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# Palm community structure association with topography, hydrography and forest density in a remote site in the Iriri river valley, Eastern Amazon

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Running title: **Environmental influences on a remote palm community in Eastern Amazon**

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## ABSTRACT

**Background and aims** – Palms (Arecaceae) are crucial to Amazonian ecosystems, contributing to biodiversity, ecosystem services, and forest resilience, and providing non-timber forest products (NTFPs) for local populations. This study investigated how topography, hydrography, and forest density influence palm community structure in a remote Eastern Amazon site, addressing knowledge gaps in this region.
**Material and methods** – A field survey was conducted in 100 plots along a 5 km transect within the Riozinho do Anfrísio Extractive Reserve, Pará, Brazil. Palm species were identified, and topographic and hydrographic data, including NDVI, altitude, proximity to permanent and intermittent streams, and terrain characteristics were collected. Species richness and composition were analysed using Redundancy Analysis (RDA), general linear models (GLM), analysis of variance (ANOVA) and Bayesian regression models.
**Key results** – Eighteen palm species were recorded, dominated by *Attalea speciosa*, *Geonoma baculifera*, and *Euterpe longibracteata*, providers of NTFPs. NDVI and altitude significantly influenced species composition, with denser forests favouring species such as *G. baculifera*, while others, such as *A. speciosa*, were found in less dense areas. The presence of *igarapés* (shallow, slow Amazonian streams) was the strongest predictor of species richness and composition, favouring *E. oleracea* and *G. baculifera*.
**Conclusion** – Palm community structure in the study area was shaped by environmental gradients, particularly NDVI, terrain shape and proximity to *igarapés*. These findings highlight the ecological importance of topographic and hydrographic features in structuring palm diversity and offer insights for conservation and management strategies in the Eastern Amazon.


**Keywords** – Arecaceae, Eastern Amazon, forest density, *igarapés*, NDVI, palm communities, species composition, terrain, topography, tropical forests.

# INTRODUCTION

Palms (Arecaceae, Bercht. & J.Presl) form one of the most important groups of arboreal species in the Amazon, with palm-dominated forests covering 20% of the Brazilian Amazonia (Emilio et al. 2014), and six of the ten most dominant tree species of the biome belonging to the family (Ter Steege et al. 2013). The family Arecaceae comprises over 2,600 species in 181 genera (Baker and Dransfield 2016), occurring in all tropical and subtropical regions of the world, and its distribution is knowingly influenced by abiotic factors at different scales (Eiserhardt et al. 2011).

Palm species have been used as surrogates to indicate biodiversity due to the challenges posed by *in situ* research in such vast natural environments. For example, palms are predictors of bird diversity, as avian species depend on these trees for food and nesting, and conservation projects can take advantage of this relationship (Menger et al. 2024). The taxon is particularly important in areas with shallow water tables – which correspond to a third of the standing Amazon forest – and show remarkable resistance to the increasingly frequent climate-change-driven droughts (Sousa et al. 2020), despite their higher vulnerability to worst-case climate scenarios in the Amazon as a whole (Esquivel-Muelbert et al. 2019). Some species, such as *Iriartela deltoidea* Ruiz & Pav., have been shown to have extremely efficient hydraulic systems, allowing the species to compete with dicotyledonous trees in tropical climates (Renninger et al. 2013). Species differ in their growth rates and stem density, as it was found in a study comparing *Attalea maripa* Mart. and *Astrocaryum aculeatum* G.May in southeastern Amazon, and differences in their oftentimes overlapped distributions may depend on physiological distinctions (Salm 2004).

Besides a higher resistance to drought, palm species may also display some resistance to fire, especially larger diameter individuals, despite lacking the heat-protecting bark of dicotyledonous species: *Bactris maraja* Mart., an understorey species of commercial value, appears to resprout after a fire even when the aerial part was completely destroyed, with *Euterpe precatoria* Mart. being the only studied species unable to regrow from the underground part after a controlled fire (Liesenfeld 2024), highlighting the role of the taxon in forest resilience.

Analyses of floristic composition in the Amazon have covered large areas, albeit with prominent geographical gaps, and found an estimated 16,000 species of trees in the Amazon, with 227 hyper-dominant species representing 50% of the individuals in the Amazonian biome. Among them, palms are particularly prominent: *E. precatoria*, *I. deltoidea*, *E. oleracea* Mart., *Oenocarpus bataua* Mart., *Socratea exorrhiza* (Mart.) H.Wendl., *Astrocaryum murumuru* Mart., and *Attalea butyracea* (Mutis ex L.f.) Wess.Boer are among the most common representatives of Arecaceae (Ter Steege et al. 2013). In the Brazilian Amazon, 11,210 species were represented, of which 20% to 30% were believed to be at risk of extinction, or already extinct (Hubbell et al. 2008), which urges the study of rarer species. Amazonia is home to at least 5% of all Arecaceae, with some spots presenting a disproportionate canopy cover from these species, and a large undocumented hotspot in Eastern Amazon, specifically in the state of Pará (Dalagnol et al. 2022). Species surveys in vast expanses of the state, one of the largest in Brazil, are scarce (e.g. Ter Steege et al. 2013, 2023; Luize et al. 2024).

Non -timber ecosystem services of Amazonian forests, such as carbon stock and non-timber forest products (NTFP), are overwhelmingly provided by the Arecaceae, with at least 56 species of the family used for the extraction of NTFPs (Smith 2015). The provision of this specific ecosystem service does not correlate with species richness (Steur et al. 2022). The development of biomass models specific for palms showed that

carbon fixation by these trees can be almost a third higher than when calculated with models developed for dicotyledons (Goodman et al. 2013). Palms were found to comprise up to 25% of the stems above 10cm of diameter at breast height (DBH) in a forest in Costa Rica (Clark and Clark 2000), and their sheer abundance means that they have a fundamental role in forest structure and composition, being the drivers of successional changes (Boukili and Chazdon 2017).

In a recent study of tree species-diversity and species-richness in 2,046 tree plots across the Amazon, location and forest type explained 70% in the variation of floristic compositions, with a non-location model including cumulative water-deficit, tree density, and temperature explaining 47% of tree-richness in *terra firme* forests; all exceeding variation should be explained by local characteristics (Ter Steege et al. 2023). Tree composition in the Amazon crosses rivers and changes gradually over large extents, leading some researchers to discourage the delimitation of clear discrete biogeographical regions within the biome, and focus on local characteristics for better models (Luize et al. 2024). Species distribution models (SDMs) vary according to the selection of predictors and interactions, and are highly scale-dependant (Elith and Leathwick 2009). While large-scale models indicate factors such as forest type and temperature as determinant for species distribution (e.g. Eiserhardt et al. 2011; Ter Steege et al. 2013, 2023; Choe et al. 2021; Marques et al. 2024), meso- and fine-scale models bring topographical, hydrological, edaphic and finer spatial elements that seem to explain variation in species composition at specific locations, often at plot level (Salm et al. 2015, Méndez-Toribio et al. 2017, Wang et al. 2019, Luize et al. 2024).

Regarding palm species, meso- and fine-scale studies found significant effects of altitude (Svenning 2001, Vormisto et al. 2004, Montufar and Pintaud 2006, Salm et al. 2007, Balslev et al. 2011), slope inclination or cardinal exposure (Normand et al. 2006, Costa et al. 2009), hydrography and drainage (Vormisto et al. 2000, Montufar and Pintaud 2006), soil characteristics (Balslev et al. 2011, Cámara-Leret et al. 2017) and forest structure (Kristiansen et al. 2011, Eiserhardt et al. 2013, Salm et al. 2015), besides chemical edaphic characteristics (Emilio et al. 2014), in various combinations, in the composition, diversity and abundance of communities of Arecaceae in the Amazon. Similar results were found in studies of tree diversity and abundance in other tropical and subtropical areas, using other tree groups as responses (Liu et al. 2014, Gonella et al. 2020, Marca-Zevallos et al. 2022, Pinho et al. 2022).

Given the importance of palm trees to the maintenance of ecosystem services in the Amazon, their resilience against fire and climate change, and their role in supporting animal biodiversity and human populations, it is necessary to understand the factors that affect the distribution of these species in Amazonian environments. There are studies focusing on several characteristics of single Amazonian palm species, especially those of commercial value (De Almeida et al. 2016, Ramos et al. 2022, De Alencar Pageú et al. 2023, Rabelo et al. 2024), but the challenges of field surveys in the region mean that community-level research fails to cover large portions of the biome, and rare species are underrepresented in large floristic meta-analyses in the region. Understanding which topographic and hydrographic factors affect the distribution of these arboreous species in the under-researched gap in the state of Pará, Eastern Amazon, can contribute to the comprehension of how the communities are structured and facilitate the development of further research in yet undocumented hotspots of Arecaceae diversity.

# MATERIALS AND METHODS

## Study area

The field survey was conducted within the federally-managed Riozinho do Anfrísio Extractive Reserve (hereafter, RESEX Riozinho), a 737,088-hectare natural reserve limited in the East by the Iriri River, a large clear-water tributary of the Xingu River in the state of Pará, Brazil (Fig. 1). The vegetation in the area is broadly defined as "Submontane Open Ombrophilous Forest" by the Brazilian Institute of Geography and Statistics (IBGE 2019), with a medium-sized canopy cover (<30 m) punctuated by taller palms. This forest lies within the Amazonas and Solimões Basin near the border of the Xingu and Iricoumé geochronological blocks on the Amazon Craton, an area characterized by Precambrian volcanic and volcaniclastic rocks, including rhyolites, dacites, and ignimbrites (Tassinari and Macambira 1999, Semblano et al. 2016). The reserve has predominantly a clay-rich podzolic soil, with mosaics of shallow, coarser soil and scattered rock outcrops (ICMBio 2010). Climate is classified as tropical wet (*Am* in the Köppen climate classification), with annual rainfall between 2000 mm and 2500 mm, mostly concentrated from December to April (Alvares et al. 2013, Santos et al. 2015). The stretch of forest surveyed was out of the way of human settlements and presented a currently undisturbed structure, with coarser soil and rocky outcrops distributed along the transect.

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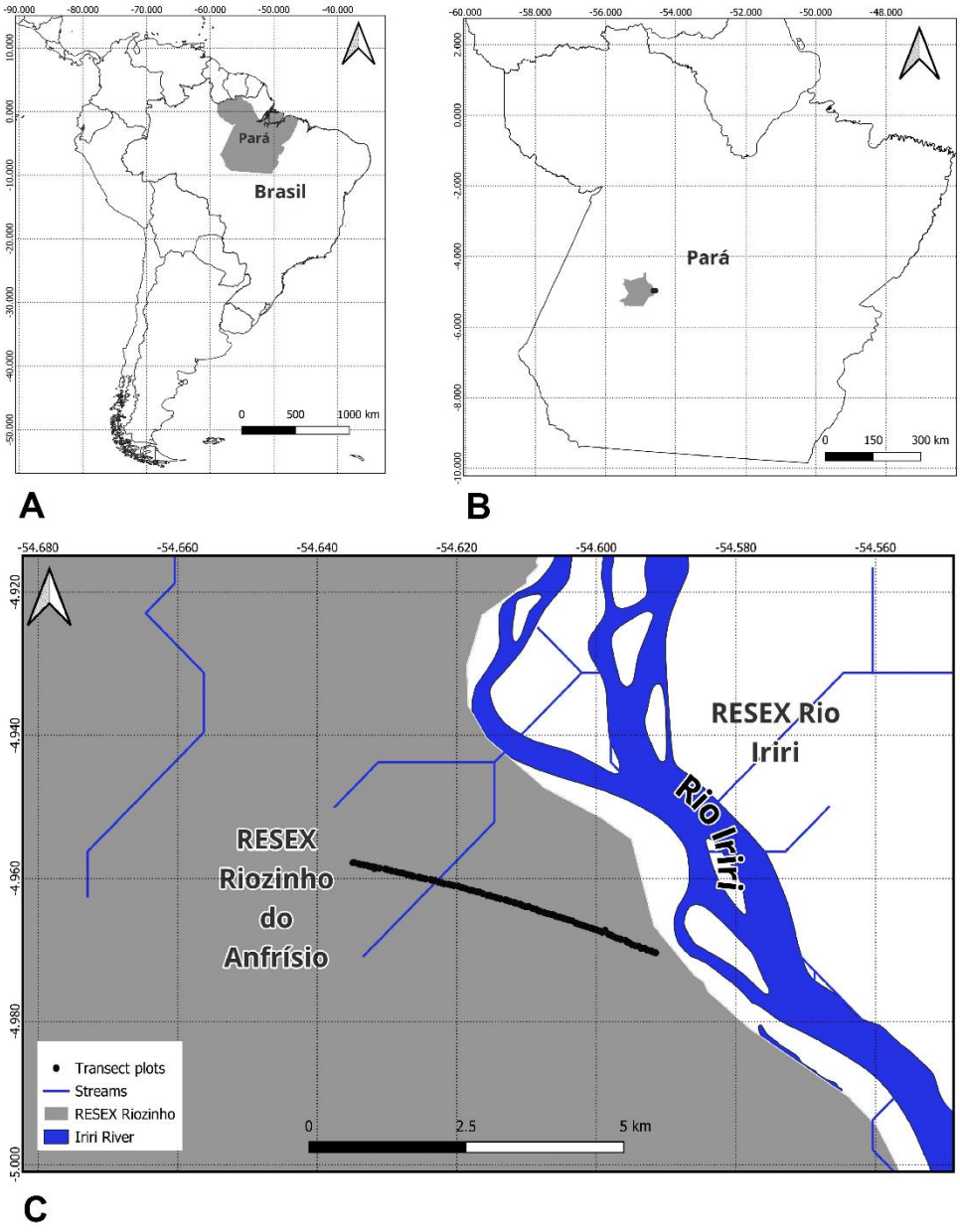


**Figure 1**: **A**. Location of the state of Pará within South America. **B.** Location of the RESEX Riozinho do Anfrísio within the state of Pará. **C.** Transect with plots surveyed at the RESEX Riozinho, Eastern Amazon, state of Pará, in the west margin of Iriri River. Sources: IBGE, 2019; Lehner et al. 2008.

