

1Small mammal responses to Amazonian forest islands are 2modulated by their forest dependence

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16*We assessed the extinction dynamics of small mammals in man-made Amazonian forest*
17*islands, providing unprecedented information that can be used in areas affected/to be*
18*affected, by hydroelectric dams.*

19

20Author Contributions: AFP, MVV and CAP conceived and designed the experiments. AFP
21performed the experiments, and MB provided additional data. AFP analysed the data and
22wrote the manuscript under the supervision and advice of MVV and CAP; MB also
23provided editorial advice.

24Abstract

25Hydroelectric dams have induced widespread loss, fragmentation and degradation of
26terrestrial habitats in lowland tropical forests. Yet their ecological impacts have been
27widely neglected, particularly in developing countries, which are currently earmarked for
28exponential hydropower development. Here we assess small mammal assemblage
29responses to Amazonian forest habitat insularization induced by the 28-year old Balbina
30Hydroelectric Dam. We sampled small mammals on 25 forest islands (0.83 – 1,466 ha) and
31four continuous forest sites in the mainland to assess the overall community structure and
32species-specific responses to forest insularization. We classified all species according to
33their degree of forest-dependency using a multi-scale approach, considering landscape,
34patch and local habitat characteristics. Based on 65,520 trap-nights, we recorded 884
35individuals of at least 22 small mammal species. Species richness was best predicted by
36island area and isolation, with small islands (<15 ha) harbouring an impoverished nested
37subset of species (mean \pm SD: 2.6 ± 1.3 species), whereas large islands (>200 ha; $10.8 \pm$
38 1.3 species) and continuous forest sites (∞ ha; 12.5 ± 2.5 species) exhibited similarly high
39species richness. Forest-dependent species showed higher local extinction rates and were
40often either absent or persisted at low abundances on small islands, where non-forest-
41dependent species became hyper-abundant. Species capacity to use non-forest habitat
42matrices appears to dictate small mammal success in small isolated islands. We suggest
43that ecosystem functioning may be highly disrupted on small islands, which account for
4462.7% of all 3,546 islands in the Balbina Reservoir.

45**Key words:** habitat fragmentation, hydroelectric dams, island biogeography, land-bridge
46islands, tropical forests.

47

48Introduction

49Hydroelectric dams have become major drivers of habitat loss and fragmentation
50worldwide (Lees et al. 2016; Jones et al. 2016). Still, their ecological and social impacts
51have been widely neglected, particularly in hyper-diverse tropical developing countries
52(Castello et al. 2013; Lees et al. 2016), which are currently the primary targets for
53hydropower development (Zarf et al. 2015). By flooding low-elevation areas, river
54damming often converts previous ridgetops into land-bridge islands, creating a complex
55insular landscape within hydroelectric reservoirs. A total of 145 dams in operation or under
56construction have flooded or will flood ~1.5 Mha of pristine forests in the Amazon basin
57alone, and current government plans include the construction of 263 additional dams
58(ECOA 2016).

59 Biological communities isolated on land-bridge islands are likely to be affected by
60several multi-scale drivers – including landscape, patch and habitat quality features of any
61given site – which may be more evident in habitat fragments than in true islands (Arroyo-
62Rodriguez et al. 2013). At the landscape scale, the degree of isolation from other islands
63and the mainland affects species colonization rates (MacArthur and Wilson 1967; Watling
64and Donnelly 2006). At the patch level, the remaining habitat area affects both population
65sizes and (micro)habitat diversity (Hutchinson 1957; MacArthur and Wilson 1967), and the
66severity of edge effects that can penetrate deeply into small islands (Benchimol and Peres
672015a). Edge effects are further linked to local habitat quality, which determines the
68spectrum of ecological niches available and, consequently, local species diversity (August
691983).

70 Species persisting in insular habitat patches are further prone to be affected by
71intrinsic eco-morphological traits (Cosson et al. 1999; Lynam and Billick 1999). In
72addition to dispersal ability, traits associated with success in disturbed habitat remnants
73play important roles in structuring animal communities isolated within land-bridge islands

74(Lynam and Billich 1999). Thus, classifying species according to their ecological traits can
75help us to understand how spatial and habitat characteristics affect species persistence
76(Ewers and Didham 2006; Santos-Filho et al. 2016), and how species composition changes
77across disturbance gradients (Pardini et al. 2009). Forest-dependent species unable to
78transverse unsuitable habitat between forest patches are therefore considered more
79extinction-prone in fragmented landscapes (Henle et al. 2004), whereas more structurally
80complex islands are expected to boost the persistence of forest-specialist species (Devictor
81et al. 2008). This pattern of selective extinctions may further result in a nested structure
82along the gradient of fragmentation, with species persisting at progressively smaller islands
83comprising subsets of assemblages retained at larger sites (Wright et al. 1998).

84 In the Neotropics, small non-volant mammals (marsupials and rodents) occupy a
85central position in forest food webs, acting either as seed predators and dispersers (Mangan
86and Adler 2000; Terborgh et al. 2001), pollinators (Vieira et al. 1991), arthropod predators
87(Carvalho et al. 2005), and as a resource for higher trophic levels (Wright et al. 1994).
88Although detailed ecological information on most species is scant, small mammals play
89critical roles in ecosystem functioning including forest regeneration (Terborgh et al. 2001;
90Galetti et al. 2015). Several studies have assessed the effects of habitat fragmentation on
91small mammals, including tropical reservoir islands (Adler and Seamon 1996; Granjon et
92al. 2002; Lambert et al. 2003; Wang et al. 2010a, Gibson et al. 2013). Indeed, islands
93isolated in the aftermath of hydroelectric dams offer several advantages over non-insular
94forest patches abutting a terrestrial matrix, including the equitability of isolation time, an
95equally hostile uniform open-water matrix, and convergent histories of anthropogenic
96disturbance (Diamond 2001; Wu et al. 2003; Benchimol and Peres 2015a). Studies in
97hydroelectric reservoirs can therefore rule out confounding effects of matrix types,
98enabling assessments of fragmentation effects *per se* (Cosson et al. 1999). Nevertheless, no

99small mammal study to date has been carried out in hyper-diverse Amazonian reservoirs,
100where currently ambitious governmental plans are expected to greatly expand hydropower
101infrastructure (Lees et al. 2016). Understanding how biodiversity is affected by
102hydropower projects is then of critical importance for management actions in lowland
103Amazonia.

104 Here, we assess small mammal assemblage responses to habitat insularization
105induced by a major hydroelectric dam in Central Amazonia 28 years after isolation. The
106Balbina Hydroelectric Dam created a reservoir of 443,772-hectares
107(FUNCATE/INPE/ANEEL, 2000), comprising 3,546 forest variable-sized islands. We
108conducted quantitative surveys on 25 forest islands and four widely-separated mainland
109sites in neighbouring continuous forests to determine the main predictors of small mammal
110persistence within forest islands, and investigate whether small mammal assemblages
111exhibited a nested structure along the gradient of habitat insularization. We used a multi-
112scale approach, initially considering potential area effects, and the combined effects of
113patch, landscape and habitat-quality metrics. We further classified each species in terms of
114their degree of forest-dependency to investigate the influence of this ecological trait in
115explaining patterns of local species extinction across islands, also testing for potential
116nestedness structure. We hypothesized that small mammal assemblages on smaller and
117more isolated islands that had been more degraded were represented by a simplified subset
118of mainly non-forest-dependent species. Conversely, nearly complete assemblages
119comprised of both forest and non-forest-dependent species are expected to persist on
120larger, less isolated islands containing high-quality forest habitat. In particular, non-forest-
121dependent species are expected to present a lower degree of nestedness than forest-
122dependent species.

