ZRDC | Zoological Research: Diversity and Conservation

Review **Open Access**

Biodiversity responses to insular fragmentation in Amazonia: two decades of research in the Balbina Hydroelectric Reservoir

Ana Filipa Palmeirim[1,2,*], Maíra Benchimol[3], Danielle Storck-Tonon[4], Anderson S. Bueno[5], Isabel L. Jones[6], Gilmar Klein[7], Carlos A. Peres[8,9]

[1] *CIBIO, Research Centre of Biodiversity and Genetic Resources, InBIO Associated Lab, Vairão Campus, University of Porto, Vairão 4485-661, Portugal*

[2] *BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Vairão Campus, University of Porto, Vairão 4485-661, Portugal*

[3] *Laboratório Laboratório de Ecologia Aplicada à Conservação, Universidade Estadual de Santa Cruz, Ilhéus, Bahia 45662-900, Brazil*

[4] *Programa de Pós-Graduação em Ambiente e Sistemas de Produção Agrícola (PPGASP), Universidade do Estado de Mato Grosso, Tangará da Serra, Mato Grosso 78301-532, Brazil*

[5] *Instituto Federal de Educação, Ciência e Tecnologia Farroupilha, Júlio de Castilhos, Rio Grande do Sul 98130-000, Brazil*

[6] *Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, UK*

[7] *REBIO Uatumã/ICMBio, Presidente Figueiredo, Amazonas 69736-000, Brazil*

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

[9] *Juruá Institute, Manaus, Amazonas 69057-060, Brazil*

ABSTRACT

As hydropower development expands across lowland tropical forests, flooding and concomitant insular fragmentation have become important threats to biodiversity. Newly created insular landscapes serve as natural laboratories to investigate biodiversity responses to fragmentation. One of these most iconic landscapes is the Balbina Hydroelectric Reservoir in Brazilian Amazonia, occupying >400 000 ha and comprising >3 500 forest islands. Here, we synthesise the current knowledge on responses of a wide range of biological groups to insular fragmentation at Balbina. Sampling has largely concentrated on a set of 22 islands and three mainland sites. In total, 39 studies were conducted over nearly two decades, covering 17 vertebrate, invertebrate, and plant taxa. Although species responses varied according to taxonomic group, island area was consistently included and played a pivotal role in 66.7% of all studies examining patterns of species diversity. Species persistence was further affected by species traits, mostly related to species capacity to use/traverse the aquatic matrix or tolerate habitat degradation, as noted for species of vertebrates and orchid bees. Further research is needed to improve our understanding of such effects on wider ecosystem functioning. Environmental Impact Assessments must account for changes in both the remaining habitat amount and configuration, and subsequent long-term species losses.

Keywords: Habitat loss; Hydropower dams; Land-bridge; Local extinctions; Species-area relationships; Species diversity; Tropical forests

INTRODUCTION

The rising global energy demand, followed by the need to decarbonize energy production, triggered the intensification of the hydropower sector, which now accounts for 73% of the renewable energy produced globally (Bucknall et al., 2014). Although extolled as "clean" energy, hydroelectricity is controversial given that the environmental and social impacts often outweigh any economic benefits (Alho, 2020; Gibson et al., 2017). This has been particularly noted across lowland tropical forests where damming, due to the typically gentle

topography, floods vast areas, creating shallow lakes that are prone to siltation, with high levels of greenhouse gas emissions, while often producing little energy (Fearnside & Pueyo, 2012; Finer & Jenkins, 2012). Moreover, low-elevation areas are flooded when dams are built, and previous ridgetops are often converted into forest islands, creating complex fragmented landscapes within hydroelectric reservoirs (Lees et al., 2016). As such, although found worldwide, these human-made insular landscapes are more frequent across the tropics (e.g., de Amorim et al., 2017; Hazard et al., 2023; Lima et al., 2015; Terborgh et al., 2001) and subtropics (e.g., Liu et al., 2019). Today, the construction of hydroelectric dams is one of the primary means of habitat loss, fragmentation, and subsequent degradation across tropical forests (Jones et al., 2016; Jones & Bull, 2020). For instance, in the Amazon basin alone, a total of 145 dams (in operation or under construction) have flooded or will flood ~1.5 Mha of pristine hyper-diverse forests (ECOA—Ecologia em Ação, 2016). Nevertheless, the hydropower sector is projected to greatly continue expanding in the Amazon basin, with 263 additional dams currently planned for construction in the next few years (ECOA—Ecologia em Ação, 2016).

In the aftermath of damming, taxa that become isolated within reservoir islands typically experience a novel hyper-disturbance regime, which may result in drastic shifts in species composition within insular communities through species extinction and turnover, which reflect biodiversity losses and ultimately altered carrying capacity of the remaining habitat (Jones et al., 2016). For instance, in the Guri Lake, Venezuela, the absence of predators from islands drove the hyper abundance of herbivores, profoundly impacting ecosystem functioning (Terborgh et al., 2001). In the forest islands of the Chiew Larn Reservoir in Thailand, an initial species assemblage of small mammals with more than 10 species has culminated in only one hyper dominant rat species after a 33-year period (Moore et al., 2022). Moreover, in the newly created islands of Serra da Mesa Reservoir, in the Brazilian Cerrado biome, a gecko species was found to rapidly modify its morphology and diet: populations on all five islands studied have proportionally larger heads than those at five nearby mainland sites, suggesting rapid evolutionary change (de Amorim et al., 2017).

Although an aquatic matrix setting is not the most common matrix type across global fragmented landscapes, the study of such insular landscapes is particularly useful because they minimise the potentially confounding matrix effects (Ewers & Didham, 2006). Indeed, these landscapes are characterised by an equally uniform and inhospitable matrix, in which time since isolation and history of anthropogenic disturbance are largely invariant (Diamond, 2001). Therefore, insular fragmented landscapes provide excellent opportunities for developing and testing theories of island biogeography and habitat fragmentation. One of the most iconic of these landscapes is that created by the construction of the Balbina Hydroelectric Dam, in central Brazilian Amazonia (Fearnside, 1989). In this landscape, 3 526 forest islands were formed throughout a shallow-water reservoir larger than 400 000 ha (Benchimol & Peres, 2015a).

Here, we review nearly two decades of research carried out to understand biodiversity responses to habitat loss and insular fragmentation in the Balbina Hydroelectric Reservoir and adjacent continuous forest areas (Figure 1). To do so, we compiled and synthesised information from all 39 existing studies focused on a wide range of biological taxa, and further discuss the effects of island area, isolation, and habitat quality, as well as species traits, in determining patterns of species persistence across a gradient of habitat loss and insular fragmentation. These studies have largely concentrated on the same subset of 22 forest islands of different sizes and degrees of isolation, in addition to three mainland continuous forest (CF) sites , used as a baseline. We further disclose the lessons and prospects of future research to continue improving our understanding of the effects of insularisation on biodiversity, as well as its consequences for ecosystem functioning. The information synthesised here is of major use for proposing effective measures to mitigate the environmental impacts of habitat loss and insularisation following river damming across lowland tropical forests.

