Determinants of population persistence and abundance of terrestrial and arboreal vertebrates stranded in tropical forest land-bridge islands

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Running head - Population loss

Article impact statement - Tropical forest islands created by major hydroelectric dams can only retain very small, if any, vertebrate populations.

Abstract

Mega-dams are among the key modern drivers of habitat and biodiversity loss in emerging economies. The Balbina Hydroelectric Dam of Central Brazilian Amazonia inundated

312,900 ha of primary forests and created ~3500 variable-sized islands that still harbor vertebrate populations after nearly three decades of post-isolation history. Here, we estimated the species richness, abundance, biomass, composition, and group size of medium to large-bodied forest vertebrates in response to patch, landscape and habitat quality metrics across 37 islands and three continuous forest sites throughout the Balbina archipelago. We recorded 34 species based on 1,168 km of diurnal censuses and 12,420 camera-trapping-days, and found that patch area was the most significant predictor explaining patterns of vertebrate populations. Additionally, the maximum group size of several group-living species was consistently larger on large islands and continuous sites. Our results show that most vertebrate populations were either locally extirpated or are now committed to future extinction events in most post-inundation islands, clearly disrupting their ecological functions. If all vertebrate species were once widely distributed across the pre-flooding reservoir area, we estimate that ~75% of all individual vertebrates were lost from all 3,546 islands, and 7.4% of the animals in all persisting insular populations are currently committed to local extinctions. Our study demonstrates that including population abundance estimates into predictions of "small island" community disassembly results in even worse biodiversity outcomes. Given the rapidly escalating hydropower infrastructure projects in developing counties, we suggest that faunal abundance and biomass estimates should be considered in environmental impact assessments and large strictly-protected reserves should be set aside to minimize the detrimental effects of future dams on biodiversity. Finally, setting-aside large tracts of continuous forests represents the most critical conservation measure to ensure that animal populations can persist at natural densities in Amazonian forests.

Introduction

Both island and continental biotas worldwide have succumbed to unprecedented biodiversity loss, with current extinction rates nearly 1000 times higher than the pre-human background rate (Pimm et al. 2014). Regional scale extirpation processes result from cumulative local extinctions, with average 60% declines in vertebrate populations worldwide since 1970 (WWF Living Planet Report 2018). Indeed, steep declines in species occupancy and abundance, which are often referred to as the hallmarks of defaunation (see Dirzo et al. 2014), have been driven by myriad anthropogenic activities inducing wholesale ecological

impacts. In particular, habitat loss and fragmentation accelerate biodiversity decay, especially in forest biotas that are sensitive to non-forest habitats (Hanski 2015). For instance, nearly three-quarters of the world's remaining forest area lies within 1 km of a forest edge, threatening the persistence of myriad species (Haddad et al. 2015). Over the last 50 years, several studies have assessed patterns of species decline and extinction, particularly in highly fragmented landscapes in tropical forests (Turner 1996; Benchimol & Peres 2015a). However, fluctuations in small numbers of individuals persisting in local populations can induce faster and more severe impacts on ecosystem functions, thus providing a more sensitive indicator of biodiversity loss (Ceballos & Ehrlich 2002; Dirzo et al. 2014). The demographic and effective sizes of populations persisting in isolated habitat remnants are critical, but have rarely been quantified in fragmented tropical landscapes.

Medium and large-sized forest vertebrates, especially birds and mammals, are widely recognized as high-performing bioindicator taxa of intact tropical landscapes (Ahumada et al. 2011). Indeed, large-scale monitoring programs and rapid assessment surveys frequently focus on large-bodied homeotherms to better elucidate their main threats and monitor species fluctuations over the time (Luzar et al. 2011). In hyper-diverse tropical forests, large terrestrial and arboreal vertebrates often comprise the most important sources of protein for local communities given their population biomass (Robinson & Bennett, 2004). Yet several large-bodied vertebrates have been locally extirpated or severely depleted in tropical forests (Ripple et al. 2017), including the Amazon (Peres & Palacios 2007). Species occupancy in small and highly disturbed patches is often exceedingly low (Thornton et al. 2011), reflecting the strong species-area relationships (SARs) explaining local vertebrate assemblages in fragmented landscapes (Michalski & Peres 2005; Benchimol & Peres 2013,2015a). However, the size of vertebrate populations persisting in forest patches is rarely assessed, and abundance-area relationships have so far been poorly investigated (but see Michalski & Peres 2007) even though population declines are perhaps the best measure of biodiversity erosion (Gaston et al. 2002). Abundance estimates can therefore enhance our understanding of population viability and the effects of anthropogenic disturbances on insular vertebrate populations, especially in hyper-fragmented tropical landscapes.

Beyond widespread forest conversion into pasture and cropland since the 1970s, hydroelectric dams have recently become an additional threat to Amazonian biotas (Fearnside 2014; Lees et al. 2016). Terrestrial vertebrates and invertebrates experience massive local extinction rates within Amazonian forest islands formed in the aftermath of dam construction (Benchimol & Peres 2015a, 2015b; Tourinho et al. 2019). In particular, most arboreal and terrestrial species are extirpated from large numbers of small islands comprising man-made archipelagos (Benchimol & Peres 2015b), yet the status of extant insular populations remains poorly investigated. Given that 191 current dams have already been built and another 243 have been proposed to be constructed by 2024 across the Amazon basin (Lees et al. 2016), it is critical to assess population sizes in insular habitats to better understand their demographic viability in areas affected by mega-dams.

Here, we quantify the local abundance of 34 vertebrate species in forest sites created by a mega hydroelectric dam in Central Amazonia, and present evidence of either local extirpation or populations that are committed to future extinction events on small islands. We conducted well-replicated quantitative surveys at 37 variable-sized islands and three mainland sites using two robust sampling techniques to survey a wide range of forest vertebrate species, including mammals, large birds and tortoises. We further assess community-wide patterns of abundance, biomass, species richness, species composition, and the socioecology of group-living species in response to patch, landscape and habitat quality metrics. Finally, we predict both the number of individuals lost considering all vertebrate populations and the number of populations that may be committed to local extinctions across all reservoir islands.

Methods

Study landscape

This study was conducted at the Balbina Hydroelectric Reservoir landscape in central Brazilian Amazonia (1°01'–1°55'S; 60°29'–59°28'W, see Appendix S1). The Balbina Dam was built in 1986 by impounding the Uatumã River, flooding an area of 312,900 ha and creating 3,546 islands ranging in size from 0.2 ha to 4,878 ha (Benchimol & Peres 2015a). In 1990, the left bank of the reservoir and the adjacent mainland continuous forests (CFs) were protected through the creation of the ~940,000-ha Uatumã Biological Reserve. The main

vegetation type is sub-montane dense closed-canopy *terra firme* forests, with mean annual rainfall of ~2,376 mm and mean temperature of 28°C (Benchimol & Peres 2015c).

Vertebrate surveys

Surveys were conducted at 37 variable-sized islands and three CFs (Appendix S1). Islands were selected on the basis of their size (0.83 to 1,690 ha), degree of isolation (distance from the mainland), spatial distribution (spaced by >1 km from one another), and absence of hunting pressure, particularly in the upper watershed of the reservoir, which is far away from the nearest village. Both islands and CFs were also unaffected by logging, but some of our study islands succumbed to ephemeral understorey fire disturbance during the 1997-1998 El-Niño drought, which affected several islands in the reservoir.

