



# Predicting local extinctions of Amazonian vertebrates in forest islands created by a mega dam



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## ABSTRACT

Hydropower projects are rapidly expanding across lowland Amazonia, driving the conversion of large tracts of once-continuous forests into archipelagos embedded within a vast open-water matrix. Forest vertebrate populations thus become stranded in habitat islands, with their persistence governed by a combination of species life-history traits, habitat patch, and landscape context. We investigate the patterns of species extinction of 34 arboreal and terrestrial vertebrate species within three continuous forest sites and 37 land-bridge islands within one of the largest South American hydroelectric reservoirs, based on a combination of camera trapping, line-transect censuses, sign surveys, and armadillo burrow counts. Forest area was the best predictor of species persistence, so we classified all species into three levels of vulnerability to habitat insularization, with most species defined as 'area-sensitive'. However, island occupancy was decisively determined by individual species traits, with wide-ranging species and poor dispersers showing high local extinction rates. We detected higher island occupancy rates of large vertebrate species compared to other Neotropical fragmented forest landscapes, suggesting that this is critically attributed to the absence of hunting pressure at Balbina. Nevertheless, most terrestrial and arboreal species have been driven to local extinction within the vast majority of islands, which have been largely defaunated. We predicted species composition across all 3546 islands within the reservoir, indicating that only  $\leq 2\%$  of all islands continue to harbour at least 75% of all species. To minimise loss of vertebrate diversity, future hydroelectric dam projects in lowland tropical forests, if unavoidable, should consider their geographic location and landscape structure to maximise both island size and landscape connectivity, and set aside strictly protected reserves within reservoir areas.

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## 1. Introduction

Mega hydroelectric dams have become a major driver of forest habitat loss and fragmentation across several Amazonian river basins, with dozens of new major hydropower projects either planned or currently under construction (Finer and Jenkins, 2012; Fearnside, 2014). In Brazilian Amazonia, a total of 1,105,400 ha of pristine forests have already been inundated by eleven major hydroelectric dams (ECO, 2012), but over 10 million ha of forests are expected to become permanently inundated following the planned construction of new dams (Fearnside, 2006). Assessments of the social and environmental impacts of large dams

worldwide have so far primarily focused on flooding of indigenous territories and displacements of local communities (Esselman and Opperman, 2010), alterations in fluvial hydrology (Nilsson et al., 2005), augmented emissions of greenhouse gases (Almeida et al., 2013), and losses in fisheries and aquatic biodiversity (Barthem et al., 1991; Alho, 2011; Liermann et al., 2012; Palmeirim et al., 2014). In contrast, the performance of terrestrial vertebrate populations in tropical ecosystems affected by dams has received comparatively little attention (but see Terborgh et al., 1997; Cosson et al., 1999; Gibson et al., 2013; Benchimol and Venticinque, 2014). Given hugely escalating investments in hydropower infrastructure worldwide, impact assessments of mega-dams on terrestrial biodiversity in many terrestrial systems, including the Amazonian basin, are conspicuously missing.

As mega-consumers and apex predators, large-bodied vertebrates are often considered as good bioindicators of intact tropical forests, as they provide key ecological services for ecosystem dynamics and are sensitive to forest disturbance and hunting

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(Dirzo et al., 2014). Local extinctions from forest patches can induce a series of trophic cascades, promoting unexpected shifts in forest composition and function. For instance, predator-free land-bridge islands in Venezuela are typically denuded by hyper-abundant herbivores, decimating seedling recruitment of canopy trees (Terborgh et al., 2001). Also, rising floodwaters drastically reduced vertebrate species diversity in newly formed islands compared to continuous forest areas only four years after French Guiana's Petiti Saut Dam was built (Cosson et al., 1999), suggesting that isolation effects in true islands are more severe than in habitat patches surrounded by a non-water matrix.

Newly isolated vertebrate assemblages could undergo nonrandom drifts in species composition within tropical land-bridge islands following a long relaxation time, but this is a function of species-specific responses to patch- and landscape-scale variables and life-history traits. Vertebrate persistence in Neotropical fragmented landscapes is likely to be affected by landscape structure and the history of human disturbance (Michalski and Peres, 2005; Canale et al., 2012), with a range of species responses to habitat fragmentation. Rare, matrix-intolerant species unable to disperse amongst remnant patches are usually considered more extinction-prone in fragmented landscapes (Davies et al., 2000; Henle et al., 2004). Hence, some life-history traits can be excellent predictors of forest patch occupancy, and coupled with patch and landscape-scale site attributes, can help predict species survival within forest remnants and inform species-specific conservation guidelines.

Here, we assess how 34 terrestrial and arboreal vertebrate species responded to the insularization process induced by a major hydroelectric dam in lowland Central Amazonia, based on intensive, well-replicated field surveys in a large number of islands and neighbouring continuous forests. Specifically, we examine (1) the observed and estimated forest patch occupancy of each species (accounting for imperfect detection), assessing minimum critical area required to ensure their persistence; (2) how different patch, landscape and habitat quality metrics affect patterns of occupancy for individual species; and (3) the relative importance of landscape context and species traits in explaining pattern of local extinction across all islands. Based on these results, we predict the aggregate vertebrate species richness and composition across >3500 islands within the reservoir, pinpointing priority sites for conservation, and dissect how large hydroelectric dams affect terrestrial vertebrate diversity in lowland Amazonia.

## 2. Material and methods

### 2.1. Study area

This study was conducted within the Balbina Hydroelectric Reservoir (BHR), a man-made reservoir within the Uatumã River basin of central Brazilian Amazonia (1°48'S; 59°29'W). The Balbina Dam was completed in 1986 to supply hydropower to Manaus, the state of Amazonas capital city. The rising floodwaters inundated an area of 312,900 ha, resulting in the formation of 3546 land-bridge islands ranging in size from <1 to 4878 ha. In 1990, the lake became protected by the creation of the ~940,000-ha Uatumã Biological Reserve, the largest protected area of this type in Brazil. Most islands consist of dense closed-canopy *terra firme* forest. There is no history of logging nor hunting in the study area within the reservoir (Benchimol and Venticinque, 2014), but many islands experienced ephemeral understorey fires during the El Niño drought of late-1997 to early-1998 (Benchimol and Peres, 2015).

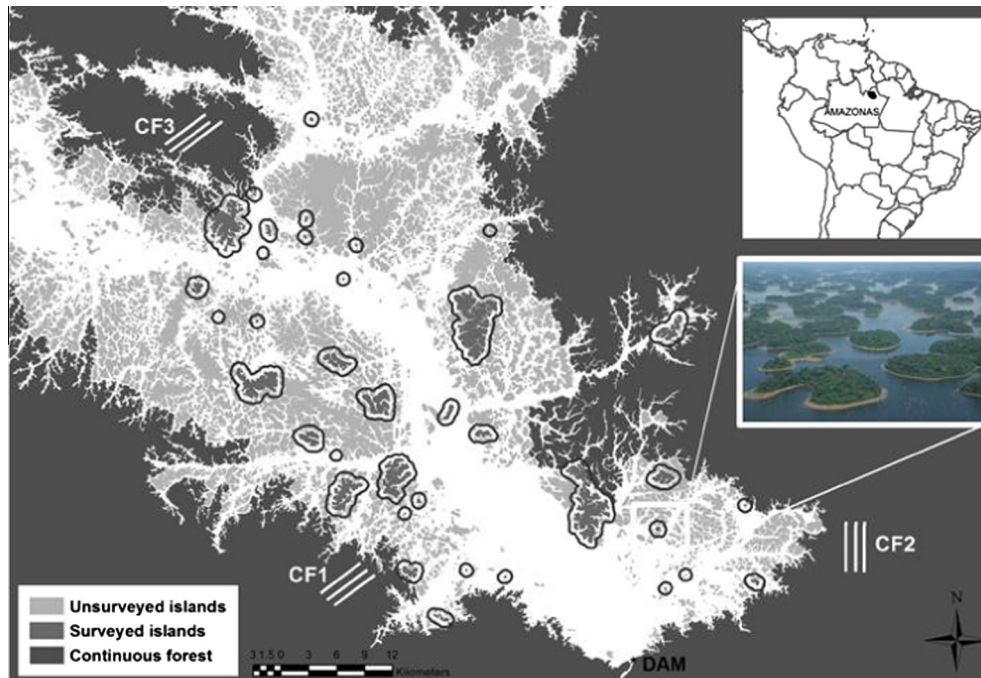
We conducted intensive vertebrate surveys within a subset of 37 islands and three widely spaced neighbouring continuous forest sites adjacent to the lake, which were spaced by at least 1 km from one another, spanning a study area of 396,400 ha (Fig. 1). Islands

were selected on the basis of their size, isolation and spatial distribution, to represent a wide range of island configurations within the reservoir. We assigned arbitrary area values of one order of magnitude greater than our largest island for mainland continuous forest sites. Surveyed islands ranged in forest area from 0.55 to 1685.38 ha, and isolation distances from each focal island to the nearest mainland continuous forest ranged from 40 m to 17.73 km (Table 1).

