

Instability of insular tree communities in an Amazonian mega-dam is driven by impaired recruitment and altered species composition

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Abstract

1. Mega-dams create highly fragmented archipelagos, affecting biodiversity and ecosystem functioning in remnant forest isolates. This study assessed the long-term impact of dam-induced fragmentation on insular tropical tree communities, with the aim of generating robust recommendations to mitigate some of the detrimental biodiversity impacts associated with future dam development.
2. We inventoried adult and sapling trees across 89 permanent plots, located on 36 islands and in three mainland continuous forest sites in the Balbina Dam, Brazilian Amazon. We examined differences in recruitment, structure, and composition of sapling and adult tree communities, in relation to plot-, patch- and landscape-scale attributes including area, isolation, and fire severity.
3. Islands harboured significantly lower sapling (mean \pm 95% CI 48.6 ± 3.8) and adult (5 ± 0.2) tree densities per 0.01 ha, than nearby mainland continuous forest (saplings, 65.7 ± 7.5 ; adults, 5.6 ± 0.3). Insular sapling and adult tree communities were more dissimilar than in mainland sites, and species compositions showed a directional shift away from mainland forests, induced by fire severity, island area, and isolation.
4. Insular sapling recruitment declined with increasing fire severity; tree communities with higher community-weighted mean wood density showed the greatest recruitment declines. Our results suggest that insular tree communities are unstable, with rare species becoming extinction-prone due to reduced tree recruitment and density on islands, potentially leading to future losses in biodiversity and ecosystem functioning across Balbina's >3,500 reservoir islands.
5. *Policy implications.* In Balbina, fire and reduced habitat area and connectivity were drivers of tree community decay after only 28 years of insularization, despite strict protection provided by the ~940,000 ha Uatumã Biological Reserve. Given that many dams are planned for lowland, moderately undulating Amazonia, we recommend that dam development strategy explicitly considers (a) dam location, aiming to

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minimize creation of small (<10 ha) and isolated islands, (b) maintaining reservoir water levels during droughts to reduce fire risk, and (c) including aggregate island area in environmental impact and offset calculations. Ideally, we recommend that alternatives to hydropower be sought in lowland tropical regions, due to the far-reaching biodiversity losses and ecosystem disruption caused by river impoundment.

KEYWORDS

environmental impact assessment, fire, floristic change, fragmentation, habitat connectivity, hydropower, mega-dam, tropical forest

1 | INTRODUCTION

Major hydroelectric dams contribute to landscape-scale loss and fragmentation of terrestrial and aquatic environments (Gibson, Wilman, & Laurance, 2017). Across the Amazon watershed, 191 dams are in operation with a further 246 planned or under construction. Amazonian dams cause wholesale changes in the functioning of riverine systems, displace people, release methane and CO₂, and drastically affect biodiversity (Benchimol & Peres, 2015a; Fearnside & Pueyo, 2012; Latrubesse et al., 2017; Lees, Peres, Fearnside, Schneider, & Zuanon, 2016). While hydropower may provide energy for burgeoning human populations, the energy output versus environmental, social, and carbon emission impacts is debated (Fearnside, 2016; Gibson et al., 2017). Amazonian forests are vital for biodiversity and global carbon cycling (Gibson et al., 2011; Pan et al., 2011). However, the construction of dams induces extensive forest loss and fragmentation by converting former hilltops into reservoir island archipelagos (Benchimol & Peres, 2015a).

Tropical forest tree communities are highly vulnerable to fragmentation, and once fragmented, undergo rapid species loss and community composition change. Tree species turnover in forest isolates is variable through time, causing local extinctions and instability in community composition, resulting in reduced ecosystem functioning and service provision (Laurance, Nascimento, Laurance, Andrade, Ribeiro, et al., 2006; Santo-Silva, Almeida, Tabarelli, & Peres, 2016). Alterations in abiotic conditions in fragments—such as increased light and desiccation—can cause substantial mortality of slow-growing shade-adapted tree species (Laurance, Nascimento, Laurance, Andrade, Ribeiro, et al., 2006). Edge-mediated fires can exacerbate and accelerate tree mortality and species turnover (Balch, Massad, Brando, Nepstad, & Curran, 2013; Barlow & Peres, 2008). Fast-growing pioneer tree species can exploit disturbed conditions in fragments, resulting in a shift towards more homogeneous low wood-density tree communities (Laurance, Nascimento, Laurance, Andrade, Fearnside, et al., 2006; Lôbo, Leão, Melo, Santos, & Tabarelli, 2011). Additionally, fragmentation reduces carbon stocks in remnant forest compared to core forest areas (25% and 10% reduction in carbon storage <500 m and 500–1,500 m from the edge, respectively; Chaplin-Kramer et al., 2015; Qie et al., 2017), increasing the rate of carbon cycling (Laurance et al., 2014; Santos et al., 2008).

Following the classic equilibrium theory of island biogeography (MacArthur & Wilson, 1967), species numbers on islands primarily depend on island area and distance to mainland species source pools. However, this theory does not necessarily apply to man-made reservoir island systems, as these islands undergo a process of species disassembly rather than assembly (Jones, Bunnefeld, Jump, Peres, & Dent, 2016; Lomolino, 2000). Remnant forest communities isolated on reservoir islands cannot buffer edge effects, and experience dispersal limitation and decreased species retention (Ewers & Didham, 2006; Jones et al., 2016; Mendenhall, Karp, Meyer, Hadly, & Daily, 2014). Reservoir islands can also experience edge-mediated fires, which propagate through deadwood standing in reservoirs (Benchimol & Peres, 2015a). Insular adult neotropical tree communities undergo rapid change, becoming dominated by pioneer tree species and lianas, and experience local extinctions of some tree species (Benchimol & Peres, 2015a; Jones, Peres, Benchimol, Bunnefeld, & Dent, 2017; Terborgh, Feeley, Silman, Nunez, & Balukjian, 2006). Thus, erosion of hyper-diverse remnant tree communities could represent significant biodiversity loss (particularly of rare species) and carbon, not yet accounted for in future dam development strategy (Gibson et al., 2017).