We first collated a vertebrate species checklist (including terrestrial and arboreal species) expected to occur across the reservoir, which included two tortoise and nearly 40 forest mammal and bird species. To carry out vertebrate surveys, we established one to five variable-length (0.5-3.0 km) linear transects at each island, and three parallel 4-km transects at each CF site, amounting to 81 transects and a total length of 108.5 km (see Benchimol & Peres 2015b). We then used line-transect censuses (LTC) and camera trapping, which are widely recognized as the two most efficient sampling techniques to survey homeotherm vertebrates >500g in tropical forests (Peres 1999; Michalski & Peres 2007). LTCs were conducted eight times at each site by two well-trained observers, following a standardized protocol (Peres 1999), accumulating 1,168 km of survey effort. For camera-trapping surveys, we deployed two to fifteen Reconyx HC500-Hyperfire digital camera traps (CTs) at each sampling site, according to island size, repeated over two continuous 30-day periods in consecutive years. CTs were unbaited, placed 30-40 cm above ground, and spaced by at least 500 m (except in very small islands). We deployed a total of 207 camera-trapping stations, which sampled a total of 12,420 CT-days (mean [SD] = 310.5 [251.83], range = 120-900 CT-days/site). All surveys were carried out between June 2011 and December 2012, and LTCs were never conducted at any site during camera-trapping sampling periods.

Patch and landscape variables

We used 28 commercial tiles of high-resolution multispectral RapidEye© (5-m pixel) imagery of the entire Balbina landscape to quantify spatial metrics for all surveyed sites. We specifically used RapidEye© tiles that matched our field time (from March 2011 to September 2012), and exhibited low (<10%) cloud cover. After image processing and mosaicing, we used the Maximum Likelihood Classification supervised method in ArcGIS to obtain four land cover classes (closed-canopy forest, open-canopy forest, bare ground, and water) for the entire Balbina archipelago and neighboring landscape. We further confirmed this supervised method using our ground-truthed georeferenced data belonging to each of our fours land-cover classes, and used the percentage of closed-canopy forest (CC%) within each surveyed site as a measure of habitat quality. We also quantified fire severity (BURN) and the aggregate basal area of all trees ≥10 cm DBH (diameter at breast height) bearing fleshy fruits (BA_{FF}) at each site. BURN and BA_{FF} were estimated from floristic surveys based on 87 quarter-hectare plots inventoried at all survey sites (Benchimol & Peres 2015c).

At the patch scale, we measured total island area (AREA, $\log_{10}$ x); the distance between each focal island and the nearest CF (ISOLATION); the perimeter of focal islands divided by their total area (SHAPE), and a modified proximity index (PROX), which considers the total size and distance to any land mass within each buffer (see Benchimol & Peres 2015a). We considered multiple buffer sizes (250 m, 500 m and 1000 m) outside the perimeter of each site, given that multi-scale analysis is considered the most suitable approach to determine landscape size when the scale of species responses is unknown (Jackson & Fahrig, 2015). At the landscape scale, we quantified the proportion of forest cover (COVER) within each buffer. We assigned a value one order of magnitude greater than our largest island (i.e., 16,900 ha) for every CF included within the buffer area of a focal island. We performed a Pearson correlation matrix among all variables, and excluded COVER from subsequent analyses because it was highly correlated (r >0.70) with other variables.

Data analysis

For each species recorded by at least one sampling technique, we obtained abundance estimates defined as either the number of individuals (or groups) detected per 10 km walked (for mostly arboreal species surveyed by LTC), or the number of independent photographs per 10 CT-days (for terrestrial species surveyed by CT). Given the wide discrepancy in units of abundance provided by either LTC or CT, we tested which sampling technique most efficiently detected any given species, and for that species used those estimates for subsequent analyses. In doing so, we constructed cumulative detection curves for each species based on that technique as a function of all possible detections based on the same technique (Appendix S2). Because total numbers of records provided by each survey technique were not equivalent, we rescaled all observations between 0.0 to 1.0. In those cases where the 'best technique' failed in record a species within a certain site, we used the rescaled values obtained from another technique, avoiding therefore zero estimates of species within a site that it was indeed detected. Besides the abundance estimate of each species per site, we also estimated (1) the overall vertebrate abundance at each site, by summing all abundance estimates of all recorded species per site; (2) a metric of biomass density for each species at each sampling site by multiplying its abundance estimate by its body mass (according to values in Benchimol & Peres 2015b), and thus obtaining (3) the overall vertebrate biomass, by summing all biomass estimates of all recorded species per site; (4) the overall species richness, considering the sum of all species recorded by both techniques at each site; and (5) the species composition, defined as the first two nonmetric multidimensional scaling (NMDS) ordination axes based on the Bray-Curtis similarity matrix of abundance data for each sampling technique. All analyses were performed using the 'vegan' R-package (Oksanen et al. 2018).

We performed Generalized Linear Models (GLMs) to assess the importance of habitat quality, patch, and landscape variables in explaining patterns of overall vertebrate abundance, overall biomass, species richness and species composition across all survey sites. Models were fitted using the 'lme4' package (Bates 2007). We tested for multicollinearity among our seven variables using Variation Inflation Factors (VIF) using the 'HH' package (Heiberger 2016), and given that PROX was moderately redundant/collinear (VIF>3) for all response

variables, we excluded this variable in subsequent models. We ran all possible models and used model-averaged estimates using the 'MuMIn' package (Barton 2018), subsequently identifying all significant variables (i.e., P≤0.05). We also determined the relative importance of each variable (i.e. the contribution of each variable to overall model variance) using hierarchical partitioning (HP) in the 'hier.part' package (Walsh & MacNally 2003). We performed GLMs considering (1) only the 37 surveyed islands, including all our six explanatory variables; and (2) all 40 surveyed sites, but excluding those explanatory variables inherently associated with islands (ISOLATION, SHAPE and PROX). We further investigated the relationships between each of our four response variables (overall abundance, overall biomass, richness and composition) focusing on the variable showing the highest explanation (based on HP). For this, we performed a model selection procedure and compared differences in Akaike Information Criterion (ΔAIC) to select the most parsimonious model (i.e., all models exhibiting ΔAIC ≤2.00), which was subsequently presented as figures. In all cases, we tested four models used to investigate relationships in fragmented tropical landscapes: null (constant), linear, power-law and piecewise.

We further obtained relativized abundance estimates of each species, accordingly to its most efficient sampling technique, by rescaling all abundance estimates between 0.0 to 1.0. For this, we divided the observed abundance estimate of each species at each sampling site by the highest abundance observed for that species across all sites. We also summed the relativized abundances for all species per site, which enabled us to obtain an 'aggregate relative abundance' considering both sampling techniques on a common scale. We subsequently obtained a 'proxy of population size' for each sampling site by multiplying the aggregate relative abundance by island area. We performed the same procedure to obtain estimates of 'aggregate relative biomass' and a 'proxy of biomass size'. Finally, we used empirical models based on the variable showing the highest hierarchical partitioning (HP, i.e., the contribution towards explained variance) for abundance (i.e., abundance-area relationship; AAR) and biomass estimates across all surveyed islands to predict local population abundances at all unsurveyed islands.

