

Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation

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Summary

1. Islands formed upstream of mega hydroelectric dams are excellent experimental landscapes to assess the impacts of habitat fragmentation on biodiversity. We examined the effects of plot-, patch- and landscape-scale variables on the patterns of floristic diversity across 34 forest islands that had experienced 26 years of isolation since the creation of the 4437 km² Balbina Hydroelectric Reservoir of central Brazilian Amazonia. In addition, three undisturbed continuous forest sites in neighbouring mainland areas were also sampled across a comparable elevational gradient.

2. We identified all live trees ≥ 10 cm DBH at species level within a total of 87 quarter-hectare forest plots and conducted a comprehensive compilation of functional attributes of each tree species. We then examined species-area relationships (SARs) and the additional effects of patch and landscape-scale metrics on patterns of tree assemblage heterogeneity, both in terms of taxonomic and functional diversity.

3. Despite a clearly positive SAR, edge-mediated forest disturbance was the single most important driver of species composition and abundance within islands. Our results suggest that non-random floristic transitions within island plots followed a predictable pattern, with different life-history traits either penalizing or rewarding local persistence of different functional groups. Distance to edges mediated the probability of tree mortality induced by windfalls and episodic surface fires, clearly resulting in faster species turnover and unidirectional changes in guild structure within small islands where light-wooded fast-growing pioneers largely replaced heavy-wooded species of the old-growth flora.

4. *Synthesis.* Following a simultaneous 26-year post-isolation history, we disentangle the effects of habitat loss and insularization on tree assemblages within a large set of Amazonian ‘true’ forest islands, of variable sizes, sharing a uniform open-water matrix. Area effects are expressed via a response to edge effects, with trees in smaller islands being more vulnerable to edge-related surface fires and wind-throws. Additionally, forest edge effects can be a powerful driver of non-random floristic transitions across islands within the Balbina archipelago via a process of rapid pioneer proliferation, drastically affecting both the taxonomic and functional composition of insular tree communities. Finally, our results indicate that detrimental effects of forest fragmentation induced by hydroelectric dams are considerably stronger than those of forest patches embedded within a terrestrial vegetation matrix.

Key-words: Amazon, habitat fragmentation, hydropower projects, island biogeography, landscape attributes, life-history traits, species-area relationship, tree communities

Introduction

Although vast, unbroken tracts of undisturbed tropical primary forests are quintessential to sustain tropical biodiversity

(Barlow *et al.* 2007; Gibson *et al.* 2011), the fate of tropical forests has increasingly become inextricably linked to fragmented landscapes. Each year, 13 Mha of tropical forests world-wide are converted into agriculture and cattle pastures, reducing once continuous forests to small isolated remnants (FAO 2010). Consequently, understanding how species diversity and ecological processes are shaped within newly isolated

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forest ecosystems is critical to identify the mechanisms governing the persistence of former tropical biotas in fragmented forest landscapes.

Tree communities play key roles in providing the structural architecture of forest ecosystems, regulating microclimatic conditions (Laurance *et al.* 1998), storing carbon and producing essential trophic resources for a wide variety of consumers (Richards 1998). Although the ecological effects of forest fragmentation on tropical and subtropical tree assemblages have been examined by a growing number of studies (e.g. Tabarelli, Mantovani & Peres 1999; Laurance *et al.* 2006a; Michalski, Nischi & Peres 2007; Yu *et al.* 2012), the key predictors of community composition following a history of isolation remain inconsistent across studies. For instance, edge effects are a dominant force controlling tree community dynamics in forest patches within the Biological Dynamics of Forest Fragments Project (BDFFP) of Central Amazonia (Laurance *et al.* 2011). In contrast, the interaction of habitat area and habitat disturbance best predicts the species composition of Atlantic Forest fragments in south-eastern Brazil (Santos, Kinoshita & dos Santos 2007), whereas time since isolation, distance to edges and fire severity best explains patterns of tree composition in a fragmented forest landscape in southern Amazonia (Michalski, Nischi & Peres 2007). Furthermore, these studies have not always found a strong positive species-area relationship, which is often hailed as the most ironclad law in ecology (Lomolino 2000). Tree community responses may diverge substantially among fragmented landscapes because of varying pre- and post-isolation histories of forest remnants, including differences in the structure of surrounding vegetation matrices and exposure to different forms of human perturbation that often synergise with the effects of forest fragmentation alone (Cochrane 2001; Peres, Barlow & Laurance 2006).

Islands isolated in the aftermath of large hydroelectric projects are superb experimental settings for fragmentation ecology studies, providing several advantages over habitat patches of variable isolation time in gradually fragmented terrestrial landscapes (Diamond 2001; Terborgh *et al.* 2001; Wu *et al.* 2003; Hu *et al.* 2011). First, hundreds to thousands of forest islands associated with varying landscape configurations are formed simultaneously, enabling the assessment of how biodiversity responds to habitat fragmentation in a large number of variable-sized islands isolated concurrently and subjected to the same history of anthropogenic disturbances. Secondly, these man-made archipelagos are embedded within a structurally uniform open-water matrix that is equally inhospitable to most terrestrial organisms, thereby eliminating the confounding effects of varying degrees of matrix habitat use and permeability, which affect the functional connectivity of terrestrial landscapes (Cosson *et al.* 1999; Mendenhall *et al.* 2014). Thirdly, mainland forest areas adjacent to hydropower reservoirs are often near ideal control sites to test ecological hypotheses, as they contain the same biota that once occurred in all newly created islands (Terborgh 1974). Finally, habitat islands created by hydroelectric impoundments consist of truly unplanned large-scale natural field experiments.

The Balbina Hydroelectric Dam of Central Brazilian Amazonia is an unrivalled experimental laboratory which aims to examine tree responses to habitat fragmentation and isolation. This is the largest Amazonian dam and it includes one of the most diverse tree floras world-wide, containing over 3500 even-aged forest islands ranging in size from < 1 ha to > 4500 ha, offering a long-term relaxation-time experiment for ecological studies (Fearnside 1989). Furthermore, similar tree floras sharing the same species functional attributes have been studied in the same biogeographic province (e.g. Guianan forest reserves: Steege & Hammond 2001 and BDFFP: Laurance *et al.* 2004a), providing an excellent comparative perspective. The history of human and natural disturbances rarely occurs homogeneously in space and cannot be easily reconstructed, thus differentially affecting the structure of insular tree assemblages, often aggravating the effects of forest fragmentation (Gascon, Williamson & da Fonseca 2000). However, Balbina also has the critical advantage of spatial congruence with REBIO Uatumã, the largest strictly protected Biological Reserve in Brazil, which has effectively suppressed spontaneous in-migration, small settlements, and timber and non-timber forest resource extraction throughout the vast archipelago and neighbouring areas. Yet islands after ~10 years of isolation were differently affected by ephemeral accidental understorey fires. Although fire effects on tree assemblages have not been previously investigated in true islands within a Neotropical fragmented landscape, studies focussed on habitat islands (i.e. surrounded by a terrestrial matrix) indicate that fire often operates as a form of edge effect (Cochrane & Laurance 2002; Alencar, Solórzano & Nepstad 2004; Broadbent *et al.* 2008). Given an inhospitable matrix consisting of a large body of open water, which is likely to be subjected to greater wind forcing (Leigh *et al.* 1993), fires may have propagated within and across forest islands, leading to profound changes in forest composition and function.

