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Author-formatted, not peer-reviewed document posted on 28/01/2025

DOI: <https://doi.org/10.3897/arphapreprints.e148043>

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

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5 **forest density in a remote site in the Iriri river valley, Eastern Amazon**

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ABSTRACT

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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 understory 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 (Steuer et al. 2022). The development of biomass models specific for palms showed that

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

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

122 Regarding palm species, meso- and fine-scale studies found significant effects of
123 altitude (Svenning 2001, Vormisto et al. 2004, Montufar and Pintaud 2006, Salm et al.
124 2007, Balslev et al. 2011), slope inclination or cardinal exposure (Normand et al. 2006,
125 Costa et al. 2009), hydrography and drainage (Vormisto et al. 2000, Montufar and
126 Pintaud 2006), soil characteristics (Balslev et al. 2011, Cámara-Leret et al. 2017) and
127 forest structure (Kristiansen et al. 2011, Eiserhardt et al. 2013, Salm et al. 2015), besides
128 chemical edaphic characteristics (Emilio et al. 2014), in various combinations, in the
129 composition, diversity and abundance of communities of Arecaceae in the Amazon.
130 Similar results were found in studies of tree diversity and abundance in other tropical
131 and subtropical areas, using other tree groups as responses (Liu et al. 2014, Gonella et
132 al. 2020, Marca-Zevallos et al. 2022, Pinho et al. 2022).

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

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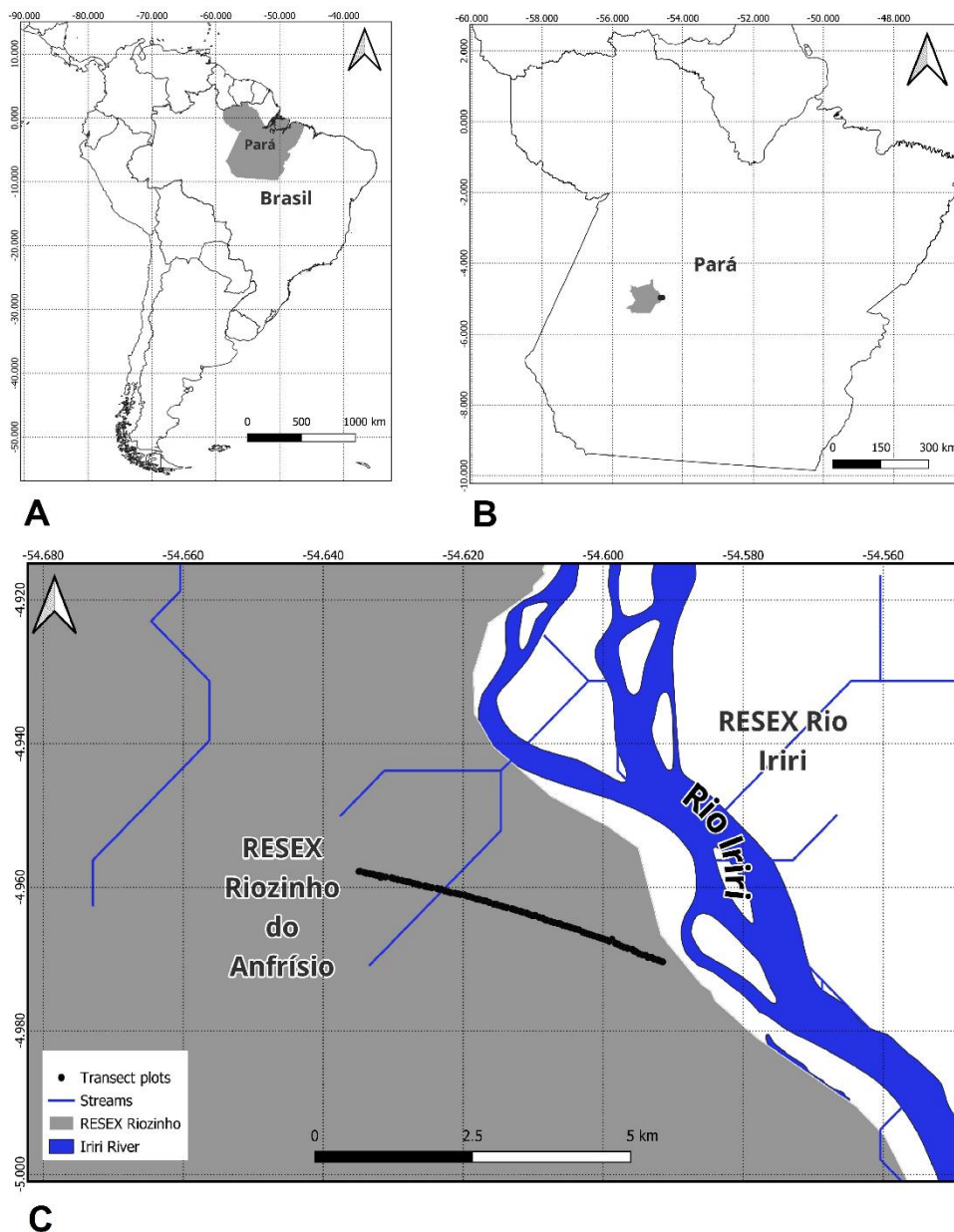
MATERIALS AND METHODS

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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 volcanoclastic 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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174 **Figure 1:** A. Location of the state of Pará within South America. B. Location of the
175 RESEX Riozinho do Anfrísio within the state of Pará. C. Transect with plots
176 surveyed at the RESEX Riozinho, Eastern Amazon, state of Pará, in the west
177 margin of Iriri River. Sources: IBGE, 2019; Lehner et al. 2008.