We also estimated the numbers of individuals likely to become extirpated in the near future due to small local population sizes. Here, we assumed that populations across all sites that were below the 25th percentile of abundance did not meet a minimum viability threshold. We further summed the relativized abundances for all 'viable' populations per site, thereby obtaining the 'viable aggregate relative abundance'. We further used empirical models based on the variable showing the highest HP to predict the 'viable aggregate relative abundance' at all unsurveyed islands.

We finally investigated species-specific responses, by examining the relationship between the variable presenting the highest explanation power and (*i*) abundance estimates for each species, derived from its most efficient survey technique, and (*ii*) in the case of group-living species, the maximum group size recorded at each survey site. Because all social species were exclusively or primarily detected using line-transect surveys and the best group counts were derived from this census technique, we examine between-site variation in group sizes for social species considering only line-transect data. All the statistical analyses were based on the R platform (R Development Core Team, 2018).

Results

Overall, we recorded 34 vertebrate forest-dwelling species representing different mammal, bird and reptile families, assigned to different threat categories according to the IUCN Red List of Threatened Species (IUCN 2019; Table 1). Ten species were exclusively recorded by line-transect censuses, six exclusively recorded by camera trapping, and 18 by both techniques (Table 1). We therefore performed data analysis considering all species best detected by [1] line-transect censuses (N=14), and [2] camera trapping (N=20).

Considering our six explanatory variables and all 37 surveyed islands, GLMs showed that patch size was the most significant predictor of species richness, overall abundance, overall biomass, and species composition. Island size also exhibited the highest explanatory power in hierarchical partitioning analysis (Appendix S3). Additionally, only fire accounted for a significant predictor of species composition considering line-transect data, albeit with a lower fraction of HP. The same pattern was observed from GLMs considering all 40 surveyed sites: patch area was the only variable included in all models, and showed the highest fraction of

HP in explaining patterns of species richness (75.1% for both techniques), overall abundance (76.5% for LTC and 76.1% for CT), overall biomass (67.9% for LTC and 84.1% for CT), and composition (69.4% for LTC and 53.6% for CT). We thus performed model selection to investigate the relationship between patch area and all four response variables (Appendix S3). Piecewise and linear models were considered equally 'good' in explaining patterns of overall abundance and overall biomass based on LTC data and species composition based on CT data, whereas only a piecewise model could explain patterns of species composition based on LTC data. Linear and power-law models best explained patterns of abundance and biomass considering CT data only, whereas the power-law and piecewise were the best models explaining species richness considering both survey techniques (Appendix S4).

Both the relative abundance (mean ± SD = 5.1 ± 3.7, range: 0-12.5) and relative biomass (105.3 ± 88.3, range: 0-309.6) summed across all species greatly increased with forest area (Figure 1a,c), so that large islands and CFs retained the largest animal numbers (Figure 1b,d). However, large islands retained higher aggregate relative abundances than CFs. In contrast, our 15 small islands (<10 ha) retained few, if any, vertebrate populations, which were mostly comprised of a small set of species exhibiting low abundances – including the nine-banded armadillo (N=11 islands), followed by the great tinamou (N=7) and black curassow and howler monkey (N=6) (Figure 2). The abundance of all vertebrate species considered here, except for the nine-banded armadillo, substantially increased in increasingly larger islands (Figure 3).

Based on parameters obtained from the linearized model considering all 37 islands, we predicted the aggregate relative abundance of all non-surveyed islands as a function of island size. We then estimated the proportion of all population sizes that were either retained or lost by assuming that the highest abundance obtained across all sites reflects the maximum abundance likely to be recorded at any site. We then identified which islands had likely lost most of their collective population sizes across the entire archipelago, which reveals a drastic loss in overall numbers of individuals across all islands (Figure 4). Assuming that all vertebrate species were once widely distributed across the pre-flooding reservoir area, we estimate a relative loss of 61.7% (284,99 of 461,76) of all individuals within our 37 surveyed islands. However, this rate increased to 74.3% (32,874 of 44,254) of all individuals when

extrapolated to all 3,546 islands across the archipelago. Only 10 large islands (>1,200 ha) in the entire archipelago could harbor healthy population sizes across all vertebrate species, with CFs serving as the main regional-scale refugia of vertebrate assemblages (Figure 4).

If we assume that populations across all sites below the 25th percentile of abundance could not meet a minimum viability threshold, one-quarter of the populations of eight species within our 40 sites (howler monkey, spider monkey, golden-handed tamarin, squirrel monkey, lowland paca, collared peccary, black curassow and marail guan) are currently committed to local extinctions, with several other species also vulnerable to many additional local extinctions in the near future (Table 1). Mirroring these estimates, the 'viable aggregate relative abundance' decreased by 8% (187.1 of 203.3 individuals) for all surveyed islands (mean ± SD = 4.68 ± 3.53, range: 0-12.1) contrasting with our observed 'aggregate relative abundances'. Our predictions considering all reservoir islands show that 7.4% (918.7 of 12,399.3) of the extant individuals across all insular populations are currently committed to local extinctions.

Additionally, the maximum group size of several social species was consistently larger in increasingly larger islands and CFs (Figure 5). In particular, significantly smaller group sizes were found on smaller islands for four primate species — howler monkeys (R^2=0.395; P=0.000); spider monkeys (R^2=0.267; P=0.019); bearded saki monkeys (R^2=0.416; P=0.008) and brown capuchin monkeys (R^2=0.293; P=0.008). Collared peccaries also showed a similar pattern of reduced herd sizes on smaller islands (R^2=0.202; P=0.147).

Discussion

Our results clearly show that the vast majority of islands created by a vast hydro- reservoir can only retain small numbers of vertebrate species that collectively sustain small population sizes and low overall biomass density, and that these differences are primarily driven by habitat area effects. Island size also largely explained patterns of conspecific group size of several social species. These patterns indicate that most islands failed to sustain sufficiently large populations, and thereby cannot ensure long-term population persistence of virtually all solitary and group-living species. Although most conservation ecology studies on tropical forest vertebrate persistence in habitat remnants have focused on binary patterns of patch

occupancy (Sampaio et al. 2010; Benchimol & Peres 2015b), we show that more severe area-effects can only be detected when local population abundance and AARs are quantified. Considering the overall numerical losses (in terms of relative numbers of individuals) across all populations, we show that nearly three-quarters of all vertebrate populations are committed to become extirpated within the entire reservoir. This occurred despite the effective protection from hunting pressure conferred on the Balbina landscape over its nearly 3-decade isolation history, not least because of active enforcement by the Uatumã Biological Reserve. Under any alternative scenario of typical game offtake in rural Amazonia, we expect a far worse outcome for isolated large vertebrate populations, which would be expected to succumb to the synergistic ravages of small habitat isolates exposed to hunting-induced mortality (Peres 2001). Our results therefore indicate that, even under a 'best-case' scenario, small islands are highly susceptible to severe vertebrate population losses and any ecosystem functions they may provide (Ceballos & Ehrlich 2002).