### 2.2. Vertebrate sampling

We used a combination of four different sampling techniques to determine occupancy of the midsized to large-bodied vertebrate fauna at each island and mainland site between June 2011 and December 2012: camera trapping, line-transect censuses, sign surveys, and armadillo burrow counts. These methods were selected considering the wide range of ecological and behavioural characteristics of target species, with different activity times (diurnal, nocturnal and cathemeral), and use of vertical space (terrestrial, arboreal and scansorial). Indeed, all of these methods have been widely used for quantitative surveys (see Silveira et al., 2003; Michalski and Peres, 2007; Munari et al., 2011; Thornton et al., 2011a, 2012). Although nocturnal line transect censuses have been used as a complementary wildlife survey technique in tropical forests, this provided little additional information for most nocturnal species in a pristine Amazonian landscape (Munari et al., 2011) so we opted not to conduct night surveys on foot. We restricted surveys to non-flying medium- and large-bodied terrestrial and arboreal mammals (except sloths), terrestrial birds and tortoises, which were widely distributed across the study landscape. Only tortoise congeners (*Chelonoidis carbonaria* and *Chelonoidis denticulata*) were pooled under a single genus, given that they could not usually be identified to species and their strong ecological similarities. To facilitate surveys, we cut linear transects of 0.5–3 km in length at each island, according to island size and shape, so that a representative island area could be covered (see Table A1). On each continuous forest site, three parallel 4-km linear transects were established, separated from each other by 1 km (Fig. 1).

We deployed two to ten *Reconyx Hyperfire* camera traps (hereafter, CTs) at each island according to its size, and 15 CTs at continuous forest sites (five along each transect) to maximise the heterogeneity of environments sampled in each survey site and minimise variation in density of CT stations (Table A1; Michalski and Peres, 2007). In all sites, CTs were deployed for two continuous periods of 30 days each. We placed unbaited CTs 30 cm above ground along transects, spaced by at least 500 m (except for small islands). We configured each CT to obtain a sequence of five photographs for each animal or animal cluster recorded, using 15-s intervals between records. Additionally, we conducted eight visits including line-transect surveys per island, each of which at different times either in the morning (06:15 h to 10:30 h) or afternoon (14:00 h to 17:30 h), following standardised guidelines proposed by Peres (1999). Two trained observers walked quietly at a constant speed (~1 km/h) on all transects established on each site. We recorded all visual or acoustic encounters of individuals or groups of any target species. On return walks along each transect, we conducted sign surveys, intensively searching for any indirect evidence of any target terrestrial species, including tracks, superficial digging, burrows, fecal material, hair, and partly consumed fruits/seeds. Finally, we searched for armadillo burrows to enhance our detection and identification of the four armadillo species occurring in the study area. In doing so, we searched all burrows ≥50 cm depth within a 5-m strip either side of each transect and measured them following Michalski and Peres (2007). This was done during return census walks, but only once per transect per survey session, during the first day of censuses. In total,



**Fig. 1.** Distribution and size of the 37 land-bridge islands (grey) and three mainland undisturbed continuous forest (CF) sites (CF1, CF2 and CF3; dark grey) surveyed using several methods within the Balbina Hydroelectric Reservoir (BHR) landscape of Amazonas, Brazil. Black contours indicate 500-m buffer polygons around each island. All unsurveyed islands are shown in light grey. A group of small islands are shown in the inset aerial photograph (photo credit: E. M. Venticinque).

we obtained 12,420 CT-days (mean [SD] = 310.5 [251.83], range = 120–900 CT days/site) from 207 camera trap stations; 1168 km of total line-transect census effort (including 592 km in islands and 576 km in continuous forest sites); 1168 km of sign surveys; and 217 km of armadillo-burrow counts (Table A1).

### 2.3. Landscape structure and habitat quality variables

We used RapidEye© high-resolution (5-m pixel) imagery for the entire BHR landscape to quantify forest patch and landscape metrics, and forest habitat quality of all surveyed sites. We selected RapidEye© tiles on the basis of low cloud cover (<10%) and months matching our field sampling. A total of 28 tiles covering an area of 698,000 ha, available from March 2011 to September 2012, were processed. At the patch scale, we measured total island (SIZE) and total forest area (AREA), both as  $\log_{10}X$ ; the distance between each focal island and the nearest continuous forest (ISOLATION); the perimeter length of focal islands divided by the total island area (SHAPE); and modified the proximity index of McGarigal et al. (2012) by considering the total size of any land mass within the buffer, rather than excluding land areas outside the buffer for patches contained within the buffer (PROXIMITY; Table 1). All patch metrics were measured for all surveyed and unsurveyed islands within the reservoir. At the landscape scale, we considered multiple buffers (250 m, 500 m and 1000 m) outside the perimeter of each focal island and mainland forest sites and quantified both the percentage of total forest cover (COVER). We assigned a value one order of magnitude greater than our largest island (i.e., 16,900 ha) for every mainland continuous forest site included within a focal island buffer area. Finally, we considered three descriptors of forest habitat quality of each surveyed site: the understory burn or fire severity (BURN) on each island, measured as a composite ordinal score (0–3) based on both the number of charred trees, the height of char marks on each burnt tree, and the extent to which each island/mainland site had been affected by fires (see Benchimol and Peres, 2015); the percentage of closed-forest canopy (cc%) within each surveyed site, following a

semi-supervised image classification using ArcMap (version 10.1) to obtain four land cover classes (closed-canopy forest, open-canopy forest, bare ground, and water); and the aggregate basal area of all trees  $\geq 10$  cm diameter at breast height bearing fleshy fruits ( $BA_{ff}$ ), estimated from floristic surveys based on 87 quarter-hectare forest plots inventoried at all forest sites [see Benchimol and Peres (2015) for details, Table 1 and Table A1].

### 2.4. Species traits

We performed a literature search using Google Scholar with various combinations of traits and species as keywords, to obtain five morpho-ecological traits: body mass, group size, home range size, diet category and ranked trophic status for all vertebrate species considered here (Table 2). These species traits are commonly associated with susceptibility to habitat fragmentation in Neotropical mammals (Henle et al., 2004; Ewers and Didham, 2006; Urquiza-Haas et al., 2009; Thornton et al., 2011b; Benchimol and Peres, 2014). Values from studies conducted within Amazonian continuous forests were obtained for most species; mean values were calculated if two or more studies were available. However, values from extra-Amazonian Neotropical sites were used for species traits that were unavailable for any Amazonian landscape. In total, we obtained a full set of ecological attributes from 28 different studies (Table A2).

