



Palm distribution patterns in the southwestern Brazilian Amazon: Impact of a large hydroelectric dam

Ednéia A. dos Santos^a, Marcelo B. Medeiros^{b,*}, Evandro J.L. Ferreira^c, Marcelo F. Simon^b, Washington L. Oliveira^d, Flávia R.C. Costa^e

^a Programa de Pós-Graduação em Botânica do Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil

^b Embrapa Recursos Genéticos e Biotecnologia – Embrapa, Parque Estação Biológica, PqEB, Av.W5 Norte (final), 70770-917 Brasília, Distrito Federal, Brazil

^c Departamento de Botânica, Universidade Federal do Acre, Rio Branco, Brazil

^d Departamento de Botânica, Instituto de Ciências Biológicas – Universidade de Brasília, 70910-900 Brasília, Distrito Federal, Brazil

^e Coordenação de Pesquisas em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil



ARTICLE INFO

Keywords:

Arecaceae

Campinarana

Environmental impacts

Extreme weather events

Madeira River

Várzea forests

Terra-firme forests

ABSTRACT

Mega hydroelectric dams cause loss of habitat for many species and lead to local or regional extinction. Despite these dire facts, little is known about the impact of these mega-dams on Amazonia. Using palms as a model, we investigated this question by sampling 26 1-ha plots distributed in the influence areas of the Jirau mega-dam in southwestern Brazilian Amazonia. We examined palm community patterns and species distributions as a function of environmental variables, as well as the effect of this large dam on plant survival. Palm communities on the banks of the Madeira River differ among three main habitats sampled (*campinarana*, *terra-firme* and *várzea* forests), and these differences are associated with the gradient of C, pH, N, P, soil texture, slope, and depth to the water-table. The level of the Madeira River raised after the construction of the Jirau mega-dam, directly affecting the populations of 61.3% of the palm species, particularly those species associated to areas with silty soils, low slope, and low depth to the water-table. *Várzea* and *terra-firme* forests near the river, as well as low-lying plots, even those distant from the river, were affected by the filling of the reservoir. *Várzea* forests and *campinaranas* had a greater proportion of palm species flooded by the reservoir and the reduction of water-table depth. *Várzea* forests and *campinaranas* harbor distinct palm communities from the *terra-firme* forests and require priority in conservation policies and management to mitigate harmful environmental impacts in the Amazon.

1. Introduction

As a result of its large hydroelectric potential, the nine countries that encompass the Amazon plan the construction of 243 new hydroelectric dams (Lees et al., 2016). Damming Andean-Amazonian rivers, which provide the vast majority of sediments, nutrients, and organic matter to the Amazon River, can affect aquatic communities and ecosystem processes in marine environments thousands of miles away (Finer and Jenkins, 2012). Studies carried out in the first hydroelectric dams built in the region showed direct and indirect negative impacts on the biota, owing to the fragmentation and degradation of riparian and terrestrial habitats (Fearnside, 1989; 2009; Lees et al., 2016) and these hydrological disturbances are rapidly degrading freshwater ecosystems, both independently and via complex feedbacks and synergistic interactions (Castello and Macedo, 2016; Moser et al., 2019). These impacts have negatively affected the habitat of more vulnerable taxa, such as

rare tree species, with loss of significant suitable areas (Silva et al., 2017). In some impacted areas, such as the Balbina hydroelectric dam in Central Amazonia, primary forests have been replaced by secondary forests, resulting in declines of taxonomic and functional diversity (Benchimol and Peres, 2015) and rare tree species are becoming extinction-prone due to reduced tree recruitment and density on islands, potentially leading to future losses in biodiversity and ecosystem functioning (Jones et al., 2019). Liana community will likely exacerbate the degradation of remnant tree communities on these islands induced by the Balbina mega-dam through direct and indirect competition (Jones et al., 2017). Also in this region, forests flooded by black waters (*igapó* forests) downstream of the hydroelectric dam presented high mortality by the loss of seasonality of flood pulses, indicating that the natural flood tolerance of this forest typology provides no protection to changes in these pulses (Resende et al., 2019). Extreme flooding over the last few decades, most likely associated with global warming, is an

* Corresponding author.

E-mail address: marcelo.brilhante@embrapa.br (M.B. Medeiros).

<https://doi.org/10.1016/j.foreco.2020.118032>

Received 19 November 2019; Received in revised form 21 February 2020; Accepted 25 February 2020

0378-1127/ © 2020 Elsevier B.V. All rights reserved.

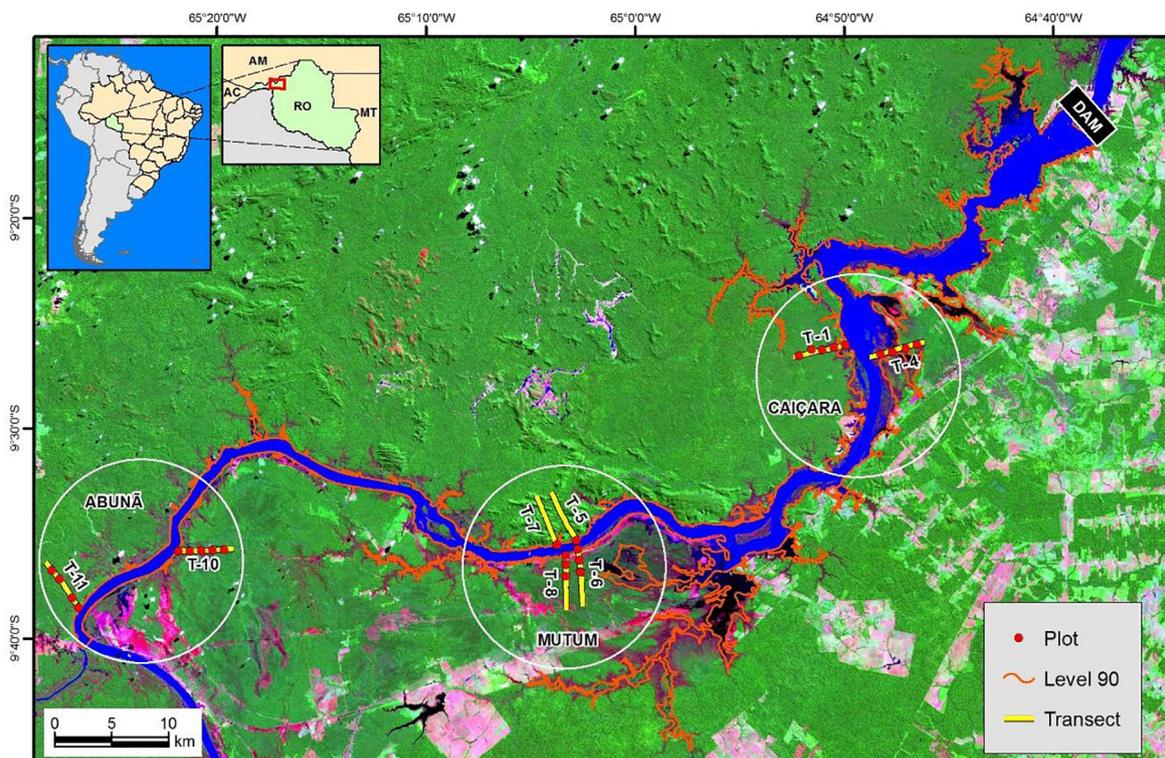


Fig. 1. Study area with 26 plots along upper Madeira River in southern Brazilian Amazonia. Level 90 (m) indicates the extension of reservoir due to the dam for the Jirau's hydroelectric.

additional factor increasing the forest degradation and losses of biodiversity caused directly by the presence and operation of large hydroelectric dams in the Amazon (Castello and Macedo, 2016; Resende et al., 2019; Moser et al., 2019).

However, controversy continues over the magnitude and extent of hydroelectric impacts in the Amazon, especially between the power-producing sector and conservationists (Fearnside, 2009; Latrubesse et al., 2017). Therefore, it is important to document the environmental impacts of these new, large hydroelectric dams that have been built in recent years and to understand their effects on the various components of Amazon biodiversity.