MATERIALS AND METHODS

Study area

The vast Balbina Hydroelectric Reservoir, created in Central Brazilian Amazonia (S1°48′, W59°29′; Figure 1), resulted from
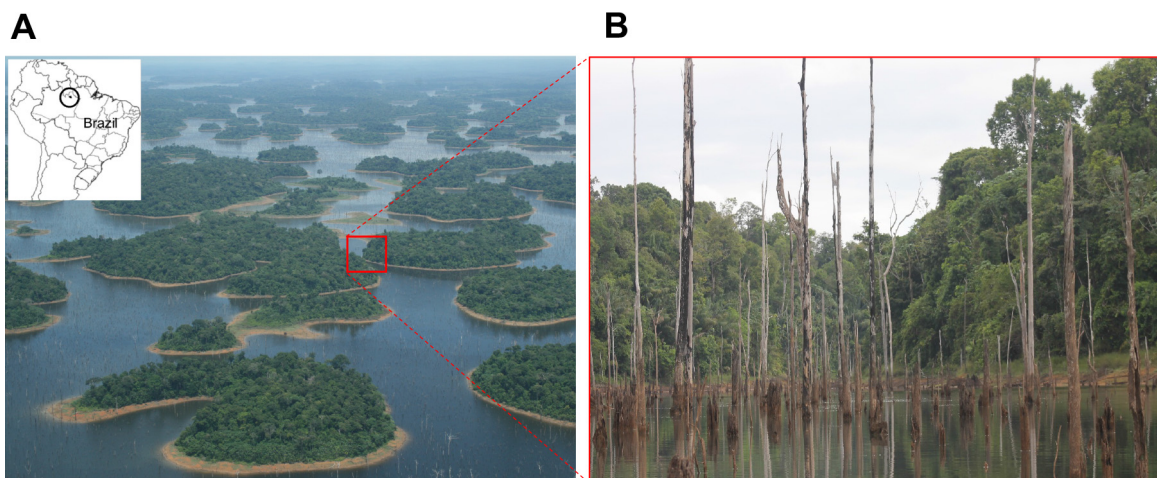

Figure 1 The Balbina landscape

A: Inset map showing the location of the Balbina Hydroelectric Dam and aerial photograph illustrating the Balbina insular landscape (photo credit: E. M. Venticinque). B: Photograph depicting the aquatic matrix surrounding forest islands as occupied by long-standing dead trees. Photo by A. F. Palmeirim.

a major dam built in 1987 on the Uatumã River, a left-bank tributary of the Amazon River. Damming resulted in a 443 772-ha reservoir and the creation of 3 546 forest islands. After 35 years, dead relics of large canopy trees remain standing in the shallow waters of the reservoir as the vegetation of the submerged area was never cleared, except for the area immediately adjacent to the dam. As lower elevation areas were mostly associated with riparian habitats, this habitat type has virtually vanished after damming and consequent flooding of the lowland areas (Palmeirim et al., 2017).

The Balbina landscape is characterised by an annual mean temperature of 26.7°C, with low variation between the wet and dry seasons. Annual precipitation is on average 2 420 mm, but as low as 80 mm during dry months (Alvares et al., 2013). The vegetation is broadly characterised by dense submontane rain forest (Benchimol & Venticinque, 2014). In particular, islands and the neighbouring continuous forest sites consist of dense closed‑canopy non-flooded terra firme forest (Benchimol & Peres, 2015a). Forest islands within the reservoir have not been subject to logging nor hunting, but many islands experienced understorey fires during the El Niño drought of late‑1997 to early‑1998 (Benchimol & Peres, 2015b). In addition, a vast area within and around the former left bank of the Uatumã river has been strictly protected since the dam was built by the 440 358-ha Uatumã Biological Reserve, the largest protected area in its category in Brazil. The implementation of this protected area aimed to offset the environmental impacts generated by the dam and it largely explains the reasonably low levels of post-damming anthropogenic disturbance throughout the reservoir (IBAMA, 1997).

Literature review

Information on the research carried out at the Balbina landscape was compiled between January and July 2023, based on a comprehensive search of published and unpublished studies (i.e., reports and dissertations) reporting the impacts of habitat loss and fragmentation in the study area. To do so, we used both Web of Science and Google Scholar with the search queries (habitat fragmentation* AND Balbina Hydroelectric Reservoir*). These searches were then repeated using keyword combinations translated into Portuguese. Any additional studies were further checked by searching the literature cited in the selected studies. We only retained studies that targeted the effects of habitat loss and fragmentation. As such, studies that perceived or approached the effects of insular forest fragmentation differently were not further discussed in this review. This included one study on the responses of giant otters (Palmeirim et al., 2014) and tapirs (using a genetic approach) to river damming (Pinho et al., 2014).

Since Benchimol and Peres (2015a) , most studies carried out in Balbina largely allocated their sampling effort to the same subset of 22 forest islands from the total of 37 islands surveyed in that study, in addition to three mainland CF sites (Figure 2). Focal islands were pre-selected according to their size, degree of isolation and spatial distribution, so that a wide spectrum of island configurations could be surveyed within the reservoir. The 22 most frequently sampled islands were at least 1‑km apart from one another, with island size ranging from 1.5 to 1 466 ha and isolation distances to the nearest mainland varying from 44 to 11 872 m (Supplementary Table S1). Continuous forest sites were also widely distributed around the reservoir and placed between 200 and 4 000 m from the nearest reservoir margin (Figure 2). For each reviewed study, we compiled information on the topic of
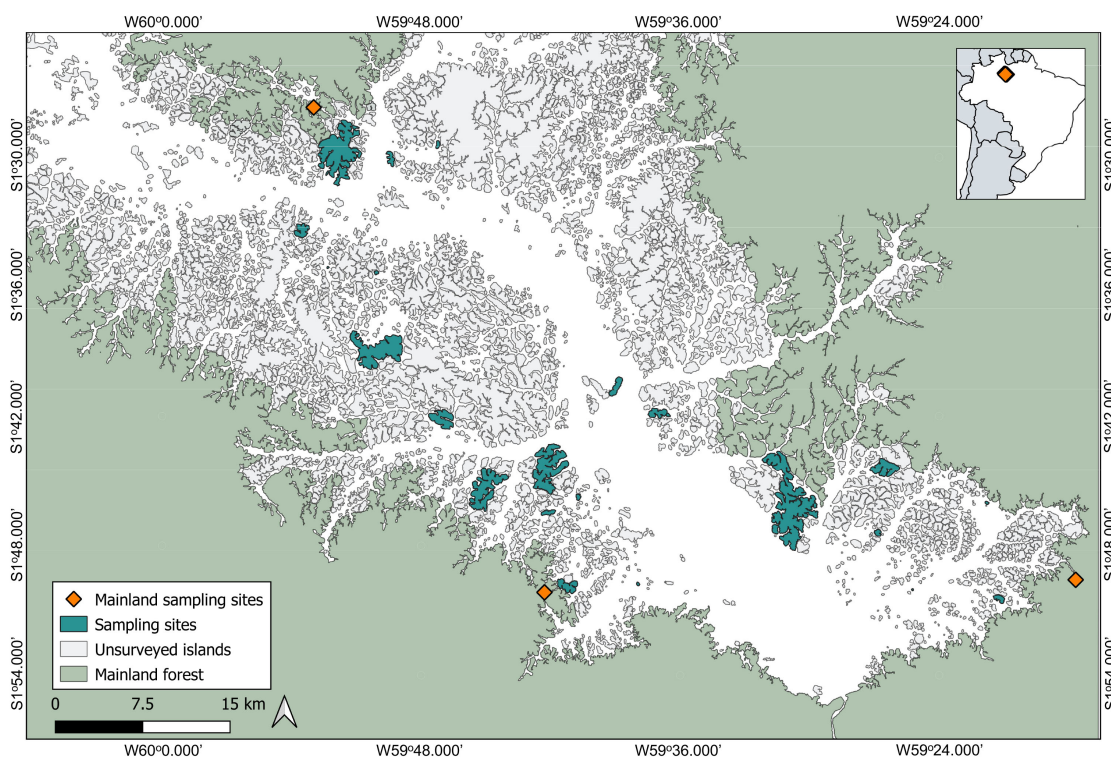

Figure 2 Survey sites within the Balbina Hydroelectric Reservoir of Central Brazilian Amazonia: 22 islands (in darker greenish and highlighted by a 500-m buffer contour line) and three continuous forest sites (indicated by orange triangles)

research, biological group, number of sampled sites, evaluated metrics, year of publication, and main findings. For studies targeting patterns of species taxonomic α-diversity in relation to insular fragmentation, we further recorded which variables affected any of the species diversity metrics considered.