## Data collection

The survey was realised in May 2019, at the end of the rainy season. Palm trees were counted on 100 adjacent plots measuring 20 m x 50 m along a 5 km-long transect previously marked for mammal surveys, totalling a 10 ha cover area. Distances were measured using the portable measuring tool HipChain®, with every 50 m marked with flagging tape and mapped with a Garmin® 78S handheld GPS receiver. The transect was slowly censused on foot at ~1 km/h by a minimum of two experienced observers. All adult palms within ten meters on either side of the transect were recorded and

identified to species level whenever possible using species descriptions from Lorenzi et al. (Lorenzi et al. 2010). Their positions along the transect were then noted to the nearest 50 meters. The presence or absence of *igarapés*, shallow, narrow and slow streams typical of Amazonian environments, was recorded for each plot, generating a binary variable, as those are generally not visible from satellite imagery.

Coordinates representing each 20 m x 50 m plot were later used to extracted data from the digital elevation model (DEM) database TOPODATA (Valeriano and Rossetti 2012), from the Brazilian Spatial Research Institute (INPE), a country-wide resource which refined data from the Shuttle Radar Topography Mission (SRTM) (Jarvis et al. 2008) and offers images with resolution of 30 m, containing measures such as altitude, slope, relief, exposure and terrain shape (Fig. 2). We used HydroSHEDS data (Lehner et al. 2008) to calculate the distance from each transect sub-unit to the nearest perennial stream as registered by the SRTM, which did not record recently formed *igarapés*. As a proxy to measure forest density, we extracted the normalized difference vegetation index (NDVI) for the coordinates representing each of the 100 plots, using satellite imagery from Cbers 4A and the method described by Ponzoni et al.(2012). NDVI has been shown to be an adequate value to represent vegetation health and density in tropical forests (Freitas et al. 2005), and ranged, in the study area, between 0.597 and 0.662 (mean 0.634±0.014).The calculations of NDVI, and topographical and hydrological variables, were conducted in QGIS 3.34 “Prizren” (QGIS.org 2024). For the analysis, our dataset contained eight environmental variables, being three continuous (altitude in meters, distance to stream in meters, and NDVI), four categorical ones (slope, relief, exposure and terrain shape), and the binary presence/absence of *igarapé*. The specific measurements and categories of the latter variables can be seen on the Supplementary Table S1.

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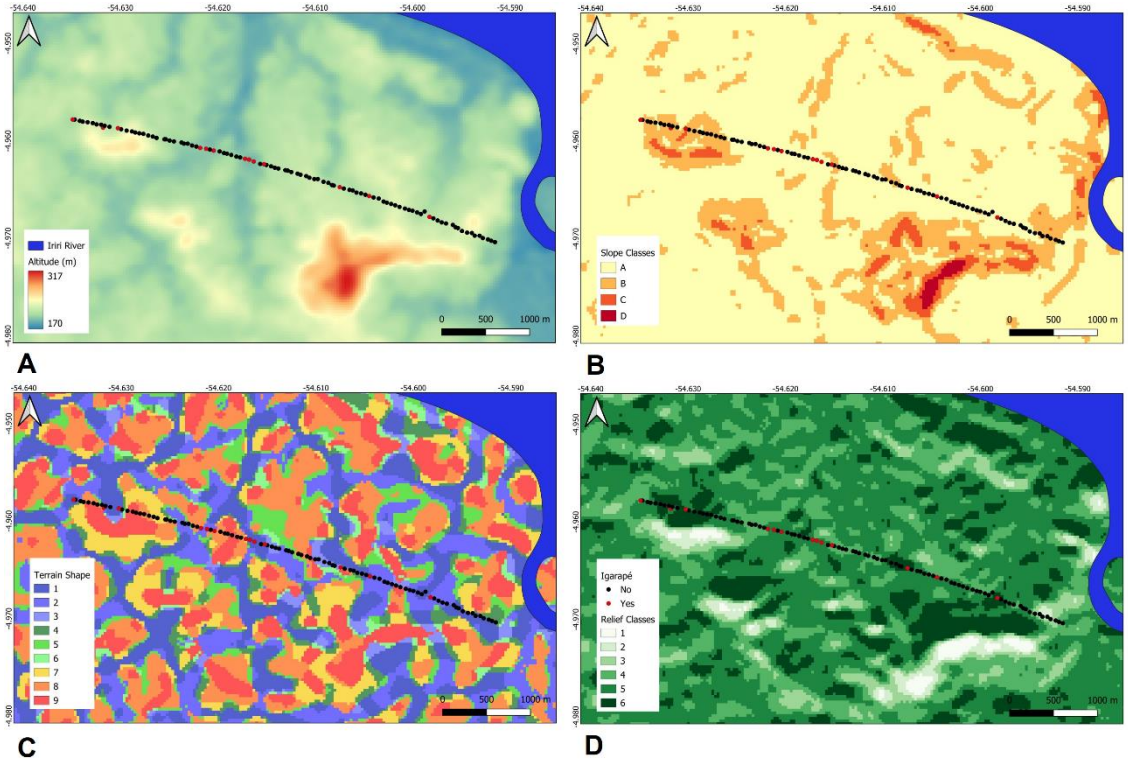


**Figure 2:** Examples of topographical data available at the TOPODATA project. **A.** Altitude. **B.** Slope classes: Flat (A); Moderate (B); Inclined (C); Steep (D). **C.** Terrain shape: Concave convergent (1); Concave neutral (2); Concave divergent (3); Flat convergent (4); Flat neutral (5); Flat divergent (6); Convex convergent (7); Convex neutral (8); Convex divergent (9). **D.** Relief classes: Flat (1); Gentle (2); Slightly undulating (3); Moderately undulating (4); Rolling (5); Hilly (6). The resolution of all maps is 30 m; red dots represent the presence of an *igarapé*.

## Sampling effort

The identification of 18 distinct palm species within the studied area concur with estimations of richness using the methods of Chao (18±0), Jackknife1 (18±0) and Jackknife2 (17.03), suggesting that our sampling adequately captured the species present in the environment. The bootstrapped richness estimate, which accounts for sampling variability, was 18.14, with a standard error of 0.34, further indicating that our sampling was effective in documenting the palm community. These results are confirmed by the species accumulation curve of this sampling effort (Supplementary Fig. S1).

## Data analysis

For data analysis, each of the 100 20 m x 50 m segments of the transect, or plots, was considered a sampling unit. Species richness and abundance were calculated for each plot, and data extracted from remote sensing databases were ascertained for each coordinate. All statistical analysis and graphs were produced using RStudio version 2024.09.1+394 (RStudio Team 2024) and R-4.4.2 for Windows “Pile of Leaves” (R Core Team 2024).

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We calculated density per species by dividing the individual count in each plot of the transect by 0.1 ha. This provided an initial density value per species per hectare, effectively scaling each plot's count to a comparable per-hectare measure.

Alpha-diversity indices calculated from the data were Shannon's Diversity Index (H'), Simpson's Diversity Index (D) and the Inverse Simpson's Index (1 – D). Similarity of floristic composition between plots was calculated using Jaccard similarity index (*J*), leading to the creation of a similarity matrix, and the dissimilarity index (1 – *J*) was used to create a hierarchical clustering dendrogram with the "Complete" method. All composition measurements and dendrograms were created with the package "vegan" (Oksanen et al. 2022).

To understand differences in floristic composition, we performed a Redundancy Analysis (RDA) to assess the relationships between aggregated species abundances and continuous environmental variables (NDVI, altitude and distance to stream) using the package "vegan". *Post hoc* tests on RDA results were performed with the package "car" (Fox and Weisberg 2019), which was also used to calculate variance inflation factors (VIF) and test for collinearity. The gamma-distribution general linear model (γ-GLM, to correct for the positively-skewed *J*-values), and the gaussian-distribution general linear model (GLM) and analysis of variance (ANOVA) applied in the normally-distributed species richness were performed with the package "glmmTMB" (Brooks et al. 2017). To understand factors affecting the distribution of the most abundant species, and to deal with zero-inflated, highly-scattered species distributions, we applied Bayesian regression models (Box and Tiao 1992) using the package "brms" (Bürkner 2017) on count or presence/absence data, and calculated the Bayesian $R^2$ with "bayestestR" (Makowski et al. 2019). *Post hoc* estimated marginal means and pairwise comparison tests with Tukey's method (Tukey 1949) were performed using the package "emmeans" (Lenth 2024). Mantel tests for checking geographical correlations were performed with the package "vegan", using Spearman's correlation method for non-normally distributed responses and Pearson's correlation method for normally distributed responses (Legendre and Anderson 1999).

Graphs showing variation of species richness and Shannon *H'* in relation to geographical positions were created with the package "sp" (Bivand et al. 2013), and the heatmap with Jaccard distance was created with "pheatmap" over "vegan" data (Kolde 2018). All other graphs were produced with the package "ggplot2", and all data was organised with the help of "dplyr", both part of the package "tidyverse" (Wickham et al. 2019). Multiple graphs were organised with the package "patchwork" (Pedersen 2024).

All p-values resulting from hypothesis testing were adjusted by the Holm-Bonferroni method (Holm 1979) to control family-wise error rates and minimise the probability of type-I errors, and are indicated hereafter as $p_{Holm}$. *Post hoc* p-values were not Holm-Bonferroni-adjusted and are represented as p.

**Selection of response variables**

Due to the distribution of abundance data not reaching the parameters needed for the application of threshold analyses such as Threshold Indicator Taxa Analysis - TITAN (King and Baker 2014), it was necessary to select a response variable to represent the differences in species composition between sampling units, while correcting for possible geographical correlations which would mask any potential effect from topographic and hydrographic data. Species richness did not differ significantly with geographic coordinates (Mantel test: r = -0.03581; $p_{Holm}$ = 1; 999 permutations), and presented an approximate normal distribution when log-transformed. Jaccard's

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Similarity Index *J* was very high throughout the studied area (Supplementary Fig. S2), but there was also no significant correlation between geographical coordinates and floristic similarity (Mantel test: r = -0.0557; $p_{Holm}$ = 1; 999 permutations). The distribution of this variable was highly right-skewed even after log-transformed, and the model including it was based on gamma distribution. There was a significant relation between Shannon's *H'* and geographic position (Mantel test: r = 0.1029; $p_{Holm}$ = 0.039; 999 permutations), which excluded Shannon's index as a response variable for further analyses due to possible multicollinearity issues skewing the results. Shannon's *H'* and Simpson's *D* indices are frequently correlated, which is the case in our data (Pearson: t = 35.544, df = 98, $p_{Holm}$ < 0.001), also excluding Simpson's and inverse Simpson's indices as response variables. Species richness and diversity were not correlated (Pearson: t = 0.36381, df = 98, $p_{Holm}$ = 1). Therefore, species richness was chosen as a response variable for verifying the effect of categorical topographic and hydrographic variables in an analysis of variance test, and Jaccard's similarity was chosen for a gamma model with continuous environmental variables.

For the Bayesian analysis, species abundance of the six most numerous species was used as a response variable, either as binary (presence/absence) or count (number of individuals) data. Predictors were chosen based on species selection factors found on the literature or the distribution of abundance against factors in simple scatterplots.

