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

Ana Filipa Palmeirim[*,1,2], Maíra Benchimol[3], Marcus Vinícius Vieira[1], Carlos A. Peres[2]

[1] Laboratório de Vertebrados, Departamento de Ecologia, Universidade Federal do Rio de Janeiro, CP 68020, Rio de Janeiro RJ, CEP 21941- 590, Brazil

[2] Center for Ecology, Evolution and Conservation, School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK

[3] Laboratório de Ecologia Aplicada à Conservação, Universidade Estadual de Santa Cruz, Rodovia Ilhéus-Itabuna, km 16, Ilhéus, BA, CEP 45662-900, Brazil

[*] Corresponding author: Tel.: +351961836044. E-mail address: anafilipapalmeirim@gmail.com. Orcid ID: 0000-0003-3931-0578.

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

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

Abstract

Hydroelectric dams have induced widespread loss, fragmentation and degradation of terrestrial habitats in lowland tropical forests. Yet their ecological impacts have been widely neglected, particularly in developing countries, which are currently earmarked for exponential hydropower development. Here we assess small mammal assemblage responses to Amazonian forest habitat insularization induced by the 28-year old Balbina Hydroelectric Dam. We sampled small mammals on 25 forest islands (0.83 – 1,466 ha) and four continuous forest sites in the mainland to assess the overall community structure and species-specific responses to forest insularization. We classified all species according to their degree of forest-dependency using a multi-scale approach, considering landscape, patch and local habitat characteristics. Based on 65,520 trap-nights, we recorded 884 individuals of at least 22 small mammal species. Species richness was best predicted by island area and isolation, with small islands (<15 ha) harbouring an impoverished nested subset of species (mean ± SD: 2.6 ± 1.3 species), whereas large islands (>200 ha; 10.8 ± 1.3 species) and continuous forest sites (∞ ha; 12.5 ± 2.5 species) exhibited similarly high species richness. Forest-dependent species showed higher local extinction rates and were often either absent or persisted at low abundances on small islands, where non-forest-dependent species became hyper-abundant. Species capacity to use non-forest habitat matrices appears to dictate small mammal success in small isolated islands. We suggest that ecosystem functioning may be highly disrupted on small islands, which account for 62.7% of all 3,546 islands in the Balbina Reservoir.

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

Introduction

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

Biological communities isolated on land-bridge islands are likely to be affected by several multi-scale drivers – including landscape, patch and habitat quality features of any given site – which may be more evident in habitat fragments than in true islands (Arroyo-Rodriguez et al. 2013). At the landscape scale, the degree of isolation from other islands and the mainland affects species colonization rates (MacArthur and Wilson 1967; Watling and Donnelly 2006). At the patch level, the remaining habitat area affects both population sizes and (micro)habitat diversity (Hutchinson 1957; MacArthur and Wilson 1967), and the severity of edge effects that can penetrate deeply into small islands (Benchimol and Peres 2015a). Edge effects are further linked to local habitat quality, which determines the spectrum of ecological niches available and, consequently, local species diversity (August 1983).

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

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

In the Neotropics, small non-volant mammals (marsupials and rodents) occupy a central position in forest food webs, acting either as seed predators and dispersers (Mangan and Adler 2000; Terborgh et al. 2001), pollinators (Vieira et al. 1991), arthropod predators (Carvalho et al. 2005), and as a resource for higher trophic levels (Wright et al. 1994). Although detailed ecological information on most species is scant, small mammals play critical roles in ecosystem functioning including forest regeneration (Terborgh et al. 2001; Galetti et al. 2015). Several studies have assessed the effects of habitat fragmentation on small mammals, including tropical reservoir islands (Adler and Seamon 1996; Granjon et al. 2002; Lambert et al. 2003; Wang et al. 2010a, Gibson et al. 2013). Indeed, islands isolated in the aftermath of hydroelectric dams offer several advantages over non-insular forest patches abutting a terrestrial matrix, including the equitability of isolation time, an equally hostile uniform open-water matrix, and convergent histories of anthropogenic disturbance (Diamond 2001; Wu et al. 2003; Benchimol and Peres 2015a). Studies in hydroelectric reservoirs can therefore rule out confounding effects of matrix types, enabling assessments of fragmentation effects *per se* (Cosson et al. 1999). Nevertheless, no small mammal study to date has been carried out in hyper-diverse Amazonian reservoirs, where currently ambitious governmental plans are expected to greatly expand hydropower infrastructure (Lees et al. 2016). Understanding how biodiversity is affected by hydropower projects is then of critical importance for management actions in lowland Amazonia.

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

Methods

Study area

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

Small mammal sampling

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

The number of transect placed at different sites varied according to their area. This allowed us to obtain a higher number of individuals at larger forest sites, where overall trap density, and consequently the probability of an individual passing near a trap, were lower (Table S1). Due to spatial restrictions in small islands, alternative smaller transects were established therein. Thus, all islands smaller than 2 ha and those between 2 and 10 ha were sampled by transects containing only three LT stations followed by an array of one pitfall, and by six LT stations followed by an array of two pitfalls, respectively. Larger islands were sampled by as many as four transects, according to their size classes: 10 to 50 ha, 50 to 200 ha, 200 to 500 ha and >500 ha, respectively; CF sites were sampled by either six (CF_1 and CF_3), 10 (CF_2) and 12 transects (CF_4). Due to logistic restrictions, CF_2 and CF_4

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

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

Patch, landscape and habitat quality variables

Patch and landscape metrics were calculated using ArcMap 10.1 (ESRI 2012), based on high-resolution multi-spectral RapidEye imagery (5-m resolution with 5-band color imagery) of the entire study landscape. At the patch scale, we measured island area and shape, and at landscape-scale, we obtained for each surveyed island a proximity (PROX) metric to other islands and CF sites, and their nearest distances to CF (Table 1; for further details on imagery processing and landscape metrics, see Benchimol and Peres 2015a, 2015b). We used Generalized Linear Models (GLMs) to analyse the relationship between the species richness in the islands and the proximity index considering in separate models at multiple scales of effects in terms of increasing buffer radius (Jackson and Fahrig 2012) – 250 m, 500 m and 1 000 m. We then ordered the models according to its Akaike Information Criteria (AIC; Burnham and Anderson 2002). For further analyses, we retained the PROX index obtained using the 500 m-radius (AIC = 129.2), rather than 1 000 m (129.2) or 250 m (130.64).