To understand the long-term impact of dam-induced forest fragmentation on remnant insular tree communities, the tree sapling community recruited post-inundation must be described, as adult tree communities tend to represent only the degraded relics of formerly continuous forest (Benchimol & Peres, 2015a). Describing sapling and adult trees in concert sheds light on potential trajectories of floristic and functional change within insular tree communities (Ewers et al., 2017; Santo-Silva et al., 2016; Tabarelli, Lopes, & Peres, 2008). Here, we investigate tree sapling communities recruited after ~28 years of isolation in relation to trees ≥10 cm diameter at breast height (DBH; hereafter, adult trees) to investigate the cross-generational impact of dam-induced habitat insularization on tree communities. We answer the following questions: (a) how do sapling and adult tree communities respond to environmental variables associated with habitat fragmentation across islands, in terms of density, species richness, diversity, and community-weighted mean wood density? How do these metrics compare to mainland continuous forest? (b) How do patterns of dissimilarity between sapling and adult communities vary across islands and mainland continuous forest sites? (c) How do per-species sapling-to-adult ratios differ across islands in relation to environmental variables and wood density, and

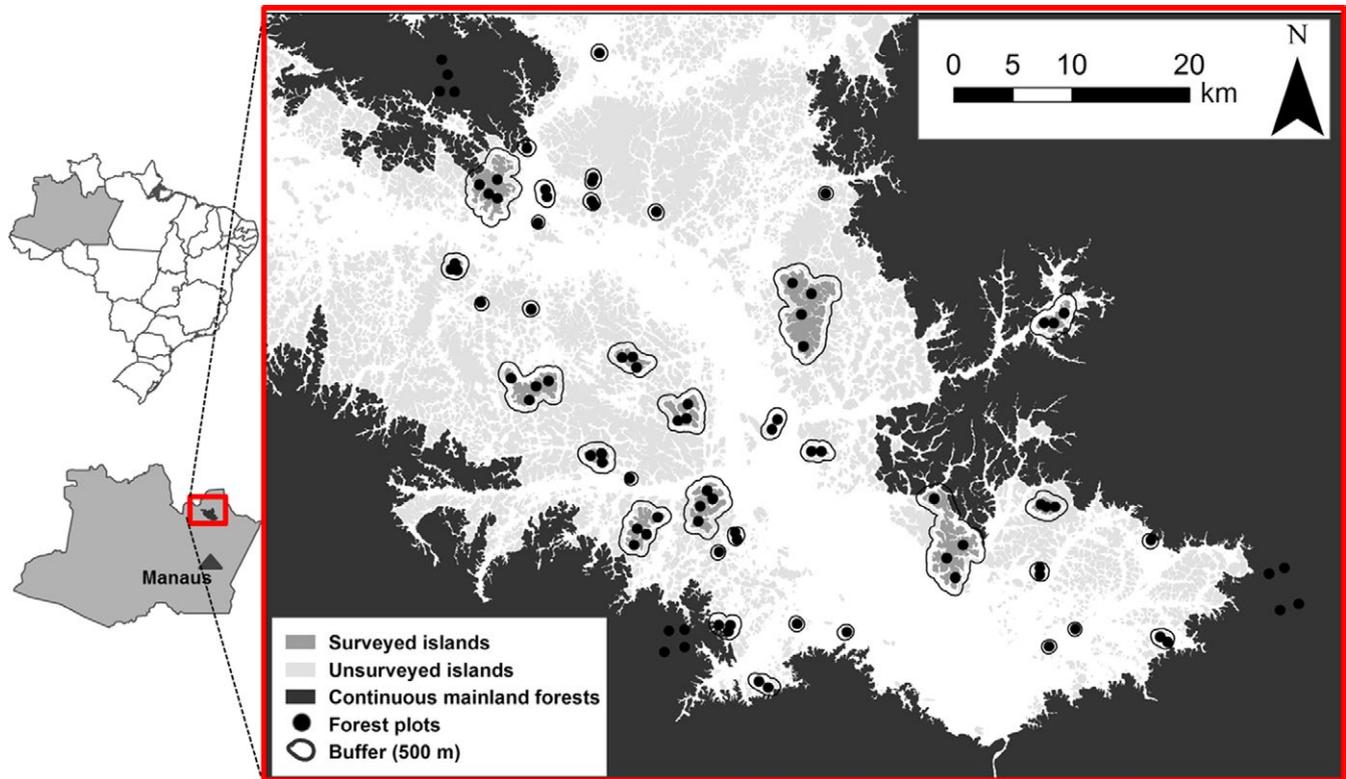


FIGURE 1 Geography of the 89 permanent plots within the Balbina landscape, Brazil; 77 plots are located on 36 islands, and 12 plots are located within three separate areas of continuous mainland forest. The 500-m buffer marked is used to calculate the percentage of forest cover surrounding each island (the “Cover” metric)

in comparison to mainland continuous forest? Through answering these key ecological questions, we provide dam infrastructure decision-makers with robust evidence of the long-term fate of insular tree communities, enabling more comprehensive assessment of the biodiversity and carbon costs/benefits of future dams. Moreover, we provide specific recommendations to minimize some of the detrimental impacts of dam development on lowland tropical regions.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted this study in the Balbina Hydroelectric Dam system, central Brazilian Amazon (1°010–1°550S; 60°290–59°280 W). Balbina was created when the Uatumã River was dammed in 1986, flooding 312,900 ha of continuous lowland old-growth wet tropical forest, transforming the landscape into an archipelago of >3,500 islands. The landscape was not logged prior to inundation, and thousands of dead trees remain standing within the reservoir. All islands and mainland *terra firme* forest to the east of the former Uatumã River bank is strictly protected within the ~940,000 ha Uatumã Biological Reserve. In 1997 a fire was accidentally started in the unprotected portion, which spread through standing above-water deadwood, and penetrated into many islands to varying extents.

We used a network of 89 permanent 0.25 ha survey plots (Benchimol & Peres, 2015a), established on 36 islands and in three

widely spaced mainland continuous forest sites, over a comparable elevation gradient (Figure 1). These 36 islands were selected based on cloudless georeferenced Landsat ETM+ scenes from 2009 (230/061 and 231/061). Islands were selected to ensure spatial independence, and were at least 1 km apart. Survey islands were also selected to span the range of island sizes found within the reservoir (0.83–1,690 ha; mean \pm SD = 210.7 \pm 392.1 ha), to be located at varying distances from the mainland (0.04–17.7 km; mean \pm SD = 4.9 \pm 4.4 km), and to represent the fire severity gradient. Between one and four permanent plots were established per island: one plot on islands <10 ha (mean \pm SD island size = 4.0 \pm 2.9 ha, range 0.8–9.5 ha, n = 14 islands); two plots per island 10–90 ha (44.4 \pm 30.1 ha, 13.4–78.4 ha, n = 9); three plots per island 91–450 ha (230.8 \pm 116.5 ha, 98.8–471 ha, n = 7); and four plots per island >450 ha (952.6 \pm 454.2 ha, 487.5–1,690 ha, n = 6) and at mainland continuous forest sites (n = 3). All permanent plots were distributed within each site considering the island shape, and were \geq 50 m from the nearest edge. Mean pairwise distances between midpoints of plots were 29.3 km \pm 17.1 km (range = 0.3–86.6 km, n = 3,741).