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179 **Data collection**

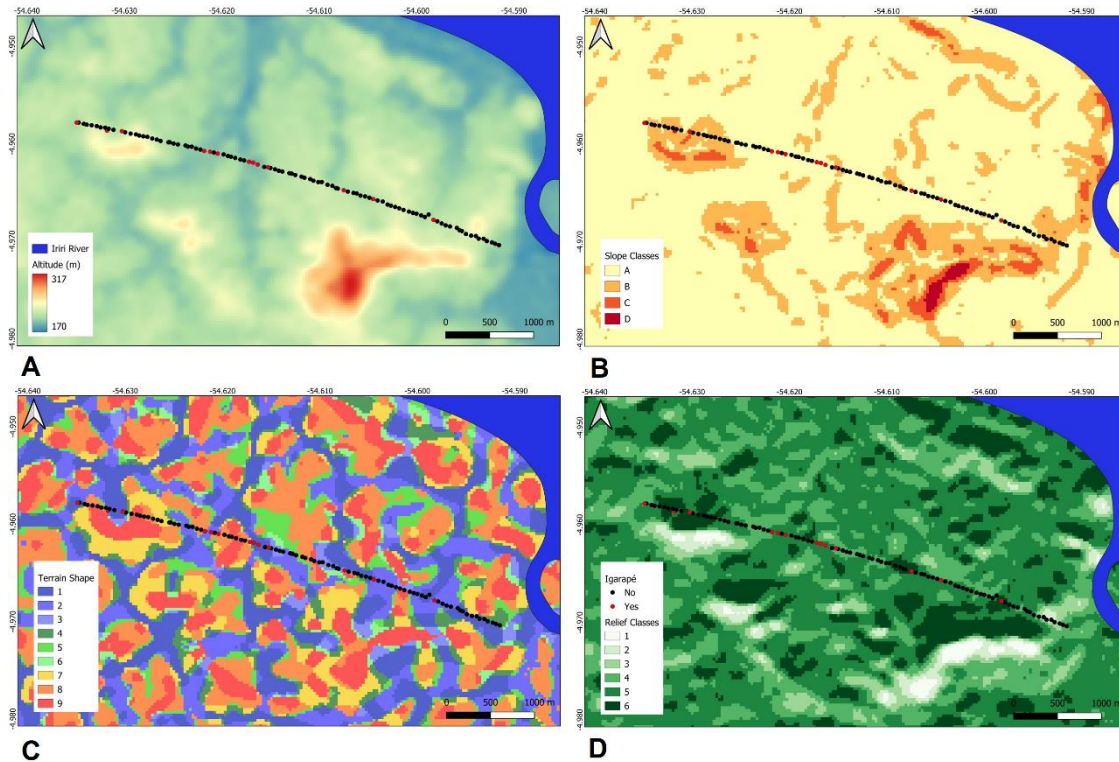
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181 The survey was realised in May 2019, at the end of the rainy season. Palm trees
182 were counted on 100 adjacent plots measuring 20 m x 50 m along a 5 km-long transect
183 previously marked for mammal surveys, totalling a 10 ha cover area. Distances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

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

193 Coordinates representing each 20 m x 50 m plot were later used to extracted data
194 from the digital elevation model (DEM) database TOPODATA (Valeriano and Rossetti
195 2012), from the Brazilian Spatial Research Institute (INPE), a country-wide resource
196 which refined data from the Shuttle Radar Topography Mission (SRTM) (Jarvis et al.
197 2008) and offers images with resolution of 30 m, containing measures such as altitude,
198 slope, relief, exposure and terrain shape (Fig. 2). We used HydroSHEDS data (Lehner et
199 al. 2008) to calculate the distance from each transect sub-unit to the nearest perennial
200 stream as registered by the SRTM, which did not record recently formed *igarapés*. As a
201 proxy to measure forest density, we extracted the normalized difference vegetation
202 index (NDVI) for the coordinates representing each of the 100 plots, using satellite
203 imagery from Cbers 4A and the method described by Ponzoni et al.(2012). NDVI has
204 been shown to be an adequate value to represent vegetation health and density in
205 tropical forests (Freitas et al. 2005), and ranged, in the study area, between 0.597 and
206 0.662 (mean 0.634 ± 0.014). The calculations of NDVI, and topographical and
207 hydrological variables, were conducted in QGIS 3.34 “Prizren” (QGIS.org 2024). For
208 the analysis, our dataset contained eight environmental variables, being three
209 continuous (altitude in meters, distance to stream in meters, and NDVI), four categorical
210 ones (slope, relief, exposure and terrain shape), and the binary presence/absence of
211 *igarapé*. The specific measurements and categories of the latter variables can be seen on
212 the Supplementary Table S1.

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

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

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239 Data analysis

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241 For data analysis, each of the 100 20 m x 50 m segments of the transect, or plots,
242 was considered a sampling unit. Species richness and abundance were calculated for
243 each plot, and data extracted from remote sensing databases were ascertained for each
244 coordinate. All statistical analysis and graphs were produced using RStudio version
245 2024.09.1+394 (RStudio Team 2024) and R-4.4.2 for Windows “Pile of Leaves” (R
Core Team 2024).

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

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

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

275 Graphs showing variation of species richness and Shannon H' in relation to
276 geographical positions were created with the package "sp" (Bivand et al. 2013), and the
277 heatmap with Jaccard distance was created with "pheatmap" over "vegan" data (Kolde
278 2018). All other graphs were produced with the package "ggplot2", and all data was
279 organised with the help of "dplyr", both part of the package "tidyverse" (Wickham et al.
280 2019). Multiple graphs were organised with the package "patchwork" (Pedersen 2024).

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

285 286 **Selection of response variables**

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

296 Similarity Index J was very high throughout the studied area (Supplementary Fig. S2),
297 but there was also no significant correlation between geographical coordinates and
298 floristic similarity (Mantel test: $r = -0.0557$; $p_{\text{Holm}} = 1$; 999 permutations). The
299 distribution of this variable was highly right-skewed even after log-transformed, and the
300 model including it was based on gamma distribution. There was a significant relation
301 between Shannon's H' and geographic position (Mantel test: $r = 0.1029$; $p_{\text{Holm}} = 0.039$;
302 999 permutations), which excluded Shannon's index as a response variable for further
303 analyses due to possible multicollinearity issues skewing the results. Shannon's H' and
304 Simpson's D indices are frequently correlated, which is the case in our data (Pearson: t
305 $= 35.544$, $df = 98$, $p_{\text{Holm}} < 0.001$), also excluding Simpson's and inverse Simpson's
306 indices as response variables. Species richness and diversity were not correlated
307 (Pearson: $t = 0.36381$, $df = 98$, $p_{\text{Holm}} = 1$). Therefore, species richness was chosen as a
308 response variable for verifying the effect of categorical topographic and hydrographic
309 variables in an analysis of variance test, and Jaccard's similarity was chosen for a
310 gamma model with continuous environmental variables.