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

Forest-dependency index

Degree of forest habitat-dependency (FD) was defined as the species-specific ratio between the capture rate in the open habitat matrix and in continuous primary forest. Forest-dependency estimates were based on small mammal data obtained during a 5-year study by J. R. Malcolm (1991) at the Biological Dynamics of Forest Fragments Project (BDFFP), a fragmented landscape ~100 km from the Balbina reservoir, which shares the same small mammal fauna. Forest and non-forest-dependent species were those for which a FD < 1 and FD > 1, respectively. We obtained the community-averaged FD values by summing the FD values of all individuals recorded at each survey site, and dividing this by the number of individuals therein. Community-averaged FD values ranged between 0.061 – 0.688, higher values corresponding to an increased prevalence of non-forest-dependent species. Species FD were previously transformed to range between 0 (highest forest-dependency) and 1 (lowest forest-dependency). Information on capture rates at the BDFFP landscape within either primary forest or the matrix was unavailable only for the squirrel *Guerlinguetus aestuans*, which occurs chiefly in primary forests (Patton et al. 2007). Based on ecological similarities between closely related taxa (Jones et al. 2009), we assigned FD values to congener species for which information was unavailable (*Oecomys*, *Neacomys* and *Marmosops*). Capture rates and FD values are summarized for all species in Table S2.

Data analysis

We excluded from analysis two Echimyidae ─ *Makalata didelphoides* and *Echimys chrysurus* ─ that were recorded only once during the study. These species feed on seeds and leaves, in addition to some fruit (Patton et al. 2000), and consequently are rarely attracted to the bait used here. The adequacy of small mammals sampling was evaluated using the sample coverage estimator (*sensu* Chao and Jost 2012), which estimates the proportion of the total number of individuals in an assemblage that belong to the species represented in the sample. Our small mammal trapping was satisfactorily accurate in relation to our sampling effort, averaging 0.92 ± 0.07 per site in the most complete assemblage, except for two small islands (‘Xibé’ and ‘Abu’), in which sample coverage was zero (Table S1). Despite the lack of sampling representativeness in those two islands, we still retained them in the analysis because trap density therein was much higher (~4.57 traps/ha) than in islands larger than 100 ha (0.08 – 0.54 traps/ha) and CF sites (~0.002 traps/ha; Table S1). Nevertheless, to account for any eventual undetected species and avoid any potential bias in species richness values, we estimated a bootstrapped number of species. To do so, we applied a bootstrap method that determines confidence intervals around Hill numbers, facilitating the comparison of multiple assemblages of extrapolated samples (Chao et al. 2014). For each site, the bootstrapped number of species was obtained from the extrapolation of individual-based Hill numbers assuming twice the number of individuals recorded at that site, using the R codes provided by Chao et al. (2014). We further verified if the variable number of traps deployed per site caused any bias on observed numbers of species. To do so, we correlated the number of traps deployed per site with sample coverage estimations and the number of individuals recorded. Spatial autocorrelation was examined by correlating matrices of binary species composition and geographic distances among sites, applying a Mantel test using the '*vegan*' R package (Oksanen et al. 2007).

Considering all 25 islands and their bootstrapped species richness, we performed species-area relationships (SARs) comparing eight possible SAR models: power, exponential, negative exponential, Monod, rational function, logistic, Lomolino and cumulative Weibull (for each model formula, see Table S3), using the '*mmSAR*' R package (Guilhaumon et al. 2010). In addition, given the importance in identifying critical thresholds beyond which species responses change abruptly, we also included a piecewise regression model to explain small mammal SARs (Toms and Lesperance 2003), using the '*segmented*' R package (Muggeo 2017). Data fitting for each model was compared according to Akaike Information Criterion values corrected for small sample sizes (AICc: Burnham and Anderson 2002).

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

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

To evaluate the combined effects of patch, landscape and habitat quality metrics on small mammal assemblages (bootstrapped species richness, species composition, standardized abundance, and aggregate biomass), we performed Generalized Additive Models (GAMs). GAMs do not require a linear relationship between the response and the explanatory variables, and were performed using a Gaussian error structure. We controlled for high levels of variable inter-dependence by performing a Pearson correlation matrix, retaining weakly correlated variables ($r < 0.70$, $P > 0.05$). ‘Island shape’, ‘percentage of old-growth trees’ and ‘fire severity’ were correlated and therefore excluded from further analysis. We did not include CF sites in this analysis because that additionally overinflated the correlation between ‘island area’ and ‘proximity’ ($r = 0.86$, $P < 0.0001$), further invalidating the inclusion of one these variables in the model. We also calculated the Variation Inflation Factors (VIFs), any of the remaining variables was moderately redundant, presenting VIF < 5 (Dormann et al. 2013). A candidate model set was further constructed, using all additive combinations of the eight explanatory variables retained, and models were ranked based on their AICc, using the ‘*MuMIn*’ R package (Bartoń 2014). To account for model uncertainty in multi-model inference, a model-averaging approach was performed using only the most plausible models (i.e., $0 < \Delta\mathrm{AICc} > 2$, $\Delta\mathrm{AIC} = \mathrm{AIC}_i - \mathrm{AIC}_{min}$ in which $i = i^{\mathrm{th}}$ model). The relative importance (RI) of each variable contained in that model set was obtained by the sum of the Akaike weights of the models in which that variable had been included (Rhodes et al. 2009). Explanatory variables were previously standardized ($x = 0$, $\sigma = 1$) to place coefficient estimates into the same scale. The same modelling procedures were repeated considering the number and abundance of forest and non-forest-dependent species separately. When analysing graphically the isolated effects of island area and proximity on species richness and abundance of forest and non-forest-dependent species, we improved data fitting by performing simple GLMs, both including and excluding the quadratic term of each explanatory variable. AIC values were compared between the models including and excluding the quadratic term of the explanatory variable (Burnham and Anderson 2002). We then added the quadratic term of the explanatory variable when examining the relationship between the number of forest-dependent species and island area, and between the number of non-forest-dependent species and island proximity (Table S4). All data analyses were performed in R (R Development Core Team 2015).

Results

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

Species-area relationships and nestedness

The power, rational function, logistic and cumulative Weibull SAR models performed similarly well in explaining the bootstrapped species richness (S) of small mammals across all 25 sampled islands, explaining 68.7 – 71.0% of the variation in S (Table S3). Henceforth, to facilitate comparisons with most other studies, we focused our results on the power model. As such, the observed SAR clearly showed fewer species over a decreasing gradient of island size (z-value = 0.289, c-value = 2.089, $R^2 = 0.687$; Table S3). Islands smaller than 15 ha retained highly impoverished small mammal assemblages (mean ± SD: 2.6 ± 1.3 species), whereas islands larger than 200 ha on average harboured 10.8 ± 1.3 species, which was comparable to CF sites in the mainland (12.5 ± 2.5; Fig. 2).

