

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

3

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

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17 **Abstract**

18

19 **Aim** Mega hydroelectric dams have become one of the main drivers of biodiversity loss
20 in the lowland tropics. Vertebrate studies in tropical reservoirs have focused on local (α)
21 diversity measures, whereas between-site (β) diversity remains poorly assessed despite
22 its pivotal importance in understanding how species diversity is structured and
23 maintained in these anthropogenic landscapes. Here we unravel the patterns and
24 predictors of mammal β -diversity including both small (SM) and midsized to large
25 mammal species (LM) across 23 islands and 2 continuous forest sites within one of the
26 largest South American hydroelectric reservoirs.

27 **Location** Balbina Hydroelectric Dam, Central Brazilian Amazonia.

28 **Methods** Small mammals were sampled using live and pitfall traps (48,350 trap-nights),
29 and larger mammals using camera traps (8,160 trap-nights). β -diversity was examined
30 for each group separately using multiplicative diversity decomposition of Hill numbers
31 to test to what extent β -diversity of SMs and LMs was related to a set of environmental
32 characteristics measured at different spatial scales.

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

37 **Main conclusions** Although island size plays a major role in structuring mammal α -
38 diversity in several land-bridge islands, local vegetation characteristics were key
39 predictors of between-site β -diversity for both mammal groups within this large
40 Amazonian archipelago. Moreover, the lower β -diversity of LMs between smaller
41 islands suggests subtractive homogenization of this group. Maintaining the integrity of
42 vegetation characteristics and preventing the formation of a large set of small islands
43 within reservoirs should be considered in long-term management plans in both existing
44 and planned hydropower development in lowland tropical forests.

45

46 **Keywords:** Biotic homogenization, Habitat fragmentation, Habitat quality,
47 Hydroelectric dams, Species turnover, Tropical forest.

48

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50

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63

64 **Introduction**

65

66 Mega hydroelectric dams have become one of the main drivers of habitat loss and
67 fragmentation worldwide (Jones *et al.*, 2016; Winemiller *et al.*, 2016; Gibson *et al.*,
68 2017). In the aftermath of damming, lower elevation areas are flooded and the previous
69 hilltops are converted into land-bridge forest islands, creating a complex archipelagic
70 landscape within hydroelectric reservoirs. Despite their relatively flat terrain, rivers at
71 hyper-diverse tropical developing countries are often targets for hydropower expansion
72 (Zarf *et al.*, 2015). As such, the hydropower sector has greatly expanded in the Amazon
73 Basin (Lees *et al.*, 2016), with 145 existing or under-construction dams that are
74 expected to flood ~1.5 Mha of pristine forests, and 263 additional dams earmarked for
75 construction by current government plans (ECOFA, 2016). Therefore, understanding how
76 the biota responds to the insularization created by dams poses as pivotal for long-term
77 conservation actions in these novel landscapes.

78 The vast majority of studies in land-bridge island systems have assessed changes
79 in local (α) diversity (reviewed by Jones *et al.*, 2016; see also Si *et al.*, 2015, 2016),
80 showing that biological communities isolated within land-bridge islands are prone to
81 experience high local extinction rates (Jones *et al.*, 2016). However, local diversity
82 typically represents only a small fraction of the regional species pool (MacArthur,
83 1972), and restricting our inferences to such measures of diversity may mask the true
84 impact of anthropogenic disturbances on ecosystem functioning (González-Maya *et al.*,

85 2015), further hindering the application of more effective management actions (Socolar
86 *et al.*, 2016). To understand how the total number of species is organized and
87 maintained in human-modified landscapes, or under alternative scenarios of
88 anthropogenic disturbance, it is necessary to consider the variation in community
89 composition among habitat patches (β -diversity; Whitakker, 1972), which is an
90 important component of regional diversity (γ -diversity; Kadmon and Pulliam, 1993;
91 Cottenie, 2005). Moreover, mechanisms generating species turnover between sites are
92 not necessarily the same as those operating on local species diversity, but are equally
93 important to be considered in effective management strategies (Bergamin *et al.*, 2017;
94 Edge *et al.*, 2017). Yet studies assessing patterns of β -diversity within reservoir islands
95 are restricted to birds and lizards in a Chinese dam (Si *et al.*, 2015, 2016),
96 demonstrating the importance of further studies focused on other taxonomic groups.

97 Mammals are widely hailed as regional conservation icons and critical
98 components of tropical forest dynamics through their ecological roles as hyper-
99 consumers, large predators, seed dispersal vectors, and structural habitat modifiers
100 (Dirzo *et al.*, 2014; Mangan and Adler, 2000; Terborgh *et al.*, 2001). Mammals can be
101 extremely diverse, particularly in the Amazon, where they are represented by 427
102 species (Mittermeier *et al.*, 2002), ranging in body mass from <15 g to >150 kg (Paglia
103 *et al.*, 2012). As different components of the mammal fauna require different survey
104 methods, ecological studies typically focus on surveying either small non-volant
105 mammals (i.e., those usually sampled using live or pitfall trapping; hereafter, SMs) or
106 mid-sized to large terrestrial mammals (i.e., those sampled using direct or indirect
107 observation, such as camera traps; hereafter, LMs).

108 Small and large mammals may differ not only in their sampling methods, but
109 also may show contrasting responses to insularization created by dams due to the
110 intrinsic characteristics of these two mammal groups. In fact, body size is known to
111 interact with species dispersal ability and trophic position, differently affecting β -
112 diversity patterns (Soininen *et al.*, 2017). Because of lower vagility, including flotation
113 and swimming endurance (Schoener and Schoener, 1984; Cosson *et al.*, 1999), SM
114 assemblages should be mainly related to local habitat characteristics (Delciellos *et al.*,
115 2015; Pardini *et al.*, 2005; Olifiers, 2002), and present a higher species turnover among
116 islands. Conversely, the higher vagility, larger spatial requirements and smaller
117 population sizes of LMs (Chiarello, 1999) should result in assemblages that converge
118 across a large number of islands. These two hypotheses, related to small and large body

119 sizes, have not yet been tested comparing species turnover of SMs and LMs at the same
120 set of sites. In addition, the effect of major environmental drivers of compositional
121 shifts across space remains poorly understood for both groups.

122 Here, we provide the first quantitative assessment of the habitat insularization
123 effects on β -diversity of SM and LM species, conducted at one of the largest man-made
124 archipelago in South America — the 28-year old Balbina Hydroelectric Reservoir.
125 Previous studies carried out in Balbina showed that island area and isolation were the
126 strongest predictors of SM α -diversity (AF Palmeirim, pers. comm.), whereas island
127 area was the single best predictor for LM α -diversity (Benchimol and Peres, 2015a,
128 2015b). We test the hypothesis that the low and high vagilities of SM and LM,
129 respectively, generate different patterns of β -diversity for these two groups.
130 Multiplicative diversity decomposition of Hill numbers was used, an approach that
131 considers the importance of rare, common and dominant species in generating β -
132 diversity patterns (Jost, 2007; Tuomisto, 2010). We further examine how patterns of β -
133 diversity are predicted by a set of environmental characteristics related to the local
134 habitat structure, forest patch and landscape scales, which are widely recognised as
135 important in enhancing mammal diversity (Chiarello, 1999; Delciellos *et al.*, 2015;
136 Pardini *et al.*, 2005). Specifically, we predict that (1) β -diversity of both mammal
137 groups should be higher for rare species, compared to dominant species; (2) between-
138 island β -diversity of SMs should be higher than that of LMs; and, (3) local habitat
139 features should be the key predictors of SM β -diversity, whereas LM β -diversity should
140 be most affected by patch and landscape metrics, such as island size and isolation.

