage of closed-canopy forest within each forest site.	37.5–10.65% (76.2 \pm 15.5)
Fire severity (FIRE)	Fire severity within each forest site, scored on an ordinal scale based on the extent of each forest site affected by surface (understorey) fires and the number of charred trees and height of char marks on each tree.	0–3 (1.96 \pm 0.60)
Old-growth trees (OGT)	Percentage of old-growth trees calculated from floristic surveys in 0.25-ha forest plots within each focal island and mainland site.	10.71–82.34% (64.1 \pm 17.0)
Basal area of trees bearing fleshy fruits (BA _{FF})	Basal area of trees bearing fleshy fruits, derived from floristic surveys of all live trees ≥ 10 cm DBH in 0.25-ha forest plots within each focal island and mainland site.	12.1–35.0 cm (20.6 \pm 5.0)
Lianas (LIANA)	Mean number of woody lianas (>2.5 cm DBH) calculated from floristic surveys in 0.25-ha forest plots within each focal island and mainland site.	0.0–40.5 (21.5 \pm 10.3)
Patch scale		
Island size (AREA)	Island area of each focal island ($\log_{10} \times$; CF = 14,660 ha).	0.8–1,466.0 ha (199.0 \pm 344.1)
Island shape (SHAPE)	Perimeter length of each focal island divided by the total island area (CF = 0.592).	0.004–0.592 (0.061 \pm 0.152)
Distance (DIST.C)	Euclidean distance from each island to the nearest neighbouring mainland forest site (CF = 0 m).	0–11,872 m (4,143 \pm 3,339)
Landscape scale		
Forest cover (COVER)	Percentage of land mass area within a 500-m buffer (CF = 100%).	5.91–100.00% (37.50 \pm 22.28)
Proximity (PROX)	The sum of all island areas divided by the squared sum of edge-to-edge distances from each focal island to all islands within a 500-m buffer. Instead of considering the area of each island within the buffer (as in McGarigal et al., 2012), we considered the total ("true") area of each island ($\log_{10} \times$; CF = 1.00×10^{10}).	$2.75\text{--}1.00 \times 10^{10}$ ($9.10 \times 10^7 \pm 2.71 \times 10^9$)

focal island divided by the AREA. We further considered DIST.C to be equal to zero; PROX to be one order of magnitude greater than our largest island; and COVER to be the maximum value of 100% (Table 1).

2.4 | Data analysis

We excluded from the analyses two Echimyid rodents—*Makalata didelphoides* and *Echimyus chrysurus*—which had been recorded only once throughout the study. Both species are primarily folivores (Patton, Da Silva, & Malcolm, 2000), and consequently are rarely attracted to the bait used here. Due to differential sampling effort per site, species abundances were standardized for each site, considering 2,095 and 319 trap-nights, which is the average sampling effort per site for SMs and LMs, respectively. Because camera trapping cannot quantify numbers of individuals, we used the number of captures for SMs rather than the number of individuals recorded, testing whether these variables were correlated. This allowed us to improve convergence in the comparison of β -diversity estimates for SMs and

LMs. The number of SM captures was indeed highly correlated with the number of individuals (15 species detected ≥ 5 sites: $r = .97 \pm .05$ (mean \pm SD); Table S2).

The accuracy of mammal surveys was assessed using the coverage estimator recommended by Chao and Jost (2012), which estimates the proportion of the total number of individuals in an assemblage that belongs to the species represented in the sample. Overall sample coverage was high, representing on average (\pm SD) $95\% \pm 0.07\%$ and $99\% \pm 0.01\%$ of the SM and LM species recorded, respectively (Table S1). This indicates that our sampling effort provided satisfactory estimates of species richness within each forest site.