# RESULTS

## Species occurrence

In the 10ha of *terra firme* forest covered by the transect, 1506 individuals of 17 species were identified at species level, and one identified at genus level (Table 1), of which 14 had specific traits listed on the PalmTraits 1.0 database (Kissling et al. 2019). The most abundant species, with more than 100 individuals recorded, were *Attalea speciosa* Mart. (527 individuals, occurring in 85 plots), *Euterpe longibracteata* Barb. Rodr. (267 in 56 plots), *Geonoma baculifera* Kunth (263 in 11 plots) and *Euterpe oleracea* (105 in 15 plots). Species with more than 50 specimens were *Astrocaryum gynacantum* Mart. (77 in 45 plots) and *Astrocaryum aculeatum* (57 in 42 plots). *Iriartela deltoidea* had only 37 specimens in eight plots, but up to 18 individuals were found in the same 100²m area. *Oenocarpus bataua* (30 individuals in 11 plots), *Astrocaryum murumuru* (29 in 14 plots), *Socratea exorrhiza* (20 in 12 plots), *Bactris acanthocarpa* Mart. (19 in 11 plots) and *Oenocarpus minor* Mart. (16 in nine plots) were found more sparsely. Rarer species, with fewer than 15 individuals, were *Attalea maripa* (15 individuals in nine plots), *Syagrus cocoides* Mart. (13 in ten plots) and *Oenocarpus distichus* Mart. (11 in nine plots). Very rare species, with fewer than 10 individuals in the 10ha area and found in isolation in a plot, were *Bactris dahlgreniana* Govaerts, with seven specimens, and *Geonoma maxima* Kunth, with only two individuals. An unidentified species of the genus *Bactris* Jacq. Ex Scop. appeared in six plots, totalling eleven individuals (Fig. 3).

342 **Table 1**: Summary of field-collected data of 18 species of Arecaceae found in 100 plots covering 10ha of *terra firme* forest at the Riozinho do
343 Anfrísio Extractive Reserve in the west margin of Iriri River, Eastern Amazon, State of Pará, Brazil, and the corresponding traits of 14
344 species available on the database PalmTraits 1.0 (Kissling et al. 2019).
345

| Species | Field Data | | | | Traits (Kissling et al. 2019) | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Inds. | Occurrence (no. of plots) | Highest no. of ind./ha | Avg. Density per ha | Habit | Stem | Armature | Max. Stem Height (m) | Max. Stem Diameter (cm) | Forest Level | Appearance |
| *Astrocaryum aculeatum* | 57 | 42 | 50 | 5.7 | Erect | Solitary | Stem; Leaves | 20 | 25 | Canopy | Conspicuous |
| *Astrocaryum gynacantum* | 77 | 45 | 60 | 7.7 | - | - | - | - | - | - | - |
| *Astrocaryum murumuru* | 29 | 14 | 50 | 2.9 | Erect | Both | Stem; Leaves | 15 | 30 | Canopy | Conspicuous |
| *Attalea maripa* | 15 | 9 | 40 | 1.5 | Erect | Solitary | None | 20 | 35 | Canopy | Conspicuous |
| *Attalea speciosa* | 527 | 85 | 270 | 52.7 | Erect | Solitary | None | 20 | 41 | Canopy | Cryptic |
| *Bactris acanthocarpa* | 19 | 11 | 40 | 1.9 | Caulesc. | Both | Leaves | 2 | 7 | Understorey | Conspicuous |
| *Bactris dahlgreniana* | 7 | 7 | 10 | 0.7 | - | - | - | - | - | - | - |
| *Euterpe longibracteata* | 267 | 56 | 380 | 26.7 | Erect | Both | None | 20 | 8 | Canopy | Cryptic |
| *Euterpe oleracea* | 105 | 15 | 280 | 10.5 | Erect | Non-solitary | None | 20 | 20 | Canopy | Cryptic |
| *Geonoma baculifera* | 263 | 11 | 630 | 26.3 | Erect | Both | None | 4 | 3 | Understorey | Cryptic |
| *Geonoma maxima* | 2 | 2 | 10 | 0.2 | Erect | Non-solitary | None | 9 | 5 | Canopy | Conspicuous |
| *Iriartela deltoidea* | 37 | 8 | 180 | 3.7 | - | - | - | - | - | - | - |
| *Oenocarpus bataua* | 30 | 11 | 90 | 3 | Erect | Solitary | None | 26 | 45 | Canopy | Cryptic |
| *Oenocarpus distichus* | 11 | 9 | 20 | 1.1 | Erect | Solitary | None | 10.2 | 26 | Canopy | Cryptic |
| *Oenocarpus minor* | 16 | 9 | 40 | 1.6 | Erect | Both | None | 10 | 7 | Canopy | Cryptic |
| *Socratea exorrhiza* | 20 | 12 | 50 | 2 | Erect | Solitary | None | 20 | 20 | Canopy | Cryptic |
| *Syagrus cocoides* | 13 | 10 | 30 | 1.3 | Erect | Solitary | None | 9 | 12 | Canopy | Cryptic |
| *Bactris sp.* | 11 | 6 | 40 | 1.1 | - | - | - | - | - | - | - |
| **Total individuals** | **1506** | | | | | | | | | | |

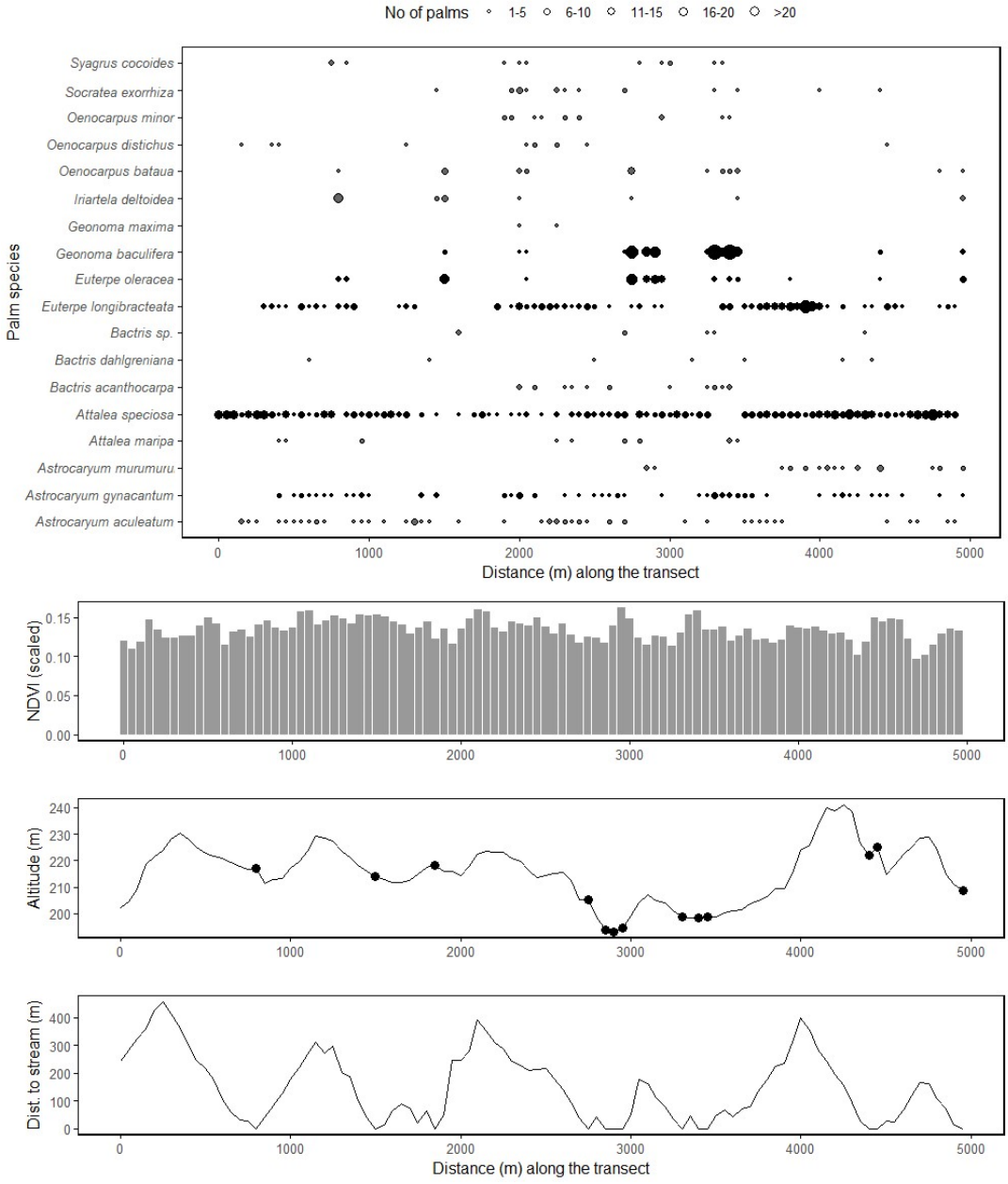


**Figure 3**: Summary of Arecaceae communities in 100 0.1-ha plots in a 5km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil. Dots in the altitude line indicate the presence of *igarapés*. NDVI is scaled for better visualization.

Palm density ranged from 0 to 860 individuals/ha (mean 151.4±143.13), demonstrating the large variability between plots. Considering the maximum estimated density of individuals of each species per hectare, the highest values were displayed by *G. baculifera* (630 ind/ha), *E. longibracteata* (380 ind/ha), *E. oleracea* (280 ind/ha), *Attalea speciosa* (270 ind/ha), *Iriartela deltoidea* (180 ind/ha), *O. bataua* (90 ind/ha) and *Astrocaryum gynacantum* (60 ind/ha). All other species presented estimated maximum densities below 50 ind/ha, with *B. dahlgreniana* and *G. maxima* having maximum estimated densities of only 10 ind/ha. *Bactris acanthocarpa* and *G.*

*baculifera* were the only two species displaying an understorey stature in the database PalmTraits 1.0. In both canopy and understorey species, the standard deviation of density per hectare was higher than the average, with average density and standard deviation higher for understory species (canopy species: 7.65± 13.7; understorey species: 14.1±17.3).

According to Kissling et al. (2019), all species found in the area, except the caulescent *B. acanthocarpa*, present an erect habit. Most species are considered cryptic, except the conspicuous *B. acanthocarpa*, the three species of the genus *Astrocaryum*, and the rare *G. maxima*.

## Diversity indices

Species diversity in the 100 20mx50m plots ranged from 0 to 10 (average 3.64 ± 1.9). The only plot with no species was later removed for further analysis. Shannon's diversity index *H'* ranged from 0.000 to 1.547 (average 0.713 ± 0.326), while Simpson's Diversity Index *D* went from 0.000 to 0.702 (average 0.355 ± 0.168). Inverse Simpson's index (1 – *D*) ranged from1.000 to 3.350 (average 1.686 ± 0.556). Species diversity and Shannon's *H'* changed with plot coordinate (Supplementary Fig. S3).

## Redundancy analysis

The Redundancy Analysis (RDA) revealed that the predictor variables (NDVI, altitude and distance to a stream) explained 17.82% of the variance between plots (Table 2), while the unconstrained variance (82.18%) cannot be explained by these characteristics alone. The three contained axes (RDA1, RDA2 and RDA3) accounted for 100% of the constrained variance, with RDA1 bearing the most part (81.84%), followed by RDA2(10.92%) and RDA3 (7.34%). Species scores (Table 3) indicated differences in species occurrence regarding these three environmental variables. The two most abundant species showed important interactions with environmental gradients. *Geonoma baculifera* displayed a positive association with RDA1, indicating a possible trend to occur in samples with higher NDVI, and a weak positive response to plots farther from streams, while *Attalea speciosa* showed a negative association with this component, suggesting an opposite response to these variables. The other two most abundant species, *Euterpe longibracteata* and *Euterpe oleracea*, displayed only mild preferences along these gradients, indicating that they are relatively generalist in this habitat. All other species had either very low numbers (abundance <50) or appeared in too few plots for the differences in environmental gradients to be detected (Fig. 4). Samples with *igarapés* clustered predominantly at lower altitudes and lower NDVI, consistent with the ecological characteristics of these streamside areas (Fig. 5).