2.2 | Sapling and adult tree surveys

Sapling and adult tree surveys were conducted in each of the 89 permanent plots. All live adult trees and arborescent palms \geq 10 cm DBH were surveyed in 87 plots (10 \times 250 m) in 2012 and in two additional

plots in 2014. One 0.025 ha subplot (1 × 250 m along the central axis of plots) was surveyed for sapling trees and arborescent palms in all plots in 2014. We chose a 0.025 ha subplot area for sapling surveys because, based on pilot data, this subplot area contained the same species richness for tree saplings as found in the 0.25 ha plot for adult trees.

Species-level identification was performed by A.E.S. Santos, an expert botanist with >20 years' experience of field and herbarium work in Central Amazonia, including within the Balbina landscape (Benchimol & Peres, 2015a). After obtaining species identification, only saplings of tree and palm species that could potentially reach ≥10 cm DBH were surveyed (i.e. excluding shrubs, lianas, and herbaceous species) to ensure that sapling and adult tree inventories were comparable in terms of species composition. Tree saplings were defined as ≥1 m height, with a diameter of ≤2 cm at 1 m height. Arborescent palm saplings were defined as lacking woody tissue at 1 m height with fronds reaching ≥1 m height. The species lists from sapling and adult surveys were updated for any changes in nomenclature between surveys.

2.3 | Tree community attributes

Four plot-level attributes of sapling and adult tree communities were investigated: (a) density—the number of individuals per 0.01 ha—used because saplings and adults were surveyed over different areas; (b) rarefied species richness, whereby species richness was rarefied to the mean number of individuals recorded per plot within the corresponding size class (\bar{x} = 124 saplings [0.025 ha]; \bar{x} = 127 adults [0.25 ha]). Where the observed number of individuals was lower than the mean value, species richness was rarefied to the observed number of individuals (Oksanen et al., 2016). We used the mean number of individuals per plot rather than the minimum observed number of individuals (n = 16, saplings; n = 40, adults) to enable inclusion of all plots, and to avoid potential undersampling that may have introduced bias, particularly in mainland plots. When using rarefied species richness values of saplings and adults within the same analysis, species richness was rarefied to the lowest mean number of individuals observed (\bar{x} = 124, saplings); (c) Fisher's α diversity, which is a measure of diversity robust to low and varying numbers of individuals (Beck & Schwanghart, 2010); and (d) community-weighted mean wood density, calculated using species-specific wood density data from the Global Wood Density database (Chave et al., 2009; Zanne et al., 2009). Wood density values from Central Amazonia were used when possible, followed by the nearest geographical region (e.g. the Guiana Shield). Where species-level data were unavailable, genus-level data were used as wood density tends to be a well-conserved trait (Chave et al., 2006).

2.4 | Environmental variables

Five variables of ecological importance at plot-, patch- (i.e., island or mainland site), and landscape-scales were used in analyses.

These included at the plot-scale: (a) distance to the nearest edge (D_{EDGE} , metres) the mean shortest linear distance between each permanent plot and the forest edge. At the patch-scale: (b) island area (AREA, in hectares), based on the area of 5 m pixels in a seamless Rapid-Eye® composite image assembled for the study area; (c) the shortest linear distance from the perimeter of a survey island to continuous mainland forest (ISOLATION, metres); and because of ephemeral surface fires in late 1997, (d) a measure of the fire severity gradient (FIRE). The FIRE metric was based on the difference in NDVI between pre-fire (June 1997) and post-fire (July 1998) Landsat 5 TM scenes. Images from June 1997 and July 1998 were used to reduce the potential for phenological differences in vegetation. Orthorectified surface reflectance data, corrected for atmospheric differences, were downloaded and image pairs mosaicked using histogram matching and the result visually inspected (R package "RStoolbox"; Leutner & Horning, 2017). The NDVI vegetation index was calculated from each mosaicked image (pre- and post-fire) and the difference calculated. The mean change in NDVI (FIRE) was calculated for each focal island, which correlated with a visual inspection of char marks in 2012 (Benchimol & Peres, 2015a). All mainland continuous forest was unaffected by fire, while all islands showed evidence of slight to severe fire damage. Finally, at the landscape-scale, we used (e) the percentage of forest cover (COVER) within a 500 m buffer extending from the perimeter of each survey island and the mainland sites. COVER provides a measure of landscape connectivity, encompassing both the degree of isolation from, and extent of, surrounding forested habitat (Fahrig, 2013).

2.5 | Statistical analyses

2.5.1 | Community attributes

Overall differences in community attributes (density, rarefied species richness, Fisher's α diversity, and community-weighted mean wood density) between saplings and adults, on islands and in mainland sites, were tested using linear mixed effects models (LMMs; with Gaussian error structure). "Site" (i.e., each surveyed island or mainland continuous forest site) was fitted as a random effect to account for our nested sampling design and potential within-plot variation.

We conducted analyses of tree community attributes across islands, separately for sapling and adult trees. We regressed each community attribute with the five environmental variables using LMMs as described above. We did not include data from mainland sites in regression analyses to avoid assigning arbitrary values for AREA and ISOLATION to continuous forest plots, and because any mainland/island effect is confounded with the FIRE effect.

In order to directly compare effect sizes of explanatory variables, all explanatory variables were rescaled (Schielzeth, 2010) prior to modelling, using "rescale" within the "arm" R package (Gelman & Su, 2016). For each model, a pairwise Pearson's correlation matrix

was inspected, and if a pair of environmental variables was highly correlated ($r > 0.7$) only one variable was retained: D_{EDGE} was highly correlated with AREA and thus we included only AREA in analyses. The distribution of each response variable was inspected and transformed if required, to achieve an approximately normal distribution (Zuur, Ieno, & Elphick, 2010). Proportion data were modelled using generalized linear mixed effects models (GLMMs) with a binomial error structure.

Models were simplified through stepwise deletion of nonsignificant terms (t -values < -2 or > 2 were deemed significant) and inspection of AIC values, whereby a difference of < 2 between model AIC values indicated that models were not significantly different (Burnham & Anderson, 2002). Model fit was assessed by visually inspecting the distribution of model residuals. Residuals were plotted on a map of the study area, and revealed no spatial autocorrelation. We calculated 95% confidence intervals around coefficient estimates by multiplying the standard error by 1.96. LMMs were run using “lmer” within the “lme4” R package (Bates, Maechler, Bolker, & Walker, 2017). All analyses were conducted using R (version 3.4.4; R Core Team, 2018).