141

142 **Methods**

143

144 **Study area**

145 This study was carried out at 23 islands and two continuous forest sites (hereafter, CFs)
146 in the forest archipelago of the Balbina Hydroelectric Reservoir (1°48'S, 59°29'W; Fig.
147 1) located in the Brazilian Amazonia. This dam was created in 1986 following the
148 permanent closure of the Uatumã River, a left-bank tributary of the Amazon River.
149 Given the typically flat to undulating topography of the study region, a vast area of
150 312,900 ha of primary forest was flooded within the 443,772-ha hydroelectric reservoir
151 (FUNCATE/INPE/ANEEL, 2000). The former hilltops of the pre-inundation forest area
152 were converted into 3,546 land-bridge islands that are widely distributed throughout the

153 reservoir lake. Islands and the neighbouring continuous forest sites consist of dense
154 closed-canopy *terra firme* forest (Benchimol and Peres, 2015a). Forest islands within
155 the reservoir have not been subject to logging nor hunting, but many islands
156 experienced understorey fires during the El Niño drought of late-1997 to early-1998
157 (Benchimol and Peres, 2015c). The mean annual temperature and rainfall in this region
158 is 28°C and 2,376 mm, respectively (IBAMA, 1997). Part of the reservoir and a vast
159 area of continuous forest on the left bank of the Uatumã River have been legally
160 protected since this dam was built by the 942,786-hectare Uatumã Biological Reserve,
161 the largest Brazilian protected area in this category.

162 We pre-selected 23 forest islands according to their size, degree of isolation and
163 spatial distribution, so that a wide spectrum of island configurations could be sampled
164 within the reservoir. Surveyed islands as CFs were at least 1-km apart from one another,
165 with island size ranging from 0.83 to 1,466 ha (mean \pm SD: 213.47 \pm 352.31 ha; Table
166 S1) and isolation distances to the nearest mainland varying from 44 to 11,872 m (4,503
167 \pm 3,352 m).

168

169 **Mammal surveys**

170 Small and midsized to large mammal assemblages were sampled twice at each forest
171 site, during two field seasons. In 2014 and 2015, SMs were sampled along two
172 continuous periods of 16 consecutive nights, using linear trapping plots. Each plot
173 consisted of a set of nine live trap stations (hereafter, LTs), followed by an array of
174 three pitfall-trap units. Each LT station was placed 20 m apart from each other and
175 included two Sherman traps (23 x 9 x 8 cm, H. B. Sherman Traps, Inc., Tallahassee,
176 Florida) and one wire mesh trap (30 x 17.5 x 15 cm, Metal Miranda, Curitiba, Paraná).
177 At each LT station, one trap was set on the ground, one in the understorey (~1.5 m
178 high), and one in the (sub)canopy (>10 m high). Traps of different types were placed
179 alternatively on the ground and in the understorey across consecutive stations, but only
180 Sherman traps were placed in the canopy due to logistic limitations. At the forest
181 canopy stratum, small mammals were sampled using an adaptation of the method
182 described by Lambert *et al.* (2005). LTs were baited with a mix of bananas, peanut
183 powder, sardines and oak florets. Pitfall traps (100 L) were also spaced apart by 20-m
184 intervals and connected by a 50-cm high plastic fence that was buried 10 cm
185 underground, and included 10 m of overhanging fence farther extended beyond the two
186 external pitfalls. Due to spatial restrictions in small islands, alternative smaller trapping

187 plots were established therein. Thus, all islands smaller than 2 ha and those between 2
188 and 10 ha were sampled by trapping plots containing only three LT stations followed by
189 an array of one pitfall, and six LT stations followed by an array of two pitfalls,
190 respectively. All traps were inspected daily and whenever live captures could not be
191 identified in the field, a maximum of five voucher specimens per species per survey site
192 were collected during the first trapping season, and deposited at the Mammal Collection
193 of the Instituto Nacional de Pesquisas da Amazônia (INPA), in Manaus, Brazil. All
194 other individuals recorded were weighted and tagged (Fish and Small Animal Tag, size
195 1; National Band and Tag Co., Newport, Kentucky), so that any subsequent recaptures
196 could be distinguished. Additionally, tissue samples were collected from all individuals
197 recorded and deposited at the INPA Mammal Collection. However, we were not always
198 able to identify at the species-level records of sympatric congeners of *Proechimys* spp.
199 (*P. cuvieri* and *P. guyanensis*) and *Oecomys* spp. 1 (*O. roberti* and *O. bicolor*). Because
200 these congeners are ecologically very similar (Jones *et al.*, 2009), we further refer to
201 those taxa as ‘ecospecies’. To streamline, we use hereafter ‘species’ to refer to both
202 species and ecospecies. Data collection followed ASM guidelines (Sikes *et al.*, 2016)
203 and was approved by an institutional animal care and use Brazilian committee (SISBIO
204 License No. 39187-4).

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

214 To maximise the heterogeneity of environments sampled at each site and
215 minimise variation in trap density, sampling effort was proportional to forest patch size
216 for both mammal groups. As such, depending on their size, islands were sampled by one
217 to four trapping plots and two to ten CT stations; whereas both CF sites were sampled
218 by six trapping plots and 15 CT stations. This amounted to a total sampling effort of
219 48,350 trap-nights for SMs, and 8,160 trap-nights for LMs.

220

221 **Local habitat, patch and landscape variables**

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

238 Patch and landscape variables were also calculated from RapidEye imagery,
239 using ArcMap 10.1. At the patch scale, we measured island AREA, island SHAPE (total
240 perimeter length of each focal island divided by AREA), and its nearest distance to any
241 CF site in the mainland (DIST). At the landscape scale, we obtained for each surveyed
242 island, the total amount of land mass area within a buffer threshold (COVER), and a
243 proximity index that considers both area and isolation of each land mass within that
244 buffer (PROX). Because previous studies used a 500-m radial buffer to predict both
245 small (AF Palmeirim *et al.*, pers. comm.) and midsized to large mammal richness
246 (Benchimol and Peres, 2015a) at the same islands, our COVER and PROX metrics
247 considered this radius threshold for analyses (see Table 1 and Benchimol and Peres,
248 2015a for further details on imagery processing, and patch and landscape metrics).
249 Additionally, this buffer size minimises or eliminates overlap between neighbouring
250 landscapes, conferring greater spatial independence.

251

252 **Data analysis**

253 We excluded from the analyses two Echimyid rodents — *Makalata didelphoides* and
254 *Echimyys chrysurus* — which had been recorded only once throughout the study. Both

255 species feed on leaves and seeds , in addition to some fruit (Patton *et al.*, 2000), and
256 consequently are rarely attracted to the bait used here. Due to differential sampling
257 effort per site, species abundances were standardized for each site, considering 2,095
258 and 319 trap-nights, which is the average sampling effort per site for SMs and LMs,
259 respectively. Because camera trapping cannot quantify numbers of individuals, we used
260 the number of captures for SMs rather than the number of individuals recorded, testing
261 whether these variables were correlated. This allowed us to improve convergence in the
262 comparison of β -diversity estimates for SMs and LMs. The number of SM captures was
263 indeed highly correlated with the number of individuals (15 species detected ≥ 5 sites: r
264 = 0.97 ± 0.05 (mean \pm SD); Table S2).