123

124 **Methods**

125 *Study area*

126 This study was carried out in the archipelagic landscape of the Balbina Hydroelectric
127 Reservoir and its immediate surroundings, in Central Brazilian Amazonia (1°48'S,
128 59°29'W; Fig. 1). The Balbina dam was built in 1986 on the Uatumã River, a left-bank
129 tributary of the Amazon River. Given the typically flat topography of the area, this dam
130 flooded a vast area of 312,900 ha of primary forest, within the 443,772-ha hydroelectric
131 reservoir (FUNCATE/INPE/ANEEL 2000). In the aftermath of damming, the former
132 hilltops of the pre-inundation forest area remained above-water as 3,546 land-bridge
133 islands widely distributed across the reservoir lake. Many dead relics of emergent trees are
134 still standing within the open-water matrix, as the submerged primary forest had not been
135 clear-cut. Most islands consist of dense closed-canopy *terra firme* forest, but many small
136 islands were strongly affected by edge-related windfalls and ephemeral wildfires, which
137 occurred during a late-1997 to early-1998 El Niño drought (Benchimol and Peres 2015a).
138 The area within and around the former left bank of the Uatumã river has been legally
139 protected since 1990 by the 942,786-ha Uatumã Biological Reserve, the largest reserve in
140 its category in Brazil. This contributes to low levels of post-damming human disturbance
141 across the reservoir. The mean annual temperature in this region is 28°C and the mean
142 annual rainfall is 2,376 mm (IBAMA 1997). Small mammal communities were sampled on
143 25 islands and four continuous forest sites (hereafter, CF; Fig. 1). Islands were selected
144 according to their size, degree of isolation and spatial distribution, resulting in a wide range
145 of island configurations. Surveyed islands ranged in area from 0.55 to 14,660 ha (mean ±
146 SD: 199 ± 344 ha; Table S1), and isolation distances from each focal island to the nearest
147 mainland continuous forest ranged from 44 to 11,872 m (4,351 ± 3,386 m).

148

149 *Small mammal sampling*

150 Small mammals were sampled using transects during sessions of 16 consecutive nights
151 over two field seasons, from April to November 2014 and April to November 2015. Each
152 transect consisted of a set of nine stations of live traps (hereafter, LTs), followed by an
153 array of three pitfall units. Each LT station was placed 20-m apart from others and included
154 two Sherman traps (23 x 9 x 8 cm, H. B. Sherman Traps, Inc., Tallahassee, Florida) and
155 one wire mesh trap (30 x 17.5 x 15 cm, Metal Miranda, Curitiba, Paraná). At each LT
156 station, one trap was set on the ground, one in the understory (~1.5 m high), and one in the
157 (sub)canopy (>10 m high). Traps of different types were placed alternatively on the ground
158 and in the understory across consecutive stations, but only Sherman traps were placed in
159 the canopy due to logistic limitations. The forest canopy stratum was sampled using an
160 adaptation of the method described by Lambert et al. (2006). LTs were baited with a mix of
161 bananas, peanut powder, sardines and oatmeal. Pitfall traps (100L) were also spaced at 20-
162 m intervals and connected by a plastic drift fence 50-cm high and 10-cm underground, with
163 10 m of fence extending beyond the two terminal pitfalls.

164 The number of transect placed at different sites varied according to their area. This
165 allowed us to obtain a higher number of individuals at larger forest sites, where overall trap
166 density, and consequently the probability of an individual passing near a trap, were lower
167 (Table S1). Due to spatial restrictions in small islands, alternative smaller transects were
168 established therein. Thus, all islands smaller than 2 ha and those between 2 and 10 ha were
169 sampled by transects containing only three LT stations followed by an array of one pitfall,
170 and by six LT stations followed by an array of two pitfalls, respectively. Larger islands
171 were sampled by as many as four transects, according to their size classes: 10 to 50 ha, 50
172 to 200 ha, 200 to 500 ha and >500 ha, respectively; CF sites were sampled by either six
173 (CF₁ and CF₃), 10 (CF₂) and 12 transects (CF₄). Due to logistic restrictions, CF₂ and CF₄

174 were only sampled during either the first (2014) or second (2015) field season,
175 respectively, which reflects the higher number of transects placed therein (for further
176 details on sampling effort per site, see Table S1).

177 We conducted a total 65,520 trap-nights across 79 transects. All traps were
178 inspected daily and whenever live captures could not be identified in the field, a maximum
179 of five voucher specimens per species per site were collected during the first season, and
180 deposited at the Mammal Collection of the Instituto Nacional de Pesquisas da Amazônia
181 (INPA), in Manaus, Brazil. All other individuals recorded were weighted and tagged (Fish
182 and Small Animal Tag, size 1; National Band and Tag Co., Newport, Kentucky), so that
183 any subsequent recaptures could be distinguished. Additionally, tissue samples were
184 collected from all individuals recorded and deposited at INPA. However, we were not
185 always able to identify at the species-level records of *Proechimys* spp. (*P. cuvieri* and *P.*
186 *guyanensis*) and *Oecomys* spp. 1 (*O. roberti* and *O. bicolor*) at all sites. Because these
187 congeners are ecologically very similar (Jones et al. 2009), we further refer to those taxa as
188 ‘ecospecies’. To streamline, we hereafter use ‘species’ to refer to both species and
189 ecospecies. We followed ASM guidelines (Sikes et al. 2016), and the study was approved
190 by the appropriate Brazilian institutional animal care and use committee (SISBIO license
191 No. 39187-4).

192

193 *Patch, landscape and habitat quality variables*

194 Patch and landscape metrics were calculated using ArcMap 10.1 (ESRI 2012), based on
195 high-resolution multi-spectral RapidEye imagery (5-m resolution with 5-band color
196 imagery) of the entire study landscape. At the patch scale, we measured island area and
197 shape, and at landscape-scale, we obtained for each surveyed island a proximity (PROX)
198 metric to other islands and CF sites, and their nearest distances to CF (Table 1; for further

199 details on imagery processing and landscape metrics, see Benchimol and Peres 2015a,
200 2015b). We used Generalized Linear Models (GLMs) to analyse the relationship between
201 the species richness in the islands and the proximity index considering in separate models
202 at multiple scales of effects in terms of increasing buffer radius (Jackson and Fahrig 2012)
203 – 250 m, 500 m and 1 000 m. We then ordered the models according to its Akaike
204 Information Criteria (AIC; Burnham and Anderson 2002). For further analyses, we
205 retained the PROX index obtained using the 500 m-radius (AIC = 129.2), rather than 1 000
206 m (129.2) or 250 m (130.64).

207 Small mammal species responses to habitat fragmentation are closely linked to
208 habitat structure, such as overstory and understory vegetation density (Delciellos et al.
209 2015). We thus obtained habitat variables by measuring forest composition and vegetation
210 structure, which further reflect the habitat quality for small mammals. Vegetation variables
211 were obtained from floristic surveys within 0.25-ha (250m × 10m) forest plots established
212 on each focal island and CF site, where all trees ≥ 10 cm diameter at breast height (DBH)
213 were measured and identified at species-level. The number of plots surveyed per site varied
214 to the area of each site, ranging from one to four plots (see Table 1 for a description of
215 floristic variables; details in Benchimol and Peres 2015c). Additionally, we conducted a
216 semi-supervised classification to obtain four land cover classes (closed-canopy forest,
217 open-canopy forest, bare ground, and water) using ArcMap 10.1, and obtained the
218 percentage of closed-canopy forest within the island from the RapidEye imagery (Table 1).

219

220 *Forest-dependency index*

221 Degree of forest habitat-dependency (FD) was defined as the species-specific ratio
222 between the capture rate in the open habitat matrix and in continuous primary forest.
223 Forest-dependency estimates were based on small mammal data obtained during a 5-year

224study by J. R. Malcolm (1991) at the Biological Dynamics of Forest Fragments Project
225(BDFFP), a fragmented landscape ~100 km from the Balbina reservoir, which shares the
226same small mammal fauna. Forest and non-forest-dependent species were those for which
227a $FD < 1$ and $FD > 1$, respectively. We obtained the community-averaged FD values by
228summing the FD values of all individuals recorded at each survey site, and dividing this by
229the number of individuals therein. Community-averaged FD values ranged between 0.061
230– 0.688, higher values corresponding to an increased prevalence of non-forest-dependent
231species. Species FD were previously transformed to range between 0 (highest forest-
232dependency) and 1 (lowest forest-dependency). Information on capture rates at the BDFFP
233landscape within either primary forest or the matrix was unavailable only for the squirrel
234*Guerlinguetus aestuans*, which occurs chiefly in primary forests (Patton et al. 2007). Based
235on ecological similarities between closely related taxa (Jones et al. 2009), we assigned FD
236values to congener species for which information was unavailable (*Oecomys*, *Neacomys*
237and *Marmosops*). Capture rates and FD values are summarized for all species in Table S2.

