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

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Abstract: Megadams 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 approximately 3500 variable-sized islands that still harbor vertebrate populations after nearly 3 decades after isolation. 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 3 continuous forest sites throughout the Balbina archipelago. We conducted 1168 km of diurnal censuses and had 12,420 camera-trapping days along 81 transects with 207 camera stations. We determined the number of individuals (or groups) detected per 10 km walked and the number of independent photographs per 10 camera-trapping days, respectively, for each species. We recorded 34 species, and patch area was the most significant predictor of vertebrate population relative abundance and aggregate biomass. The maximum group size of several group-living species was consistently larger on large islands and in continuous patches than on small islands. Most vertebrate populations were extirpated after inundation. Remaining populations are unlikely to survive further ecological disruptions. If all vertebrate species were once widely distributed before inundation, we estimated that approximately 75% of all individual vertebrates were lost from all 3546 islands and 7.4% of the animals in all persisting insular populations are highly likely to be extirpated. Our results demonstrate that population abundance estimates should be factored into predictions of community disassembly on small islands to robustly predict biodiversity outcomes. Given the rapidly escalating hydropower infrastructure projects in developing counties, we suggest that faunal abundance and biomass estimates be considered in environmental impact assessments and large strictly protected reserves be established to minimize detrimental effects of dams on biodiversity. Conserving large tracts of continuous forests represents the most critical conservation measure to ensure that animal populations can persist at natural densities in Amazonian forests.

Keywords: Amazon, homeotherms, hydroelectric, island biogeography, mammals, population abundance

Determinantes de la Persistencia Poblacional y la Abundancia de Vertebrados Terrestres y Arbóreos Varados en Islas con Puentes Terrestres en los Bosques Tropicales

Resumen: Las megapresas se encuentran entre los causantes modernos de la pérdida de hábitat y biodiversidad en las economías emergentes. La Presa Hidroeléctrica Balbina de la Amazonia central en Brasil inundó 312, 900 ha de bosques primarios y creó ~3500 islas de tamaños variables que todavía albergan poblaciones de vertebrados

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después de casi tres décadas de aislamiento. Estimamos la riqueza de especies, abundancia, biomasa, composición y tamaño grupal de los vertebrados de talla mediana a grande del bosque como respuesta a la a las medidas de calidad del fragmento, paisaje y hábitat en 37 islas y tres sitios de bosque continuo en todo el archipiélago de Balbina. Realizamos censos diurnos a lo largo de 1,168 km y tuvimos 12,420 días de trampeo con cámaras a lo largo de 81 transectos con 207 estaciones de cámara. Determinamos el número de individuos (o grupos) detectados en cada diez kilómetros recorridos y el número de fotografías independientes para cada diez días de trampeo con cámara, respectivamente, para cada especie. Registramos 34 especies y el área del fragmento fue el pronosticador más importante de la población de vertebrados en relación con la abundancia y la biomasa agregada. El tamaño grupal máximo de varias de las especies gregarias fue sistemáticamente mayor en las islas grandes y en los fragmentos continuos que en las islas pequeñas. La mayoría de las poblaciones de vertebrados fueron extirpadas después de la inundación. Las poblaciones remanentes tienen pocas probabilidades de sobrevivir más perturbaciones ecológicas. Si todas las especies de vertebrados tuvieron alguna vez una distribución amplia previa a la inundación, estimamos que se perdió ~75% de todos los vertebrados individuales en todas las 3, 546 islas y el 7.4% de los animales en las poblaciones insulares remanentes tienen una alta probabilidad de desaparecer. Nuestros resultados demuestran que las estimaciones de abundancia poblacional deberían incluirse en las predicciones del desmontaje comunitario en islas pequeñas para predecir con solidez los resultados de biodiversidad. Ya que cada vez existen más proyectos de infraestructura hidroeléctrica en los países en desarrollo, sugerimos que las estimaciones de abundancia de fauna y de biomasa sean consideradas en las evaluaciones de impacto ambiental y que se establezcan grandes reservas con protección estricta para minimizar los efectos dañinos que tienen las presas sobre la biodiversidad. La conservación de grandes tramos continuos de bosque representa la medida de conservación más crítica para asegurar que las poblaciones animales puedan persistir con densidades naturales en los bosques de la Amazonia.

