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

Short running-title: Mammal β-diversity in land-bridge islands

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Abstract

Aim Mega hydroelectric dams have become one of the main drivers of biodiversity loss in the lowland tropics. Vertebrate studies in tropical reservoirs 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 in these anthropogenic landscapes. Here we unravel the patterns and predictors of mammal β-diversity including both small (SM) and midsized to large mammal species (LM) across 23 islands and 2 continuous forest sites within one of the largest South American hydroelectric reservoirs.

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 separately using multiplicative diversity decomposition of Hill numbers to test to what extent β-diversity of SMs and LMs was related to a set of environmental characteristics measured at different spatial scales.

Results Habitat variables, such as tree richness and percentage of old-growth trees, were the strongest predictors of β-diversity among sites for both mammal groups. Conversely, β-diversity was weakly related to patch and landscape characteristics, except for LMs, for which β-diversity was predicted by differences in island sizes.

Main conclusions Although island size plays a major role in structuring mammal α-diversity in several land-bridge islands, local vegetation characteristics were key predictors of between-site β-diversity for both mammal groups within this large Amazonian archipelago. Moreover, the lower β-diversity of LMs between smaller islands suggests subtractive homogenization of this group. 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.

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Introduction

Mega hydroelectric dams have become one of the main drivers of habitat loss and fragmentation worldwide (Jones *et al*., 2016; Winemiller *et al*., 2016; Gibson *et al.*, 2017). 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 (Zarf *et al*., 2015). As such, the hydropower sector has greatly expanded in the Amazon Basin (Lees *et al*., 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 (ECOA, 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 *et al*., 2015, 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), and restricting our inferences to such measures of diversity may mask the true impact of anthropogenic disturbances on ecosystem functioning (González-Maya *et al*., 2015), further hindering the application of more effective management actions (Socolar *et al*., 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; Whitakker, 1972), which is an important component of regional diversity (γ-diversity; Kadmon and 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 and Adler, 2000; Terborgh *et al*., 2001). Mammals can be extremely diverse, particularly in the Amazon, where they are represented by 427 species (Mittermeier *et al.*, 2002), 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 midsized to large terrestrial 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 *et al.*, 2017). Because of lower vagility, including flotation and swimming endurance (Schoener and Schoener, 1984; Cosson *et al.*, 1999), SM assemblages should be mainly related to local habitat characteristics (Delciellos *et al*., 2015; Pardini *et al.*, 2005; Olifiers, 2002), 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 that converge across a large number of islands. 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 drivers of 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 (AF Palmeirim, pers. comm.), whereas island area was the single best predictor for LM α-diversity (Benchimol and Peres, 2015a, 2015b). 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. Multiplicative diversity decomposition of Hill numbers was used, 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 predicted by a set of environmental characteristics related to the local habitat structure, forest patch and landscape scales, which are widely recognised 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 SMs should be higher than that of LMs; and, (3) local habitat features should be the key predictors of SM β-diversity, whereas LM β-diversity should be most affected by patch and landscape metrics, such as island size and isolation.

Methods

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; Fig. 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 and 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 and Peres, 2015c). The mean annual temperature and rainfall in this region is 28ºC 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 as CFs were at least 1-km apart from one another, with island size ranging from 0.83 to 1,466 ha (mean ± SD: 213.47 ± 352.31 ha; Table S1) and isolation distances to the nearest mainland varying from 44 to 11,872 m (4,503 ± 3,352 m).

Mammal surveys

Small and midsized 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 x 9 x 8 cm, H. B. Sherman Traps, Inc., Tallahassee, Florida) and one wire mesh trap (30 x 17.5 x 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 *et al.* (2005). LTs were baited with a mix of bananas, peanut powder, sardines and oak flocks. 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 *et al.*, 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-sec 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 recognised on the basis of natural marks.

To maximise the heterogeneity of environments sampled at each site and minimise 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.

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 and 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 nearest distance to any CF site in the mainland (DIST). 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 (AF Palmeirim *et al*., pers. comm.) and midsized to large mammal richness (Benchimol and Peres, 2015a) at the same islands, our COVER and PROX metrics considered this radius threshold for analyses (see Table 1 and Benchimol and Peres, 2015a for further details on imagery processing, and patch and landscape metrics). Additionally, this buffer size minimises or eliminates overlap between neighbouring landscapes, conferring greater spatial independence.