2.5.2 | Community composition

We visually examined the plot-level similarity between sapling and adult tree communities using nonmetric multidimensional scaling

(NMDS; Anderson et al., 2011). We constructed a “species abundance \times plot” matrix considering saplings and adults simultaneously. Abundance-based dissimilarity values were produced using the Bray–Curtis index. The Bray–Curtis index assumes consistent survey area (Chao, Chazdon, Colwell, & Shen, 2006), however, the observed species richness of saplings and adults was comparable, and the Bray–Curtis index provided the best fit to the data (see Figure S1.1: Supporting Information Appendix S1). We generated incidence-based dissimilarity values using the Jaccard index. Distance values were produced using “vegdist,” and ordination performed using “metaMDS”. Patch and landscape environmental variables were fitted to ordinations using “envfit” and their significance ascertained ($p < 0.05$) using 999 permutations (“vegan” R package; Oksanen et al., 2016).

We used plot-level abundance- (Bray–Curtis) and incidence-based (Jaccard) distance values for sapling and adult communities, to test for overall differences in community dissimilarity between island and mainland plots. To investigate the drivers of plot-level dissimilarity between saplings and adults across islands, we regressed log-transformed ($\ln x$) distance values and environmental variables using LMMs.

The proportion of species in each plot that were present only as (a) saplings, (b) adults, or (c) as both saplings and adults simultaneously, were calculated. GLMMs were used to test for overall differences between island and mainland plots. To investigate variation in

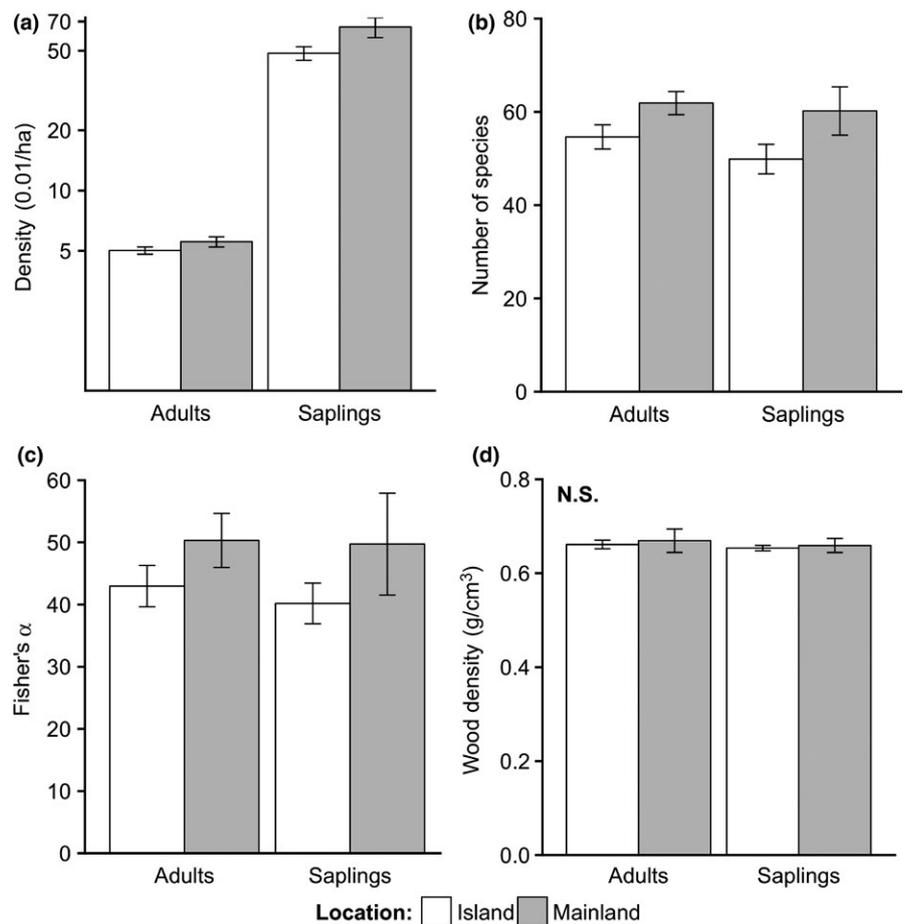


FIGURE 2 Sapling and adult tree community attributes across islands and mainland continuous forest plots. Mean values with 95% confidence intervals are shown. Mainland forest sites had significantly higher sapling and adult tree densities, than islands (Table S1.2: Supporting Information Appendix S1). N.S.: nonsignificant difference

sapling recruitment across islands and mainland continuous forest, we calculated the \log_{10} ratio of saplings: adults (S:A) per species per plot. We added one to all sapling and adult populations to remove zero values to allow calculation of S:A. We generated plot-level mean values of S:A ($S:A_m$) and modelled $S:A_m$ with environmental variables and sapling community-weighted mean wood density using LMMs.

3 | RESULTS

3.1 | Sapling and adult tree surveys

The 89 permanent plots harboured 484 tree species in total, across 11,046 saplings (396 species) and 11,330 adults (376 species), with 288 species (60%) common to sapling and adult layers. Tree saplings were surveyed over 2.225 ha in total, and adult trees over 22.25 ha. Per 0.025 ha plot, 16–240 saplings (mean \pm SD; 124 ± 46) of 10–89 species (56 ± 17) were recorded. Per 0.25 ha plot, 40–180 adult trees (127 ± 23) of 14–78 species (58 ± 12) were recorded. Wood density data were obtained for 465 species, representing 99.1% of saplings and 99.8% of adult trees. Wood density per species ranged from 0.24 to 1.08 g/cm³ (0.65 ± 0.15).

3.2 | Structural differences between saplings and adults on islands and in continuous forest

Density of individuals (per 0.01 ha) ranged from 8 to 96 (mean \pm SD; 51 ± 17) for saplings, and from 2 to 7 (5 ± 1) for adult trees. Densities of both saplings and adults were significantly higher in mainland continuous forest plots compared to island plots (Figure 2a; Table S1.2: Supporting Information Appendix S1), but rarefied species richness, diversity, and community-weighted mean wood density did not significantly differ between island and mainland plots (Figure 2b–d; Table S1.2: Supporting Information Appendix S1).

3.3 | Determinants of sapling and adult tree community attributes on islands

The density of sapling and adult trees increased with higher surrounding forest cover; sapling density was negatively affected by fire severity (Figure 3a,e; Table S1.3: Supporting Information Appendix S1). Species richness and diversity of sapling and adult tree communities increased with surrounding forest cover (Figures 3b,c,f,g; Table S1.3: Supporting Information Appendix S1), and sapling species richness and diversity was significantly lower on more isolated islands and when fire severity was higher (Figure 3c; Table S1.3: Supporting Information Appendix S1). Community-weighted mean wood density of adult trees significantly decreased with fire severity (Figure 3h; Table S1.3: Supporting Information Appendix S1) whereas the mean wood density of sapling communities significantly increased with isolation, although this effect was marginal (Figure 3d; Table S1.3: Supporting Information Appendix S1).