Palabras Clave: abundancia poblacional, Amazonia, biogeografía de islas, hidroeléctrica, homeotermos, mamíferos

Introduction

Both island and continental biotas worldwide have succumbed to unprecedented losses; current extinction rates are nearly 1000 times higher than the prehuman background rate (Pimm et al. 2014). Regional extirpation processes result from cumulative local extinctions; average decline in vertebrate populations worldwide since 1970 is 60% (WWF 2018). Steep declines in species occupancy and abundance, which are often considered hallmarks of defaunation (Dirzo et al. 2014), have been driven by myriad anthropogenic activities that have induced wide-scale ecological impacts. In particular, habitat loss and fragmentation accelerate biodiversity decay, especially for forest biotas sensitive to habitat disturbance (Hanski 2015). For instance, nearly three quarters of the world's remaining forests lie within 1 km of a forest edge, which threatens 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 2015*a*). However, fluctuations in small numbers of individuals persisting in local populations can lead to rapid acceleration of negative effects and increase severity of negative effects on ecosystem functions; thus, they provide a 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 bioindicators 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 hyperdiverse 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 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 that explain local vertebrate assemblages in fragmented landscapes (Michalski & Peres 2005; Benchimol & Peres 2013, 2015*a*). However, the size of vertebrate populations persisting in forest patches is rarely assessed, and abundance–area relationships (AARs) 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. 2000). Abundance estimates can therefore enhance understanding of population viability and the effects of anthropogenic disturbances on insular vertebrate populations, especially in hyperfragmented 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 have been extirpated at massive rates on Amazonian forest islands formed in the aftermath of dam construction (Benchimol & Peres 2015*a*, 2015*b*; Tourinho et al. 2020). In particular, most arboreal and terrestrial species have been extirpated from large numbers of small islands that are human-made archipelagos (Benchimol & Peres 2015*b*), yet the status of extant insular populations remains poorly investigated. Given that there are currently 191 dams and another 243 have been proposed for construction by 2024 across the Amazon basin (Lees et al. 2016), it is critical to assess population sizes in insular areas to better understand their demographic viability in areas affected by megadams.

We quantified the local abundance of 34 vertebrate species in forest sites to evaluate the species-specific responses to habitat insularization induced by a mega hydroelectric dam in central Amazonia. For this we used 2 sampling techniques to survey a wide range of forest vertebrate species, including mammals, large birds, and tortoises, on 37 variable-sized islands and 3 mainland sites. We also assessed 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 predicted the number of individuals lost in all vertebrate populations and the number of populations that are likely to be extirpated 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) (Appendix S1). The Balbina Dam was built in 1986 by impounding the Uatumã River, flooding 312,900 ha and creating 3,546 islands ranging in size from 0.2 to 4878 ha (Benchimol & Peres 2015*a*). In 1990 the left bank of the reservoir and the adjacent mainland continuous forests (CFs) were protected through the creation of the approximately 940,000-ha Uatumã Biological Reserve. The main vegetation type is submontane dense closed-canopy terra firme forests. Mean annual rainfall is approximately 2376 mm and mean temperature is 28 °C (Benchimol & Peres 2015*c*).

Vertebrate Surveys

Surveys were conducted at 37 variable-sized islands and 3 CFs (Appendix S1). Islands were selected on the basis of size (0.83–1690 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 from the nearest village. Both islands and CFs were unaffected by logging, but some of our study islands were affected by ephemeral understory fire during the 1997–1998 El-Niño drought, which affected several islands in the reservoir.

We collated a vertebrate species list (including terrestrial and arboreal species) expected to occur across the reservoir, which included 2 tortoise and nearly 40 forest mammal and bird species. To carry out vertebrate surveys, we established 1–5 variable-length (0.5–3.0 km) linear transects on each island and 3 parallel 4-km transects at each CF site, amounting to 81 transects (total length of 108.5 km) (Benchimol & Peres 2015*b*). We used line transect censuses (LTC) and camera trapping, which are widely recognized as the 2 most efficient sampling techniques to survey homeotherm vertebrates >500 g in tropical forests (Peres 1999; Michalski & Peres 2007). The LTCs were conducted 8 times at each site by 2 well-trained observers, who surveyed 1168 km following a standardized protocol (Peres 1999). For camera-trapping surveys, we deployed 2–15 digital-camera traps (CTs) (HC500-Hyperfire, Reconyx, Holmen, Wisconsin) at each sampling site, according to island size. Cameras were deployed over 2 continuous 30-day periods in consecutive years. The CTs were unbaited, placed 30–40 cm above ground, and spaced at least 500 m apart (except on very small islands). We deployed a total of 207 CT stations, total of 12,420 CT days (mean [SD] = 310.5 [251.83], range 120–900 CT days/site). All surveys were carried out from June 2011 to December 2012, and LTCs were never conducted at any site during CT 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 (RapidEye, Berlin, Germany) tiles that matched our field time (from March 2011 to September 2012) and exhibited low (<10%) cloud cover. After image processing and creating a mosaic, we used the maximum likelihood classification supervised method in ArcGIS to obtain 4 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 with our ground-truthed georeferenced data for each of our 4 land-cover classes and used the percentage of closed-canopy forest (CC%) in 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. The burn and (BA_{FF}) variables were estimated from floristic surveys based on 87 quarter-hectare plots inventoried at all survey sites (Benchimol & Peres 2015*c*).