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

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RESULTS

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Species occurrence

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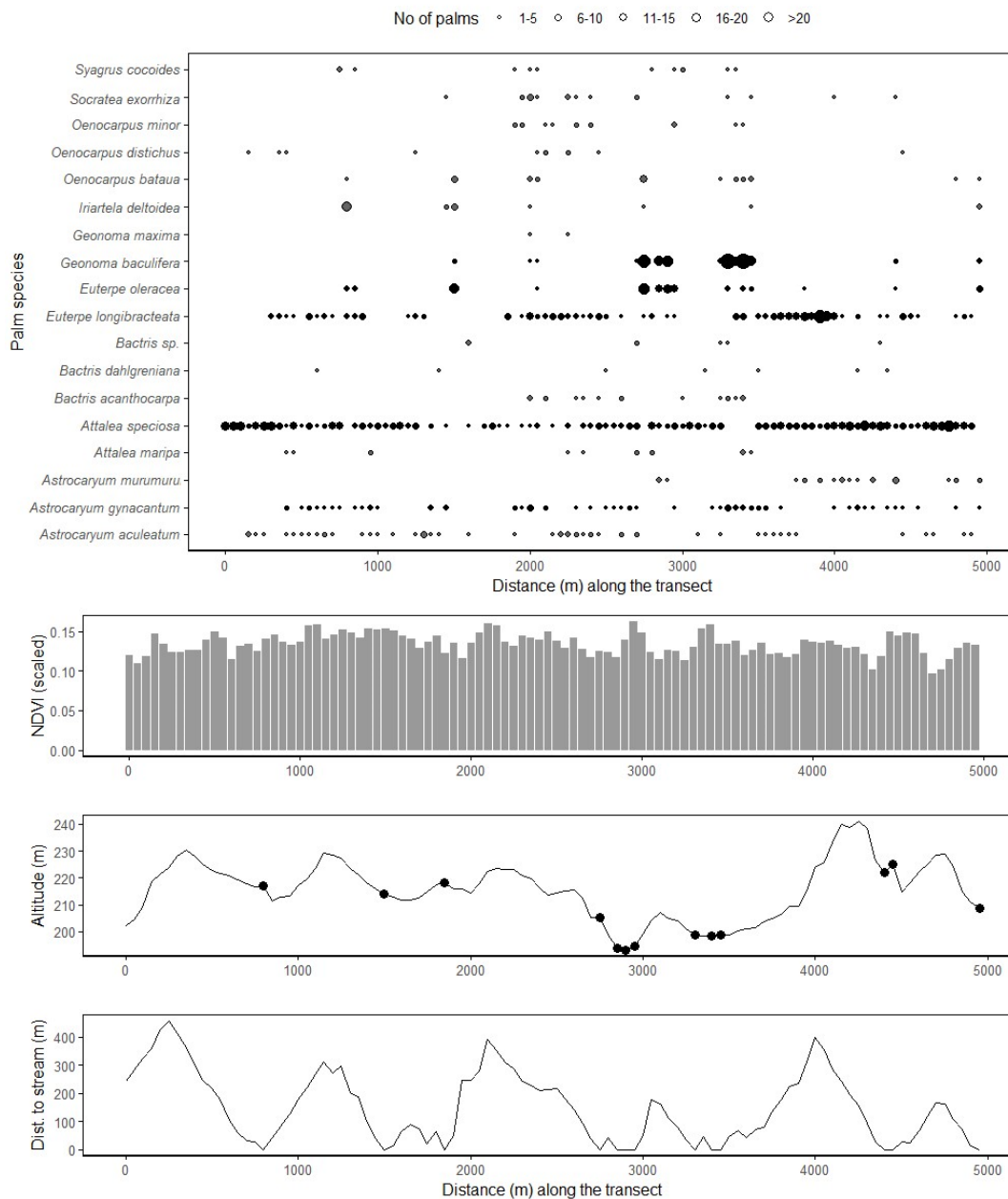
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In the 10ha of *terra firme* forest covered by the transect, 1506 individuals of 17 species were identified at species level, and one identified at genus level (Table 1), of which 14 had specific traits listed on the PalmTraits 1.0 database (Kissling 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).

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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.*

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

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

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374 Diversity indices

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376 Species diversity in the 100 20mx50m plots ranged from 0 to 10 (average $3.64 \pm$
377 1.9). The only plot with no species was later removed for further analysis. Shannon's
378 diversity index H' ranged from 0.000 to 1.547 (average 0.713 ± 0.326), while Simpson's
379 Diversity Index D went from 0.000 to 0.702 (average 0.355 ± 0.168). Inverse Simpson's
380 index ($1 - D$) ranged from 1.000 to 3.350 (average 1.686 ± 0.556). Species diversity and
381 Shannon's H' changed with plot coordinate (Supplementary Fig. S3).

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384 Redundancy analysis

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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: $F_{3,95}$, $p_{\text{Holm}} = 0.0140$, 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 of this analysis (Supplementary Table S2)

417 **Table 2:** Summary of Redundancy Analysis (RDA) of floristic composition in 100 0.1-
 418 ha plots in a 5km-transect surveyed for Arecaceae species at the RESEX
 419 Riozinho, Eastern Amazon, state of Pará, Brazil.
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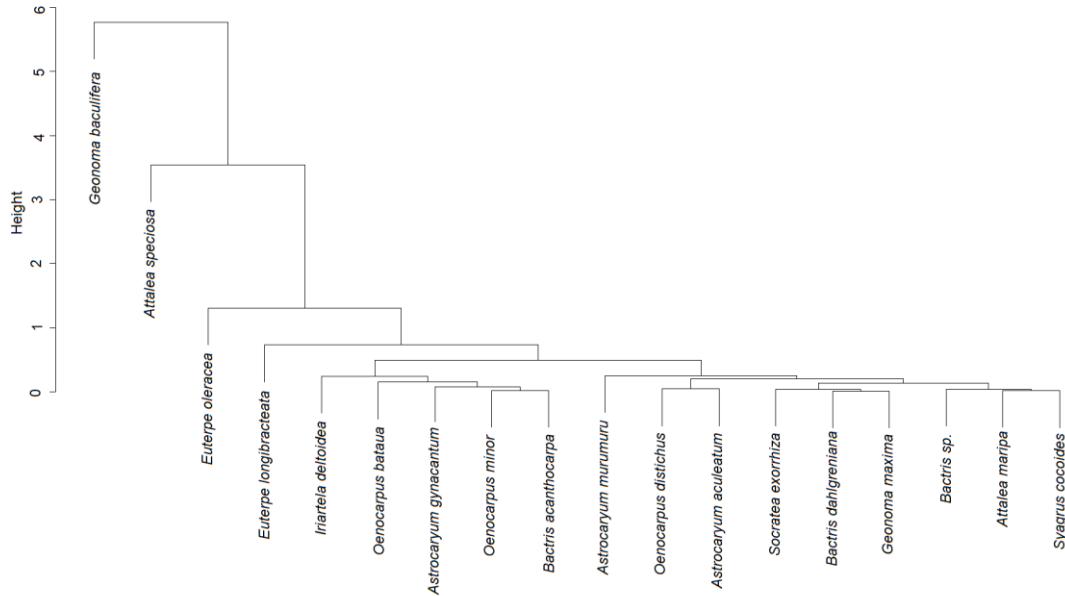
Variance Partitioning		Inertia			Proportion	
Total		181.01			1.0000	
Constrained		32.26			0.1782	
Unconstrained		148.75			0.8218	
Importance of Components	RDA1	RDA2	RDA3	PC1	PC2	PC3
Eigenvalue	26.4039	3.5218	2.3363	92.8842	23.2660	13.7153
Proportion Explained	0.1459	0.0195	0.0129	0.5131	0.1285	0.0758
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	

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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.