3.4 | Tree community composition

There was clear differentiation between sapling and adult community composition along the NMDS1 axis, for both abundance- and incidence-based metrics (Figure 4). In both ordinations, the NMDS2 axis was significantly correlated with area, degree of isolation, and surrounding forest cover ($p < 0.05$). For sapling and adult communities, mainland plots were tightly clustered, indicating higher similarity in community composition. Sapling communities were more widely scattered in ordination space than adults, indicating a greater variation in species composition among plots. The smallest islands had the most variable species compositions of both sapling and adult trees, and were positioned towards higher values of NMDS2, corresponding to higher degrees of isolation and fire severity and lower surrounding forest cover ($p < 0.05$). Larger islands were more similar to mainland plots, particularly for adult tree communities. The composition of sapling and adult layers were less similar to one another on islands compared to the mainland, considering the incidence-based but not abundance-based dissimilarity (Table S1.2: Supporting Information Appendix S1). Patterns in abundance- and incidence-based dissimilarity were not significantly related to environmental variables across islands when modelled using LMMs (Table S1.3: Supporting Information Appendix S1).

3.5 | Sapling: adult ratio

Significantly fewer species were present as both saplings and adults simultaneously, than in either size class independently (Figure 5a; Table S1.2: Supporting Information Appendix S1), indicating that species within adult tree communities are not readily recruiting into the sapling layer, further highlighted by the significantly greater proportion of species present only as adults compared to saplings (Figure 5a; Table S1.2: Supporting Information Appendix S1). The species-level \log_{10} ratio of saplings: adults (S:A) was not significantly different between islands and mainland continuous forests (Figure 5b; Table S1.2: Supporting Information Appendix S1). However, across islands, the degree of fire severity was the strongest driver of declines in plot-level mean \log_{10} sapling: adult ratios ($S:A_m$; Figure 6a; Table S1.3: Supporting Information Appendix S1). Tree communities with higher community-weighted mean wood density displayed the greatest declines in $S:A_m$ (Figure 6b; Table S1.3: Supporting Information Appendix S1).

4 | DISCUSSION

We investigated the cross-generational impact of dam-induced habitat fragmentation on Amazonian tropical forest tree communities, considering both sapling and adult life stages, on islands ~28 years post-isolation and in mainland continuous forest. Compared to continuous forest, islands supported significantly fewer sapling and adult trees. Across islands, tree sapling communities were negatively impacted by island isolation and fire. Furthermore, island tree communities were less stable in terms of recruitment and replacement of

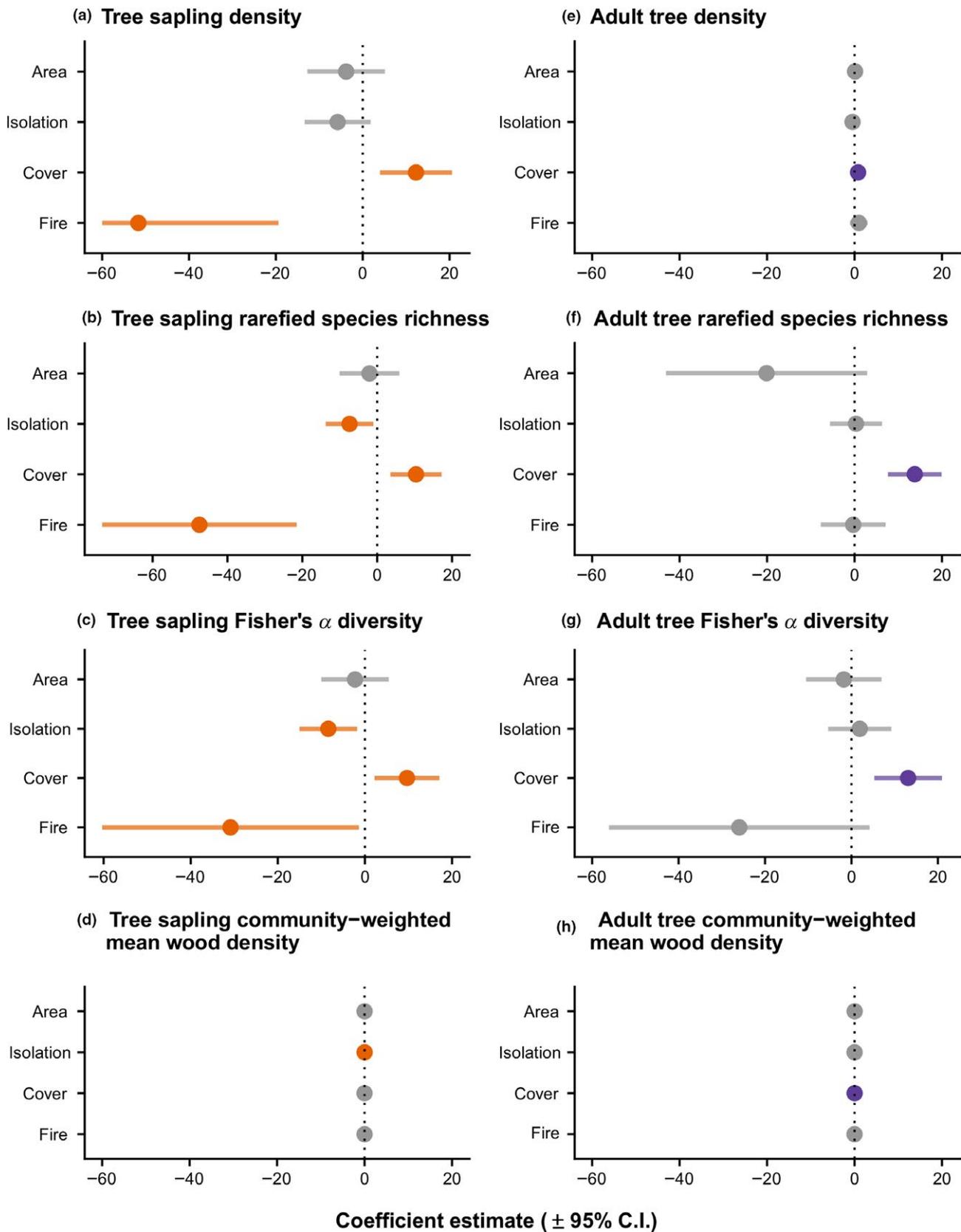


FIGURE 3 Standardized effect sizes of plot-, patch-, and landscape-scale variables on sapling and adult tree community attributes on islands. Coefficient estimates from maximal models are plotted with 95% confidence intervals. Orange (saplings) and purple circles (adults) indicate that coefficient estimates and confidence intervals do not overlap zero, evidence that variables have a significant effect; points <0 indicate a negative effect and >0 indicate a positive effect. The most parsimonious models are summarized in Table S1.3: Supporting Information Appendix S1