Data analysis

We excluded from the analyses two Echimyid rodents ─ *Makalata didelphoides* and *Echimys chrysurus* ─ which had been recorded only once throughout the study. Both species feed on leaves and seeds , in addition to some fruit (Patton *et al.*, 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: $r = 0.97 \pm 0.05$ (mean ± 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 (± SD) 95 ± 0.07% and 99 ± 0.01% of the SM and LM species recorded, respectively (Table S1). This indicates that our sampling effort provided satisfactory estimates of β-diversity within each forest site. However, to account for any undetected species, particularly of SMs, and avoid any potential bias in β-diversity patterns due to small differences in sample coverage among sites, we additionally assessed the expected β-diversity values using coverage-based extrapolations for both mammal groups (Chao and Jost, 2012, Sánches-de-Jesús *et al.*, 2016). We further retained the expected values for subsequent analysis.

Patterns of mammal β-diversity were analysed using multiplicative diversity decomposition of Hill numbers: ${}^{q}D_{\beta} = {}^{q}D_{\gamma}/{}^{q}D_{\alpha}$. Here, ${}^{q}D_{\gamma}$ corresponds to the observed total number of species (γ-diversity); ${}^{q}D_{\alpha}$ to the mean local number of species recorded per site (α-diversity); and, ${}^{q}D_{\beta}$ to the 'effective number of completely distinct communities' (β-diversity). The equations for ${}^{q}D_{\gamma}$ and ${}^{q}D_{\alpha}$ are detailed elsewhere (Jost, 2007; Tuomisto, 2010); ${}^{q}D_{\beta}$ was calculated for each pairwise comparison of 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 (${}^{0}D_{\beta}$), 1 (${}^{1}D_{\beta}$) and 2 (${}^{2}D_{\beta}$), in which ${}^{0}D_{\beta}$ gives disproportionate weight to rare species, as it is not sensitive to species abundances; ${}^{1}D_{\beta}$ weights each species according to its abundance in the community, measuring the turnover of ‘common’ or ‘typical’ species in the community; and ${}^{2}D_{\beta}$ favours very abundant species and is therefore interpreted as the turnover of ‘dominant’ species in the community (Jost, 2007; Tuomisto, 2010). These analyses were performed using the ‘*entropart*’ R package (Marcon and Herault, 2013). Further, we used paired *t*-tests (Zar, 1999) to compare β-diversity in the different *q* orders between each mammal group. We used Mantel tests performed using the ‘*vegan*’ R package (Oksanen *et al.*, 2017) to assess whether β-diversity was correlated to site location (i.e., geographic distance matrix among all 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), and in landscape (i.e., COVER, PROX). All analyses were performed using R (R Development Core Team, 2013), assuming a significance level of 0.05 (Zar, 1999).

Results

We obtained 1,481 captures of SMs (*N* = 853 individuals) representing 20 species (17 genera; 3 families), and 6,290 camera-trapping records of LMs representing 22 species (18 genera; 13 families; Table S3). The number of species per site ranged from 2 to 15 (mean ± SD = 7.0 ± 4.2 species) 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, this species was replaced by other locally common species (e.g., *Philander opossum*, *Hylaeamys megacephalus* and *Marmosa murina*; Fig. 2a). 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 (Fig. 2b). At each site, the number of uncommon or occasional species, i.e. those recorded only once or twice, averaged 41.5% (± 19.9) and 33.1% (± 31.2) for SM and LM assemblages, respectively.

Patterns and predictors of β-diversity

Both SMs and LMs exhibited similarly high β-diversity (SM: 1.63 ± 0.27; LM: 1.62 ± 0.28; P = 0.624) when considering only the number of species (q = 0). When species abundance was considered (q = 1 and 2), however, β-diversity was significantly higher (P <0.0001) for SM ($^{1}\beta$ = 1.48 ± 0.28; $^{2}\beta$ = 1.47 ± 0.31) than for LM assemblages ($^{1}\beta$ = 1.34 ± 0.31; $^{2}\beta$ = 1.32 ± 0.37; Fig. 3). Overall, levels of β-diversity of 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 considering rare species than when only common or dominant species were considered (Fig. 3).