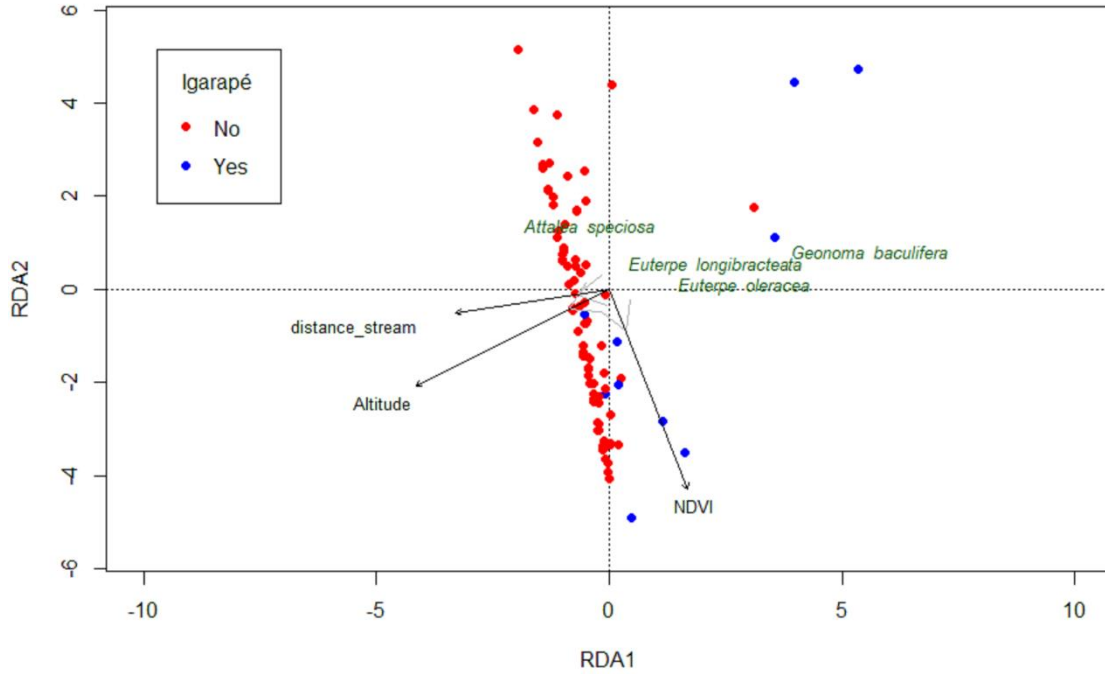
Species	RDA1	RDA2	RDA3	PC1	PC2	PC3
<i>Attalea speciosa</i>	-2.09414	1.301685	-0.370149	-0.3819282	-0.896400	2.931234
<i>Oenocarpus distichus</i>	-0.05943	-0.075526	0.080924	0.0098484	0.006552	-0.042265
<i>Astrocaryum aculeatum</i>	-0.05345	-0.124100	0.096595	-0.1011135	-0.002171	-0.127921
<i>Euterpe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

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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



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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.

448 **Effects of environmental variables on Jaccard’s Similarity Index**

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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.

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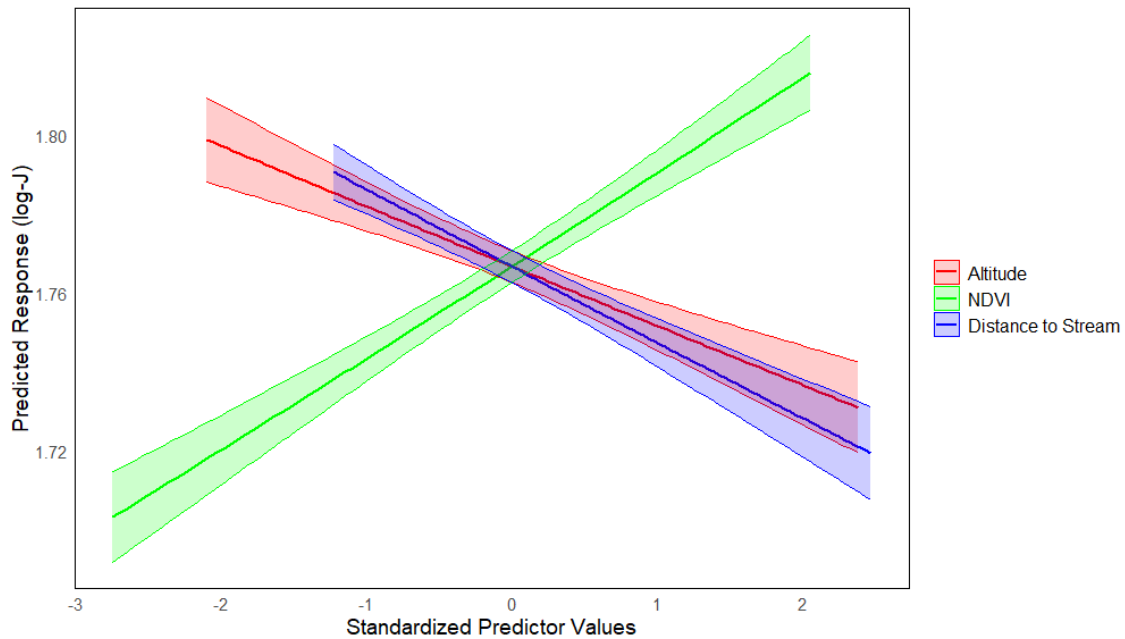
464 **Table 4:** Summary of gamma-distribution General Linear Model of the effect of
 465 continuous environmental variables on the Jaccard similarity index *J* between 100
 466 0.1-ha plots in a 5km-transect surveyed for Arecaceae species at the RESEX
 467 Riozinho, Eastern Amazon, state of Pará, Brazil.

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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%

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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.

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Effects of continuous environmental variables on species richness

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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 ($t = 1.218$; $p_{\text{Holm}} = 1$), suggesting no baseline difference in richness when all variables are at zero. NDVI ($t = 0.28451$; $p_{\text{Holm}} = 1$), altitude ($t = -2.588$; $p_{\text{Holm}} = 0.11$) and distance to stream ($t = -2.662$; $p_{\text{Holm}} = 0.10$) 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.

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Effects of categorical environmental variables on species richness

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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 ($R^2 = 50\%$; $R^2 \text{ adj.} = 47.3\%$), 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 ($F_1 = 16.060$; $p_{\text{Holm}} = 0.0022$) was highly significant, and the significant difference in estimated marginal

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

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

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

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

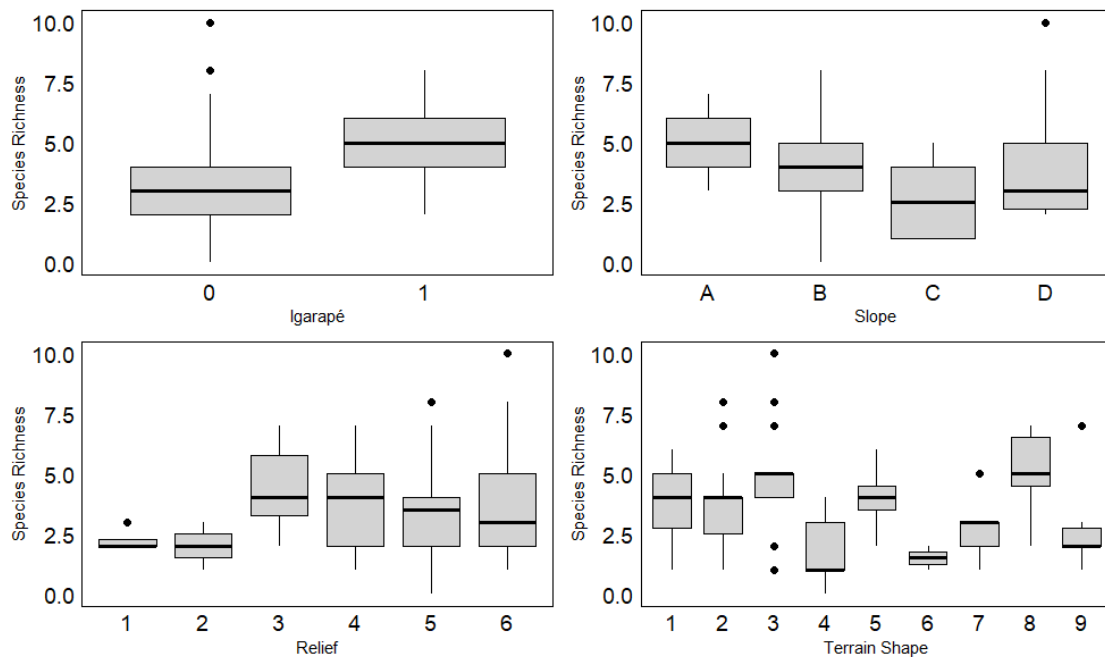
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Factor	Df	Sum Sq	Mean Sq	F value	p_{Holm}
<i>Igarapé</i>	1	2.765	2.7649	16.060	0.0022
Slope	3	2.595	0.8649	5.024	0.0390
Relief	5	2.063	0.4125	2.396	0.3125
Exposure	3	0.974	0.3247	1.886	0.8322
Shape	8	5.209	0.6511	3.782	0.0126
Residuals	79	13.601		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