Patterns of mammal β -diversity were analysed using multiplicative diversity decomposition of Hill numbers: ${}^qD_\beta = {}^qD_\gamma / {}^qD_\alpha$. Here, ${}^qD_\gamma$ corresponds to the observed total number of species (γ -diversity); ${}^qD_\alpha$ to the mean local number of species recorded per site (α -diversity); and, ${}^qD_\beta$ to the "effective number of completely distinct communities" (β -diversity). The equations for ${}^qD_\gamma$ and ${}^qD_\alpha$

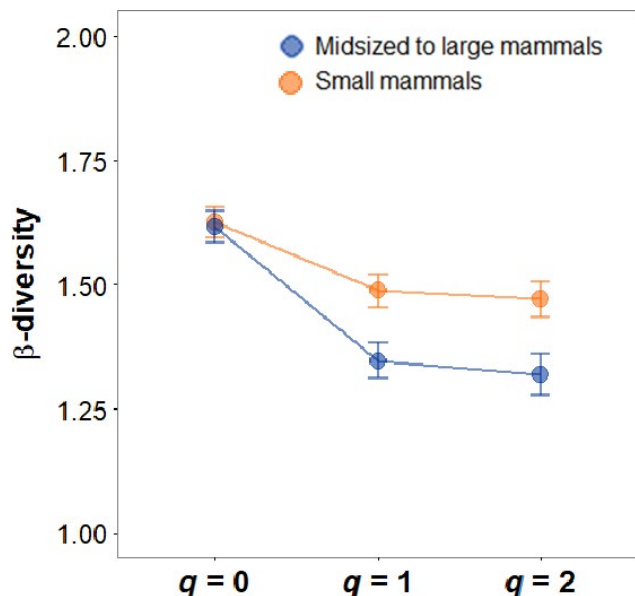


FIGURE 2 Mean β -diversity estimates of small and mid-sized-large mammals surveyed at 25 forest sites within the Balbina archipelago considering all possible combinations of sites ($N = 300$ pairwise comparisons). β -diversity was assessed using three orders of q (0, 1 and 2), which determines the sensitivity of the measure to relative species abundances. For each mammal group, we indicate the mean β -diversity, and the corresponding 95% confidence intervals [Colour figure can be viewed at wileyonlinelibrary.com]

are detailed elsewhere (Jost, 2007; Tuomisto, 2010); $^qD_\beta$ was calculated for each pairwise comparison considering all forest sites (i.e., islands and CF sites; $N = 300$) and ranges between 1, when both communities are identical, and 2, when both communities are completely distinct from each other (Jost, 2007). In addition, β -diversity depends on the parameter q , which determines the sensitivity of the measure to species relative abundances (Jost, 2007; Tuomisto, 2010). We considered β -diversity estimates of order 0 ($^0D_\beta$), 1 ($^1D_\beta$) and 2 ($^2D_\beta$), in which $^0D_\beta$ gives disproportionate weight to rare species, as it is not sensitive to species abundances; $^1D_\beta$ weights each species according to its abundance in the community, measuring the turnover of “common” or “typical” species in the community; and $^2D_\beta$ favours very abundant species and is therefore interpreted as the turnover of “dominant” species in the community (Jost, 2007; Tuomisto, 2010). In spite of the small differences in sample coverage observed among sites, particularly across the SM data (Table S1), we further obtained expected β -diversity values for both mammal groups to improve the estimation of entropy (Beck, Holloway, & Schwanghart, 2013; Marcon & Hérault, 2015). To do so, we used the “ENTROPART” R package (Marcon & Hérault, 2017), which uses the best available diversity estimator according to the data. We then compared observed and expected values of SM and LM β -diversity for each order of q , using paired t tests (Zar, 1999). Because we found significant differences between observed and expected β -diversity for both mammal groups for some orders of q (Table S3), we used the expected values for subsequent analyses.

We used paired t tests (Zar, 1999) to compare β -diversity in the different q orders between each mammal group. Further, we used Mantel tests performed using the “VEGAN” R package (Oksanen et al., 2007) to assess whether β -diversity was correlated with distance (i.e., geographic distance matrix among all islands and CF sites) and to the matrices showing between-site differences in local habitat variables (i.e., S.TREE, N.TREE, OGT, BA_{FF}, LIANA, FIRE, CC), in patch (i.e., AREA, SHAPE, DIST.C) and in landscape (i.e., COVER, PROX). For all environmental variables, matrices were based on Euclidian distances. All analyses were performed using R (R Development Core Team, 2013), assuming a significance level ≤ 0.05 (Zar, 1999).