265 The accuracy of mammal surveys was assessed using the coverage estimator
266 recommended by Chao and Jost (2012), which estimates the proportion of the total
267 number of individuals in an assemblage that belongs to the species represented in the
268 sample. Overall sample coverage was high, representing on average (\pm SD) $95 \pm 0.07\%$
269 and $99 \pm 0.01\%$ of the SM and LM species recorded, respectively (Table S1). This
270 indicates that our sampling effort provided satisfactory estimates of β -diversity within
271 each forest site. However, to account for any undetected species, particularly of SMs,
272 and avoid any potential bias in β -diversity patterns due to small differences in sample
273 coverage among sites, we additionally assessed the expected β -diversity values using
274 coverage-based extrapolations for both mammal groups (Chao and Jost, 2012, Sánchez-
275 de-Jesús *et al.*, 2016). We further retained the expected values for subsequent analysis.

276 Patterns of mammal β -diversity were analysed using multiplicative diversity
277 decomposition of Hill numbers: ${}^qD_\beta = {}^qD_\gamma / {}^qD_\alpha$. Here, ${}^qD_\gamma$ corresponds to the observed
278 total number of species (γ -diversity); ${}^qD_\alpha$ to the mean local number of species recorded
279 per site (α -diversity); and, ${}^qD_\beta$ to the ‘effective number of completely distinct
280 communities’ (β -diversity). The equations for ${}^qD_\gamma$ and ${}^qD_\alpha$ are detailed elsewhere (Jost,
281 2007; Tuomisto, 2010); ${}^qD_\beta$ was calculated for each pairwise comparison of forest sites
282 (i.e. islands and CF sites; $N = 300$) and ranges between 1, when both communities are
283 identical, and 2, when both communities are completely distinct from each other (Jost,
284 2007). In addition, β -diversity depends on the parameter q , which determines the
285 sensitivity of the measure to species relative abundances (Jost, 2007; Tuomisto, 2010).
286 We considered β -diversity estimates of order 0 (${}^0D_\beta$), 1 (${}^1D_\beta$) and 2 (${}^2D_\beta$), in which ${}^0D_\beta$
287 gives disproportionate weight to rare species, as it is not sensitive to species
288 abundances; ${}^1D_\beta$ weights each species according to its abundance in the community,

289 measuring the turnover of ‘common’ or ‘typical’ species in the community; and ${}^2D_\beta$
290 favours very abundant species and is therefore interpreted as the turnover of ‘dominant’
291 species in the community (Jost, 2007; Tuomisto, 2010). These analyses were performed
292 using the ‘*entropart*’ R package (Marcon and Herault, 2013). Further, we used paired *t*-
293 tests (Zar, 1999) to compare β -diversity in the different *q* orders between each mammal
294 group. We used Mantel tests performed using the ‘*vegan*’ R package (Oksanen *et al.*,
295 2017) to assess whether β -diversity was correlated to site location (i.e., geographic
296 distance matrix among all sites) and to the matrices showing between-site differences in
297 local habitat variables (i.e., S.TREE, N.TREE, OGT, BA_{ff}, LIANA, FIRE, CC), in patch
298 (i.e., AREA, SHAPE, DIST), and in landscape (i.e., COVER, PROX). All analyses were
299 performed using R (R Development Core Team, 2013), assuming a significance level of
300 0.05 (Zar, 1999).

301

302 **Results**

303

304 We obtained 1,481 captures of SMs ($N = 853$ individuals) representing 20 species (17
305 genera; 3 families), and 6,290 camera-trapping records of LMs representing 22 species
306 (18 genera; 13 families; Table S3). The number of species per site ranged from 2 to 15
307 (mean \pm SD = 7.0 ± 4.2 species) for SMs, and from 1 to 19 (8.8 ± 5.8) for LMs. The
308 most abundant SM species was *Marmosa demerarae*, an arboreal marsupial recorded at
309 18 sites and corresponding to nearly one-third of all captures ($N = 499$). Despite the
310 local commonness of this species, others were often similarly abundant (e.g., *Didelphis*
311 *marsupialis* and *Proechimys* spp.), and whenever absent, this species was replaced by
312 other locally common species (e.g., *Philander opossum*, *Hylaeamys megacephalus* and
313 *Marmosa murina*; Fig. 2a). Considering LMs, the red acouchy *Myoprocta acouchy* was
314 the most abundant species, detected at 21 sites and accounting for 59% of all records (N
315 = 3,593). This small-bodied dasyproctid rodent was consistently the most abundant
316 species at nearly all islands larger than 5 ha ($N = 20$) and mainland CF sites (Fig. 2b). At
317 each site, the number of uncommon or occasional species, i.e. those recorded only once
318 or twice, averaged 41.5% (± 19.9) and 33.1% (± 31.2) for SM and LM assemblages,
319 respectively.

320

321 **Patterns and predictors of β -diversity**

322 Both SMs and LMs exhibited similarly high β -diversity (SM: 1.63 ± 0.27 ; LM: $1.62 \pm$
323 0.28 ; $P = 0.624$) when considering only the number of species ($q = 0$). When species
324 abundance was considered ($q = 1$ and 2), however, β -diversity was significantly higher
325 ($P < 0.0001$) for SM (${}^1\beta = 1.48 \pm 0.28$; ${}^2\beta = 1.47 \pm 0.31$) than for LM assemblages (${}^1\beta =$
326 1.34 ± 0.31 ; ${}^2\beta = 1.32 \pm 0.37$; Fig. 3). Overall, levels of β -diversity of both groups
327 decreased when species were weighted proportionally to their abundances, especially
328 for LM assemblages. In fact, β -diversity of LMs was 1.23 times higher considering rare
329 species than when only common or dominant species were considered (Fig. 3).

330 For both small and medium to large mammals, β -diversity was more strongly
331 related to environmental variation among sites than to their spatial setting in the
332 landscape. Indeed, β -diversity estimates (for any order q) of both mammal groups were
333 not influenced by geographic distance among forest sites (Table 2). Local habitat
334 variables were the most important predictors of β -diversity for both small and mid-sized
335 to large mammals. In particular, differences in tree species richness, percentage of old-
336 growth tree and basal area of trees bearing fleshy fruiting increased mammal β -diversity
337 among sites (Table 2). Additionally, β -diversity of LMs was significantly positively
338 related to greater differences in the number of lianas among sites.

339 Patch and landscape variables influenced the β -diversity for some q orders,
340 especially for LMs. In fact, β -diversity of LMs was influenced by some measures of
341 isolation (including COVER, PROX and DIST), particularly when considering only rare
342 species (${}^0\beta$; Table 2). Island size influenced β -diversity of LMs at all orders of q , but
343 explained patterns of β -diversity for SMs only when rare species were considered
344 (Table 2). In other words, across the archipelagic landscape of Balbina, β -diversity for
345 SMs was generally high, compared to that of LMs, regardless of pairwise differences in
346 island sizes. On the other hand, β -diversity for LMs was higher between islands of
347 contrasting sizes, and lower between small islands, or between large islands and CF
348 sites (Fig. S1).