Here, we examine how tree assemblages have responded to the 26-year post-isolation history of landscape alteration in true forest islands within one of the world's largest hydroelectric reservoirs. We measured a set of local and landscape-scale variables to identify the main environmental predictors of species richness and composition within 34 variable-sized islands and three mainland continuous forest sites. We also selected a set of key tree functional traits to examine the degree to which forest insularization affects different tree functional groups and used these traits to quantify functional diversity across all sites. We hypothesized that islands created by hydroelectric dams will become heavily affected by habitat fragmentation effects due to elevated wind exposure and that tree assemblage composition and functional diversity will be governed by non-random floristic transitions. Specifically we predict that (i) the species richness and diversity of tree assemblages will increase in larger islands, following predictions from island biogeography theory (MacArthur & Wilson 1967); (ii) over and above area effects, other patch and landscape features will affect patterns of taxonomic and functional diversity of tree species, such as distance to the edge, distance

to continuous forest areas and surrounding forest cover (Michalski, Nischi & Peres 2007; Santos *et al.* 2008); (iii) fire severity will interact synergistically with habitat fragmentation leading to severe compositional changes in tree assemblages (Cochrane & Schulze 1999; Cochrane 2001); and (iv) edge-dominated forests will tend towards greater representation of pioneer species, severe declines in the abundance of emergent, large-seeded animal-dispersed species and overall reduction in mean wood density (Laurance *et al.* 2002; Magnago *et al.* 2014).

Materials and methods

STUDY SITE

We conducted this study in a large set of forest islands created in 1986 following the permanent closure of the Balbina Hydroelectric Dam (1°01' – 1°55' S; 60°29' – 59°28' W), subsequently flooding a reservoir lake area of 4437 km² along the Uatumã River, a first-order tributary of the Amazon. Consequently, an undisturbed upland (*terra firme*) primary forest area of 3129 km² was converted into 3525 forest islands surrounded by a large body of freshwater punctuated by dead trees rising above the maximum water level. Sub-montane dense closed-canopy forests at Balbina are subjected to an average annual rainfall and temperature of ~2376 mm [range = 2113.1–2716.3 mm] and 28 °C [range = 21–35 °C]. These forests are relatively diverse, averaging 143 tree species of ≥10 cm diameter-at-breast-height [DBH] ha⁻¹ in continuous upland *terra firme* forests (range = 124–156 species ha⁻¹). The mean water column depth across the entire reservoir is 7.4 m but as deep as 30 m near the former river channel (Eletronorte 1997). The reservoir water level has remained remarkably stable over the past 26 years (Melack & Wang 1998) due to a tight hydraulic system control at the dam site. Forest islands at Balbina, which range in size from 0.2 to 4878 ha, have never been selectively logged, neither before nor after dam construction. To mitigate the environmental impact of the dam, part of the reservoir area (left bank of the Uatumã river) and adjacent mainland continuous forests became strictly protected in 1990 with the creation of the ~940 000 ha Uatumã Biological Reserve, the largest forest reserve of

this kind in Brazil. During a severe El Niño drought from late 1997 to early 1998, ephemeral understorey fires accidentally affected much of the Balbina Reservoir region and adjacent areas, often penetrating into previously unburnt primary forest islands and rapidly propagating to islands in other parts of the reservoir. A fisherman on the right bank of the river was likely the primary source of fire ignition, given that both navigation and fishing are permitted on this portion of the reservoir.

STUDY DESIGN

In 2012, we conducted floristic inventories within 87 quarter-hectare forest plots distributed across 34 variable-sized forest islands and three continuous forest sites in undisturbed mainland areas adjacent to the reservoir (Fig. 1), spanning a study area of ~3964 km². These plots measured 250 m × 10 m at all forest sites, except for 10 small islands where rectangular plots were 125 m × 20 m. Floristic inventories were compiled considering the location of stems within 'sub-plots' of 50 m × 10 m (or 25 m × 20 m), providing five subplots per plot.

The widely distributed forest islands and mainland sites were pre-selected using two cloudless georeferenced Landsat ETM+ scenes (230/061 and 231/061; year 2009) on the basis of their size and degree of isolation. Islands and continuous forest sites were spaced by at least 1 km from one another. On each island and mainland site, we inventoried one to four 0.25 ha forest plot according to island size as following: 1 plot per island < 10 ha (mean ± SD island size = 4.0 ± 2.9 ha, range 0.8–9.5 ha, *N* = 12 islands); 2 plots per island of 10–90 ha (44.4 ± 30.1 ha, 13.4–78.4 ha, *N* = 9); 3 plots per island of 91–450 ha (230.8 ± 116.5 ha, 98.8–471 ha, *N* = 7); and 4 plots per island > 450 ha (952.6 ± 454.2 ha, 487.5–1690 ha, *N* = 6) and mainland forest sites [to which, depending on the analysis, we assigned arbitrary area values of either infinity (∞) or one order of magnitude greater than our largest island] (see Table S1 in Supporting Information). A similar sampling design consisting of establishing 0.25 ha forest plots according to fragment area was previously adopted in another Amazonian fragmented landscape by one of us and colleagues, providing a robust data set (Michalski, Nischi & Peres 2007). Island plots were always spaced by ≥50 m from the nearest forest edge to avoid sampling areas that may have been

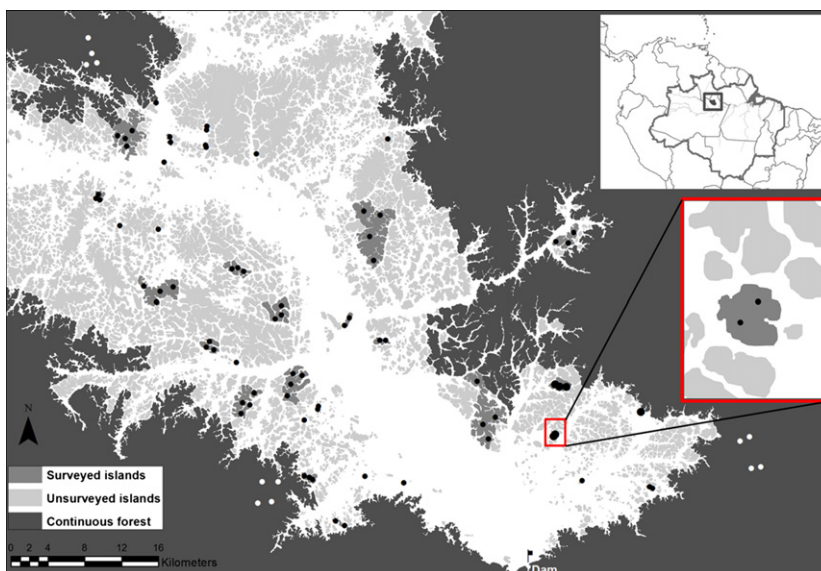


Fig. 1. Spatial distribution of the 87 forest plots of 0.25 ha surveyed within 34 islands (black circles; *N* = 75 plots) and 3 continuous forest sites (white circles; *N* = 12 plots) within the Balbina Hydroelectric Reservoir of central Brazilian Amazonia. Inset rectangle is amplified to highlight the location of plots within a 26 ha island that was surveyed.