RESULTS

Nearly two decades of research at Balbina

The onset of research activities examining the effects of insular forest fragmentation in the Balbina landscape dates from 20 years post-damming. These studies culminated in 33 peer-reviewed publications, Five MSc unpublished theses, and one book chapter. About 70% of these 39 studies were produced between 2017 and 2022, corresponding to a period of data collection between 2012 and 2018 (Figure 3A). Over the years, a total of 17 biological groups have been surveyed, including vertebrates (snakes, primates, lizards, aerial insectivorous bats, frogs, small mammals, birds, and mid-sized to large arboreal and terrestrial vertebrates), invertebrates (termites, spiders, orchid bees, harvestmen, dung beetles, and leafcutter ants) and plants (lianas, ferns, trees ≥10 cm DBH (diameter at breast height), and saplings). Overall, vertebrates received most of the research attention (Figure 3B). The topics covered varied from single-taxon studies examining α-diversity metrics to multi-taxa or multi-scale studies (Table 1). Additional topics covered include mutualistic (Emer et al., 2013) and predator-prey interactions (Pires et al., 2023), species-habitat networks (Palmeirim et al., 2022), and the diversity of sound in the acoustic space (Luypaert et al., 2023). The number of sampling sites in each study varied widely, being highest for studies using passive acoustic monitoring (74 islands: Bueno et al., 2020) (Table 1). A total of 33 variables have been considered to assess biodiversity responses to insular forest fragmentation (Supplementary Table S2). The core variables considered most commonly were island area, distance to mainland, proximity index, island shape, and tree species richness, but the set of metrics considered varied according to the biological group surveyed (Table 1).

Landscape, patch and local habitat drivers of species diversity

The most important driver of species diversity in the Balbina landscape is island size (or insular forest area, excluding any non-forest part of the island). This variable has been consistently included in all 18 studies examining overall species diversity patterns, being an important predictor of species diversity in 67% of these studies (Figure 4). Island isolation, as measured using either the linear distance to mainland forest (included in 72% of the studies) or a Proximity index (that considers not only the area of any landmass included in any given buffer but also the distance to those landmasses (McGarigal et al., 2012), included in 72% of the studies), were important drivers of species diversity in 46% and 39% of the studies. Habitat quality has been inferred from 21 variables at either forest patch- or plot-scale. Overall, the most examined habitat variables were fire severity (44%), density of trees ≥10 cm DBH (33%) and percentage of closed-canopy forest (28%), which predicted species diversity in 50%, 33%, and 20% of the studies, respectively (Figure 4). Below we provide a detailed summary of the main findings for each of the biological groups considered to date.

Vertebrates: Mid- to large-bodied terrestrial and arboreal vertebrates at Balbina, as surveyed using a combination of camera trapping, line-transect censuses, sign surveys, and armadillo burrow counts, amounted to 35 species. Forest habitat area explained 91% of their species richness, which was further affected by edge-mediated surface fire disturbance, which was most noticeable on islands smaller than 10 ha (Benchimol & Peres, 2015a). Primates' species diversity was additionally affected by tree density and vertical stratification (Benchimol & Venticinque, 2014). When accounting for species abundance, most vertebrate populations were observed to be either locally extirpated or committed to future extinction events on most islands (Benchimol & Peres, 2021). For small non-volant mammals, including a total of 20 species of rodents and marsupials (Palmeirim et al., 2018a), species richness was best predicted by both island area and isolation (Borges, 2007). However, the responses to these variables further depended on the species-specific ability to cross the matrix (Palmeirim et al., 2018a). Between-site (β) diversity of both small mammals and midsize to large mammals was additionally affected by local vegetation characteristics (Palmeirim et al., 2018b). When considering taxonomic, functional, and phylogenetic diversity, island area stood out as the most important predictor. These same
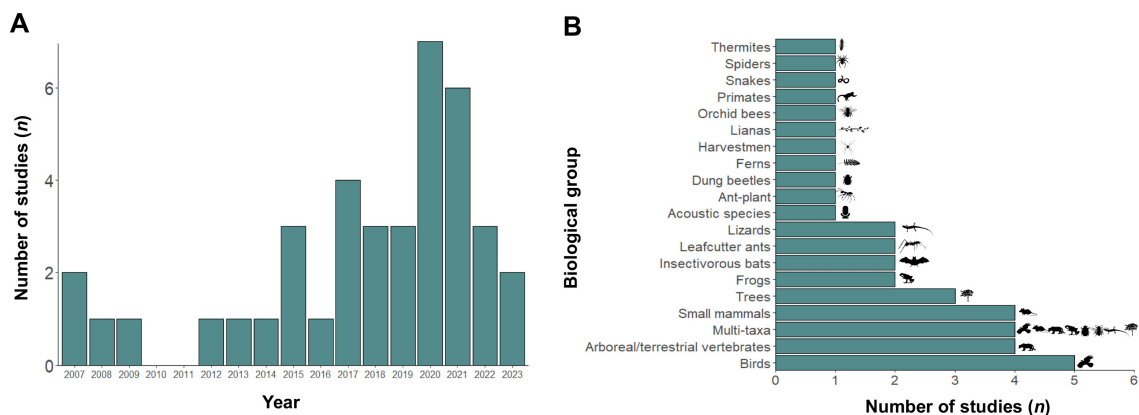
Figure 3 Studies carried out in Balbina focused on the effects of insular forest fragmentation

A, B: Number of studies (A) per year and (B) per biological group in the Balbina insular landscape, Brazilian Amazonia. Studies include published scientific papers (n=33), MSc theses (if no corresponding paper has been published; n=5), and book chapters (n=1). Only studies published until the end of August 2023 have been included.

Table 1 References of studies carried out in Balbina to quantify biodiversity responses to insular forest fragmentation as organised by topic covered, biological group targeted, number of surveyed sites —islands, continuous forest (CF) sites and open-water matrix sites—and the variables assessed

Topic	Biological group	Reference	No. surveyed sites	Variables assessed
Overall species diversity				
	Frogs	Bueno et al., 2020	74 islands, 4 CF sites	i.area
	Midsized-large vertebrates	Benchimol & Peres, 2015a	37 islands, 3 CF sites	f.area, dist, prox, shape, burn, %closed-canopy, fruit-area
	Birds	Aurelio-Silva et al., 2016	27 islands, 3 CF sites	i.area, dist, prox, dist.river
	Dung beetles	Storck-Tonon et al., 2020	30 islands, 3 CF sites	f.area, i.area, dist, prox, shape, %closed-canopy, n.islands, burn, S-trees, D-trees, Simpson-trees, %old-growth, Area-trees
	Ferns	Zuquim et al., 2022	10 islands	i.area, dist, %cover, burn, %pioneer
	Harvestmen	Tourinho et al., 2020	20 islands, 1 CF sites	i.area, dist, prox, %cover, litter, D-trees, D-palms, fallen steams
	Insectivorous bats	Di Ponzio et al., 2023	28 islands, 3 CF sites	f.area, dist, dist-neighbour, %cover, D-trees, S-trees, Area-trees, burn, clutterness, edge-area
	Lianas	Jones et al., 2017	36 islands, 3 CF sites	i.area, dist, %cover, burn, wind-angle, dist-edge, slope
	Lizards	Bittencourt, 2008	20 islands, 4 CF sites	i.area, prox, shape, litter, D-palm, D-trees
		Palmeirim et al., 2017	25 islands, 4 CF sites	i.area, dist, prox, shape
	Orchid bees	Storck-Tonon & Peres, 2017	34 islands, 3 CF sites, 14 matrix sites	i.area, f.area, dist, dist-neighbour, dist-edge, prox, cover, %closed-canopy, %open-canopy, S-trees, Simpson-trees, %old-growth
	Primates	Benchimol & Venticinque, 2014	20 islands	i.area, prox, n.islands, %cover, openness, height, v.stratification, D-trees, lianas
	Small mammals	Borges, 2007	8 islands, 1 CF site	i.area, prox
		Palmeirim et al., 2018a	25 islands, 4 CF sites	i.area, dist, prox, shape, S-trees, D-trees, %closed-canopy, burn, %old-growth, fruit-area, lianas
	Snakes	Palmeirim et al., 2021a	25 islands, 4 CF sites	i.area, dist, prox, shape
	Spiders	Ferreira, 2007	20 islands, 1 CF site	i.area, prox, shape
	Trees (adult)	Benchimol & Peres, 2015b	34 islands, 3 CF sites	i.area, f.area, dist, prox, %cover, edge-dist, burn, slope, wind-angle
	Trees (saplings)	Jones et al., 2019	36 islands, 3 CF sites	i.area, dist, %cover, burn
Species-specific responses				
	Midsized-large vertebrates	Benchimol & Peres, 2015c	37 islands, 3 CF sites	i.area, f.area, dist, prox, shape, %cover, burn, %closed-canopy, fruit-area
Beta-diversity				
	Mammals	Palmeirim et al., 2018b	23 islands, 2 CF sites	i.area, dist, prox, shape, %cover, S-trees , D-trees, %closed-canopy, burn, %old-growth , fruit-area, lianas
Multiple dimensions/scales of diversity				
	Small mammals and lizards	Palmeirim et al., 2021c	26 islands, 4 CF sites	i.area, dist, prox, shape, S-trees
Functional diversity				
	Insectivorous bats	Colombo et al., 2023	28 islands, 3 CF sites	f.area, dist, %cover, burn, S-tree, D-tree, Area-tree, cluterness, dist-edge
Phylogenetic diversity				
	Trees	Santo‑Silva et al., 2021	34 islands, 3 CF sites	i.area, dist, %cover, brun, wind-angle, slope, dist-edge
Habitat Amount Hypothesis				
	Birds	Bueno & Peres, 2019	33 islands	f.area, %cover (multiple circular buffers)
Importance of baseline suitability				
	Birds	Bueno & Peres, 2020	33 islands, 4 CF sites	f.area
	Multi-taxa	Jones et al., 2021	72 islands, 4 CF sites	i.area
Inter-trophic relationships				
	Leafcutter ants	Nogueira, 2009	25 islands, 25 CF sites	islands vs CF sites
		Palmeirim et al., 2021b	34 islands, 3 CF sites	f.area, burn, Ab-pioneer
Species-habitat networks				
	Multi-taxa	Palmeirim et al., 2022	22 islands, 3 CF sites	f.area, dist, burn, %water
Prey-predator networks				
	Midsized-large vertebrates	Pires et al., 2023	37 islands, 3 CF sites	i.area, f.area, closed-canopy.area, dist, prox, shape, %cover, %closed-canopy

