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Research Article

Palm community structure in relation to topography, hydrography, and forest structure in the Iriri River Valley, eastern Amazon

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Abstract

The distribution of palm (Arecaceae) species distribution is closely associated with topography, hydrology, and forest architecture, but site- and species-specific studies remain scarce in the Amazon. Here, we describe patterns of palm community structure and their associations with environmental gradients in a remote area of the eastern Amazon, helping fill an approximately 500-km geographic knowledge gap. We hypothesized that local environmental heterogeneity, particularly hydrographic conditions, topography, and forest structure, would promote spatial variation in palm community structure, with species richness and composition varying along these gradients and dominant species showing species-specific associations with local environmental conditions. A field survey across a 5-km transect, subdivided into 100 plots in the Riozinho do Anfrísio Extractive Reserve, Pará, Brazil, identified palm species and collected environmental data, including NDVI, altitude, terrain characteristics, and proximity to permanent and intermittent streams. We assessed associations between species richness, community composition, and environmental variables using multivariate and regression-based analyses. Eighteen palm species were recorded, with the palm community overwhelmingly dominated by *Attalea speciosa*, which reached exceptionally high local abundance, followed by *Geonoma baculifera* and *Euterpe longibracteata*. Variation in species composition was significantly associated with NDVI, altitude, and distance to streams, whereas species richness showed stronger associations with the presence of igarapés and terrain shape. *A. speciosa* was associated with lower NDVI values and areas away from igarapés, whereas *Euterpe oleracea* and *G. baculifera* were positively associated with the presence of igarapés. The observed patterns partially support the hypothesis that local environmental heterogeneity promotes spatial variation in palm community structure by creating habitats differing in environmental suitability for palm species. These findings provide a baseline characterization of palm communities in a poorly documented region of the Eastern Amazon and contribute to understanding how local environmental gradients shape palm community structure and species distribution.

Key words: Arecaceae, forest density, *igarapés*, palm communities, tropical forests

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Introduction

The influence of environmental factors such as topography, hydrology, soil type, and forest structure on the diversity and abundance of palm communities was recognized in early plot-based studies in the Amazon (Kahn and de Castro 1985; Kahn et al. 1988). Among these factors, topographic variation has been repeatedly associated with Amazonian forest palm distribution patterns. However, its role cannot be stated with absolute certainty, as topography is closely interconnected with other variables, such as soil chemistry, texture, and hydrology, which exert a more direct influence on plant communities (Cámara-Leret et al. 2017).

Meso- and fine-scale studies have shown that variation in palm communities is associated with multiple environmental and ecological factors, including hydrography and drainage (Vormisto et al. 2000; Montufar and Pintaud 2006), forest structure (Kristiansen et al. 2011; Salm et al. 2015), altitude (Salm et al. 2007), slope inclination and exposure (Normand et al. 2006; Costa et al. 2009), and soil characteristics (Cámara-Leret et al. 2017). Chemical edaphic factors (Emilio et al. 2014) and biotic interactions such as predation (Salm 2006) also shape the abundance and composition of Amazonian Arecaceae communities. Similar ecological patterns have been observed in studies examining tree diversity and abundance across other tropical and subtropical regions (Marca Zevallos et al. 2022; Pinho et al. 2022).

Amazonia harbors at least 5% of the world's Arecaceae species (Dransfield et al. 2008), with certain regions exhibiting exceptionally high palm abundance and canopy dominance, yet many areas remain poorly documented. Recent remote-sensing analyses based on airborne LiDAR data and deep learning have identified extensive areas of high canopy palm cover in the eastern Brazilian Amazon, particularly in remote forests associated with the Iriri River Basin in the state of Pará (Dalagnol et al. 2022). Biomass models developed specifically for palms suggest that their carbon fixation capacity may be nearly a third higher than estimates based on dicotyledonous trees (Goodman et al. 2013). In some forests, palms constitute up to 25% of stems exceeding 10 cm in diameter at breast height (Clark and Clark 2000), playing a crucial role in forest structure and succession (Boukili and Chazdon 2017). Unlike distinct biogeographical zones, tree composition in the Amazon changes gradually across vast areas, reinforcing the need to incorporate local-scale environmental information when describing patterns of species occurrence (Luize et al. 2024). Despite their ecological importance, insufficient knowledge from several regions across the Amazon still constrains our understanding of palm community composition and its spatial variation along environmental gradients.