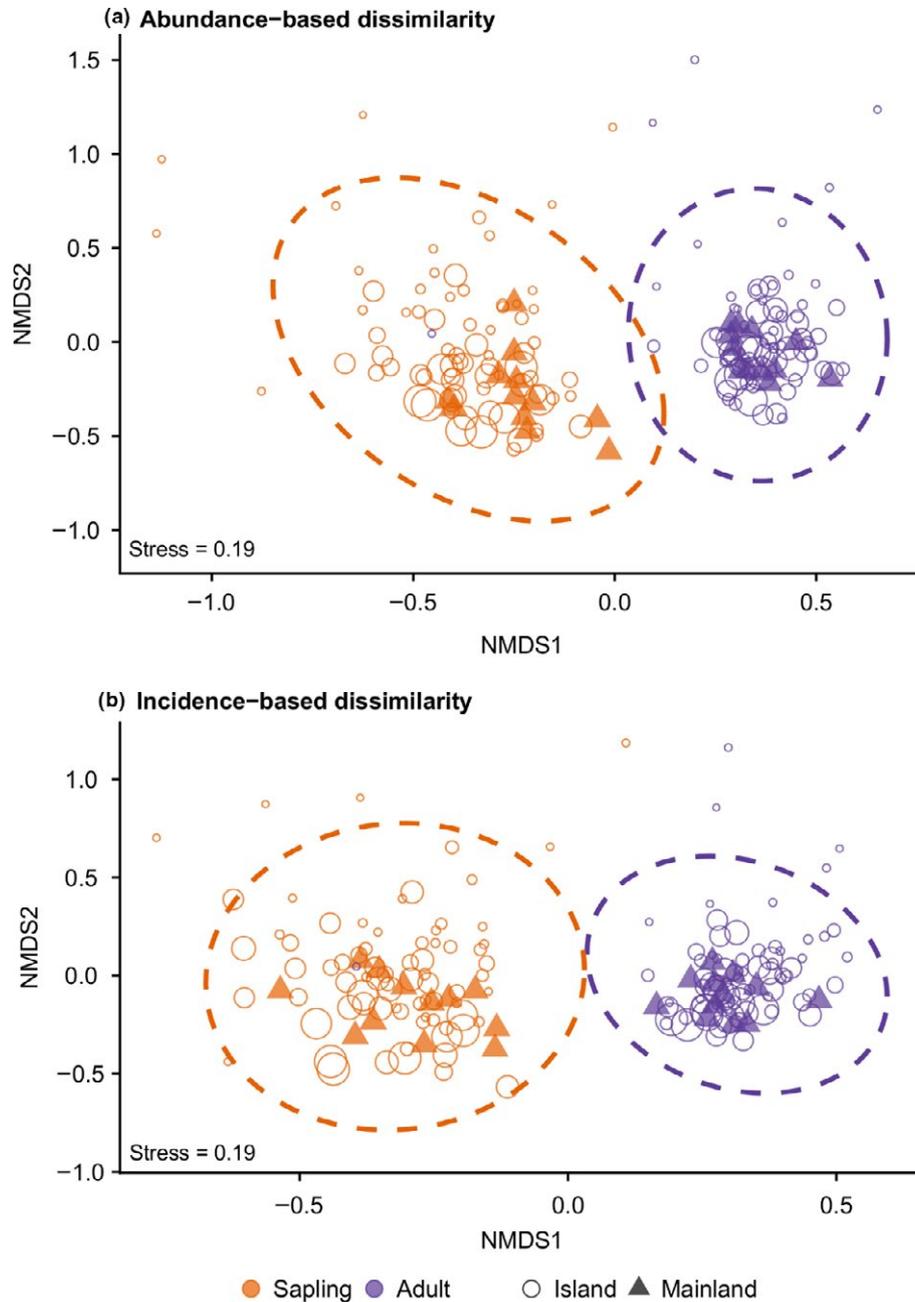


FIGURE 4 NMDS ordinations of abundance-based (Bray-Curtis) and incidence-based (Jaccard) plot-level species dissimilarities for sapling and adult communities. Circles are scaled by island size (0.83–1,690 ha; mean \pm SD = 210.7 \pm 392.1 ha). Dashed lines represent 95% confidence intervals

adult individuals due to fire, and sapling and adult communities had significantly different species compositions; island tree communities showed a directional shift in composition away from mainland communities, highlighting the cross-generational impacts of landscape scale habitat fragmentation.

4.1 | Islands support lower tree densities than continuous forest

Our finding that mainland continuous forest supports higher tree densities is in line with previous studies of fragmented Amazonian

forest systems (Benchimol & Peres, 2015a; Michalski, Nishi, & Peres, 2007; Terborgh et al., 2006). In the nearby Biological Dynamics of Fragmented Forests Project (BDFFP), tree density was reduced within fragments following high rates of mortality and species turnover (Laurance, Nascimento, Laurance, Andrade, Ribeiro, et al., 2006). Similarly, in Atlantic Forest fragments, tree density and species richness were lower than in undisturbed forests, most notably in small fragments and forest edges (Santos et al., 2008; Tabarelli et al., 2008). While we do not see an overall significant difference in richness and diversity between island and mainland tree communities, our findings highlight that tree density is lower, and structural