At the patch scale, we measured total island area (area, $\log_{10} x$); distance between each focal island and the nearest CF (isolation); perimeter of focal islands divided by their total area (shape); and a modified proximity index (prox), which accounts for the total size and distance to any land mass (Benchimol & Peres 2015*a*), of 250, 500, and 1000 m (hereafter buffer areas) outside the perimeter of each site, given that multiscale 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 Analyses

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 LTC and 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 from 0.0 to 1.0. In those cases where the best technique failed to record a species within a certain site, we used the rescaled values obtained from another technique, therefore avoiding 0 estimates of species occurrences in a site where the species was indeed detected. Besides the abundance estimate of each species per site, we also estimated the overall vertebrate abundance at each site by summing all abundance estimates of all recorded species per site; 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 [2015*b*]) and thus obtaining the overall vertebrate biomass by summing all biomass estimates of all recorded species per site; overall species richness based on the sum of all species recorded with both techniques at each site; and species composition, defined as the first 2 nonmetric multidimensional scaling ordination axes based on the Bray–Curtis similarity matrix of abundance data for each sampling technique. All analyses were performed with 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 7 variables with variation inflation factors (VIF) that we derived using the HH package (Heiberger 2016). Given that prox was moderately redundant or collinear (VIF > 3) for all response variables, we excluded this variable in subsequent models. We ran all possible models and used model-averaged estimates in the MuMIn package (Barton 2018) to identify significant variables (i.e., $p \leq 0.05$). We also determined the relative importance of each variable (i.e., contribution of each variable to overall model variance) with hierarchical partitioning (HP), carried out in the hier.part package (Walsh & Mac Nally 2003). We performed GLMs considering only the 37 surveyed islands, including all 6 explanatory variables, and 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 4 response variables (overall abundance, overall biomass, richness, and composition), and the variable showing the highest HP in each GLM. For this, we performed a model-selection procedure and compared differences in Akaike information criterion (ΔAIC) to select the most parsimonious model (i.e., models exhibiting $\Delta\text{AIC} \leq 2.00$). In all cases, we tested 4 widely used models to investigate relationships in fragmented tropical landscapes: null (constant), linear, power law, and piecewise.

We calculated relativized abundance estimates for each species, based on the most efficient sampling technique for each species, by rescaling all abundance estimates from 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 based on 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 with the highest HP (i.e., the contribution toward explained variance) for abundance (i.e., 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. 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 with the highest HP to predict the viable aggregate relative abundance at all unsurveyed islands.

We investigated species-specific responses by examining the relationship between the variable presenting the highest explanation power and abundance estimates for each species, derived from its most efficient survey technique, and, 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 LTCs and the best group counts were derived from this census technique, we examined between-site variation in group sizes for social species based only on LTC data. All the statistical analyses were conducted with R (R Development Core Team 2018).

Results

Overall, we recorded 34 vertebrate forest-dwelling species, including from mammal, bird, and reptile families belonging to different threat categories (Table 1). Ten species were recorded only from LTC, 6 were recorded only from CTs, and 18 were recorded from both techniques (Table 1). Fourteen species were best detected in LTC and 20 species were best detected with CT.

For all 6 explanatory variables at all 37 surveyed islands, the GLMs showed that area was the most significant predictor of species richness, overall abundance, overall biomass, and species composition. Island size had the highest explanatory power in HP analysis (Appendix S3). Only fire was a significant predictor of species composition for LTC, albeit with a lower fraction of HP. The same pattern was observed with GLMs of all 40 surveyed sites. Island area was the only variable included in these models, and it 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 area and all 4 response variables (Appendix S3). Piecewise and linear models performed equally well 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 explained patterns of species composition based on LTC data. Linear and power-law models best explained patterns of abundance and biomass based only on CT data, whereas the power-law and piecewise models best explained species richness with data from both survey techniques (Appendix S4).

Both 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 as island area increased (Figs. 1a & 1c), so large islands and CFs had the largest animal numbers (Figs. 1b and 1d). 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 composed of a small set of species exhibiting low abundances—including the nine-banded armadillo (*Dasypus novemcinctus*) (n = 11 islands), the Great Tinamou (*Tinamus major*, n = 7), and Black Curassow (*Crax alector*) and howler monkey (*Alouatta macconnelli*, n = 6) (Fig. 2). The abundance of all vertebrate species, except for the nine-banded armadillo, substantially increased as island size increased (Fig. 3).

We used parameters obtained from the linearized model with all 37 islands to predict aggregate relative abundance of all unsurveyed 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 likely had lost most of their collective population sizes across the entire archipelago. Based on our assumption that all vertebrate species were once widely distributed across the reservoir area before flooding, there was a drastic loss in overall numbers of individuals across all islands (Fig. 4). We estimated a relative loss of 61.7% (28,499 of 46,176) of all individuals on the surveyed islands. This level increased to 74.3% (32,874 of 44,254) of all individuals when extrapolated to all 3546 islands across the archipelago. Only 10 large islands (>1200 ha) in the entire archipelago could harbor healthy population sizes across all vertebrate species; CFs served as the main regional-scale refugia of vertebrate assemblages (Fig. 4).