For both small and medium to large mammals, β-diversity was more strongly related to environmental variation among sites than to their spatial setting in the landscape. Indeed, β-diversity estimates (for any order q) of both mammal groups were not influenced by geographic distance among forest sites (Table 2). Local habitat variables were the most important predictors 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 increased mammal β-diversity among sites (Table 2). Additionally, β-diversity of LMs was significantly positively related to greater differences in the number of lianas among sites.

Patch and landscape variables influenced the β-diversity for some q orders, especially for LMs. In fact, β-diversity of LMs was influenced by some measures of isolation (including COVER, PROX and DIST), particularly when considering only rare species ($^{0}\beta$; Table 2). Island size influenced β-diversity of LMs at all orders of q, but explained 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 (Fig. S1).

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 predictors of β-diversity for both small and midsized to large terrestrial and arboreal mammals within a 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, with patch and landscape variables exerting a key influence on β-diversity of only midsized to large-bodied mammals. In particular, the severe local extinctions of LMs in smaller islands (Benchimol and Peres, 2015a) resulted in the biotic homogenization of assemblages therein.

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 *et al*., 2015), plant (Arroyo-Rodríguez *et al*., 2013) and bird assemblages (Si *et al.*, 2016; Morante-Filho *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 therefore cover a reasonable range of habitat patches (Meza-Parral and 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 and Peres, 2015b), may actually correspond to transient species, rather than true residents in forest islands created by dams (Terborgh *et al*., 1997). This can inflate differences in species composition of LM between sites when considering only species richness. 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 minimised possible underestimates for SMs, or overestimates for LMs, by using expected β-diversity values (Chao and Jost, 2012).

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).As such, the SM species turnover was higher than that for LMs. Indeed, while only one LM species (*M. acouchy*) was consistently the commonest species across nearly all forest sites surveyed, whereas local composition of common SM species was much more variable across the spectrum of island sizes/CF sites (Fig. 2). Differences in vagility between SMs and LMs could also partly explain the higher abundance-based β-diversities of SMs. However, the larger effect of abundance-based β-diversity on SMs, compared to those based on species richness only, suggest an additional mechanism. SM assemblages are closely linked to local habitat conditions, being mainly determined by local characteristics related to habitat structure (e.g., overstory and understorey vegetation density and number of fallen logs; 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 et al. in revision). Indeed, habitat conditions are highly variable across Balbina forest islands, for example, in terms of vertical stratification of the vegetation (Benchimol and 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-Rodriguez *et al.*, 2013).

In the case of the LM assemblages, the observed correlation between β-diversity and differences in island sizes indicates that these mammal assemblages share a more similar species composition either between larger islands and CF sites, or between smaller islands (Fig. S1). That is expected for larger islands/CF sites, which harbour the same full, or nearly full, species assemblage (Benchimol and Peres, 2015a). Yet, the lower LM β-diversity between smaller islands, occupied by a smaller subset of species (Benchimol and Peres, 2015a), denotes 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 (Vellend *et* *al.*, 2007; Karp *et al.*, 2012). 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 *et al.*, 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 compromised across most of the landscape, further posing a major threat to the maintenance of regional scale biodiversity (Olden *et al.*, 2011; Solar *et al.*, 2015).

Predictors 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 range of body sizes covered in 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 in the islands is a proxy of the degree of forest ecosystem integrity (Benchimol and Peres, 2015c). All of these habitat variables may therefore represent a gradient of forest habitat quality for mammals (Delciellos *et al.*, 2015; Lomolino and Perault, 2000; Pardini *et al.*, 2005, 2009). Therefore, maintaining habitat integrity should preclude the homogenization of mammal species assemblages across the landscape.