3 | RESULTS

We obtained 1,481 captures of SMs ($N = 853$ individuals) representing 20 species (17 genera; three families), and 6,290 camera-trapping records of LMs representing 22 species (18 genera; 13 families; Table S4). The number of species per site ranged from 2 to 15 (7.0 ± 4.2 species; mean \pm SD) for SMs, and from 1 to 19 (8.8 ± 5.8) for LMs. The most abundant SM species was *Marmosa demerarae*, an arboreal marsupial recorded at 18 sites and corresponding to nearly one-third of all captures ($N = 499$). Despite the local commonness of this species, others were often similarly abundant (e.g., *Didelphis marsupialis* and *Proechimys* spp.), and whenever absent, *M. demerarae* was replaced by other locally common species (e.g., *Philander opossum*, *Hylaeamys megacephalus* and *Marmosa murina*; Figure S1a). Considering LMs, the red acouchy *Myoprocta acouchy* was the most abundant species, detected at 21 sites and accounting for 59% of all records ($N = 3,593$). This small-bodied dasyproctid rodent was consistently the most abundant species at nearly all islands larger than 5 ha ($N = 20$) and mainland CF sites (Figure S1b). At each site, the number of uncommon or occasional species, that is those recorded only once or twice, averaged $41.5\% (\pm 19.9)$ and $33.1\% (\pm 31.2)$ for SM and LM assemblages, respectively.

3.1 | Patterns and environmental correlates of β -diversity

Considering all combinations of forest sites ($N = 300$ pairwise comparisons), both SMs and LMs exhibited similarly high β -diversity (SM: 1.63 ± 0.27 , mean \pm SD; LM: 1.62 ± 0.28 ; $t = 0.491$, $df = 299$, $p = .624$) when considering only the number of species ($q = 0$). When species abundance was considered ($q = 1$ and 2), however, β -diversity was significantly higher for SM ($^1\beta = 1.48 \pm 0.28$; $^2\beta = 1.47 \pm 0.31$) than for LM assemblages ($^1\beta = 1.34 \pm 0.31$, $t = 8.113$, $df = 299$, $p < .001$; $^2\beta = 1.32 \pm 0.37$, $t = 7.678$, $df = 299$, $p < .001$; Figure 2). Overall, levels of β -diversity for both groups decreased when species were weighted proportionally to their abundances, especially for LM assemblages. In fact, β -diversity of LMs was 1.23 times higher when we considered presence-absence data ($q = 0$) rather than relative abundances ($q = 1$ and 2; Figure 2).

TABLE 2 Correlation between β -diversity estimates among forest sites of small and midsized to large mammals and geographic distance among sampled sites, inter-site differences (Δ) in local habitat, patch and landscape variables at 25 forest sites sampled at the Balbina Hydroelectric Reservoir ($N = 300$ pairwise comparisons). Three orders of q (0, 1 and 2), which determine the sensitivity of each β -diversity component to the relative abundance of species. Pearson correlation coefficients and significance were calculated using Mantel tests (* $p < .05$; ** $p \leq .001$)

Variables	β -diversity order	Small mammals	Midsized-large mammals
DISTANCE	0	0.046	0.015
	1	0.070	0.051
	2	0.085	0.069
Local habitat scale			
Δ S.TREES	0	0.307*	0.430**
	1	0.331*	0.427*
	2	0.327*	0.387*
Δ N.TREES	0	0.133	0.083
	1	0.039	0.076
	2	0.007	0.049
Δ OGT	0	0.305*	0.319**
	1	0.312*	0.476*
	2	0.293*	0.445*
Δ BA _{FF}	0	0.161	0.245*
	1	0.269*	0.396*
	2	0.275*	0.434*
Δ LIANA	0	0.056	0.357**
	1	0.075	0.287*
	2	0.083	0.244*
Δ FIRE	0	-0.181	0.201*
	1	-0.145	-0.026
	2	-0.142	-0.048
Δ CC	0	0.070	0.114
	1	0.113	0.191
	2	0.100	0.151
Patch scale			
Δ AREA	0	0.293*	0.751**
	1	0.141	0.465**
	2	0.150	0.418*
Δ SHAPE	0	-0.116	0.228
	1	-0.189	-0.069
	2	-0.160	-0.077
	0	-0.070	0.214*
Δ DIST.C	1	-0.167	-0.075
	2	-0.156	-0.082
Landscape scale			
Δ COVER	0	0.105	0.386**
	1	0.053*	0.199
	2	0.074	0.182
Δ PROX	0	0.071	0.369*
	1	-0.134	0.043
	2	-0.127	0.019