subjected to the worst ravages of edge effects, although some edge disturbance may affect areas up to 400 m into forests (Laurance *et al.* 2002). Pairwise distances between midpoints of tree plots were on average $29.3 \text{ km} \pm 17.1 \text{ km}$ (range = 0.3–86.6 km, $N = 3741$).

All live trees (including arborescent palms) $\geq 10 \text{ cm}$ DBH within each plot were measured, tagged and identified at species level by A.E.S. Santos, an expert botanist with > 20 years of fieldwork and herbarium experience in floristic inventories throughout Central Amazonia, including 8 years of tree identification work at BDFPP and the Ducke Reserve. These two landscapes are located ~60 km and ~120 km from the Balbina Reservoir, respectively, and share a similar tree flora (Ribeiro *et al.* 2002). Voucher specimens of all trees that could not be unambiguously identified *in situ* were collected and subsequently identified at the INPA (National Institute for Amazon Research) herbarium, which houses the largest voucher collection of the Amazonian tree flora (220 000 specimens), with a strong geographic bias towards the Manaus–Balbina region.

FUNCTIONAL ATTRIBUTES

We assigned five functional traits widely recognized as important determinants of tree recruitment, growth and survival (see Hammond *et al.* 1996; Steege & Hammond 2001; Santos *et al.* 2008) to each tree species sampled across the Balbina landscape. These included regeneration strategy (short-lived pioneer, long-lived pioneer and old-growth species); vertical stratification (understorey, canopy, and emergent species); seed-dispersal mode (vertebrate-dispersed or abiotically dispersed); dry seed mass (eight classes on a log scale: $1 = 10^{-5} - 10^{-4} \text{ g}$, $2 = 10^{-4} - 10^{-3} \text{ g}$, ..., $8 = > 100 \text{ g}$); and wood density (g cm^{-3}), based on a comprehensive literature review encompassing data obtained across several Amazonian sites, but primarily the Guiana Shield which includes the regional scale tree flora of our study area (Guevara, Purata & Van der Maarel 1986; Granville 1992; Hammond & Brown 1995; Hammond *et al.* 1996; Harms & Dalling 1997; Steege & Hammond 2001; Laurance *et al.* 2004a,b; van Uft 2004; Baraloto & Forget 2007; SID 2008; Amaral *et al.* 2009; Herault *et al.* 2010). Species-specific wood density (WD) measurements were obtained for 67.3% of the 368 tree species and 100% of the 189 genera included in the analysis. For those species for which species level data were lacking, we used the mean genus-level WD value from Guianan Shield sites or, if those were unavailable, from any lowland Amazonian site. We also calculated the total and proportional abundance of different functional groups within each plot – (i) emergent species, (ii) pioneer species, (iii) large-seeded species (seeds $\geq 1 \text{ g}$) and (iv) vertebrate-dispersed species – and the mean WD per stem, as they have been widely considered as important indicators of habitat disturbance in Neotropical forests (Laurance *et al.* 2006a,b; Michalski, Nischi & Peres 2007; Santos, Kinoshita & dos Santos 2007; Santos *et al.* 2008).

MEASURES OF DIVERSITY

Based on the species presence/absence and abundance data, we derived five robust metrics of tree taxonomic diversity (Magurran 2004) within each of the 87 plots to investigate patterns of species heterogeneity across islands and mainland sites: species richness (S), Simpson's Diversity Index (D_s), Fisher's alpha, Dominance (D) and functional diversity (FD). We quantified FD for each forest plot based on a dendrogram approach proposed by Petchey & Gaston (2002), using the five species traits considered in this study (regeneration strategy, vertical stratification, seed-dispersal mode, dry seed mass

and wood density). This method encompasses four steps: (i) design of the trait matrix, (ii) conversion of this matrix into a distance matrix, (iii) hierarchical clustering of the distance matrix to produce a functional dendrogram and (iv) calculation of the total branch length of the dendrogram, providing a continuous FD measure. We used the Euclidean distance and the unweighted paired-group clustering method using arithmetic averages and performed the analysis using Petchey's (2013) R code.

EXPLANATORY VARIABLES

Following a two-stage unsupervised classification of the two georeferenced Landsat images, we used ArcView 10.1 (ESRI 2011) to extract seven plot-, forest patch- and surrounding landscape-scale variables associated with each of our 87 forest plots. At the plot scale, we estimated the distance to forest edges (defined as the mean linear distance between the five midpoints of every 50-m section of each plot and the nearest points along the island perimeter; hereafter, 'EDGE DISTANCE'); the difference between maximum and minimum plot elevations based on the Shuttle Radar Topography Mission – SRTM – raster data (hereafter, 'SLOPE'); and the angular difference ($0-90^\circ$) between the main axis of each rectangular plot and the median angular direction of prevailing strong winds recorded prior to and during convective windstorms (hereafter, 'WINDSTORM' angle). At the island scale, we measured the total area in hectares ($\log_{10} x$; 'AREA'); the shortest linear distance from each island to the nearest mainland (' D_{MAINLAND} '); and the understorey burn or fire severity (hereafter, 'FIRE'), measured according to a composite ordinal score (0–3) of both fire severity (based on both the proportion of charred trees $\geq 10 \text{ cm}$ DBH and height of char marks on the bole of each tree) and the extent to which each island had been affected by surface fires, which were estimated by three independent observers during detailed *in situ* surveys. At the wider landscape scale, we measured the percentage of FOREST COVER within a 500-m external buffer from the perimeter of each island and the survey area of mainland forests. We also modified the McGarigal *et al.* (2012) proximity index by considering both the aggregate area and distance to any land mass within 500 m of each island ('PROXIMITY').