To support the robustness of these RDA results and provide statistical backing, we conducted a permutation test to assess the significance of the overall RDA model, assessing whether the amount of variance explained by the RDA is significantly greater than expected by chance. The test was significant, indicating that the environmental variables collectively explain a meaningful amount of variation in species composition (ANOVA: $F_{3,95}$, $p_{Holm} = 0.0140$, 999 permutations). To ensure that multicollinearity among environmental variables did not distort the RDA results, we calculated Variance Inflation Factors (VIFs) for each environmental variable. All VIFs were below the commonly used threshold of 10, indicating that collinearity is unlikely to bias the interpretation if this analysis (Supplementary Table S2)

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**Table 2**: Summary of Redundancy Analysis (RDA) of floristic composition in 100 0.1-ha plots in a 5km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil.

| **Variance Partitioning** | | | **Inertia** | | **Proportion** | |
|---|---|---|---|---|---|---|
| Total | | | 181.01 | | 1.0000 | |
| Constrained | | | 32.26 | | 0.1782 | |
| Unconstrained | | | 148.75 | | 0.8218 | |
| **Importance of Components** | **RDA1** | **RDA2** | **RDA3** | **PC1** | **PC2** | **PC3** |
| Eigenvalue | 26.4039 | 3.5218 | 2.3363 | 92.8842 | 23.2660 | 13.7153 |
| Proportion Explained | 0.1459 | 0.0195 | 0.0129 | 0.5131 | 0.1285 | 0.0758 |
| Cumulative Proportion | 0.1459 | 0.1653 | 0.1782 | 0.6914 | 0.8199 | 0.8957 |
| **Accumulated Constrained Eigenvalues** | | | | **RDA1** | **RDA2** | **RDA3** |
| Eigenvalue | | | | 26.4039 | 3.5218 | 2.3363 |
| Proportion Explained | | | | 0.8184 | 0.1092 | 0.0724 |
| Cumulative Proportion | | | | 0.8184 | 0.9276 | 1.0000 |
| **Contribution of Variables** | | | | | | |
| **Variable** | | | | **RDA1** | **RDA2** | **RDA3** |
| NDVI | | | | 0.3521374 | -0.8983006 | 0.2627838 |
| Altitude | | | | -0.8715911 | -0.4338066 | -0.2283438 |
| Distance to Stream | | | | -0.6949290 | -0.1034342 | 0.7116003 |

**Table 3**: Species scores calculated from the Redundancy Analysis (RDA) applied on the floristic composition of 100 0.1-ha plots in a 5km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil.

| **Species** | **RDA1** | **RDA2** | **RDA3** | **PC1** | **PC2** | **PC3** |
|---|---|---|---|---|---|---|
| *Attalea speciosa* | -2.09414 | 1.301685 | -0.370149 | -0.3819282 | -0.896400 | 2.931234 |
| *Oenocarpus distichus* | -0.05943 | -0.075526 | 0.080924 | 0.0098484 | 0.006552 | -0.042265 |
| *Astrocaryum aculeatum* | -0.05345 | -0.124100 | 0.096595 | -0.1011135 | -0.002171 | -0.127921 |
| *Euterpe longibracteata* | 0.15940 | 0.487333 | 1.143004 | -0.3845590 | 4.023363 | 0.598681 |
| *Euterpe oleracea* | 1.22260 | 0.049299 | -0.313831 | 1.4716192 | -0.241431 | -0.848796 |
| *Astrocaryum gynacantum* | 0.17975 | -0.101610 | -0.063376 | 0.3478556 | 0.074254 | -0.033829 |
| *Attalea maripa* | 0.09477 | 0.010021 | 0.015928 | 0.1646713 | -0.003764 | 0.051507 |
| *Bactris dahlgreniana* | -0.01182 | 0.012274 | -0.030337 | -0.0131801 | -0.002707 | -0.035350 |
| *Syagrus cocoides* | 0.10196 | -0.005841 | -0.007938 | -0.0055956 | -0.021731 | 0.026323 |
| *Iriartela deltoidei* | 0.24614 | -0.241116 | -0.309794 | -0.0715330 | 0.068867 | -0.432230 |
| *Oenocarpus bataua* | 0.23438 | 0.001759 | -0.068660 | 0.4446005 | 0.017232 | -0.280574 |
| *Socratea exorrhiza* | -0.02407 | 0.040832 | 0.063044 | 0.0436201 | 0.041686 | -0.132059 |
| *Geonoma baculifera* | 3.64888 | 0.734421 | -0.132932 | 8.0914162 | 0.186482 | 0.332494 |
| *Bactris sp* | 0.06055 | 0.003489 | -0.055454 | 0.0048451 | -0.030310 | -0.008123 |
| *Oenocarpus minor* | 0.10351 | -0.078681 | 0.076685 | -0.0003393 | -0.015063 | -0.031384 |
| *Bactris acanthocarpa* | 0.11087 | -0.056753 | 0.100447 | 0.2121724 | 0.053579 | 0.008067 |
| *Geonoma maxima* | -0.01029 | 0.001349 | 0.012973 | 0.0013189 | 0.010290 | -0.017825 |
| *Astrocaryum murumuru* | -0.08328 | 0.129311 | -0.120026 | 0.0728578 | 0.134610 | -0.042807 |

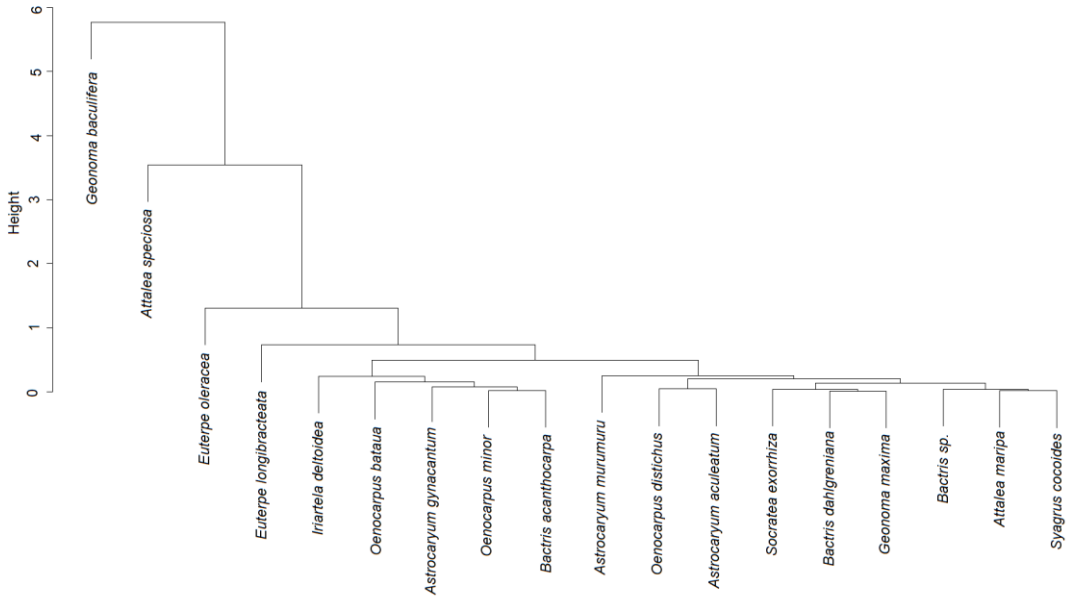


**Figure 4**: Dendrogram species scores distances in relation to environmental gradients calculated by RDA of 18 species of Arecaceae in 100 0.1-ha plots in a 5km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil

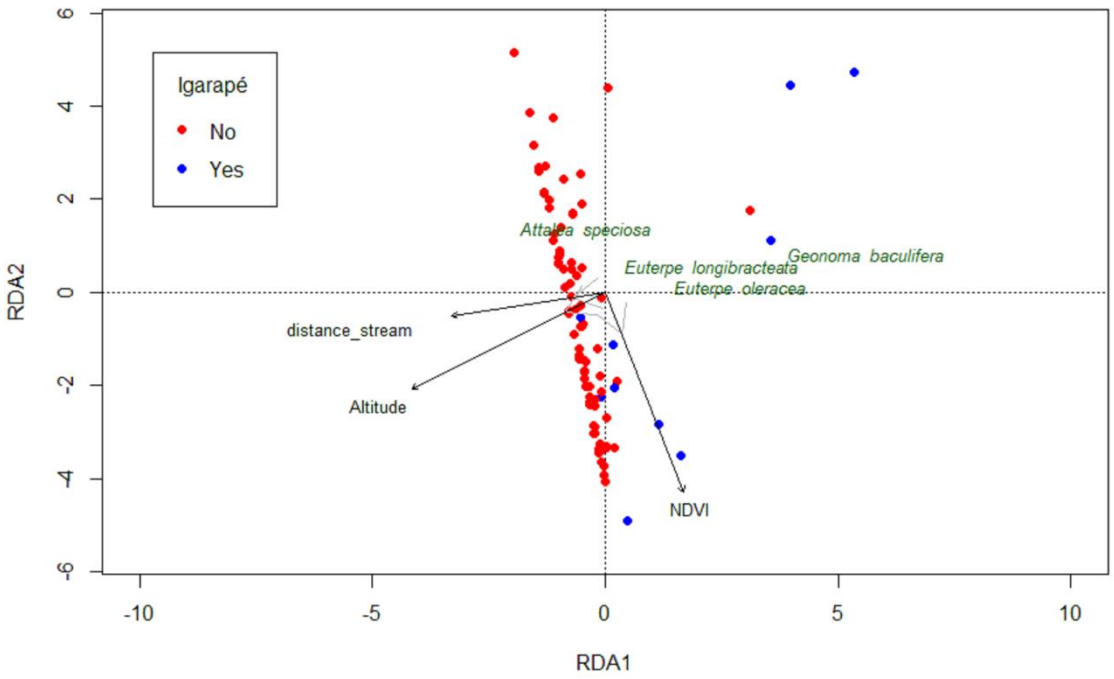


**Figure 5**: Biplot of the RDA of 18 species of Arecaceae in 100 0.1-ha plots in a 5km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil, with indication of plots containing an *igarapé*. Only the four most abundant species are displayed.

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448 **Effects of environmental variables on Jaccard's Similarity Index**
449
450 As established in the methodological set up of this analysis, the Jaccard similarity
451 index (*J*) between plots was not explained by geographic positioning. To ascertain if any
452 of the continuous environmental variables (NDVI, altitude and distance to stream)
453 affected the floristic similarity between plots, a gamma-distribution general linear
454 model (GLM) was applied, with the log-transformed *J* index as a response. All three
455 environmental variables were highly significant, with NDVI having a strong positive
456 influence in composition similarity, and both altitude and distance to streams having a
457 negative influence, meaning that floristic composition became more similar in denser
458 forests, and altitude and distance to streams causing the composition to become more
459 dissimilar (Table 4; Fig. 6). Although highly significant, the model has a high AIC and
460 low pseudo-$R^2$ (McFadden's Pseudo-$R^2$: 9.6%), which indicates that a low percentage
461 of the variance in similarity between plots may be explained by these predictors.
462
463
464 **Table 4**: Summary of gamma-distribution General Linear Model of the effect of
465 continuous environmental variables on the Jaccard similarity index *J* between 100
466 0.1-ha plots in a 5km-transect surveyed for Arecaceae species at the RESEX
467 Riozinho, Eastern Amazon, state of Pará, Brazil.
468

| **Coefficients:** | | | | |
|---|---|---|---|---|
| | **Estimate** | **Std. Error** | **t-value** | **$p_{Holm}$** |
| **(Intercept)** | 0.14496165 | 0.05952864 | 2.435 | 0.1192 |
| **Altitude** | -0.00080383 | 0.00012567 | -6.396 | <0.0001 |
| **NDVI** | 0.96334743 | 0.08450848 | 11.399 | <0.0001 |
| **Distance to stream** | -0.00008896 | 0.00001086 | -8.194 | <0.0001 |
| (Dispersion parameter for Gamma family taken to be 0.01336545) | | | | |
| Null deviance: 153.00 on 9800 degrees of freedom | | | | |
| Residual deviance: 148.57 on 9797 degrees of freedom | | | | |
| Number of Fisher Scoring iterations: 4 | | | | |
| AIC: -2201.7 | | | | |
| Pseudo-$R^2$ (Nagelkerke): 9.6% | | | | |

469

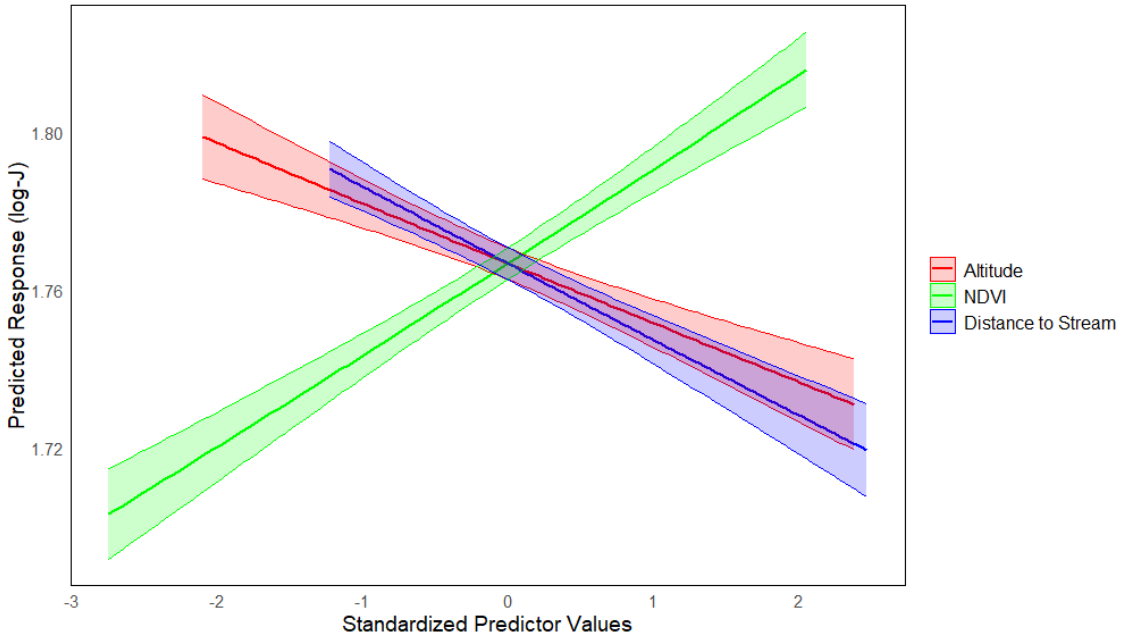


**Figure 6:** Standardised predictor values of altitude (m), NDVI and distance to stream (m) against log-transformed Jaccard similarity indices of 100 0.1-ha plots in a 5km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil.