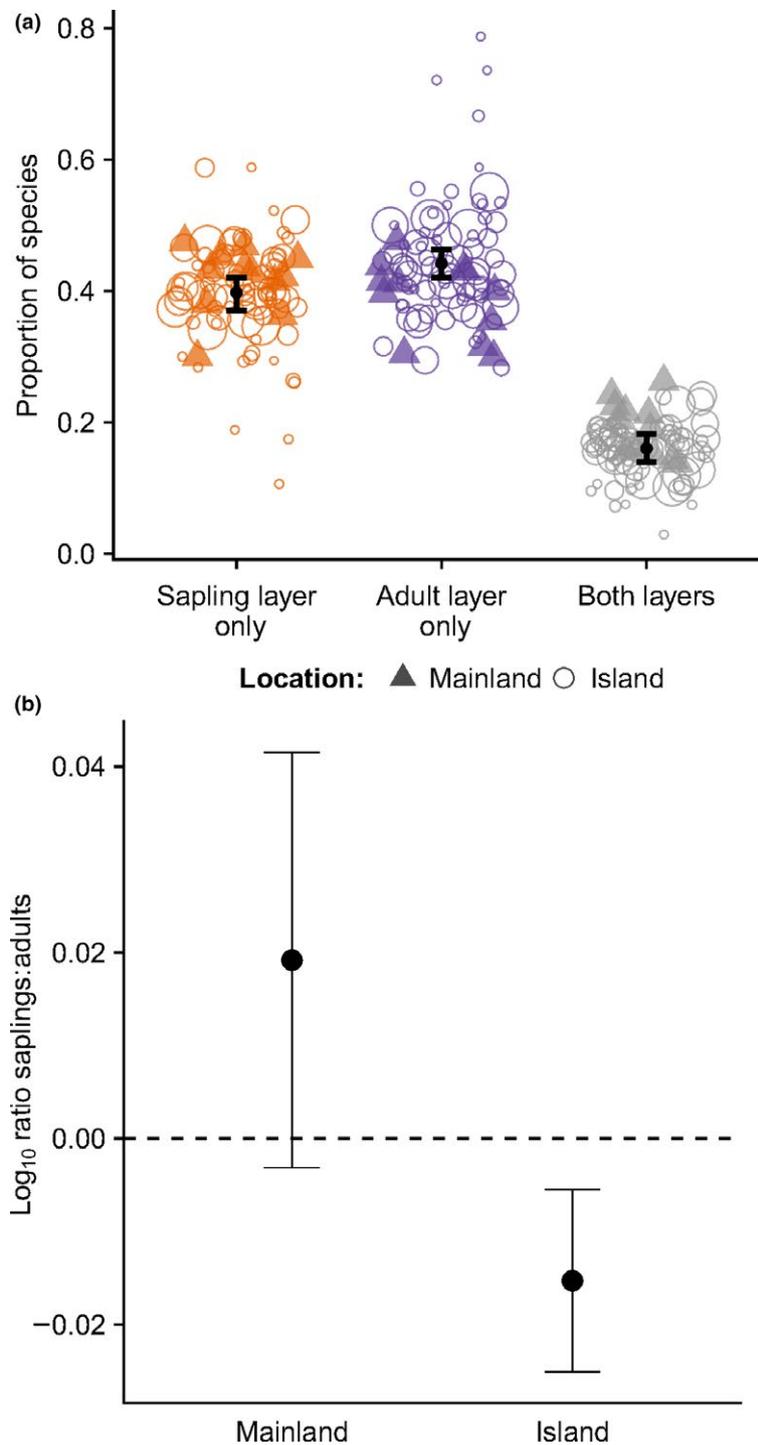


FIGURE 5 (a) Proportion of species within each plot represented only in the (i) sapling layer, (ii) adult layer, or (iii) sapling and adult layers simultaneously. Significantly fewer species occurred as saplings and adults simultaneously, than in either class independently (Table S1.2: Supporting Information Appendix S1). There was no significant difference between island and mainland plots (Table S1.2: Supporting Information Appendix S1); (b) Species-level \log_{10} of sapling: adult communities in mainland continuous forest and on islands; there was no significant difference between island and mainland plots (Table S1.2: Supporting Information Appendix S1)

and compositional integrity is lost, in insular tree communities; the diminished number of trees on islands likely increases tree community vulnerability to further degradation and local species extinctions, particularly rare species, in such a hyper-diverse tropical forest system (Gibson et al., 2011; Haddad et al., 2015).

4.2 | Tree communities in small, isolated and highly disturbed islands are more degraded

Islands surrounded by more forest sustained greater tree diversity and stem densities, which is similar to patterns seen in Atlantic

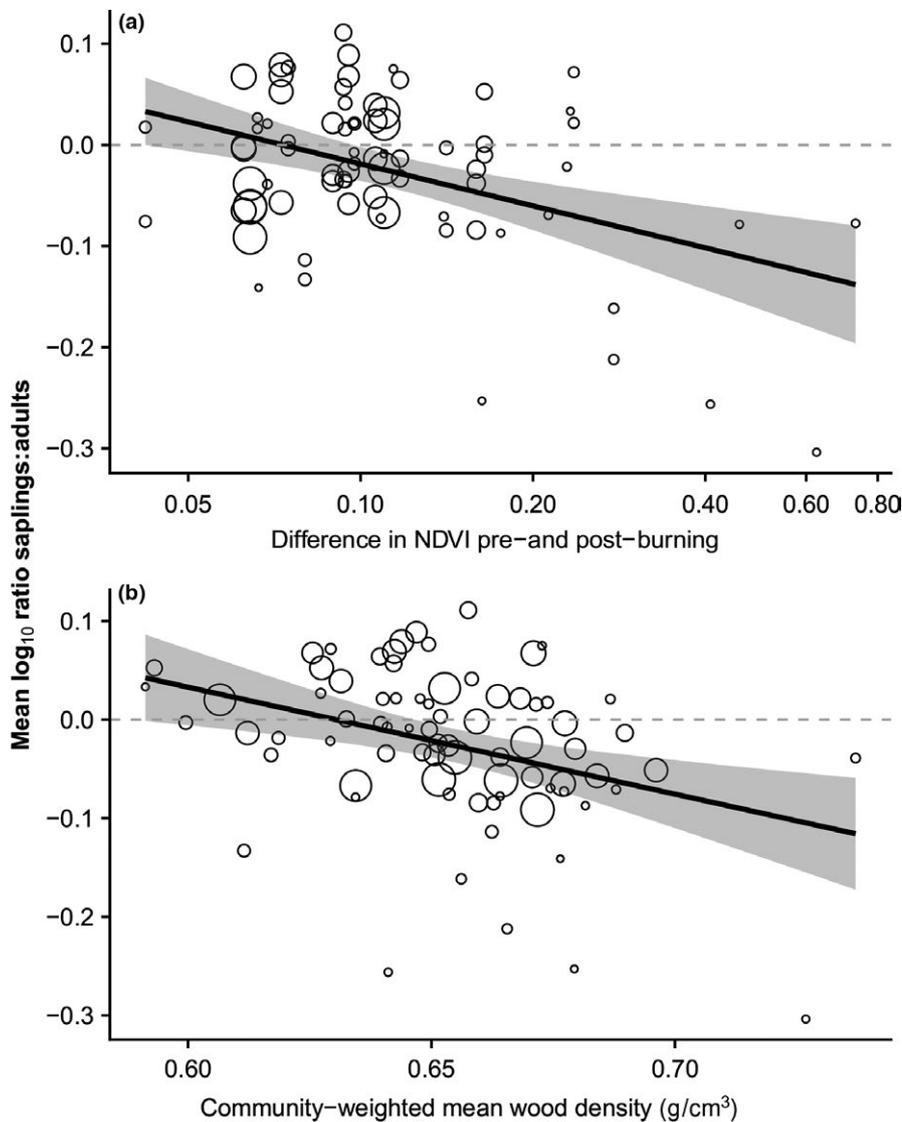


FIGURE 6 Plot-level mean \log_{10} ratio of sapling: adult communities across islands with (a) difference in NDVI pre- and post-fire; and (b) plot-level sapling community-weighted mean wood density. Points are scaled by island size, and the 95% CI is represented by grey shading. The x-axis in (a) uses a \log_{10} scale