238

239*Data analysis*

240We excluded from analysis two Echimyidae — *Makalata didelphoides* and *Echimys*
241*chrysurus* — that were recorded only once during the study. These species feed on seeds
242and leaves, in addition to some fruit (Patton et al. 2000), and consequently are rarely
243attracted to the bait used here. The adequacy of small mammals sampling was evaluated
244using the sample coverage estimator (*sensu* Chao and Jost 2012), which estimates the
245proportion of the total number of individuals in an assemblage that belong to the species
246represented in the sample. Our small mammal trapping was satisfactorily accurate in
247relation to our sampling effort, averaging 0.92 ± 0.07 per site in the most complete
248assemblage, except for two small islands ('Xibé' and 'Abu'), in which sample coverage

249 was zero (Table S1). Despite the lack of sampling representativeness in those two islands,
250 we still retained them in the analysis because trap density therein was much higher (~4.57
251 traps/ha) than in islands larger than 100 ha (0.08 – 0.54 traps/ha) and CF sites (~0.002
252 traps/ha; Table S1). Nevertheless, to account for any eventual undetected species and avoid
253 any potential bias in species richness values, we estimated a bootstrapped number of
254 species. To do so, we applied a bootstrap method that determines confidence intervals
255 around Hill numbers, facilitating the comparison of multiple assemblages of extrapolated
256 samples (Chao et al. 2014). For each site, the bootstrapped number of species was obtained
257 from the extrapolation of individual-based Hill numbers assuming twice the number of
258 individuals recorded at that site, using the R codes provided by Chao et al. (2014). We
259 further verified if the variable number of traps deployed per site caused any bias on
260 observed numbers of species. To do so, we correlated the number of traps deployed per site
261 with sample coverage estimations and the number of individuals recorded. Spatial
262 autocorrelation was examined by correlating matrices of binary species composition and
263 geographic distances among sites, applying a Mantel test using the ‘*vegan*’ R package
264 (Oksanen et al. 2007).

265 Considering all 25 islands and their bootstrapped species richness, we performed
266 species-area relationships (SARs) comparing eight possible SAR models: power,
267 exponential, negative exponential, Monod, rational function, logistic, Lomolino and
268 cumulative Weibull (for each model formula, see Table S3), using the ‘*mmSAR*’ R package
269 (Guilhaumon et al. 2010). In addition, given the importance in identifying critical
270 thresholds beyond which species responses change abruptly, we also included a piecewise
271 regression model to explain small mammal SARs (Toms and Lesperance 2003), using the
272 ‘*segmented*’ R package (Mugge 2017). Data fitting for each model was compared

273 according to Akaike Information Criterion values corrected for small sample sizes (AICc:
274 Burnham and Anderson 2002).

275 We further estimated the degree of nestedness in small mammal assemblages for
276 each sampling site using NODF, a metric based on overlap and decreasing fill of presence-
277 absence matrix data (Almeida-Neto et al. 2008). Using this method, probability levels can
278 be assessed using *Z* scores, i.e., by comparing the observed nestedness value with the mean
279 of a series of values obtained by reshuffling the original matrix to produce a number of
280 random matrices according to a certain null model (Strona et al. 2014). These analyses
281 were performed using the ‘Nestedness for Dummies’ Program (Strona et al. 2014),
282 considering the ‘proportional column and row totals’ algorithm to construct 999 simulated
283 random matrices. Interaction matrices of small mammal species and sites ordered by
284 species richness were further obtained using the ‘*Vegan*’ R package. Prior to analysis, we
285 added the data from all four mainland continuous forest sites. Nestedness analyses were
286 further repeated separately for each species grouping (i.e., forest- and non-forest-
287 dependent), using the same procedure

288 Species composition was also analysed using Principal Coordinate Analysis
289 (PCoA) based on a quantitative Bray-Curtis similarity matrix of species composition.
290 Species abundances were previously standardized for each site due to differences in
291 sampling effort per site. Aggregate biomass ($\log_{10} x$) was defined as the sum of the body
292 mass of all individuals recorded at any given site per unit of trapping effort. For that, we
293 considered the body mass of each live capture weighted during the field work.

294 To evaluate the combined effects of patch, landscape and habitat quality metrics on
295 small mammal assemblages (bootstrapped species richness, species composition,
296 standardized abundance, and aggregate biomass), we performed Generalized Additive
297 Models (GAMs). GAMs do not require a linear relationship between the response and the

298explanatory variables, and were performed using a Gaussian error structure. We controlled
299for high levels of variable inter-dependence by performing a Pearson correlation matrix,
300retaining weakly correlated variables ($r < 0.70$, $P > 0.05$). ‘Island shape’, ‘percentage of
301old-growth trees’ and ‘fire severity’ were correlated and therefore excluded from further
302analysis. We did not include CF sites in this analysis because that additionally overinflated
303the correlation between ‘island area’ and ‘proximity’ ($r = 0.86$, $P < 0.0001$), further
304invalidating the inclusion of one these variables in the model. We also calculated the
305Variation Inflation Factors (VIFs), any of the remaining variables was moderately
306redundant, presenting $VIF < 5$ (Dormann et al. 2013). A candidate model set was further
307constructed, using all additive combinations of the eight explanatory variables retained,
308and models were ranked based on their AICc, using the ‘*MuMIn*’ R package (Bartoń 2014).
309To account for model uncertainty in multi-model inference, a model-averaging approach
310was performed using only the most plausible models (i.e., $0 < \Delta AICc < 2$, $\Delta AIC = AIC_i -$
311 AIC_{min} in which $i = i^{th}$ model). The relative importance (RI) of each variable contained in
312that model set was obtained by the sum of the Akaike weights of the models in which that
313variable had been included (Rhodes et al. 2009). Explanatory variables were previously
314standardized ($x = 0$, $\sigma = 1$) to place coefficient estimates into the same scale. The same
315modelling procedures were repeated considering the number and abundance of forest and
316non-forest-dependent species separately. When analysing graphically the isolated effects of
317island area and proximity on species richness and abundance of forest and non-forest-
318dependent species, we improved data fitting by performing simple GLMs, both including
319and excluding the quadratic term of each explanatory variable. AIC values were compared
320between the models including and excluding the quadratic term of the explanatory variable
321(Burnham and Anderson 2002). We then added the quadratic term of the explanatory
322variable when examining the relationship between the number of forest-dependent species

323 and island area, and between the number of non-forest-dependent species and island
324 proximity (Table S4). All data analyses were performed in R (R Development Core Team
325 2015).

326

327 Results

328 A total of 884 small mammal individuals was recorded across the 29 sampled sites,
329 amounting to an overall mean capture success of 1.35% per trap-night (excluding
330 recaptures). A total of 22 species was recorded considering all sites, representing 12
331 rodents and 10 marsupials (see Table S5). Excluding the two singleton records of *E.*
332 *chrysurus* and *M. didelphoides*, the number of species recorded per site ranged from 1 to
333 16 (mean \pm SD: 5.76 ± 3.80 species) for all islands, and from 9 to 16 for CF sites ($12.5 \pm$
334 2.5 species). Nearly all species recorded on islands were also present in at least one CF
335 site, except for the small terrestrial rodent *Neacomys paracou*, which was recorded at only
336 one island ($N = 2$ individuals). The most abundant species were the arboreal marsupial
337 *Marmosa demerarae* ($N = 195$) and the terrestrial rodent *Hylaeamys megacephalus* ($N =$
338 187); while the arboreal echimyid rodent *Isothrix pagurus* ($N = 6$) and sciurid
339 *Guerlinguetus aestuans* ($N = 4$) were among the least detected species across all sites (see
340 Table S3). On the basis of those species, our index of forest-dependency resulted in 11
341 species classed as forest-dependent and 9 species as non-forest-dependent (Table S2).
342 Furthermore, the number of traps deployed at each site was neither correlated with sample
343 coverage estimations ($r = -0.012$, $P = 0.951$) nor with the overall number of individuals
344 recorded ($r = 0.245$, $P = 0.200$), supporting the notion that the number of traps deployed at
345 any given site did not induce any bias in the number of species recorded therein. Also,
346 small mammal species composition was largely unaffected by the geographic distance
347 between sites ($r = 0.037$, $P = 0.269$, $N = 406$ pairwise comparisons).