## Effects of continuous environmental variables on species richness

Using each plot's species richness transformed by the square root (to approach normality), we ran a gaussian general linear model including the three continuous variables: NDVI, altitude, and distance to stream. The intercept of the model was not statistically significant ($t = 1.218$; $p_{Holm} = 1$), suggesting no baseline difference in richness when all variables are at zero. NDVI ($t = 0.28451$; $p_{Holm} = 1$), altitude ($t = -2.588$; $p_{Holm} = 0.11$) and distance to stream ($t = -2.662$; $p_{Holm} = 0.10$) were non-significant after correcting p-values. The distribution of residuals and fitted values indicate a good model fit (Supplementary Fig. S4), and the Nagelkerke pseudo-$R^2$ was 17.2%. This indicated that other factors are influencing the difference in Arecaceae species richness between the plots, such as the presence of *igarapés* or terrain characteristics, which are indirect indicators whether a determined area collects or drains rainwater and nutrients.

## Effects of categorical environmental variables on species richness

Species richness, adjusted by square root, was the response variable for an analysis of variance (ANOVA) including all five categorical variables: presence of an *igarapé*, slope, relief, exposure and shape of terrain. The ANOVA results (Table 5) reveal that the model explains a meaningful portion of the variability in the response variable ($R^2 = 50\%$; $R^2$ adj. = 47.3%), suggesting that roughly half of the variance in species richness is explained by these factors. Three of the five factors included in the model had significant effects on species richness. *Igarapé* presence ($F_1 = 16.060$; $p_{Holm} = 0.0022$) was highly significant, and the significant difference in estimated marginal

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means (as seen in the *post hoc* tests on the Supplementary Table S4) shows that the average species richness is higher when an *igarapé* is present (mean = 2.07), compared to when it is absent (mean = 1.56), with a significant difference of -0.509 (p = 0.0006).

Slope inclination ($F_3$ = 5.024; $p_{Holm}$ = 0.039) was significant, but *post hoc* pairwise contrasts reveal no significant differences between individual levels of inclination after Tukey comparisons, with the lowest p-value between moderately inclined and steep slopes (t-ratio = -2.341; p = 0.0975). This suggests that, although terrain inclination had an overall effect, individual differences between specific steepness levels are not particularly strong or consistent. The relief of the terrain was non-significant ($F_5$ = 2.396; $p_{Holm}$ = 0.3125).

Terrain shape was significant in the model ($F_8$ = 3.7820; $p_{Holm}$ = 0.0126). *Post hoc* pairwise comparisons revealed specific significant contrasts between concave, water-divergent areas and flat, water-convergent ones (t-ratio = 3.420; p = 0.0262), and between the latter and convex, water-neutral plots (t-ratio = -3.522; p = 0.0194). The differences can be seen on Figure 7.

**Table 5:** Results of an Analysis of Variance (ANOVA) of the effect of topographical and hydrographical categorical variables on species richness (square root transformed) in 100 0.1-ha plots in a 5km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil.

| Factor | Df | Sum Sq | Mean Sq | F value | $p_{Holm}$ |
|---|---|---|---|---|---|
| ***Igarapé*** | 1 | 2.765 | 2.7649 | 16.060 | 0.0022 |
| **Slope** | 3 | 2.595 | 0.8649 | 5.024 | 0.0390 |
| **Relief** | 5 | 2.063 | 0.4125 | 2.396 | 0.3125 |
| **Exposure** | 3 | 0.974 | 0.3247 | 1.886 | 0.8322 |
| **Shape** | 8 | 5.209 | 0.6511 | 3.782 | 0.0126 |
| **Residuals** | 79 | 13.601 | | | |
| **$R^2$** | 50.01% | | | | |
| **$R^2$ adjusted** | 47.35% | | | | |

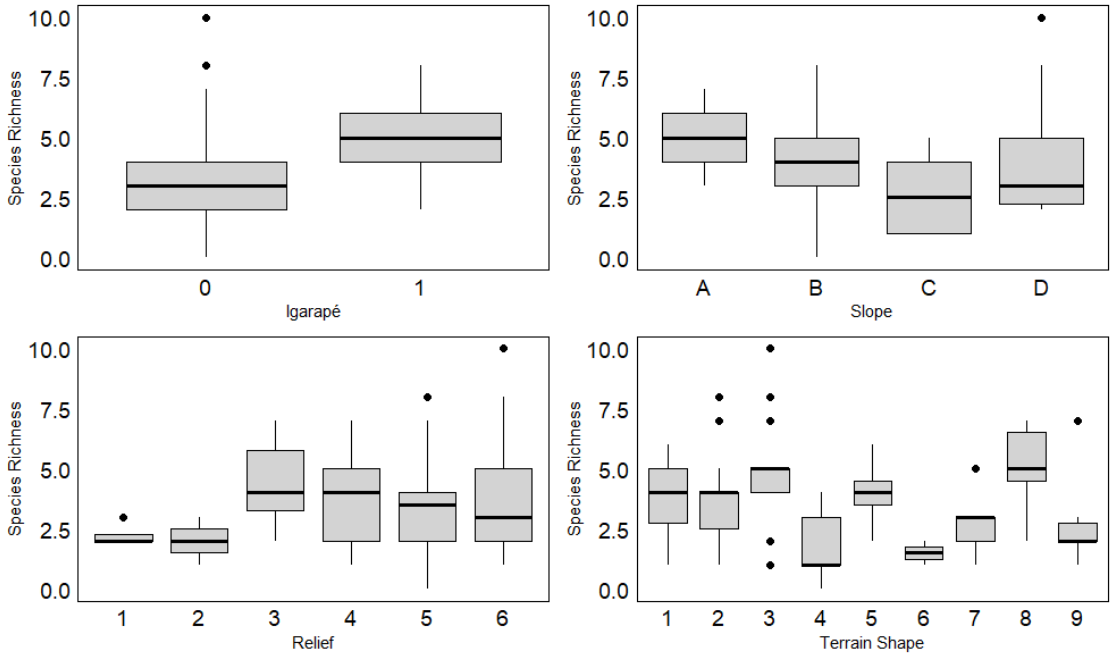


**Figure 7:** Boxplots of the effects of presence of *igarapés*, slope steepness, and terrain relief and shape on the species richness of Arecaceae in 100 0.1-ha plots in a 5km-transect at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil. Thick horizontal lines represent means and dots represent outliers.

## Habitat characteristics related to abundant species

To understand the differences in distribution of the six most abundant species, we ran Bayesian regression models on the abundance – counts or presence/absence – of each against NDVI and either the presence/absence of *igarapé* or the type of terrain shape, as these were the most relevant variables when species' abundance distributions were plotted against environmental variables. The models varied in their setup according to the distribution of data (Table 6).

**Table 6:** Summary of the Bayesian regression models to explain the distribution of the six most abundant Arecaceae species recorded in 100 0.1-ha plots in a 5km-transect at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil. Predictors were NDVI (continuous), terrain shape (categorical) and presence of *igarapé* (binary). A positive sign after a predictor under "Potential Effects" means higher abundance or probability of presence of the species; a negative sign means lower abundance or probability of presence of the species.

| Species | Model Type | Predictors | Potential Effects | Bayesian $R^2$ |
|---|---|---|---|---|
| *Attalea speciosa* | Poisson | NDVI, *Igarapé* | NDVI (-), Igarapé (-) | 0.36 |
| *Euterpe longibracteata* | Poisson | NDVI, Shape | NDVI (-), Shape5 (+), Shape7 (+) | 0.46 |
| *Geonoma baculifera* | Negative Binomial | NDVI, *Igarapé* | NDVI (+), Igarapé (+) | 0.46 |
| *Euterpe oleracea* | Negative Binomial | NDVI, *Igarapé* | NDVI (+), Igarapé (+) | 0.50 |
| *Astrocaryum gynacantum* | Logistic | NDVI, Shape | NDVI (-), Shape6 (-), Shape8 (+) | 0.24 |
| *Astrocaryum aculeata* | Logistic | NDVI, Shape | NDVI (+), Shape6 (-), Shape7 (-) | 0.18 |

*Attalea speciosa* counts yielded the most reliable results. NDVI had a strong negative effect on the species presence (Estimate: -29.59), indicating it is more likely to be present in lower-density forests. The proximity to an *igarapé* also showed a significant negative effect (Estimate: -1.31), suggesting avoidance of these watercourses. The model explained 36% of the variation in distribution, and, of all models, it is the strongest due to the high numbers of individuals throughout the samples. The Region of Practical Equivalence analysis (ROPE) indicated the high relevance of these predictors (Supplementary Table S4).

NDVI had a negative but broad effect on *Euterpe longibracteata* distribution (Estimate: -4.56, CI includes zero), suggesting a potential association with more open forest areas, although the effect is not definitive. Two terrain shapes appeared to have a positive effect in this species: Shape5, a flat water-neutral contour (Estimate: 1.61) and Shape7, convex water-convergent contour (Estimate: 2.08), suggesting an avoidance of areas prone to waterlogging. The model fit was reasonable, with 46% of the variance explained by these terms (Supplementary Table S5). For *Geonoma baculifera*, broad credible intervals resulted from the very sparse distribution of the species, with individuals recorded in only eleven plots, despite being the third most abundant species in the study area. NDVI appeared to have a positive effect (Estimate: 45.74) that is broadly estimated, showing a trend toward denser forests, though the effect is inconclusive as the CI includes zero. The presence of an *igarapé* appeared to favour the occurrence of the species (Estimate: 5.01), and this effect seemed to be confirmed by ROPE analysis. Despite these shortcomings, the explanatory power of the model reached 46% (Supplementary Table S6). Broad estimates were also a setback of the models for *Euterpe oleracea*, *Astrocaryum gynacantum* and *Astrocaryum aculeatum*, and results must be interpreted carefully. For *E. oleracea*, NDVI appeared to have a positive effect (Estimate: 29.17), although the association is uncertain as the CI includes zero, but proximity to an *igarapé* presented a stronger positive association (Estimate:

5.00), which may be responsible for the model's higher explanatory power (Bayesian $R^2$ = 50%; Supplementary Table S7). The models for the two species of *Astrocaryum* yielded very different results. *A. gynacantum* appeared to have negative effects of NDVI (Estimate: -20.83), although CI includes zero. The species reacted differently to two terrain shapes, with a flat water-divergent contour having a strong negative effect (Estimate: -130.76) and convex, water-neutral areas having a weak positive effect (Estimate: 3.23). The model, however, has a modest explanatory power (Bayesian $R^2$ = 24%, Supplementary Table S8). For *A. aculeatum*, NDVI appeared to affect positively (Estimate: 14.03), although with high uncertainty, while two terrain shapes had strong negative impacts in this species' distribution: flat water-divergent (Estimate: -167.24) and convex water-convergent contours (Estimate: -45.31), which are not prone to water-logging and can be washed by rains. The model Bayesian $R^2$, however, is low at 18% (Supplementary Table S9). A graphical summary of the relations between species distributions and environmental variables can be seen on Figure 8.