Based on the assumption that populations across all sites below the 25th percentile of abundance could not meet a minimum viability threshold, one quarter of the populations of 8 species in our 40 sites (howler monkey, spider monkey [*Ateles paniscus*], golden-handed tamarin [*Saguinus midas*], squirrel monkey [*Guerlinguetus aestuans*], lowland paca [*Cuniculus paca*], collared peccary [*Pecari tajacu*], Black Curassow, and Marail Guan [*Penelope marail*]) are likely to be extirpated, and several other species are vulnerable to many additional extirpations 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), a result that contrasted with our observed aggregate relative abundances. When all reservoir islands were

Table 1. The 34 vertebrate species recorded in 37 forest islands across the Balbina archipelagic landscape and 3 neighboring mainland sites in Brazil and the sampling techniques used to quantify relative abundance of each species.

Taxonomic group	*Scientific name*	*English common name*	*IUCN*[a]	*Bodymass (kg)*[b]	*Sampling technique*[c]		*Observed occurrence*	*No. populations highly likely to be extirpated (%)*
					line transect censuses	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 yagouaroundi*	jaguarundi	LC	6.75	×	*	6	0 (0)
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*	9-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)

Continued

Table 1. Continued.

Taxonomic group	*Scientific name*	*English common name*	*IUCN*[a]	*Bodymass (kg)*[b]	*Sampling technique*[c]		*Observed occurrence*	*No. populations highly likely to be extirpated (%)*
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 midas*	golden-handed tamarin	LC	0.54	*		12	3 (25)
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)

[a] *Abbreviations: DD, data deficient; LC, least concern; VU, vulnerable; NT, near threatened. Classification based on IUCN (2019).*

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

[c] *Asterisk (*), abundance estimates not made due to low number of records; ×,* Chelonoidis carbonaria *and* C. denticulata *pooled given that they could not always be identified to species and their strong ecological similarities.*