Species distribution models (SDMs) are highly scale-dependent. Large-scale models tend to emphasize forest type and temperature (Eiserhardt et al. 2011; ter Steege et al. 2013, 2023), whereas meso- and fine-scale models highlight the importance of topographical, hydrological, and edaphic variables in explaining species composition at the plot level (Salm et al. 2015; Méndez-Toribio et al. 2017; Luize et al. 2024). Understanding how palm communities relate to local environmental gradients is essential given the ecological significance of palms in maintaining ecosystem services, their resilience to fire and climate change, and their role in supporting both animal biodiversity and human populations. While studies have focused on individual Amazonian palm species,

particularly those of commercial importance (de Alencar Pageú et al. 2023), community-level research remains limited because field surveys in the region are challenging. Consequently, large portions of the Amazon remain underrepresented in floristic meta-analyses, leading to gaps in knowledge about rare species. Documenting palm communities and their associations with local environmental heterogeneity in poorly sampled regions of Pará may improve our understanding of species distributions and provide a valuable baseline for future ecological studies in the Eastern Amazon.

In this study, we characterized the palm community of a remote area in the Eastern Amazon and described how species composition, richness, and abundance varied along local environmental gradients represented by remotely sensed variables related to forest structure, topography, and hydrography. We also provide the first description of a palm community for this poorly documented region, helping fill an approximately 500-km geographic gap in floristic information within an area of high predicted palm abundance in the state of Pará (Dalagnol et al. 2022). We aimed to characterize palm community structure and examine its associations with local environmental gradients related to forest structure, topography, and hydrography.

Because topography, hydrography, and forest structure can create local differences in habitat conditions and resource availability, we expected environmental heterogeneity to be associated with spatial variation in palm community structure. Therefore, we tested the hypothesis that local environmental heterogeneity, particularly variation in hydrographic conditions, forest structure, and topography, promotes spatial variation in palm diversity and community structure by creating habitats that differ in environmental suitability for palm species. In light of this hypothesis, we made the following predictions: (i) palm species richness would differ between plots subjected to contrasting hydrographic and topographic conditions; (ii) palm community composition would vary along environmental gradients associated with hydrography, forest structure, and topography; and (iii) dominant palm species would exhibit species-specific associations with local environmental variables, reflecting differences in habitat preference.

Material and methods

Study site

The field survey was conducted within the federally managed Riozinho do Anfrísio Extractive Reserve (hereafter, RESEX Riozinho), a 737,088-hectare natural reserve bounded on 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-height canopy (<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). The reserve has predominantly clay-rich podzolic soil, with mosaics of shallow, coarser soil and scattered rock outcrops (ICMBio 2010). The climate is classified as tropical wet (*Am* in the Köppen climate