DATA ANALYSIS

Spatial correlation and area effects

We first performed a Mantel test with a Weighted Spearman rank correlation using the package 'ade4' (Dray & Dufour 2007) to examine the spatial effect associated with plot location on species richness. We then fitted both semi-loglinearized models and nonlinear multi-model tree species-area relationships (SARs) considering all 87 plots distributed across the 37 forest sites inventoried to evaluate the effects of area alone on the number of tree species. We rarefied species richness to the minimum number of individuals recorded across all forest plots to account for differences in tree density, and then fitted SAR models considering both the rarefied estimates and raw data. We used the 'mmSAR' R package (Guilhaumon, Mouillot & Gimenez 2010) to evaluate model performance among eight possible nonlinear models – including four convex (power, exponential, negative exponential and Monod) and four sigmoidal models (rational function, logistic, Lomolino and cumulative Weibull) based on the Akaike information criterion (AIC; Burnham & Anderson 2002).

We also assessed the area effects on patterns of species composition. For this, we first performed non-metric multidimensional scaling

(NMDS) ordinations for all 87 plots using the Bray–Curtis dissimilarity matrix based on both qualitative (presence/absence) data and quantitative species composition (standardized and sqrt-transformed abundance data). We then used the axis of both NMDS (qualitative and quantitative) to relate to island area using linear regression. Additionally, we investigated patterns of tree diversity according to island size, using Simpson (D_s), Fisher's alpha, Dominance (D) and functional diversity (FD) as response variables.

Furthermore, we examined the effects of island area on the abundance of functional groups. These included the percentage of stems within plots defined as emergents, pioneers, large-seeded and vertebrate-dispersed, as well as the mean wood density per live stem. We also performed a Mantel test to examine the effects of spatial structure on each of these functional responses.

Plot, patch and landscape effects

We performed generalized linear mixed models (GLMMs) to examine the effects of plot-, patch- (i.e. island or mainland site) and landscape-scale metrics on species richness. We initially used the variance inflation factor (VIF) to test for multicollinearity among all variables for each GLMM (Dormann *et al.* 2013) and deleted those factors that were at least moderately redundant/collinear ($VIF \geq 6$). In all GLMMs explaining plot-scale tree species richness and diversity, VIF analyses indicated high multicollinearity between our modified proximity index and landscape-scale forest cover ($VIF > 10.00$). We therefore excluded forest cover, which consistently showed the highest VIF value, with the other seven plot- and patch-scale metrics subsequently showing low multicollinearity ($VIF < 6.00$). Also, pairwise Pearson correlations of fixed effects were consistently < 0.50 . We therefore retained seven explanatory variables in the models (see Table 1). We then calculated pairwise Pearson correlation coefficients among all plot-, patch- and landscape-scale metrics within each GLMM and considered any two variables as autocorrelated if $r \geq 0.70$. Our global models incorporated a random term nesting 'plots' within island and mainland sites to account for potential spatial autocorrelation (Bolker *et al.* 2009). Models were fitted using the 'lme4' package (Bates 2007) within the R platform. We ran all predictor subsets using the 'MuMIn' package (Bartón 2009), retained all 'best' models that differed by $\Delta AIC \leq 2.00$ (Burnham & Anderson 2002) and obtained the relative importance of each variable. A model-averaging approach was further performed if at least five models were retained within the 'best' models. We further determined the unique and joint fractions of variation explained for each significant variable using variance partitioning (VP) within the 'vegan' package (Oksanen *et al.* 2013) and used hierarchical partitioning (HP) to determine the relative importance of each significant variable. We also performed GLMMs considering FD and Fisher alpha as response variables.

We further performed canonical redundancy analysis (RDA) to assess the importance of our seven environmental variables in explaining changes in community composition using both the binary and abundance data. Finally, we assessed the effects of plot, patch and landscapes variables on functional attributes across all plots using GLMMs, considering both (i) 87 plots nested within the 37 forest sites and (ii) 435 'subplots' of 50 m \times 10 m (or 25 m \times 20 m) nested within the 87 plots, which were in turn nested within the 37 sites, to account for potential within-plot differences in edge distance effects. For this second approach, we defined edge distances as the linear distances between the midpoint of each subplot and the nearest forest edge along island perimeters. We considered the number of live stems within each functional group but included the total number of

stems as an offset variable using a Poisson error structure, to account for plot-scale variation in stem density. We performed GLMMs using the same steps described above, including multicollinearity and correlation tests, model selection, VP and HP.

Effects of fire disturbance

We conducted permutational multivariate analysis of variance (PERMANOVA) using the software PRIMER to test for differences in species composition in response to different levels of fire intensity, using data from the 87 plots. We then performed ANCOVAs using subplot-scale data (435 'subplots' of 50 m \times 10 m) to examine the effects of burn severity on the relative abundance of different functional groups, with edge distance as a covariate. Given the edge penetration distances documented elsewhere (e.g. BDFFP landscape: Laurance *et al.* 2002), we considered 4 edge distance classes: 0–100 m, 100–200 m, 200–300 m and > 300 m.

Results

We recorded a total of 11 230 live trees belonging to 368 species, 189 genera and 59 families within 21.75 ha of forest sampled across all 87 plots (Table S2 in Supporting Information). All trees were identified at the family level, 99.2% at the genus level and 98.1% at the species level. Quarter-hectare plots contained between 14 and 78 tree species (mean \pm SD = 58.9 ± 10.3). On the basis of 365 of the 368 species in our overall sample, we classified 27 species as emergents, 118 as pioneers, 167 as large-seeded species and 327 exhibiting seed and fruit morphology traits typical of vertebrate dispersal. Wood density per species ranged from 0.24 to 1.03 g cm⁻³.

SPATIAL CORRELATION AND AREA EFFECTS

A Mantel test failed to reveal any large-scale spatial effect on species richness across all 87 plots ($r = 0.002$, $P = 0.442$), so the forest islands we surveyed can be considered as spatially independent. There was a positive semi-loglinear relationship between island size and tree species richness per plot, whether we included ($R^2_{adj} = 0.286$, $N = 87$, $P < 0.001$) or excluded continuous forest plots ($R^2_{adj} = 0.250$, $N = 75$, $P < 0.001$; Fig. 2a). This explanatory power was further improved using eight nonlinear models, which explained up to 32.5% of the species-area relationships (mean $R^2_{adj} = 0.282$), with the cumulative Weibull providing the best-fit model, followed by the logistic model. This pattern held true when we considered the plot-scale rarefied species richness to account for any post-isolation variation in tree density due to differential tree mortality and recruitment across islands, whether we included ($R^2_{adj} = 0.172$, $N = 87$, $P < 0.001$) or excluded continuous forest plots ($R^2_{adj} = 0.157$, $N = 75$, $P < 0.001$).