Topic	Biological group	Reference	No. surveyed sites	Variables assessed
Mutualistic networks				
	Ants and plants	Emer et al., 2013	20 islands, 5 CF sites	i.area, dist, prox; island interior vs island edge vs CF
Acoustic space				
	Soundscape	Luypaert et al., 2023	49 islands	f.area, %water
Acoustic signal				
	Birds	Bicudo et al., 2016	13 islands, 2 CF sites	i.area, prox, D-trees, Area-trees
Activity patterns				
	Frogs	Masseli, 2021	74 islands, 4 CF sites	i.area
Physiological mechanisms				
	Birds	Bicudo et al., 2020	13 islands, 2 CF sites	i.area
Check list				
	Thermites	de Sales Dambros et al., 2012	5 CF sites, 5 matrix sites	matrix vs CF
Methodological insights				
	Midsized-large vertebrates	Benchimol & Peres, 2020	37 islands, 3 CF sites	i.area, dist, prox, %cover, %closed-canopy, brun, fruit-area
	Small mammals	Palmeirim et al., 2019	23 islands, 2 CF sites	-
	Small mammals	Palmeirim et al., 2020	14 islands, 2 CF sites	i.area

The description of each metric can be found in Supplementary Table S2. As further indicated in the table, some studies have compared biodiversity metrics between islands, mainland CF sites and matrix sites. The assessed variables included: total island area (i.area), forest island area (f.area), island distances to the nearest mainland forest site (dist), nearest island (dist-neighbour), and nearest portion of the once river channel (dist-river), the Proximity index, or an adaptation of that (prox), island shape (shape), proportion of forest cover (%cover), proportion of open-water cover (%water), degree of fire severity (burn), percentage of closed-canopy forest (%closed-canopy), percentage of open-canopy forest (%open-canopy), basal area of trees bearing fleshy fruits (fruit-area), number of tree species (S-trees), density of trees (D-trees), Simpson diversity index of tree species (Simpson-trees), aggregated tree basal area (Area-trees), percentage of pioneer tree stems (%pioneer), abundance of pioneer trees (Ab-pioneer), percentage of old-growth trees (%old-growth), density of palms (D-palms), number of fallen woody stems (fallen-stems), degree of vegetation clutter (cluterness), mean number of lianas (lianas), litter depth (litter), windstorm angle (wind-angle), terrain slope (slope) and distance to the nearest edge (dist-edge).
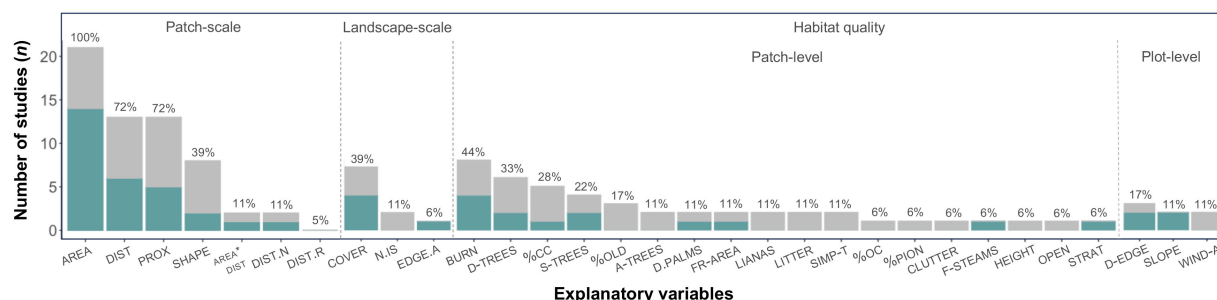

Figure 4 Number of studies targeting overall species diversity including each of the explanatory variables
At the patch-scale: Island total area/island forest area (area), distance from mainland (dist), proximity index (prox), island shape (shape), interaction between area and dist (area*dist), neighbour island distance (dist.n), river distance (dist.r); at the landscape-scale: forest cover (cover), number of neighbour islands (n.is), edge area (edge.a); and regarding habitat quality at the patch-level: fire severity (burn), density of trees (d-trees), percentage of closed-canopy forest (%cc), species richness of trees (s-trees), percentage of old-growth trees (%old), basal area of trees (a-trees), density of palms (d.palms), basal area of fleshy-fruiting trees (fr-area), number of lianas (lianas), tree diversity (simp-t), percentage of open-canopy forest (%oc), percentage of pioneer trees (%pion), vegetation clutter (cluter), number of fallen steams (f-steams), canopy height (height), canopy openness (open), vertical stratification (strat); and, at the plot-level: edge distance (d-edge), terrain slope (slope), windstorm angle (wind-a). Bars are colour-coded according to the number of studies on which that variable was statistically important/unimportant at explaining species diversity in the fragmented landscape. The percentage of studies on which each variable has been included is indicated above each bar. A total of 18 studies regarding 15 biological groups (i.e., considering adult and sapling trees in the same biological group) were included in this plot.

patterns are echoed by those noted for diurnal lizard assemblages, which consisted of 17 taxa (Bittencourt, 2008; Palmeirim et al., 2017; Palmeirim et al., 2021a). Likewise, the persistence of 37 anuran species, recorded via passive acoustic monitoring at a large number of sites (compared to other studies), including 74 islands and four mainland CF sites, was also best predicted by island size (Bueno et al., 2020). Island size further positively affected the vocal activity time of these assemblages (Masseli, 2021). Considering 61 forest bird species, diversity was primarily affected by island size (Aurélio-Silva et al., 2016), but small islands were unlikely to translate into higher physiological stress for birds, given the

lack of a relationship between corticosterone levels (measured from bird feathers) and island area (except for the Guianan Antwarbler *Hypocnemis cantator*) (Bicudo et al., 2020). Furthermore, considering a limited sample of 50 snakes belonging to 16 species, species richness was also positively affected by forest area, explaining 48% of the number of species, and negatively affected by island isolation (Palmeirim et al., 2021b). Notwithstanding, species richness of aerial insectivorous bats (including 23 sonotypes, each of which corresponds to one or more species that emit calls of similar shape and peak frequency), was unaffected by island size or isolation. Yet, bat species composition was affected by the island area (Di Ponzio et al., 2023).