We also derived a species-specific index of water matrix dispersal (swimming) capacity based on the number of times each species had been observed traversing the water body anywhere on the Balbina Lake. This was based on systematic interviews conducted with boatmen, sports fishermen, and the Uatumã Reserve surveillance staff at Vila Balbina who had frequently navigated the lake over many years. As a precondition, the interviewee had previously travelled on the lake during at least 30 days per year. A total of 49 informants were independently interviewed from September to December 2012. During interviews, we presented colour plates and photographs of each of the 34 species individually, asking if and how often each interviewee had ever seen that

**Table 1**  
Patch, landscape and habitat quality variables considered in the analyses.

Variable name	Code names	Type	Description	Range (mean $\pm$ SD)
Size	SIZE	Patch	Total island area of each focal island	0.83–1690.04 ha (210.67 $\pm$ 392.08)
Area	AREA	Patch	Total forest area within each focal island	0.55–1685.38 ha (209.06 $\pm$ 390.04)
Isolation	ISOLATION	Patch	Euclidean distance from each island to the nearest neighbouring mainland forest site	0.04–17.43 km (4.87 $\pm$ 4.41)
Shape	SHAPE	Patch	Total perimeter length of each focal island divided by the total island area	0.004–0.106 (0.017 $\pm$ 0.019)
Proximity	PROXIMITY	Patch	Represents the sum of all island areas divided by the squared edge-to-edge distances from each focal island to all islands within a specified buffer. Instead of considering the area of each island within the buffer (as in McGarigal et al., 2012), we considered the total (“true”) area of each island. Buffer threshold considered in the final analysis: 500 m	0.0–9.65 (3.17 $\pm$ 1.97), (log <sub>x</sub> + 1)
Forest cover	COVER	Landscape	Percentage of forest cover within a 500-m buffer	0.0–56.1% (30.55 $\pm$ 16.72)
Fire severity	BURN	Habitat quality	Fire severity within each focal island or mainland site, scored as an ordinal scale based on the extent of each forest site affected by fires and the number of charred trees and height of char marks on each tree	0–3 (2.05 $\pm$ 0.70)
Closed-canopy	cc%	Habitat quality	Percentage of closed-canopy forest within the focal island	0–100% (74.79 $\pm$ 20.93)
Basal area of fleshy-fruited trees	BA <sub>ff</sub>	Habitat quality	Basal area of trees bearing fleshy fruits, calculated from floristic surveys of all live trees $\geq$ 10 cm DBH in 0.25-ha forest plots within each focal island or mainland site	0.2–8.76 m <sup>2</sup> /ha (5.03 $\pm$ 1.52)

species traversing between islands or the mainland forest since the lake was created. Despite observer differences in the number of days per year spent on the lake and the number of years they had travelled on the lake, we assumed that all interviewees had the same probability of visually detecting a matrix dispersal event of any given species. Large-bodied species may have been more easily detected than small-bodied species (Pearson  $r=0.542$  between dispersal index and body mass) but correcting for true detectability is far from straight-forward here. We therefore summed all independently detected swimming events for each species to obtain an index of dispersal capacity over water (mean [SD] = 61.79 [87.06], range = 0–467; Table 2).

### 2.5. Data analysis

We first controlled for high levels of variable inter-dependence by performing a Pearson correlated matrix, retaining non-correlated variables ( $r < 0.70$ ). These were seven patch- and landscape-scale variables (area, isolation, shape, proximity defined as a 500-m buffer, fire severity, percentage of closed-canopy forest, and tree basal area bearing fleshy fruits) and five species traits (body mass, group size, home range size, dietary status, and water dispersal capacity). Some of these variables were log-transformed to normalise the data.

Second, we obtained the *observed site occupancy* for all vertebrate species considered here, based on the species detected by any of the four sampling techniques during any sampling session. Because false absences are likely to occur during surveys, we further obtained the *estimated site occupancy* using a maximum likelihood approach (MacKenzie et al., 2002), which computes the proportion of sites occupied accounting for detection probabilities  $< 1$ . We opted to use the *estimated site occupancy* values for further analyses, given that they improved island occupancy estimates. For this, we constructed a detection (1) and non-detection (0) matrix for each species per visit per site (40 sites), using data either combined from the three sampling techniques related to transects (line-transect, sign and armadillo surveys; hereafter, *transect data*) or only camera trapping surveys (hereafter, *CT data*). We opted to separate these two methodological approaches because they diverge markedly in the type of sampling visit. Visits were defined as a single day for transect data and 6 days

for CT data, resulting in 8 and 10 visit-sessions, respectively. Each species was then examined using either the transect or CT data, given that some species were either exclusively or most efficiently detected by only one method (e.g. arboreal species during line-transect censuses). For species detected by more than one method, we selected the method providing the highest detection probability and lowest variance in occupancy estimates – CT and transect data were used for 18 and 16 species, respectively (Table 3). Data from all transects and all CT stations per island or continuous forest were pooled together per visit. Using the PRESENCE© software (Hines, 2006), we then modelled both site occupancy and detection probabilities. We defined a set of simple models that we hypothesised might explain site occupancy and detection probability of vertebrate species, considering only a small number of covariates in each model because of the reduced data set (Burnham and Anderson, 2002). We therefore considered only one landscape structure variable in each model (i.e., one of seven non-correlated patch, landscape and habitat quality variables individually) to model site occupancy ( $\Psi$ ); and including sampling effort according to the method (number of km walked or CT-nights) to model the detection probability ( $p$ ), accounting for potential biases in unequal sampling in different survey sites. We also tested the null model, which assumes constant species presence and detection probability across time and sites [ $\Psi(\cdot)$ ;  $p(\cdot)$ ]. We used Akaike's Information Criterion (AIC) to rank models and to calculate Akaike weights (Burnham and Anderson, 2002) to indicate the best model in the candidate set. For those species exhibiting high dispersal capacity and large home range sizes, we interpret occupancy estimates as the probability of island use, rather than occupancy probability per se (MacKenzie et al., 2006; Thornton et al., 2011b).

We then performed logistic regression models based on the estimated site occupancy as a function of forest area, considering all species pooled together and each species individually. Based on these models, we further determined the minimum critical area required to ensure local persistence for each species, considering a threshold of occupancy probability of 60%. We opted to use a threshold  $>50\%$  as frequently adopted (see Benchimol and Peres, 2014) to enhance the probability of ensuring species occurrence. We thus predicted the proportion of all islands within the reservoir likely to contain any given species based on a 60% occupancy threshold.

**Table 2**

Critical area, percentage of islands expected to be occupied and species traits for 34 species within 37 islands at the BHR landscape.

Species	English vernacular name	Critical area <sup>a</sup> (ha)	% of islands expected to be occupied <sup>b</sup>	Species traits				
				Body mass <sup>c</sup> (kg)	Group size <sup>c</sup>	Home range <sup>c</sup>	Diet category <sup>c</sup>	Dispersal ability <sup>d</sup>
<i>Mammals</i>								
<i>Alouatta macconnelli</i>	Red howler monkey	4.46	73.38	6.15	8.2	53	1	77
<i>Ateles paniscus</i>	Black spider monkey	25.12	24.39	7.90	2.5	224	3	23
<i>Cabassous unicinctus</i>	Southern naked-tailed armadillo	151.36	3.24	4.80	1	101.6	5	0
<i>Chiropotes sagulatus</i>	Bearded saki	74.99	7.53	3.10	21.8	336	4	3
<i>Cuniculus paca</i>	Lowland paca	9.66	50.71	9.00	1	2.46	2	81
<i>Dasyprocta leporina</i>	Red-rumped agouti	19.72	30.91	3.50	1.5	5.66	3	39
<i>Dasyopus kappleri</i>	Greater long-nosed armadillo	61.66	9.39	9.50	1	7	5	27
<i>Dasyopus novemcinctus</i>	Nine-banded armadillo	0.20	97.43	3.50	1	3.4	5	51
<i>Eira Barbara</i>	Tayra	363.08	0.85	3.91	1.2	1420	5	8
<i>Guerlinguetus aestuans</i>	Brazilian squirrel	446.68	0.73	0.19	1	1.5	3	0
<i>Leopardus pardalis</i>	Ocelot	20.01	31.39	11.90	1	162	6	37
<i>Leopardus wiedii</i>	Margay	912.00	0.34	3.25	1	2295	6	0
<i>Mazama americana</i>	Red brocket deer	37.15	16.89	22.80	1	100	1	130
<i>Mazama nemorivaga</i>	Amazonian brown brocket deer	141.25	3.47	16.30	1	100	1	45
<i>Myoprocta acouchy</i>	Red acouchi	5.49	67.32	0.95	1	1.5	3	15
<i>Myrmecophaga tridactyla</i>	Giant anteater	45.71	13.56	22.33	1	2500	5	116
<i>Nasua nasua</i>	South American coati	371.53	0.82	3.79	30	166	5	4
<i>Panthera onca</i>	Jaguar	131.82	3.72	80.00	1	20,650	6	122
<i>Pecari tajacu</i>	Collared peccary	112.20	4.46	21.27	4.5	500	4	100
<i>Pithecia chrysocephala</i>	Golden-faced saki	181.97	2.48	1.38	3.4	103	3	10
<i>Priodontes maximus</i>	Giant armadillo	363.08	0.85	38.00	1	726.5	5	5
<i>Puma concolor</i>	Puma	95.50	5.61	51.60	1	3177	6	71
<i>Puma yagouaroundi</i>	Jaguarundi	1288.25	0.25	6.75	1	10,000	6	6
<i>Saguinus midas</i>	Golden-handed tamarin	251.19	1.47	0.54	5.7	50	4	7
<i>Saimiri sciureus</i>	Squirrel monkey	398.11	0.76	0.90	22.5	500	4	1
<i>Sapajus apella</i>	Brown capuchin monkey	22.91	26.48	2.75	14.3	429	4	43
<i>Tamandua tetradactyla</i>	Southern tamandua	933.25	0.31	5.52	1	380	5	12
<i>Tapirus terrestris</i>	South American tapir	11.75	44.90	160.00	1	275	1	467
<i>Tayassu pecari</i>	White-lipped peccary	1202.26	0.28	32.23	500	2970	4	116
<i>Birds</i>								
<i>Crax alector</i>	Black curassow	9.44	51.41	3.40	2	20	4	198
<i>Penelope marail</i>	Marail guan	37.15	16.89	0.95	2.2	30	4	119
<i>Psophia crepitans</i>	Grey-winged trumpeter	107.15	4.77	1.50	8	120	4	52
<i>Tinamus major</i>	Great tinamou	7.94	56.54	1.20	1	20	3	30
<i>Reptiles</i>								
<i>Chelonoidis</i> spp.	Red and Yellow-footed tortoise	118.85	4.20	4.00	1	28.7	2	86