We also detected a significant area effect on species composition across all plots. Island size explained 22.7% ($P < 0.001$) of the variation in the species presence/absence data, with NMDS plots in small islands showing a lower overall similarity compared to plots in large islands and

Table 1. Summary of best-fit generalized linear mixed models (GLMMs) examining tree assemblage structure and functionality in relation to explanatory variables considering all 87 plots nested within 37 forest sites. Coefficient estimates (β), their respective standard error values (SE), their relative importance, and both the hierarchical partition and the independent power based on variation partition of each significant variable are shown. Significant variables are indicated as: *** $P \leq 0.001$, ** $P \leq 0.01$, and * $P \leq 0.05$

Community attribute	Explanatory variable	Estimate (\pm SE)	Relative Importance	Hierarchical partitioning (%)	R^2
Species richness	Intercept***	3.888 (0.153)			
	AREA**	0.091 (0.034)	0.90		
	D_{MAINLAND}	0.001 (0.001)	0.37		
	FIRE	-0.025 (0.034)	0.28		
	PROXIMITY	0.024 (0.017)	0.49		
	EDGE DISTANCE	-0.106 (0.102)	0.32		
	SLOPE	-0.003 (0.003)	0.37		
	WINDSTORM	-0.001 (0.001)	0.34		
Functional diversity	Intercept***	3.497 (0.083)			
	AREA***	0.067 (0.018)	1.00	53.03	0.165
	D_{MAINLAND}	—			
	FIRE**	-0.057 (0.022)	1.00	24.32	0.099
	PROXIMITY	—			
	EDGE DISTANCE	—			
	SLOPE*	0.006 (0.003)	0.82	22.65	0.060
	WINDSTORM	—			
Fisher alpha	Intercept***	2.675 (0.347)			
	AREA	0.123 (0.074)	0.70		
	D_{MAINLAND} *	0.162 (0.075)	0.77		
	FIRE	—			
	PROXIMITY	0.078 (0.044)	0.45		
	EDGE DISTANCE	—			
	SLOPE	—			
	WINDSTORM	—			
Pioneers (%)	Intercept	-0.605 (0.354)			
	AREA	—			
	D_{MAINLAND} **	-0.006 (0.002)	0.96	18.77	0.066
	FIRE***	0.332 (0.083)	1.00	63.83	0.123
	PROXIMITY	—			
	EDGE DISTANCE***	-0.420 (0.122)	0.99	17.40	0.014
	SLOPE	—			
	WINDSTORM	—			
Emergents (%)	Intercept***	-1.966 (0.486)			
	AREA***	0.261 (0.077)	0.97	60.35	0.081
	D_{MAINLAND} **	0.005 (0.002)	0.95	19.55	0.088
	FIRE*	-0.181 (0.076)	0.68	20.10	0.010
	PROXIMITY	—			
	EDGE DISTANCE*	-0.455 (0.228)	0.57		0.009
	SLOPE	-0.012 (0.006)	0.57		
	WINDSTORM	—			
Large-seeded (%)	Intercept***	-0.400 (0.107)			
	AREA	—			
	D_{MAINLAND} *	0.003 (0.001)	0.68	11.21	0.031
	FIRE***	-0.225 (0.062)	0.95	88.79	0.171
	PROXIMITY	—			
	EDGE DISTANCE	—			
	SLOPE	—			
	WINDSTORM	—			
Wood density (mean)	Intercept***	4.238 (0.027)			
	AREA	—			
	D_{MAINLAND} *	0.001 (0.001)	0.69	19.64	0.010
	FIRE***	-0.059 (0.018)	0.85	80.36	0.011
	PROXIMITY	—			
	EDGE DISTANCE	—			
	SLOPE	—			
	WINDSTORM	—			

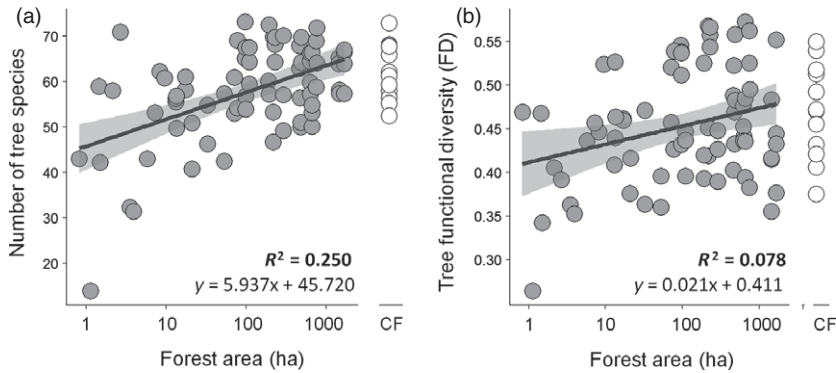


Fig. 2. Relationship between forest island size and (a) the total number of tree species per plot, and (b) functional diversity of trees per plot, considering all 87 forest plots inventoried. Values for plots embedded within continuous forest sites (CF) are shown in white circles, but are not included in linear fits.

continuous forest sites. A similar pattern was found for abundance-weighted species composition ($R^2_{\text{adj}} = 0.177$, $P < 0.001$).

Forests on small islands had lower functional diversity than those on large islands or continuous forest tracts, although the relationship was not strong ($R^2 = 0.08$, Fig. 2b). Moreover, forests on islands < 100 ha had consistently lower tree species diversity and higher dominance than those on islands > 100 ha (Fig. S1 in Supporting Information).

Island size was a good predictor of the abundance of different tree functional groups across all 87 forest plots (Fig. S2 in Supporting Information). Small island forest plots contained a significant lower proportion of both emergent and large-seeded tree stems, and a lower mean wood density per stem. Conversely, pioneer stems were more prevalent in small islands, although the proportion of vertebrate-dispersed stems was unrelated to island area ($R^2_{\text{adj}} < 0.001$, $P = 0.998$). We failed to detect spatial autocorrelation among the 87 plots in mean wood density ($r = 0.009$, $P = 0.399$) and the proportions of pioneer (Mantel test, $r = -0.061$, $P = 0.882$), emergent ($r = -0.060$, $P = 0.905$), large-seeded ($r = 0.015$, $P = 0.348$) and vertebrate-dispersed stems ($r = -0.093$, $P = 0.974$).

PLOT, PATCH AND LANDSCAPE EFFECTS

Island size was the only significant predictor of tree species richness across all 87 forest plots nested within the 37 sites (Table 1). Island size, burn severity and topographic slope were good predictors of functional diversity, whereas Fisher's alpha tree diversity was only explained by distance to the mainland (Table 1).

Redundancy analysis showed that the abundance-based plot-by-species matrix was significantly ($P \leq 0.05$) related to distance to the mainland, burn severity and distance to nearest forest edges; all combined environmental data explained 18.8% of the overall variance. Similarly, these three environmental variables also explained the presence/absence composition matrix, with all combined environmental data explaining 10.8% of the variance. Unburned forest plots in large forest areas had remarkably similar tree assemblages on the basis of the first NMDS axes, which represent tree species assemblage based on either the presence/absence or abundance data (Fig. 3).