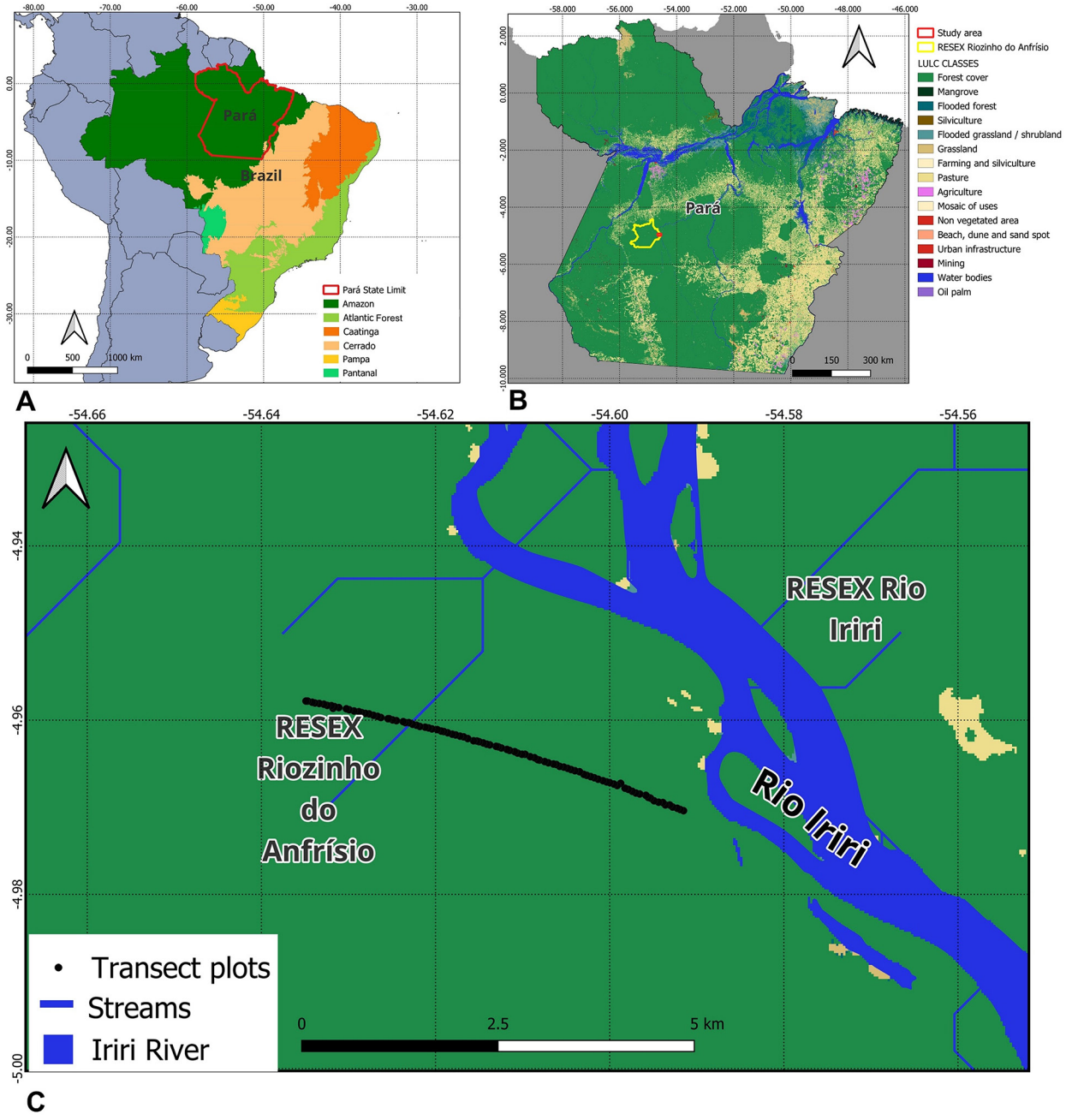

Figure 1. A. Location of the state of Pará within Brazil and the Brazilian ecodomains; **B.** Location of the Riozinho do Anfrísio Extractive Reserve (RESEX Riozinho) within the state of Pará; **C.** Location of the sampling units in RESEX Riozinho, Iriri River Valley, Eastern Amazon, Pará, Brazil. Only the main permanent hydrographic features are shown for geographic reference; small intermittent streams (igarapés) recorded during field surveys are not represented because of their local scale.

classification), with annual rainfall between 2000 mm and 2500 mm, mostly concentrated from December to April (Alvares et al. 2013). Altitude along the 5-km surveyed transect ranged from 193 to 241 m (mean = 215.57 ± 10.65 m; N = 100 plots), whereas elevations in the surrounding landscape ranged from 170 to 317 m. No roads or trails provide access to the study area, and it can only be reached by small motorboats departing from the nearest city, Altamira, over 400 km away. The journey requires about two days of navigation along the Xingu and Iriri rivers. Nevertheless, the study area lies a little more than 100 km to the south of the Trans-Amazon Highway and 150 km from the Cuiabá-San-

tarém Highway to the east, two of the main road corridors associated with deforestation in the Brazilian Amazon. The reserve's remoteness has contributed to the scarcity of floristic surveys in the region, highlighting the value of documenting its palm community.

Data sampling

The survey was conducted in May 2019, at the end of the rainy season, using a 5-km-long linear belt transect established specifically for a comprehensive palm inventory. Palm trees were recorded within a continuous 20-m-wide belt transect (10 m on each side of the central line), which was subsequently partitioned into 100 contiguous sampling units of 20 m × 50 m, with the end of each unit directly coinciding with the beginning of the next, totaling a sampled area of 10 ha. 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 at least two experienced observers. Adult palms located within the 20-m-wide sampling belt (i.e., up to 10 m on either side of the transect line) were recorded and identified to species level whenever possible using species descriptions from 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 sampling unit (20 m × 50 m segment), generating a binary variable, because these small streams are generally not visible in satellite imagery. These contiguous sampling units were used to characterize spatial variation in palm community composition and associated environmental conditions along the surveyed transect.