Invertebrates: Considering the eight invertebrate taxa examined at Balbina, dung beetles were thought to be the most affected by insular forest fragmentation (Palmeirim et al., 2022). Only two out of 34 dung-beetle species in the regional species pool were found on islands smaller than 10 ha. Given that most Balbina islands are small, Storck-Tonon et al. (2020) estimated that one third of all islands are highly defaunated in terms of their dung-beetle assemblages. For scarabeine beetles, species richness was instead best predicted by island isolation, followed by an interaction between isolation and island size, with both variables determining species composition (Storck-Tonon et al., 2020). Conversely, orchid bees (Euglossinae), which were represented by 25 species, were seemingly most resilient group to insular fragmentation, showing the least steep species-area relationship (Jones et al., 2021), and the most robust species-habitat networks (Palmeirim et al., 2022). Orchid bee species richness was predicted by both island area, isolation, and distance to forest edges. This has been the only group to date that was surveyed throughout the aquatic matrix, ensuring a better understanding of the variation in matrix dispersal as a key determinant of the community structure (Storck-Tonon & Peres, 2017).

Similarly to insectivorous bats, species richness of harvestmen (31 species recorded) was unaffected by any local patch or landscape variables. Yet, species composition was affected by landscape-scale forest cover and fallen woody stems, while species abundance was affected by vegetation density, forest cover, island area, abundance of arborescent palms, and fallen woody stems (Tourinho et al., 2020). From a total of 34 species, spider species richness was affected by isolation, and species composition was more similar between continuous forest sites than between islands (Ferreira, 2007). Likewise, termite assemblages (26 species recorded) were also more similar in composition between mainland continuous forest than between the dead tree snags surveyed in the aquatic matrix (de Sales Dambros et al., 2012).

Plants: Based on a floristic inventory including 368 species of trees ≥10 cm DBH, adult tree species richness at Balbina was mostly predicted by forest area. However, forest edge effects were responsible for non-random floristic transitions across islands via a process of rapid pioneer proliferation (Benchimol & Peres, 2015b). Santo-Silva et al. (2021) further showed a reduction in phylogenetic diversity on small (<10 ha), isolated islands, particularly in more fire-prone areas near forest edges surrounded by low amounts of forest cover. Considering tree saplings, islands harboured lower stem densities than nearby CF sites. Altogether, these findings highlight the instability of insular tree communities at Balbina, with rare species

becoming extinction-prone due to reduced tree recruitment and density on islands (Jones et al., 2019).

Woody lianas comprise a group that was hypothesised to generally benefit from insular forest fragmentation (Wright et al., 2015). As such, Jones et al. (2017) noted that community composition remained similar between islands and CF sites. Lianas further increased in dominance relative to trees in the sapling layer in the most degraded islands, with both the amount of forest cover surrounding islands and history of fire disturbance predicting liana dominance. Considering ferns or lycophytes, here sampled through a citizen science approach using photographs systematically recorded by a non-expert, species richness across a pool of 23 species was positively related to island size and negatively related to isolation and fire severity (Zuquim et al., 2022).

Patterns of trait-based persistence

Species persisting on the forest islands were further prone to being affected by insularisation due to their intrinsic eco-morphological traits. Patterns of remaining species diversity on islands were thus deterministically induced by nonrandom local extinctions. In addition to dispersal capacity, traits associated with success in disturbed habitat remnants play important roles in structuring biological communities isolated within forest islands (Palmeirim et al., 2022). Below, we provide a general overview of the trait-related responses reported for each of the biological groups surveyed at Balbina.

In the case of mid- to large-bodied terrestrial and arboreal vertebrates, higher extinction rates were noted for wide-ranging species with large spatial requirements (Benchimol & Peres, 2015c). Considering small mammals, forest-dependent species experienced higher local extinction rates and were often either absent or persisted at low abundances on small islands, where non-forest-dependent species became particularly abundant (Palmeirim et al., 2018a). In addition, small-bodied rodents and marsupials were less extinction-prone (Palmeirim et al., 2021a). Lizard assemblages inhabiting small, isolated islands consisted almost exclusively of an oversimplified set of widely distributed, large-bodied, habitat generalist, heliophile species that are energetically subsidised by sun flecks in open areas and forest edges, and that feed on a wide spectrum of prey sizes. In one of the surveyed CF sites, additional lizard trapping transects were deployed along stream banks, in which two lizard species have been exclusively recorded. Those riparian species are likely to be virtually absent from the whole insular landscape as lowland areas along perennial streams have been flooded (Palmeirim et al., 2017).

The most dam-affected bird guilds included terrestrial omnivores and insectivores, small understorey frugivores and large-bodied frugivores and faunivores (Aurélio-Silva et al., 2016). Colombo et al. (2023) found that understorey foraging large insectivorous bats exhibiting greater dispersal capacity, constant frequency–modulated calls, and higher frequency of maximum energy were associated with small, isolated islands. A recent study including eight biological groups further added that large-bodied orchid bees and smaller-bodied anurans were more widely distributed across the landscape (Palmeirim et al., 2022). At the extreme end of the fragmentation gradient characterised by the smaller islands, tree species were mostly light-wooded, fast-growing pioneers, which have largely replaced the heavy-wooded species of the former old-growth flora (Benchimol & Peres, 2015b; Jones et al., 2019).

Additional studies

Studies carried out in the Balbina landscape to examine species interactions included: ant-plant mutualistic interactions (Emer et al., 2013), vertebrate predator-prey interactions (Pires et al., 2023), and two studies focused on leafcutter ants and their inter-trophic relationships (Nogueira, 2009; Palmeirim et al., 2021c). In mutualistic ant-plant interactions, the myrmecophyte plants provide domatia nesting space to their symbiotic ants. In 31 ant-myrmecophyte networks in undisturbed and disturbed sites surrounding Balbina, networks were found to be highly compartmentalised in undisturbed forests, and the compartments had few strongly connected mutualistic partners. In contrast, networks at lake edges and on islands were poorly compartmentalised and negatively affected by island area and isolation in terms of species richness, density, and composition (Emer et al., 2013). Using data from forest vertebrate surveys, combined modelling and network analysis, Pires et al. (2023) investigated how the structure of predator-prey networks was affected by habitat insularisation. Network complexity, here measured by interaction diversity, decayed non-linearly with decreasing forest area (Pires et al., 2023). The leafcutting ants (*Atta* spp.) are dominant herbivores in Neotropical forests, and their colony density typically increases in the aftermath of habitat disturbance (Leal et al., 2014). At Balbina, leafcutter ant colony density, wherever they were present, was a negative function of island size (Palmeirim et al., 2021c), being lower than that in adjacent CF sites around the lake (Nogueira, 2009).

To understand how the effects of insular fragmentation scale up to entire landscapes, Palmeirim et al. (2022) applied species-habitat networks on multiple taxa surveyed across a common set of 22 forest islands and three CF sites. Here, a species-habitat network represented a landscape in which each species is a node that is linked to another set of nodes matching the forest islands where that species occurs. Interaction links within the network are established by the occurrence of a given species at a given island. Emerging properties of entire species-habitat networks were then quantified using traditional metrics largely used in network studies. Overall, this study revealed that widespread, non-random local species extinctions were translated into highly nested networks of low connectance and modularity. Network robustness considering the sequential removal of large-to-small sites was further noted to be generally low, with between 5% (dung beetles) and 50% (orchid bees) of species persisting when the landscape retained only islands smaller than 10 ha.

Bueno & Peres (2019) tested the Habitat Amount Hypothesis (Fahrig, 2013), and found that the relative importance of island size in determining the species richness of understorey insectivorous birds on forest islands was higher than that of the surrounding habitat amount. As such, their findings provided stronger support for the island biogeography paradigm (MacArthur & Wilson, 1967). Other studies have examined species responses to insular fragmentation at Balbina by excluding species that were not present in CF sites (e.g., birds: Bueno & Peres, 2020; eight biological groups: Jones et al., 2021). Both studies highlight the importance of the intactness of reference sites to accurately assess the impacts of land-use change on biodiversity and establish conservation strategies. The multi-taxa study further found that adult trees comprise the biological group showing the

species-area relationship that best represents the remaining groups (Jones et al., 2021). In addition, scaling of biodiversity has been recently extended to the realm of ecoacoustics. Here, Luypaert et al. (2023) used eco-acoustic metrics to investigate ecological patterns without requiring biodiversity assessments at the species-level. Instead, environmental sounds were grouped into bins with shared acoustic traits in the time-frequency domain of the acoustic space in which sound is produced. These soundscape metrics were shown to be sensitive to ecological patterns that were largely predicted by island area.