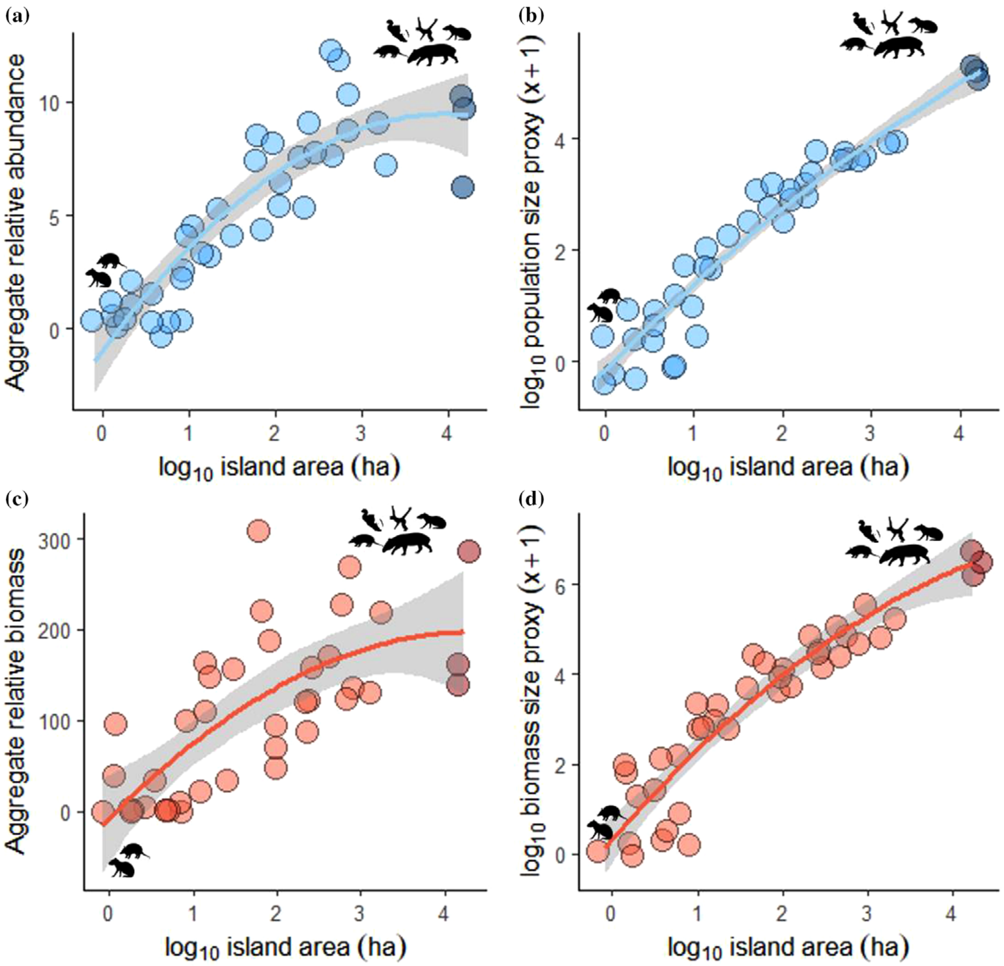

Figure 1. Relationships between forest patch (island and mainland) area and (a) aggregate relative abundance, (b) population size (proxy aggregate relative abundance × island area), (c) aggregate relative biomass, and (d) biomass density (proxy aggregate relative biomass × island area) for 37 islands and 3 continuous forest sites across the Balbina landscape (shading, 95% CI).

considered, we found that 7.4% (918.7 of 12,399.3) of the extant individuals across all insular populations are likely to be extirpated.

The maximum group size of several social species was consistently larger on increasingly larger islands and CFs (Fig. 5). In particular, significantly smaller group sizes were found on small islands for howler monkeys ($R^2 = 0.395$, $p = 0.000$), spider monkeys ($R^2 = 0.267$, $p = 0.019$), bearded saki monkeys (*Chiropotes sagulatus*) ($R^2 = 0.416$, $p = 0.008$), and brown capuchin monkeys (*Sapajus apella*) ($R^2 = 0.293$, $p = 0.008$). Collared peccaries also showed a similar pattern of reduced herd sizes on small islands ($R^2 = 0.202$, $p = 0.147$).

Discussion

Our results clearly showed that the vast majority of islands created by a vast hydroreservoir retained only a few vertebrate species that collectively had small population sizes and low overall biomass density and that these differences were primarily driven by habitat area effects. Island size also largely explained patterns of conspecific group size of several social species. These patterns indicated 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 2015*b*), we found that more severe area effects can be detected only when local population abundance and AARs are quantified. In considering the overall numerical losses (in terms of relative numbers of individuals) across all populations, we found that nearly three quarters of all vertebrate populations are likely to be extirpated throughout the reservoir. These substantial population losses are