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

Combined effects of patch, landscape and habitat quality metrics

Multiple-scale landscape, patch and habitat quality variables clearly affected the overall persistence of small mammal species across all 25 islands surveyed, with species composition best predicted by both island area ($\beta_{AREA} = 0.229$, $P = 0.023$, RI = 0.84) and tree species richness ($\beta_{S.TREES} = 0.148$, $P = 0.033$, RI = 0.67; Fig. 4a, Table S6). In fact, despite the lack of significant nestedness among the survey sites, the narrow set of non-forest-dependent species persisting at all islands smaller than 2 ha was virtually the same. Most of the other islands, ranging from 2 to 800 ha, retained highly idiosyncratic species compositions, as indicated by the poorly predicted PCoA1 values obtained for those islands ($R^2 = 0.417$; Fig. S1).

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

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

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

Discussion

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

Island biogeography revisited

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

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

Biogeography Theory (IBT), in which islands experiencing higher colonization rates should harbour more species (MacArthur and Wilson 1967). However, higher colonization rates were primarily a function of the functional connectivity of an island in the landscape (as inferred by the Proximity index) rather than the distance to the mainland, as predicted by IBT. Studies in terrestrial landscapes have found similar patterns of fragmentation effects in terrestrial landscapes for both small mammals (e.g. Goodman and Rakotondravony 2000; Pardini et al. 2005), and other taxa (see Predevello and Vieira 2010). Our findings therefore unequivocally support the notion that small, isolated reservoir islands have more limited conservation value than non-island habitat fragments in entirely terrestrial landscapes, which agrees with paleotropical small mammal data from reservoir islands in southern Thailand (Gibson et al. 2013).

Determinants of community composition

Communities isolated in land-bridge islands may exhibit nested structures over time, as has already been detected for small mammal, birds and lizard assemblages within the ~50 year old Thousand Island Lake, China (Wang et al. 2010a). In Balbina, the nested structure observed in small mammal assemblages are probably related to the differential species susceptibility to extinction (Lynam and Billick 1999). Indeed, the subset of small mammal species persisting at Balbina islands was closely related to both patch and local habitat characteristics, as suggested by the importance of island area and tree species richness in predicting species composition. Small islands likely retain a very limited spectrum of habitat resources (August 1983), so they are consistently occupied by the same subset of species, which were mainly non-forest-dependent. As island area increases, more ecological niches become available (Pardini et al. 2005), which facilitates higher species packing, including forest-dependent species. Similarly, habitat structure was one of the main determinants of small mammal assemblages in Brazilian Atlantic Forest fragments (Pardini et al. 2005; Delciellos et al. 2015). Nevertheless, although forest-dependent species exhibited an expected nested structure, the same was observed for non-forest-dependent species. This might be due to the inclusion of certain species rarely captured throughout the sampling, that were particularly evident at larger islands and continuous forest sites (e.g., *Monodelphis arlindoi*, *N. paracou*, and *N. guianae*).

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

Vulnerability of forest-dependent species

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

In contrast to species richness, the abundance of forest-dependent species was not affected by island isolation. The abundance of these species may therefore be mainly determined by within-island processes rather than movement between islands. For forest-dependent species, such processes may be idiosyncratic in relation to each island, and unrelated to landscape variables. In contrast, non-forest-dependent species were hyper-abundant in small isolated islands, so that overall species abundance was compensated for at those sites. Because only non-forest-dependent species increased in abundance in small islands, higher species abundances there are unlikely a consequence of “fence effects” in which increased island isolation limits dispersal (Adler et al. 1986). Previous neotropical small mammal studies also reported relatively higher abundances in small fragments compared to continuous forest (Malcolm 1991; Passamani and Fernandez 2011; but see Santos-Filho et al. 2012), including both true islands (Glanz et al. 1990; Lambert et al. 2006), and forest patch isolates embedded within terrestrial matrices (Laurance 1994; Lynam and Billick 1999; Pardini et al. 2005; Vieira et al. 2009). Apparently, species that could persist in small isolated islands were additionally well positioned to increase their abundances therein. This over-inflated abundance could be explained by the absence of predators (Glanz et al. 1990; Adler and Seamon 1996; Terborgh et al. 1997; Lambert et al. 2006) or density compensation in the absence of other small mammal species (Fonseca and Robinson 1990). Benchimol and Peres (2015b) reported the local extinction of most medium and large-bodied vertebrates in small Balbina islands, including mammalian predators of small mammals, and this is also the case of diurnal and nocturnal raptors (A.S. Bueno, unpubl. data). Moreover, despite the low trophic resource availability at small disturbed islands, non-forest-dependent species may increase in abundance by additionally exploring novel resources (Pardini et al. 2005; Wang et al. 2010b), which may become available once other species have become locally extirpated (Fonseca and Robinson 1990). The negative relationship between the abundance of forest-dependent species and the aggregate basal area of trees bearing fleshy fruits was unexpected. This could be due to the higher occupancy or abundance of large-bodied terrestrial mammals, such as white-lipped peccary *Tayassu pecari* (Benchimol and Peres 2015b), which could negatively affect the abundance of forest-dependent species. Further studies should investigate interspecific interactions between large and small mammals.

Conservation implications

In line with previous findings in non-insular forest fragments (Watling and Donnelly 2006; Vieira et al. 2009), fragmentation effects on small mammal assemblages across a true archipelagic landscape were best predicted by island area and isolation. As explained above, however, this illustrates a slight departure from the central tenets of Island Biogeography Theory, and highlights the importance of taking into account the spatial configuration of habitat remnants in landscape-scale conservation plans. This should be extended to environmental impact assessments (EIAs) prior to licensing of hydropower development, or other infrastructure projects resulting in fragmented forest landscapes (Fahrig 2003). In addition, species classification according to degree of forest-dependency could efficiently distinguish species exhibiting different patterns of persistence across the archipelagic landscape. Species ability to traverse the matrix should therefore also be considered, as previously noted (Pardini et al. 2010; Santos-Filho et al. 2016). Moreover, as the aquatic matrix acts as a strong environmental filter, ecosystem functioning could undergo severe changes at small, isolated islands occupied by the same set of hyperabundant species, including the loss of ecosystem processes such as forest regeneration and arthropod control (Terborgh et al. 1997, 2001). As the vast majority of Balbina islands are small, their biodiversity and ecosystem functioning trajectories can already be seriously compromised. In this way, creation of myriad small islands within vast hydroelectric archipelagos is not conducive to maintaining high levels of biodiversity and forest functionality in the long term (Jones et al. 2016), which should be considered prior to licensing future hydropower projects. If any given mega-dam becomes completely unavoidable, hydraulic engineers should prioritize the creation of large islands by reassessing the relationship between maximum operational water level of a reservoir and the spatial configuration of its archipelago.