349

350 **Discussion**

351

352 Habitat insularization in the aftermath of river damming has led to wholesale local
353 extinctions of tropical forest species (Jones *et al.*, 2016). However, understanding how
354 diversity is organized and maintained in biological communities is still poorly
355 investigated in archipelagic systems, including islands created by hydroelectric

356 reservoirs (Si *et al.*, 2015, 2016). Indeed, no study to date had examined patterns of β -
357 diversity for any taxonomic group within a major Neotropical reservoir, a region
358 experiencing a boom in dam building (Lees *et al.*, 2016). Hence, this is the first study
359 that examines the main predictors of β -diversity for both small and mid-sized to large
360 terrestrial and arboreal mammals within a fragmented tropical forest landscape. As
361 expected, when considering common and dominant species, SMs exhibited higher levels
362 of β -diversity than LMs. We also showed that habitat quality plays a major role in
363 mammal species turnover for both groups, with patch and landscape variables exerting a
364 key influence on β -diversity of only mid-sized to large-bodied mammals. In particular,
365 the severe local extinctions of LMs in smaller islands (Benchimol and Peres, 2015a)
366 resulted in the biotic homogenization of assemblages therein.

367

368 **Patterns of mammal β -diversity**

369 For both SMs and LMs, β -diversity estimates were higher when considering rare
370 species. This is expected given the observed patterns of dominance, with only one or
371 two records obtained for more than one third of all SM and LM species detected,
372 respectively. Other studies in fragmented forest landscapes showed similar results for
373 small mammal (Püttker *et al.*, 2015), plant (Arroyo-Rodríguez *et al.*, 2013) and bird
374 assemblages (Si *et al.*, 2016; Morante-Filho *et al.*, 2016). Thus, to maintain the regional
375 pool of species (γ -diversity), including rare mammal species, conservation efforts at
376 Balbina and analogous landscapes must therefore cover a reasonable range of habitat
377 patches (Meza-Parral and Pineda, 2015; Socolar *et al.*, 2016). Nevertheless, the LM
378 species exhibiting a small number of occurrences, including jaguar, tapir and giant
379 anteaters, which are able to transverse the aquatic matrix and visit multiple land masses
380 (Benchimol and Peres, 2015b), may actually correspond to transient species, rather than
381 true residents in forest islands created by dams (Terborgh *et al.*, 1997). This can inflate
382 differences in species composition of LM between sites when considering only species
383 richness. In contrast, differences in SM species composition for $q = 0$ could be
384 underestimated due to the lower probability of arboreal species to approach any trap in
385 the three-dimensional forest canopy. Although our sampling effort provided satisfactory
386 estimates of species richness for both mammal groups, we minimised possible
387 underestimates for SMs, or overestimates for LMs, by using expected β -diversity values
388 (Chao and Jost, 2012).

389 We also considered abundance-based measures of β -diversity (i.e., $q = 1$ and $q =$
390 2), which are dominated by common species, given their importance to inform
391 ecosystem processes (Socolar *et al.*, 2016). As such, the SM species turnover was
392 higher than that for LMs. Indeed, while only one LM species (*M. acouchy*) was
393 consistently the commonest species across nearly all forest sites surveyed, whereas local
394 composition of common SM species was much more variable across the spectrum of
395 island sizes/CF sites (Fig. 2). Differences in vagility between SMs and LMs could also
396 partly explain the higher abundance-based β -diversities of SMs. However, the larger
397 effect of abundance-based β -diversity on SMs, compared to those based on species
398 richness only, suggest an additional mechanism. SM assemblages are closely linked to
399 local habitat conditions, being mainly determined by local characteristics related to
400 habitat structure (e.g., overstorey and understorey vegetation density and number of
401 fallen logs; Delciellos *et al.*, 2015; Olifiers, 2002). Such trophic and structural resources
402 for small mammals tend to be patchy distributed, so that populations are often clustered
403 over large forest areas (Charles-Dominique *et al.*, 1981). This may contribute with the
404 overall higher abundance-based β -diversity values recorded for SMs. Interestingly, such
405 heterogeneity in SM assemblages was also recorded between smaller islands, where
406 only a reduced set of species persist (Palmeirim *et al.* in revision). Indeed, habitat
407 conditions are highly variable across Balbina forest islands, for example, in terms of
408 vertical stratification of the vegetation (Benchimol and Peres, 2015c). Such a link to
409 local habitat conditions may lead to multiple compositional pathways in which SM
410 species differ in abundance between sites according to locally available resource
411 spectra, habitat structure and ecological niches, as observed for plant species (Arroyo-
412 Rodriguez *et al.*, 2013).

413 In the case of the LM assemblages, the observed correlation between β -diversity
414 and differences in island sizes indicates that these mammal assemblages share a more
415 similar species composition either between larger islands and CF sites, or between
416 smaller islands (Fig. S1). That is expected for larger islands/CF sites, which harbour the
417 same full, or nearly full, species assemblage (Benchimol and Peres, 2015a). Yet, the
418 lower LM β -diversity between smaller islands, occupied by a smaller subset of species
419 (Benchimol and Peres, 2015a), denotes a subtractive homogenization in species
420 composition of LMs (Karp *et al.*, 2012; Püttker *et al.*, 2015; Socolar *et al.*, 2016) —
421 involving the hyperdominance of a similar subset of species (Chase, 2007). Common
422 species typically have relatively high dispersal abilities and generalist habits (Vellend *et*

423 *al.*, 2007; Karp *et al.*, 2012). Such unidirectional pattern of species turnover is expected
424 to promote cascading effects onto lower trophic levels, which can further disrupt the
425 structure of the entire forest ecosystem at small islands (Tabarelli *et al.*, 2012). In
426 Balbina, where 94.7% of all 3,546 islands are smaller than 100 ha, evidence for biotic
427 homogenization suggests that any ecosystem functions provided by LMs are
428 compromised across most of the landscape, further posing a major threat to the
429 maintenance of regional scale biodiversity (Olden *et al.*, 2011; Solar *et al.*, 2015).

430

431 **Predictors of mammal β -diversity**

432 We expected assemblages of SMs, rather than those of LMs, to be context-dependent in
433 terms of local habitat structure. The unexpected association between β -diversity of LMs
434 and local habitat variables could be related to the large range of body sizes covered in
435 this group, from small-bodied (e.g. the squirrel *Guerlinguetus aestuans*, 210 g), to very
436 large-bodied species (e.g. jaguar, 158 kg; lowland tapir, 260 kg). As such, variables
437 related to local habitat-quality – tree species richness, prevalence of old-growth trees
438 and basal area of trees bearing fleshy fruits – played a major role in predicting species
439 turnover for both mammal groups. Those latter two habitat variables can increase the
440 amount of food and structural resources available to at least small mammal species
441 (Malcolm, 1991), while the proportion of old-growth trees remaining in the islands is a
442 proxy of the degree of forest ecosystem integrity (Benchimol and Peres, 2015c). All of
443 these habitat variables may therefore represent a gradient of forest habitat quality for
444 mammals (Delciellos *et al.*, 2015; Lomolino and Perault, 2000; Pardini *et al.*, 2005,
445 2009). Therefore, maintaining habitat integrity should preclude the homogenization of
446 mammal species assemblages across the landscape.

447 Variables at both the forest patch and landscape scale also predicted β -diversity,
448 particularly for LMs. As stated above, at the patch scale, island area predicted β -
449 diversity of LMs, while β -diversity of SMs was only predicted by area when rare
450 species were considered. In comparison to SMs, most LMs require larger areas and
451 sustain lower population densities (Wright *et al.*, 1998). Therefore, assemblages of
452 large-bodied mammals are expected to be greatly affected by the remaining habitat area
453 in fragmented landscapes (Chiarello, 1999; Michalski and Peres, 2005; Newmark,
454 1996). Indeed, forest area alone explained 91% of the overall variation in species
455 richness for medium and large-sized vertebrates surveyed at 37 Balbina islands
456 (Benchimol and Peres, 2015a). In the case of SMs, island area predicted the turnover of

457 only rare species, which probably matches those species with the largest spatial
458 requirements or higher habitat specificity, both of which are primarily accommodated
459 by larger forest sites (Palmeirim et al., in revision). Although large islands and mainland
460 forest sites can retain a larger number of rare species, those sites must still meet
461 appropriate conditions in terms of habitat quality to sustain viable populations.