Three studies have provided methodological insights. Palmeirim et al. (2020), using small mammal data, observed that potential sampling biases are more likely at larger forest sites, which should be more intensively sampled to reduce any such bias. Although not testing the effects of insular forest fragmentation, co-sampling of multiple taxa at the same sites further allowed testing the efficiency of alternative methods for surveying small mammals (Palmeirim et al., 2019). Likewise, by identifying the most reliable survey method for any given species (diurnal censuses vs. camera-trapping), Benchimol & Peres (2021) were able to integrate measures of species abundance based on different methods to quantify abundance-area relationships (AARs) and assess how extinction proneness is governed by local population sizes.

DISCUSSION

To date, the economic benefits of hydropower development in lowland tropical forests have been overestimated, whereas the environmental costs have been broadly neglected (Moran et al., 2018). Nevertheless, large hydroelectric projects will continue to be justified by an ever-larger world population and growing per capita rates of energy consumption (Chen et al., 2016). The Balbina Hydroelectric Reservoir is an emblematic case study for its socio-environmental "disaster" (Fearnside, 1989). Here, we focused on the archipelagic Balbina landscape upstream of the dam and synthesised the current knowledge of the detrimental effects of insular forest fragmentation on terrestrial biodiversity, as gathered from the 39 studies covering 17 biological groups.

Drivers of dam-induced biodiversity loss

Overall, island area was the most important driver of species diversity, consistently affecting species persistence in all biological groups. Indeed, habitat area affects local extinction probability (MacArthur & Wilson, 1967), which directly reflects the number of species able to persist on each island. Conversely, island isolation effects were relatively weak, yet still noticeable for some groups (e.g., dung-beetles and orchid bees). Habitat quality, as considered by a different set of variables according to the study (Supplementary Table S2), often affected the assemblage-wide metrics of diversity. For instance, fire perturbation underpinned the turnover of tree assemblages, favouring fast-growing pioneers at the expense of old-growth tree species (Benchimol & Peres, 2015b). As such, this type of disturbance contributed to the decline of several vertebrate species (Barlow & Peres, 2004). Edge effects drastically affect the integrity of plant assemblages, and consequently that of other species that depend on them, as noticed for orchid bees (Storck-Tonon and Peres, 2017).

Furthermore, species persistence was highly variable across taxa, with orchid bees and dung beetles likely the least and the most affected taxa, respectively. This differential

vulnerability shown by different biological groups is possibly related to their ability to use the aquatic matrix or to tolerate habitat degradation (Newbold et al., 2014). This is further supported by the studies considering species-specific traits (e.g., mid-sized to large vertebrates, small mammals, lizards, orchid bees, and lianas). For instance, swimming capacity in vertebrates >1 kg traversing a large body of open-water, which was measured over 25 years of empirical observation, partly explained which species persisted on islands (Benchimol & Peres, 2015a), presumably because this proxy of dispersal ability affected species-specific recolonization rates. These findings further suggest that non-random species extirpations in Balbina are likely to affect the ecological processes underpinning ecosystem functioning, so that future studies should further cover that topic.

Patterns of remaining species diversity tend to contrast with those observed in other tropical and sub-tropical reservoirs. In the Guri Lake, top-down forces have been weakened with the local extinction of predators, causing a marked increase in herbivore abundance and herbivory (Terborgh et al., 2001). In contrast, mechanisms controlling species diversity at Balbina are more likely to be bottom-up-mediated, being most likely related the overall low foliage palatability typical of wet evergreen forests (Palmeirim et al., 2021c). As such, lower trophic guilds would not be "released" and considerably increase their abundance even in the absence of predators, as observed at the Guri Lake (Rao, 2000; Terborgh et al., 2001). In the Chiew Larn Reservoir, where small mammals have been extensively surveyed, Gibson et al. (2017) reported the collapse of these species, which was attributed to habitat loss and fragmentation, was further boosted by the hyper-dominance of a rat species (*Rattus tiomanicus*) which gradually displaced all other small mammal species over time (Moore et al., 2022). In Balbina, we have failed to observe clear evidence of hyper abundance in any animal taxa. In the Kenyir Lake, Malaysia, non-random species extinctions were observed for insectivorous bats (Hazard et al., 2023) and dung-beetles (Qie et al., 2011), resembling the scenario observed for Balbina (Palmeirim et al., 2022). Furthermore, while island area is commonly the best predictor of species diversity at Balbina (Palmeirim et al., 2022), species diversity in the Thousand Island Lake in China is more often suggesting a "small island effect", i.e., when species richness varies independently of island area (e.g., Chen et al., 2019; López-Bosch et al., 2022; Wang et al., 2015, 2018).

Lessons from the Balbina landscape
The information synthetised here illustrates the detrimental ecological effects of insular fragmentation as induced by damming across lowland tropical forests. Indeed, as in other dam-induced archipelagos, most Balbina islands are relatively small (e.g., 90% of all islands are smaller than 100 ha), and thus sustain impoverished species assemblages. Forest islands in Balbina contribute low conservation values compared to forest fragments left in terrestrial matrix settings (Jones et al., 2021). Indeed, extinction rates are reported to be higher in insular than in terrestrial forest fragments for both birds (Wolfe et al., 2015) and lizards (Palmeirim et al., 2017). Moreover, overall habitat quality of insular forest fragments will only get worse over the time, a process that will be faster on smaller islands which are more edge-affected (Benchimol & Peres, 2015a). This will contribute to the overall decline in species diversity and payment of any extinction debt (Jones et al., 2016). In comparison, even small forest remnants <10 ha in a southern Amazonian landscape dominated by cattle

pastures contribute significantly to the overall regional scale diversity in both dung beetles (Noble et al., 2023) and leaflitter ants (Dambros et al., 2024).

Immediately after the Balbina dam construction, a strictly protected area was created as a mitigation measure for the negative effects of insular fragmentation on biodiversity (Fearnside, 1989). This protection likely contributes to maintaining part of the biodiversity (Benchimol & Peres, 2015c). Indeed, hunting and logging are not pervasive anthropogenic stressors in Balbina. This makes Balbina a "best-case" scenario in terms of additional anthropogenic threats. This highly contrasts with the eastern Amazonian Tucuruí Hydroelectric Reservoir, where a considerable part of the islands and margins of the lake were occupied by small farmers and are now deforested (Velastegui-Montoya et al., 2020), contributing to wholesale regional scale extinctions in at least birds (Henriques et al., 2021). Both types of additional human disturbances are widely known to interact synergistically with habitat fragmentation and lead to increased depletion rates of species persistence (Peres, 2001). In the case of large-bodied vertebrates, overall species island occupancy rates were higher in Balbina compared to other Neotropical fragmented forest landscapes (Benchimol & Peres, 2015c, but see Michalski & Peres, 2005). It is therefore likely that forest loss, fragmentation and subsequent degradation after impoundment has been far worse in other major Amazonian dams.

Based on our findings throughout the Balbina landscape, our main recommendation to maximise the persistence of biodiversity in tropical forest contexts, is preventive rather than remedial: future hydropower projects need to avoid flooding large expanses of forest and creating myriad small islands. This can be achieved through the appropriate dam site selection. Guidelines to improve site selection exist and are known to those who fund large hydropower infrastructure (e.g., Ledec & Quintero, 2003). Making compliance in following such guidelines mandatory would contribute towards more ecologically sustainable hydropower development, if they cannot be avoided, across lowland tropical forests. Also, given differences in species responses to insular habitat fragmentation across the tropics, assessing ecological impacts from damming should be site-specific. Finally, the robust amount of evidence provided here indicates that key reforms in Environmental Impact Assessments are needed, including the incorporation of accurate estimates of both habitat loss and biodiversity erosion through space and time. This would allow us to truly account for the long-term ecological impacts on natural environments within insular landscapes created by river impoundment.

REFERENCES
Alho CJR. 2020. Hydropower dams and reservoirs and their impacts on

Brazil's biodiversity and natural habitats: a review. *World Journal of Advanced Research and Reviews*, **6**(3): 205–215.

Alvares CA, Stape JL, Sentelhas PC, et al. 2013. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift*, **22**(6): 711–728.