We finally emphasize that our study illustrates a ‘best-case’ scenario in terms of ecological impacts caused by habitat insularization, given that the Balbina flooded area and its surroundings have been strictly protected by the Uatumã Biological Reserve since 1990. Other hydroelectric reservoirs in the Brazilian Amazon lacking protection were rapidly occupied and deforested by smallholders (e.g. Tucuruí Hydroelectric Reservoir; Fearnside 2001). As such, we highlight the importance of implementing protected areas as a mitigation measure, preventing subsequent hunting, fire disturbance and unplanned settlements therein. To make matters worse, insular ecosystems are likely to pay an extinction debt by gradually losing species even many years in the aftermath of island creation (Jones et al. 2016). Careful planning of hydropower development is therefore critical to avoid mass species extinctions and losses in ecosystem services in the world's mega-diverse tropical forests.

Acknowledgements

We thank all 15 volunteers/field assistants who assisted in the field; the Reserva Biológica do Uatumã and its staff for logistical support; M.N.F. da Silva for help with species identification and D. Storck-Tonon for assistance with landscape metrics. This study was funded by the Amazon Region Protected Areas Program (ARPA), Amazonas Distribuidora de Energia S.A., and Associação Comunidade Waimiri Atroari; Rufford Foundation (grant number 13675-1); Idea Wild; and a NERC grant (NE/J01401X/1) awarded to CAP. AFP and MB were funded by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) scholarship, and MVV was funded by Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

References

Adler GH, Seamon JO (1996) Distribution of four-eyed opossum, *Philander opossum* (Marsupialia, Didelphidae) on small islands In Panama. Mammalia 60:91–100

Adler GH, Wilson ML, Derosa MJ (1986). Influence of island area and isolation on population characteristics of *Peromyscus leucopus*. J Mammal 67:406–40

Almeida-Neto M, Guimarães P, Guimarães PR., Loyola RD, Ulrich W (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117:1227–1239

Arroyo-Rodríguez V, Rös M, Escobar F, Melo FP, Santos BA, Tabarelli M, Chazdon R (2013) Plant β-diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. J Ecol 101:1449–1458

August PV (1983) The role of habitat complexity and heterogeneity in structuring tropical mammal communities. Ecology 64:1495–1507

Aurélio-Silva M, Anciães M, Henriques LMP, Benchimol M, Peres CA (2016) Patterns of local extinction in an Amazonian archipelagic avifauna following 25 years of insularization. Biol Cons 199:101–109

Bartoń K (2016) MuMIn: multi-model inference. R package version 1.15.6

Benchimol M, Peres CA (2015a) Widespread forest vertebrate extinctions induced by a mega hydroelectric dam in lowland Amazonia. PLoS ONE 10:e0129818

Benchimol M, Peres CA (2015b) Predicting local extinctions of Amazonian vertebrates in forest islands created by a mega dam. Biol Cons 187:61–72

Benchimol M, Peres CA (2015c) Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. J Ecol 103:408–420

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York

Carvalho FMV, Fernandez FAS, Nessimian JL (2005) Food habits of sympatric opossums coexisting in small Atlantic Forest fragments in Brazil. Mamm Biol 70:366–375

Castello L, McGrath DG, Hess LL, Coe MT, Lefebvre PA, Petry P, Macedo MN, Renó VF, Arantes CC (2013) The vulnerability of Amazon fresh water ecosystems. Conserv Lett 6:217–229

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

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol Monogr 84:45–67

Charles-Dominique P, Atramentowicz M, Charles-Dominique M, Gerard H, Hladik A, Hladik CM, Prévost MF (1981) Les mamiferes arboricoles nocturnes d'une foret guyanaise: interrelations plantes-animaux. Rev Ecol-Terre Vie 35:341–435

Cosson JF, Ringuet S, Claessens O, De Massary JC, Dalecky A, Villiers JF, Grajon L, Pons JM (1999). Ecological changes in recent land-bridge islands in French Guiana, with emphasis on vertebrate communities. Biol Cons 91:213–222

Delciellos AC, Vieira MV, Grelle CE, Cobra P, Cerqueira R (2016) Habitat quality versus spatial variables as determinants of small mammal assemblages in Atlantic Forest fragments. J Mammal 97:253–265

Devictor V, Julliard R, Jiguet F (2008) Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117:507–514

Diamond J (2001) Damned experiments! Science 294:1847–1848

Dormann, CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46

ECOA – Ecologia em Ação (2016). International Rivers and Fundacion Proteger, Dams in Amazonia. http://www.dams-info.org/en. Accessed 05 June 2017

ESRI (2012) ArcMap 10.1, Environmental Systems Research Institute, Inc. Redlands

Estavillo C, Pardini R, da Rocha PLB (2013) Forest loss and the biodiversity threshold: an evaluation considering species habitat requirements and the use of matrix habitats. PLoS ONE 8:e82369

Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev 81:117–142

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol, 34:487–515.

Fearnside PM (2001) Environmental impacts of Brazil's Tucuruí Dam: Unlearned lessons for hydroelectric development in Amazonia. Environ Manage 27:377–396

Fearnside PM, Pueyo S (2012) Greenhouse-gas emissions from tropical dams. Nat Clim Change 2:382–384

Fonseca GA, Robinson JG (1990) Forest size and structure: competitive and predatory effects on small mammal communities. Biol Cons 53:265–294

FUNCATE/INPE/ANEEL (2000) Mapeamento por satélite das áreas inundadas por reservatórios de hidrelétricas brasileiras. Unpublished Report

Galetti M, Guevara R, Galbiati LA, Neves CL, Rodarte RR, Mendes CP (2015) Seed predation by rodents and implications for plant recruitment in defaunated Atlantic forests. Biotropica 47:521–525

Gibson L, Lynam AJ, Bradshaw CJ, He F, Bickford DP, Woodruff DS, Bumrungsri S, Laurance WF (2013) Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. Science 341:1508–1510

Glanz WE (1990) Neotropical mammal densities: how unusual is the community on Barro Colorado Island, Panama. In: Gentry A H (ed) Four neotropical rainforests. Yale University Press, New Haven, pp. 287-313

Goodman SM, Rakotondravony D (2000) The effects of forest fragmentation and isolation on insectivorous small mammals (Lipotyphla) on the Central High Plateau of Madagascar. J Zool 250:193–200