<sup>a</sup> Critical area required to ensure a minimum occupancy probability of 60% based on our logistic regression models (see Fig. 3).<sup>b</sup> Percentage of all islands within the Balbina reservoir (considering a total of 3546 islands). Estimation based on critical area.<sup>c</sup> See Table A2 for list of references used for life-history trait values.<sup>d</sup> Based on interviews conducted in this study (see Methods).

We also assessed the relative importance of landscape context and life-history traits in explaining patterns of local extinction for all species across the surveyed islands through Generalised Linear Mixed Models (GLMMs). We first tested for multicollinearity amongst our 12 variables (seven patch- and landscape-scale variables and five species traits) using the Variation Inflation Factor (VIF; Dormann et al., 2013) but none of those factors were moderately to highly redundant/collinear ( $VIF \leq 3$  for all variables). We then constructed a matrix pooling all 34 species within 37 surveyed islands, assigned [1] or [0] for each species, based on either observed detections or non-detections, respectively. As previously explained, a species was considered present if it had been detected by any of the four sampling techniques during any sampling session. We then performed GLMMs with a binomial error structure including the 'SPECIES' random factor to account for

differential species representation within the dataset. Models were fitted using the 'lme4' package (Bates, 2007) within the R platform, and selected based on a multimodel approach considering a  $\Delta AIC < 2.00$  (Burnham and Anderson, 2002). Due to the large number of models below the  $\Delta AIC$  threshold, we obtained model-averaged estimates.

We finally used the most significant patch and landscape variables of island occupancy for 37 islands examined in this study to predict the completeness of vertebrate species composition for all 3546 islands across the Balbina reservoir. We assumed that each species is likely to either occupy or temporarily use an island if it meets a minimum local occupancy probability of 60%, based on logistic regression models. We therefore created a presence/absence likelihood matrix of all islands versus 34 species, obtaining the estimated species richness per island by summing all potential

**Table 3**  
The best models and parameter estimations of occupancy and detectability for 34 vertebrate species predicted by a maximum likelihood hierarchical approach (accounting for imperfect detection) within 40 forest sites examined in this study.

Species	Observed occupancy	Method <sup>b</sup>	Estimated occupancy ( $\Psi$ ) <sup>c</sup> (SE) <sup>d</sup>	Mean detection probability (p) <sup>c</sup> (SE) <sup>d</sup>	Best model(s) <sup>a</sup>			
					Models	AIC	$\Delta$ AIC	Weight
<i>Mammals</i>								
<i>Alouatta macconnelli</i>	0.77	Transect	0.77 (0.07)	0.78 (0.03)	$\Psi$ (area); p (effort)	232.72	0.00	0.99
<i>Ateles paniscus</i>	0.57	Transect	0.57 (0.08)	0.54 (0.04)	$\Psi$ (area); p (effort)	247.27	0.00	1.00
<i>Cabassous unicinctus</i> *	0.40	Transect	0.40 (0.13)	0.07 (0.06)	–			
<i>Chiropotes sagulatus</i>	0.45	Transect	0.45 (0.08)	0.50 (0.04)	$\Psi$ (area); p (effort)	201.35	0.00	1.00
<i>Cuniculus paca</i>	0.70	Camera	0.70 (0.07)	0.54 (0.03)	$\Psi$ (prox); p (effort)	364.30	0.00	0.79
<i>Dasyprocta leporina</i>	0.62	Transect	0.62 (0.08)	0.58 (0.04)	$\Psi$ (area); p (effort)	248.61	0.00	0.96
<i>Dasypros kappleri</i>	0.50	Camera	0.50 (0.15)	0.21 (0.08)	–			
<i>Dasypros novemcinctus</i>	0.97	Camera	0.97 (0.02)	0.67 (0.02)	$\Psi$ (closed-canopy); p (effort)	483.07	0.00	0.75
<i>Eira Barbara</i>	0.27	Camera	0.30 (0.08)	0.21 (0.04)	$\Psi$ (area); p (effort)	139.87	0.00	0.75
<i>Guerlinguetus aestuans</i>	0.30	Transect	0.37 (0.09)	0.18 (0.05)	$\Psi$ (area); p (effort)	134.46	0.00	0.93
<i>Leopardus pardalis</i>	0.62	Camera	0.62 (0.05)	0.41 (0.04)	$\Psi$ (area); p (effort)	329.51	0.00	0.74
<i>Leopardus wiedii</i>	0.22	Camera	0.26 (0.08)	0.17 (0.05)	$\Psi$ (area); p (effort)	111.08	0.00	0.43
<i>Mazama americana</i>	0.52	Transect	0.52 (0.08)	0.53 (0.04)	$\Psi$ (area); p (effort)	194.43	0.00	0.99
<i>Mazama nemorivaga</i>	0.37	Camera	0.37 (0.08)	0.46 (0.05)	$\Psi$ (area); p (effort)	186.80	0.00	0.97
<i>Myoprocta acouchy</i>	0.75	Camera	0.75 (0.03)	0.91 (0.02)	$\Psi$ (area); p (effort)	154.15	0.00	1.00
<i>Myrmecophaga tridactyla</i> *	0.50	Camera	0.54 (0.09)	0.20 (0.03)	–			
<i>Nasua nasua</i>	0.22	Camera	0.25 (0.08)	0.20 (0.05)	$\Psi$ (area); p (effort)	115.73	0.00	0.99
<i>Panthera onca</i>	0.42	Camera	0.52 (0.14)	0.11 (0.03)	$\Psi$ (prox); p (effort)	139.08	0.00	0.80
<i>Pecari tajacu</i>	0.40	Transect	0.40 (0.08)	0.62 (0.04)	$\Psi$ (area); p (effort)	171.02	0.00	1.00
<i>Pithecia chrysocephala</i>	0.37	Transect	0.42 (0.09)	0.25 (0.05)	$\Psi$ (area); p (effort)	169.37	0.00	0.99
<i>Priodontes maximus</i> *	0.27	Camera	0.27 (0.07)	0.19 (0.05)	–			
<i>Puma concolor</i>	0.47	Camera	0.47 (0.08)	0.28 (0.04)	$\Psi$ (area); p (effort)	249.20	0.00	0.96
<i>Puma yagouaroundi</i>	0.15	Camera	0.30 (0.18)	0.07 (0.04)	$\Psi$ (area); p (effort)	66.78	0.00	0.84
<i>Saguinus midas</i>	0.30	Transect	0.30 (0.07)	0.71 (0.05)	$\Psi$ (area); p (effort)	124.65	0.00	1.00
<i>Saimiri sciureus</i>	0.30	Transect	0.30 (0.07)	0.45 (0.05)	$\Psi$ (area); p (effort)	159.56	0.00	0.81
<i>Sapajus apella</i>	0.57	Transect	0.57 (0.08)	0.78 (0.03)	$\Psi$ (area); p (effort)	194.50	0.00	1.00
<i>Tamandua tetradactyla</i> *	0.27	Transect	0.38 (0.22)	0.08 (0.05)	–			
<i>Tapirus terrestris</i>	0.65	Camera	0.65 (0.07)	0.44 (0.03)	$\Psi$ (area); p (effort)	359.80	0.00	0.60
					$\Psi$ (prox); p (effort)	360.65	0.85	0.39
<i>Tayassu pecari</i>	0.12	Transect	0.12 (0.05)	0.29 (0.09)	$\Psi$ (basal area); p (effort)	52.99	0.00	0.37
					$\Psi$ (area); p (effort)	54.52	1.53	0.17
					$\Psi$ (closed canopy); p (effort)	54.93	1.94	0.14
<i>Birds</i>								
<i>Crax alector</i>	0.70	Camera	0.70 (0.07)	0.53 (0.03)	$\Psi$ (area); p (effort)	367.73	0.00	0.94
<i>Penelope marail</i>	0.55	Transect	0.58 (0.08)	0.31 (0.04)	$\Psi$ (area); p (effort)	225.61	0.00	0.95
<i>Psophia crepitans</i>	0.42	Camera	0.42 (0.08)	0.91 (0.02)	$\Psi$ (area); p (effort)			
<i>Tinamus major</i>	0.72	Camera	0.72 (0.07)	0.46 (0.03)	$\Psi$ (prox); p (effort)	372.59	0.00	0.74
<i>Reptiles</i>								
<i>Chelonoidis</i> spp.	0.40	Transect	0.40 (0.08)	0.41 (0.04)	$\Psi$ (area); p (effort)	181.06	0.00	0.98