348

349 *Species-area relationships and nestedness*

350 The power, rational function, logistic and cumulative Weibull SAR models performed
351 similarly well in explaining the bootstrapped species richness (S) of small mammals across
352 all 25 sampled islands, explaining 68.7 – 71.0% of the variation in S (Table S3).

353 Henceforth, to facilitate comparisons with most other studies, we focused our results on the
354 power model. As such, the observed SAR clearly showed fewer species over a decreasing
355 gradient of island size (z -value = 0.289, c -value = 2.089, $R^2 = 0.687$; Table S3). Islands
356 smaller than 15 ha retained highly impoverished small mammal assemblages (mean \pm SD:
357 2.6 ± 1.3 species), whereas islands larger than 200 ha on average harboured 10.8 ± 1.3
358 species, which was comparable to CF sites in the mainland (12.5 ± 2.5 ; Fig. 2).

359 Across the decreasing gradient of island size, small mammal community
360 disassembly further appears to be mediated primarily by the selective extirpation of forest-
361 dependent species, in that small islands mostly retained non-forest-dependent species, as
362 denoted from the high community-averaged FD values. In contrast, community-averaged
363 FD values remained relatively low across CF sites (range = 0.08 – 0.11; Fig. 2). Moreover,
364 overall small mammal assemblages presented a significantly nested structure (matrix size:
365 520, fill = 0.313; $NODF_{row} = 62.493$, $Z = 9.731$, $P < 0.001$). Similar nestedness results
366 were obtained when considering only either forest-dependent species (matrix size: 220, fill
367 = 0.341; $NODF_{row} = 56.055$, $Z = 4.086$, $P < 0.001$), or non-forest-dependent (matrix size:
368 234, fill = 0.376; $NODF_{row} = 60.682$, $Z = 4.645$, $P < 0.001$; Fig. 3).

369

370 *Combined effects of patch, landscape and habitat quality metrics*

371 Multiple-scale landscape, patch and habitat quality variables clearly affected the overall
372 persistence of small mammal species across all 25 islands surveyed, with species

373 composition best predicted by both island area ($\beta_{AREA} = 0.229$, $P = 0.023$, $RI = 0.84$) and
374 tree species richness ($\beta_{S.TREES} = 0.148$, $P = 0.033$, $RI = 0.67$; Fig. 4a, Table S6). In fact,
375 despite the lack of significant nestedness among the survey sites, the narrow set of non-
376 forest-dependent species persisting at all islands smaller than 2 ha was virtually the same.
377 Most of the other islands, ranging from 2 to 800 ha, retained highly idiosyncratic species
378 compositions, as indicated by the poorly predicted PCoA1 values obtained for those
379 islands ($R^2 = 0.417$; Fig. S1).

380 The bootstrapped number of species at each island was best predicted by both
381 island area ($\beta_{AREA} = 4.227$, $P = 0.001$, $RI = 0.75$) and proximity ($\beta_{PROX} = 3.312$, $P = 0.002$,
382 $RI = 1.00$; Fig. 4b, Table S5). When species were distinguished based on their degree of
383 forest-dependency, the number of forest-dependent species responded similarly, being
384 positively affected by both island area ($\beta_{AREA} = 3.107$, $P = 0.001$, $RI = 1.00$) and proximity
385 ($\beta_{PROX} = 1.289$, $P = 0.039$, $RI = 1.00$; Fig. 4c). Richness of non-forest-dependent species,
386 however, was positively affected only by proximity to other land-masses ($\beta_{PROX} = 1.227$, P
387 $= 0.011$, $RI = 0.88$; Fig. 4d, Table S7). Again, the turnover in the number of forest and non-
388 forest-dependent species can be observed across the size gradient from insular and
389 continuous forest sites: forest-dependent species were often missing from small islands but
390 were more abundant than non-forest-dependent species at CF sites (Fig. 5a). The same was
391 not clearly observed across the gradient of proximity to other land-masses (Fig. 5c).

392 Although none of the variables considered here performed well in predicting
393 overall species abundance (Fig. 4e, Table S6), the abundance of forest-dependent species
394 was positively affected by island area ($\beta_{AREA} = 6.597$, $P = 0.005$, $RI = 0.84$) and negatively
395 affected by the aggregate basal area of trees bearing fleshy fruits ($\beta_{FRUIT} = -2.799$, $P =$
396 0.027 , $RI = 0.16$; Fig. 4d). The abundance of non-forest-dependent species was negatively
397 affected by both island area ($\beta_{AREA} = 6.597$, $P = 0.005$, $RI = 0.49$) and proximity ($\beta_{PROX} =$

3986.597, $P = 0.005$, $RI = 0.35$; Fig. 4g, Table S7). Non-forest-dependent species accounted
399for a disproportionate fraction of the overall abundance at islands smaller than 15 ha
400(median (min – max) = 100% (50 –100%); Fig. 5b), while the abundance of the two
401functional groups in terms of forest habitat-dependency was comparable between weakly
402isolated large islands and CF sites (Fig. 5b, d). Indeed, except for the least detected species
403(*N. guianensis*, *N. paracou* and *Monodelphis arlindoi*), non-forest-dependent species were
404clearly widespread across all island sizes and CF sites. Forest-dependent species instead
405are completely absent from very small islands (< 2 ha) and 45.5% only occurred in islands
406larger than 200 ha (Fig. S2). Finally, the aggregate biomass of small mammals across all 25
407islands could not be predicted by any of the variables considered here (Table S6).

408

409**Discussion**

410As new capital investment fuels hydropower frontier expansion across wilderness regions
411in tropical countries (Castello et al. 2013; Zarf et al. 2015), decision-makers should
412carefully weigh the landscape-wide ecological impacts of this infrastructure against their
413overall socioeconomic benefits (Fearnside and Pueyo 2012; Lees et al. 2016). In lowland
414Amazonia, damming creates disproportionately large reservoirs and highly fragmented
415archipelagos of land-bridge forest islands (Junk and Mello 1990). Under this landscape
416context, we document widespread local extinctions of small mammal species across the
417archipelago, which is comprised of myriad of small islands. Small mammal assemblages
418further exhibited a nested structure, so that smaller and more isolated Balbina islands
419exhibited depauperate small mammal assemblages, in which forest-dependent species were
420typically either missing or persisted at very low abundances.