Granjon L, Ringuet S, Cheylan G (2002) Evolution of small terrestrial mammal species richness on newly formed islands in primary tropical forest of French Guiana: A 6 year study. Rev Ecol-Terre Vie 57:131–144

Guilhaumon F, Mouillot D, Gimenez O (2010) mmSAR: an R-package for multimodel species–area relationship inference. Ecography 33:420–424

Henle K, Davies KF, Kleyer M, Margules C, Settele J (2004) Predictors of species sensitivity to fragmentation. Biodivers Conserv 13:207–251

Hutchinson GE (1957) Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22:415–427

IBAMA (1997) Plano de Manejo Fase I: Reserva Biológica do Uatumã. http://www.icmbio.gov.br. Accessed 05 June 2017

Jackson HB, Fahrig L (2012) What size is a biologically relevant landscape? Landscape Ecol 27:929–941

Jones IL, Bunnefeld N, Jump AS, Peres CA, Dent DH (2016) Extinction debt on reservoir land-bridge islands. Biol Cons 199:75–83

Jones KE, et al. (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90:2648–2648

Junk WJ, Mello JAS (1990) Impactos ecológicos das represas hidrelétricas na bacia amazônica brasileira. Estudos avançados 4:126–143

Lambert TD, Adler GH, Riveros CM, Lopez L, Ascanio R, Terborgh J (2003) Rodents on tropical land-bridge islands. J Zool 260:179–187

Lambert TD, Malcolm JR, Zimmerman BL (2006) Amazonian small mammal abundances in relation to habitat structure and resource abundance. J Mammal 87:766–776

Laurance WF (1994) Rainforest fragmentation and the structure of small mammal communities in tropical Queensland. Biol Cons 69:23-32

Lees AC, Peres CA, Fearnside PM, Schneider M, Zuanon JA (2016) Hydropower and the future of Amazonian biodiversity. Biodivers Conserv 25:451–466

Lynam AJ, Billick I (1999) Differential responses of small mammals to fragmentation in a Thailand tropical forest. Biol Cons 91:191–200

MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography, Press Princeton, USA.

Malcolm JR (1991) The small mammals of Amazonian forest fragments: pattern and process. PhD dissertation, Department of Zoology, Gainesville, Florida, USA.

Mangan SA, Adler GH (2000) Consumption of arbuscular mycorrhizal fungi by terrestrial and arboreal small mammals in a Panamanian cloud forest. J Mammal 81:563–570.

McGarigal K, Cushman SA, Ene E (2012) FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. http://www.umass.edu/landeco/research/fragstats/fragstats.html. Accessed 05 June 2017

Muggeo VRM (2017) Segmented: Regression Models with Break-Points / Change-Points Estimation. R package version 0.5-2.1

Oksanen J, Kindt R, Legendre P, O’Hara B, Stevens MHH (2007) Vegan: the community ecology package. R package version 2.4-2

Pardini R (2004) Effects of forest fragmentation on small mammals in an Atlantic Forest landscape. Biodivers Conserv 13:2567–2586

Pardini R, de Souza SM, Braga-Neto R, Metzger JP (2005) The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. Biol Cons 124:253–266

Pardini R, Faria D, Accacio GM, Laps RR, Mariano-Neto E, Paciencia ML, Dixo M, Baumgarten J (2009) The challenge of maintaining Atlantic forest biodiversity: a multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia. Biol Cons 142:1178–1190

Pardini R, de Arruda Bueno A, Gardner TA, Prado PI, Metzger JP (2010) Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. PLoS ONE 5:e13666

Passamani M, Fernandez FAS (2011) Abundance and richness of small mammals in fragmented Atlantic Forest of Southeastern Brazil. J Nat Hist 45:553–565

Patton JL, Da Silva MNF, Malcolm JR (2000) Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. Bull. Am. Mus. Nat. Hist. 244:1–306

Patton JL, Pardiñas UFJ, D’Elía G (2007) Mammals of South America - volume 2, 1st edn. The University of Chicago Press, Chicago

Prevedello JA, Vieira MV (2010) Does the type of matrix matter? A quantitative review of the evidence. Biodivers Conserv 19:1205–1223

R Development Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing. http://www.R-project.org/. Accessed 05 June 2017

Rhodes JR, McAlpine CA, Zuur AF, Smith GM, Ieno EN (2009) GLMM applied on the spatial distribution of koalas in a fragmented landscape. In: Zuur AF, Leno EN, Walker NJ, Saveliev AA, Smith GM (eds) Mixed effects models and extensions in ecology with R. Springer, New York, pp. 469–492

San-José M, Arroyo-Rodríguez V, Sánchez-Cordero V (2014) Association between small rodents and forest patch and landscape structure in the fragmented Lacandona rainforest, Mexico. Trop Conserv Sci 7:403–422

Santos-Filho M, Peres CA, Da Silva DJ, Sanaiotti TM (2012) Habitat patch and matrix effects on small-mammal persistence in Amazonian forest fragments. Biodivers Conserv 21:1127–1147

Santos-Filho M, Bernardo CS, Silva DJD, Ignácio ARA, Canale GR (2016) The importance of considering both taxonomic and habitat guild approaches in small mammal research. Austral Ecol 41:854–863

Sikes RS (2016) 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. J Mammal 97:663–688

Strona G, Galli P, Seveso D, Montano S, Fattorini S (2014) Nestedness for Dummies (NeD): a user-friendly web interface for exploratory nestedness analysis. J. Stat. Softw 59:1–9

Terborgh J, Lopez L, Nuñez P, Rao M, Shahabuddin G, Orihuela G, Riveros M, Ascanio R, Adler GH, Lambert TD, Balbas L (2001) Ecological meltdown in predator-free forest fragments. Science 294:1923–1926

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

Toms JD, Lesperance ML (2003) Piecewise regression: a tool for identifying ecological thresholds. Ecology 84:2034–2041

Umetsu F, Pardini R (2007) Small mammals in a mosaic of forest remnants and anthropogenic habitats – evaluating matrix quality in an Atlantic forest landscape. Landscape Ecol 22:517–530

Vieira MF, Carvalho-Okano RM, Sazima, M (1991) The common opossum (*Didelphis marsupialis*), as a polinator of *Mabea fistulifera* (Euphorfiaceae). Ciência e Cultura 43:390–393

Vieira MV, Olifiers N, Delciellos AC, Antunes VZ, Bernardo LR, Grelle CE, Cerqueira R (2009) Land use vs. fragment size and isolation as determinants of small mammal composition and richness in Atlantic Forest remnants. Biol Cons 142:1191–1200