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

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534 **Habitat characteristics related to abundant species**

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

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544 **Table 6:** Summary of the Bayesian regression models to explain the distribution of the
 545 six most abundant Arecaceae species recorded in 100 0.1-ha plots in a 5km-
 546 transect at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil. Predictors
 547 were NDVI (continuous), terrain shape (categorical) and presence of *igarapé*
 548 (binary). A positive sign after a predictor under “Potential Effects” means higher
 549 abundance or probability of presence of the species; a negative sign means lower
 550 abundance or probability of presence of the species.
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Species	Model Type	Predictors	Potential Effects	Bayesian R ²
<i>Attalea speciosa</i>	Poisson	NDVI, <i>Igarapé</i>	NDVI (-), <i>Igarapé</i> (-)	0.36
<i>Euterpe longibracteata</i>	Poisson	NDVI, Shape	NDVI (-), Shape5 (+), Shape7 (+)	0.46
<i>Geonoma baculifera</i>	Negative Binomial	NDVI, <i>Igarapé</i>	NDVI (+), <i>Igarapé</i> (+)	0.46
<i>Euterpe oleracea</i>	Negative Binomial	NDVI, <i>Igarapé</i>	NDVI (+), <i>Igarapé</i> (+)	0.50
<i>Astrocaryum gynacantum</i>	Logistic	NDVI, Shape	NDVI (-), Shape6 (-), Shape8 (+)	0.24
<i>Astrocaryum aculeata</i>	Logistic	NDVI, Shape	NDVI (+), Shape6 (-), Shape7 (-)	0.18

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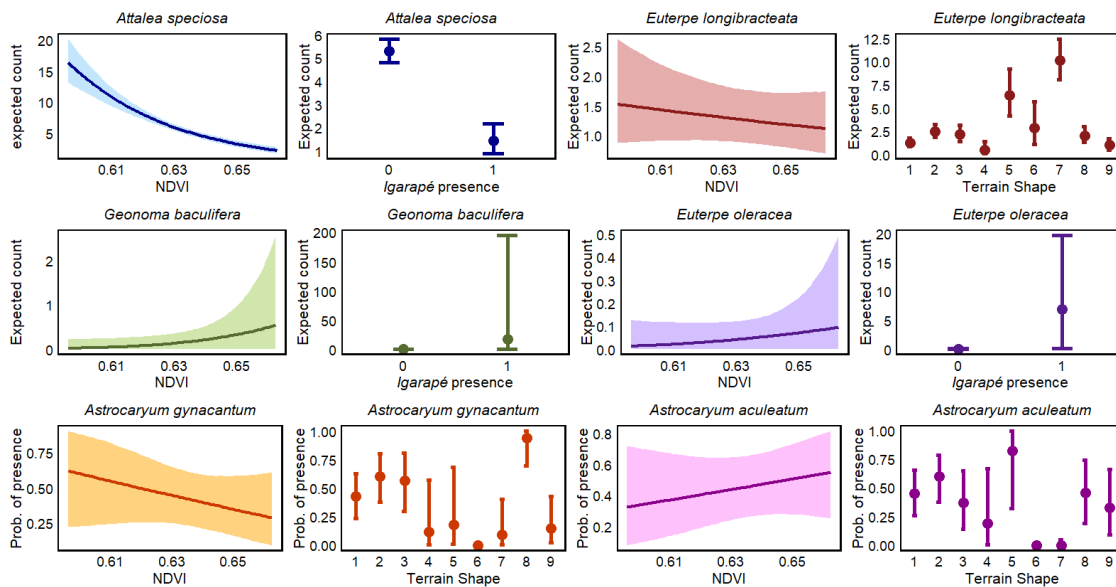
554 *Attalea speciosa* counts yielded the most reliable results. NDVI had a strong
 555 negative effect on the species presence (Estimate: -29.59), indicating it is more likely to
 556 be present in lower-density forests. The proximity to an *igarapé* also showed a
 557 significant negative effect (Estimate: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

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563 NDVI had a negative but broad effect on *Euterpe longibracteata* distribution
 564 (Estimate: -4.56, CI includes zero), suggesting a potential association with more open
 565 forest areas, although the effect is not definitive. Two terrain shapes appeared to have a
 566 positive effect in this species: Shape5, a flat water-neutral contour (Estimate: 1.61) and
 567 Shape7, convex water-convergent contour (Estimate: 2.08), suggesting an avoidance of
 568 areas prone to waterlogging. The model fit was reasonable, with 46% of the variance
 569 explained by these terms (Supplementary Table S5). For *Geonoma baculifera*, broad
 570 credible intervals resulted from the very sparse distribution of the species, with
 571 individuals recorded in only eleven plots, despite being the third most abundant species
 572 in the study area. NDVI appeared to have a positive effect (Estimate: 45.74) that is
 573 broadly estimated, showing a trend toward denser forests, though the effect is
 574 inconclusive as the CI includes zero. The presence of an *igarapé* appeared to favour the
 575 occurrence of the species (Estimate: 5.01), and this effect seemed to be confirmed by
 576 ROPE analysis. Despite these shortcomings, the explanatory power of the model
 577 reached 46% (Supplementary Table S6). Broad estimates were also a setback of the
 578 models for *Euterpe oleracea*, *Astrocaryum gynacantum* and *Astrocaryum aculeatum*,
 579 and results must be interpreted carefully. For *E. oleracea*, NDVI appeared to have a
 580 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:

581 5.00), which may be responsible for the model’s higher explanatory power (Bayesian R^2
 582 = 50%; Supplementary Table S7). The models for the two species of *Astrocaryum*
 583 yielded very different results. *A. gynacantum* appeared to have negative effects of NDVI
 584 (Estimate: -20.83), although CI includes zero. The species reacted differently to two
 585 terrain shapes, with a flat water-divergent contour having a strong negative effect
 586 (Estimate: -130.76) and convex, water-neutral areas having a weak positive effect
 587 (Estimate: 3.23). The model, however, has a modest explanatory power (Bayesian R^2 =
 588 24%, Supplementary Table S8). For *A. aculeatum*, NDVI appeared to affect positively
 589 (Estimate: 14.03), although with high uncertainty, while two terrain shapes had strong
 590 negative impacts in this species’ distribution: flat water-divergent (Estimate: -167.24)
 591 and convex water-convergent contours (Estimate: -45.31), which are not prone to water-
 592 logging and can be washed by rains. The model Bayesian R^2 , however, is low at 18%
 593 (Supplementary Table S9). A graphical summary of the relations between species
 594 distributions and environmental variables can be seen on Figure 8.