Aurélio-Silva M, Anciães M, Henriques LMP, et al. 2016. Patterns of local extinction in an Amazonian archipelagic avifauna following 25 years of insularization. *Biological Conservation*, **199**: 101–109.

Barlow J, Peres CA. 2004. Ecological responses to El Niño-induced surface fires in central Brazilian Amazonia: management implications for flammable tropical forests. *Philosophical Transactions of the Royal Society B:Biological Sciences*, **359**(1443): 367–380.

Benchimol M, Peres CA. 2015a. Widespread forest vertebrate extinctions induced by a mega hydroelectric dam in lowland Amazonia. *PLoS One*, **10**(7): e0129818.

Benchimol M, Peres CA. 2015b. Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. *Journal of Ecology*, **103**(2): 408–420.

Benchimol M, Peres CA. 2015c. Predicting local extinctions of Amazonian vertebrates in forest islands created by a mega dam. *Biological Conservation*, **187**: 61–72.

Benchimol M, Peres CA. 2021. Determinants of population persistence and abundance of terrestrial and arboreal vertebrates stranded in tropical forest land-bridge islands. *Conservation Biology*, **35**(3): 870–883.

Benchimol M, Venticinque EM. 2014. Responses of primates to landscape change in Amazonian land-bridge islands —a multi-scale analysis. *Biotropica*, **46**(4): 470–478.

Bicudo T, Anciães M, Arregui L, et al. 2020. Effects of forest fragmentation on feather corticosterone levels in an Amazonian avian community. *Ardeola*, **67**(2): 229–245.

Bicudo T, Anciães M, Benchimol M, et al. 2016. Insularization effects on acoustic signals of 2 suboscine Amazonian birds. *Behavioral Ecology*, **27**(5): 1480–1490.

Bittencourt S. 2008. A Insularização Como Agente de Fragmentação Florestal em Comunidades de Lagartos na Amazônia Central. Master thesis, Instituto Nacional de Pesquisas da Amazônia, Manaus.

Borges MLDO. 2007. A Comunidade de Pequenos Mamíferos e o Processo de Regeneração de Palmeiras em Fragmentos Florestais Isolados por Água na Amazônia Central. Master thesis, Instituto Nacional de Pesquisas da Amazônia, Manaus.

Bucknall J, Foster V, Liden MJR, et al. 2014. Supporting hydropower: an overview of the World Bank Group's engagement. The World Bank. https://documents.worldbank.org/pt/publication/documents-reports/documentdetail/628221468337849536/supporting-hydropower-an-overview-of-the-world-bank-groups-engagement.

Bueno AS, Peres CA. 2019. Patch-scale biodiversity retention in fragmented landscapes: Reconciling the habitat amount hypothesis with the island biogeography theory. *Journal of Biogeography*, **46**(3): 621–632.

Bueno AS, Peres CA. 2020. The role of baseline suitability in assessing the impacts of land-use change on biodiversity. *Biological Conservation*, **243**: 108396.

Bueno AS, Masseli GS, Kaefer IL, et al. 2020. Sampling design may obscure species-area relationships in landscape-scale field studies. *Ecography*, **43**(1): 107–118.

Chen CW, Xu AC, Ding P, et al. 2019. The small-island effect and nestedness in assemblages of medium-and large-bodied mammals on Chinese reservoir land-bridge islands. *Basic and Applied Ecology*, **38**: 47–57.

Chen J, Shi HY, Sivakumar B, et al. 2016. Population, water, food, energy and dams. *Renewable and Sustainable Energy Reviews*, **56**: 18–28.

Colombo GT, Di Ponzio R, Benchimol M, et al. 2023. Functional diversity and trait filtering of insectivorous bats on forest islands created by an Amazonian mega dam. *Functional Ecology*, **37**(1): 99–111.

Dambros CS, Izzo TJ, de Oliveira LC, et al. 2024. Beta-diversity buffers fragmented landscapes against local species losses. *Oikos*, **2024**(3): e10401.

de Amorim ME, Schoener TW, Santoro GRCC, et al. 2017. Lizards on newly created islands independently and rapidly adapt in morphology and diet. *Proceedings of the National Academy of Sciences of the United States of America*, **114**(33): 8812–8816.

de Sales Dambros C, de Mendonça DRM, Rebelo TG, et al. 2012. Termite species list in a terra firme and ghost forest associated with a hydroelectric plant in Presidente Figueiredo, Amazonas, Brazil. *Check List*, **8**(4): 718–721.

Di Ponzio R, Colombo GT, Bicudo T, et al. 2023. Aerial insectivorous bat responses to 30 years of forest insularization in a dam-created Amazonian archipelagic landscape. *Biological Conservation*, **285**: 110222.

Diamond J. 2001. Dammed experiments! *Science*, **294**(5548): 1847–1848.

ECOA —Ecologia em Ação. 2016[2017-06-05]. International rivers and fundacion proteger, dams in Amazonia.

Emer C, Venticinque EM, Fonseca CR. 2013. Effects of dam-induced landscape fragmentation on Amazonian ant–plant mutualistic networks. *Conservation Biology*, **27**(4): 763–773.

Ewers RM, Didham RK. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**(1): 117–142.

Fahrig L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, **40**(9): 1649–1663.

Fearnside PM. 1989. Brazil's Balbina Dam: environment versus the legacy of the pharaohs in Amazonia. *Environmental Management*, **13**(4): 401–423.

Fearnside PM, Pueyo S. 2012. Greenhouse-gas emissions from tropical dams. *Nature Climate Change*, **2**(6): 382–384.

Ferreira RS. 2007. Efeitos do Isolamento e da Perda de Área de Floresta Sobre Comunidades Insulares de Aranhas, Amazônia Central, Brasil. Master thesis, Instituto Nacional de Pesquisas da Amazônia, Manaus.

Finer M, Jenkins CN. 2012. Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes-Amazon connectivity. *PLoS One*, **7**(4): e35126.

Gibson L, Wilman EN, Laurance WF. 2017. How green is 'green' energy?. *Trends in Ecology & Evolution*, **32**(12): 922–935.

Hazard QC, Froidevaux JS, Yoh N, et al. 2023. Foraging guild modulates insectivorous bat responses to habitat loss and insular fragmentation in peninsular Malaysia. *Biological Conservation*, **281**: 110017.

Henriques LMP, Dantas S, Santos LB, et al. 2021. Avian extinctions induced by the oldest Amazonian hydropower mega dam: evidence from museum collections and sighting data spanning 172 years. *PeerJ*, **9**: e11979.

IBAMA. 1997[2023-06-05]. Plano de Manejo Fase I: Reserva Biológica do Uatumã. http://www.icmbio.gov.br.

Jones IL, Bull JW. 2020. Major dams and the challenge of achieving "No Net Loss" of biodiversity in the tropics. *Sustainable Development*, **28**(2): 435–443.

Jones IL, Bunnefeld N, Jump AS, et al. 2016. Extinction debt on reservoir land-bridge islands. *Biological Conservation*, **199**: 75–83.

Jones IL, Peres CA, Benchimol M, et al. 2017. Woody lianas increase in dominance and maintain compositional integrity across an Amazonian dam-induced fragmented landscape. *PLoS One*, **12**(10): e0185527.

Jones IL, Peres CA, Benchimol M, et al. 2019. Instability of insular tree communities in an Amazonian mega-dam is driven by impaired recruitment and altered species composition. *Journal of Applied Ecology*, **56**(3): 779–791.

Jones IL, Bueno AS, Benchimol M, et al. 2021. Using relict species-area relationships to estimate the conservation value of reservoir islands to improve environmental impact assessments of dams. *In*: Matthews TJ, Triantis KA, Whittaker RJ. The Species-Area Relationship: Theory and Application. Cambridge: Cambridge University Press, 417–437.

Leal IR, Wirth R, Tabarelli M. 2014. The multiple impacts of leaf-cutting ants and their novel ecological role in huma-modified neotropical forests. *Biotropica*, **46**(5): 516–528.

Ledec G, Quintero JD. 2003. Good dams and bad dams: environmental criteria for site selection of hydroelectric projects. Latin America and

Caribbean Region: Environmentally and Socially Sustainable Development Sector Management Unit.