Our analysis shows that forest area was by far the strongest predictor of overall numerical abundance, population biomass density, species richness and species composition of vertebrates on islands, contributing most of the explanatory power among all patch, landscape and habitat quality predictors. In fact, islands smaller than 10 ha were either entirely 'empty' or retained very depauperate vertebrate populations, followed by a linear increase in overall abundance as a function of island size beyond this area threshold. Given that half (50.3%) of all 3,546 Balbina islands are smaller than 10 ha, and 87.8% of all islands are <50 ha, a vast proportion of all habitat remnants in this archipelagic landscape retained very few, if any, vertebrate populations. This likely led to a process of defaunation and biomass collapse with cascading effects on ecosystem functioning. For instance, considering a subset of Balbina islands, those smaller than 13 ha experienced massive losses in dung beetle assemblages, likely as a partial response to depletion of mammal populations and their fecal resources (Storck-Tonon et al. 2020). This suggests that a wide range of ecosystem functions provided by dung beetles, including nutrient cycling, topsoil fertilization and secondary seed dispersal, are severely disrupted on small islands, via the indirect effect of community disassembly of resource populations. Likewise, the decline of mammal and gamebird abundance following patch reduction was also documented in another Amazonian fragmented landscape (Michalski & Peres 2007). Additionally, richness and composition of rodents and marsupials

(Palmeirim et al. 2018) and bird assemblages (Aurélio-Silva et al. 2016) were best predicted by island size, with patches smaller than 15 and 55 ha retaining an impoverished nested subset of each of these taxa, respectively. Therefore, our study provides evidence that preserving large tracts of non-hunted Amazonian forest is essential to sustain natural populations of vertebrate species, which should be prioritized in conservation efforts.

Patterns of vertebrate abundance in fragmented landscapes are highly variable, with 'winner' and 'loser' species either benefiting from habitat modification or declining towards local extirpation (Laurance et al. 2011; Michalski & Peres 2007). In Balbina, nearly all species can be described as 'losers', as they either succumbed to local extinctions or exhibited extremely low relativized abundance estimates on small islands, which encompasses the vast majority of islands within the reservoir. Nine-banded armadillo can be considered an exceptional case, as they occurred in almost all surveyed sites and even exhibited over-inflated abundances on some islands. This ubiquitous species, which has been previously classified as area-insensitive (Benchimol & Peres 2015b), has been recorded in much greater densities in small patches in other fragmented landscapes (Michalski & Peres 2007; Thornton et al. 2011). Yet other area-insensitive species including the red acouchi, lowland paca, tapir, black curassow and great tinamou occurred at low abundances on small islands, where their natural population densities are likely curbed by low resource availability. Conversely, some species exhibited higher abundances on islands compared to continuous forest sites, provided that they were able to persist. For instance, the small-bodied Brazilian squirrel tolerates habitat perturbation (Mendes et al. 2019), and the small-herd-living collared peccary can thrive in secondary forests and small fragments (Keuroghlian et al. 2004), suggesting that viable populations can persist on medium-sized to large islands. However, these results can also be attributed to a sampling artefact if the same individuals are detected repeatedly on small islands, thereby overestimating their abundance estimates. Furthermore, swimming capacity and therefore the probability of traversing the open-water matrix between islands varied substantially among species (Benchimol & Peres 2015b), with potential metapopulation consequences for population persistence within islands. In particular, species that were most adept at swimming and frequently dispersed over open-water were most likely to either recolonize vacant islands or boost small populations compared to those exhibiting low or no vagility. On the basis of a comprehensive compilation of data on dispersal events (Benchimol

& Peres 2015b), many species were indeed observed swimming across islands in Balbina. Across all species, however, the number of populations committed to local extinctions was positively associated with dispersal capacity across the open-water matrix (rs = 0.476). Species showing the highest proportions of populations committed to extinction (see Table 1), such as collared peccary and terrestrial birds, could be rescued by successful colonization events provided patch area and habitat quality are suitable.

Island size also affected the maximum operational group size of several social species, such as primates and grey-winged trumpeters, in which the large groups typical of continuous sites were apparently suppressed on small islands. Group size comprises a tradeoff between the costs of reduced foraging efficiency and the benefits of reduced predation risk (Pulliam & Caraco, 1984), with large groups constrained by either small food clusters or habitat patches (Oderdonk & Chapman 2000). Given that food resource availability is reduced in small patches, our results indicate that islands retaining group-living species are unlikely to accommodate the natural range of group sizes typical of undisturbed continuous forest. In fact, tree assemblages on small Balbina islands were species-poor and functionally impoverished (Benchimol & Peres 2015c), resulting in reduced availability of fleshy fruits for frugivores. Habitat area effects on group sizes have also been observed in bearded saki monkeys in other fragmented landscape (Boyle & Smith 2010). Fission-fusion groups of spider monkeys were also smaller in fragments in Colombia, with potential consequences to population persistence (Marsh et al. 2016). The small group size effect may carry long-term costs for population persistence, given that inbreeding and limited gene flow become more likely, ultimately threatening long-term genetic viability (Knapp 2013). All other things being equal, reduced group sizes may not affect group densities but depress the size of breeding populations, ultimately reducing demographic viability.

Conclusions

Our study clearly reinforces the notion that land-bridge archipelagos formed by large hydroelectric dams are extremely detrimental to medium to large-bodied vertebrates, which either undergo local extinctions or are retained in small numbers in most reservoir islands. We have previously shown that most species drop out of small forest islands following 25 years post-isolation, including invertebrates and vertebrates (Benchimol & Peres 2015a,b;

Palmeirim et al. 2018; Tourinho et al. 2019). Our new findings consistently show that population sizes and biomass density are generally low on most islands even for those species that have somehow avoided local extinctions so far. This highlights the precarious demographic viability that likely characterizes the small population syndrome of all small islands, which can further contribute to a time-lagged extinction debt. Furthermore, most vertebrate species assessed here are forest specialists, with correlated effects of island size and habitat degradation (Benchimol & Peres 2015c) further affecting their abundance. As a result, key ecological processes directly or indirectly provided by forest-dwelling species can be lost, threatening the maintenance of ecosystem integrity (Terborgh et al. 2001).

If current trends in hydropower expansion continues, the long-term ecosystem functionality of newly formed land-bridge islands will likely be strongly compromised. Other planned or under-construction large dams in lowland Amazonia are also located in relatively flat terrains, which create shallow lakes inundating extensive areas where ridgetop archipelagos will be largely comprised of small islands (Fearnside 2014). As shown here, these small islands will likely succumb to severe defaunation of area-sensitive species, resulting in massive population declines if not local extinctions. We therefore suggest that policy-makers should explicitly consider the overall topography of planned reservoir areas, favoring dams associated with large-island creation but embargoing those located in unfavorable terrains and river basins. Additionally, we consider that biodiversity loss should be explicitly included into Environmental Impacts Assessments (EIAs) of large hydropower projects in developing countries, with data acquisition including population abundance estimates. For those dams that have already been approved, we recommend setting-aside extensive tracts of strictly protected forest adjacent to reservoir areas to maximize the retention of healthy animal populations. This conservation strategy becomes crucial, given that only mainland forest sites can safeguard natural population sizes. Finally, maintaining, restoring or otherwise protecting large tracts of tropical forests are the only safe options to ensure population viability in our charismatic large vertebrate fauna.

Data Availability Statement.

Data will be available from the Figshare Repository.