<sup>a</sup> AIC, Akaike Information Criteria;  $\Delta$ AIC, difference between the model with the lowest AIC and the given model. Only models with  $\Delta$ AIC  $\leq$  2.00 are shown.

<sup>b</sup> Method used for analyses accounting for imperfect detection.

<sup>c</sup> Estimated proportion of forest sites occupied and estimated detection probability provided by the null model.

<sup>d</sup> Standard errors.

\* The variance–covariance matrix could not be calculated successfully.

species presences per island. We then performed non-metric multidimensional scaling (NMDS) ordinations for all 3546 islands using the Bray–Curtis dissimilarity matrix based on qualitative (presence/absence) data, and related the NMDS axes to island area. Finally, we were able to pinpoint priority areas for vertebrate conservation for all islands within the Balbina Hydroelectric Reservoir based on the species richness estimates.

### 3. Results

#### 3.1. Forest island occupancy

A total of 34 species was recorded across all 40 survey sites (Table 2), including 29 mammal, four large terrestrial bird, and two tortoise species (see Fig. A1 for CT photos; data available from

the Dryad Digital Repository). However, we failed to record several highly inconspicuous, nocturnal, or low-density species which almost certainly occurs in the study area (e.g. *Coendou prehensilis*, *Cyclops didactylus*, *Atelocynus microtis*, *Speothus venaticus*, *Galictis vittata* and *Potos flavus*). The 37 islands contained from 0 to 32 species (mean [SD] = 14.6 [10.9]), whereas the three continuous forests harboured 33 species each, on the basis of 10,110 independent CT records (mean [SD] = 273.24 [264.6], range = 0–857); 5765 visual and auditory records during line-transect censuses (mean [SD] = 155.8 [219.8], range = 0–1051); 1850 sign records (mean [SD] = 50.0 [61.9], range = 0–251); and 427 armadillo burrows (mean [SD] = 14.72 [15.23], range = 0–47).

Despite large overall sample sizes, site-specific occupancy rates were low for most species: the overall occupancy matrix for all 37 islands filled only 42.5% of the 1258 cells, increasing to 46.6% when

continuous forest sites were included (Fig. 2). Species ranged widely in their observed island occupancy rates, from the most to the ubiquitous: nine-banded armadillo, *Dasyurus novemcinctus* (97.3% of islands) and white-lipped peccary, *Tayassu pecari* (8.1% of islands; Fig. 2). Occupancy estimates from the maximum likelihood approach differed from those based on site-scale sampling surveys for 10 species. Detectability varied greatly amongst species (Table 3), with red acouchi and grey-winged trumpeter (*Psophia crepitans*) showing the highest detection probability ( $p = 0.91$ ) across all sites, whereas southern naked-tailed armadillo (*Cabassous unicinctus*) and jaguarundi showed the lowest detection probabilities ( $p = 0.07$ ). Models for three armadillo species (southern naked-tailed; greater long-nosed, *Dasyurus kappleri*; and giant armadillo, *Priodontes maximus*), and two anteaters (giant anteater, *Myrmecophaga tridactyla* and southern tamandua, *Tamandua tetradactyla*) yielded poor parameter estimates and the variance-covariance matrix could not be successfully calculated.

Accounting for imperfect detection, forest patch area was by far the best predictor of site occupancy for most species: 83% of 29 species for which the variance-covariance matrix could be adequately estimated included AREA in their best model (Table 3). PROXIMITY was the second best predictor amongst seven patch, landscape and habitat quality variables, appearing in the top model for lowland paca (*Cuniculus paca*), great tinamou (*Tinamus major*) and jaguar (*Panthera onca*), and in the second-best model for tapir (*Tapirus terrestris*). The percentage of closed-canopy forest was included in the best model for nine-banded armadillo, whereas basal area of trees bearing fleshy fruits was included in the top ranking model explaining the occupancy of white-lipped peccary. Therefore, the estimated occupancy rates were highly variable but strongly responsive to forest patch area, with all species occupying gradually fewer smaller islands (Fig. 3). The jaguarundi (*Puma yagouaroundi*) and the white-lipped peccary were the most area-sensitive species, exhibiting low occupancy even in large forest tracts – the smallest estimated insular forest patch required to capture a >60% occupancy probability for these species were 1288.2 and 1202.3 ha, respectively (Table 2). Conversely, nine-banded armadillos were least area-sensitive, showing a >60%

occupancy probability in islands as small as 0.2 ha. Howler monkeys (*Alouatta macconnelli*), red acouchi (*Myoprocta acouchy*), lowland paca, great tinamou and black curassow (*Crax alector*) also exhibited high occupancy rates in small islands, with critical areas smaller than 10 ha. Considering the species-specific logistic regression models pooled across all species, a minimum forest island of 95 ha would be required to ensure an aggregate 60% occupancy probability for the entire vertebrate assemblage, yet only 5.7% of all 3546 BHR islands are larger than this threshold.

### 3.2. Landscape and life-history predictors of island occupancy

Considering all 34 species within 37 surveyed islands, GLMMs showed that forest area ( $\beta = 2.816$ ,  $P < 0.001$ ), home range size ( $\beta = -1.204$ ,  $P < 0.001$ ) and non-habitat dispersal capacity ( $\beta = 1.466$ ,  $P < 0.001$ ) were the main predictors of the probability of species occupancy, with the highest relative importance across all variables (Table 3). Indeed, when we related the estimated species occupancy rate to their swimming capacity, we observed that adept swimmers capable of frequent dispersal over open-water had the highest occupancy rates across all islands ( $R^2 = 0.255$ ,  $P = 0.005$ ), whereas those using larger home ranges showed the most negative residuals in this relationship (Fig. 4). Other significant variables identified in the averaged model included the patch SHAPE ( $\beta = 23.330$ ,  $P = 0.001$ ) and PROXIMITY to other land masses ( $\beta = 0.208$ ,  $P = 0.026$ ).