Wang Y, Bao Y, Yu M, Xu G, Ding P (2010a) Nestedness for different reasons: the distributions of birds, lizards and small mammals on islands of an inundated lake. Divers Distrib 16:862–873

Wang J, Huang J, Wu J, Han X, Lin G (2010b) Ecological consequences of the Three Gorges Dam: insularization affects foraging behavior and dynamics of rodent populations. Front. Ecol. Environ 8:13–19

Watling JI, Donnelly MA (2006) Fragments as islands: a synthesis of faunal responses to habitat patchiness. Conserv Biol 20:1016–1025

Wright DH, Patterson BD, Mikkelson GM, Cutler A, Atmar W (1998) A comparative analysis of nested subset patterns of species composition. Oecologia, 113:1–20

Wright SJ, Gompper ME, DeLeon B (1994) Are large predators keystone species in neotropical forests? The evidence from Barro Colorado Island. Oikos 71:279–294

Wu J, Huang J, Han X, Gao X, He F, Jiang M, Primack RB, Shen Z (2004) The three gorges dam: an ecological perspective. Front Ecol Environ 2:241–248

Zarfl C, Lumsdon AE, Berlekamp J, Tydecks L, Tockner K (2015) A global boom in hydropower dam construction. Aquatic Sciences 77:161–170

Figure legends

Figure 1. Surveyed sites within the Balbina Hydroelectric Reservoir of Central Brazilian Amazonia: 25 land-bridge islands (in red and highlighted by a 1,000-m buffer contour) and four continuous forest sites (CF_1, CF_2, CF_3 and CF_4; indicated by red rectangles). Inset photographs illustrate an aerial view of the Balbina archipelagic landscape (photo credit: E. M. Venticinque) including the aquatic matrix. Histogram represents the size distribution of all 3,546 islands; red dots in the histogram represent the size distribution of surveyed islands.

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

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

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

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

Table

Table 1. Description of patch, landscape, and habitat quality variables quantified to examine small mammal assemblage properties within the Balbina landscape. The overall range, mean and standard deviation are provided for each variable.

Name (code name)	Variable description	Range (mean ± 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 ± 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 ± 3,318)
Patch		
Island size (AREA)	Total island area of each focal island ($\log_{10}$ x).	0.83 – 1466.00 ha (199.0 ± 344.1)
Island shape (SHAPE)	Total perimeter length of each focal island divided by the total island area.	0.004 – 0.106 (0.018 ± 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 ± 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-fruiting 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)

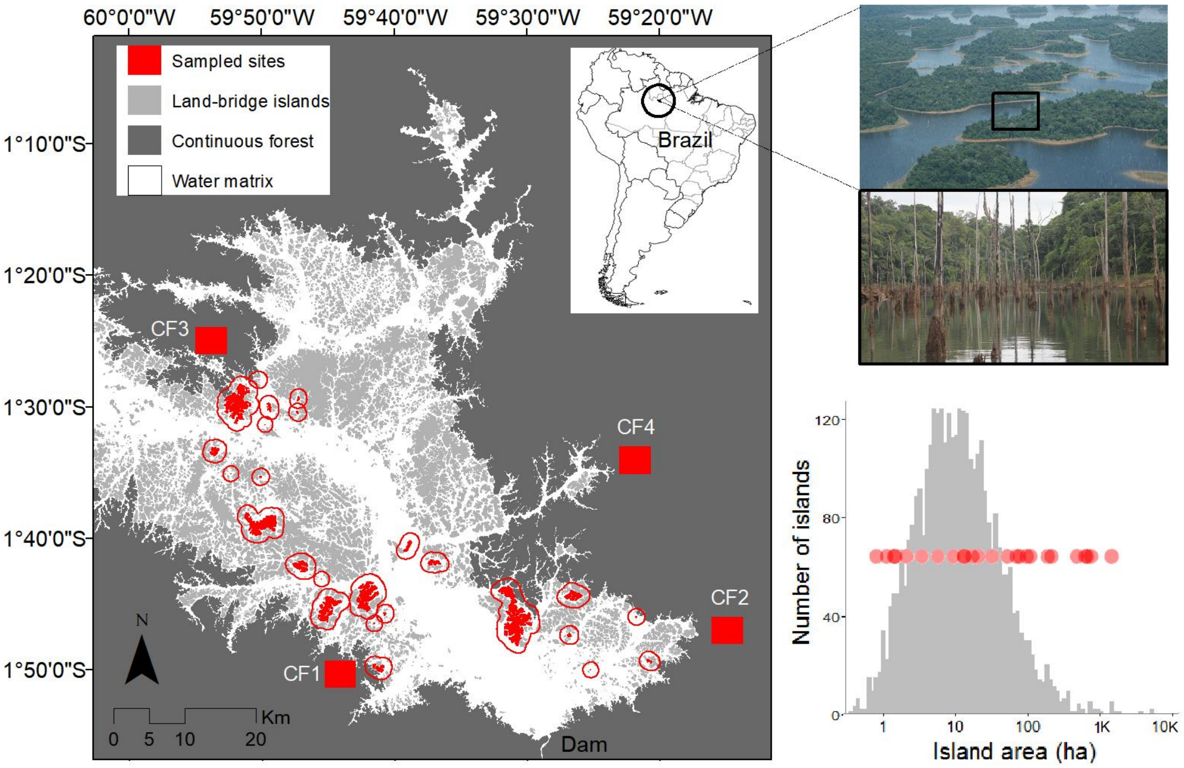
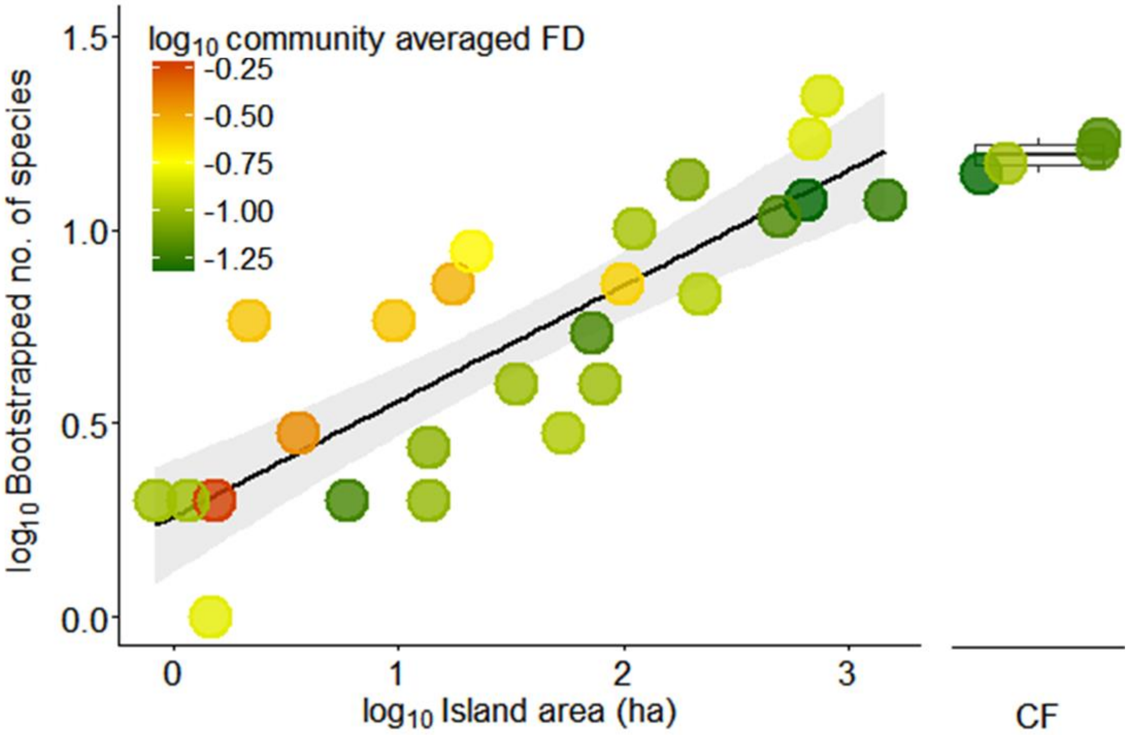