The centroid of each 20 m × 50 m sampling unit was later used to extract data from the digital elevation model (DEM) database TOPODATA (De Morisson Valeriano and De Fátima Rossetti 2012), from the Brazilian National Institute for Space Research (INPE), a country-wide resource derived from Shuttle Radar Topography Mission (SRTM) data (Jarvis et al. 2008) with a spatial resolution of 30 m, containing measures such as altitude, slope, relief, exposure, and terrain shape (Fig. 2). We extracted environmental variables from the centroid of each sampling unit, providing a standardized characterization of local environmental conditions. We used HydroSHEDS data to calculate the distance from each sampling unit to the nearest perennial stream as registered by the SRTM, which does not capture many of the small intermittent igarapés recorded during field surveys. As a proxy for forest structure, we extracted the normalized difference vegetation index (NDVI) for the centroid of each of the 100 sampling units using CBERS-4A satellite imagery and the method described by Ponzoni et al. (2012). In this study, NDVI was used as a proxy for vegetation greenness and forest structure. NDVI ranged from 0.597 to 0.662 (mean = 0.634 ± 0.014). The calculations of NDVI, topographic, and hydrological variables were conducted in QGIS 3.34 "Prizren" (QGIS 2024). Eight environmental variables were included in the analyses: three continuous (altitude in meters, distance to stream in meters, and NDVI), four categorical (slope, relief, exposure, and terrain shape), and one binary variable indicating the presence or absence of igarapé. The specific measurements and categories of the latter variables are presented in Suppl. material: table S1.