421

422*Island biogeography revisited*

423 Island size and degree of isolation were the strongest predictors of the number of small
424 mammal species at Balbina forest islands. Islands larger than 200 ha and mainland forest
425 sites contained up to 12 and 15 species, respectively, while those smaller than 15 ha
426 supported a maximum of four species, or fewer than one-third of the number of species
427 expected to persist in large islands and mainland forest sites. Although large islands
428 harboured nearly full complements of species, they account for only 1.8% of the 3,546
429 islands in Balbina reservoir, whereas those smaller than 15 ha correspond to 62.7% of all
430 islands (see histogram in Fig. 1). Our findings are consistent with the overall negative
431 response of terrestrial species and communities to isolation in man-made reservoir islands
432 reported worldwide (Jones et al. 2016). Indeed, medium and large-bodied terrestrial
433 vertebrates were greatly affected by island size within the Balbina reservoir, with 95% of
434 all islands retaining fewer than 60% of all 35 native vertebrate species (Benchimol and
435 Peres 2015a). In other tropical reservoirs containing forest islands smaller than 350 ha,
436 small mammals experienced local extinctions at similar (Guri Reservoir, Venezuela:
437 Lambert et al. 2003) or higher rates than those observed here, often culminating in the
438 persistence of only a single dominant species (Gatun Lake, Panama: Adler and Seamon
439 1996; Saint-Eugène reservoir, French Guiana: Grajon et al. 2002; Chiew Larn Reservoir,
440 Thailand: Gibson et al. 2013). Yet those studies do not provide a comprehensive scenario,
441 failing to include large islands (but see Wang et al. 2010a for a reservoir in southern
442 China). Given the observed ability of certain terrestrial mammal species to swim between
443 insular forest patches (e.g. Grajon et al. 2002), large islands play a critical biotic role in the
444 archipelagic landscape, by harbouring resident populations and operating as a source of
445 emigrants for some species, depending on island isolation (Adler and Seamon 1996).

446 Second to island area, patterns of small mammal species richness at Balbina were
447 best predicted by isolation. This is in part consistent with seminal ideas from Island

448Biogeography Theory (IBT), in which islands experiencing higher colonization rates
449should harbour more species (MacArthur and Wilson 1967). However, higher colonization
450rates were primarily a function of the functional connectivity of an island in the landscape
451(as inferred by the Proximity index) rather than the distance to the mainland, as predicted
452by IBT. Studies in terrestrial landscapes have found similar patterns of fragmentation
453effects in terrestrial landscapes for both small mammals (e.g. Goodman and
454Rakotondravony 2000; Pardini et al. 2005), and other taxa (see Predevello and Vieira
4552010). Our findings therefore unequivocally support the notion that small, isolated
456reservoir islands have more limited conservation value than non-island habitat fragments in
457entirely terrestrial landscapes, which agrees with paleotropical small mammal data from
458reservoir islands in southern Thailand (Gibson et al. 2013).

459

460*Determinants of community composition*

461Communities isolated in land-bridge islands may exhibit nested structures over time, as has
462already been detected for small mammal, birds and lizard assemblages within the ~50 year
463old Thousand Island Lake, China (Wang et al. 2010a). In Balbina, the nested structure
464observed in small mammal assemblages are probably related to the differential species
465susceptibility to extinction (Lynam and Billick 1999). Indeed, the subset of small mammal
466species persisting at Balbina islands was closely related to both patch and local habitat
467characteristics, as suggested by the importance of island area and tree species richness in
468predicting species composition. Small islands likely retain a very limited spectrum of
469habitat resources (August 1983), so they are consistently occupied by the same subset of
470species, which were mainly non-forest-dependent. As island area increases, more
471ecological niches become available (Pardini et al. 2005), which facilitates higher species
472packing, including forest-dependent species. Similarly, habitat structure was one of the

473 main determinants of small mammal assemblages in Brazilian Atlantic Forest fragments
474 (Pardini et al. 2005; Delciellos et al. 2015). Nevertheless, although forest-dependent
475 species exhibited an expected nested structure, the same was observed for non-forest-
476 dependent species. This might be due to the inclusion of certain species rarely captured
477 throughout the sampling, that were particularly evident at larger islands and continuous
478 forest sites (e.g., *Monodelphis arlindoi*, *N. paracou*, and *N. guianae*).

479 Moreover, despite the nested structure of the Balbina small mammal assemblages,
480 larger islands and continuous forest sites still presented an idiosyncratic species
481 composition (Figs. S1, S2). This result contrasts with other faunal groups at the Balbina
482 landscape, in which species composition converged along the gradient of island area
483 (Benchimol and Peres 2015b; Aurélio-Silva et al. 2016). The idiosyncrasy in species
484 composition observed in this study could result from the reduced sample coverage in larger
485 islands and continuous forest sites. Regardless of the overall satisfactory sample coverage
486 of estimators obtained, the difference between observed and bootstrapped species richness
487 was higher in continuous forest sites (Fig. S3). Even considering the higher sampling effort
488 at larger forest sites, the density of traps was 21 – 207 times lower therein (0.20 and 0.02
489 traps/ha at islands > 200 ha and CF sites, respectively) compared to small islands (4.14
490 traps/ha). Therefore, the probability of an individual passing near a trap was much higher
491 in small islands due to higher trap saturation, and also due to vertical forest compression,
492 as larger forest areas were both more saturated and multi-layered (AFP, CAP, MB, unpubl.
493 data). In addition, large islands' transects may cover a limited part of the ecological
494 distribution of species, which are often aggregated due to patchy trophic resources
495 (Charles-Dominique et al. 1981). Our results may therefore underestimate the number of
496 species in larger islands and continuous forest sites. This further amplifies the strength of
497 species-area effects, and suggesting that SAR patterns presented here are conservative.

498

499 *Vulnerability of forest-dependent species*

500 In entirely terrestrial fragmented landscapes, habitat-generalist species responses are most
501 likely due to their smaller spatial requirements, ability to access and take advantage of
502 matrix resources, and trophic plasticity (Pardini et al. 2005; Umetsu and Pardini 2007;
503 Santos-Filho et al. 2012). Interestingly, those general patterns also hold true in a real island
504 landscape such as Balbina, even though matrix resources are entirely unavailable.
505 Likewise, forest specialist small mammal species greatly declined in forest patches
506 surrounded by small amounts of forest cover in the Brazilian Atlantic Forest, whereas those
507 non-forest-dependent species were unaffected by habitat loss (Estavillo et al. 2013). Using
508 the same species classification, Santos-Filho et al. (2016) noted the same trend in species
509 richness of small mammals in southern Amazonian forest fragments. Unlike forest-
510 dependent species, habitat generalists were able to persist in tiny islands with highly
511 reduced trophic and structural resource availability. Rodent species persisting in islands
512 within China's Three Gorges Dam also exhibited dietary shifts compared to their baseline
513 diet in the mainland (Wang et al. 2010b).

514 In contrast to species richness, the abundance of forest-dependent species was not affected
515 by island isolation. The abundance of these species may therefore be mainly determined by
516 within-island processes rather than movement between islands. For forest-dependent species,
517 such processes may be idiosyncratic in relation to each island, and unrelated to landscape
518 variables. In contrast, non-forest-dependent species were hyper-abundant in small isolated
519 islands, so that overall species abundance was compensated for at those sites. Because only non-
520 forest-dependent species increased in abundance in small islands, higher species abundances
521 there are unlikely a consequence of "fence effects" in which increased island isolation limits
522 dispersal (Adler et al. 1986). Previous neotropical small mammal studies also reported relatively

523 higher abundances in small fragments compared to continuous forest (Malcolm 1991; Passamani
524 and Fernandez 2011; but see Santos-Filho et al. 2012), including both true islands (Glanz et al.
525 1990; Lambert et al. 2006), and forest patch isolates embedded within terrestrial matrices
526 (Laurance 1994; Lynam and Billick 1999; Pardini et al. 2005; Vieira et al. 2009). Apparently,
527 species that could persist in small isolated islands were additionally well positioned to increase
528 their abundances therein. This over-inflated abundance could be explained by the absence of
529 predators (Glanz et al. 1990; Adler and Seamon 1996; Terborgh et al. 1997; Lambert et al. 2006)
530 or density compensation in the absence of other small mammal species (Fonseca and Robinson
531 1990). Benchimol and Peres (2015b) reported the local extinction of most medium and large-
532 bodied vertebrates in small Balbina islands, including mammalian predators of small mammals,
533 and this is also the case of diurnal and nocturnal raptors (A.S. Bueno, unpubl. data). Moreover,
534 despite the low trophic resource availability at small disturbed islands, non-forest-dependent
535 species may increase in abundance by additionally exploring novel resources (Pardini et al. 2005;
536 Wang et al. 2010b), which may become available once other species have become locally
537 extirpated (Fonseca and Robinson 1990). The negative relationship between the abundance of
538 forest-dependent species and the aggregate basal area of trees bearing fleshy fruits was
539 unexpected. This could be due to the higher occupancy or abundance of large-bodied terrestrial
540 mammals, such as white-lipped peccary *Tayassu pecari* (Benchimol and Peres 2015b), which
541 could negatively affect the abundance of forest-dependent species. Further studies should
542 investigate interspecific interactions between large and small mammals.