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

473

474 **Conservation implications**

475 This study highlights the importance of considering β -diversity to propose conservation
476 recommendations in anthropogenic landscapes, and improves our understanding of the
477 pervasive impact of mega hydropower dams on tropical forest biodiversity. First, we
478 revealed that predictors of mammal β -diversity failed to match those observed in
479 previous vertebrate α -diversity studies carried out in the same study landscape. While
480 the number of SM species was related to island area and proximity (Palmeirim et al., in
481 revision), the species turnover of small mammals was primarily predicted by local
482 habitat characteristics. Likewise, although island size is a powerful predictor of large
483 mammal species richness (Benchimol and Peres, 2015a), the species turnover of LMs
484 was additionally driven by a set of local habitat variables. Other studies also report
485 divergent drivers of either α - or β -diversity, for example in stream fish communities
486 (Edge *et al.*, 2017). Therefore, focusing on predictors of α -diversity alone would fail to
487 understand drivers of high species turnover and consequently cannot ensure guidelines
488 for long-term conservation of full mammal assemblages in fragmented tropical forest
489 landscapes.

490 In land-bridge islands isolated within hydroelectric reservoirs, edge effects tend
491 to be stronger than in non-insular fragments, entailing more drastic changes in the forest
492 structure, particularly in smaller islands (Benchimol and Peres, 2015c). This further
493 represents a problem in maintaining the Balbina mammal regional diversity, where only
494 <10% of all islands are >100 ha. In any case, this study illustrates a relatively benign
495 scenario in terms of mammal β -diversity 28 years after damming, mainly because the
496 Balbina archipelago has been effectively protected by the largest biological reserve in
497 Brazil. In the long-term, as the Balbina islands become more degraded by edge effects,
498 insular mammal assemblages, particularly those of larger bodied species, may become
499 even more homogeneous, through further decays in β -diversity. Yet, this will depend on
500 how edge effects will continue to impact insular forest structure, which may lead to
501 either homogenization or differentiation, being stronger in smaller and more infrequent
502 in larger islands (Benchimol and Peres, 2015c). Because non-volant mammals also
503 provide key ecological services for ecosystem maintenance, their loss can substantially
504 affect tropical forest functioning (Dirzo *et al.* 2014). Therefore, future assessments of
505 hydropower development should carefully weigh the environmental partition of
506 biodiversity loss along all other environmental and socioeconomic costs.

507

508 **References**

509

- 510 Arroyo-Rodríguez, V., Rös, M., Escobar, F., Melo, F. P., Santos, B. A., Tabarelli, M., &
511 Chazdon, R. (2013). Plant β -diversity in fragmented rain forests: testing floristic
512 homogenization and differentiation hypotheses. *Journal of Ecology*, **101**, 1449–
513 1458.
- 514 Barwell, L. J., Isaac, N. J. B., & Kunin, W. E. (2015). Measuring β -diversity with
515 species abundance data. *Journal of Animal Ecology*, **84**, 1112–1122.
- 516 Benchimol, M., & Peres, C. A. (2015a). Widespread forest vertebrate extinctions
517 induced by a mega hydroelectric dam in lowland Amazonia. *PloS one*, **10**,
518 e0129818.
- 519 Benchimol, M., & Peres, C. A. (2015b). Predicting local extinctions of Amazonian
520 vertebrates in forest islands created by a mega dam. *Biological Conservation*, **187**,
521 61–72.

522 Benchimol, M., & Peres, C. A. (2015c). Edge-mediated compositional and functional
523 decay of tree assemblages in Amazonian forest islands after 26 years of
524 isolation. *Journal of Ecology*, **103**, 408–420.

525 Bergamin, R. S., Bastazini, V. A. G., Vélez-Martin, E. V., Debastiani, V., Zanini, K. J.,
526 Loyola, R., & Müller, S. C. (2017). Linking beta diversity patterns to protected
527 areas: lessons from the Brazilian Atlantic Rainforest. *Biodiversity and
528 Conservation*, **26**, doi: 10.1007/s10531-017-1315-y.

529 Chao, A., & Jost, L. (2012). Coverage-based rarefaction and extrapolation:
530 standardizing samples by completeness rather than size. *Ecology*, **93**, 2533–2547.

531 Chase, J. M. (2007). Drought mediates the importance of stochastic community
532 assembly. *Proceedings of the National Academy of Sciences*, **104**, 17430–17434.

533 Chiarello, A. G. (1999). Effects of fragmentation of the Atlantic forest on mammal
534 communities in south-eastern Brazil. *Biological Conservation*, **89**, 71–82.

535 Cosson, J. F., Ringuet, S., Claessens, O., De Massary, J. C., Dalecky, A., Villiers, J.
536 F., ... Pons, J. M. (1999). Ecological changes in recent land-bridge islands in
537 French Guiana, with emphasis on vertebrate communities. *Biological
538 Conservation*, **91**, 213–222.

539 Cottenie, K. (2005). Integrating environmental and spatial processes in ecological
540 community dynamics. *Ecology Letters*, **8**, 1175–1182.

541 Delciellos, A. C., Vieira, M. V., Grelle, C. E., Cobra, P., & Cerqueira, R. (2015).
542 Habitat quality versus spatial variables as determinants of small mammal
543 assemblages in Atlantic Forest fragments. *Journal of Mammalogy*, **97**, 253–265.

544 Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J., & Collen, B. (2014).
545 Defaunation in the Anthropocene. *Science*, **345**, 401–406.

546 ECOA (Ecologia em Ação) 2016. International Rivers and Fundacion Proteger, Dams in
547 Amazonia. Available online: <<http://www.dams-info.org/en>>

548 Edge, C. B., Fortin, M. J., Jackson, D. A., Lawrie, D., Stanfield, L., & Shrestha, N.
549 (2017). Habitat alteration and habitat fragmentation differentially affect beta
550 diversity of stream fish communities. *Landscape Ecology*, **32**, 647–662.

551 ESRI. 2012. ArcMap 10.1. Environmental Systems Research Institute Inc., Redlands,
552 CA, USA.

553 FUNCATE/INPE/ANEEL (2000). Mapeamento por satélite das áreas inundadas por
554 reservatórios de hidrelétricas brasileiras. Unpublished Report. Convênio
555 FUNCATE/INPE/ANEEL, São Paulo.

556 Gibson, L., Wilman, E. N., & Laurance, W. F. (2017). How green is 'green' energy?
557 *Trends in Ecology and Evolution*, <https://doi.org/10.1016/j.tree.2017.09.007>.

558 González-Maya, J. F., Viquez-R, L. R., Belant J. L., & Ceballos G. (2015).
559 Effectiveness of protected areas for representing species and populations of
560 terrestrial mammals in Costa Rica. *PloS one*, **10**, e0124480.

561 IBAMA (1997). Plano de Manejo Fase I: Reserva Biológica do Uatumã.
562 Eletronorte/IBAMA. Brasília/DF/Brazil. Available online:
563 <<http://www.icmbio.gov.br>>

564 Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., ... Purvis,
565 A. (2009). PanTHERIA: a species-level database of life history, ecology, and
566 geography of extant and recently extinct mammals. *Ecology*, **90**, 2648–2648.