Variables at both the forest patch and landscape scale also predicted 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. In comparison to SMs, most LMs require larger areas and sustain lower population densities (Wright *et al.*, 1998). Therefore, assemblages of large-bodied mammals are expected to be greatly affected by the remaining habitat area in fragmented landscapes (Chiarello, 1999; Michalski and Peres, 2005; Newmark, 1996). Indeed, forest area alone explained 91% of the overall variation in species richness for medium and large-sized vertebrates surveyed at 37 Balbina islands (Benchimol and Peres, 2015a). In the case of SMs, island area predicted 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 et al., in revision). Although large islands and mainland forest sites can retain a larger number of rare species, those sites must still meet appropriate conditions in terms of habitat quality to sustain viable populations.

Our results also indicate that β-diversity of LMs was further predicted by site isolation at both the patch and landscape scale (i.e., forest cover, proximity and distance to the mainland) when considering only species richness (q = 0). The ability of species to disperse between fragments is one of the main determinants of population persistence in fragmented landscapes (Moilanen and Hanski, 1998; Schooley and Wiens, 2004), including the Balbina archipelago, where intrinsic species swimming capacity was positively related to island occupancy rates for LMs (Benchimol and Peres, 2015a). Isolation-related variables also account for the availability of neighbouring habitat, and therefore to the probability of recolonization events. Thus, both species ability to disperse and habitat availability seem to shape the turnover of rare LM species (cf. Rabelo *et al*., 2017).

Conservation implications

This study highlights the importance of considering β-diversity to propose conservation recommendations in anthropogenic landscapes, and improves our understanding of the pervasive impact of mega hydropower dams on tropical forest biodiversity. First, we revealed that predictors of mammal β-diversity failed to match those 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 et al., in revision), the species turnover of small mammals was primarily predicted by local habitat characteristics. Likewise, although island size is a powerful predictor of large mammal species richness (Benchimol and Peres, 2015a), the species turnover of LMs was additionally driven by 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 high species turnover and consequently cannot ensure guidelines for 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 fragments, entailing more drastic changes in the forest structure, particularly in smaller islands (Benchimol and Peres, 2015c). This further represents a problem in maintaining the Balbina mammal regional diversity, 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 the 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. Yet, this will depend on how edge effects will continue to impact insular forest structure, which may lead to either homogenization or differentiation, being stronger in smaller and more infrequent in larger islands (Benchimol and Peres, 2015c). Because non-volant mammals also provide key ecological services for ecosystem maintenance, their loss can substantially affect tropical forest functioning (Dirzo *et al*. 2014). Therefore, future assessments of hydropower development should carefully weigh the environmental partition of biodiversity loss along all other environmental and socioeconomic costs.

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Biosketches

The authors of this study form an interdisciplinary team from a range of institutions in Brazil and the UK, and have research interests and expertise that cover the fields of tropical ecology and conservation science, including the impacts of habitat change and degradation in Amazonian and Atlantic forest landscapes.

Author contributions: A.F.P., M.B. and J.C.M.F conceived the ideas; A.F.P. and M.B. collected the data; A.F.P. and J.C.M.F. conducted the data analysis, A.F.P. led the writing; and all authors contributed with comments and revisions to all drafts of the manuscript.

Tables

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 are provided for each variable.

Name (code name)	**Variable description**	**Range (mean ± SD)**
Local habitat scale		
Trees 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 ± 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 ± 22.8)
Closed-canopy forest (CC)	Percentage of closed-canopy forest within each forest site.	37.5 – 10.65 % (76.2 ± 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 ± 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 ± 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 ± 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 – 40.5 (21.5 ± 10.3)
Patch scale		

Island size (AREA)	Island area of each focal island ($\log_{10} x$).	0.83 – 1466 ha (199.0 ± 344.1)
Island shape (SHAPE)	Perimeter length of each focal island divided by the total island area.	0.004 – 0.106 (0.018 ± 0.022)
Distance (DIST)	Euclidean distance from each island to the nearest neighbouring mainland forest site.	0 – 11,872 m (4,503 ± 3,352)
Landscape scale		
Forest cover (COVER)	Percentage of land mass area within a 500 m-buffer.	5.91 – 100% (37.50 ± 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.	0.44 – 10.65 (3.45 ± 1.84)

Table 2. Correlation between β-diversity estimates among forest sites of small and midsized to large mammals and site location (geographic distance among sampled sites), inter-site differences (Δ) in landscape, patch and local habitat variables at 25 forest sites sampled at the Balbina Hydroelectric Reservoir. Three orders of *q* (0, 1 and 2), which determines the sensitivity of each β-diversity component to the relative abundance of species. Pearson correlation coefficients and significance were calculated using Mantel tests (* P < 0.05; ** P ≤ 0.001).