Between 2008 and 2013, the Jirau and Santo Antonio hydroelectric dams were built in the Madeira River Basin, southwest of the Brazilian Amazon, and these make up the main axis of the Madeira River Hydroelectric Complex. The Santo Antonio hydroelectric has been in operation since 2012 flooding an area approximately 422 km² at its maximum level. The Jirau hydroelectric reservoir has been in operation since 2013, and the water level varies between 82.5 and 90 m during the year, flooding an area approximately 361.6 km² at its maximum level. This artificial flooding is approximately 5–10 m above the previous natural river levels and causes permanent and temporary flooding in *terra-firme*, *várzea* and *campinarana* forests in the area of influence of the Jirau reservoir (Silva et al., 2017). However, forest formations most impacted by the Jirau-Santo - Antônio hydroelectric system are the floodplain forests of the upper Madeira River, with at least 89 km² of these forests flooded and high tree mortality observed from aerial photos (Cochrane et al., 2017). The flooded area increased by 72% in the area of the two hydroelectric dams, going from 884 km² in 2011 to 1528 km² in 2015 (Cochrane et al., 2017). In addition, owing to the potential of major hydrological and biotic disturbances that will affect the floodplains of the Amazon River Basin with the construction of 83 dams, the Madeira River sub-basin is considered the most threatened in the Amazon (Latrubesse et al., 2017).

Among the many plant groups possibly affected by the large

hydroelectric dams in the Amazon, palms (Arecaceae) stand out because they are strongly associated with humid environments in valleys and floodplains (Henderson, 1995) where they can constitute a large proportion of individuals and forest biomass (Peters et al., 1989). The area of influence of the two most recent mega hydroelectric dams (Jirau and Santo Antonio) has large areas of forest dominated by palm species (IBGE, 2012; Perigolo et al., 2017). The loss of habitat from flooding of the reservoir on the banks and plains of the Madeira River can, therefore, significantly reduce local palm diversity and increase the vulnerability of species typical of forest formations in these areas (Moser et al., 2014). Understanding the potential impact of these large human disturbances on a botanical family with high diversity (195 species in the Amazon, including 62% endemic), numerical dominance and high biomass in the biome (ter Steege et al., 2013) has, thus, high relevance for conservation.

The distribution of palm species has been associated with soil characteristics (Sollins, 1998; Vormisto, 2002; Vormisto et al., 2004; Costa et al., 2009), hydrology (Skov and Borchsenius, 1997; Wittmann et al., 2006; Stefan et al., 2007; Eiserhardt et al., 2011) and topography (Kahn, 1987; Normand et al., 2006; Svenning et al., 2009; Eiserhardt et al., 2011), and the effects of these factors depend on spatial scale. Hydrological conditions and, consequently, edaphic conditions, are the first to be modified by the building of hydroelectric reservoirs. Therefore, this study asked (1) how the distribution of palm species is associated with environmental gradients in the area of influence of the Jirau hydroelectric dam, and (2) what is the impact of this reservoir on southwestern Amazonian palm communities. We believe that environmental heterogeneity in the study area is the cause of floristic and structural variations in palm communities and thus reservoir flooding would differentially impact communities and species according to their association to riparian or low-water table environments.

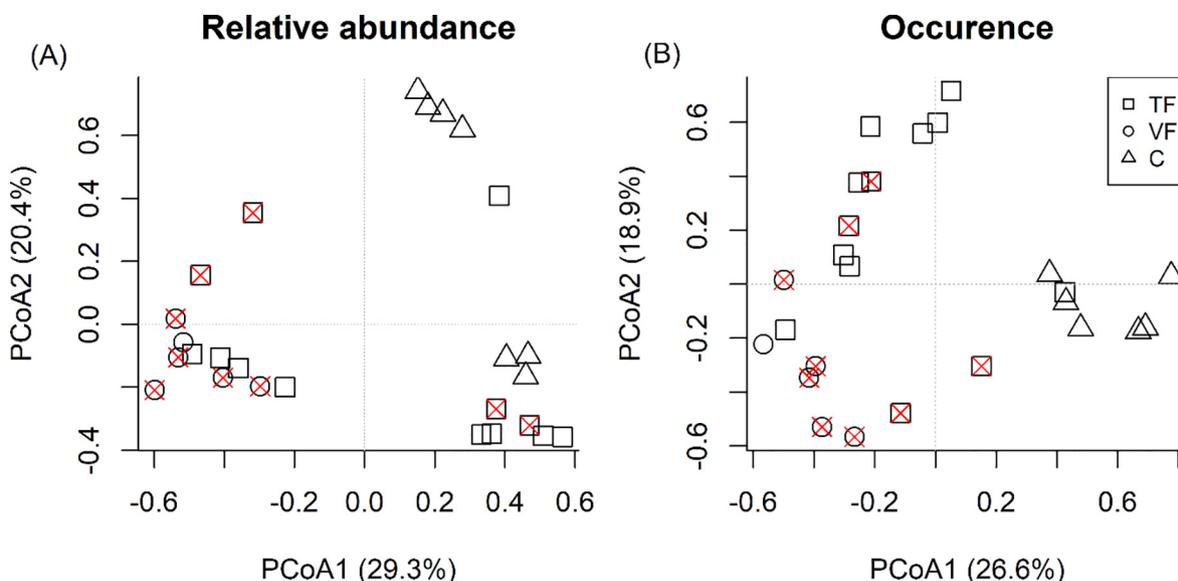


Fig. 2. Principal Coordinate Analysis (PCoA) summarizing palm community composition based on (A) relative abundance and (B) species occurrence in southern Brazilian Amazonia. TF = *Terra-firme* forest, VF = *Várzea* forest, C = *Campinarana*. Plots flooded by the Jirau reservoir are indicated with (x).

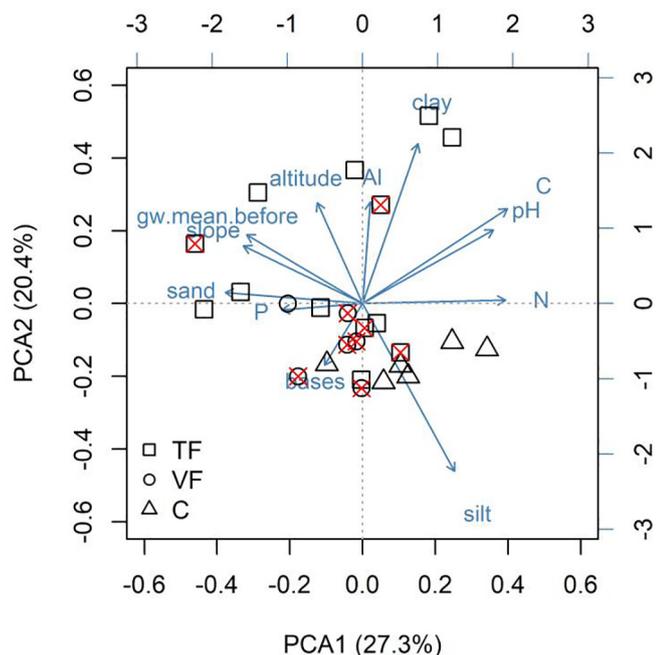


Fig. 3. Principal Components Analysis (PCA) of the environmental variables of plots along the Madeira River in southern Brazilian Amazonia. TF = *Terra-firme* forest, VF = *Várzea* forest, C = *Campinarana*. Plots flooded by the Jirau reservoir are indicated with a red x over the plot symbol.

2. Methods

2.1. Study area

The study was carried out in an area under the influence of the Jirau hydroelectric dam reservoir on the Madeira River, which is located 136 km upstream of the city of Porto Velho, Rondônia (coordinates 9°9'35"S and 9°50'25"S and 65°28'8"W and 64°35'21"W) (Fig. 1). The Madeira River basin begins in the Andes, draining an area of 1,420,000 km², and its highest flow is recorded in March and the lowest in September (Molina, 2007). The climate of the region is classified as tropical humid hyperthermic (Cochrane and Cochrane, 2010) with minimum annual average temperature varying between 20 and 22 °C

Table 1

Generalized least squares regressions (GLS), associating variation in the composition of palm species (summarized by Principal Coordinate Analysis - PCoA) and the environmental gradients summarized by the first two axes of the Principal Component Analysis - PCA (PCA axis 1 was mainly correlated to the sum of bases and average depth to the water-table; PCA axis 2 to silt and altitude). The candidate models included different spatial correlation structures associated with geographic coordinates and heterogeneity of variance between predictors, modules, or sampling transect. lme = Linear Mixed Effects models; gls = Generalized Least Squares models.