Given data from 37 islands, we were able to estimate species-specific vertebrate occupancy rates based on logistic regression models in relation to island area, since this was the most important predictor of species occupancy for most species. We therefore obtained the estimated species composition and richness for the entire Balbina archipelago of 3546 islands. This species occupancy data filled 19.42% of the overall presence-absence matrix (34 species · 3546 islands), with a mean of ~7 species persisting in each island. Furthermore, our predictive modelling showed that only 1.5% of all islands in the reservoir are likely to retain at least 26 (>75%) of all vertebrate species considered here. We thus identified priority islands for conservation based on species richness

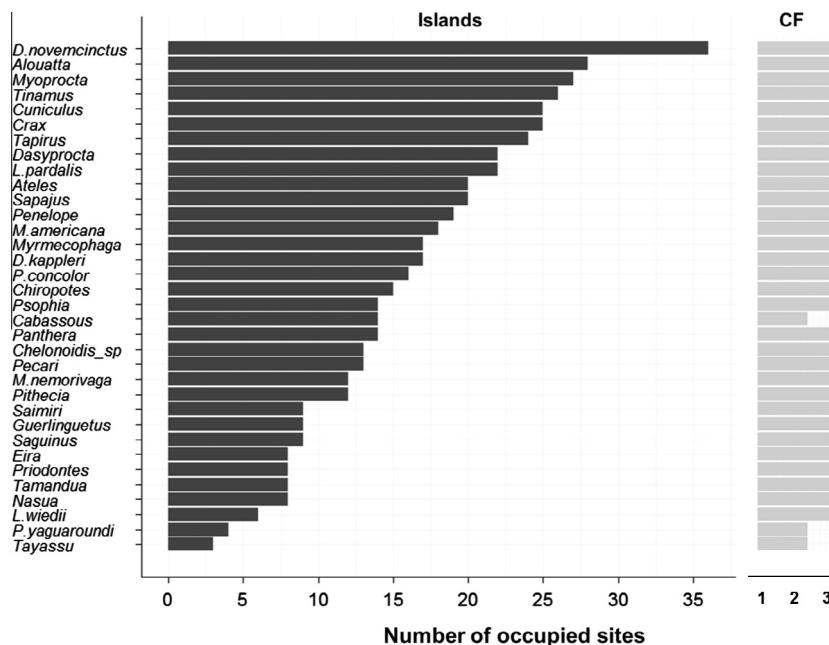
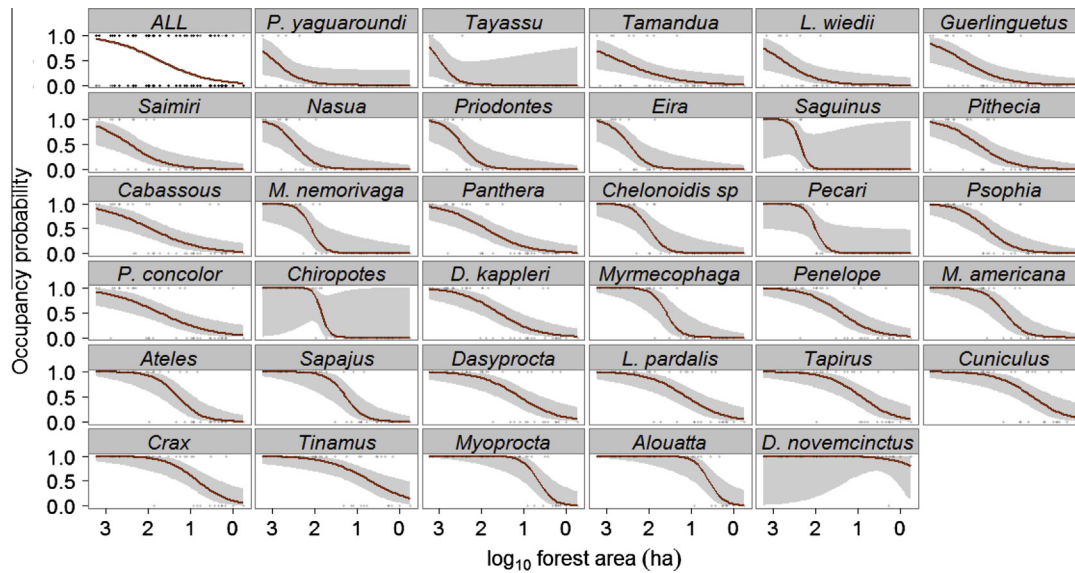


Fig. 2. Patterns of observed occupancy for 34 vertebrate species within 37 surveyed islands and three mainland continuous forest (CF) sites surveyed at the Balbina Hydroelectric Reservoir landscape. Species/genus names are ordered top to bottom from the most to the least ubiquitous across all forest islands, and correspond to those in Table 2.

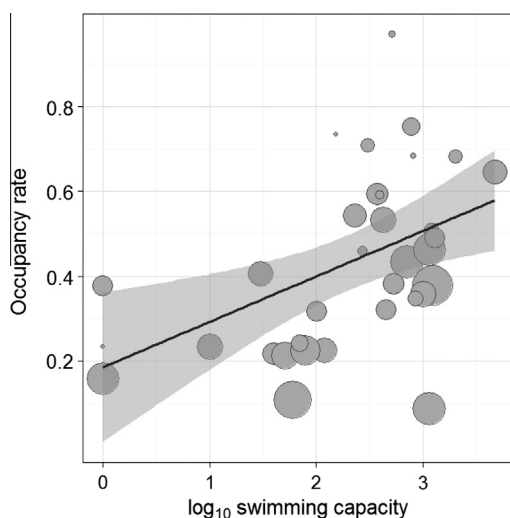


**Fig. 3.** Occupancy probability of all 34 vertebrate pooled together ('ALL') and each species individually, as a function of insular forest area, predicted using logistic regression models based on estimated occupancy for each species. Species are ordered left to right and top to bottom according to empirical logistic curves from the most to the least sensitive to forest patch area.

estimates, showing that most islands are now highly impoverished, harbouring a small number of vertebrate species (Fig. 5).

#### 4. Discussion

A number of studies have addressed large-bodied terrestrial vertebrate populations in fragmented tropical forest landscapes (Michalski and Peres, 2005; Urquiza-Haas et al., 2009; Sampaio et al., 2010; Thornton et al., 2011a, 2011b; Canale et al., 2012). However, these study areas are dominated by a terrestrial vegetation matrix of varying degrees of permeability as there are few opportunities to examine faunal assemblages in truly archipelagic landscapes where insular forest remnants have been isolated by a uniform open-water matrix. While large hydroelectric dams severely degrade both terrestrial and aquatic ecosystems of major river basins, they provide near ideal experimental landscapes that



**Fig. 4.** Relationship between matrix dispersal (swimming) capacity over open-water and site occupancy rate for 34 forest vertebrate species recorded at 37 surveyed islands. Circle sizes are proportional to empirical estimates of home range sizes for each species.