Literature Cited

Ahumada JA, Silva CE, Gajapersad K, Hallam C, Hurtado J, Martin E, McWilliam A, Mugerwa B, O'Brien T, Rovero F, Sheil D. 2011. Community structure and diversity of tropical forest mammals: data from a global camera trap network. Philosophical Transactions of the Royal Society of London B: Biological Sciences **366**:2703-2711.

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. Biological Conservation **199**:101-109.

Barton K. 2018. MuMIn: multi-modal inference. Model selection and model averaging based on information criteria (AICc and alike).

Bates DM. 2007. Linear mixed model implementation in lme4. Manuscript,University of Wisconsin.

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. Biological Conservation **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. Journal of Ecology **103**:408-420.

Benítez-López A, Alkemade R, Schipper M, Ingram DJ, Verweij PA, Eikelboom JAJ, Huijbregts MAJ. 2017. The impact of hunting on tropical mammal and bird populations. Science **356**:180-183.

Boyle SA, Smith AT. 2010. Behavioral modifications in northern bearded saki monkeys (*Chiropotes satanas chiropotes*) in forest fragments of central Amazonia. Primates **51**:43-51.

Ceballos G, Ehrlich PR. 2002. Mammal population losses and the extinction crisis. Science **296**:904-907.

Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJ, Collen B. 2014. Defaunation in the Anthropocene. Science **345**:401-406.

Fearnside PM. 2014. Impacts of Brazil's Madeira River dams: Unlearned lessons for hydroelectric development in Amazonia. Environmental Science & Policy **38**:164-72.

Gaston KJ, Blackburn TM, Greenwood JJ, Gregory RD, Quinn RM, Lawton JH. 2000. Abundance–occupancy relationships. Journal of Applied Ecology **37**:39-59.

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances **1**:p.e1500052.

Hanski I. 2015. Habitat fragmentation and species richness. Journal of Biogeography **42**:989-993.

Heiberger RM. 2016. HH: Statistical analysis and data display: Heiberger and Holland. R Package Version 3:1–31.

IUCN. 2019. The IUCN Red List of Threatened Species v. 2016-3. http://www.iucnredlist.org [accessed 10 April 2019].

Jackson HB, Fahrig L. 2015. Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography **24**:52-63.

Keuroghlian A, Eaton DP, Longland WS. 2004. Area use by white-lipped and collared peccaries (*Tayassu pecari* and *Tayassu tajacu*) in a tropical forest fragment. Biological Conservation **120**:411-425.

Knapp LA. 2013. Molecular genetic tools for evaluating the consequences of habitat fragmentation. In Primates in Fragments: Complexity and Resilience (Marsh LK, ed.), pp 389-398. New York, Springer.

Laurance WF et al. 2011. The fate of Amazonian forest fragments: A 32-year investigation. Biological Conservation **144**:56–67

Lees AC, Peres CA, Fearnside PM, Schneider M, Zuanon JA. 2016. Hydropower and the future of Amazonian biodiversity. Biodiversity and Conservation **25**:451-66.

Luzar JB, Silvus KM, Overman H, Giery ST, Read JM, Fragoso JMV. 2011. Large-scale environmental monitoring by indigenous people. BioScience **61**:771-781.

Marsh C, Link A, King-Bailey G, Donati G. 2016. Effects of fragment and vegetation structure on the population abundance of *Ateles hybridus*, *Alouatta seniculus* and *Cebus albifrons* in Magdalena Valley, Colombia. Folia Primatologica **87**:17-30.

Mendes CP, Koprowski JL, Galetti M. 2019. NEOSQUIRREL: a data set of ecological knowledge on Neotropical squirrels. Mammal Review **49**:210-225.

Michalski F, Peres CA. 2005. Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. Biological conservation **124**:383-396.

Michalski F, Peres CA. 2007. Disturbance-mediated mammal persistence and abundance-area relationships in Amazonian forest fragments. Conservation Biology **21**:1626-1640.

Onderdonk DA, Chapman CA. 2000. Coping with forest fragmentation: the primates of Kibale National Park, Uganda. International Journal of Primatology **21**:587-611.

Oksanen JFG, Blanchet R, Kindt P et al. 2018. Vegan: community ecology package. R package version 2.4–1.

Palmeirim AF, Benchimol M, Vieira MV, Peres CA. 2018. Small mammal responses to Amazonian forest islands are modulated by their forest dependence. Oecologia **187**:191-204.

Peres CA. 1999. General guidelines for standardizing line-transect surveys of tropical forest primates. Neotropical Primates **7**:11-16.

Peres CA. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. Conservation Biology **15**:1490-1505.

Peres CA, Palacios E. 2007. Basin- wide effects of game harvest on vertebrate population densities in Amazonian forests: Implications for animal- mediated seed dispersal. Biotropica **39**:304-315.

Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science **344**:1246752.

Pulliam HR, Caraco T. 1984. Living in groups: is there an optimal group size. In: Krebs J. R. and Davis N. B. (eds), Behavioural ecology, an evolutionary approach. Blackwell, Oxford, pp. 122-147.

R Development Core Team 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Ripple WJ, Wolf C, Newsome TM, Hoffmann M, Wirsing AJ, McCauley DJ. 2017. Extinction risk is most acute for the world's largest and smallest vertebrates. Proceedings of the National Academy of Sciences **114**:10678-10683.

Robinson JG, Bennett EL. 2004. Having your wildlife and eating it too: an analysis of hunting sustainability across tropical ecosystems. Animal Conservation **7**:397-408.

Sampaio R, Lima AP, Magnusson WE., Peres CA. 2010. Long-term persistence of midsized to large-bodied mammals in Amazonian landscapes under varying contexts of forest cover. Biodiversity and Conservation **19**:2421-2439.

Storck-Tonon D, da Silva RJ, Sawaris L, Vaz-de-Melo FZ, Silva DJ, Peres CA. 2020. Habitat patch size and isolation drive the near-complete collapse of Amazonian dung beetle assemblages in a 30-year-old forest archipelago. Biodiversity and Conservation **29**:2419-2438.

Tourinho AL, Benchimol M, Porto W, Peres CA, Storck- Tonon D. 2019. Marked compositional changes in harvestmen assemblages in Amazonian forest islands induced by a mega dam. Insect Conservation and Diversity.

Terborgh J, Lopez L, Nuñez P, Rao M, Shahabuddin G, Orihuela G, et al. 2001. Ecological meltdown in predator-free forest fragments. Science **294**:1923-1926.

Thornton D, Branch L, Sunquist M. 2011. Passive sampling effects and landscape location alter associations between species traits and response to fragmentation. Ecological Applications **21**:817-829.

Turner IM. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. Journal of applied Ecology **33**:200-209.

Walsh C, MacNally R. Hierarchical partitioning. R project for statistical computing. Available from. 2003.

WWF Living Planet Report - 2018: Aiming Higher. Aiming Higher (Eds M. Grooten and R. E. A. Almond). WWF International, Gland, Switzerland.

Table 1. Checklist of 34 vertebrate species surveyed within 37 forest islands across the Balbina archipelagic landscape and three neighboring mainland sites and the sampling techniques quantifying the relative abundance of each species. Solid circles (●) denote the most efficient survey technique for each species that was detected by more than one method. The number of forest sites in which the species was recorded and the number/proportion of current populations committed to local extinction is also presented.