567 Jones, I. L., Bunnefeld, N., Jump, A. S., Peres, C. A., & Dent, D. H. (2016) Extinction
568 debt on reservoir land-bridge islands. *Biological Conservation*, **199**, 75–83.

569 Jost, L. (2007). Partitioning diversity into independent alpha and beta components.
570 *Ecology*, **88**, 2427–2439.

571 Kadmon, R., & Pulliam, H. R. (1993). Island biogeography: effect of geographical
572 isolation on species composition. *Ecology*, **74**, 977–981.

573 Karp, D. S., Rominger, A. J., Zook, J., Ranganathan, J., Ehrlich, P. R., & Daily, G. C.
574 (2012). Intensive agriculture erodes β -diversity at large scales. *Ecology Letters*,
575 **15**, 963–970.

576 Lambert, T. D., Malcolm, J. R., & Zimmerman, B. L. (2005). Variation in small
577 mammal species richness by trap height and trap type in southeastern Amazonia.
578 *Journal of Mammalogy*, **86**, 982–990.

579 Lees, A. C., Peres, C. A., Fearnside, P. M., Schneider, M., & Zuanon, J.A. (2016)
580 Hydropower and the future of Amazonian biodiversity. *Biodiversity and*
581 *Conservation*, **25**, 451–466.

582 Lomolino, M. V., & Perault, D. R. (2000). Assembly and disassembly of mammal
583 communities in a fragmented temperate rain forest. *Ecology*, **81**, 1517–1532.

584 MacArthur, R. H. (1972). Geographical ecology. Princeton University Press, Princeton,
585 New Jersey, USA.

586 Malcolm, J. R. (1991). The small mammals of Amazonian forest fragments: patterns
587 and process. PhD Thesis. University of Florida.

588 Mangan, S. A., & Adler, G. H. (2000). Consumption of arbuscular mycorrhizal fungi by
589 terrestrial and arboreal small mammals in a Panamanian cloud forest. *Journal of*
590 *Mammalogy*, **81**, 563–570.

591 Marcon, E., & Hérault, B. (2013). *Entropart, an R package to partition diversity*. R
592 Foundation for Statistical Computing, Vienna, Austria. Available at:
593 <http://CRAN.R-project.org/package=entropart>.

594 Meza-Parral, Y., & Pineda, E. (2015). Amphibian diversity and threatened species in a
595 severely transformed Neotropical region in Mexico. *PloS one*, **10**, e0121652.

596 Michalski, F., & Peres, C. A. (2005). Anthropogenic determinants of primate and
597 carnivore local extinctions in a fragmented forest landscape of southern
598 Amazonia. *Biological conservation*, **124**, 383–396.

599 Mittermeier, R. A. M., Pilgrim, C. G., Fonseca, J., Konstant, G., & William, R. (2002).
600 Wilderness: Earth's last wild places. México, MX: CEMEX.

601 Moilanen, A., & Hanski, I. (1998). Metapopulation dynamics: effects of habitat quality
602 and landscape structure. *Ecology*, **79**, 2503–2515.

603 Morante-Filho, J. C., Arroyo-Rodríguez, V., & Faria, D. (2016). Patterns and predictors
604 of β -diversity in the fragmented Brazilian Atlantic forest: a multiscale analysis of
605 forest specialist and generalist birds. *Journal of Animal Ecology*, **85**, 240–250.

606 Newmark, W. D. (1996). Insularization of Tanzanian parks and the local extinction of
607 large mammals. *Conservation Biology*, **10**(6), 1549–1556.

608 Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J.,
609 Suggests, M. A. S. S. (2007). *Vegan: the community ecology package*. R
610 package version 2.4-2.

611 Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E., & Fausch, K. D. (2004).
612 Ecological and evolutionary consequences of biotic homogenization. *Trends in*
613 *ecology & evolution*, **19**, 18–24.

614 Olifiers, N., 2002. Fragmentação, Habitat e as Comunidades de Pequenos Mamíferos da
615 Bacia do Rio Macacu, RJ. MSc Thesis. Universidade Federal de Minas Gerais.

616 Paglia, A. P., Fonseca, G. A. B., Rylands, A. B., Herrmann, G., Aguiar, L. M. S.,
617 Chiarello, A. G., ... Patton, J. L. (2012). Lista Anotada dos Mamíferos do Brasil.
618 Occasional Papers in Conservation Biology 6. Conservation International,
619 Arlington, 2ª ed. 76p.

620 Pardini, R., de Souza, S. M., Braga-Neto, R., & Metzger, J. P. (2005). The role of forest
621 structure, fragment size and corridors in maintaining small mammal abundance

622 and diversity in an Atlantic forest landscape. *Biological conservation*, **124**, 253–
623 266.

624 Pardini, R., Faria, D., Accacio, G. M., Laps, R. R., Mariano, E., Paciencia, P. A., ...
625 Baumgarten, J., 2009. The challenge of maintaining Atlantic Forest biodiversity: a
626 multi-taxa conservation assessment of an agro-forestry mosaic in southern Bahia.
627 *Biological Conservation*, **142**, 1178–1190.

628 Patton, J. L., Da Silva, M. N. F., & Malcolm, J. R. (2000). Mammals of the Rio Juruá
629 and the evolutionary and ecological diversification of Amazonia. *Bulletin of the*
630 *American museum of natural history*, **244**, 1–306.

631 Pfeifer, M., Lefebvre, V., Peres, C. A., Banks-Leite, C., Wearn, O. R., Marsh, C. J., ...
632 & Ewers, R. M. (2017). Creation of forest edges has a global impact on forest
633 vertebrates. *Nature*, doi:10.1038/nature24457.

634 Püttker, T., de Arruda Bueno, A., Prado, P. I., & Pardini, R. (2015). Ecological filtering
635 or random extinction? Beta-diversity patterns and the importance of niche-based
636 and neutral processes following habitat loss. *Oikos*, **124**, 206–215.

637 R Development Core Team (2013). *R: A language and environment for statistical*
638 *computing*. R Foundation for Statistical Computing, Vienna, Austria. Available
639 online: <<http://www.R-project.org/>>.

640 Rabelo, R. M., Bicca-Marques, J. C., Aragón, S., & Nelson, B. W. (2017). Are fluvial
641 islands “real” islands for arboreal mammals? Uncovering the effect of patch size
642 under the species–area relationship. *Journal of Biogeography*, **44**, 1802–1812.

643 Sánchez-de-Jesús, H. A., Arroyo-Rodríguez, V., Andresen, E., & Escobar, F. (2016).
644 Forest loss and matrix composition are the major drivers shaping dung beetle
645 assemblages in a fragmented rainforest. *Landscape ecology*, **31**, 843–854.

646 Schoener, A., & Schoener, T. W. (1984). Experiments on dispersal: short-term
647 floatation of insular anoles, with a review of similar abilities in other terrestrial
648 animals. *Oecologia*, **63**, 289–294.

649 Schooley, R. L., & Wiens, J. A. (2004). Movements of cactus bugs: patch transfers,
650 matrix resistance, and edge permeability. *Landscape Ecology*, **19**, 801–810.

651 Si, X., Baselga, A., & Ding, P. (2015). Revealing beta-diversity patterns of breeding
652 bird and lizard communities on inundated land-bridge islands by separating the
653 turnover and nestedness components. *PloS one*, **10**, e0127692.