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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

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In our study in the Iriri river valley, all but two species were canopy species, but understory 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 understory 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 18th 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).

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

674 Species richness did not seem to be affected by forest density, altitude or
675 distance to streams, but it was highly affected by the presence of *igarapés* and the shape
676 of the terrain. As distance to streams was calculated using information from
677 HydroSHEDS, which was captured in the beginning of the 21st Century (Lehner et al.
678 2008), this variable may have not reflected the present hydrographic configuration of
679 the area as accurately as the *igarapés* recorded in the field. *Igarapés* are known to
680 present a number of adapted palm species which will colonise these areas all throughout
681 Amazonia (Kahn and de Granville 1992, Salm et al. 2015). In our study, the average
682 species richness was higher where there was an *igarapé*, although the range of species
683 was higher in its absence, indicating that the same species are found near these
684 Amazonian shallow waterways, as suggested by our redundancy analysis, with
685 *Geonoma baculifera* and *Euterpe oleracea* appearing associated to these features.
686 Again, flat, water-convergent terrains, which had higher Jaccard's similarity, presented
687 the lowest species richness, suggesting that only a few species are adapted to these
688 conditions (Kahn 1987, Kahn and de Granville 1992). Concave, water-divergent, and
689 convex, water-neutral terrains presented the highest species richness. Both shapes are
690 not prone to waterlogging, with the first retaining moisture but not holding water, and
691 the second being the quintessential *terra firme* condition, but without the excessive
692 removal of nutrients found in convex, water-divergent terrains. These results agree with
693 findings that most arborescent palms avoid both permanently waterlogged areas near
694 rivers and dry areas where the terrain is convex and water-divergent, such as the top of
695 hills (Muscarella et al. 2020, Wagner et al. 2020).

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

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

711 Smith 2015); the latter occupies from seasonally-flooded plains to altitudes up to
712 1,400m, and is frequently spread opportunistically by indigenous populations (Kahn
713 1987, Kahn et al. 1988, Smith 2015). Both species are among the ten most abundant
714 trees in the Amazon (Ter Steege et al. 2013), although they were not the most abundant
715 in our study area.

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

722 Bayesian analysis of the six most abundant species in our study area pointed out
723 how different species occur in plots with very different microhabitats in relation to
724 forest density, presence of *igarapés* and terrain shape, as it is known for palm species
725 (Svenning 1999). Three species showed a consistent relation with open forests, with
726 lower NDVI, and dry, rich soils: *A. speciosa* was predominantly found away from
727 *igarapés* in areas with lower NDVI; *E. longibracteata* also occurred in less dense plots,
728 in convex, water-convergent and flat, water-neutral terrain; and *Astrocaryum*
729 *gynacantum* occurred in open forest in convex, water-neutral terrain, avoiding flat,
730 water-divergent plots where the soil is washed-up. Two species were found in denser
731 plots where there is an *igarapé*: *G. baculifera* and *E. oleracea* occurred near *igarapés*,
732 when the NDVI was higher. *A. aculeata* occurred in denser forest, but avoided flat,
733 water-divergent and convex, water-convergent terrain: the first shape allows the soil to
734 be washed of nutrients, and the second retains water. These results are consistent with
735 the known microhabitats for each species (Kahn and de Granville 1992, Lorenzi et al.
736 2010, Smith 2015), and can instruct future reforestation and agroforestry projects
737 involving these species, which are frequently used as surrogates to indicate biodiversity
738 (Svenning et al. 2009, Cardoso et al. 2013, Ramos et al. 2022, Menger et al. 2024)
739 despite some caveats (Ritter et al. 2019), although further studies would be needed to
740 ascertain specific requirements.

741

742 CONCLUSION

743

744 The area surveyed in this study, with its relative abundance of Arecaceae and
745 submontane open ombrophilous forest, confirms the importance of this family in areas
746 with shallow water tables (Kahn and de Granville 1992, Sousa et al. 2020), especially
747 with the increased risk of drought and forest fires due to climate change in the region
748 (Silva et al. 2018), as some species appear to resprout after a fire (Noblick et al. 2020,
749 Liesenfeld 2024). An analysis of fires in the state of Acre, western Amazon, showed
750 that lowland open ombrophilous forests with palms, which suffer the most with
751 deforestation for the creation of pastures by cattle farmers, are most vulnerable to forest
752 fires during climatic extremes such as El Niño and La Niña (Da Silva Júnior et al.
753 2019). Submontane, remote forests may act as a reserve for palm species that may
754 recolonise lowland areas over time, especially through human- and fauna-assisted
755 dispersion (Heijink et al. 2024). Human management of the Amazon has at least 14,000
756 years of history, and palm species are among the first to be dispersed by indigenous
757 populations in the biome (Furquim et al. 2023), as most Arecaceae provide human
758 (Smith 2015, Dos Santos et al. 2024) and faunal subsistence, being in primary,
759 secondary, degraded or urban forests (Fragoso et al. 2003, Beck 2006, Borges et al.
760 2014, Mendes Pontes et al. 2020, Glória and Tozetti 2021, Soares et al. 2023).

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

765
 766 ACKNOWLEDGEMENTS
 767

768 We are thankful to the Chico Mendes Institute for Biodiversity Conservation
 769 (ICMbio) for authorizing and supporting this research. We are grateful to Mr. Fogoió
 770 and his wife for hosting our field team in their house. This study was not possible
 771 without the assistance of the students of the Faculdade de Ciências Biológicas, Ana
 772 Caroline Leal, Carla Campos, Emili Larissa, Geysa Raposo, Gustavo Cruz, Loyriane
 773 Sousa, Jakeline Arcanjo and Tayná Medeiros, from Universidade Federal do Pará. We
 774 thank professor Anderson Serra, Karina Dias da Silva and Thiago Bernandi Vieira for
 775 important inputs on the analysis and interpretation of the data. Karin von Schmalz
 776 would like to thank the community at ResearchGate and Stack Overflow for their
 777 generous discussions and exchange of literature.

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AUTHOR CONTRIBUTIONS

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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.

Dilailson Araújo de Souza: Data curation; formal analysis; investigation.

Angelino Pereira de Oliveira Jr.: Investigation.

Wellington De Pinho Alvarez: Data curation; investigation.

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

ONLINE SUPPLEMENTARY MATERIAL

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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

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1328 **Table S2:** Analysis of variance (ANOVA) for the permutation test of the redundancy
 1329 analysis (RDA) of Areaceae composition under reduced model and variance
 1330 inflation factors (VIF) for the environmental variables NDVI, Altitude (m) and
 1331 distance to stream (m) at the RESEX Riozinho, Eastern Amazon, state of Pará,
 1332 Brazil.