Fixed effects	B	p	Random effects
Palm community Composition			
Relative abundance			
PCoA-1	PCA1 0,1228	0,0020	lme(random intercept = module)
	PCA2 -0,1048	0,1231	
PCoA-2	PCA1 -0,0231	0,0996	gls(varExp(PCA1 module))
	PCA2 -0,0028	0,8299	
Presence-absence			
PCoA-1	PCA1 -0,0298	0,1282	gls(corGaus(Lat + Lon), weights = varIdent(module))
	PCA2 0,0403	0,2417	
PCoA-2	PCA1 0,0318	0,3581	lme(random = transect, weights = varExp(PCA2))
	PCA2 0,0680	0,2901	

and maximum between 31 and 33 °C. The relative air humidity varies between 85 and 90 percent, and the average precipitation is between 1700 and 2000 mm (Sombroek, 2001).

The right bank of the river (when facing downstream) is of recent geological formation (Cenozoic period) with past alluvial deposits corresponding to Gleysol areas on flatter terrain. On the left bank, older geological formations of the Proterozoic predominate with post-orogenic granitoids and a more hilly landscape. The predominant soils in the study area are Acrisols and Ferralsols (latosols), mainly in the open rainforest on the left bank of the Madeira River. Hydromorphic Gleysols also occur, but are more common in transition areas of the woody *campinarana* located on the right bank of the Madeira River. Fluvisols formed by alluvial sediment deposition occur at the margins of the Madeira River (Cochrane and Cochrane, 2010; Embrapa, 2011; Quesada et al., 2011). The predominant vegetation type of the region is lowland open rainforest (IBGE, 2012) which is characterized in most of

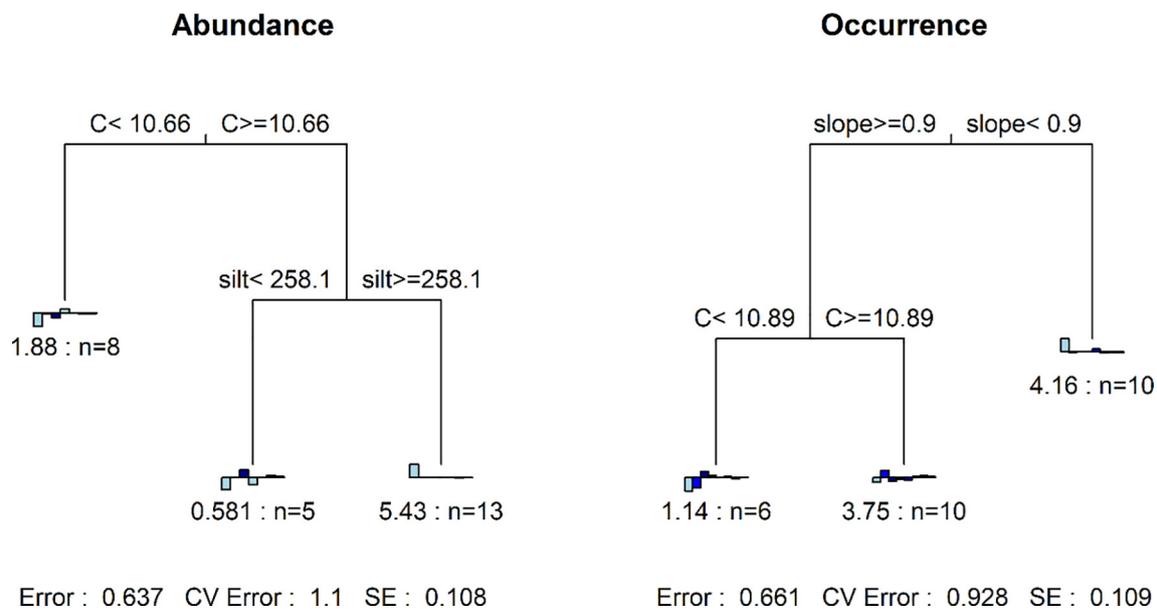


Fig. 4. Multivariate regression trees (MRT) of palm community composition based on species occurrence and relative abundance of species, in southern Brazilian Amazonia. Each split in the MV tree is indicated by the relevant independent variable and its value at the splitting point. Each leaf on the tree has an associated barplot, and each bar is a PCoA axis used as response variable. Because the data is normalized, all of the bars above the line are the ones driving the split. The number of observations represented by each leaf is also shown. At the bottom of the tree is the residual error for the overall tree, or how much variation is not explained by the tree, the cross-validation error and standard error for this size of tree. C = Carbon.

the area as an open canopy *terra firme* forest by the lack of flooding during the rainy period.

The open canopy *terra firme* forest occurs in well-drained soils and is strongly related to the presence of elements such as palms, *sororoca* (*Phenakospermum guyanense*), bamboo and lianas. Openness of canopy allows more light penetration in the understory, resulting in a denser layer of shrubs and lianas (Pires and Prance, 1985). The term *campinarana* is normally used to define a type of stunted vegetation, with thin and small trees usually growing on white-sands or less often on hydromorphic soil (podzol) in Amazon floodplains (Daly and Mitchell, 2000). Patches of *campinaranas* occur on the right bank of the Madeira River in silty, hydromorphic soil subject to seasonal waterlogging caused by the elevation of the water-table, as well as *várzea* forests (areas that are seasonally inundated by the rise of the Madeira River and its tributaries) (Perigolo et al., 2017).

2.2. Data collection: Environmental and floristic data

We systematically distributed RAPELD sampling modules (Magnusson et al., 2005) perpendicular to the Madeira River, two modules next to the hydroelectric dam (Caiçara), two modules in the intermediate portion (Mutum) and two in the final portion (Abunã) of the future UHE Jirau reservoir. Each module is made of two 5 km transects, and the longest distance between modules was 80 km. (Fig. 1). The allocation of plots followed the contour of the terrain in order to minimize internal variation in topography and soil and to allow the use of these variables as predictors of species distribution (Magnusson et al., 2005; MCT, 2005).

Twenty-six plots (250 × 40 m) were sampled before the reservoir flooding (2011), nine in the Caiçara, eight in the Mutum and nine in the Abunã modules (Fig. 1). Of the total sampled plots, 13 were in *terra-firme* forest, seven in *campinarana*, and six in *várzea* forests.

The data was collected in three sub-plots per plot, according to breast height (DAP) of the individuals and the inclusion criterion adopted for this study (individuals with height greater than, or equal to five centimeters). In a 250 × 2 m (0.05 ha) sub-plot, all individuals with height ≥ 5 cm were sampled; in a 250 × 10 m (0.25 ha) sub-plot, only individuals with DBH ≥ 10 cm were sampled; and in a

250 × 20 m sub-plot, only individuals with DBH ≥ 30 cm (0.5 ha) were sampled (Magnusson et al., 2005).