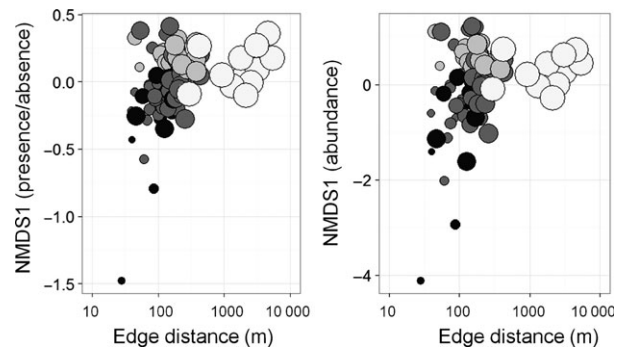


Fig. 3. Relationships between mean edge distance of forest plots and the first non-metric multidimensional scaling (NMDS) axis representing the tree species assemblage structure considering either the presence/absence (left panel) or stem abundance per species (right panel) within 87 plots across 34 islands and three continuous forest sites. Sizes of circles are proportional to the log-transformed areas of forest sites and colours indicate fire severity (greater fire severity from light grey to black; white circles indicate unburnt plots in continuous forest sites).

The relative abundance of different functional groups showed that burn severity was the most important predictor of tree guild structure across islands, appearing in all 'best' models for each functional attribute (Table 1). Distance to nearest edges and distance to the mainland were also significantly retained in the 'best' model explaining the proportion of pioneer stems across all plots nested within the 37 forest sites. Pioneer stems were most dominant in plots and subplots within 100 m from the nearest forest edge, but these rates stabilized at edge distances of ~ 300 m (Fig. 4). Island size was closely related to the proportion of emergent stems, showing the highest relative importance among all variables retained in the 'best' model. Additionally, burn severity, edge distance and distance to the mainland were also significant negative predictors of emergent tree abundance, with severely burnt islands containing very few relict emergents. Burn severity and distance to the mainland were the only significant variables retained in the 'best' model explaining both the proportion of large-seeded stems and mean WD (Table 1). In contrast, our predictors failed to explain the proportion of vertebrate-dispersed stems across the entire seed size spectrum.

Burn severity also explained most changes in tree guilds in GLMM analyses that considered all 435 subplots nested

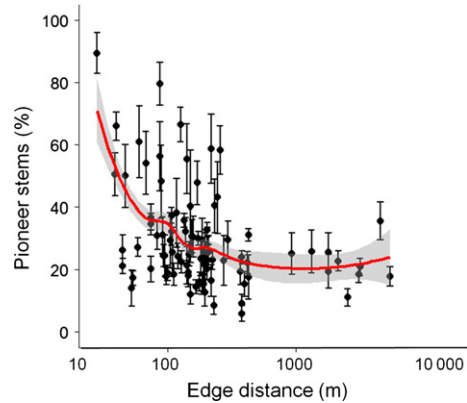


Fig. 4. Relationship between mean edge distance of forest plots and the percentage of pioneer stems considering all 435 subplots nested within 87 plots across the 37 forest sites surveyed at the Balbina Reservoir. Error bars show the subplot-scale variation for each plot. Shaded area represents the 95% confidence interval around a smoother fitted through the plot means.

within 87 plots across the 37 sites. Burn severity ($\beta = 0.299$, $P < 0.001$), island area ($\beta = -0.133$, $P < 0.05$) and distance to the mainland ($\beta = -0.005$, $P < 0.01$) were the strongest predictors retained in the ‘best’ model explaining the proportion of pioneer stems, and these same variables were significant predictors of emergent stems. Burn severity was the only significant variable retained in the ‘best’ model explaining the prevalence of both large-seeded ($\beta = -0.209$, $P < 0.001$) and vertebrate-dispersed stems ($\beta = -0.313$, $P < 0.05$), whereas burn severity ($\beta = -0.058$, $P < 0.05$) combined with distance to the mainland ($\beta = 0.002$, $P < 0.001$) was the strongest predictors of mean wood density.

EFFECTS OF FIRE DISTURBANCE

PERMANOVAS showed a significant effect of different levels of burn severity on tree species composition based on either the presence/absence (d.f. = 3, SS = 12.642, $F = 2.33$, $P < 0.001$) or abundance data (d.f. = 3, SS = 14.969, $F = 2.52$, $P < 0.001$). There was a significant effect of burn

severity on the relationship between edge distance and mean wood density (ANCOVA, $F = 8.45$, $P < 0.001$), and the relative abundance of pioneers ($F = 29.39$, $P < 0.001$), large-seeded stems ($F = 23.65$, $P < 0.001$) and vertebrate-dispersed stems ($F = 6.668$, $P < 0.001$). However, there was no significant effect of burn severity on the relationship between the proportion of emergent stems and edge distance ($F = 0.88$, $P = 0.453$).

We detected higher abundances of pioneer stems within four classes of edge distances in severely burnt islands compared to either unburnt islands or those with a history of low incidence of fire (Fig. 5). Indeed, forests with high dominance values, which resulted from a much greater abundance of pioneer stems, occurred mostly on heavily burnt islands (Fig. S3 in Supporting Information). Conversely, lower dominance values of emergent tree stems were related to either unburnt or lightly burnt forest plots (Fig. S3).

Discussion

This assessment of the ‘relaxation’ in post-isolation floristic guild structure within variable-sized forest islands was based on the largest number of forest plots and one of the largest number of tropical forest patches sampled within the context of a major tropical hydroelectric reservoir. In this unique experimental landscape, we were able to assess how tree assemblages respond to forest habitat fragmentation *sensu stricto* (controlling for habitat loss, Fahrig 2003) following a 26-year history of insularization. As expected, the fragmentation process induced by flooding strongly affected the structure of tree assemblages. Additionally, our results indicate that insular tree assemblages have so far been shaped by non-random floristic transitions that have occurred since the islands were created by the rising floodwaters, rather than pre-existing differences in tree species composition and abundance. Although island size was a good predictor of both taxonomic and functional tree diversity, other forest patch and landscape-scale variables exerted even more powerful forces on tree assemblage structure, driven primarily by edge-mediated burn disturbance.