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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

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1343 **Table S3:** *Post hoc* estimate marginal means (EMMEANS) and pairwise comparisons
 1344 (contrasts by Tukey’s method) of the analysis of variance (ANOVA) model of
 1345 species richness (sqrt-transformed) vs categorical and binary environmental
 1346 variables (presence of *igarapé*, slope inclination, terrain relief and terrain
 1347 shape) in 100 0.1-ha plots in a 5 km-transect surveyed for Arecaceae species at
 1348 the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil.
 1349

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

1351 **Table S4:** Aggregated table of the summary of a Poisson Bayesian Regression Model
 1352 for the abundance of *Attalea speciosa* in 100 0.1-ha plots in a 5 km-transect
 1353 surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state
 1354 of Pará, Brazil, with the Region of Practical Equivalence (ROPE) analysis of
 1355 the effects of NDVI and presence of *igarapé*, and the model's Bayesian R².
 1356

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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1360 **Table S5:** Aggregated table of the summary of a Poisson Bayesian Regression Model
 1361 for the abundance of *Euterpe longibracteata* in 100 0.1-ha plots in a 5 km-
 1362 transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern
 1363 Amazon, state of Pará, Brazil, with the Region of Practical Equivalence
 1364 (ROPE) analysis of the effects of NDVI and terrain shape, and the model's
 1365 Bayesian R².
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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	

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1369 **Table S6:** Aggregated table of the summary of a negative binomial Bayesian
 1370 Regression Model for the abundance of *Geonoma baculifera* in 100 0.1-ha
 1371 plots in a 5 km-transect surveyed for Arecaceae species at the RESEX
 1372 Riozinho, Eastern Amazon, state of Pará, Brazil, with the Region of Practical
 1373 Equivalence (ROPE) analysis of the effects of NDVI and presence of *igarapé*,
 1374 and the model's Bayesian R².
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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%
igarapel	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		

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1379 **Table S7:** Aggregated table of the summary of a negative binomial Bayesian
 1380 Regression Model for the abundance of *Euterpe oleracea* in 100 0.1-ha plots in
 1381 a 5 km-transect surveyed for Arecaceae species at the RESEX Riozinho,
 1382 Eastern Amazon, state of Pará, Brazil, with the Region of Practical Equivalence
 1383 (ROPE) analysis of the effects of NDVI and presence of *igarapé*, and the
 1384 model's Bayesian R².
 1385

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

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1390 **Table S8:** Aggregated table of the summary of a logistic Bayesian Regression Model
 1391 for the presence of *Astrocaryum gynacantum* in 100 0.1-ha plots in a 5 km-
 1392 transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern
 1393 Amazon, state of Pará, Brazil, with the Region of Practical Equivalence
 1394 (ROPE) analysis of the effects of NDVI and terrain shape, and the model's
 1395 Bayesian R².
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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		

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1399 **Table S9:** Aggregated table of the summary of a logistic Bayesian Regression Model
 1400 for the presence of *Astrocaryum aculeatum* in 100 0.1-ha plots in a 5 km-
 1401 transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern
 1402 Amazon, state of Pará, Brazil, with the Region of Practical Equivalence
 1403 (ROPE) analysis of the effects of NDVI and terrain shape, and the model's
 1404 Bayesian R².
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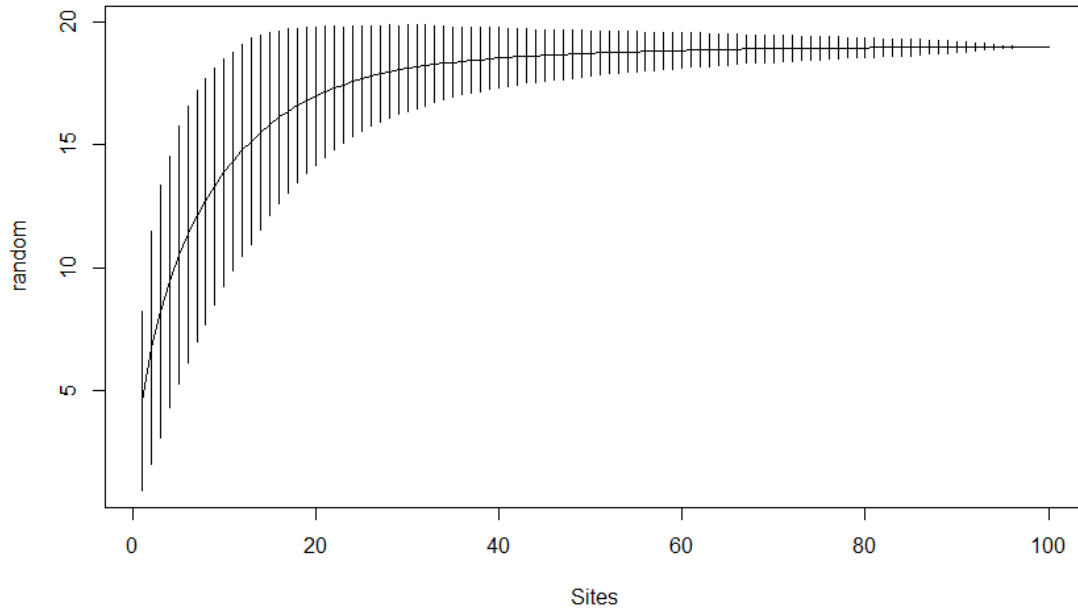
Parameter	Estimate	Est. Error	l-95% CI	u-95% CI	Bulk ESS	Tail ESS	ROPE
Intercept	-9.09	12.04	-33.33	13.97	5009	5042	0.99 %
NDVI	14.03	18.91	-22.21	52.01	5041	5181	0.78 %
Shape2	0.58	0.61	-0.62	1.78	4281	4979	15.71 %
Shape3	-0.37	0.73	-1.81	1.00	4712	5204	19.63 %
Shape4	-1.42	1.47	-4.72	1.06	5064	3895	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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1409 **Supplementary Figures**