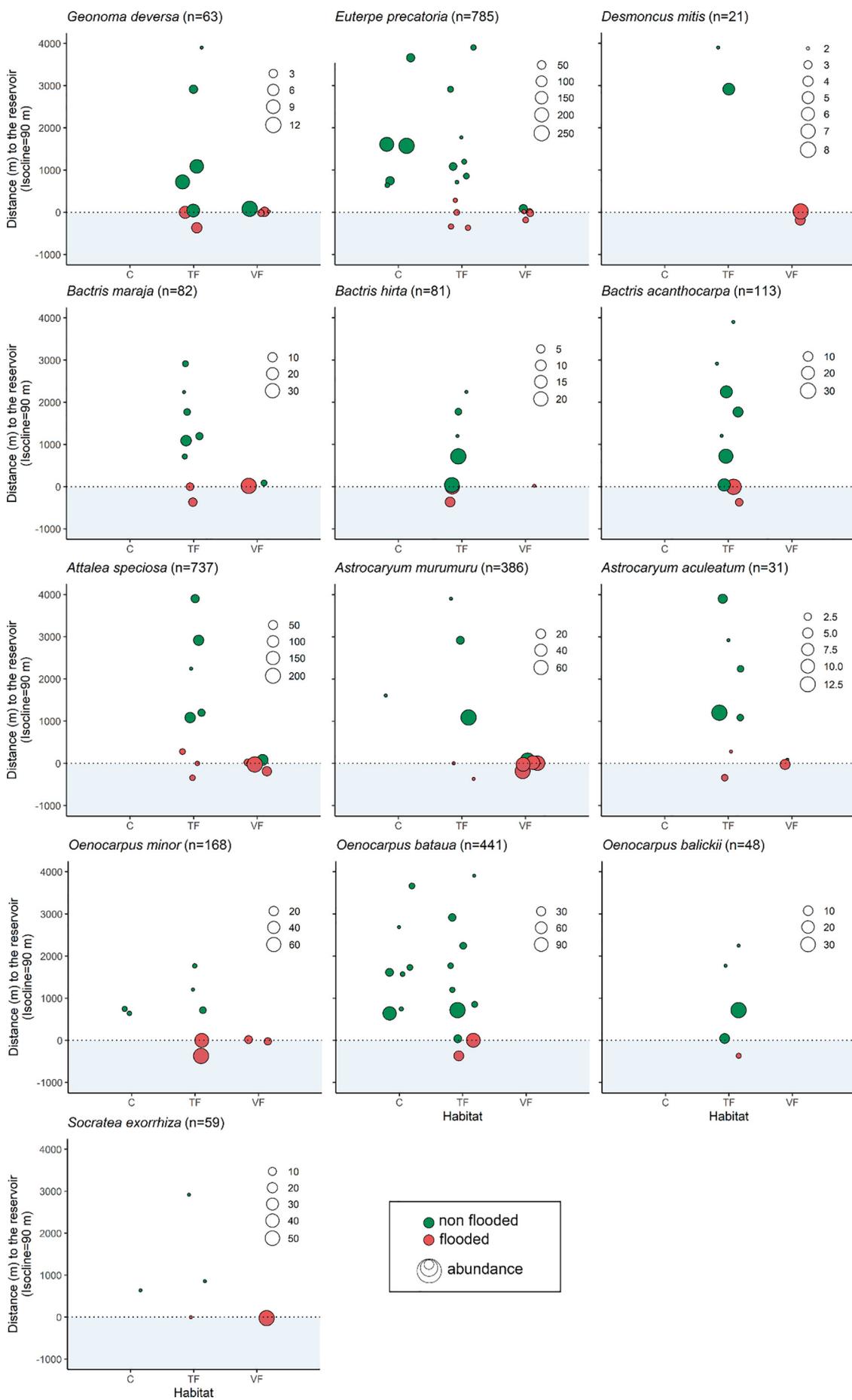
Identifications were performed in the field by taxonomists and parataxonomists with the aid of identification guides (Henderson, 1995; Lorenzi et al., 2010), following the nomenclature of Henderson (1995). We collected voucher specimens of at least one individual of each species surveyed for further identification in the Embrapa Genetic Resources and Biotechnology (CEN) herbarium, and duplicates were sent to the following herbaria: Federal University of Acre (UFACPZ) and National Institute for Amazonian Research (INPA).

We collected soil samples at six locations within each plot (0, 50, 100, 150, 200 and 250 m) and at four depths (0–5, 5–10, 10–20, and 20–30 cm), totaling 24 single samples per plot. Samples were stored at room temperature until complete drying, then aggregated by depth and analyzed following the protocol of EMBRAPA (1997) for texture (sand, clay, silt) and chemical properties (pH, Ca²⁺, K⁺, Mg²⁺, Na⁺, Al³⁺, C, N, and P). Averages from across the four depths within each plot were used to represent texture and chemical variables in the analyses. The terrain slope was measured using a PM-5/360 Suunto clinometer (Suunto, Finland) at every 50 m of each plot, perpendicular to its central axis.

Water-table measurements were carried out on a piezometer per plot (in 25 plots), and measurements were taken from June 2012 (before the reservoir flooding) to June 2013 (after the reservoir flooding) every 30 min and stored in data loggers. Each piezometer had two Solinst® data loggers for water level measurements (Levellogger Junior Model 3001) and atmospheric pressure (Barologger Gold Model 3001). The data was analyzed using Levellogger 4.0.2 software (Solinst, 2014).

2.3. Data analysis

We used Principal Coordinate Analysis (PCoA) to summarize the variation in floristic composition (presence/absence) and structure (relative abundance) of the communities using, respectively, Sørensen's distance and Bray-Curtis index (Legendre and Legendre, 2012). The environmental variables were standardized (mean zero and one unit of variance) and were included in the Principal Component Analysis (PCA) to summarize the environmental gradient. PCoA community



(caption on next page)

Fig. 5. Palm species partially affected by the Jirau reservoir in the southwestern Brazilian Amazon. TF = *Terra-firme* forest, VF = *Várzea* forest, C = *Campinarana*.

eigenvectors were used as response variables, and the axes of the environmental PCA were tested as predictors in GLS (Generalized Least Squares). The main purpose of the modelling approach employed here was to evaluate the responses of variation in community composition to the effects of environmental variation.

We are aware that our sampling design and the scale of the study area could lead to spatial autocorrelation between observations, resulting in lack of independence between samples, which is an important premise of linear regressions. It is known that spatial autocorrelation may inflate type-I error and bias estimates of *p* values (Legendre et al., 2002). Our plots are nested within modules, thus, within a module plots are relatively close to each other (1 km apart), and can be more similar to each other than plots in different modules (~25 km apart). Thus it is necessary to control this potential spatial autocorrelation between the samples. Moreover, the variation of biotic and abiotic components between modules may not be homogeneous, leading to heteroscedasticity in the distribution of model residues, another serious violation of the assumption of linear models. In order to prevent these issues, we contrasted traditional linear models with Generalized Least Squares models, allowing for the test of spatial correlation structures between sampled plots and also allowing the use of weights to control residual bias due to the variance heterogeneity between sample modules or plots. We modelled the auto-correlation based on the plot geographic coordinates (UTM coordinate system) as any of the main potential spatial structures (eg. Gaussian, linear, power, exponential, spherical), as there was no a priori hypothesis about the shape of the spatial component. Weights are also additional variation structures that can be added to decrease bias, accommodating heteroscedasticity between groups, in the case of the present study related to sampling modules or plots. Weights may correspond to different structures of variation, with no prior hypothesis, so we tested fixed variance weights ('varFixed' parameter on 'glS' function), a constant variance function structure ('varIdent') that allows different variances, one for each level of a grouping factor as the sample modules or plots, and an exponential variance, according to the group and or according to the predictor variables in each group. Candidate models were compared with models without correlation structures and the selection of the best correlation structure was done from the saturated model with all predictive variables adjusted with maximum likelihood (maximizing the restricted log-likelihood). The Akaike information criterion (AIC) (Burnham and Anderson, 2002) was used to perform model selection of correlation structures. Following this, we perform selection of the fixed predictors with a maximized log-likelihood test. The analysis protocol and the validation of the models proceeded according to recommendations of Zuur et al. (2009) and Zuur et al. (2010).

We also evaluated the hierarchical importance of the effect of each environmental predictor on the patterns of community structure through Multivariate Regression Trees (MRT; De'ath, 2002). We used PCoA axes with at least 80% of cumulative percentage of variance accounted for by the first *n* components representing the community structure and composition, as response variables on MRT analyses and examined the hierarchical effects of the environmental predictors (Pansonato et al., 2013).

All analyses were performed with the R software (R Development Core Team, 2017). We performed ordinations in the *vegan* package (Oksanen et al., 2013), regression models with 'glS' and 'lme' functions in the *nlme* packages (Pinheiro et al., 2011) and MRT analyses in the *mvp* package (Therneau et al., 2013).

3. Results

3.1. Community composition

A total of 31 species and 3571 individuals were sampled (Table S1). *Bactris* was the genus with the highest number of species (8), followed by *Astrocaryum* (4), *Attalea* (4), *Oenocarpus* (4), *Desmoncus* (3) and *Geonoma* (2). The other genera (*Chamaedorea*, *Euterpe*, *Iriarteia*, *Mauritia*, *Mauritiella* and *Socratea*) were represented by one species each. Species richness were quite unequal among forest types. *Terra-firme* forests harbours 26 palm species, *várzea* forests harbours 17 species and *campinaranas* harbours 8 species.