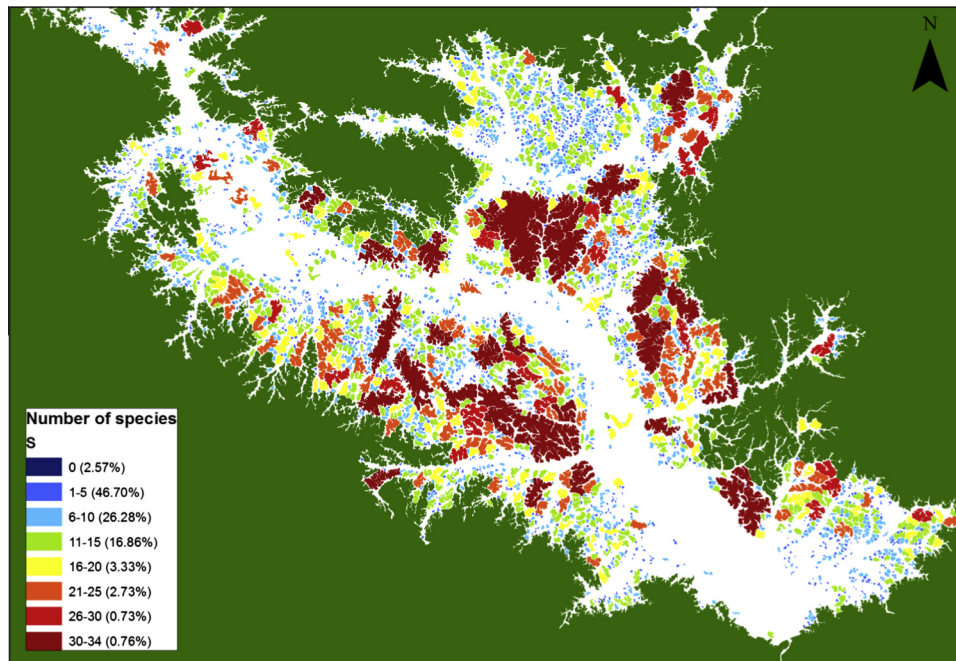
effectively control for the effects of matrix type and isolation history of habitat remnants (Cosson et al., 1999). Yet vertebrate studies in hydroelectric reservoirs usually document large-vertebrate population outcomes within the first few years of inundation (e.g. Cosson et al., 1999; Terborgh et al., 2001; Dalecky et al., 2002). To our knowledge, this is the first study examining how medium to large-bodied terrestrial and arboreal vertebrates have responded to a >25-year history of alteration in landscape structure and habitat quality by a major hydroelectric reservoir in a tropical forest region.

##### 4.1. Drivers of local extinctions

Understanding the main drivers of species extinctions in human-modified landscapes has become a central pursuit of conservation biologists. Habitat area effects have been consistently identified as the main predictors of bird and mammal occupancy in tropical forest remnants (Ferraz et al., 2007; Gibson et al., 2013; Benchimol and Peres, 2013; Benchimol and Venticinque, 2014). However, other features of the patch and surrounding landscape – including the nature of neighbouring habitats (Andr n, 1994; Prugh et al., 2008), patch habitat quality (Michalski and Peres, 2005; Holland and Bennett, 2009; Wang et al., 2010) and human disturbances (Michalski and Peres, 2005; Sampaio et al., 2010; Thornton et al., 2011b; Canale et al., 2012) – have been frequently pinpointed as strong predictors of species loss across multiple landscapes. Additionally, species life-history attributes can be excellent predictors of vertebrate species susceptibility to extinction in tropical forest remnants (Lees and Peres, 2008; Meyer et al., 2008; Urquiza-Haas et al., 2009; Thornton et al., 2011a; Benchimol and Peres, 2014). We therefore attempted to consider both intrinsic and extrinsic factors to elucidate the main drivers of local extinctions of midsized to large vertebrate species within forest islands embedded within an open-water matrix.

Considering all 12 explanatory variables, patch metrics and life-history traits were the only significant predictors of local persistence of vertebrate populations across all 37 islands. Specifically, island forest area, home range size and swimming competence of vertebrate species were the strongest predictors, attaining the maximum relative importance amongst all variables. Indeed, the





**Fig. 5.** Priority areas for forest vertebrate conservation action based on the estimated species composition and richness for all BHR islands on the basis of species-specific logistic regression equations. All islands were assumed to be 'occupied' by any given species if its occupancy probability was equal to or greater than 60%.

Balbina islands exhibit extremely powerful species-area relationships (SARs), a resounding endorsement of [MacArthur and Wilson's \(1967\)](#) island biogeography theory. Positive SARs have been observed for small mammals, bats, primates and birds in artificial land-bridge island systems worldwide ([Yu et al., 2012](#); [Gibson et al., 2013](#); [Benchimol and Peres, 2013](#); [Benchimol and Venticinque, 2014](#); [Mendenhall et al., 2014](#)). Island occupancy was also a function of individual species traits, with wide-ranging species and poor swimmers showing evidence of high local extinction rates, low recolonization rates, or both (cf. [Dale et al., 1994](#)). In Amazonian fragmented forest landscapes, large mammals exhibiting large spatial requirements are highly vulnerable to extinction in small fragments ([Timo, 2003](#); [Michalski and Peres, 2005](#)). Home range size and trophic status were amongst the main predictors of primate local extinction within 760 neotropical forest patches ([Benchimol and Peres, 2014](#)), and large-bodied trophic generalist vertebrate species were most resilient to local extinction in recently isolated land-bridge islands ([Cosson et al., 1999](#)). We also show that species that are more adept at matrix movements (through inherently greater swimming capacity) occupied more islands. Water is widely considered an effective barrier to terrestrial vertebrate dispersal ([Cosson et al., 1999](#)), but our results show that some species can frequently traverse great distances across this hostile matrix. For instance, tapirs (*T. terrestris*) were observed swimming between islands more than 450 times, corroborating genetic analyses showing high levels of gene flow within a single genetically uniform tapir population across the entire post-damming BHR landscape ([Pinho et al., 2014](#)). At Lago Guri, Venezuela, even the most remote islands isolated by several kilometres were inhabited by capybaras ([Terborgh et al., 1997](#)) which are renowned for their long-distance swimming capability. Consistent with our results in an archipelagic landscape, species persistence in isolated forest patches embedded in entirely terrestrial landscapes is also strongly associated with their ability to traverse, if not exploit, the vegetation matrix ([Gascon et al., 1999](#); [Michalski and Peres, 2005](#); [Lees and Peres, 2009](#)).

#### 4.2. Species-specific area sensitivity

Although occupancy rates ranged widely across forest vertebrate species at Balbina, forest area was the most important predictor of local extinction, appearing in the best model of 24 of the 29 species for which it was possible to account for imperfect detection ([Table 4](#)). We can therefore distinguish three classes of species according to island area: (a) area-insensitive species, showing >60% occupancy probability even in islands smaller than 12 ha (e.g. nine-banded armadillo, howler monkey, red acouchi, lowland paca, tapir, great tinamou and black curassow); (b) moderately insensitive species, requiring islands larger than 20 ha but smaller than 80 ha to exhibit a >60% occupancy probability (e.g. red brocket deer, ocelot, greater long-nosed armadillo, giant anteater, brown capuchin monkey, spider monkey, bearded saki, red-rumped agouti and marail guan); and (c) area-sensitive species, which required more than 95 ha to show a >60% occupancy probability (e.g. brown brocket deer, collared peccary, white-lipped peccary, tayra, South American coati, puma, jaguar, margay, jaguarondi, southern naked-tailed armadillo, giant armadillo, southern tamandua, golden-faced saki, golden-handed tamarin, squirrel monkey, Brazilian squirrel, grey-winged trumpeter and tortoises). For five species, however, other variables were better predictors of island persistence: the importance of land mass proximity exceeded that of patch area for jaguar, lowland paca and great tinamou; whereas closed-canopy forest and basal area of fleshy-fruited trees were the best predictors for nine-banded armadillo and white-lipped peccary, respectively. Because jaguars have large spatial requirements and favour aquatic movements, they typically occupy sufficiently accessible small islands as local transients rather than as full-time residents (see also [Dalecky et al., 2002](#)). Our interviews and field surveys show that jaguars are excellent swimmers and regularly traped neighbouring islands, with large, poorly isolated islands most likely to be used by this threatened species. Yet they were absent from medium-sized islands at Lago Guri, following a short isolation time

**Table 4**  
Summary of Generalised linear mixed models (GLMMs) showing the predictors of overall patterns of 34 vertebrate species occupancy within 37 forest islands at BHR and their relative importance. Model-averaged coefficients are presented. Significant variables and coefficients ( $P < 0.05$ ) are shown in bold and shaded grey. See text for details of each variable.