For both small and midsized to large mammals, β -diversity was more strongly related to environmental variation among sites than to spatial distance. Indeed, β -diversity estimates (for any order q) for both mammal groups were not correlated with geographic distance among forest sites (Table 2). Overall, local habitat variables were the most important correlates of β -diversity for both small and midsized to large mammals. In particular, differences in tree species richness, percentage of old-growth tree and basal area of trees bearing fleshy fruiting were positively correlated with mammal β -diversity among sites (Table 2). Additionally, β -diversity of LMs was significantly and positively related to greater differences in the number of lianas among sites.

Patch and landscape variables were correlated with β -diversity for some q orders, especially for LMs. In fact, β -diversity of LMs was related to some measures of isolation (including COVER, PROX and DIST.C), particularly when considering rare species ($^0\beta$; Table 2). Island size was correlated with β -diversity of LMs at all orders of q , but was correlated to patterns of β -diversity for SMs only when rare species were considered (Table 2). In other words, across the archipelagic landscape of Balbina, β -diversity for SMs was generally high, compared to that of LMs, regardless of pairwise differences in island sizes. On the other hand, β -diversity for LMs was higher between islands of contrasting sizes, and lower between small islands, or between large islands and CF sites (Figure S2).

4 | DISCUSSION

Habitat insularization in the aftermath of river damming has led to wholesale local extinctions of tropical forest species (Jones et al., 2016). However, understanding how diversity is organized and maintained in biological communities is still poorly investigated in archipelagic systems, including islands created by hydroelectric reservoirs (Si et al., 2015, 2016). Indeed, no study to date had examined patterns of β -diversity for any taxonomic group within a major Neotropical reservoir, a region experiencing a boom in dam building (Lees et al., 2016). Hence, this is the first study that examines the main environmental correlates of β -diversity for both small and midsized to large terrestrial and arboreal mammals within a truly fragmented tropical forest landscape. As expected, when considering common and dominant species, SMs exhibited higher levels of β -diversity than LMs. We also showed that habitat quality plays a major role in mammal species turnover for both groups. Patch and landscape variables were key correlates of β -diversity of only midsized to large-bodied mammals, when all combinations of sites were considered. Yet, when CF sites were directly compared to islands (given pairwise comparisons between any of the two CF sites and any of the 23 islands), patch and landscape variables were also important correlates of SM β -diversity (Table S5). In particular, the severe local extinctions of LMs in smaller islands (Benchimol & Peres, 2015a) resulted in the biotic homogenization of assemblages therein.