60°0'0"W
59°50'0"W
59°40'0"W
59°30'0"W
59°20'0"W
1°10'0"S
1°20'0"S
1°30'0"S
1°40'0"S
1°50'0"S
Sampled sites
Land-bridge islands
Continuous forest
Water matrix
Brazil
CF1
CF2
CF3
CF4
N
Km
0
5
10
20
Dam
Number of islands
0
40
80
120
1
10
100
1K
10K
Island area (ha)

Figure 1



851

852**Figure 2**

853

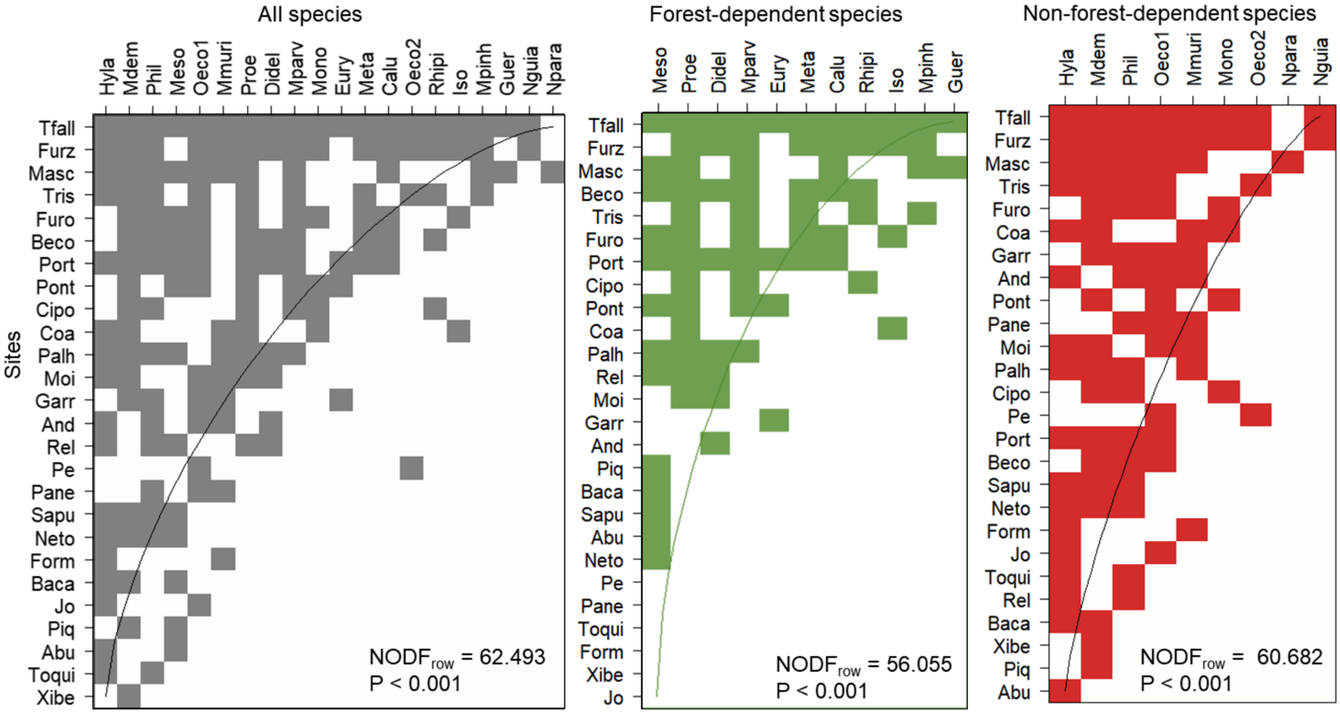

All species
Forest-dependent species
Non-forest-dependent species
Hyla
Mdem
Phil
Meso
Oeco1
Mmuri
Proe
Didel
Mparv
Mono
Eury
Meta
Calu
Oeco2
Rhipi
Iso
Mpinh
Guer
Nguia
Npara
Sites
Tfall
Furz
Masc
Tris
Furo
Beco
Port
Pont
Cipo
Coa
Palh
Moi
Garr
And
Rel
Pe
Pane
Sapu
Neto
Form
Baca
Jo
Piq
Abu
Toqui
Xibe
NODF$_{row}$ = 62.493
P < 0.001
NODF$_{row}$ = 56.055
P < 0.001
NODF$_{row}$ = 60.682
P < 0.001