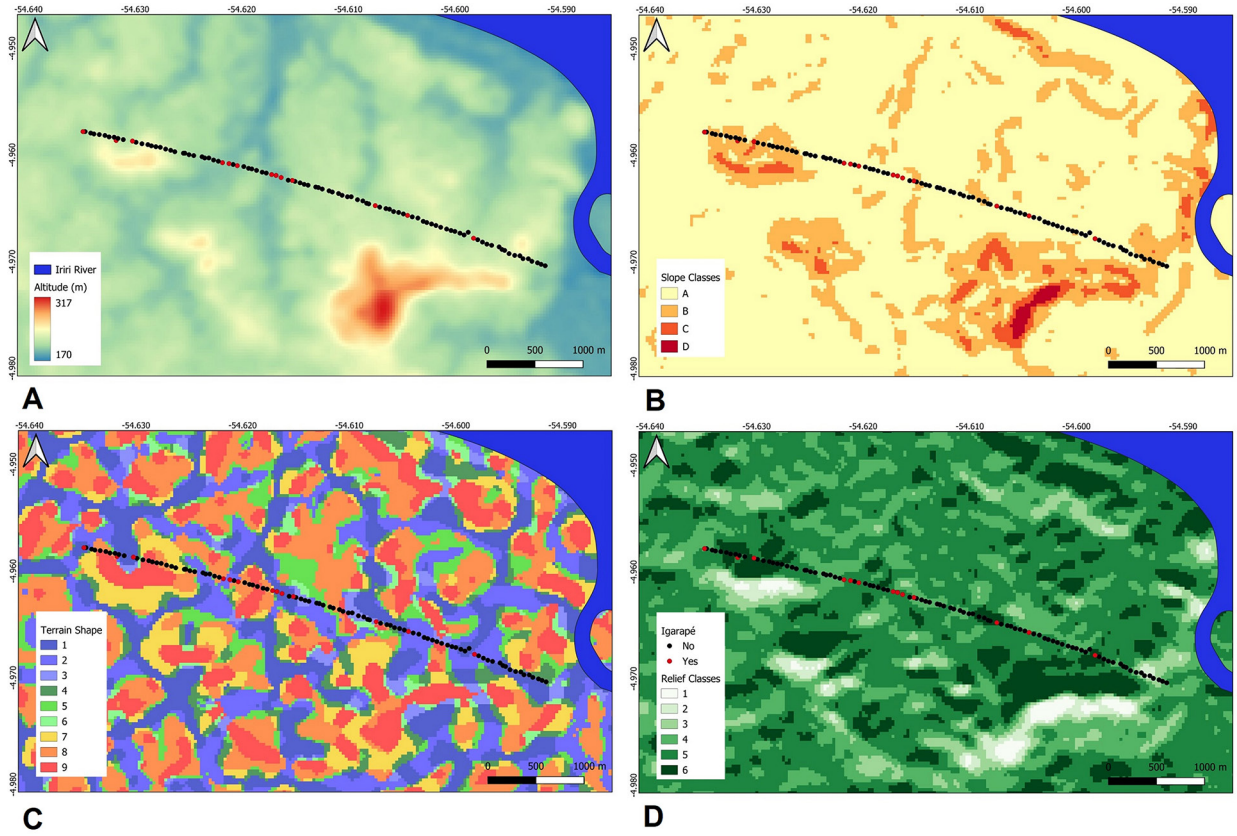

Figure 2. Examples of topographical data available in the TOPODATA project. **A.** Altitude; **B.** Slope classes: Flat (A); Moderate (B); Inclined (C); Steep (D); **C.** Terrain shape: Concave convergent (1); Concave neutral (2); Concave divergent (3); Flat convergent (4); Flat neutral (5); Flat divergent (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). All maps are at 30 m resolution; red dots indicate the presence of an *igarapé*.

Data analysis

Floristic and environmental data were summarized for the 100 contiguous 20 m × 50 m sampling units to characterize spatial variation along the 5-km transect. Species richness and abundance were calculated for each sampling unit, and environmental variables extracted from remote sensing databases were associated with the centroid of the corresponding sampling unit. All statistical analyses and graphs were produced in R (R Core Team 2025).

We calculated density per species by dividing the individual count in each plot by 0.1 ha, providing standardized density estimates per hectare. We used species richness to summarize local diversity patterns.

To describe associations between palm community composition and environmental gradients, we performed a Redundancy Analysis (RDA) using species abundance data and the continuous environmental variables NDVI, altitude, and distance to stream with the package "vegan" (Oksanen et al. 2022). We calculated Variance Inflation Factors (VIFs) to assess multicollinearity among predictor variables. We analyzed species richness using a Gaussian General Linear Model (GLM) for continuous environmental variables and an analysis of variance (ANOVA) for categorical environmental variables, and evaluated model assumptions by visually inspecting Q-Q plots of residuals. When ANOVA indicated

significant differences among categories, we performed pairwise comparisons using Tukey's Honestly Significant Difference (HSD) test with the "emmeans" package (Lenth 2024). Bayesian regression models were fitted for the six most abundant species (selected based on the total number of individuals recorded across the 100 sampling units) to explore species-specific associations with selected environmental variables while accommodating different response distributions, including zero-inflated count and presence/absence data. The six species were selected because their higher abundance provided sufficient observations across sampling units to investigate environmental associations, whereas the lower abundance of the remaining species limited the information available for reliable species-specific models. Bayesian R^2 values were calculated with "bayestestR" (Makowski et al. 2019).

Results

Sampling effort

The species accumulation curve approached an asymptote, corroborating sampling completeness (Suppl. material 1: fig. S1). Richness estimates obtained using the Chao (18 ± 0 SE), Jackknife 1 (18 ± 0 SE), Jackknife 2 (17.03), and Bootstrap (18.14 ± 0.34 SE) estimators closely matched the 18 recorded species, indicating that sampling effort was sufficient to document nearly the entire palm flora within the surveyed transect.

Species occurrence

Within the 10-ha transect, 1,506 palm individuals belonging to 18 taxa were recorded, including 17 species identified to species level and one morphospecies identified to genus (Table 1). Fourteen species were represented in the PalmTraits 1.0 database. Four species strongly dominated the community: *Attalea speciosa* Mart. (527 individuals; 85 plots), *Euterpe longibracteata* Barb. Rodr. (267 individuals; 56 plots), *Geonoma baculifera* Kunth (263 individuals; 11 plots), and *Euterpe oleracea* Mart. (105 individuals; 15 plots), which together accounted for more than three-quarters of all recorded individuals.

The remaining species occurred at considerably lower abundances. *Astrocaryum gynacanthum* Mart. (77 individuals) and *Astrocaryum aculeatum* (57 individuals) were moderately frequent, whereas the other species were sparsely distributed throughout the transect (Table 1). *Iriartea deltoidea* was represented by 37 individuals in eight plots, with local aggregations reaching up to 18 individuals within a single 0.1-ha plot. The rarest taxa included *Bactris dahlgreniana* Govaerts (seven individuals) and *Geonoma maxima* Kunth (two individuals). We recorded an additional morphospecies of the genus *Bactris* in six plots, totaling 11 individuals (Fig. 3).