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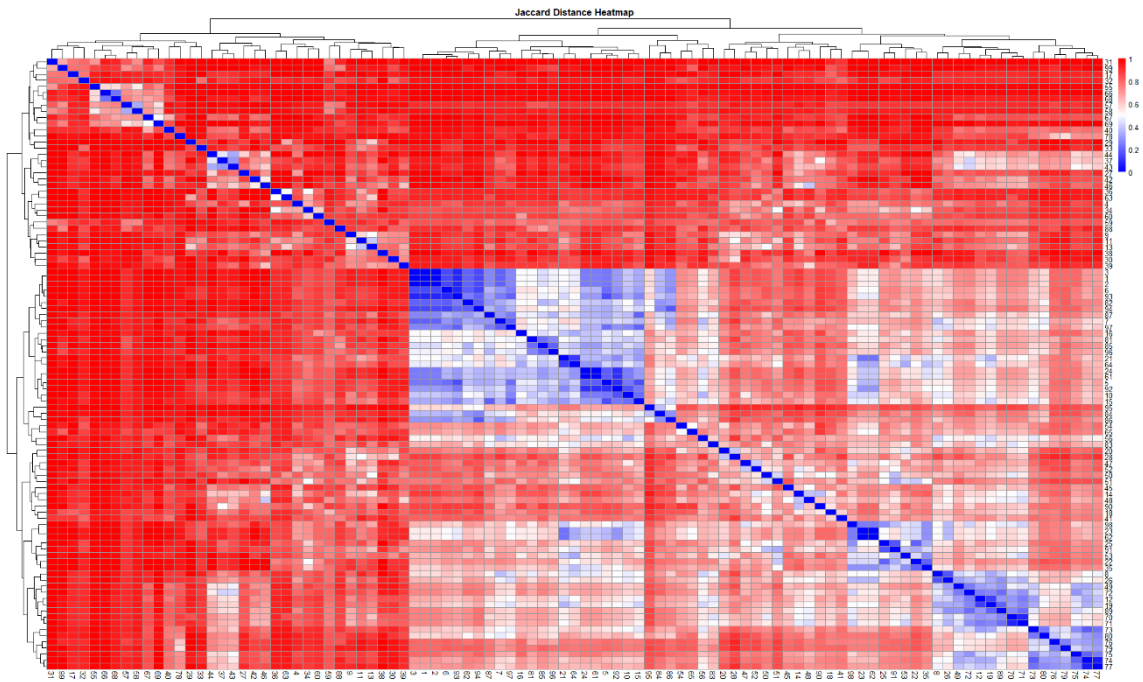
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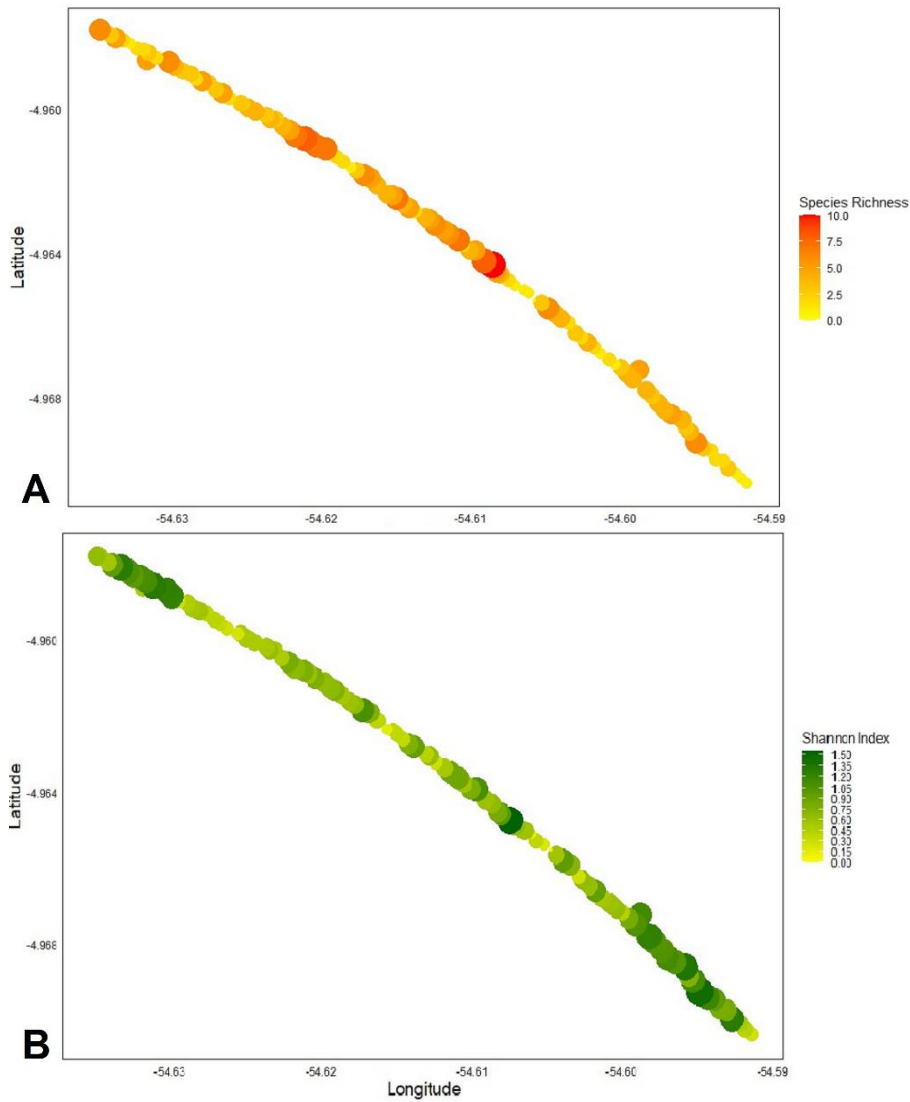
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Figure S1: Species accumulation curve of 100 0.1-ha plots in a 5km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil.



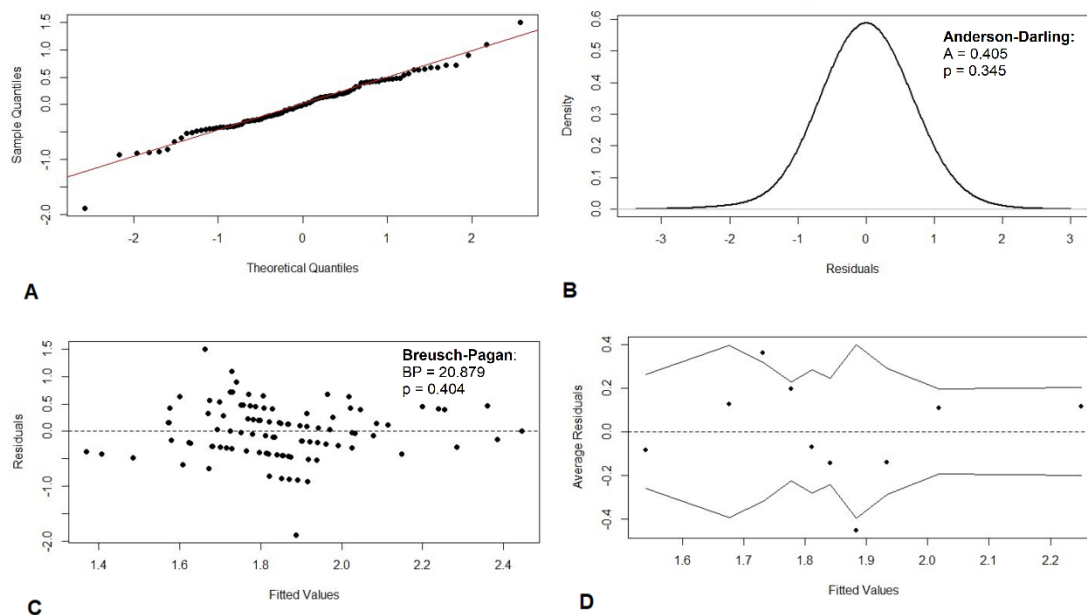
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Figure S2: Heatmap and dendrogram of Jaccard's composition distance of 100 0.1-ha plots in a 5km-transect surveyed for Arecaceae species at the RESEX Riozinho, Eastern Amazon, state of Pará, Brazil.



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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.