4.1 | Patterns of mammal β -diversity

For both SMs and LMs, β -diversity estimates were higher when considering rare species. This is expected given the observed patterns of dominance, with only one or two records obtained for more than one-third of all SM and LM species detected, respectively. Other studies in fragmented forest landscapes showed similar results for small mammal (Püttker, de Arruda Bueno, Prado, & Pardini, 2015), plant (Arroyo-Rodríguez et al., 2013) and bird assemblages (Morante-Filho, Arroyo-Rodríguez, & Faria, 2016; Si et al., 2016). Thus, to maintain the regional pool of species (γ -diversity), including rare mammal species, conservation efforts at Balbina and analogous landscapes must cover a reasonable range of habitat patches (Meza-Parral & Pineda, 2015; Socolar et al., 2016). Nevertheless, the LM species exhibiting a small number of occurrences, including jaguar, tapir and giant anteaters, which are able to transverse the aquatic matrix and visit multiple land masses (Benchimol & Peres, 2015b), may actually correspond to transient species, rather than true residents in forest islands created by dams (Terborgh, Lopez, & Tello, 1997). This can inflate differences in species composition of LMs between sites when considering only species presence-absence. In contrast, differences in SM species composition for $q = 0$ could be underestimated due to the lower probability of arboreal species to approach any trap in the three-dimensional forest canopy. Although our sampling effort provided satisfactory estimates of species richness for both mammal groups, we minimized possible underestimates for SMs, or overestimates for LMs, using expected β -diversity values (Beck et al., 2013). Furthermore, when pairwise comparisons consisted of one CF site and one island, LM β -diversity for $q = 0$ was higher than that for SMs (Figure S3). This illustrates the proportionally higher turnover of rare species from continuous to insular forests for LMs, compared to those for SMs.

We also considered abundance-based measures of β -diversity (i.e., $q = 1$ and $q = 2$), which are dominated by common species, given their importance to inform ecosystem processes (Socolar et al., 2016). In particular for LMs, the decrease in β -diversity when species abundance was considered ($q = 1$ and 2) may be due to the higher number of common species occupying most islands. Moreover, species turnover for SM was higher than that for LMs. Indeed, local composition of common SM species was more variable across the spectrum of island sizes/CF sites than that for LMs (Figure S1). Differences in vagility between SMs and LMs likely explain the higher abundance-based β -diversities of SMs. However, the larger effect of abundance-based β -diversity on SMs, compared to LMs, suggests an additional mechanism. SM assemblages are closely linked to local habitat conditions, being mainly determined by local characteristics related to habitat structure (Delciellos et al., 2015; Olifiers, 2002). Such trophic and structural resources for small mammals tend to be patchy distributed, so that populations are often clustered over large forest areas (Charles-Dominique et al., 1981). This may contribute with the overall higher abundance-based β -diversity values

recorded for SMs. Interestingly, such heterogeneity in SM assemblages was also recorded between smaller islands, where only a reduced set of species persist (Palmeirim, A. F., Benchimol, M., Vieira, M. V., & Peres, C. A., 2018). Indeed, habitat conditions are highly variable across Balbina forest islands, for example, in terms of vertical stratification of the vegetation (Benchimol & Peres, 2015c). Such a link to local habitat conditions may lead to multiple compositional pathways in which SM species differ in abundance between sites according to locally available resource spectra, habitat structure and ecological niches, as observed for plant species (Arroyo-Rodríguez et al., 2013).

The observed correlation between LM β -diversity and differences in island sizes indicates that LM assemblages shared a more similar species composition either between larger islands and CF sites, or between smaller islands (Figure S2). LM β -diversity in particular, considering the abundance data, tends to be either high between small and medium to large islands or CF sites, or low between large islands and CF sites (Figure S2b,c). Such extreme β -diversity values appear to result from different sets of common or dominant species occupying either small or medium to large islands and continuous forest sites. Indeed, nine-banded armadillos (*Dasypus novemcinctus*) represented the most abundant species in small islands, whereas large islands/CF sites were occupied by at least three relatively common rodent and ungulate species (i.e., *Dasyprocta leporina*, *Myoprocta acouchi* and *Pecari tajacu*, Figure S1b). This pattern is expected for the largest islands and CF sites, which harboured a nearly full, if not complete, species assemblage (Benchimol & Peres, 2015a). Yet, the lower LM β -diversity between smaller islands, occupied by a smaller subset of species (Benchimol & Peres, 2015a), implies a subtractive homogenization in species composition of LMs (Karp et al., 2012; Püttker et al., 2015; Socolar et al., 2016)—involving the hyperdominance of a similar subset of species (Chase, 2007). Common species typically have relatively high dispersal abilities and generalist habits (Karp et al., 2012; Vellend et al., 2007). Such unidirectional pattern of species turnover is expected to promote cascading effects onto lower trophic levels, which can further disrupt the structure of the entire forest ecosystem at small islands (Tabarelli, Peres, & Melo, 2012). In Balbina, where 94.7% of all 3,546 islands are smaller than 100 ha, evidence for biotic homogenization suggests that any ecosystem functions provided by LMs are already degraded across most of the landscape, further posing a major threat to the maintenance of regional scale biodiversity (Olden, Poff, Douglas, Douglas, & Fausch, 2004; Solar et al., 2015).