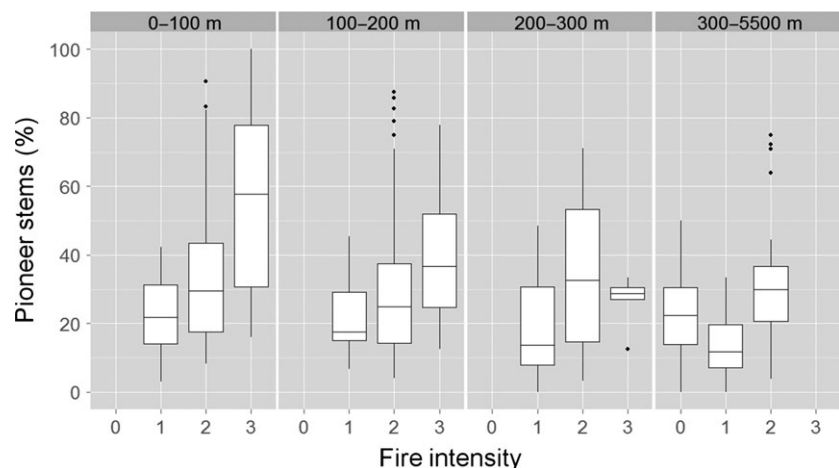


Fig. 5. Box plot showing the effect of fire severity on the percentage of pioneer stems within four classes of edge distances, considering the variation across all 435 subplots nested within 87 plots inventoried at 37 forest sites within the Balbina Reservoir.

DRIVERS OF SPECIES DIVERSITY IN TRUE FOREST ISLANDS

Large islands contained the greatest number of tree species across the Balbina landscape at both plot and island scales. It has been widely accepted that area effects play a prevailing role in the erosion of species diversity in tropical forest fragments (Bell & Donnelly 2006; Ferraz *et al.* 2007), yet this pattern remains ambiguous in tree assemblages in forest remnants embedded within a matrix of pasture and cropland. For instance, studies in southern Mexico, southern Amazonia and the Brazilian Atlantic Forest have shown that tree species richness either declines or fails to respond to patch area (Metzger 2000; Arroyo-Rodríguez & Mandujano 2006; Laurance *et al.* 2006a; Michalski, Nischi & Peres 2007; Santos, Kinoshita & dos Santos 2007; Santos *et al.* 2008; Magnago *et al.* 2014). In contrast, island area explained plant species richness within 154 sub-tropical islands in China's Thousand Island Lake, following ~50 years of isolation (Hu *et al.* 2011). Our positive species-area relationship at the Balbina archipelago suggests that forest islands experienced much higher extinction rates along transient 'relaxation' stages. In particular, islands < 100 ha often exhibited lower species diversity and much higher dominance compared to larger forest areas, indicating that tree assemblages stranded in small and many medium islands have experienced a rapid loss of tree species after only 26 years of isolation.

Over and above the underlying effects of island size, tree species richness and composition were largely predicted by the severity of a single episodic fire disturbance event, which were more prevalent near forest edges. Species density was particularly low within 100 m of the nearest edges, but relatively low species richness could also be detected in plots (and subplots) up to 500 m from island margins. Forest patch boundaries are often exposed to a hostile microclimate including elevated temperatures, increased wind speed and greater desiccation compared to forest interiors (Kapos *et al.* 1997). Trees within nine BDFFP forest fragments north of Manaus experienced higher mortality within 60 m of edges, and this was aggravated in the smallest isolates (Laurance *et al.* 1998). However, post-isolation old-growth tree mortality in the Balbina islands was primarily driven by a greater susceptibility of edge-related forest disturbance including canopy tree wind-throws and episodic surface fires coinciding with an unprecedented supra-annual drought. Moreover, matrix vegetation in terrestrial landscapes plays a strong role in the magnitude and penetration-distance of edge effects, with much higher tree mortality in patches surrounded by pastures rather than young secondary forests (Mesquita, Delamônica & Laurance 1999; Gascon, Williamson & da Fonseca 2000). Given that Balbina islands were completely exposed to an open-water matrix, which tends to propagate rather than break-up the effects of peak wind turbulence, edges facing prevailing heavy windstorms likely incurred higher rates of tree mortality (cf. Leigh *et al.* 1993). Indeed, plot slope had a significant effect on tree functional diversity, suggesting that trait loss in plots exhibiting a greater elevational range is associated with

higher rates of tree turnover. In contrast, distance to nearest edges had no effect on forest structure within Eastern Amazonian forest islands at the Tucuruí Hydroelectric Dam after ~27 years of isolation (Ferreira *et al.* 2012), likely because the 17 islands sampled in that study had a much narrower size range (8–103 ha), were entirely edge-dominated, and effectively lacked any 'core area' baseline.

TRAIT CORRELATES OF EXTINCTION RISK

Forest habitat insularization at Balbina did not affect plant species uniformly, with life-history traits explaining varying degrees of vulnerability. In particular, emergent species associated with shade-tolerant seedlings, large seeds, dense wood and slow growth rates were most extinction-prone. Island area predicted the abundance of emergents, but edge effects were again the strongest force driving changes in functional space of insular tree assemblages. We thus provide further evidence that the non-random drift in species composition and abundance experienced by tree assemblages are mediated by several species functional attributes (Laurance *et al.* 2006a,b; Tabarelli *et al.* 2010).

The proliferation of fast-growing successional trees in small patches has also been shown to occur in other Neotropical fragmented forest landscapes (Laurance *et al.* 2006a,b; Michalski, Nischi & Peres 2007; Tabarelli *et al.* 2010; Lôbo *et al.* 2011). Some disturbance-loving pioneers at the BDFFP landscape experienced a > 1000% increase in density after only < 20 years of fragmentation (Laurance *et al.* 2006b). Similarly, the number of both pioneer stems and pioneer species in the Atlantic Forest of north-eastern Brazil increased more than fourfold in small fragments after a long post-isolation period (Santos *et al.* 2008). We uncovered strong edge effects on the abundance of pioneer stems within our forest plots, with a significant decline of old-growth stems near forest edges. Additionally, burn severity apparently compounded edges effects, leading to a proliferation of disturbance-adapted pioneer species in plots that had burnt at least once. Pioneer abundance was significantly elevated in heavily burnt plots within 200 m of forest edges, compared to plots that had been moderately and lightly affected by fire. Indeed, fires interact synergistically with forest habitat fragmentation effectively inflating edge effects, given that forests borders are disproportionately more susceptible to surface fires than forest interiors (Cochrane 2001; Cochrane & Laurance 2002). Even in more extensive tracts of forests, fire is likely to exert a negative impact on tree assemblages – in Eastern Amazonia, stem densities decreased and the abundance of pioneer species increased dramatically with burn intensity (Cochrane & Schulze 1999). We also detected that surface fires were more extensive in islands far from the mainland (Fig. S4 in Supporting Information), suggesting that distance to the mainland is somehow related to burn severity, thereby operating as a secondary edge effect.

Fire history and distance to mainland were also good predictors of the abundance of large-seeded (larger than 1 g), emergent stems and mean wood density within forest plots.