543

544 *Conservation implications*

545 In line with previous findings in non-insular forest fragments (Watling and Donnelly 2006;
546 Vieira et al. 2009), fragmentation effects on small mammal assemblages across a true
547 archipelagic landscape were best predicted by island area and isolation. As explained

548above, however, this illustrates a slight departure from the central tenets of Island
549Biogeography Theory, and highlights the importance of taking into account the spatial
550configuration of habitat remnants in landscape-scale conservation plans. This should be
551extended to environmental impact assessments (EIAs) prior to licensing of hydropower
552development, or other infrastructure projects resulting in fragmented forest landscapes
553(Fahrig 2003). In addition, species classification according to degree of forest-dependency
554could efficiently distinguish species exhibiting different patterns of persistence across the
555archipelagic landscape. Species ability to traverse the matrix should therefore also be
556considered, as previously noted (Pardini et al. 2010; Santos-Filho et al. 2016). Moreover,
557as the aquatic matrix acts as a strong environmental filter, ecosystem functioning could
558undergo severe changes at small, isolated islands occupied by the same set of
559hyperabundant species, including the loss of ecosystem processes such as forest
560regeneration and arthropod control (Terborgh et al. 1997, 2001). As the vast majority of
561Balbina islands are small, their biodiversity and ecosystem functioning trajectories can
562already be seriously compromised. In this way, creation of myriad small islands within vast
563hydroelectric archipelagos is not conducive to maintaining high levels of biodiversity and
564forest functionality in the long term (Jones et al. 2016), which should be considered prior
565to licensing future hydropower projects. If any given mega-dam becomes completely
566unavoidable, hydraulic engineers should prioritize the creation of large islands by
567reassessing the relationship between maximum operational water level of a reservoir and
568the spatial configuration of its archipelago.

569 We finally emphasize that our study illustrates a ‘best-case’ scenario in terms of
570ecological impacts caused by habitat insularization, given that the Balbina flooded area and
571its surroundings have been strictly protected by the Uatumã Biological Reserve since 1990.
572Other hydroelectric reservoirs in the Brazilian Amazon lacking protection were rapidly

573occupied and deforested by smallholders (e.g. Tucuruí Hydroelectric Reservoir; Fearnside
5742001). As such, we highlight the importance of implementing protected areas as a
575mitigation measure, preventing subsequent hunting, fire disturbance and unplanned
576settlements therein. To make matters worse, insular ecosystems are likely to pay an
577extinction debt by gradually losing species even many years in the aftermath of island
578creation (Jones et al. 2016). Careful planning of hydropower development is therefore
579critical to avoid mass species extinctions and losses in ecosystem services in the world's
580mega-diverse tropical forests.

581

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593

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794 **Figure legends**

795

796 **Figure 1.** Surveyed sites within the Balbina Hydroelectric Reservoir of Central Brazilian
797 Amazonia: 25 land-bridge islands (in red and highlighted by a 1,000-m buffer contour) and
798 four continuous forest sites (CF₁, CF₂, CF₃ and CF₄; indicated by red rectangles). Inset
799 photographs illustrate an aerial view of the Balbina archipelagic landscape (photo credit: E.
800 M. Venticinque) including the aquatic matrix. Histogram represents the size distribution of
801 all 3,546 islands; red dots in the histogram represent the size distribution of surveyed
802 islands.

803

804 **Figure 2.** Species-area relationship for small mammal assemblages recorded across 25
805 land-bridge islands and species richness at four continuous forest (CF) sites surveyed at the
806 Balbina Reservoir landscape, considering the bootstrapped species richness. Data points
807 are color-coded according to the community-averaged forest habitat-dependency (FD)
808 values ($\log_{10} x$; see text). Shaded area represents the 95% confidence region. Boxplots
809 indicate the median, 1st and 3rd quartiles, and minimum and maximum values of species
810 richness in CF sites; solid dots indicate observed values.

811

812 **Figure 3.** Nested matrices of small mammal species and sites: 25 land-bridge islands and
813 an aggregation of the four continuous forest sites (*'Tfall'*). Sites are ordered top to bottom
814 by species richness. Matrices, from left to right, represent the overall small mammal
815 assemblage (grey cells), forest-dependent species (green cells), and non-forest-dependent
816 species (orange cells). For each matrix, we indicate $NODF_{row}$ and P-values. Trend lines
817 illustrate the hypothetical maximum nestedness for each data set. Sites are described in
818 Table S1, and the full species nomenclature is listed in Table S3.

819**Figure 4.** Estimates of averaged models and their 95% confident intervals for predictors of
820(a) species composition (denoted by the PCoA axis 1), (b) bootstrapped species richness,
821number of (c) forest-dependent and (d) non-forest-dependent species, (e) overall species
822abundance, and abundance of (f) forest-dependent and (g) non-forest-dependent species.
823Predictors included: proximity (Prox), distance (Dist) to the mainland, island size (Area),
824tree species richness (S.trees), tree density (D.trees), proportion of closed-canopy forest
825(CC), aggregate basal area of fleshy-fruited trees (Fruit) and density of lianas (Lianas).
826Statistically significant negative and positive coefficients are shown as red and blue
827colours, respectively.

828

829**Figure 5.** Relationships between island area (top panels; (a) and (b)) and island proximity
830(bottom panels; (c) and (d)) and the richness (left panels) and abundance (right panels) of
831forest-dependent (green circles) and non-forest-dependent species (red circles) at the
832Balbina reservoir landscape. Species abundances are standardized by sampling effort.
833Shaded areas represent the 95% confidence regions. Boxplots for CF sites indicate the
834median, 1st and 3rd quartiles, and minimum and maximum values of species richness and
835abundance. The number of forest-dependent species increases with island area ($P < 0.001$)
836and proximity ($P = 0.011$), whereas the number of non-forest-dependent species increases
837only with island area ($P = 0.011$). The abundance of forest-dependent species increases
838with island area ($P = 0.005$), while the abundance of non-forest-dependent species
839decreases with island area ($P = 0.038$) and proximity ($P = 0.035$).

840**Table**

841

842**Table 1.** Description of patch, landscape, and habitat quality variables quantified to

843examine small mammal assemblage properties within the Balbina landscape. The overall