Variables	**β-diversity order**	**Small**	**Midsized–large**
	0	0.046	0.015
Site location	1	0.070	0.051
	2	0.085	0.069
Local habitat scale			
	0	0.307*	0.430**
Δ S.TREES	1	0.331*	0.427*
	2	0.327*	0.387*
	0	0.133	0.083
Δ N.TREES	1	0.039	0.076
	2	0.007	0.049
	0	0.305*	0.319**
Δ OGT	1	0.312*	0.476*
	2	0.293*	0.445*
	0	0.161	0.245*
Δ BAFF	1	0.269*	0.396*
	2	0.275*	0.434*
	0	0.056	0.357**
Δ LIANA	1	0.075	0.287*
	2	0.083	0.244*
	0	–0.181	0.201*
Δ FIRE	1	–0.145	–0.026
	2	–0.142	–0.048
	0	0.070	0.114

Δ CC	1	0.113	0.191
	2	0.100	0.151
Patch scale			
	0	0.293*	0.751**
Δ Area	1	0.141	0.465**
	2	0.150	0.418*
	0	0.007	0.078
Δ Shape	1	–0.214	–0.063
	2	–0.213	–0.088
	0	–0.070	0.214*
Δ Dist	1	–0.167	–0.075
	2	–0.156	–0.082
Landscape scale			
	0	0.105	0.386**
Δ Cover	1	0.053*	0.199
	2	0.074	0.182
	0	0.071	0.369*
Δ Prox	1	–0.134	0.043
	2	–0.127	0.019

Figure captions

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 (CF_1 and CF_2; red rectangles).

Figure 2. Rank-abundance (ln) distribution curves for (a) small mammals and (b) midsized to large mammals across all 25 surveyed sites within the Balbina Hydroelectric Reservoir. Each data point represents the abundance of each species at each site and is colour-coded by species. Lines connect species abundances at the same site. Sites are ordered left to right in terms of area, from smallest to largest. Due to overlapping symbology, we indicate species code names only for the most abundant species (ln (abundance) > 2.85 and 2.50, for small and midsized to large mammals, respectively). Abundant small mammal species include: *Philander opossum* (Phil), *Marmosa murina* (Mmuri), *Marmosa demerarae* (Mdem), *Hylaeamys megacephalus* (Hyla), *Didelphis marsupials* (Didel), *Oecomys* sp. 1 (Oeco1) and *Proechimys* sp. (Proe); midsized to large mammal species include: *Dasypus novemcinctus* (Dno), *Myoprocta acouchy* (Myo), *Cuniculus paca* (Cu), *Tapirus terrestris* (Tap), *Mazama americana* (Ma), *Hydrochoerus hydrochaeris* (Hyd), *Dasyprocta leporina* (Das), *Pecari tajacu* (Pec), Dasypus kappleri (Dk).

Figure 3. Mean β-diversity estimates of small and medium sized mammals surveyed at 25 forest sites within the Balbina archipelago. 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 for all pairwise sites (N = 300), and the corresponding 95% confidence intervals.