Density and species richness

Palm density varied markedly along the surveyed transect, ranging from 0 to 860 individuals ha^{-1} (mean = 151.4 ± 143.13). The highest maximum densities were recorded for *Geonoma baculifera* (630 individuals ha^{-1}), *Euterpe longibracteata*

Table 1. Summary of field-collected data for the 18 Arecaceae species recorded in RESEX Riozinho, Iriri River Valley, Eastern Amazon, Pará, Brazil. Avg. = average; Ind. = individuals; No. = number.

Species	Field Data			
	No. of ind.	Occurrence (No. of plots)	Highest No. of Ind./ha	Avg. density per ha
Astrocaryum aculeatum	57	42	50	5.7
Astrocaryum gynacanthum	77	45	60	7.7
Astrocaryum murumuru	29	14	50	2.9
Attalea maripa	15	9	40	1.5
Attalea speciosa	527	85	270	52.7
Bactris acanthocarpa	19	11	40	1.9
Bactris dahlgreniana	7	7	10	0.7
Euterpe longibracteata	267	56	380	26.7
Euterpe oleracea	105	15	280	10.5
Geonoma baculifera	263	11	630	26.3
Geonoma maxima	2	2	10	0.2
Iriartea deltoidea	37	8	180	3.7
Oenocarpus bataua	30	11	90	3.0
Oenocarpus distichus	11	9	20	1.1
Oenocarpus minor	16	9	40	1.6
Socratea exorrhiza	20	12	50	2.0
Syagrus cocoides	13	10	30	1.3
Bactris sp.	11	6	40	1.1
Total individuals	**1506**			

(380 individuals ha^{-1}), *Euterpe oleracea* (280 individuals ha^{-1}), *Attalea speciosa* (270 individuals ha^{-1}), *Iriartea deltoidea* (180 individuals ha^{-1}), *Oenocarpus bataua* (90 individuals ha^{-1}), and *Astrocaryum gynacanthum* (60 individuals ha^{-1}). All remaining species exhibited maximum densities below 50 individuals ha^{-1}. Species richness ranged from 0 to 10 species per 0.1-ha plot (mean = 3.64 ± 1.90). One plot contained no palms and was excluded from subsequent analyses.

Redundancy analysis

Palm community composition was associated with variation in NDVI, altitude, and distance to streams, which together explained 17.82% of the observed variation (Suppl. material 1: table S2). The first constrained axis explained 81.84% of the constrained variation, followed by RDA2 (10.92%) and RDA3 (7.34%). Species scores (Suppl. material 1: table S3) indicated distinct associations between the dominant species and the measured environmental gradients. *Geonoma baculifera* was more closely associated with areas near streams, whereas *Attalea speciosa* was associated with lower NDVI values. *Euterpe longibracteata* and *Euterpe oleracea* also tended to occur in areas closer to streams. The remaining species occurred too infrequently for consistent patterns to be distinguished in the ordination. Plots containing igarapés were concentrated at lower elevations and generally exhibited lower NDVI values (Fig. 4).

The RDA model was significant, indicating that the observed associations between palm community composition and the measured environmental variables were unlikely to have occurred by chance (permutation ANOVA: $F_{3,95}$ = 6.868,