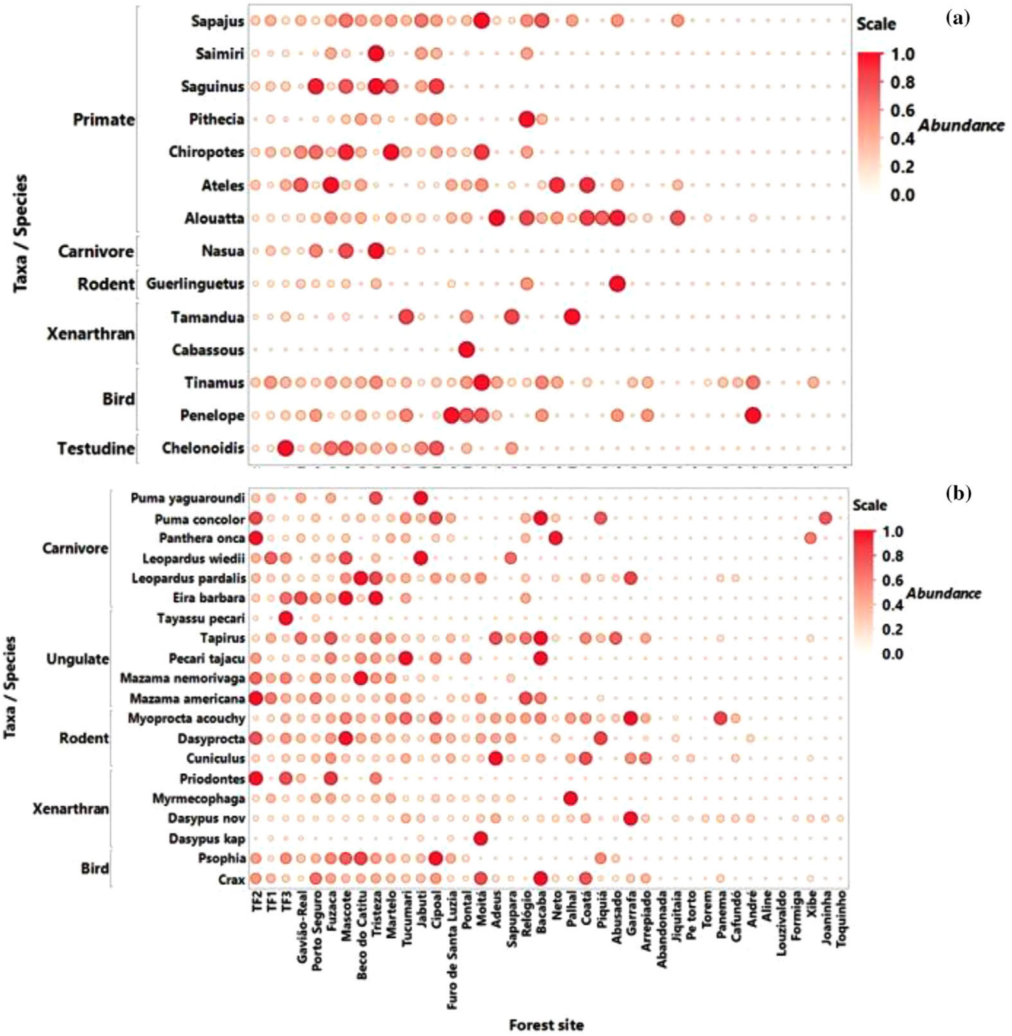

Figure 2. Species-by-site matrix of relative abundances based on the most efficient sampling method for each vertebrate species: (a) line transect censuses of mostly arboreal species and (b) camera trapping of terrestrial species (circle size, proportional to relative population abundances based on each method). Mainland and island sites are sorted according to forest area from left to right.

estimated despite 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 other scenario of typical offtake in rural Amazonia, we would expect a far worse outcome for isolated large vertebrate populations, which would be expected to be extirpated due to the synergistic effects of small habitats and 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 disruptions of ecosystem functions they may provide (Ceballos & Ehrlich 2002).

Our results showed 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. Overall abundance increased linearly as a function of island size beyond this area threshold. Given that half (50.3%) of all 3546 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 and cascading effects on ecosystem functioning. For instance, on Balbina islands smaller than 13 ha there were 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