Forest fragments (Benchimol et al., 2017). Fire severity had the greatest impact on insular tree communities and led to significant reductions in sapling richness and diversity, and reduced plot-level mean sapling: adult ratios ($S:A_m$) on islands. The smallest islands (<10 ha) experienced the lowest sapling recruitment, and communities with higher mean sapling wood density exhibited the greatest recruitment declines, indicating that hard-wooded species are particularly sensitive to disturbance (Berenguer et al., 2018; Tabarelli, Peres, & Melo, 2012).

4.3 | Island tree communities show increased variance in composition

Across all plots, sapling community composition was significantly different from that of adults due to a low proportion of shared species. Both sapling and adult communities on islands showed a consistent compositional shift away from mainland plots, related to reduced island area and surrounding forest cover, and greater isolation and fire severity. Islands subject to the most disturbance, for example small, isolated islands with a history of severe fire, showed

the greatest degree of divergence from mainland communities. Similar directional shifts in community composition were found in BDFFP fragments, where edge-dominated plots exhibited a non-random shift in composition away from those in interior forest plots (Laurance, Nascimento, Laurance, Andrade, Ribeiro, et al., 2006; Laurance et al., 2011).

There was greater variation in sapling community composition than adults, indicating that fragmentation has potentially driven compositionally unstable sapling communities (Laurance, Nascimento, Laurance, Andrade, Ribeiro, et al., 2006). There was low species overlap between saplings and adults on the smallest islands, where a high proportion of species were restricted to the adult layer, with low sapling-to-adult ratios due to fire. Many small and highly disturbed islands had high sapling community-weighted mean wood density, and the greatest declines in sapling recruitment. In such disturbed conditions, we would expect a high degree of pioneer recruitment, and hence, low sapling community-weighted mean wood density. On small disturbed islands, pioneer trees dominate adult tree communities (Benchimol & Peres, 2015a), and may have created excessive shade for new pioneers to recruit. Furthermore,

where stem density is so low, singleton or doubleton recruits of heavy-wooded species may disproportionately increase the sapling community-weighted mean wood density of the island.

4.4 | Caveats and future directions

We provide a snapshot study of insular sapling and adult tree communities. Given the high turnover of tree communities in fragmented systems, repeated inventories of saplings and adults are needed to fully understand the dynamics of remnant forest fragments created by mega-dams (Laurance et al., 2011). Saplings can remain in the understorey for decades (Green, Harms, & Connell, 2014), thus, though reasonably unlikely, we may have inadvertently sampled saplings that recruited before inundation, and the full effects of habitat fragmentation on tree communities may yet to be consolidated (Jones et al., 2016; Metzger et al., 2009; Tilman, May, Lehman, & Nowak, 1994). However, even after ~28 years of island isolation, we find significant decay in sapling community structure and composition on islands compared to mainland continuous forest. While our use of NDVI pre- and post-fire to characterize fire severity, in concert with a visual inspection of char marks (Benchimol & Peres, 2015a), is a robust method of reconstructing historic fire severity, forest canopy degradation (reflected in NDVI change) may also be due to cumulative impacts from other edge- and area-effects, and not solely fire.

5 | CONCLUSIONS

Dams typically fragment lowland tropical forests, isolating remnant forest patches on reservoir islands. These islands have been considered as a means for wildlife conservation by dam developers, and are not explicitly considered in environmental impact assessments. We show that reservoir islands in Balbina support significantly fewer trees compared to mainland continuous forest, increasing the risk of local extinctions of rare species and forest biomass loss. Furthermore, we show that tree recruitment is suppressed on islands, and that tree community composition has rapidly shifted away from mainland tree communities after only ~28 years of isolation; small islands (<10 ha) are consistently the most impacted. The systemic degradation of tree communities on islands is driven by the reduction in habitat area, degree of isolation, and level of fire disturbance; the amount of forest cover surrounding islands mediates the degree of impacts, highlighting the importance of habitat connectivity, and quality for species persistence within fragments.

The Balbina archipelago retains 3,546 islands, with a combined area of 118,000 ha and an overall island perimeter of 8,992 km. Considering the loss of biodiversity and carbon emissions associated with fragmentation, edge creation, and ongoing forest degradation (Benchimol & Peres, 2015b; Chaplin-Kramer et al., 2015), we call for more thorough consideration of these impacts, and their explicit inclusion in impact assessments and carbon cost/benefit analyses of future dams. Given that >240 dams are planned or under

construction in Amazonia alone, we recommend that future dam development strategy explicitly considers dam location, minimizing the creation of small (<10 ha) and isolated islands when flooding moderately undulating lowland habitats. We further recommend that reservoir water levels be maintained during droughts to reduce fire risk, and that aggregate island area must be included in environmental impact and offset calculations.

The Balbina archipelago has the unique advantage of being protected from potential anthropogenic disturbance by the Uatumã Biological Reserve. Hence, the long-term effects of dam-induced fragmentation on forest integrity would be expected to be far worse had the archipelago and surrounding mainland forests been left unprotected since river impoundment. We therefore emphasize the perverse detrimental effects of hydropower infrastructure development on the persistence of remnant biological communities within dammed lowland tropical forest systems, even when the resulting archipelagic landscape is protected. We stress the need to consider alternatives to dam infrastructure development in highly biodiverse and continuous lowland tropical forest regions, such as the Amazon Basin.

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AUTHORS' CONTRIBUTIONS

Research ideas were conceived by I.J., M.B., C.A.P., and D.D. Data were collected by I.J. and M.B. Analyses were conducted by I.J., with input from D.D. and L.B. The manuscript was written by I.J. All authors commented critically and approved final submission.

DATA ACCESSIBILITY

Tree sapling data available via the University of Stirling data-STORRE <http://hdl.handle.net/11667/124> (Jones, Peres, Benchimol, Bunnefeld, & Dent, 2018). Adult tree data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.2v8f9> (Benchimol & Peres, 2015c).

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SUPPORTING INFORMATION

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