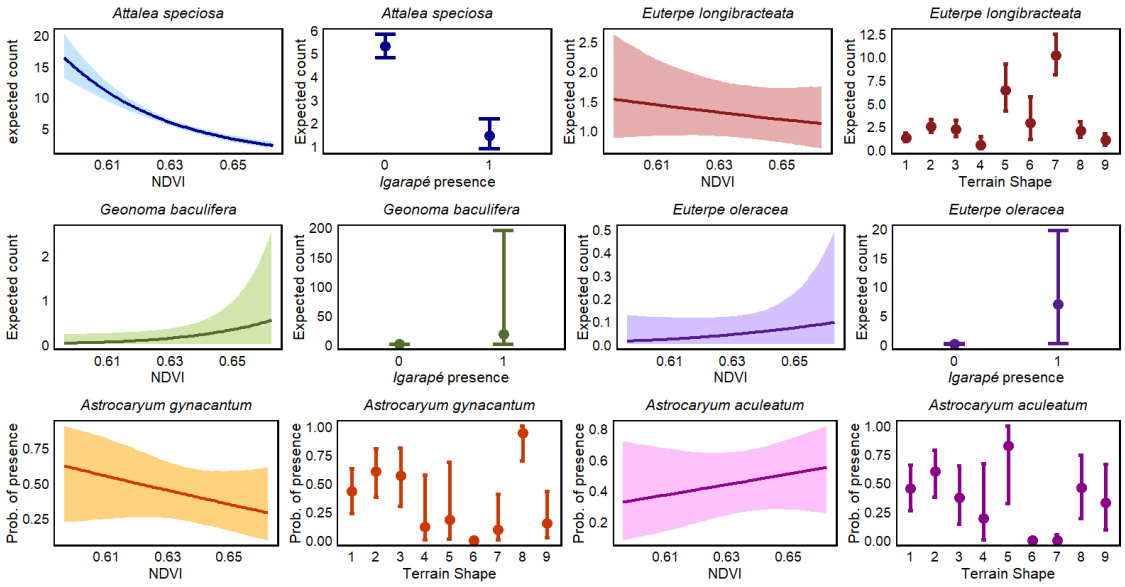


**Figure 8:** Summary of marginal effects graphs of Bayesian regression models of the distribution of six most abundant Arecaceae species recorded in 100 0.1-ha plots in a 5km-transect at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil, against NDVI, terrain shape, and presence of *igarapés*. Responses are estimates of expected individual counts (Expected count) or the probability of presence of the species (Prob. of presence). In NDVI graphs, shaded areas represent 95% confidence intervals; in interval graphs, bars represent amplitude and dots represent means.

## DISCUSSION

In our study in the Iriri river valley, all but two species were canopy species, but understorey species showed higher average density and larger standard deviation, a result also found in a research in three areas in western, central and eastern Amazonia, with the remarked difference that understorey species made the majority of recorded individuals in that study (Kahn et al. 1988). As RESEX Riozinho is an extractive reserve, the abundance of species providing NTFPs may indicate a degree of forest anthropogeny, historical or otherwise, in the area. This is reinforced by the fact that *Attalea speciosa*, the babassu palm, known for its various industrial applications (Lima et al. 2024), could be found in high density along the transect. In our study, the species reached a density of 270 adult individuals per hectare, a very high value when considering that the average tree density in the Amazon, counting all arboreal species, is 563 ind./ha, and that eastern Amazon has a lower tree density than other areas of the biome (Kahn et al. 1988, Ter Steege et al. 2023). In a recent study in the RESEX Rio Iriri, on the other margin of the river, the species was also found to hyper-dominant, and is considered an indicator of historic forest disturbance (Smith 2015); in that case, archaeological excavations showed that the disturbance dates to the 18$^{th}$ Century, when the area was populated by indigenous peoples, and despite being anthropogenic in origin, the area was not degraded or modified by intermittent extractive activities from *beiradeiros*, or forest peasants, that are allowed to enter the reserve (Balée et al. 2020).

The remoteness of our study area means that this is the first description of a palm community in the region, closing a gap on a potential hotspot of palm diversity, in the state of Pará, where Arecaceae density is higher than in other parts of the Amazon (Dalagnol et al. 2022), despite displaying lower species richness when compared to western Amazon, and being more threatened by deforestation (Alvez-Valles et al. 2018).

Species richness at the RESEX Riozinho, with 17 identified species, is higher than in other two areas we previously sampled on the eastern border of the Xingu basin. At the Kayapo Indigenous Territory, 400km to the southwest of RESEX Riozinho, we found ten species of Arecaceae (Salm et al. 2007), while eleven species were recorded near the city of Altamira, Pará (Salm et al. 2015). These represent lower species richness than those reported in central and western Amazon, resulting from the westward gradient of increasing rainfall, as it was previously described for Amazonian palms (Balslev et al. 2011, Eiserhardt et al. 2011, Alvez-Valles et al. 2018, Muscarella et al. 2020).

Differences in species composition, as measured by the Jaccard similarity index in our study, were not explained by simple geographical position, but were positively influenced by NDVI, used here as a proxy for forest density, and negatively by altitude and distance to streams, suggesting that a certain cohort of species tends to colonise areas with similar topography, hydrography and shading (Wagner et al. 2020), although these similarities were only partially explained by these three factors. The same results were found on our redundancy analysis (RDA), with NDVI, altitude and distance to stream only explaining around 17% of the difference in species composition between plots. The RDA also pointed out that plots where an *igarapé* was present were clustered around low altitudes and had lower NDVI, although the difference was not significant.

Edaphic characteristics have been known to affect Arecaceae communities in western Amazon, with soil macronutrients shaping both abundance and presence of species (Cámara-Leret et al. 2017). Furthermore, soil physical characteristics limit arborescent palms' basal area, with palms being predominant in weakly structured soils, while other trees are more affected by species turnover and rainfall (Emilio et al. 2014).

Soil characteristics are highly influenced by topography and hydrography, with aspects such as altitude, exposure, inclination and terrain shape determining from levels of erosion to organic carbon and macronutrient levels and, therefore, species composition (Liu et al. 2014, Måren et al. 2015, Wang et al. 2019, Zhou et al. 2023). The effect of topography and hydrography on arborescent palms is well-known (Kahn 1987, Svenning et al. 2009, Gomes De Freitas et al. 2012, Salm et al. 2015). In our study, similarity of species composition was affected by terrain inclination and shape, with species being more similar in terrains with inclination below 8% and with a shape that is neither concave nor convex, but where rainwater converges, although further studies would be needed to ascertain to which extent this effect is real. By far, the most important predictor of species composition was the presence of an *igarapé*, as some species seem to only occur in such areas (Kahn and Castro 1985, Kahn 1987, Kahn and de Granville 1992, Wagner et al. 2020).

Species richness did not seem to be affected by forest density, altitude or distance to streams, but it was highly affected by the presence of *igarapés* and the shape of the terrain. As distance to streams was calculated using information from HydroSHEDS, which was captured in the beginning of the 21$^{st}$ Century (Lehner et al. 2008), this variable may have not reflected the present hydrographic configuration of the area as accurately as the *igarapés* recorded in the field. *Igarapés* are known to present a number of adapted palm species which will colonise these areas all throughout Amazonia (Kahn and de Granville 1992, Salm et al. 2015). In our study, the average species richness was higher where there was an *igarapé*, although the range of species was higher in its absence, indicating that the same species are found near these Amazonian shallow waterways, as suggested by our redundancy analysis, with *Geonoma baculifera* and *Euterpe oleracea* appearing associated to these features. Again, flat, water-convergent terrains, which had higher Jaccard's similarity, presented the lowest species richness, suggesting that only a few species are adapted to these conditions (Kahn 1987, Kahn and de Granville 1992). Concave, water-divergent, and convex, water-neutral terrains presented the highest species richness. Both shapes are not prone to waterlogging, with the first retaining moisture but not holding water, and the second being the quintessential *terra firme* condition, but without the excessive removal of nutrients found in convex, water-divergent terrains. These results agree with findings that most arborescent palms avoid both permanently waterlogged areas near rivers and dry areas where the terrain in convex and water-divergent, such as the top of hills (Muscarella et al. 2020, Wagner et al. 2020).

At the Iriri site, we found clusters of *G. baculifera* with densities of up to 630 individuals per hectare. These are common in seasonally-flooded and waterlogged sandy soils all throughout eastern Amazon, with the species being found in densities over 700 ind./ha. These clusters indicate present or past reproductive activity, as the species sets new stems by rooting and fragmentation, originating closely distributed individuals where conditions are optimal (Kahn and de Granville 1992).

Another species found in clusters was *Euterpe olereacea*, the assai tree, which is an important food product for local populations (Leão et al. 2021), despite not being commercially exploited in this area. The species is the only Arecaceae among the most abundant in our study, with densities of up to 280 ind./ha, to be considered hyper-abundant in the whole Amazonian biome (Ter Steege et al. 2013). Two common palm species found in forests of the Xingu river basin (Salm et al. 2007, 2015) and also found at the RESEX Riozinho were *Socratea exorriza* and *Oenocarpus bataua*. The former is known as the walking palm, due to trunk adjustments in flooded soil with lateral rooting stilts that give the impression of movement over time (Kahn and de Granville 1992,

Smith 2015); the latter occupies from seasonally-flooded plains to altitudes up to 1,400m, and is frequently spread opportunistically by indigenous populations (Kahn 1987, Kahn et al. 1988, Smith 2015). Both species are among the ten most abundant trees in the Amazon (Ter Steege et al. 2013), although they were not the most abundant in our study area.

Our research recorded the occurrence of *Iriartea deltoidea* for the first time in the state of Pará, Eastern Amazonia, as the species, which spreads as far north as Nicaragua, was only registered in Central and Western Amazonia (Lorenzi et al. 2010, Smith 2015, Henderson 2019), illustrating the lack of studies in the region. *I. deltoidea* is one of the five most abundant trees in the Amazon, albeit being found only 18.5% of all surveyed areas of the biome (Ter Steege et al. 2013, 2023),

Bayesian analysis of the six most abundant species in our study area pointed out how different species occur in plots with very different microhabitats in relation to forest density, presence of *igarapés* and terrain shape, as it is known for palm species (Svenning 1999). Three species showed a consistent relation with open forests, with lower NDVI, and dry, rich soils: *A. speciosa* was predominantly found away from *igarapés* in areas with lower NDVI; *E. longibracteata* also occurred in less dense plots, in convex, water-convergent and flat, water-neutral terrain; and *Astrocaryum gynacantum* occurred in open forest in convex, water-neutral terrain, avoiding flat, water-divergent plots where the soil is washed-up. Two species were found in denser plots where there is an *igarapé*: *G. baculifera* and *E. oleracea* occurred near *igarapés*, when the NDVI was higher. *A. aculeata* occurred in denser forest, but avoided flat, water-divergent and convex, water-convergent terrain: the first shape allows the soil to be washed of nutrients, and the second retains water. These results are consistent with the known microhabitats for each species (Kahn and de Granville 1992, Lorenzi et al. 2010, Smith 2015), and can instruct future reforestation and agroforestry projects involving these species, which are frequently used as surrogates to indicate biodiversity (Svenning et al. 2009, Cardoso et al. 2013, Ramos et al. 2022, Menger et al. 2024) despite some caveats (Ritter et al. 2019), although further studies would be needed to ascertain specific requirements.

## CONCLUSION

The area surveyed in this study, with its relative abundance of Arecaceae and submontane open ombrophilous forest, confirms the importance of this family in areas with shallow water tables (Kahn and de Granville 1992, Sousa et al. 2020), especially with the increased risk of drought and forest fires due to climate change in the region (Silva et al. 2018), as some species appear to resprout after a fire (Noblick et al. 2020, Liesenfeld 2024). An analysis of fires in the state of Acre, western Amazon, showed that lowland open ombrophilous forests with palms, which suffer the most with deforestation for the creation of pastures by cattle farmers, are most vulnerable to forest fires during climatic extremes such as El Niño and La Niña (Da Silva Júnior et al. 2019). Submontane, remote forests may act as a reserve for palm species that may recolonise lowland areas over time, especially through human- and fauna-assisted dispersion (Heijink et al. 2024). Human management of the Amazon has at least 14,000 years of history, and palm species are among the first to be dispersed by indigenous populations in the biome (Furquim et al. 2023), as most Arecaceae provide human (Smith 2015, Dos Santos et al. 2024) and faunal subsistence, being in primary, secondary, degraded or urban forests (Fragoso et al. 2003, Beck 2006, Borges et al. 2014, Mendes Pontes et al. 2020, Glória and Tozetti 2021, Soares et al. 2023).

Preserving the continuity of these palm communities in remote areas may act as a refuge that will guarantee the survival of flora and fauna diversity throughout the climate crisis the Amazonia biome will face in the next decades, and further research in Arecaceae hotspots, such as the state of Pará, is urgent.

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## AUTHOR CONTRIBUTIONS

**Karin Elisabeth von Schmalz:** Conceptualization; data curation; formal analysis; investigation; methodology; supervision; validation; visualization; writing: original draft; writing: review.

**Emil Hernandez Ruz:** Conceptualization; writing: original draft; writing: review.

**Dilaílson Araújo de Souza**: Data curation; formal analysis; investigation.

**Angelino Pereira de Oliveira Jr.:** Investigation.

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**Rodolfo Salm:** Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; supervision; writing: original draft.

ONLINE SUPPLEMENTARY MATERIAL

All supplementary material will be available on FigShare.