Large-seeded species are consistently adversely affected in Amazonian forest fragments (Cramer, Mesquita & Williamson 2007) and are more susceptible to forest fragmentation than small-seeded species, showing a reduction of a third in density in Atlantic Forest patches (Santos *et al.* 2008). Trees bearing large seeds are more specialized in their dispersal agents, primarily medium and large vertebrates, which are also more extinction-prone in semi-defaunated forest remnants (Cordeiro & Howe 2001). For instance, Silva & Tabarelli (2000) predicted that 34% of tree species bearing large fruits will become extinct in Atlantic forest fragments of northeast Brazil, due to vertebrate dispersal bottlenecks. Frugivorous vertebrates in small and medium islands in hydroelectric reservoirs elsewhere were extirpated following a short period of isolation (Cosson *et al.* 1999; Terborgh *et al.* 2001), and several key dispersers of large-seeded plants also met a similar fate at the Balbina lake, aggravating dispersal limitation. However, we failed to uncover a relationship between biotic-dispersed species and island area, which may be related to the fact that many bird and bat species are able to easily cross the water matrix and disperse certain tree species.

The overall mean wood density per stem was lower within severely burnt plots, which is consistent with the greater susceptibility of heavy-wooded species to desiccation (Borchert 1994). In Australian forest isolates, tree species with low wood density were more prone to stem damage due to wind disturbance (Curran *et al.* 2008), yet this functional trait was considered to be a poor predictor of successional species' responses to habitat fragmentation at the BDFFP landscape (Laurance *et al.* 2006b). Wood density can be a good measure of sensitivity to habitat disturbance (Steege & Hammond 2001) and provides another indication that thermal stress through unprecedented surface fires induced high levels of tree mortality within the Balbina islands. Finally, fire severity also depressed the abundance of emergent stems, although this was primarily mediated by area effects. Large trees are particularly vulnerable in isolated forest patches, given their susceptibility to the detrimental effects of wind turbulence, desiccation and liana infestation (Laurance *et al.* 2000).

Conclusions

Our unique experimental setting of thousands of forest islands within one of the largest tropical hydroelectric reservoirs indicates that the detrimental effects of fragmentation in islands formed by a hydroelectric dam are considerably stronger than in forest isolates embedded within a terrestrial landscape, confirming other Neotropical studies in analogous archipelagos (Cosson *et al.* 1999; Emer, Venticinque & Fonseca 2013). In contrast to other Neotropical fragmentation ecology studies on tree assemblages (Metzger 2000; Arroyo-Rodríguez & Mandujano 2006; Laurance *et al.* 2006a; Michalski, Nischi & Peres 2007; Santos, Kinoshita & dos Santos 2007; Santos *et al.* 2008), we uncovered a significantly positive species-area relationship, indicating a rapid decay in tree diversity in most islands. Yet our results clearly show that edge effects – including edge-related fires and forest disturbance – were the

main predictors of directional floristic transitions at Balbina. This suggests that area effects are expressed via a response to edge effects, given that trees in smaller islands were most susceptible to edge-related fires and wind-throws, which is consistent with the biotic and abiotic changes occurring at forest patch boundaries (Murcia 1995; Laurance *et al.* 1998).

Secondly, the inhospitable open-water matrix seems to exert a key role in determining patterns of tree assemblage composition and functional space in our study landscape. Water is an unconditionally unsuitable habitat for tree species of upland forests and operates as a strong barrier for many vertebrate species, thus severing matrix movements of key seed dispersers. For example, primates and small mammals were unable to cross inundated areas only a few years after the flooding of the Sinnamary River in French Guiana (Cosson *et al.* 1999) and a decline of tree diversity in small Gatun Lake islands (Panama) was apparently induced by the absence of seed-burying agoutis (Leigh *et al.* 1993). Large predators were extirpated in several islets within Lago Guri just after isolation, resulting in hyper-herbivory and a sharp decline in saplings (Terborgh *et al.* 2006). Furthermore, islands are strongly affected by edge effects, given that their boundaries cannot be buffered by the attenuating protection of second-growth vegetation and therefore directly exposed to prevailing windstorms. In fact, edge-related tree mortality in Amazonian forest patches is largely a function of the surrounding vegetation structure (Mesquita, Delamônica & Laurance 1999). In other words, the dynamics of tree assemblages within islands created by hydroelectric impoundments appears to be more strongly sensitive to edge effects than most terrestrial fragmented forest landscapes. In light of the burgeoning hydro-power engineering sector in several South American countries (Finer & Jenkins 2012; Kareiva 2012), our results highlight the drastic floristic erosion that new mega hydroelectric dams are expected to induce in future archipelagic landscapes.

Finally, we uncovered the pervasive additive effect of El Niño surface fires within forest isolates, which were more prevalent in islands far from the mainland and along peripheral portions of all islands. These ground fires led to a near complete species turnover characterized by a pronounced proliferation of pioneer species, severe decline in the abundance of emergent and large-seeded species, and overall reduction in mean wood density. Fire disturbance operates as a large-scale edge effect and represents a serious risk for fragmented tropical forest landscapes. We suspect that fires induced a more destructive effect due to the large amounts of combustible fuel from dead trees surrounding all islands. The Balbina archipelago has the unique advantage of being protected by the Uatumã Biological Reserve from a panoply of human disturbances, such as logging and hunting activities, that may interact synergistically with forest fragmentation (Laurance & Peres 2006). Hence, medium-term effects on forest structure and composition would be expected to be far worse had these islands been left unprotected since the rise of floodwaters. Preventing or mitigating the compounding effects of anthropogenic forest disturbance in artificial archipelagos formed by mega hydroelectric dams can therefore decelerate ecological

processes leading to forest degradation and losses in forest ecosystem services such as carbon retention.

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Data accessibility

Data available from the Dryad Digital Repository (Benchimol & Peres, 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Number of individuals and species of trees ≥ 10 cm DBH within all 87 plots inventoried across 34 islands and three continuous forest sites across the Balbina Hydroelectric Dam landscape of Central Brazilian Amazonia.

Table S2. List of 368 tree species belonging to 59 families, and their frequency (number of plots within which the species occurred) within 87 forest plots sampled across 37 forest sites throughout the Balbina dam landscape.

Figure S1. Relationship between floristic diversity metrics and island area for 87 forest plots across 34 islands (light grey; $N = 75$ plots) and three continuous forest sites (dark grey; $N = 12$ plots) surveyed throughout the Balbina Reservoir landscape. Circle sizes are proportional to the log-transformed areas of forest sites.

Figure S2. Relationships between island area and functional attributes representing the tree species assemblage structure within 87 forest plots across 37 forest sites surveyed at the Balbina Reservoir landscape.

Figure S3. Patterns of species dominance in tree assemblages within 87 plots across 37 forest sites surveyed at the Balbina Reservoir landscape

in relation to the proportion of either the proportion of pioneer stems and emergent stems, according to levels of fire severity [(0)= Unburnt; (1) = Lightly fire disturbed; (2) Moderately fire disturbed; and (3) Heavily fire disturbed].

Figure S4. Relationship between surface fire severity and the shortest linear distance to the mainland across 87 plots nested within 37 forest sites surveyed at the Balbina Reservoir landscape. Jitter points are used to avoid overplotting.