Family	Species	English vernacular name	IUCN[1]	Body mass (kg)[2]	Sampling technique		Observed occurrence	Populations committed to local extinction (Number/%)
					Census	Camera trapping		
Mammals								
Cervidae	*Mazama americana*	Red brocket deer	DD	22.80	×	●	18	4/22
Cervidae	*Mazama nemorivaga*	Amazonian brown brocket deer	LC	16.30	×	●	14	3/21
Tayassuidae	*Pecari tajacu*	Collared peccary	LC	21.27	×	●	16	4/25
Tayassuidae*	*Tayassu pecari*	White-lipped peccary	VU	32.23		×	3	0/0
Mustelidae	*Eira barbara*	Tayra	LC	3.91	×	●	11	2/18
Felidae	*Leopardus pardalis*	Ocelot	LC	11.90	×	●	24	3/13
Felidae	*Leopardus wiedii*	Margay	NT	3.25		●	9	0/0
Felidae	*Panthera onca*	Jaguar	NT	80.00	×	●	15	2/13
Felidae	*Puma concolor*	Puma	LC	51.60	×	●	18	4/22
Felidae	*Puma*	Jaguaru	LC	6.75	×	●	6	0/0

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Procyonidae	*Nasua nasua*	South American coati	LC	3.79	●	×	9	2/22
Dasypodidae*	*Cabassous unicinctus*	Southern naked-tailed armadillo	LC	4.80	×		1	0/0
Dasypodidae	*Dasypus kappleri*	Greater long-nosed armadillo	LC	9.50		●	6	0/0
Dasypodidae	*Dasypus novemcinctus*	Nine-banded armadillo	LC	3.50		●	37	9/24
Dasypodidae	*Priodontes maximus*	Giant armadillo	VU	38.00		●	5	1/20
Tapiridae	*Tapirus terrestris*	South American tapir	VU	160.00	×	●	26	6/23
Myrmecophagidae	*Myrmecophaga tridactyla*	Giant anteater	VU	22.33	×	●	19	3/16
Myrmecophagidae	*Tamandua tetradactyla*	Southern tamandua	LC	5.52	●	×	9	2/18
Atelidae	*Alouatta macconnelli*	Red howler monkey	LC	6.15	●		28	7/25
Atelidae	*Ateles paniscus*	Black spider monkey	VU	7.90	●		20	5/25
Pitheciidae	*Chiropotes sagulatus*	Northern bearded saki	-	3.10	●		17	4/24
Pitheciidae	*Pithecia chrysocephala*	Golden-faced saki	LC	1.38	●		13	3/23
Callithrichidae	*Saguinus*	Golden	LC	0.54	●		12	3/25

	midas	-handed tamarin						
Cebidae	*Saimiri sciureus*	Squirrel monkey	LC	0.90	●		12	3/25
Cebidae	*Sapajus apella*	Brown capuchin monkey	LC	2.75	●		23	5/22
Cuniculidae	*Cuniculus paca*	Lowland paca	LC	9.00		●	28	7/25
Dasyproctidae	*Dasyprocta leporina*	Red-rumped agouti	LC	3.50	×	●	23	5/22
Dasyproctidae	*Myoprocta acouchy*	Red acouchi	LC	0.95	×	●	30	7/23
Sciuridae	*Guerlinguetus aestuans*	Brazilian squirrel	-	0.19	●	×	11	2/18
Birds								
Cracidae	*Penelope marail*	Marail guan	LC	0.95	●		20	5/25
Cracidae	*Crax alector*	Black curassow	VU	3.40	×	●	28	7/25
Psophiidae	*Psophia crepitans*	Grey-winged trumpeter	NT	1.50	×	●	17	4/24
Tinamidae	*Tinamus major*	Great tinamou	NT	1.20	●	×	29	7/24
Reptiles								
Testudines/Testudinidae×	*Chelonoidis carbonaria, C. denticulata*	Red-footed and Yellow-footed tortoises	VU	4.00	●		15	3/20

* Due to the low number of records we were unable to obtain abundance estimates

× *Chelonoidis carbonaria* and *C. denticulata* were pooled under a single group, given that they could not always be identified to species and their strong ecological similarities.

[1] DD = Data deficient; LC = Least concern; VU = vulnerable; NT = Near Threatened. Classification based on IUCN (2019).

[2] See Benchimol & Peres (2015b) for details on body mass acquisition.

FIGURE LABELS

Figure 1 – Relationships between forest patch (island and mainland) area and (A) aggregate relative abundance, (B) a proxy of population size (aggregate relative abundance × island area), (C) aggregate relative biomass, and (D) a proxy of biomass density (aggregate relative biomass × island area), for 37 islands and three continuous forest sites across the Balbina landscape. Shaded area represents the 95% confidence region.

Figure 2 – Species-by-site matrix of relative abundances considering the most efficient sampling method for each vertebrate species, including (A) line-transect censuses of mostly arboreal species, and (B) camera-trapping of terrestrial species. Circle sizes are proportional to the relative population abundances based on each method. Mainland and island sites are sorted according to forest area from left to right. Species/genera are grouped into orders or higher taxa.

Figure 3 – Abundance-area relationships (AARs), defined in terms of the relativized population abundance estimates based on the most efficient sampling technique per species, considering all 40 forest sites surveyed throughout the Balbina archipelagic landscape. Unoccupied sites are shown in light pink; orange circles indicate insular populations and green circles represent populations in continuous forest sites. Species panels are shown according to taxonomic groupings (birds, tortoises, carnivores, primates, rodents, ungulates and xenarthrans).

Figure 4 – (A) Proportion of the relative numbers of all individuals across all species predicted to have been lost as a function of forest patch area modelled for all 3,546 forest islands across the Balbina archipelagic landscape, and (B) Heatmap indicating the degree of overall losses of individuals considering all populations (more severe losses colour-coded from yellow to red) based on empirical estimates derived from our 37 surveyed islands.