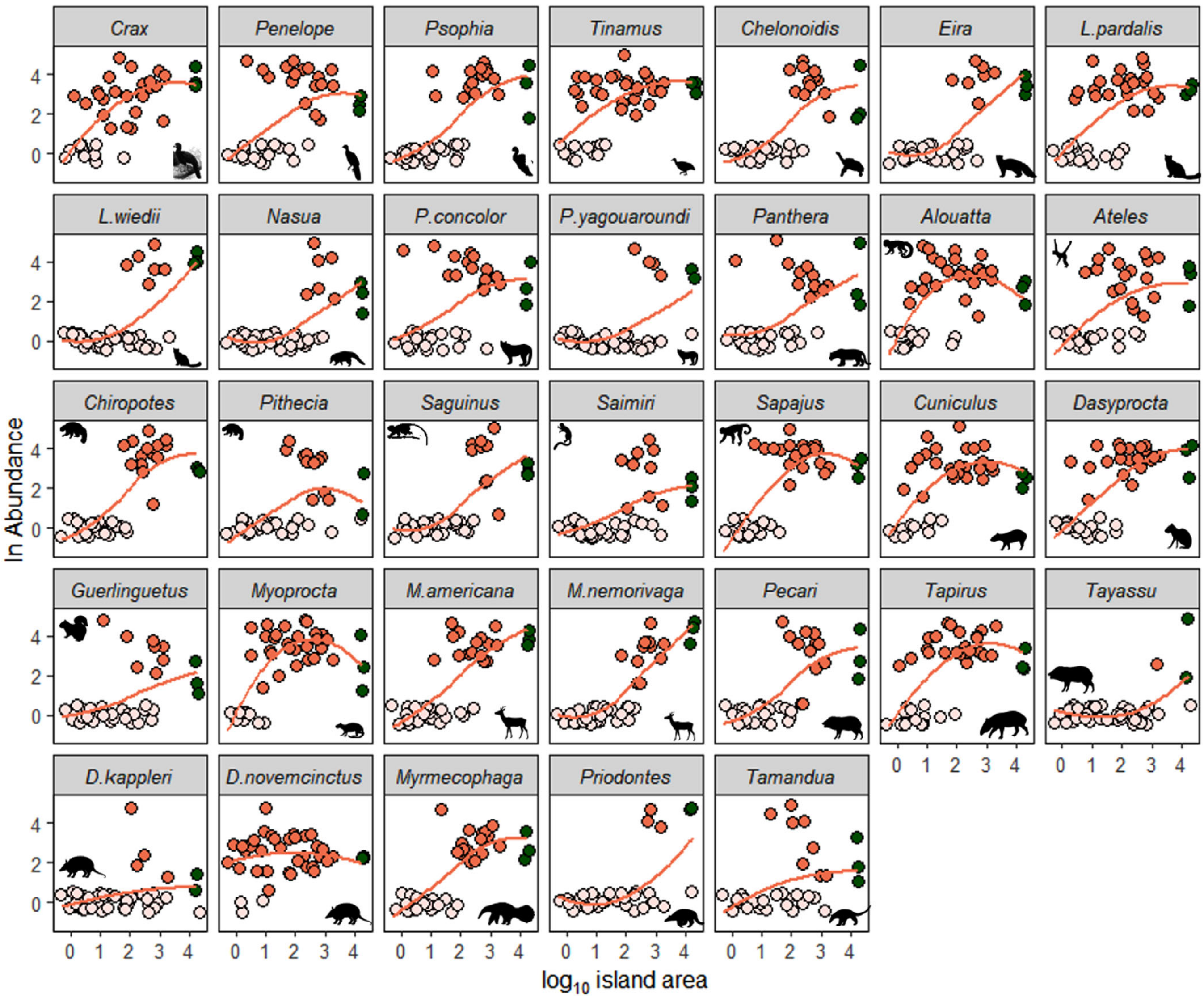

Figure 3. Abundance–area relationships defined in terms of the relativized population abundance estimates based on the most efficient sampling technique per species, considering all 40 forest sites surveyed throughout the Balbina archipelagic landscape (light pink, unoccupied sites; orange circles, insular populations; green circles, populations in continuous forest sites).

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; patches smaller than 15 and 55 ha retained an impoverished nested subset of each of these taxa, respectively. Therefore, our results provide evidence that preserving large tracts of unhunted 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; species either benefit from habitat modification or decline toward extirpation (Michalski & Peres 2007; Laurance et al. 2011). In Balbina, nearly all species either succumbed to local extinctions or exhibited extremely low relativized abundance estimates on small islands, which comprise the vast majority of islands within the reservoir. Nine-banded armadillo is an exception because it occurred in almost all surveyed sites and even exhibited overabundance on some islands. This ubiquitous species, which has been previously classified as area insensitive (Benchimol & Peres 2015*b*), has been recorded in much greater den-