## Supplementary Tables

**Table S1**: Categorical variables extracted from the TOPODATA database (Valeriano and Rossetti 2012) used in models to explain the differences in floristic composition in 100 0.1-ha plots in a 5km-transect surveyed for Arecaceae species at the ResEx Riozinho, Eastern Amazon, state of Pará, Brazil.

| Variables | Description | Categories |
|---|---|---|
| Slope | Angle of steepness of terrain; punctual | A – Flat; B – Moderate; C – Inclined; D - Steep |
| Relief | Difference in altitude between highest and lowest points of pixel | 1 – Flat; 2 – Gentle; 3 - Slightly undulating; 4 – Moderately undulating; 5 – Rolling; 6 - Hilly |
| Exposure | Cardinal exposure of terrain; implicates sun exposure | North, South, East and West |
| Shape | Combination of vertical and horizontal curvatures, giving the tridimensionality of the pixel (if concave, convex or flat) and the proneness to hold or drain water (convergent, divergent or neutral) | 1- Concave convergent; 2 – Concave neutral; 3 – Concave divergent; 4 – Flat convergent; 5 – Flat neutral; 6 – Flat divergent; 7 – Convex convergent; 8 – Convex neutral; 9 Convex divergent |

**Table S2:** Analysis of variance (ANOVA) for the permutation test of the redundancy analysis (RDA) of Arecaceae composition under reduced model and variance inflation factors (VIF) for the environmental variables NDVI, Altitude (m) and distance to stream (m) at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil.

| **Permutation test for RDA under reduced model** | | | | |
|---|---|---|---|---|
| Number of free permutations: 999 | | | | |
| | **DF** | **Variance** | **F** | **p-value** |
| Model | 3 | 32.262 | 6.8681 | 0.014 |
| Residual | 95 | 148.750 | | |
| **Variance Inflation Factors (VIF)** | | | | |
| **Variables** | | NDVI | Altitude | Dist. to stream |
| **VIF** | | 1.001282 | 1.312764 | 1.313711 |

**Table S3**: *Post hoc* estimate marginal means (EMMEANS) and pairwise comparisons (contrasts by Tukey's method) of the analysis of variance (ANOVA) model of species richness (sqrt-transformed) vs categorical and binary environmental variables (presence of *igarapé*, slope inclination, terrain relief and terrain shape) in 100 0.1-ha plots in a 5 km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil.

| ***Igarapé* Presence** | | | | | |
|---|---|---|---|---|---|
| ***Igarapé*** | **EMMEANS** | **SE** | **DF** | **Lower CL** | **Upper CL** |
| 0 | 1.56 | 0.119 | 79 | 1.33 | 1.8 |
| 1 | 2.07 | 0.162 | 79 | 1.75 | 2.4 |
| Pairwise Contrasts: | | | | | |
| **Contrast** | **Estimate** | **SE** | **DF** | **t-ratio** | **p-value** |
| 0 - 1 | -0.509 | 0.142 | 79 | -3.578 | 0.0006 |
| **Slope Inclination** | | | | | |
| **Slope** | **EMMEANS** | **SE** | **Df** | **Lower CL** | **Upper CL** |
| A | 1.96 | 0.281 | 79 | 1.40 | 2.52 |
| B | 1.79 | 0.131 | 79 | 1.52 | 2.05 |
| C | 1.59 | 0.134 | 79 | 1.33 | 1.86 |
| D | 1.94 | 0.130 | 79 | 1.68 | 2.20 |
| Pairwise Contrasts: | | | | | |
| **Contrast** | **Estimate** | **SE** | **DF** | **t-ratio** | **p-value** |
| C - D | -0.3440 | 0.147 | 79 | -2.341 | 0.0975 |
| **Relief** | | | | | |
| **Relief** | **EMMEANS** | **SE** | **DF** | **Lower CL** | **Upper CL** |
| 1 | 1.28 | 0.311 | 79 | 0.657 | 1.90 |
| 2 | 1.51 | 0.360 | 79 | 0.798 | 2.23 |
| 3 | 2.04 | 0.179 | 79 | 1.683 | 2.39 |
| 4 | 2.01 | 0.138 | 79 | 1.740 | 2.29 |
| 5 | 1.92 | 0.190 | 79 | 1.540 | 2.30 |
| 6 | 2.15 | 0.228 | 79 | 1.696 | 2.60 |
| Pairwise Contrasts: | | | | | |
| **Contrast** | **Estimate** | **SE** | **DF** | **t-ratio** | **p-value** |
| 1 - 3 | -0.7622 | 0.288 | 79 | -2.643 | 0.0990 |
| **Terrain Shape** | | | | | |
| **Shape** | **EMMEANS** | **SE** | **DF** | **Lower CL** | **Upper CL** |
| 1 | 2.02 | 0.125 | 79 | 1.768 | 2.26 |
| 2 | 1.83 | 0.144 | 79 | 1.547 | 2.12 |
| 3 | 2.16 | 0.164 | 79 | 1.832 | 2.48 |
| 4 | 1.33 | 0.240 | 79 | 0.854 | 1.81 |
| 5 | 2.06 | 0.253 | 79 | 1.556 | 2.56 |
| 6 | 1.18 | 0.335 | 79 | 0.519 | 1.85 |
| 7 | 1.97 | 0.203 | 79 | 1.569 | 2.38 |
| 8 | 2.19 | 0.176 | 79 | 1.838 | 2.54 |
| 9 | 1.63 | 0.186 | 79 | 1.255 | 2.00 |
| Pairwise Contrasts: | | | | | |
| **Contrast** | **Estimate** | **SE** | **DF** | **t-ratio** | **p-value** |
| 3 - 4 | 0.8269 | 0.242 | 79 | 3.420 | 0.0262 |
| 4 - 8 | -0.8575 | 0.243 | 79 | -3.522 | 0.0194 |

**Table S4:** Aggregated table of the summary of a Poisson Bayesian Regression Model for the abundance of *Attalea speciosa* in 100 0.1-ha plots in a 5 km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil, with the Region of Practical Equivalence (ROPE) analysis of the effects of NDVI and presence of *igarapé*, and the model's Bayesian $R^2$.

| **Parameter** | **Estimate** | **Est. Error** | **l-95% CI** | **u-95% CI** | **Bulk ESS** | **Tail ESS** | **ROPE** |
|---|---|---|---|---|---|---|---|
| Intercept | 20.43 | 1.95 | 16.54 | 24.29 | 2647 | 2594 | 0.00% |
| NDVI | -29.59 | 3.10 | -35.70 | -23.42 | 2629 | 2559 | 0.00% |
| igarape1 | -1.31 | 0.24 | -1.80 | -0.86 | 2871 | 2579 | 0.00% |
| **Model Explanatory Power** | | | | | | | |
| Metric | Estimate | | Est. Error | | 2.5% CI | | 97.5% CI |
| $R^2$ | 0.3639364 | | 0.04693397 | | 0.2713759 | | 0.4489915 |

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**Table S5:** Aggregated table of the summary of a Poisson Bayesian Regression Model for the abundance of *Euterpe longibracteata* in 100 0.1-ha plots in a 5 km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil, with the Region of Practical Equivalence (ROPE) analysis of the effects of NDVI and terrain shape, and the model's Bayesian $R^2$.

| **Parameter** | **Estimate** | **Est. Error** | **l-95% CI** | **u-95% CI** | **Bulk ESS** | **Tail ESS** | **ROPE** |
|---|---|---|---|---|---|---|---|
| Intercept | 3.13 | 3.53 | -4.05 | 10.00 | 3755 | 2755 | 1.92% |
| NDVI | -4.56 | 5.55 | -15.45 | 6.65 | 3842 | 2815 | 1.05% |
| Shape2 | 0.67 | 0.23 | 0.24 | 1.11 | 1306 | 2182 | 0.00% |
| Shape3 | 0.53 | 0.26 | -0.00 | 1.04 | 1604 | 2428 | 2.87% |
| Shape4 | -0.98 | 0.65 | -2.42 | 0.16 | 3039 | 2603 | 4.18% |
| Shape5 | 1.61 | 0.27 | 1.07 | 2.14 | 1518 | 2478 | 0.00% |
| Shape6 | 0.76 | 0.48 | -0.24 | 1.61 | 2833 | 2675 | 5.39% |
| Shape7 | 2.08 | 0.21 | 1.67 | 2.50 | 1107 | 1726 | 0.00% |
| Shape8 | 0.47 | 0.27 | -0.08 | 0.99 | 1521 | 2216 | 7.66% |
| Shape9 | -0.25 | 0.36 | -0.99 | 0.43 | 2419 | 2347 | 18.79% |

**Model Explanatory Power**

| Metric | Estimate | Est. Error | 2.5% CI | 97.5% CI |
|---|---|---|---|---|
| $R^2$ | 0.265 | 0.043 | 0.184 | 0.354 |

**Table S6:** Aggregated table of the summary of a negative binomial Bayesian Regression Model for the abundance of *Geonoma baculifera* in 100 0.1-ha plots in a 5 km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil, with the Region of Practical Equivalence (ROPE) analysis of the effects of NDVI and presence of *igarapé*, and the model's Bayesian $R^2$.

| **Parameter** | **Estimate** | **Est. Error** | **l-95% CI** | **u-95% CI** | **Bulk ESS** | **Tail ESS** | **ROPE** |
|---|---|---|---|---|---|---|---|
| Intercept | -30.62 | 16.30 | -62.60 | 0.64 | 3399 | 2715 | 0.05% |
| NDVI | 45.74 | 25.50 | -3.18 | 95.51 | 3397 | 2715 | 0.03% |
| igarape1 | 5.01 | 1.19 | 3.03 | 7.84 | 2969 | 1866 | 0.00% |
| **Model Explanatory Power** | | | | | | | |
| Metric | Estimate | | Est. Error | | 2.5% CI | | 97.5% CI |
| $R^2$ | 0.4634218 | | 0.1359437 | | 0.08449929 | | 0.5898195 |

**Table S7:** Aggregated table of the summary of a negative binomial Bayesian Regression Model for the abundance of *Euterpe oleracea* in 100 0.1-ha plots in a 5 km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil, with the Region of Practical Equivalence (ROPE) analysis of the effects of NDVI and presence of *igarapé*, and the model's Bayesian $R^2$.

| **Parameter** | **Estimate** | **Est. Error** | **l-95% CI** | **u-95% CI** | **Bulk ESS** | **Tail ESS** | **ROPE** |
|---|---|---|---|---|---|---|---|
| Intercept | -21.37 | 15.80 | -55.74 | 6.40 | 2358 | 2278 | 0.29% |
| NDVI | 29.17 | 24.72 | -14.42 | 82.65 | 2402 | 2305 | 0.29% |
| igarape1 | 5.00 | 0.68 | 3.83 | 6.48 | 1585 | 1816 | 0.00% |
| **Model Explanatory Power** | | | | | | | |
| Metric | Estimate | | Est. Error | | 2.5% CI | | 97.5% CI |
| $R^2$ | 0.5015063 | | 0.1150297 | | 0.2052507 | | 0.6309078 |

**Table S8:** Aggregated table of the summary of a logistic Bayesian Regression Model for the presence of *Astrocaryum gynacantum* in 100 0.1-ha plots in a 5 km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil, with the Region of Practical Equivalence (ROPE) analysis of the effects of NDVI and terrain shape, and the model's Bayesian $R^2$.

| **Parameter** | **Estimate** | **Est. Error** | **l-95% CI** | **u-95% CI** | **Bulk ESS** | **Tail ESS** | **ROPE** |
|---|---|---|---|---|---|---|---|
| Intercept | 12.91 | 12.19 | -11.11 | 36.72 | 2931 | 2839 | 0.45 % |
| NDVI | -20.83 | 19.16 | -58.52 | 16.98 | 2950 | 2842 | 0.32 % |
| Shape2 | 0.74 | 0.62 | -0.44 | 1.98 | 2393 | 2622 | 13.08 % |
| Shape3 | 0.58 | 0.74 | -0.90 | 2.06 | 2689 | 2438 | 15.45 % |
| Shape4 | -1.88 | 1.54 | -5.40 | 0.65 | 2617 | 1693 | 4.76 % |
| Shape5 | -1.32 | 1.47 | -4.52 | 1.22 | 3031 | 1882 | 8.47 % |
| Shape6 | -130.76 | 131.83 | -492.69 | -5.15 | 1000 | 617 | 0.00 % |
| Shape7 | -2.14 | 1.39 | -5.30 | 0.15 | 2865 | 1879 | 2.92 % |
| Shape8 | 3.23 | 1.43 | 0.97 | 6.50 | 2309 | 1736 | 0.00 % |
| Shape9 | -1.58 | 1.04 | -3.84 | 0.28 | 2647 | 2265 | 4.29 % |
| **Model Explanatory Power** | | | | | | | |
| Metric | Estimate | | Est. Error | | 2.5% CI | | 97.5% CI |
| $R^2$ | 0.2421246 | | 0.03832866 | | 0.1594421 | | 0.3100903 |

**Table S9:** Aggregated table of the summary of a logistic Bayesian Regression Model for the presence of *Astrocaryum aculeatum* in 100 0.1-ha plots in a 5 km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil, with the Region of Practical Equivalence (ROPE) analysis of the effects of NDVI and terrain shape, and the model's Bayesian $R^2$.