Figure 5 - Relationships between island size and maximum observed group sizes for all social species, based on the largest number of individuals recorded during any line-transect census, provided that any given species was recorded at least once. Darker circles represent continuous forest sites.
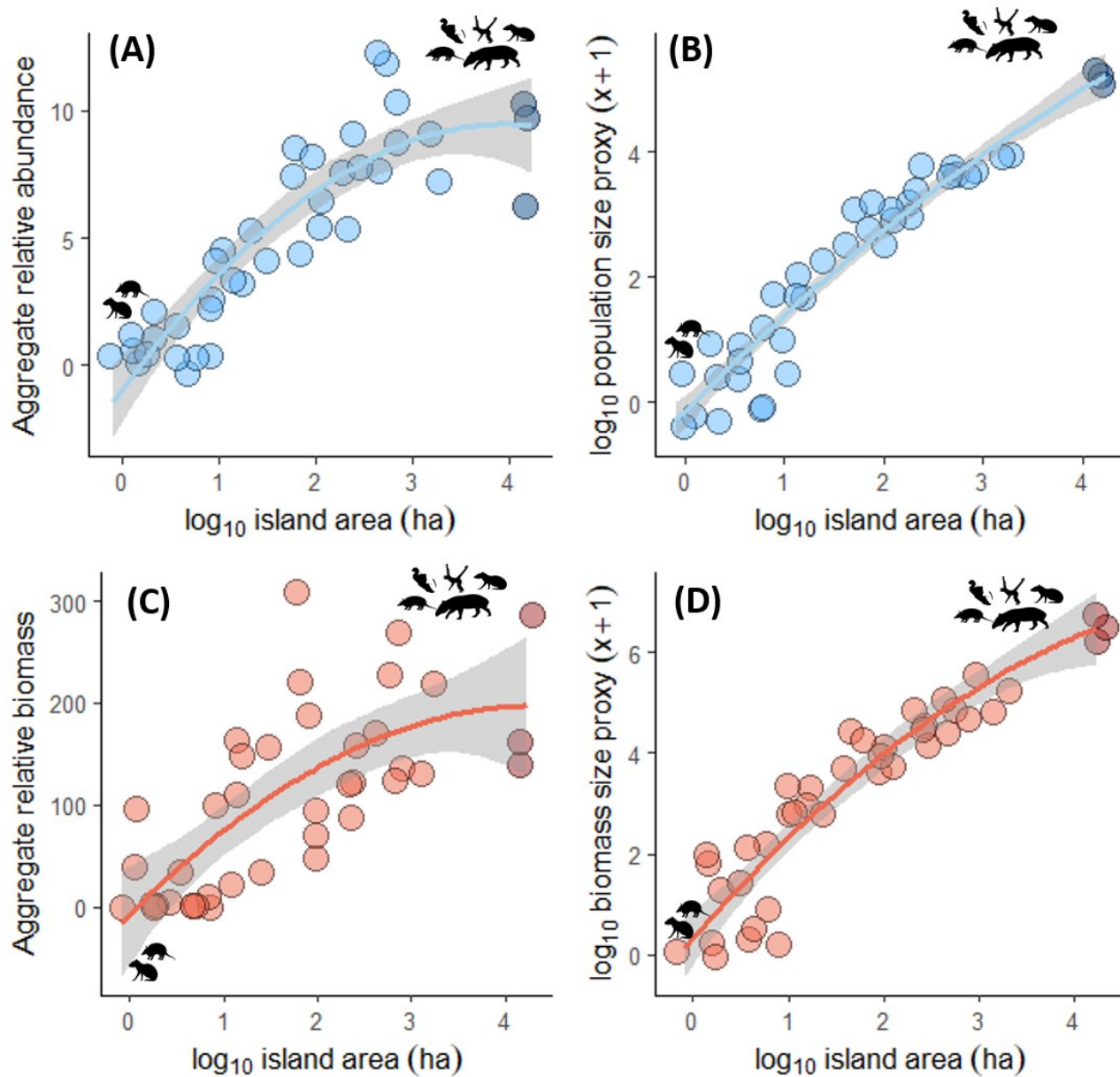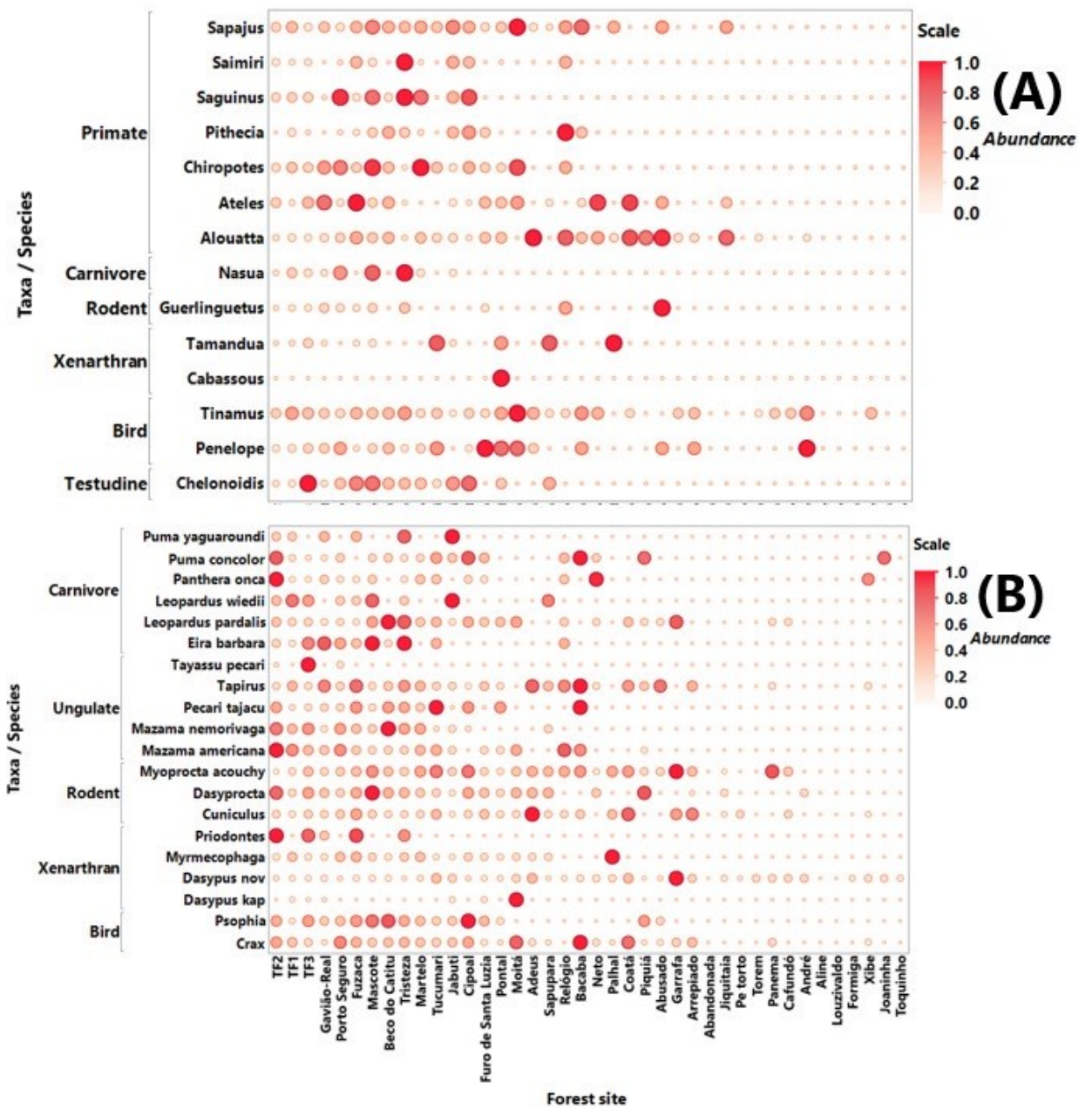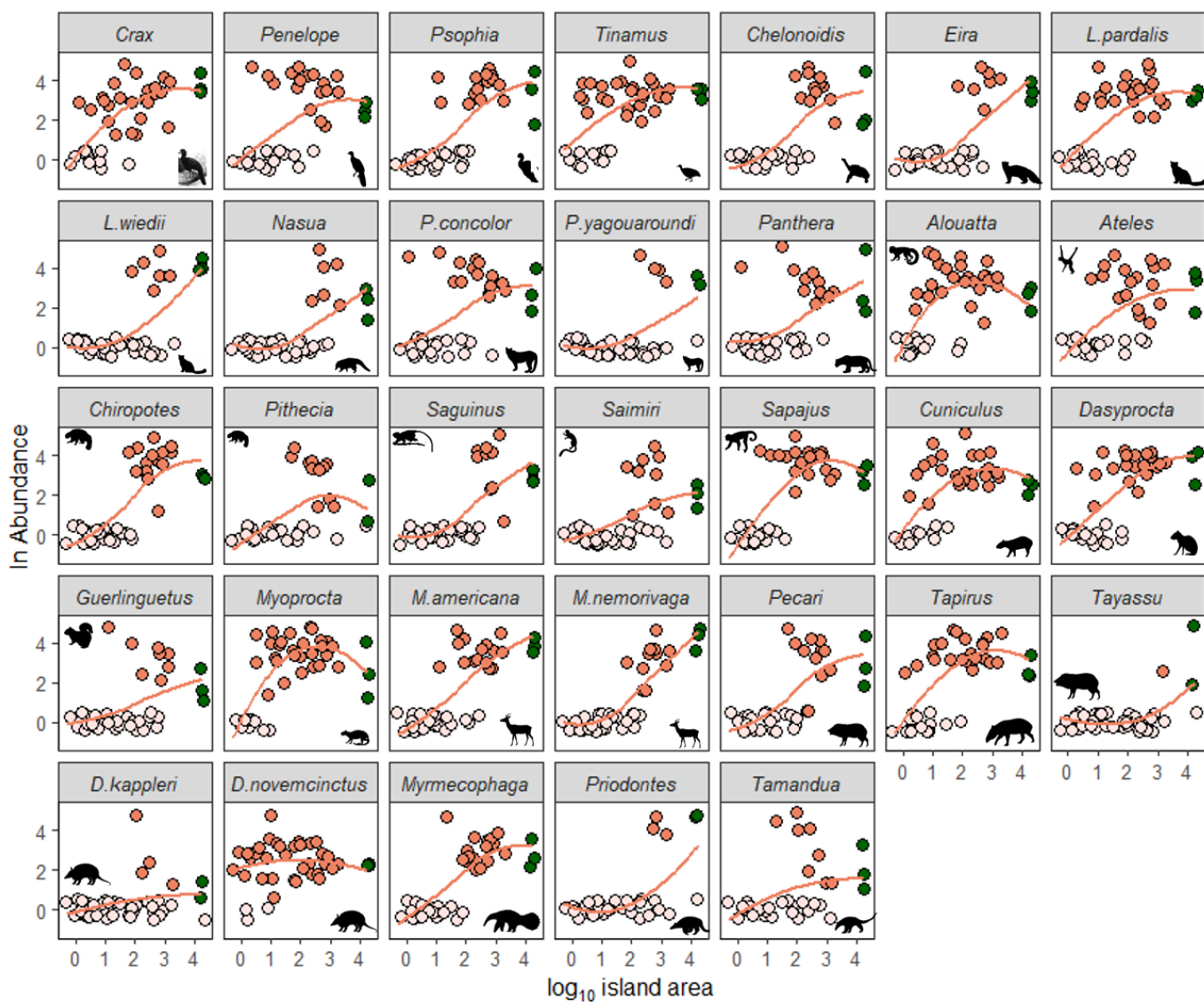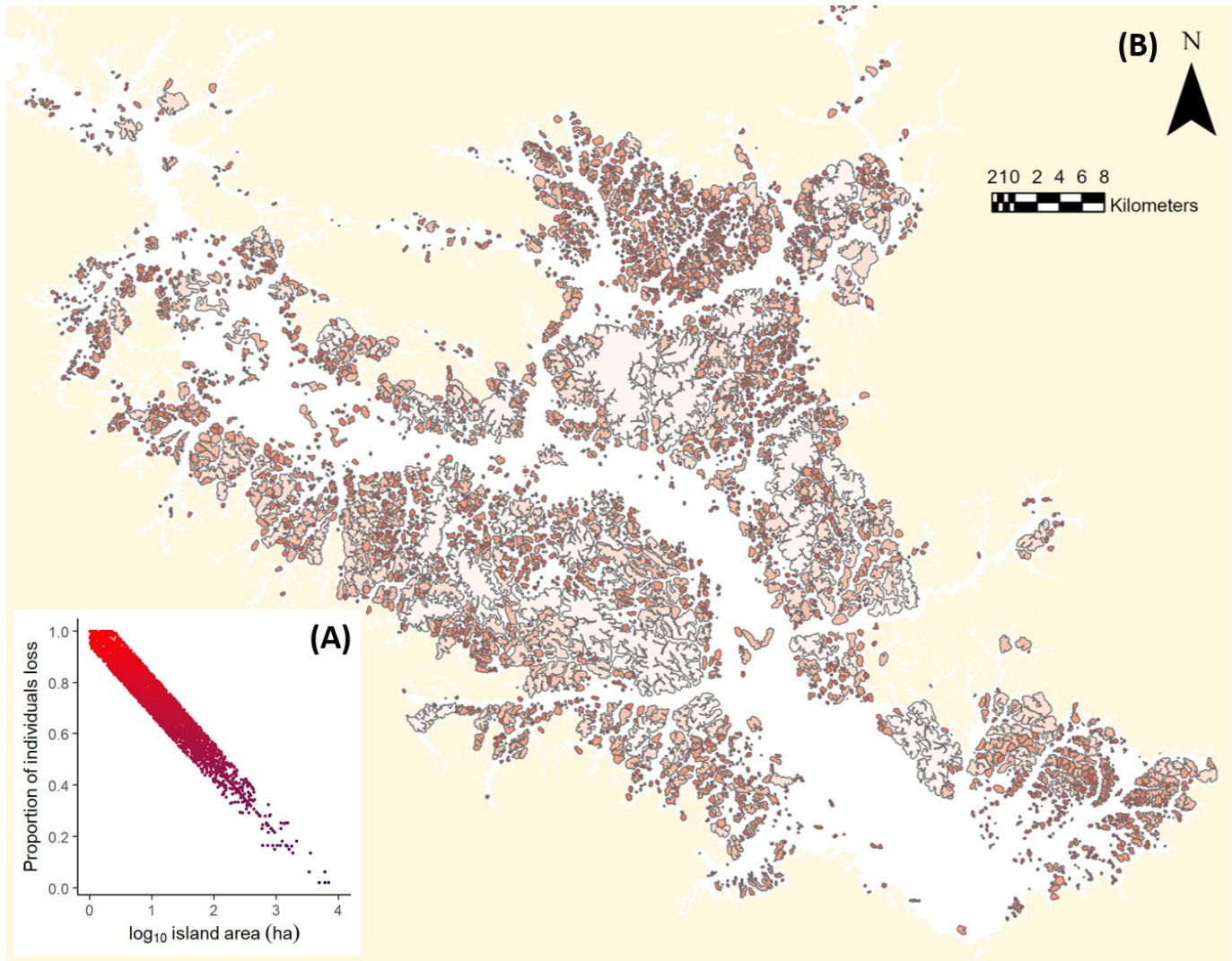
Figure 1

Figure 2

Figure 3

Figure 4

Figure 5