Figure 3

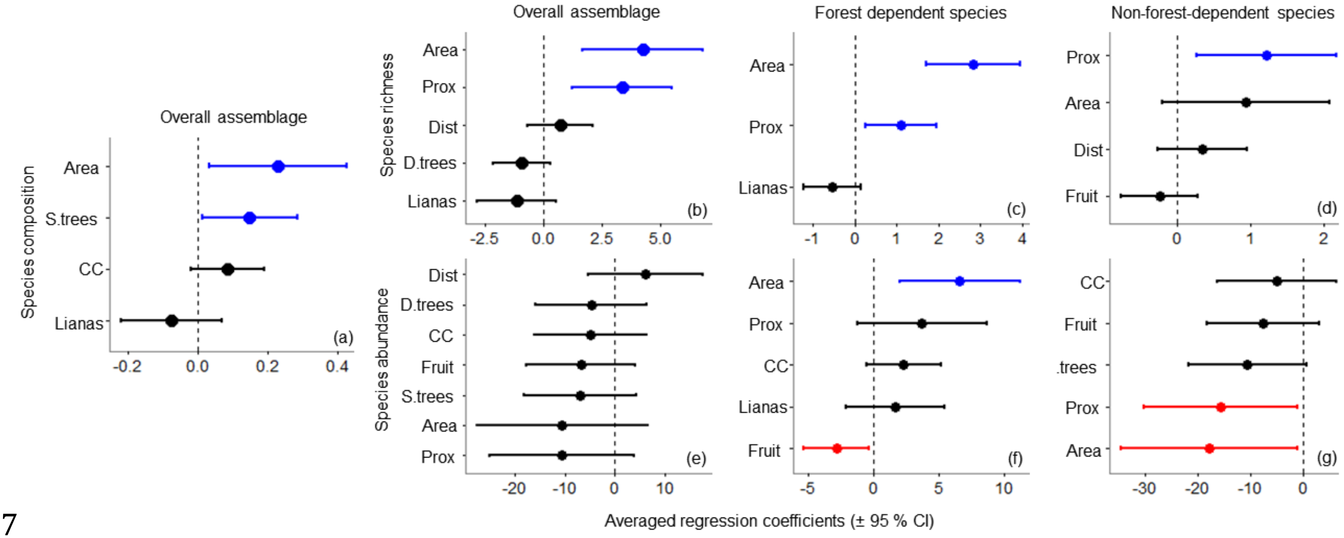
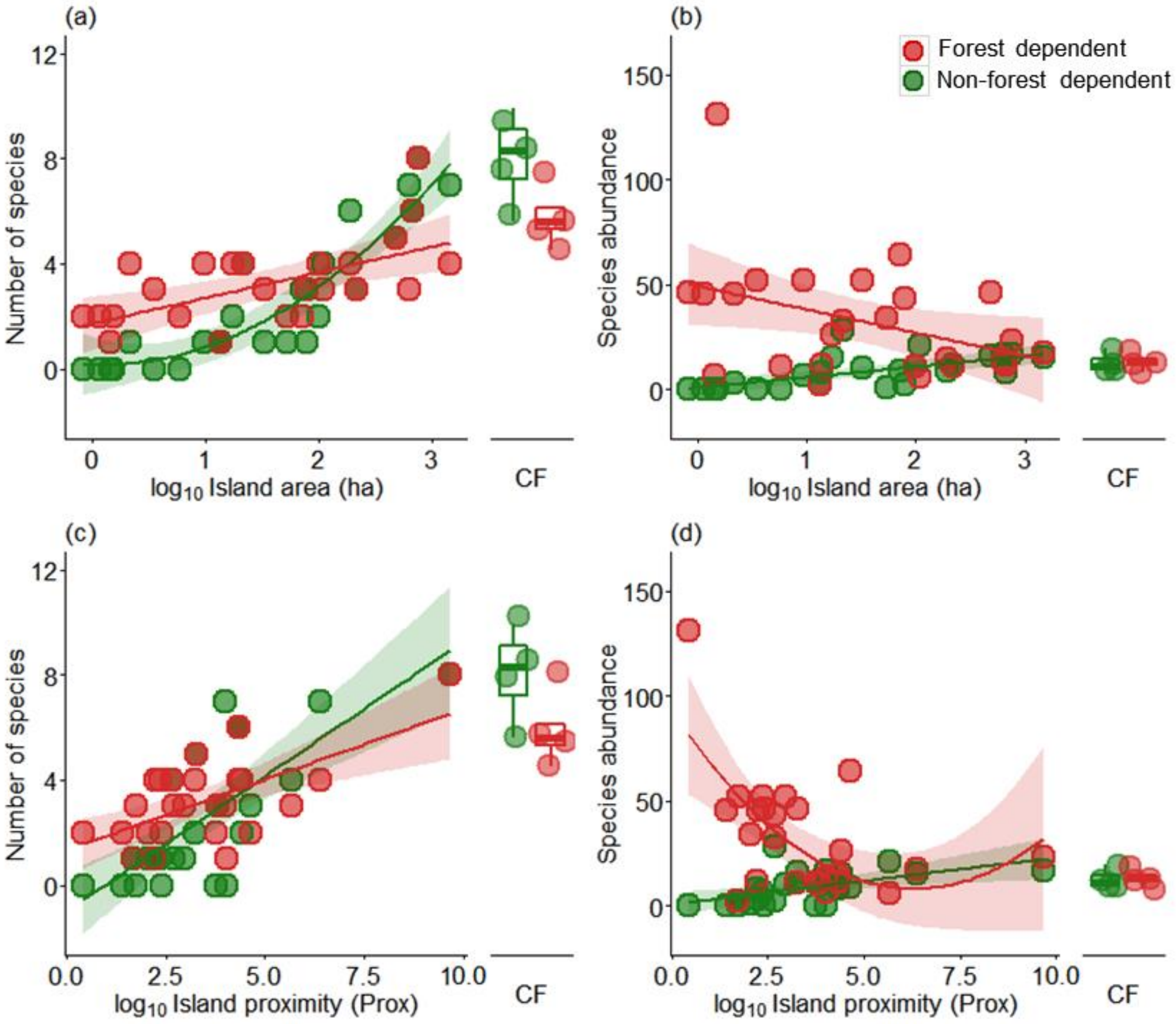

Overall assemblage
Species composition
Area
S.trees
CC
Lianas
-0.2
0.0
0.2
0.4
(a)
Overall assemblage
Species richness
Area
Prox
Dist
D.trees
Lianas
-2.5
0.0
2.5
5.0
(b)
Forest dependent species
Area
Prox
Lianas
-1
0
1
2
3
4
(c)
Non-forest-dependent species
Prox
Area
Dist
Fruit
0
1
2
(d)
Species abundance
Dist
D.trees
CC
Fruit
S.trees
Area
Prox
-20
-10
0
10
(e)
Area
Prox
CC
Lianas
Fruit
-5
0
5
10
(f)
CC
Fruit
.trees
Prox
Area
-30
-20
-10
0
(g)
Averaged regression coefficients (± 95 % CI)

Figure 4



860

861 **Figure 5**