3.2. Determinants of community composition

Palm community composition based on both occurrence or relative abundances differed among *campinaranas*, *várzea* and *terra-firme* forests (Fig. 2 A and B). *Campinaranas* was the most distinctive group among the palm communities. The PCoA based on abundance data shows that terra firme forests can have very variable compositions, even very similar to *campinaranas*. On the other hand the PCoA based on occurrence suggests the three forest formations have different compositions. The Principal Component Analysis (PCA) based on soil, altitude and slope also indicates distinct clusters relative to forest formations. *Terra-firme* forests have a greater environmental amplitude relative to *várzea* and *campinarana* forests. Higher silt concentrations on lower altitude sites were associated mainly with *campinarana* and *várzea* forests, whereas *terra-firme* forests had a greater association with sandy or clayey soils and greater depth to the water-table (Fig. 3). Axis 1 of the PCA indicated a gradient positively correlated with C, pH, N and silt content and negatively correlated with P, sand, slope and mean depth to the water-table. Axis 2 indicated a gradient positively correlated with clay, C, Al and altitude and negatively correlated with silt and sum of exchangeable bases (Table S2).

The community composition based on the abundance of palm species was strongly associated with axis 1 of the environmental PCA and, therefore, with the gradient of C, pH, N, silt, P, sand, slope and mean depth to the water-table, as indicated by the linear mixed effects models taking into account the random variation of the intercept related to the sampling modules (Fig. S1; Table 1). The palm community composition based on the presence-absence of the species was not associated with the two axes of the PCA (Table 1; Fig. S1). MRT analysis emphasized the importance of C content, silt and slope for the variation in structure and floristic composition of palm communities (Fig. 4).

3.3. Impacts of the dam

Upon filling the reservoir, nine of the 26 sampled plots were completely flooded annually during the flood months (December to April) of the Madeira River. Four plots were in *terra-firme* forest and five in *várzea* forests. However, the populations of palm species most affected (flooded) by the reservoir were concentrated in *várzea* forests (Fig. S2). Palm species less affected by the reservoir were concentrated in areas with greater depth to the water-table (Fig. S3).

In addition to the annual flooding of these nine plots, the ground-water level has undergone significant changes in all habitats, including *campinarana* and *terra-firme* forests, even in plots farther from the reservoir, which do not suffer reservoir-induced flooding (Fig. S4). The mean value of the water-table depth across plots was -3.75 ± 1.79 m before the reservoir (2012–2013), but raised to -1.99 ± 1.87 m after the reservoir filling (2014–2015). In *campinaranas*, a forest formation not flooded annually by the reservoir, the average values of the water-table depth went from -2.13 ± 1.69 m before to -1.15 ± 1.46 m

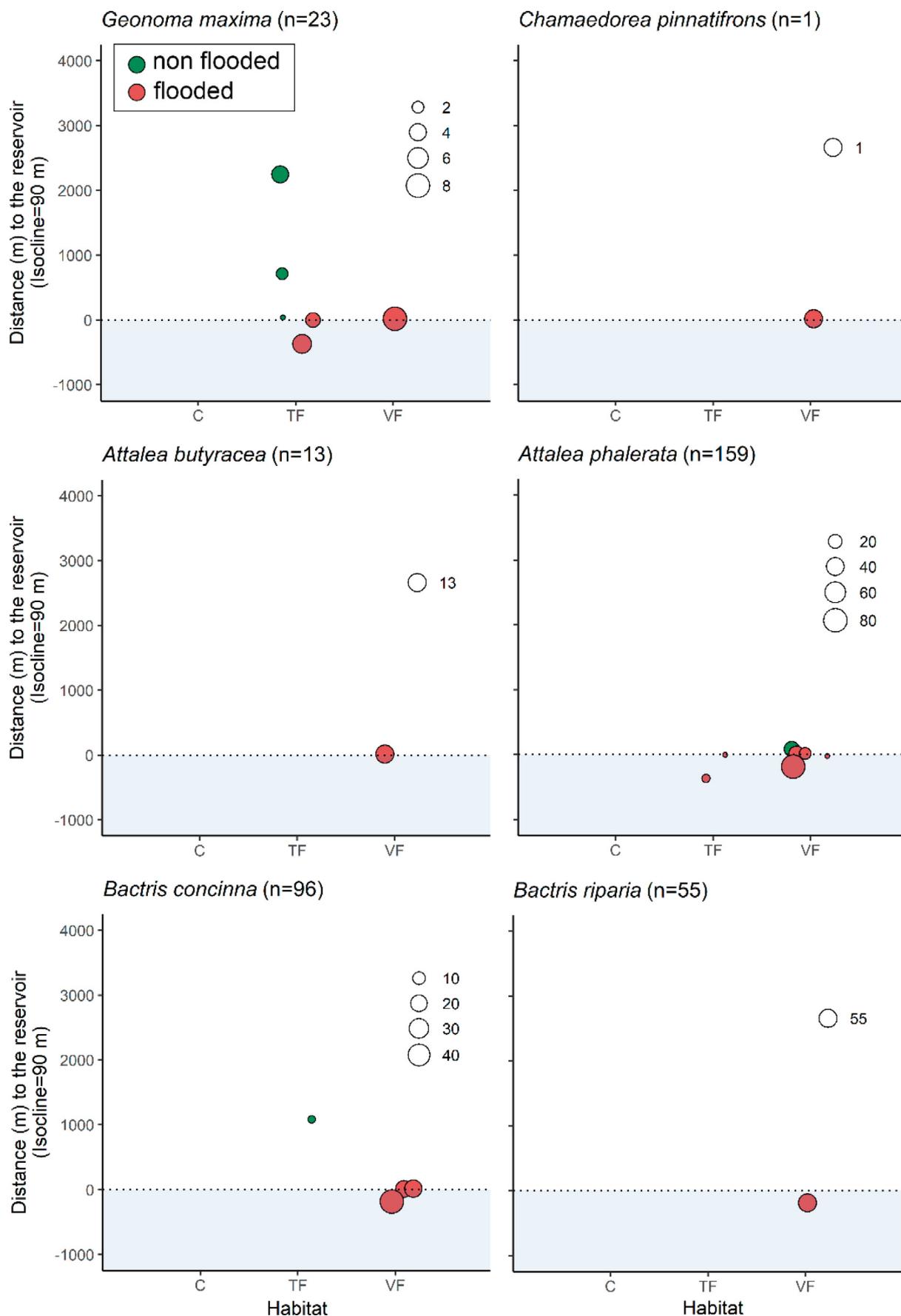


Fig. 6. Palm species with populations severely affected by the Jirau reservoir in the southwestern Brazilian Amazon. TF = Terra-firme forest, VF = Várzea forest, C = Campinarana.

after the reservoir filling, in *terra-firme* forests from -4.56 ± 2.2 m to -3.28 ± 2.2 m, and in *várzea* forests from -4.06 ± 1.45 m to -1.04 ± 1.9 m.

Of the 31 species sampled, twelve (*A. acaule*, *A. gynacanthum*, *B. elegans*, *B. gastoniana*, *B. simplicifrons*, *D. giganteus*, *D. polyacanthos*, *Iriartea deltoidea*, *M. flexuosa*, *A. maripa*, *M. armata* and *O. bacaba*; Fig. S5) had no individuals in the area flooded by the reservoir and, in general, were sampled in one or two sampling modules where they presented low abundance (except *A. gynacanthum*). Thirteen species (*A. murumuru*, *A. aculeatum*, *A. speciosa*, *B. maraja*, *B. hirta*, *B. acanthocarpa*, *D. mitis*, *E. precatória*, *G. deversa*, *O. minor*, *O. bataua*, *O. balickii* and *S. exorrhiza*; Fig. 5) had many individuals in the area flooded by the reservoir, and include some very abundant species, such as *E. precatória*, *A. speciosa*, *O. bataua* and *A. murumuru*. Six species (*A. phalerata*, *A. butyracea*, *B. riparia*, *B. concinna*, *C. pinnatifrons* and *G. maxima*) had most of their individuals flooded by the reservoir, ranging from species with only one individual (*C. pinnatifrons*) to more abundant species, such as *A. phalerata*, *B. riparia* and *B. concinna* (Fig. 6).

4. Discussion

We have shown here that: (1) palm communities on the banks of the Madeira River differ among forest formations (*campinarana*, *várzea* and *terra-firme* forests), and these differences are associated with the gradients of C, pH, N, P, soil texture, slope and mean depth to the water-table; (2) the increase in the level of the Madeira River, associated with the operation of the Jirau dam, directly flooded the populations of 61.3% of the palm species in the region; and (3) six palm species had all populations flooded by the reservoir, and another 13 species had part of their populations flooded by the reservoir.