Predictor	Estimate	Standard Error	z-Value	Confidence interval	Relative importance
Intercept	-5.820	1.423	4.091	(-8.609; -3.031)	
AREA	2.816	0.240	11.744	(2.346; 3.286)	1.00
ISOLATION	0.292	0.152	1.916	(-0.007; 0.590)	0.70
SHAPE	23.330	7.316	3.189	(8.991; 37.668)	0.99
PROXIMITY	0.208	0.094	2.222	(0.024; 0.392)	0.85
BURN	-0.173	0.165	1.051	(-0.496; 0.150)	0.39
CC%	-0.004	0.007	0.586	(-0.0189; 0.010)	0.30
BA <sub>ff</sub>	0.058	0.088	0.655	(-0.115; 0.231)	0.33
BODY MASS	0.320	0.618	0.518	(-0.891; 1.531)	0.29
GROUP SIZE	-0.540	0.416	1.297	(-1.356; 0.276)	0.45
HOME RANGE SIZE	-1.204	0.298	4.043	(-1.788; -0.620)	1.00
DIET CATEGORY	0.202	0.199	1.014	(-0.188; 0.593)	0.37
DISPERSAL ABILITY	1.466	0.398	3.683	(0.686; 2.246)	1.00

(Terborgh et al., 2001), and no longer occur in the ~1500-ha Barro Colorado Island, Panama (Moreno et al., 2006). Additionally, other adept swimmers, including tapir, puma, giant anteater and even large ground-dwelling birds, can be defined as transients rather than true small island residents at Balbina.

The most ubiquitous species – nine-banded armadillo – occurred in all surveyed sites, except for a single island degraded to scrub vegetation and no longer supporting a tree canopy. Even tiny islands were large enough to contain this species, provided they retained forested, mirroring small forest patches in other landscapes (Michalski and Peres, 2007; Urquiza-Haas et al., 2009; Thornton et al., 2011a). Although white-lipped peccaries exhibited high dispersal capacity at the Balbina Lake, their large herds require vast forest areas that are sufficiently productive in terms of concentrations of large-seeded trees (Keuroghlian et al., 2004; Tobler et al., 2009). Unsurprisingly, given the strong ecological relationships of white-lipped peccary and large-seeded fruits (Beck, 2006), fleshy-fruited tree basal area was the most important predictor for this species. In contrast to other Neotropical fragmentation ecology studies in terrestrial landscapes (Estrada et al., 1994; Michalski and Peres, 2005; Sampaio et al., 2010; Thornton et al., 2011a; Canale et al., 2012), we detected an overall greater habitat area effect on local extinctions of mid- to large-sized vertebrate species. However, sufficiently large islands and mainland sites retained a larger proportion of species than that reported in those studies, which can be explained by the absence at Balbina of some negative extrinsic factors, such as hunting pressure. Additive mortality induced by hunters accelerates local extinction rates of large-bodied vertebrates in tropical forest fragments (Peres, 2001), often overriding the effects of fragment size on vertebrate species persistence (Thornton et al., 2011b; Canale et al., 2012). Comparing occupancy rates of frequently hunted forest ungulates between Balbina and a set of 50 overhunted forest patches in northern Guatemala (Thornton et al., 2011a) reveals clear differences in estimated forest isolate occupancy of approximately the same age (30 years; see Fig. A2). In Guatemala, fragments were also comprehensively surveyed using both camera trapping and visual-acoustic censuses, and patch occupancy estimates also accounted for imperfect detectability; these differences are almost certainly related to hunting pressure and matrix type. Water is much more hostile to matrix movements for cursorial species compared to terrestrial landscapes embedded within a matrix of secondary forest, pasture and cropland. Likewise, other game species exhibited higher levels of island occupancy compared to forest patches intensively hunted elsewhere in the Neotropics. Large bodied-primates are often extirpated in hunted

forest patches (Sampaio et al., 2010; Canale et al., 2012; Benchimol and Peres, 2014) whereas the largest primates at Balbina (howler monkey, spider monkey, and brown capuchin monkey) showed the highest levels of occupancy (see also Benchimol and Venticinque, 2014). Large game birds also showed high occupancy rates compared to their congeners in a densely settled forest landscape in southern Mexico (Urquiza-Haas et al., 2009) and in a fragmented landscape of northern Guatemala (Thornton et al., 2012). Tortoises, which are frequently consumed by local communities (Souza-Mazurek et al., 2000), were detected in 13 of 37 islands.

Dasyproctids (agouties and acouchies) only occurred in Balbina islands larger than 10 ha, a pattern observed in other artificial archipelagos (Asquith et al., 1997; Terborgh et al., 2001; Dalecky et al., 2002). However, this is at odds with the Biological Dynamic Forest Fragment Project (BDFFP) where agoutis occur in ~1-ha forest fragments, which again is likely related to a matrix dominated by young second-growth (Jorge, 2008). The three largest carnivore species – jaguar, puma and ocelot – also showed high island occupancy rates compared to forest patches at other Neotropical fragmented landscapes (Estrada et al., 1994; Michalski and Peres, 2005; Thornton et al., 2011a), which is presumably related to their adept locomotion in water. We therefore surmise that – compared to hunted, terrestrial landscapes elsewhere – the absence of hunting pressure and the uniform aquatic matrix elevates the intercept and increases the SAR slope for large vertebrates at Balbina because of the simultaneous processes of local extinction and recolonization of forest patches.

As a cautionary note, the high observed and estimated occupancy rates for most vertebrate species examined in this study masks a cryptic local extinction debt as many resident (meta)populations appear to be too small and will likely fail to persist in most islands in the long-term (see Dalecky et al., 2002). Small populations combined with edge effects, stochastic disturbance events, and imbalances in trophic cascades render forest isolates extremely vulnerable to further biodiversity loss (Terborgh et al., 2001; Laurance et al., 2011), even if they remain effectively protected against human perturbation. Indeed, edge effects are a powerful driver of non-random floristic transitions in forest islands within the Balbina archipelago (Benchimol and Peres, 2015) and a single convective windstorm event led to the complete canopy implosion of a 6.1-ha island, resulting in the extirpation of the only remaining howler monkey group (M.B., pers. obs.). We therefore encourage follow-up studies to better understand the long-term viability of vertebrate populations stranded on islands created by large dams.

### 4.3. Conservation implications

To satisfy burgeoning energy demands, the increasingly affluent Brazilian economy is required to add ~6000 MW each year for the next decade to its current 121,000 MW generating capacity (MME/EPE, 2012). This sector is expected to greatly increase in the near future: a total of 154 hydroelectric dams currently operate in the Amazon, 21 are under construction, and a further 277 are on the brink of approval (Castello et al., 2013). Understanding the long-term impacts of major dams on forest biodiversity and designing strategies to mitigate their detrimental impacts are thus a critical policy priority. Most islands within the Balbina Lake had experienced a colossal rate of vertebrate extirpation following ~26 years of isolation, and even the largest islands could not retain all species recorded in mainland continuous forest sites. Given data from 37 islands, we were able to estimate species-specific vertebrate occupancy rates, and subsequently species composition and richness, for the entire Balbina archipelago of 3546 islands. This scaling-up scenario represents a gloomy outcome in that the species occupancy data filled less than one-fifth of the overall presence-absence matrix. Worse still, fewer than 2% of all islands are likely to harbour at least 26 vertebrate species (Fig. 5). This suggests that even in the context of a strictly-protected Biological Reserve, the vast majority of islands formed by the dam cannot ensure the local persistence of even a modest fraction of the original mid- and large-sized vertebrate fauna. Simply put, Balbina and many other planned or under-construction major dams in lowland Amazonia still target relatively flat terrains with a moderately dissected topography, which apart from a highly undesirable inundated area to hydropower output ratio, creates vast shallow lakes favouring the formation of myriad small islands (Fearnside, 1995, 2014). Likewise, the Tucuruí Hydroelectric Dam of eastern Amazonia also created a large shallow lake containing 2200 variable-sized but increasingly degraded islands (Ferreira et al., 2012). Hence, blueprints of new hydropower projects will likely experience a similar fate: creation of vast archipelagos of small islands that cannot retain a legacy of most of the biota from once continuous forests. Policy-makers and hydropower engineers should thus explicitly consider the overall topography of planned reservoirs to both maximise landscape connectivity resulting from legally approved dams or reject plans targeting unfavourable river basins – those ones located in lowland forests that will create shallow reservoirs and therefore large number of small islands.

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### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.04.005>.

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