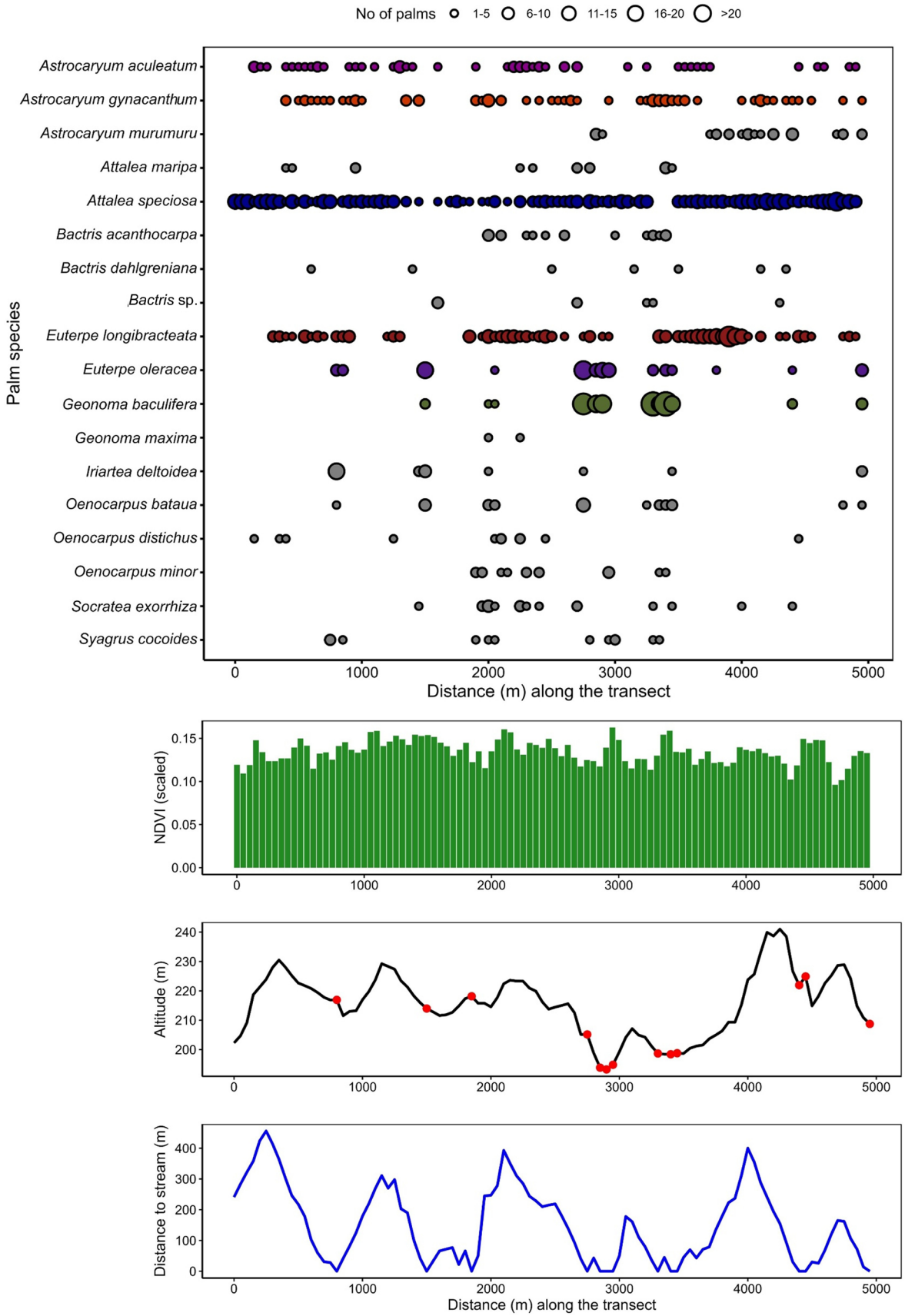

Figure 3. Spatial distribution of the Arecaceae community in RESEX Riozinho, Iriri River Valley, Eastern Amazon, Pará, Brazil. Colored circles represent the six most abundant species. Red dots on the altitude profile indicate igarapé presence. NDVI values are shown on a rescaled axis for visualization purposes.