654 Si, X., Baselga, A., Leprieur, F., Song, X., & Ding, P. (2016). Selective extinction
655 drives taxonomic and functional alpha and beta diversities in island bird
656 assemblages. *Journal of Animal Ecology*. doi: 10.1111/1365-2656.12478

657 Sikes, R. S. & Animal Care and Use Committee of the American Society of
658 Mammalogists (2016). 2016 Guidelines of the American Society of
659 Mammalogists for the use of wild mammals in research and education. *Journal of*
660 *Mammalogy*, **97**, 663–688.

661 Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How should beta-
662 diversity inform biodiversity conservation? *Trends in ecology & evolution*, **31**,
663 67–80.

664 Soininen, J., Heino, J., & Wang, J. A. (2017) A meta-analysis of nestedness and
665 turnover components of beta diversity across organisms and ecosystems. *Global*
666 *Ecology and Biogeography*. doi:10.1111/geb.12660.

667 Solar, R. R. D. C., Barlow, J., Ferreira, J., Berenguer, E., Lees, A. C., Thomson, J. R., ...
668 & Chaul, J. (2015). How pervasive is biotic homogenization in human-modified
669 tropical forest landscapes? *Ecology Letters*, **18**, 1108-1118.

670 Tabarelli, M., Peres, C. A., & Melo, F. P. (2012). The ‘few winners and many losers’
671 paradigm revisited: emerging prospects for tropical forest biodiversity. *Biological*
672 *Conservation*, **155**, 136–140.

673 Terborgh, J., Lopez, L., & Tello, S. (1997). Bird communities in transition: the Lago
674 Guri islands. *Ecology*, **78**, 1494–1501.

675 Terborgh, J., Lopez, L., Nuñez, P. V., Rao, M., Shahabuddin, G., Orihuela, G., ...
676 Balbas, L. (2001). Ecological meltdown in predator-free forest fragments.
677 *Science*, **294**, 1923–1926.

678 Tuomisto, H. (2010). A diversity of beta diversities: straightening up a concept gone
679 awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity.
680 *Ecography*, **33**, 2–22

681 Vellend, M., Verheyen, K., Flinn, K. M., Jacquemyn, H., Kolb, A., Van Calster, H., ...
682 & Brunet, J. (2007). Homogenization of forest plant communities and weakening
683 of species–environment relationships via agricultural land use. *Journal of*
684 *Ecology*, **95**, 565-573.

685 Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, **21**,
686 213–51.

- 687 Winemiller, K. O., McIntyre, P. B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T.,
688 Nam, S., ... Sáenz, L. (2016). Balancing hydropower and biodiversity in the
689 Amazon, Congo, and Mekong. *Science*, **351**, 128–129.
- 690 Wright, D. H., Patterson, B. D., Mikkelsen, G. M., Cutler, A., & Atmar, W. (1998). A
691 comparative analysis of nested subset patterns of species composition. *Oecologia*,
692 **113**, 1–20.
- 693 Zar, J. H. (1999). *Biostatistical Analysis*. Prentice Hall, Upper Saddle River, New
694 Jersey.
- 695 Zarfl, C., Lumsdon, A. E., Berlekamp, J., Tydecks, L., & Tockner, K. (2015). A global
696 boom in hydropower dam construction. *Aquatic Sciences*, **77**, 161–170.

697

698 **Biosketches**

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

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

707

708 **Tables**

709

710 **Table 1.** Local habitat quality, patch and landscape variables measured, potentially
 711 affecting mammal β -diversity among 25 forest sites within the Balbina Hydroelectric
 712 Reservoir archipelagic landscape. The overall range, mean and standard deviation are
 713 provided for each variable.

714

Name (code name)	Variable description	Range (mean \pm SD)
Local habitat scale		
Trees richness (S.TREES)	Number of tree species \geq 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 \geq 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 _{FP})	Basal area of trees bearing fleshy fruits, derived from floristic surveys of all live trees \geq 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 – 40.5 (21.5 \pm 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 <i>et al.</i> , 2012), we considered the total (“true”) area of each island.	0.44 – 10.65 (3.45 ± 1.84)

715

716 **Table 2.** Correlation between β -diversity estimates among forest sites of small and
717 midsized to large mammals and site location (geographic distance among sampled sites),
718 inter-site differences (Δ) in landscape, patch and local habitat variables at 25 forest sites
719 sampled at the Balbina Hydroelectric Reservoir. Three orders of q (0, 1 and 2), which
720 determines the sensitivity of each β -diversity component to the relative abundance of
721 species. Pearson correlation coefficients and significance were calculated using Mantel
722 tests (* $P < 0.05$; ** $P \leq 0.001$).
723

Variables	β-diversity order	Small	Midsized–large
	0	0.046	0.015
Site location	1	0.070	0.051
	2	0.085	0.069
<i>Local habitat scale</i>			
	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
<hr/>			
<i>Patch scale</i>			
Δ AREA	0	0.293*	0.751**
	1	0.141	0.465**
	2	0.150	0.418*
<hr/>			
Δ SHAPE	0	0.007	0.078
	1	-0.214	-0.063
	2	-0.213	-0.088
<hr/>			
Δ DIST	0	-0.070	0.214*
	1	-0.167	-0.075
	2	-0.156	-0.082
<hr/>			
<i>Landscape scale</i>			
Δ COVER	0	0.105	0.386**
	1	0.053*	0.199
	2	0.074	0.182
<hr/>			
Δ PROX	0	0.071	0.369*
	1	-0.134	0.043
	2	-0.127	0.019
<hr/>			

725 **Figure captions**

726

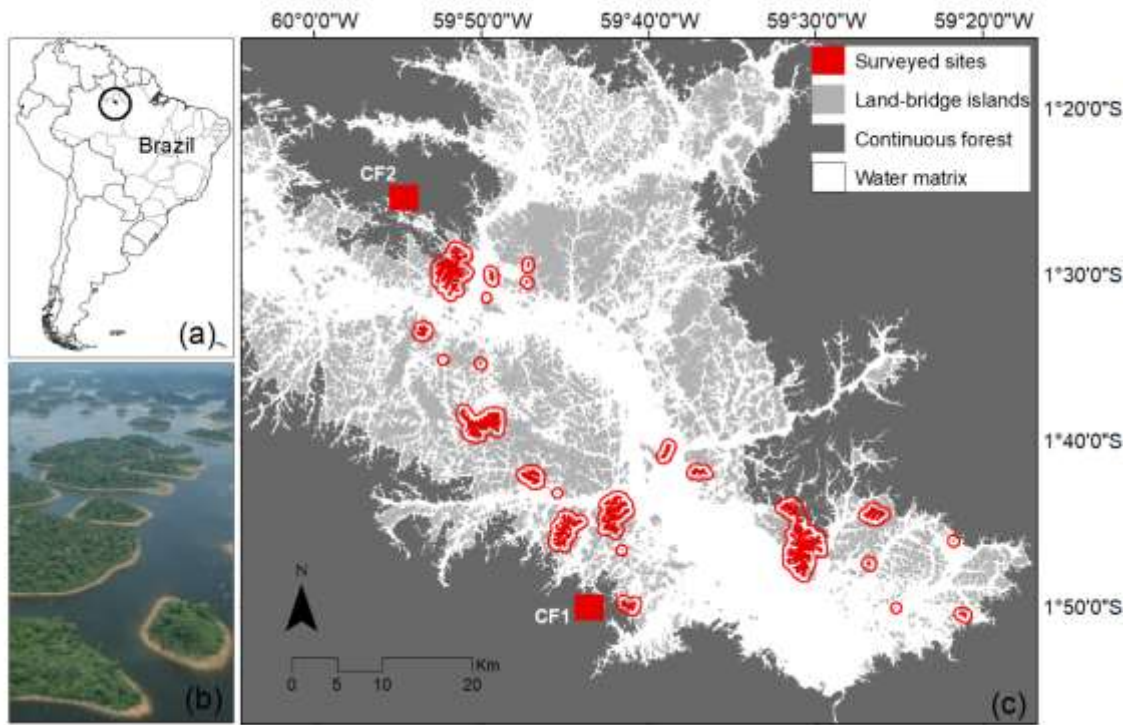
727 **Figure 1.** (a) Overview of the Balbina Hydroelectric Reservoir location in the Central
728 Brazilian Amazon; (b) aerial photograph illustrating the archipelagic landscape (photo
729 credit: E. M. Venticinque); and (c) spatial distribution of the 23 land-bridge islands (in
730 red and highlighting the 500-m buffer polygons) and two continuous forest sites
731 surveyed in the mainland (CF₁ and CF₂; red rectangles).