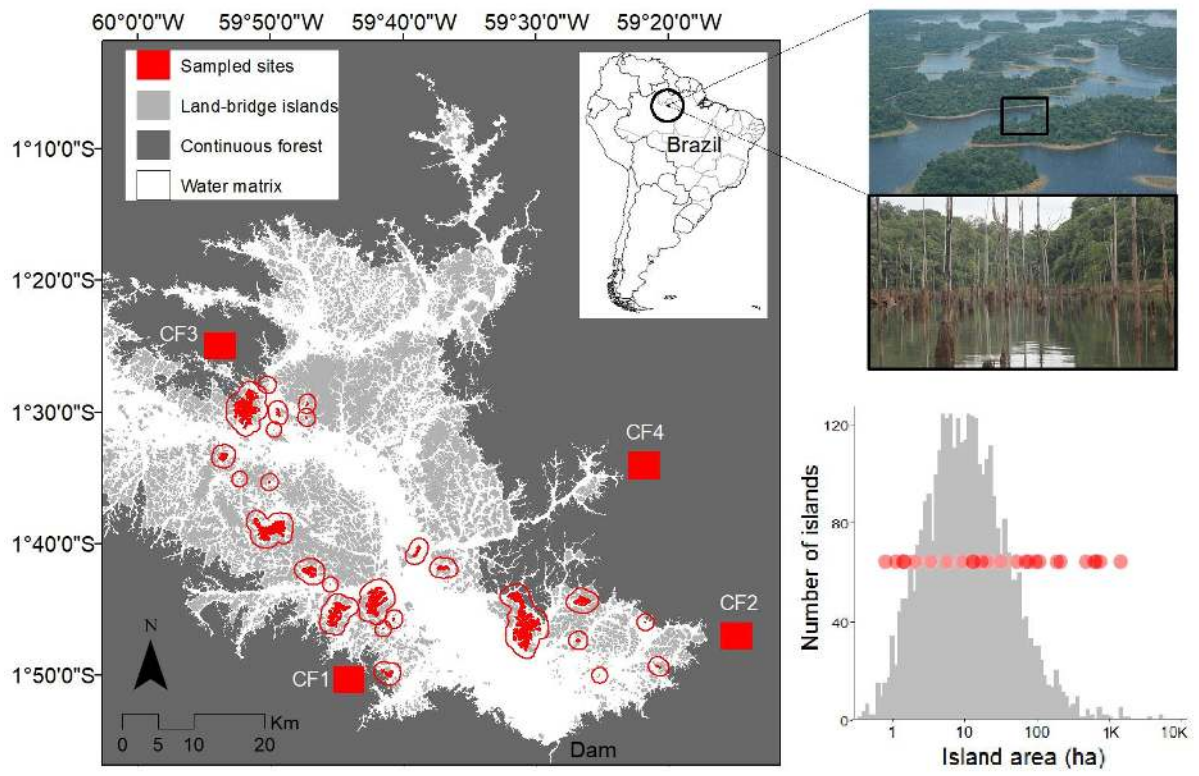
844range, mean and standard deviation are provided for each variable.

845

Name (code name)	Variable description	Range (mean \pm SD)
Landscape		
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 ($\log_{10} x + 1$; McGarigal et al. 2012).	2.75 – 4.54 x 10 ⁹ (1.89 x 10 ⁸ \pm 9.07 x 10 ⁸)
Distance (DIST)	Euclidean distance from each island to the nearest neighbouring mainland forest site.	44 – 11,872 m (4,351 \pm 3,318)
Patch		
Island size (AREA)	Total island area of each focal island ($\log_{10} x$).	0.83 – 1466.00 ha (199.0 \pm 344.1)
Island shape (SHAPE)	Total perimeter length of each focal island divided by the total island area.	0.004 – 0.106 (0.018 \pm 0.022)
Habitat quality		
Trees richness (S.TREES)	Number of tree species calculated from floristic surveys in 0.25-ha forest plots within each focal island or mainland site.	14 – 66 (54.6 \pm 11.5)
Trees density	Trees density calculated from floristic surveys in 0.25-ha forest plots within each focal island or mainland site.	84 – 176

(D.TREES)		(123.4 ± 22.8)
Closed-canopy forest (CC)	Percentage of closed-canopy forest within the focal island.	37.5 – 99.35 (76.2 ± 15.5)
Fire severity (FIRE)	Fire severity within each focal island or mainland site, scored as an ordinal scale based on the extent of each forest site affected by surface fires and the number of charred trees and height of char marks on each tree.	1 – 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 or mainland site.	10.71 – 82.34 (64.1 ± 17.0)
Basal area of fleshy-fruited trees (FRUIT)	Basal area of trees bearing fleshy fruits, calculated from floristic surveys of all live trees ≥10 cm DBH in 0.25-ha forest plots within each focal island or mainland site.	12.1 – 33.0 (20.6 ± 5.0)
Lianas (LIANAS)	Mean number of lianas (> 2.5 cm DBH) calculated from floristic surveys in 0.25-ha forest plots within each focal island or mainland site.	0 – 40.5 (21.5 ± 10.3)

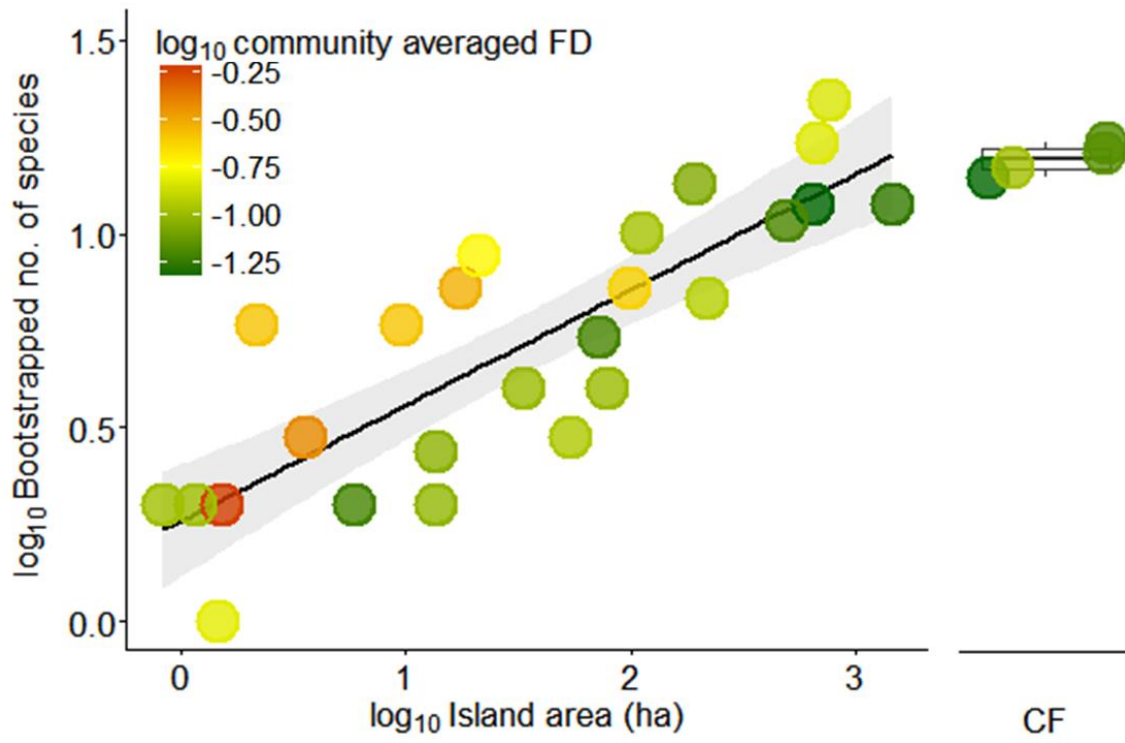
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849 **Figure 1**