The species distribution and, therefore, the composition based on the abundance of the palm communities differed according to edaphic factors (texture, C, pH, N and P), slope and depth to the water-table, as has been documented in other sites (Jirka et al., 2007; Balslev et al., 2011; Vormisto et al., 2004; Costa et al., 2009). We observed a gradient in species distribution, with some restricted to drier (*terra-firme* forests) and others to more humid areas (*várzea* and *campinarana* forests). Forests flooded with black-waters (*igapó* forests) also have their floristic composition, species richness, forest structure and diversity related to variation of flood pulses (Ferreira, 1997). Both *Igapó* and *varzea* forests comprise Amazonian wetlands periodically inundated (or periodically waterlogged), differing on ecological attributes such as water physico-chemical parameters and water sediment loads (Junk et al., 2011). Soil water conditions, as determined by the flood pattern and depth to the water-table, have a strong influence on species richness and composition of palm communities, and, generally, richness decreases with the increase of the flood intensity. This can be explained by the stress suffered by plants in this type of environment, which requires adaptations for survival in hypoxic to anoxic soil conditions (Balslev et al., 2011). Disruption of seasonal inundation regimes impacts species composition and biogeochemical cycling in river floodplains (Castello and Macedo, 2016). Over time, Amazonian species have evolved and adapted to natural variation in the level of rivers and groundwater (Wittmann et al., 2010), and a drastic change in these levels can lead to a high mortality of individuals in the first years after the formation of a reservoir (Vale et al., 2013; Moser et al., 2019). Furthermore, Assahira et al. (2017) observed tree mortality during periods of consecutive years of inundation, up to two decades after the implementation of a large hydroelectric dam.

The existence of different palm floristic communities implies that the loss by reservoir flooding of some environments with distinctive characteristics generates a corresponding loss of floristic diversity at landscape scale on the banks of the Madeira River. In fact, populations of 61.3% of species associated with silt and shallow water depths were drastically reduced by the flooding of the Madeira River banks by the Jirau reservoir. This includes floodplains near the river, as well as plots

with low altitudes that, even when distant from the river, were affected by the reservoir filling. Among these 19 species (61.3%) locally threatened by the dam on the banks of the Madeira River in Jirau, some (*A. butyracea*, *B. riparia* and *C. pinnatifrons*) were recorded from a single plot, and 100% of their abundance in the study area lies within the flood-affected area. Two species (*A. butyracea*, *C. pinnatifrons*) have a small number of observed individuals in addition to low frequency. *A. butyracea* and *C. pinnatifrons* are part of the palm flora of western Amazonia and occur in *terra-firme* and *várzea* forests (Henderson, 1995). *B. riparia* was abundant in only one plot, and it is a species more common on the banks of black water rivers, occurring only rarely on the banks of white waters (Henderson, 1995) such as the Madeira River.

Some species had only part of their abundances affected by reservoir filling, such as *A. murumuru*, *A. phalerata*, *A. speciosa*, *E. precatória* and *O. bataua*, but still had large abundance in the study area. These are also among the most abundant palm species found in other studies (Vormisto, 2002; Vormisto et al., 2004; ter Steege et al., 2013) and are widely distributed in the Amazon region or adjacent areas, such as Central America, Cerrado and Atlantic Forest. *Astrocaryum murumuru* occurs in *várzea* forests, and sparsely in *terra firme* forests (Henderson, 1995), and in the study area, more than 77% of their individuals were found in plots with periodic natural flooding and temporary streams. On the other hand, *E. precatória* and *O. bataua* occur in both *várzea* and *terra firme* forests, and these two species were widely found in the study area, both in *terra-firme* forests and in *campinaranas*, and their abundances varied between and within each physiognomy. Thus, the mega dam does not imply local loss of these species, but potentially a loss of genetic diversity.

The loss of habitat is more impactful for species that are restricted to riparian environments (Cochrane et al., 2017; Resende et al., 2019) and reproduce preferably in clonal form, even if they have large local abundances. For example, *B. concinna* and *O. minor* form clonal clusters and had more than 90% of their individuals occurring in the flood-affected area by the reservoir. In addition, species that occur in specific environments, such as *B. riparia*, or in areas that have been most severely flooded by the reservoir, such as *A. phalerata*, may be more vulnerable to habitat loss. Thus, the more susceptible species to habitat loss are those associated with floodplain environments or with low altitude sites, even if these are far from the riverbanks.

Other risk factors for palm species are the rise in groundwater level and changes in the pattern of flooding after the reservoir. Species potentially intolerant of flooded soils, such as *B. acanthocarpa*, *B. elegans* and *B. gastoniana*, found exclusively in areas of *terra-firme* forest or with well-drained soil (Henderson, 1995), may be the first species to suffer extinction locally if their habitat undergoes periodic flooding or changes in groundwater levels. Considering the significant changes that have occurred in groundwater levels in *campinarana* and *terra-firme* forests in areas away from the reservoir, long-term negative effects may still occur on populations not directly affected by reservoir flooding. The synergistic effect between mega hydroelectric dams and the increased frequency of extreme flooding over the last few decades (Castello and Macedo, 2016; Marengo and Espinoza, 2016; Barichivich et al., 2018) is likely to result in mega-floods, such as the one that affected the Madeira River in 2014. Harmful consequences for biodiversity are expected as the frequency of such events is likely to increase over the Amazon basin (Moser et al., 2019).

Palm fruits are important sources of food for many animals and zoochory is common in several palm species (Zona and Henderson, 1989). Benchimol et al. (2017) observed the strong influence of habitat loss on the overall structure of *Arecaceae* assemblages in the Brazilian Atlantic forest, where the reduction of species richness and the abundance of palm trees have the potential to impoverish the fauna of specialist frugivores. In addition, these authors note that extinctions of key palm dispersers may have affected the dispersal and regeneration of large-seeded palm species, such as *Attalea humilis*. Defaunation of seed dispersers in forest fragments with less than 1000 ha in the Atlantic

Forest collapsed the seedling recruitment of *Astrocaryum aculeatissimum* (Galetti et al., 2006). Southwestern Brazilian Amazon is facing this scenario of forest fragmentation where deforestation for intensive agricultural activities and the construction of large hydroelectric dams have been significant in recent decades (Ferraz et al., 2005). Therefore, other important negative implications for palm species of the upper Madeira River may be triggered by the forest fragmentation.

The results presented here indicate direct and indirect effects of environmental changes due to dam flooding on the diversity, abundance, and distribution of palm species. These can be used to guide the environmental licensing process of new reservoirs, the recovery of populations and the collection of germplasm, with priority to species with populations in more vulnerable forest formations, such as the *campinaranas* and *várzea* forests of the upper Madeira River.

CRedit authorship contribution statement

Ednéia A. dos Santos: Conceptualization, Investigation, Methodology, Writing - original draft, Data curation, Formal analysis. **Marcelo B. Medeiros:** Conceptualization, Investigation, Methodology, Writing - original draft, Data curation, Formal analysis, Funding acquisition, Supervision. **Evandro J.L. Ferreira:** Conceptualization, Methodology. **Marcelo F. Simon:** Conceptualization, Investigation, Methodology, Writing - review & editing, Data curation, Formal analysis, Funding acquisition, Supervision. **Washington L. Oliveira:** Investigation, Methodology, Writing - review & editing, Data curation, Formal analysis. **Flávia R.C. Costa:** Conceptualization, Investigation, Methodology, Writing - original draft, Formal analysis, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank Pamela Moser, Isabela P. L. Lima, Natália Perigolo, Glocimar Pereira da Silva, Ocírio de Souza Pereira (Juruna), Antônio José Barreto dos Santos (Tonico), Riba, Valdeci Ferreira Gomes (Dudu), Gledson Alves Moreira, Márcio Honorato, Samanta Gianni, Victor Vinicius Ferreira Lima, Aécio Amaral, Nilton Ferreira, Juarez Amaral and João Benedito Pereira for support in the field. We also thank Conselho Nacional de Pesquisas-CNPq – for a M.Sc. scholarship to E. A. Santos, Embrapa Genetic Resources and Biotechnology, Energia Sustentável do Brasil- ESBR and Eliseu Alves Foundation for financial supporting.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118032>.