4.2 | Environmental correlates of mammal β -diversity

We expected assemblages of SMs, rather than those of LMs, to be context-dependent in terms of local habitat structure. The unexpected association between β -diversity of LMs and local habitat variables could be related to the large spectrum of body

sizes spanned by this group, from small-bodied (e.g., the squirrel *Guerlinguetus aestuans*, 210 g), to very large-bodied species (e.g., jaguar, 158 kg; lowland tapir, 260 kg). As such, variables related to local habitat quality—tree species richness, prevalence of old-growth trees and basal area of trees bearing fleshy fruits—played a major role in predicting species turnover for both mammal groups. Those latter two habitat variables can increase the amount of food and structural resources available to at least small mammal species (Malcolm, 1991), while the proportion of old-growth trees remaining on islands is a proxy of the degree of forest ecosystem integrity (Benchimol & Peres, 2015c). All of these habitat variables may therefore represent a gradient of forest habitat quality for mammals (Delciellos et al., 2015; Lomolino & Perault, 2000; Pardini et al., 2005, 2009). Therefore, maintaining habitat integrity should minimize the homogenization of mammal species assemblages across the landscape.

Variables at both the forest patch and landscape scale were also strong predictors of β -diversity, particularly for LMs. As stated above, at the patch scale, island area predicted β -diversity of LMs, while β -diversity of SMs was only predicted by area when rare species were considered, or when CF sites were compared to islands (Table S5). In comparison to SMs, most LMs require larger areas and sustain lower population densities (Wright, Patterson, Mikkelsen, Cutler, & Atmar, 1998). Therefore, assemblages of large-bodied mammals are expected to be greatly affected by the remaining habitat area in fragmented landscapes (Chiarello, 1999; Michalski & Peres, 2005; Newmark, 1996). Indeed, forest area alone explained 91% of the overall variation in species richness for medium and large-bodied vertebrates surveyed at 37 Balbina islands (Benchimol & Peres, 2015a). In the case of SMs, island area was correlated with the turnover of only rare species, which probably matches those species with the largest spatial requirements or higher habitat specificity, both of which are primarily accommodated by larger forest sites (Palmeirim, A. F., Benchimol, M., Vieira, M. V., & Peres, C. A., 2018). Although large islands and mainland forest sites can retain a larger number of rare species, those sites must still meet appropriate habitat quality conditions to sustain viable populations. Moreover, when comparing CF sites with islands, β -diversity right across the mammal size spectrum was negatively correlated with island shape (Table S5). This shape index reflects the extent of forest edges weighted by the respective island area, further denoting the intensity of edge effects. This reinforces the negative effects of forest edges on mammal assemblages (Pfeifer et al., 2017), further contributing to the overall homogenization of mammal assemblages.

Our results also indicate that β -diversity of LMs, and β -diversity of SMs when pairwise comparisons between mainland and island sites were considered, were further correlated with degree of site isolation at both the patch and landscape scale (i.e., forest cover, proximity and distance to the mainland). The ability of species to disperse between fragments is one of the main determinants of population persistence in fragmented landscapes (Moilanen & Hanski, 1998; Schooley & Wiens, 2004), including the Balbina archipelago, where the intrinsic swimming capacity of different species

was positively related to island occupancy rates for LMs (Benchimol & Peres, 2015b). Isolation-related variables also account for the availability of neighbouring habitat, and therefore the probability of recolonization events. Thus, both species ability to disperse and habitat availability apparently shape the turnover of LM species in an archipelagic landscape (cf. Rabelo, Bicca-Marques, Aragón, & Nelson, 2017) and that of SMs between mainland continuous forest and forest islands.