Lees AC, Peres CA, Fearnside PM, et al. 2016. Hydropower and the future of Amazonian biodiversity. *Biodiversity and Conservation*, **25**(3): 451–466.

Lima JR, Galatti U, Lima CJ, et al. 2015. Amphibians on Amazonian land-bridge islands are affected more by area than isolation. *Biotropica*, **47**(3): 369–376.

Liu JJ, Slik F, Coomes DA, et al. 2019. The distribution of plants and seed dispersers in response to habitat fragmentation in an artificial island archipelago. *Journal of Biogeography*, **46**(6): 1152–1162.

López-Bosch D, Rocha R, López-Baucells A, et al. 2022. Passive acoustic monitoring reveals the role of habitat affinity in sensitivity of sub-tropical East Asian bats to fragmentation. *Remote Sensing in Ecology and Conservation*, **8**(2): 208–221.

Luypaert T, Bueno AS, Haugaasen T, et al. 2023. Extending species-area relationships into the realm of ecoacoustics: the soundscape-area relationship. *BioRxiv*, doi:https://doi.org/10.1101/2023.02.08.527658.

MacArthur RH, Wilson EO. 1967. The Theory of Island Biogeography. Princeton: Princeton University Press.

Masseli GS. 2021. Diferentes Padrões de Atividade Vocal de Espécies de Anuros Amazônicos Formam Assembleias Acústicas em Escala Diária. Master thesis, Instituto Nacional de Pesquisas da Amazônia, Manaus.

McGarigal K, Cushman SA, Ene E. 2012. FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. University of Massachusetts, Amherst, MA, USA.

Michalski F, Peres CA. 2005. Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biological Conservation*, **124**(3): 383–396.

Moore JH, Palmeirim AF, Peres CA, et al. 2022. Invasive rat drives complete collapse of native small mammal communities in insular forest fragments. *Current Biology*, **32**(13): 2997–3004.e2.

Moran EF, Lopez MC, Moore N, et al. 2018. Sustainable hydropower in the 21st century. *Proceedings of the National Academy of Sciences of the United States of America*, **115**(47): 11891–11898.

Newbold T, Scharlemann JPW, Butchart SHM, et al. 2014. Functional traits, land-use change and the structure of present and future bird communities in tropical forests. *Global Ecology and Biogeography*, **23**(10): 1073–1084.

Noble CD, Gilroy JJ, Berenguer E, et al. 2023. Many losers and few winners in dung beetle responses to Amazonian forest fragmentation. *Biological Conservation*, **281**: 110024.

Nogueira CA. 2009. Efeito do Isolamento e Perda de Área de Floresta Sobre Populações de Saúvas (Hymenoptera, Formicidae, *Atta*) e Seus Inimigos Naturais em Ilhas do Reservatório da UHE Balbina, Amazônia Central, Brasil. Master thesis, Instituto Nacional de Pesquisas da Amazônia, Manaus.

Palmeirim AF, Benchimol M, Morante-Filho JC, et al. 2018b. Ecological correlates of mammal β-diversity in Amazonian land-bridge islands: from small- to large-bodied species. *Diversity and Distributions*, **24**(8): 1109–1120.

Palmeirim AF, Benchimol M, Peres CA, et al. 2019. Moving forward on the sampling efficiency of neotropical small mammals: insights from pitfall and camera trapping over traditional live trapping. *Mammal Research*, **64**(3): 445–454.

Palmeirim AF, Benchimol M, Vieira MV, et al. 2018a. Small mammal responses to Amazonian forest islands are modulated by their forest dependence. *Oecologia*, **187**(1): 191–204.

Palmeirim AF, de Fraga R, Vieira MV, et al. 2021b. Species-area relationships induced by forest habitat fragmentation apply even to rarely detected organisms. *Tropical Conservation Science*, **14**: 1–7.

Palmeirim AF, Emer C, Benchimol M, et al. 2022. Emergent properties of species-habitat networks in an insular forest landscape. *Science Advances*, **8**(34): eabm0397.

Palmeirim AF, Farneda FZ, Vieira MV, et al. 2021a. Forest area predicts all

dimensions of small mammal and lizard diversity in Amazonian insular forest fragments. *Landscape Ecology*, **36**(12): 3401–3418.

Palmeirim AF, Benchimol M, Leal IR, Peres CA. 2021c. Drivers of leafcutter ant populations and their inter-trophic relationships in Amazonian forest islands. *Ecosphere*, **12**(5): e03518.

Palmeirim AF, Peres CA, Rosas FCW. 2014. Giant otter population responses to habitat expansion and degradation induced by a mega hydroelectric dam. *Biological Conservation*, **174**: 30–38.

Palmeirim AF, Peres CA, Vieira MV. 2020. Optimizing small mammal surveys in Neotropical fragmented landscapes while accounting for potential sampling bias. *Mammalian Biology*, **100**(1): 81–90.

Palmeirim AF, Vieira MV, Peres CA. 2017. Non-random lizard extinctions in land-bridge Amazonian forest islands after 28 years of isolation. *Biological Conservation*, **214**: 55–65.

Peres CA. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conservation Biology*, **15**(6): 1490–1505.

Pinho GM, da Silva AG, Hrbek T, et al. 2014. Kinship and social behavior of lowland tapirs (*Tapirus terrestris*) in a central Amazon landscape. *PLoS One*, **9**(3): e92507.

Pires MM, Benchimol M, Cruz LR, et al. 2023. Terrestrial food web complexity in Amazonian forests decays with habitat loss. *Current Biology*, **33**(2): 389–396.e3.

Qie L, Lee TM, Sodhi NS, Lim SL. H. , 2011. Dung beetle assemblages on tropical land-bridge islands: small island effect and vulnerable species. *Journal of Biogeography*, **38**(4), 792–804.

Rao M. 2000. Variation in leaf-cutter ant (*Atta* sp.) densities in forest isolates: the potential role of predation. *Journal of Tropical Ecology*, **16**(2): 209–225.

Santo-Silva EE, Benchimol M, Peres CA. 2021. Phylogenetic homogenization of Amazonian tree assemblages in forest islands after 26 years of isolation. *Applied Vegetation Science*, **24**(3): e12601.

Storck-Tonon D, Peres CA. 2017. Forest patch isolation drives local extinctions of Amazonian orchid bees in a 26 years old archipelago. *Biological Conservation*, **214**: 270–277.

Storck-Tonon D, da Silva RJ, Sawaris L, et al. 2020. Habitat patch size and isolation drive the near-complete collapse of Amazonian dung beetle assemblages in a 30-year-old forest archipelago. *Biodiversity and Conservation*, **29**(7): 2419–2438.

Terborgh J, Lopez L, Nuñez P, et al. 2001. Ecological meltdown in predator-free forest fragments. *Science*, **294**(5548): 1923–1926.

Tourinho AL, Benchimol M, Porto W, et al. 2020. Marked compositional changes in harvestmen assemblages in Amazonian forest islands induced by a mega dam. *Insect Conservation and Diversity*, **13**(5): 432–444.

Velastegui-Montoya A, de Lima A, Adami M. 2020. Multitemporal analysis of deforestation in response to the construction of the Tucuruí Dam. *ISPRS International Journal of Geo-Information*, **9**(10): 583.

Wang YP, Wang X, Wu Q, et al. 2018. The small-island effect in amphibian assemblages on subtropical land-bridge islands of an inundated lake. *Current Zoology*, **64**(3): 303–309.

Wang YP, Wu Q, Wang X, et al. 2015. Small-island effect in snake communities on islands of an inundated lake: the need to include zeroes. *Basic and Applied Ecology*, **16**(1): 19–27.

Wolfe JD, Stouffer PC, Mokross K, et al. 2015. Island vs. countryside biogeography: an examination of how Amazonian birds respond to forest clearing and fragmentation. *Ecosphere*, **6**(12): 1–14.

Wright SJ, Sun IF, Pickering M, Fletcher CD, Chen YY. 2015. Long-term changes in liana loads and tree dynamics in a Malaysian forest. *Ecology*, **96**(10): 2748–2757.

Zuquim G, Benchimol M, Tonon R, et al. 2022. Effects of forest degradation on Amazonian ferns in a land‐bridge island system as revealed by non‐specialist inventories. *Ecological Solutions and Evidence*, **3**(1): e12123.