References

Assahira, C., Piedade, M.T.F., Trumbore, S.E., Wittmann, F., Cintra, B.B.L., Batista, E.S., et al., 2017. Tree mortality of a flood-adapted species in response of hydrographic changes caused by an Amazonian river dam. *For. Ecol. Manage.* 396, 113–123. <https://doi.org/10.1016/j.foreco.2017.04.016>.

Balslev, H., Kahn, F., Millan, B., Svenning, J.C., Kristiansen, T., Borchsenius, F., et al., 2011. Species diversity and growth forms in tropical American palm communities. *Bot. Rev.* 77, 381–425. <https://doi.org/10.1007/s12229-011-9084-x>.

Barichivich, J., Gloor, E., Peylin, P., Brienen, R.J.W., Schöngart, J., Espinoza, J.C., Pattanayak, K.C., 2018. Recent intensification of Amazon flooding extremes driven by strengthened Walker circulation. *Sci. Adv.* 4, eaat8785. <https://doi.org/10.1126/sciadv.aat8785>.

Benchimol, M., Peres, C.A., 2015. Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. *J. Ecol.* 103, 408–420. <https://doi.org/10.1111/1365-2745.12371>.

Benchimol, M., Talora, D.C., Mariano-Neto, E., Oliveira, T.L.S., Leal, A., Mielke, M.S., Faria, D., 2017. Losing our palms: the influence of landscape deforestation on the Arecaeae diversity in the Atlantic forest. *For. Ecol. Manage.* 384, 314–322. <https://doi.org/10.1016/j.foreco.2016.11.014>.

Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multi-model Inference: A Practical Information-theoretic Approach* (2nd edition). Springer Verlag.

Castello, L., Macedo, M.N., 2016. Large-scale degradation of Amazonian freshwater ecosystems. *Glob. Change Biol.* 22, 990–1007. <https://doi.org/10.1111/gcb.13173>.

Cochrane, S.M.V., Matricardi, E.A.T., Numata, I., Lefebvre, P.A., 2017. Landsat-based analysis of mega dam flooding impacts in the Amazon compared to associated environmental impact assessments: Upper Madeira River example 2006–2015. *Remote Sens. Appl.: Society Environ.* 7, 1–8. <https://doi.org/10.1016/j.rsase.2017.04.005>.

Cochrane, T.T., Cochrane, T.A., 2010. *Amazon Forest and Savanna Lands: A Guide to the Climates, Vegetation, Landscapes and Soils of Central Tropical South America*. Scotts Valley, Create Space.

Costa, F.R.C., Guillaumet, J.L., Lima, A.P., Pereira, O.S., 2009. Gradients within gradients: the mesoscale distribution patterns of palms in a central Amazonian forest. *J. Veg. Sci.* 20, 69–78. <https://doi.org/10.1111/j.1654-1103.2009.05314.x>.

Daly D.C., Mitchell J.D., 2000. Lowland vegetation of tropical South America – an overview. In: Lentz D. (Ed.), *Imperfect balance: landscape transformations in the pre-Columbian Americas*. Columbia University Press. New York, pp. 391–454.

De'ath, G., 2002. Multivariate regression trees: a new technique for modeling species-environment relationships. *Ecology* 83, 1105–1117. <https://doi.org/10.1890/0012-9658>.

Eiserhardt, W.L., Svenning, J.C., Kissling, W.D., Balslev, H., 2011. Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. *Ann. Bot.* 108, 1391–1416. <https://doi.org/10.1093/aob/mcr146>.

EMBRAPA. (1997). *Manual de Métodos de Análise de Solo*. Centro Nacional de Pesquisa de Solos. Rio de Janeiro: EMBRAPA, Centro Nacional de Pesquisa de Solos.

EMBRAPA. (2011). *O Novo Mapa de Solos do Brasil Legenda Atualizada escala 1:5.000.000*. Embrapa Solos.

Fearnside, P.M., 1989. Brazil's Balbina Dam: Environment versus the legacy of the pharaohs in Amazonia. *Environ. Manage.* 13, 401–423. <https://doi.org/10.1007/BF01867675>.

Fearnside, P.M., 2009. As hidrelétricas de Belo Monte e Altamira (Babaquara) como fontes de gases de efeito estufa. *Novos Cadernos NAEA* 12 (2), 5–56. <https://doi.org/10.5801/ncn.v12i2.315>.

Ferraz, S.F.D.B., C.A. Vettorazzi, D.M. Theobald, M.V.R. Ballester., 2005. Landscape dynamics of Amazonian deforestation between 1984 and 2002 in central Rondônia, Brazil: assessment and future scenarios. *For. Ecol. Manage.* 204, 69–85. <https://doi.org/10.1016/j.foreco.2004.07.073>.

Ferreira, L.V., 1997. Effects of the duration of flooding on species richness and floristic composition in three hectares in the Jaú National Park in floodplain forests in central Amazonia. *Biodivers. Conserv.* 6, 1353–1363. <https://doi.org/10.1023/A:1018385529531>.

Finer, M., Jenkins, C.N., 2012. Proliferation of hydroelectric dams in the Andean Amazon and implications for Andean-Amazon connectivity. *PLoS One* 7 (4), e35126. <https://doi.org/10.1371/journal.pone.0035126>.

Galetti, M., Donatti, C.I., Pires, A.S., Guimarães, P.R., Jordano, P., 2006. Seed survival and dispersal of an endemic Atlantic forest palm: the combined effects of defaunation and forest fragmentation. *Bot. J. Linn. Soc.* 151, 141–149. <https://doi.org/10.1111/j.1095-8339.2006.00529.x>.

Henderson, A., 1995. *The Palms of the Amazon*. Oxford University Press.

IBGE, 2012. *Manual técnico da vegetação brasileira*. Instituto Brasileiro de Geografia e Estatística – IBGE. Séries Manuais técnicos em geociências.

Jirka, S., McDonald, A.J., Johnson, M.S., Feldpausch, T.R., Couto, E.G., Riha, S.J., 2007. Relationships between soil hydrology and forest structure and composition in the southern Brazilian Amazon. *J. Veg. Sci.* 18, 183–194. [https://doi.org/10.1658/1100-9233\(2007\)18\[183:RBSHAF\]2.0.CO;2](https://doi.org/10.1658/1100-9233(2007)18[183:RBSHAF]2.0.CO;2).

Jones, I.L., Peres, C.A., Benchimol, M., Bunnefeld, L., Dent, D.H., 2017. Woody lianas increase in dominance and maintain compositional integrity across an Amazonian dam-induced fragmented landscape. *PLoS One* 12, 1–19. <https://doi.org/10.1371/journal.pone.0185527>.

Jones, I.L., Peres, C.A., Benchimol, M., Bunnefeld, L., Dent, D.H., 2019. Instability of insular tree communities in an Amazonian mega-dam is driven by impaired recruitment and altered species composition. *J. Appl. Ecol.* 56, 779–791. <https://doi.org/10.1111/1365-2664.13313>.

Junk, J.J., Piedade, M.T.F., Schongart, J., Cohn-Haft, M., Adeney, J.M., Wittmann, F., 2011. A classification of major naturally-occurring Amazonian lowland wetlands. *Wetlands* 31, 623–640. <https://doi.org/10.1007/s13157-011-0190-7>.

Kahn, F., 1987. The distribution of palms as a function of local topography in Amazonian terra-firme forests. *Experientia* 43, 251–259. <https://doi.org/10.1007/BF01945548>.

Latrubesse, E.M., Aryma, E.Y., Dunne, T., Park, E., Baker, V.R., D'horta, F.M., et al., 2017. Damming the rivers of the Amazon Basin. *Nature* 546 (15), 363–369. <https://doi.org/10.1038/nature22333>.

Lees, A.C., Peres, C.A., Fearnside, P.M., Schneider, M., Zuanon, J.A.S., 2016. Hydropower and the future of Amazonian biodiversity. *Biodivers. Conserv.* 25, 451–466. <https://doi.org/10.1007/s10531-016-1072-3>.

Legendre, P., Legendre, L., 2012. *Numerical Ecology*. Elsevier.

Legendre, P., Dale, M.R., Fortin, M.J., Gurevitch, J., Hohn, M., Myers, D., 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* 25, 601–615. <https://doi.org/10.1034/j.1600-0587.2002.250508.x>.