| **Parameter** | **Estimate** | **Est. Error** | **l-95% CI** | **u-95% CI** | **Bulk ESS** | **Tail ESS** | **ROPE** |
|---|---|---|---|---|---|---|---|
| Intercept | -9.09 | 12.04 | -33.33 | 13.97 | 5009 | 5042 | 0.99 % |
| NDVI | 14.03 | 18.91 | -22.21 | 52.01 | 5041 | 5181 | 0.78 % |
| Shape2 | 0.58 | 0.61 | -0.62 | 1.78 | 4281 | 4979 | 15.71 % |
| Shape3 | -0.37 | 0.73 | -1.81 | 1.00 | 4712 | 5204 | 19.63 % |
| Shape4 | -1.42 | 1.47 | -4.72 | 1.06 | 5064 | 3895 | 7.57 % |
| Shape5 | 1.86 | 1.49 | -0.74 | 5.07 | 4669 | 3629 | 4.95 % |
| Shape6 | -167.24 | 232.92 | -820.04 | -4.08 | 1443 | 931 | 0.00 % |
| Shape7 | -45.31 | 62.11 | -211.44 | -2.98 | 967 | 769 | 0.00 % |
| Shape8 | 0.01 | 0.77 | -1.52 | 1.53 | 4569 | 4972 | 19.45 % |
| Shape9 | -0.58 | 0.91 | -2.38 | 1.15 | 4594 | 4788 | 14.14 % |
| **Model Explanatory Power** | | | | | | | |
| Metric | Estimate | | Est. Error | | 2.5% CI | | 97.5% CI |
| $R^2$ | 0.1820384 | | 0.03483247 | | 0.1152493 | | 0.250035 |

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## Supplementary Figures

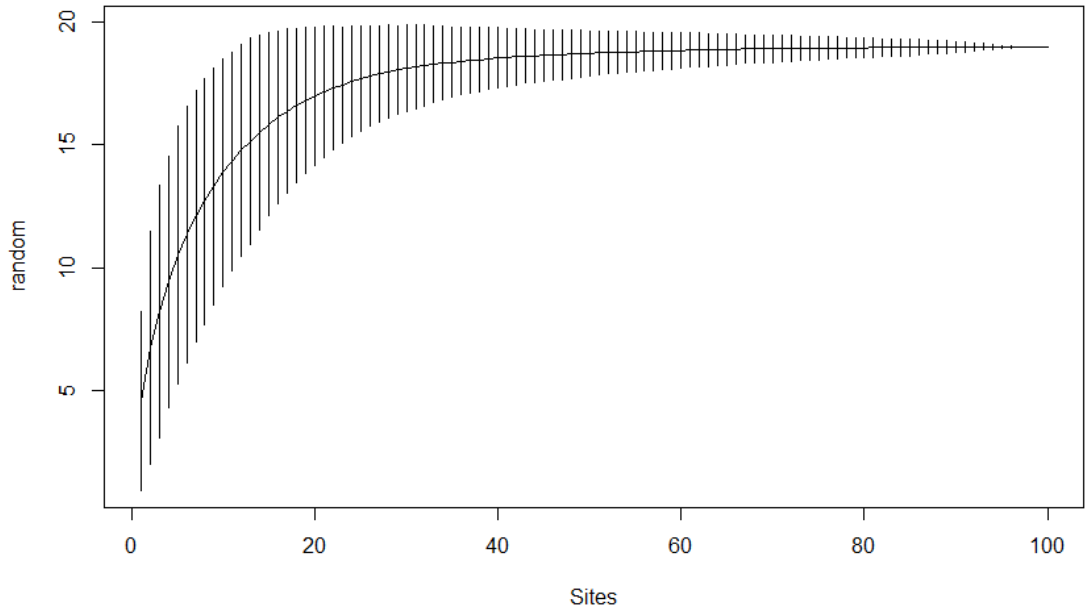


**Figure S1**: Species accumulation curve of 100 0.1-ha plots in a 5km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil.

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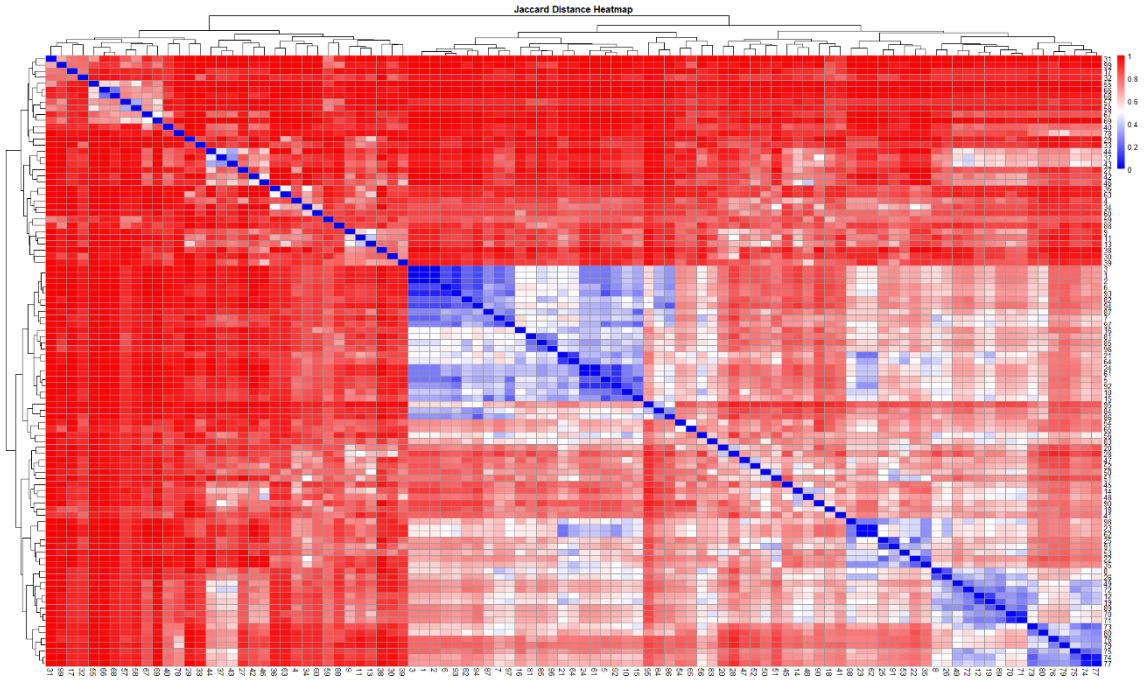


**Figure S2:** Heatmap and dendrogram of Jaccard's composition distance of 100 0.1-ha plots in a 5km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil.

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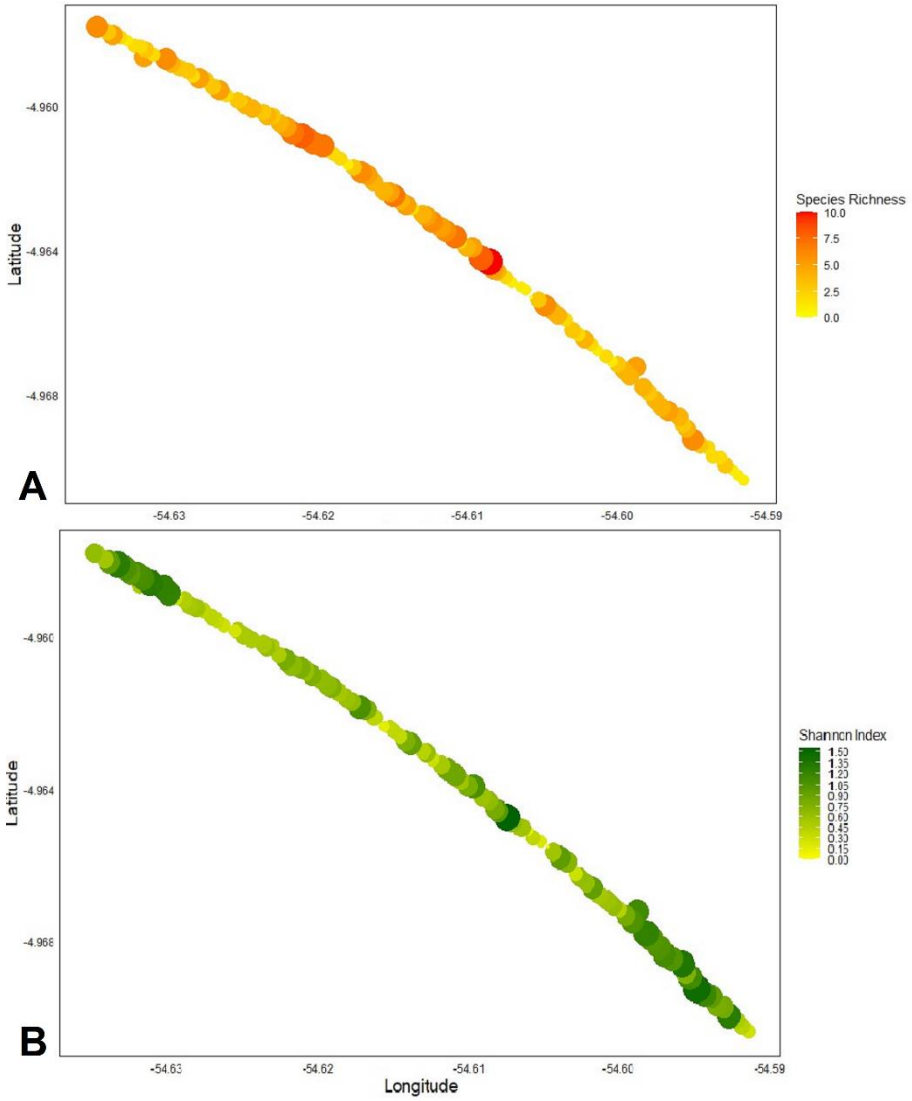


**Figure S3**: **A.** Species richness; and **B.** Shannon's Diversity Index in 100 0.1-ha plots in a 5km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil.

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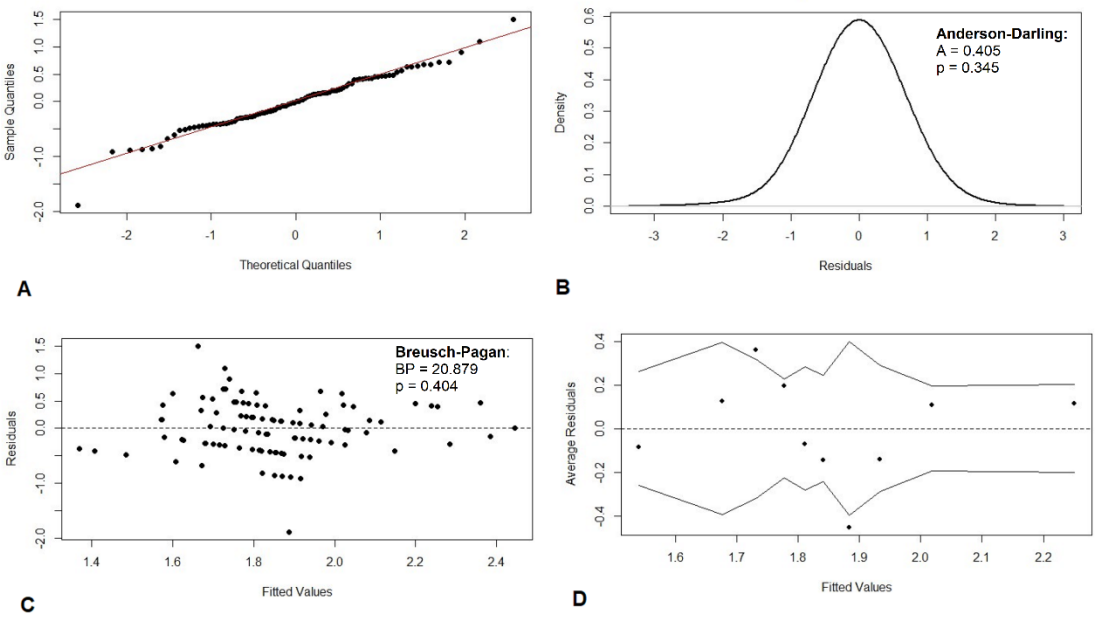


**Figure S4:** *Post hoc* analysis of residuals and fitted values of the general linear model (GLM) of species richness (sqrt-transformed) in 100 0.1-ha plots in a 5 km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil, versus continuous environmental variables (NDVI, altitude and distance to stream). **A**. Q-Q plot of residuals. **B.** Residual normal curve with Anderson-Darling test confirming the normal distribution. **C.** Residuals versus fitted values scatterplot and Breusch-Pagan test confirming homoskedasticity. **D.** Binned residuals versus fitted values plot showing few, non-systematic deviations from zero, confirming the model's validity.