Figures

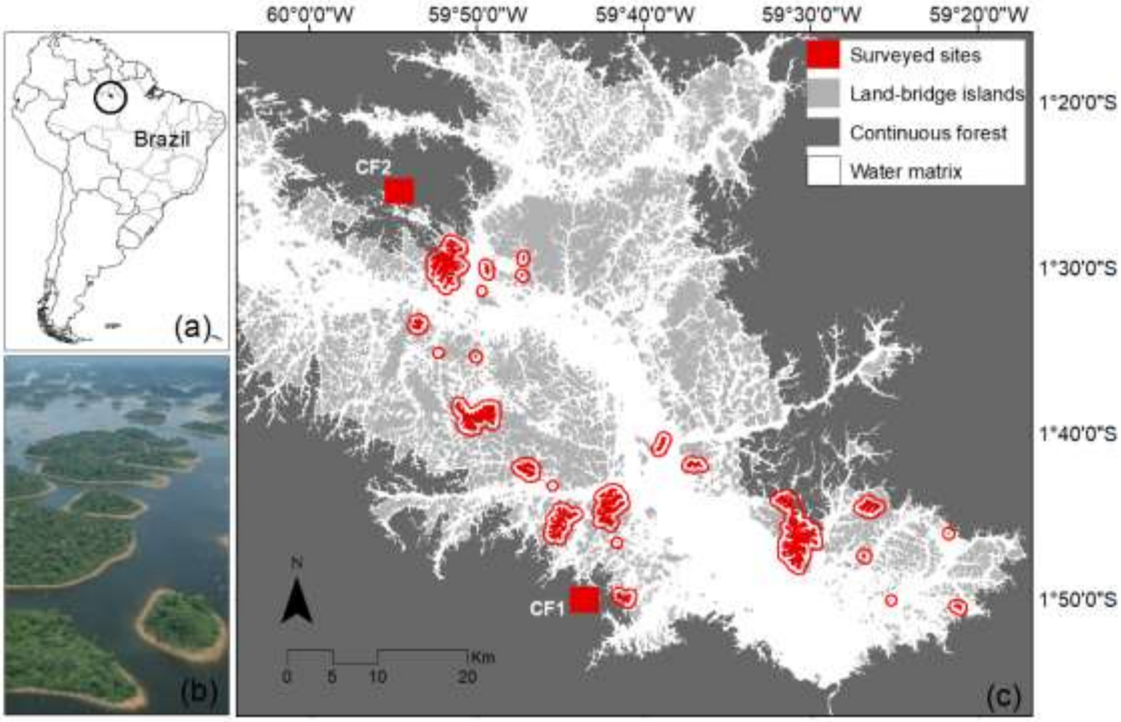
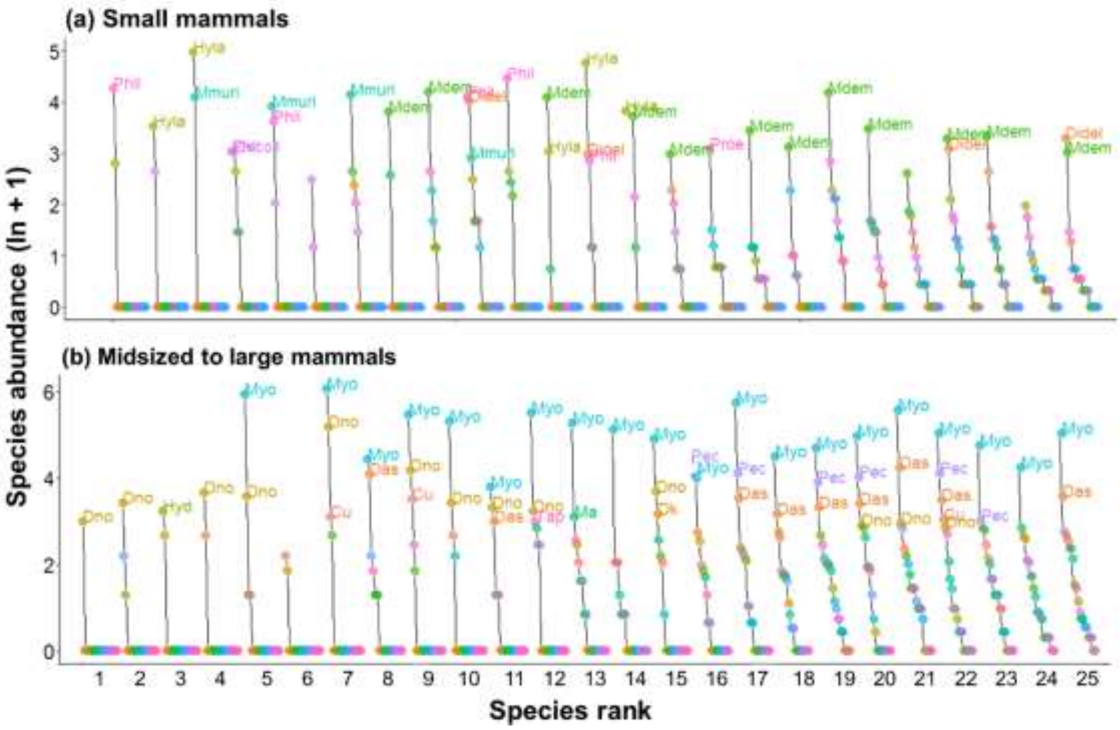