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

746 **Figure 3.** Mean β -diversity estimates of small and medium sized mammals surveyed at
747 25 forest sites within the Balbina archipelago. β -diversity was assessed using three
748 orders of q (0, 1 and 2), which determines the sensitivity of the measure to relative
749 species abundances. For each mammal group, we indicate the mean β -diversity for all
750 pairwise sites ($N = 300$), and the corresponding 95% confidence intervals.

751

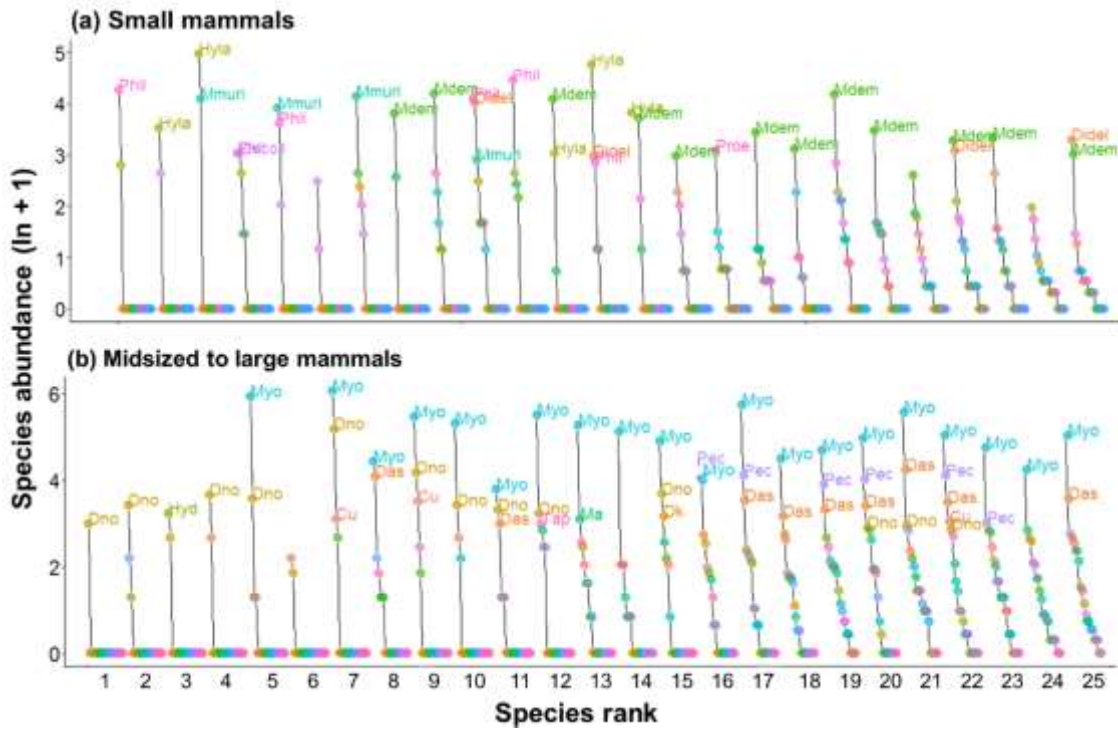
752 **Figures**



753

754 **Fig. 1**

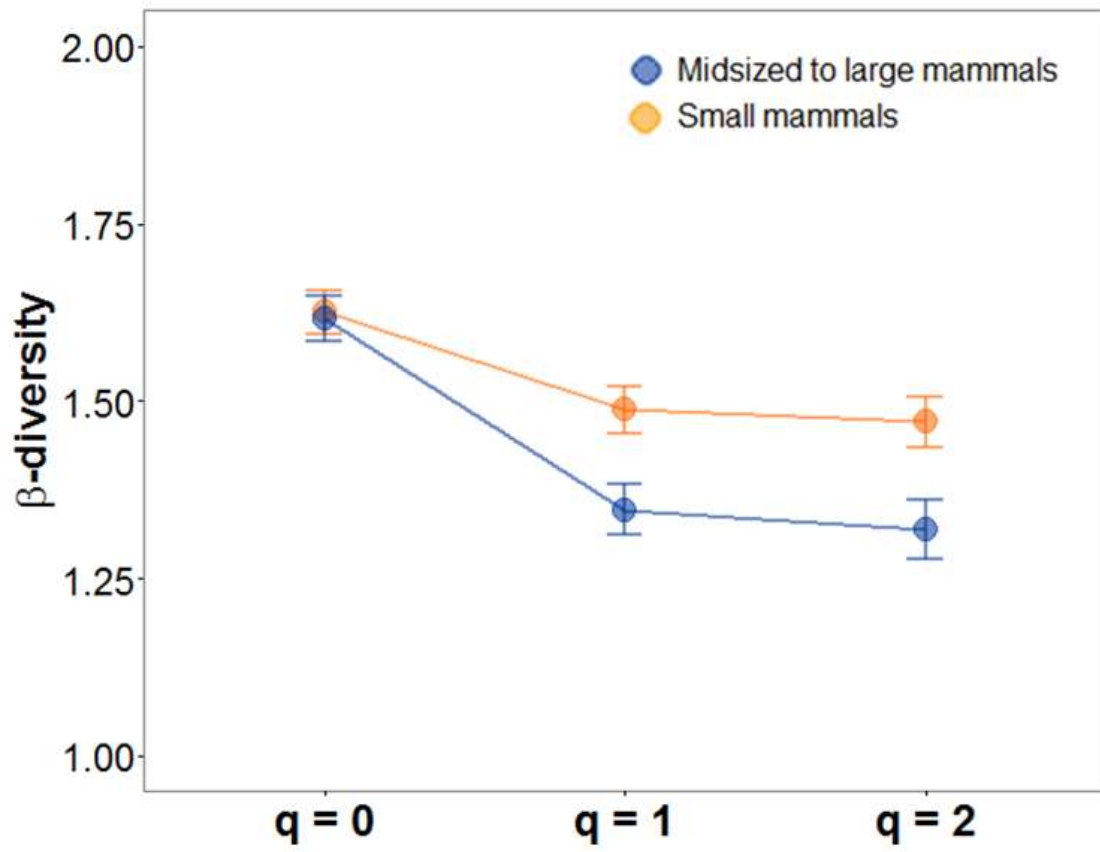
755



756

757 Fig. 2

758



759

760 **Fig. 3**