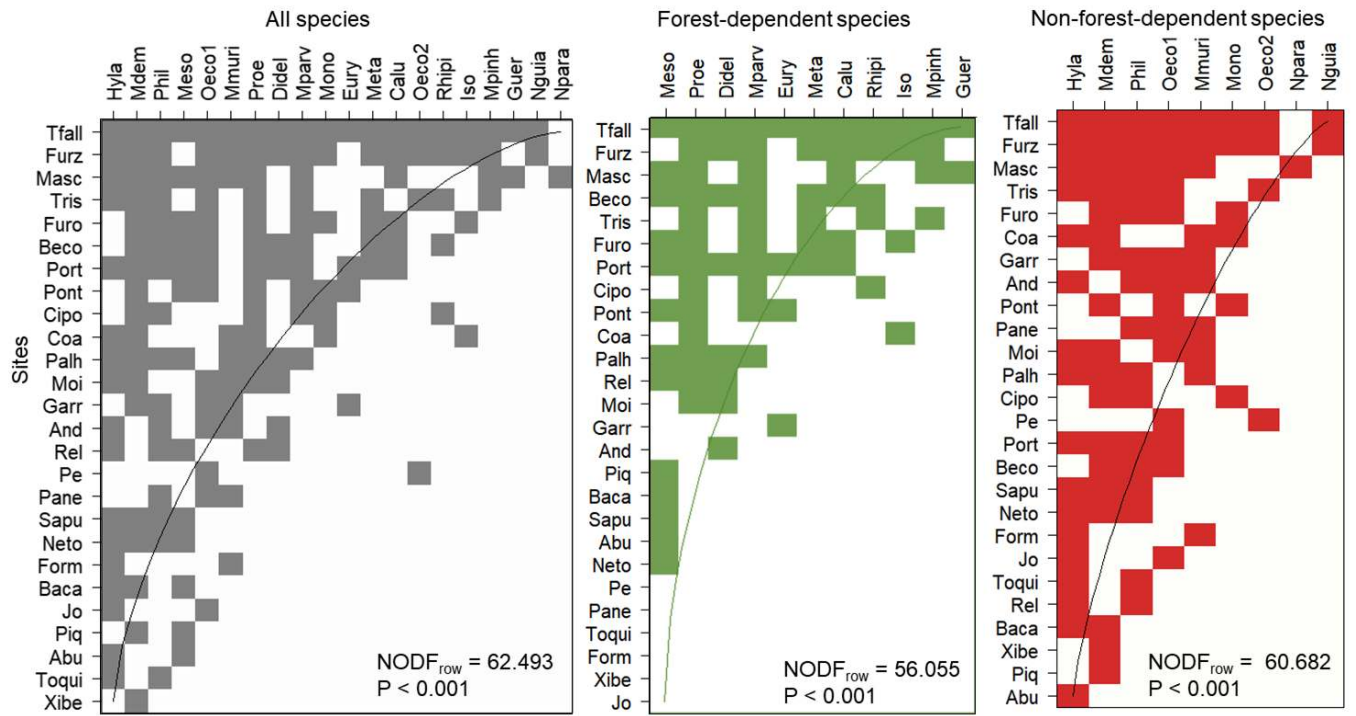
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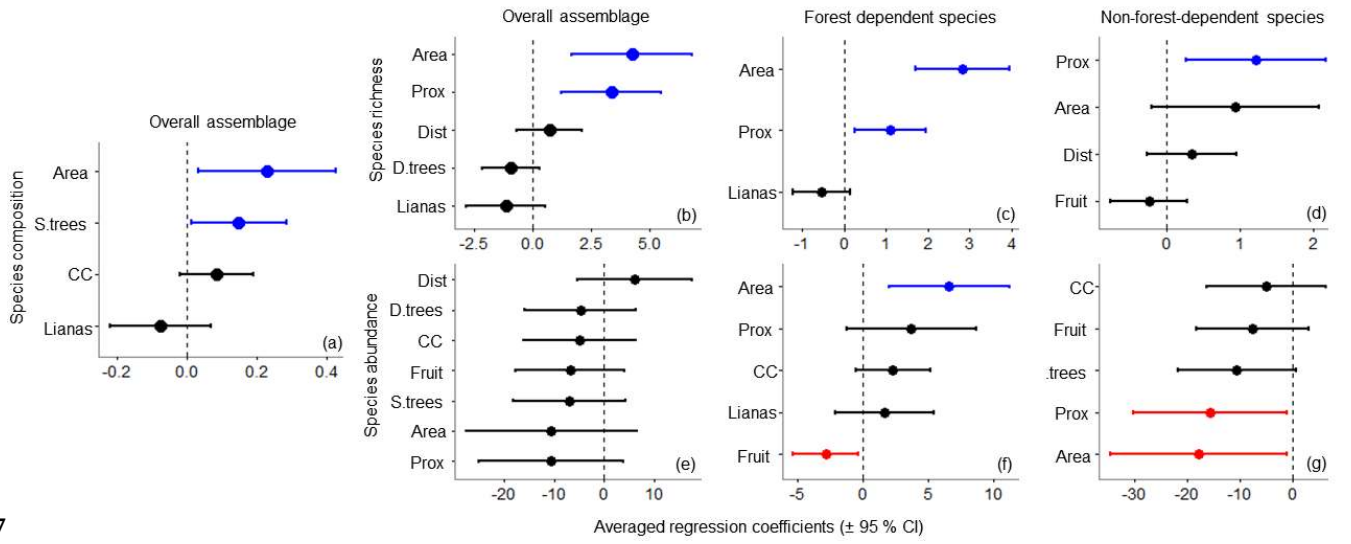
852 **Figure 2**

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854
855 **Figure 3**

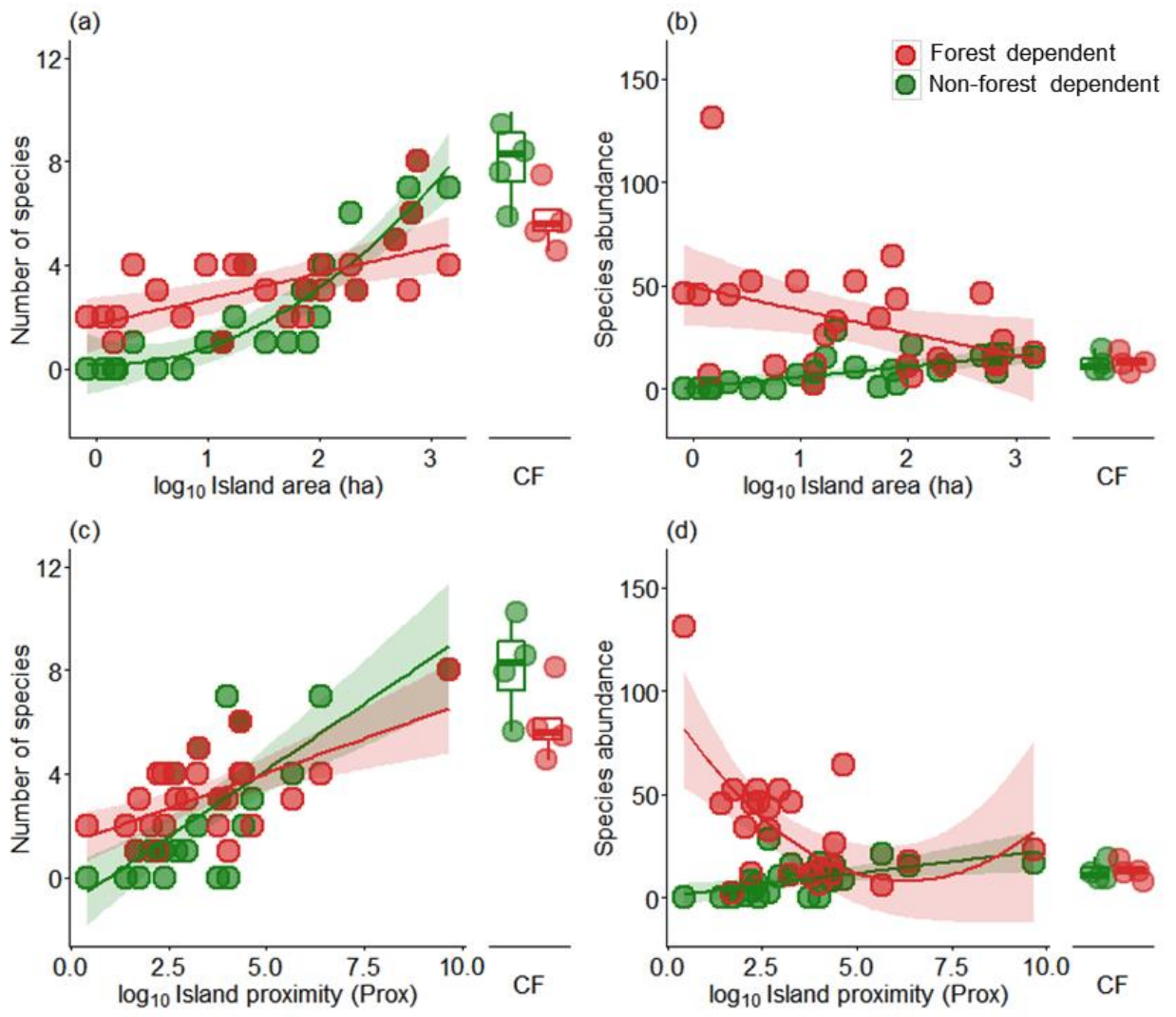
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858 **Figure 4**

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861 **Figure 5**