In general, correlation values between β -diversity and environmental variables were lower for SMs (Table 2). The large amount of variation that cannot be explained by these correlations suggests that other habitat variables may be important to SM β -diversity (e.g., overstorey and understorey vegetation density and number of fallen logs; Delciellos et al., 2015; Olifiers, 2002). As such, a finer scale study would be required to improve our understanding of correlates of SMs β -diversity.

4.3 | Conservation implications

This study highlights the importance of considering β -diversity in informing conservation recommendations in anthropogenic landscapes, and improving our understanding of the pervasive impacts of mega hydropower dams on tropical forest biodiversity. First, we revealed that environmental factors correlated with mammal β -diversity failed to match the predictors observed in previous vertebrate α -diversity studies carried out in the same study landscape. While the number of SM species was related to island area and proximity (Palmeirim, A. F., Benchimol, M., Vieira, M. V., & Peres, C. A., 2018), the small mammal species turnover across the archipelagic landscape was primarily correlated with local habitat features. Yet, when pairwise comparisons were restricted to those between CF sites and islands, patch and landscape variables were also important correlates of SM β -diversity (Table S5). Likewise, although island size is a powerful predictor of large mammal species richness (Benchimol & Peres, 2015a), the species turnover of LMs is additionally correlated with a set of local habitat variables. Other studies also report divergent drivers of either α - or β -diversity, for example in stream fish communities (Edge et al., 2017). Therefore, focusing on predictors of α -diversity alone would fail to understand drivers of species turnover, and consequently cannot ensure appropriate guidelines for the long-term conservation of full mammal assemblages in fragmented tropical forest landscapes.

In land-bridge islands isolated within hydroelectric reservoirs, edge effects tend to be stronger than in non-insular habitat fragments, entailing more drastic changes in forest structure, particularly in smaller islands (Benchimol & Peres, 2015c). This further represents a challenge in maintaining the regional scale mammal diversity at Balbina, where only <10% of all islands are >100 ha. In any case, this study illustrates a relatively benign scenario in terms of mammal β -diversity 28 years after damming, mainly because the Balbina archipelago has been effectively protected by the largest Biological Reserve in Brazil. In the long-term, as Balbina islands

become more degraded by edge effects, insular mammal assemblages, particularly those of larger bodied species, may become even more homogeneous, through further decays in β -diversity. This will however depend on how edge effects will continue to impact insular forest structure, which may lead to either homogenization or differentiation, as smaller and larger islands will likely burn more or less frequently, respectively (Benchimol & Peres, 2015c). Because non-volant mammals also provide key ecological services for ecosystem maintenance (Dirzo et al., 2014), their loss can substantially affect tropical forest functioning. Therefore, future assessments of hydropower development should carefully weigh environmental costs in terms of biodiversity loss against any socioeconomic benefits.

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DATA AVAILABILITY

The ecological data used in this manuscript are available on the supplementary material of this manuscript, in Palmeirim, A. F., Benchimol, M., Vieira, M. V., & Peres, C. A. (2018) and in Benchimol and Peres (2015a,b,c).

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BIOSKETCHES

The authors of this study form an interdisciplinary team from a range of institutions in Brazil (A.F.P. and M.V.V.: <http://www.intranet.biologia.ufrj.br/labvert/equipe.html>; M.B. and J.M.F.: <https://www.appliedecologylab.org/main-researchers>), and the UK (C.A.P.: <https://www.uea.ac.uk/environmental-sciences/people/profile/c-peres>). This team has research interests and expertise that cover the fields of tropical ecology and conservation science, including the impacts of habitat change and degradation in tropical forest landscapes. This research is part of a project aiming to improve our understanding of the impacts of habitat fragmentation on biodiversity loss in Neotropical forests, by evaluating the patterns of both faunal extinctions and floristic changes in insular forest habitat patches (<https://www.researchgate.net/project/Predicting-biodiversity-loss-in-forest-islands-created-by-a-mega-dam-in-Brazilian-Amazonia>).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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