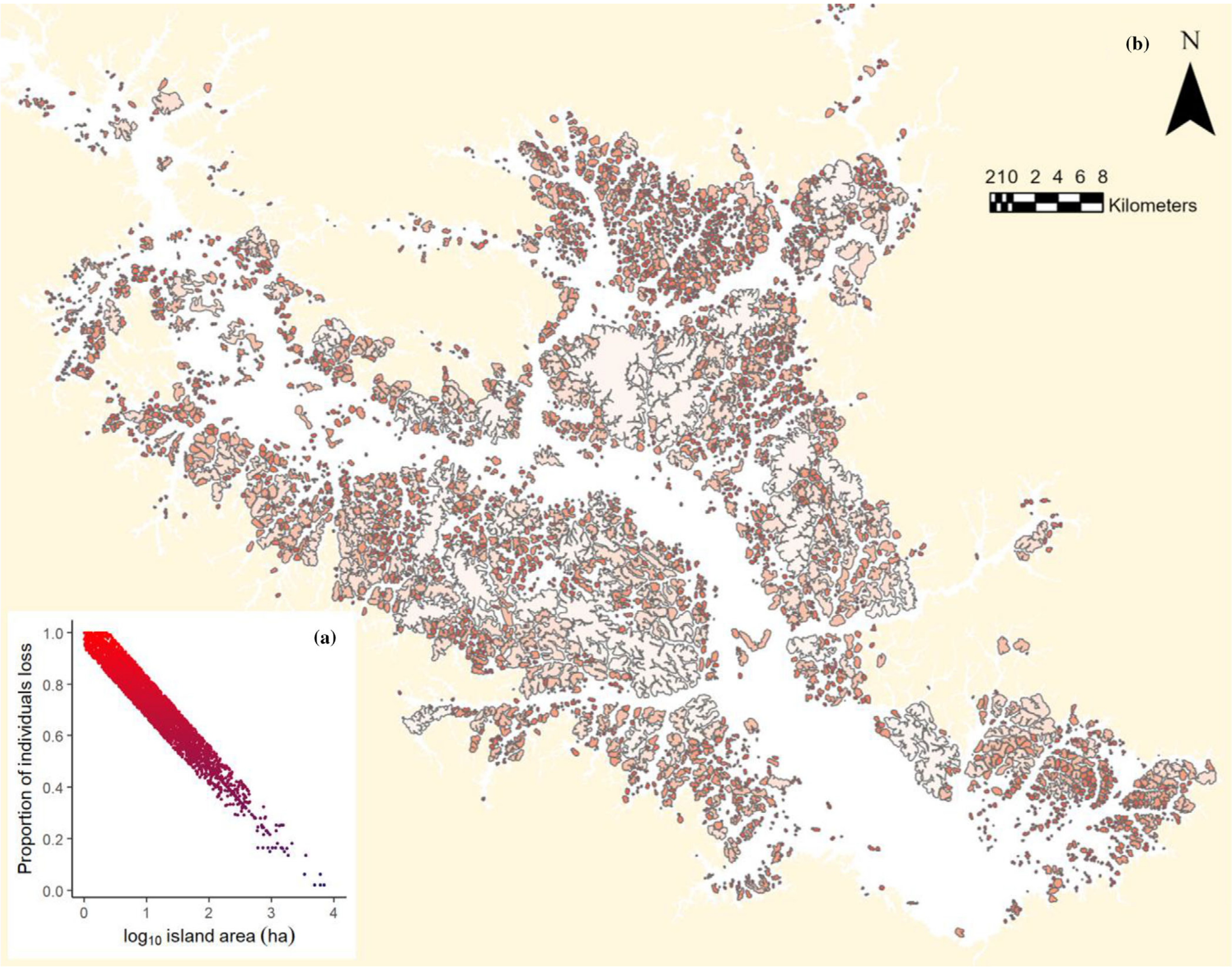

Figure 4. (a) Proportion of the relative number of all individuals across all species predicted to have been extirpated as a function of forest patch area modeled for all 3546 forest islands across the Balbina archipelagic landscape and (b) level of overall losses of individuals based on all populations (losses increase from yellow to red) and on empirical estimates derived from the 37 surveyed islands.

sities 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 with CF sites. 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 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. Furthermore, swimming capacity and therefore the probability of traversing the open-water matrix between islands varied substantially among species (Benchimol & Peres 2015*b*), 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 with those exhibiting low or no vagility. On the basis of a comprehensive compilation of data on dispersal events (Benchimol & Peres 2015*b*), many species are indeed observed swimming across islands in Balbina. Across all species, however, the number of populations likely to be extirpated was positively associated with dispersal capacity across open water (Spearman rank correlation = 0.476).

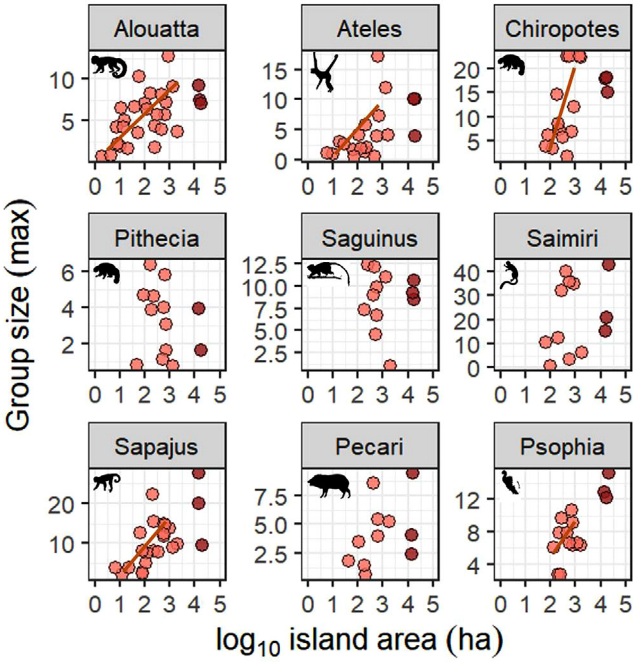

Figure 5. Relationships between island size and maximum observed group sizes for all social species based on the largest number of individuals recorded during any line transect census provided that any given species was recorded at least once (darker circles, continuous forest sites).

Species showing the highest proportions of populations likely to be extirpated (Table 1), such as collared peccary and terrestrial birds, could be rescued by successful colonization events provided patch area sufficient and habitat quality is high.

Island size also affected the maximum operational group size of several social species, such as primates and Gray-winged Trumpeters (*Psophia crepitans*); large groups typical of continuous sites were apparently suppressed on small islands. Group size comprises a trade-off between the costs of reduced foraging efficiency and the benefits of reduced predation risk (Pulliam & Caraco 1984); large groups are 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 CF. In fact, tree assemblages on small Balbina islands were species poor and functionally impoverished (Benchimol & Peres 2015*c*), 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 effect of small group size may have 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 rather depress the size of breeding populations, ultimately reducing demographic viability.

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 are either extirpated or retained in small numbers in most reservoir islands. We previously found that most species are absent on small forest islands after 25 years of isolation, including invertebrates and vertebrates (Benchimol & Peres 2015*a*, 2015*b*; Palmeirim et al. 2018; Tourinho et al. 2020). Our new findings consistently showed that population sizes and biomass density were generally low on most islands even for those species that had somehow avoided extirpation 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 were forest specialists; correlated effects of island size and habitat degradation (Benchimol & Peres 2015*c*) further affected 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 functioning of newly formed land-bridge islands will likely be strongly compromised. Other planned or large dams under construction in lowland Amazonia are also located in relatively flat terrains, which creates shallow lakes inundating extensive areas where ridgetop archipelagos will be largely composed of small islands (Fearnside 2014). As shown here, these small islands will likely be subject to severe defaunation of area-sensitive species, resulting in massive population declines if not extirpations. We therefore suggest that policy makers 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 in environmental impacts assessments 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 functioning 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 of charismatic large vertebrate fauna.

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Supporting Information

Additional information is available online in the Supporting Information section at the end of the online article. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. Data are available on Figshare (https://doi.org/10.6084/m9.figshare.12996686.v1).

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