Fig. 1



(a) Small mammals
(b) Midsized to large mammals
Species abundance (ln + 1)
Species rank

Fig. 2

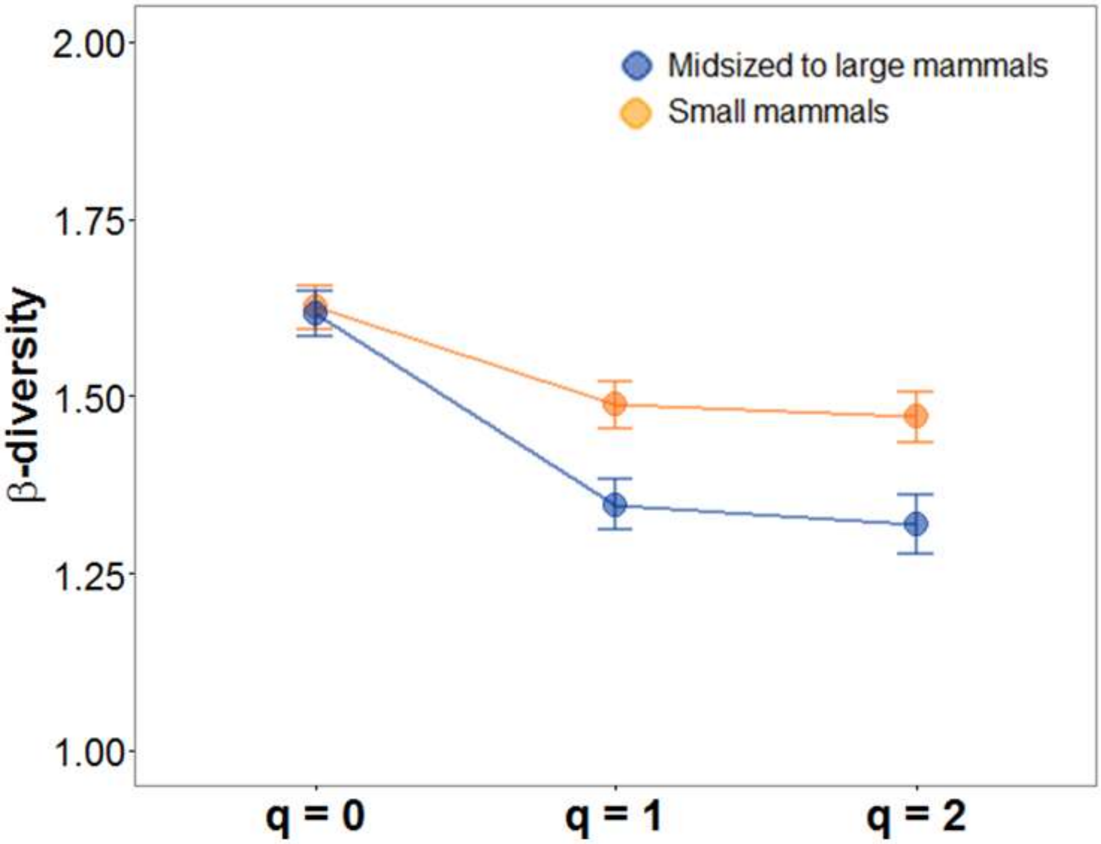

Midsized to large mammals
Small mammals
β-diversity
2.00
1.75
1.50
1.25
1.00
q = 0
q = 1
q = 2

Fig. 3