Lorenzi, H., Noblick, L.R., Kahn, F., Ferreira, E., 2010. *Flora brasileira Lorenzi: Arecaceae (palmeiras)*. Instituto Plantarum.

Magnusson, W.E., Lima, A.P., Luizão, R., Luizão, F., Costa, F.R.C., Castilho, C.V., Kinupp, V.F., 2005. RAPELD: a modification of the Gentry method for biodiversity surveys in

- long-term ecological research sites. *Biota Neotrop.* 5, 19–24. <https://doi.org/10.1590/S1676-06032005000300002>.
- Marengo, J.A., Espinoza, J.C., 2016. Extreme seasonal droughts and floods in Amazonia: Causes, trends and impacts. *Int. J. Climatol.* 36, 1033–1050. <https://doi.org/10.1002/joc.4420>.
- MCT, 2005. Programa de biodiversidade PPBIO Amazônia: delineamento espacial protocolos de coleta. Ministério da Ciência e Tecnologia.
- Molina, C.J., 2007. Análisis de los estudios de impacto ambiental del complejo hidroeléctrico del río Madera: hidrología y sedimentos. Available online: <http://www.fobomade.org.bo>. (accessed July 2014).
- Moser, P., Oliveira, W.L., Medeiros, M.B., Pinto, J.R., Eisenlohr, P.V., Lima, I.L., Simon, M.F., 2014. Tree species distribution along environmental gradients in an area affected by a hydroelectric dam in Southern Amazonia. *Biotropica* 46 (3), 367–376. <https://doi.org/10.1111/btp.12111>.
- Moser, P., Simon, M.F., Medeiros, M.B., Gontijo, A.B., Costa, F.R.C., 2019. Interaction between extreme weather events and mega-dams increases tree mortality and alters functional status of Amazonian forests. *J. Appl. Ecol.* 56 (12), 02641–2651. <https://doi.org/10.1111/1365-2664.13498>.
- Normand, S., Vormisto, J., Svenning, J.C., Grández, C., Balslev, H., 2006. Geographical and environmental controls of palm beta diversity in paleo-riverine terrace forests in Amazonian Peru. *Plant Ecol.* 186, 161–176. <https://doi.org/10.1007/s11258-006-9120-9>.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., et al., 2013. *Vegan: Community Ecology Package*. R package version 2.0-8. URL <https://cran.r-project.org/web/packages/vegan/index.html>.
- Pansonato, M.P., Costa, F.R.C., Castilho, C.V., Carvalho, F.A.G., Zuquim, G., 2013. Spatial scale or amplitude of predictors as determinants of the relative importance of environmental factors to plant community structure. *Biotropica* 45, 299–307. <https://doi.org/10.1111/btp.12008>.
- Perigolo, N.A., Medeiros, M.B., Simon, M.F., 2017. Vegetation types in the upper Madeira River in Rondônia. *Brittonia* 69 (4), 423–446. <https://doi.org/10.1007/s12228-017-9505-1>.
- Peters, C.M., Balick, M.J., Kahn, F., Anderson, A.B., 1989. Oligarchic forests of economic plants in Amazonia: Utilization and conservation of an important tropical resource. *Conserv. Biol.* 3 (4), 341–349.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Development Core Team, R., 2011. *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-100. R Core Team, Vienna.
- Pires, J.M., Prance, G.T., 1985. The vegetation types of the Brazilian Amazon. In: Prance, G.T., Lovejoy, T.E. (Eds.), *Key Environments Amazonia*. Pergamon Press, Oxford, pp. 109–145.
- Quesada, C.A., Lloyd, J., Anderson, L.O., Fyllas, N.M., Shwarz, M., Czimczik, C.I., 2011. Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences* 8, 1415–1440. <https://doi.org/10.5194/bg-8-1415-2011>.
- Development, R., Team, C.O.R.E., 2017. *R: A language and environment for statistical computing*. ver. 3.4.2. R Foundation for Statistical Computing, Austria Vienna.
- Resende, A.F.D., Schöngart, J., Streher, A.S., Ferreira-Ferreira, J., Piedade, M.T.F., Silva, T.S.F., 2019. Massive tree mortality from flood pulse disturbances in Amazonian floodplain forests: The collateral effects of hydropower production. *Sci. Total Environ.* 659, 587–598. <https://doi.org/10.1016/j.scitotenv.2018.12.208>.
- Silva, T.R., Medeiros, M.B., Noronha, S.E., Pinto, J.R.R., 2017. Species distribution models of rare tree species as an evaluation tool for synergistic human impacts in the Amazon rainforest. *Rev. Bras. Botânica* 40 (4), 963–971. <https://doi.org/10.1007/s40415-017-0413-0>.
- Skov, F., Borchsenius, F., 1997. Predicting plant species distribution patterns using simple climatic parameters a case study of Ecuadorian palms. *Ecography* 20, 347–355.
- Solinst, 2014. Solinst Levellogger Software. Solinst Canada Ltda. URL <https://www.solinst.com/downloads/>.
- Sollins, P., 1998. Factors influencing species composition in tropical lowland rain forest: Does soil matter? *Ecology* 79 (1), 23–30. [https://doi.org/10.1890/0012-9658\(1998\)079\[0023:FISCIT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[0023:FISCIT]2.0.CO;2).
- Sombroek, W., 2001. Spatial and temporal patterns of amazon rainfall: consequences for the planning of agricultural occupation and the protection of primary forests. *Ambio* 30, 388–396. <https://doi.org/10.1579/0044-7447-30.7.388>.
- Stefan, J., McDonald, A.J., Johnson, M.S., Feldpausch, T.R., Couto, E.G., Riha, S.J., 2007. Relationships between soil hydrology and forest structure and composition in the southern Brazilian Amazon. *J. Veg. Sci.* 18, 183–194. <https://doi.org/10.1111/j.1654-1103.2007.tb02529.x>.
- Svenning, J.C., Harlev, D., Sorensen, M.M., Balslev, H., 2009. Topographic and spatial controls of palms species distributions in a montane rain forest, southern Ecuador. *Biodivers. Conserv.* 18, 219–228. <https://doi.org/10.1007/s10531-008-9468-3>.
- Ter Steege, H., Pitman, N.C.A., Sabatier, D., Silman, M.R., 2013. Hyperdominance in the Amazon tree flora. *Science* 342, 325–334. <https://doi.org/10.1126/science.1243092>.
- Therneau, T.M., Atkinson, B., Ripley, B., Oksanen, J., De'ath, G., 2013. *mvpart: Multivariate partitioning*. R package version 1.6-1. Vienna: R Core Team. (18 October 2018). Retrieved from: <http://CRAN.R-project.org/package=mvpart/>.
- Vale, V.S., Schiavini, I., Araújo, G.M., Gusson, A.E., Lopes, S.F., Oliveira, A.P.,... Dias-Neto, O.C., 2013. Fast changes in seasonal forest communities due to soil moisture increase after damming. *Rev. Biol. Trop.* 61(4), 1901–1917.
- Vormisto, J., 2002. Palms as rainforest resources: how evenly are they distributed in Peruvian Amazonia? *Biodivers. Conserv.* 11, 1025–1045. <https://doi.org/10.1023/A:1015873223350>.
- Vormisto, J., Svenning, J.C., Hall, P., Balslev, H., 2004. Diversity and dominance in palm (Arecaceae) communities in *terra firme* forests in the western Amazon basin. *J. Ecol.* 92, 577–588. <https://doi.org/10.1111/j.0022-0477.2004.00904.x>.
- Wittmann, F., Schöngart, J., Brito, J.M., Wittmann, A.O., Piedade, M.T.F., Parolin, P., et al., 2010. *Manual of trees from Central Amazonian várzea floodplains: Taxonomy, ecology and use*. Editora INPA.
- Wittmann, F., Schöngart, J., Montero, J.C., Motzer, T., Junk, W.J., Piedade, M.T.F., et al., 2006. Tree species composition and diversity gradients in white-water forests across the Amazon basin. *J. Biogeogr.* 33, 1334–1347. <https://doi.org/10.1111/j.1365-2699.2006.01495.x>.
- Zona, S., Henderson, A., 1989. A review of animal-mediated seed dispersal of palms. *Selbyana* 6–21.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer Verlag.