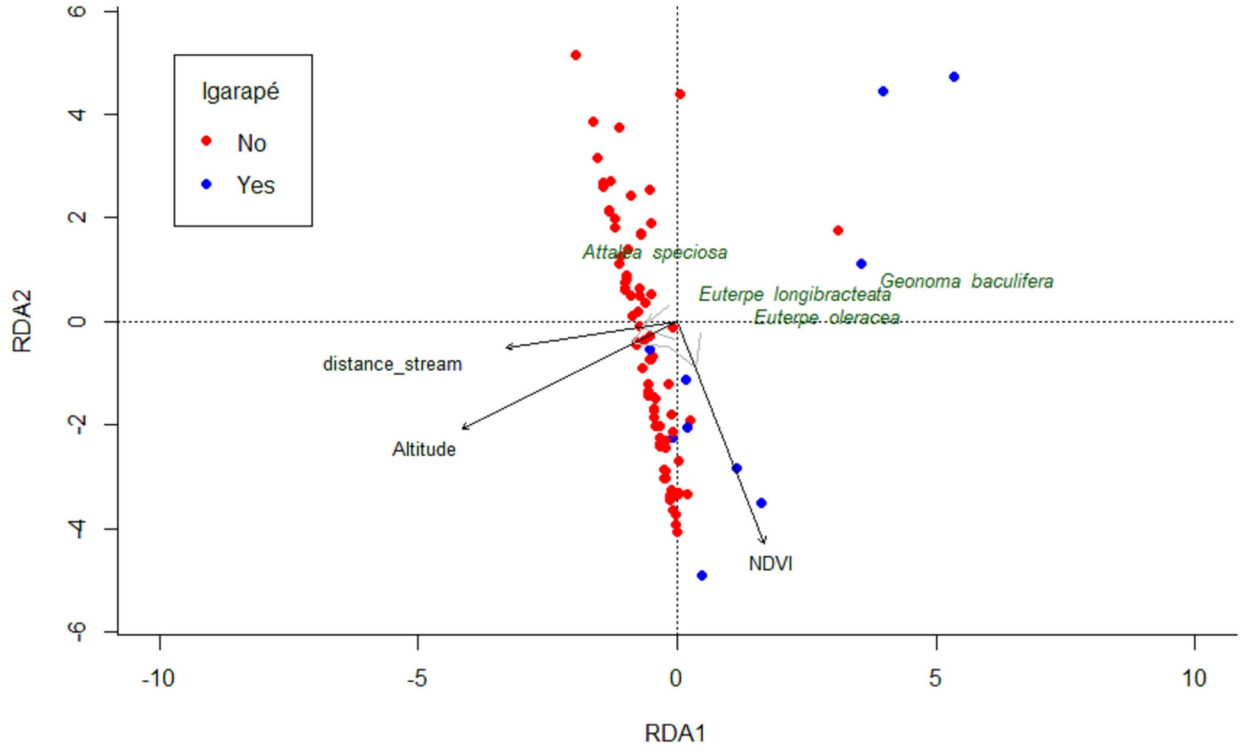

Figure 4. Redundancy analysis (RDA) biplot showing associations between the Arecaceae community and environmental variables in RESEX Riozinho, Iriri River Valley, Eastern Amazon, Pará, Brazil. Sampling units containing an igarapé are indicated. Only the four most abundant species are displayed, namely *Attalea speciosa*, *Euterpe longibracteata*, *Geonoma baculifera*, and *Euterpe oleracea*, because these species best allow visualization of the main patterns associated with the environmental gradients. The RDA was performed using all species recorded in the study, and species scores for all species included in the analysis are presented in Suppl. material 1: table S3.

P = 0.014; 999 permutations). Variance Inflation Factors (VIFs) were all below 10, indicating no evidence of problematic multicollinearity among the predictor variables (Suppl. material 1: table S4).

Effects of continuous environmental variables on species richness

Model validation

Visual inspection of the Q-Q plot indicated that residuals closely followed the theoretical normal distribution, with no substantial deviations from normality (Suppl. material 1: fig. S2). This supported the adequacy of the Gaussian error structure assumed by the General Linear Model and indicated that model assumptions were satisfactorily met for subsequent inference.

General Linear Model

Species richness was not significantly associated with NDVI, altitude, or distance to stream, indicating that none of the continuous environmental variables influenced palm species richness along the surveyed transect (Gaussian General Linear Model: NDVI: t = 0.285, P = 1.000; altitude: t = –2.588, P = 0.11; distance to stream: t = –2.662, P = 0.10). The model explained a relatively small proportion of the observed variation (Nagelkerke pseudo-R^2 = 17.2%).

Effects of categorical environmental variables on species richness

Species richness was significantly higher in plots containing igarapés than in plots without them (estimated marginal means = 2.07 and 1.56, respectively; ANOVA: $F_{1,79}$ = 16.060, P = 0.0022), indicating a positive association between the presence of igarapés and palm species richness (Suppl. material 1: tables S5, S6). Slope inclination also showed a significant overall effect on species richness (ANOVA: $F_{3,79}$ = 5.024, P = 0.039), although no pairwise comparison remained significant after Tukey adjustment, indicating relatively weak differences among slope classes (Suppl. material 1: tables S5, S6). Terrain shape was significantly associated with species richness (ANOVA: $F_{8,79}$ = 3.782, P = 0.0126). Pairwise comparisons indicated higher species richness in convex, water-divergent areas than in both flat, water-convergent and flat, water-divergent areas, whereas concave, water-neutral areas also exhibited higher richness than flat, water-convergent and flat, water-divergent areas (Suppl. material 1: tables S5, S6; Fig. 5). The ANOVA model explained 50.0% of the observed variation in species richness (adjusted R^2 = 47.3%).

Habitat characteristics related to abundant species

Bayesian regression models identified distinct associations between habitat characteristics and the six most abundant palm species (Table 2). NDVI, igarapé presence, and terrain shape were the environmental variables most frequently associated with species distribution, although the strength and direction of these relationships varied among species. Model structure was selected according to the distribution of each response variable (Table 2).

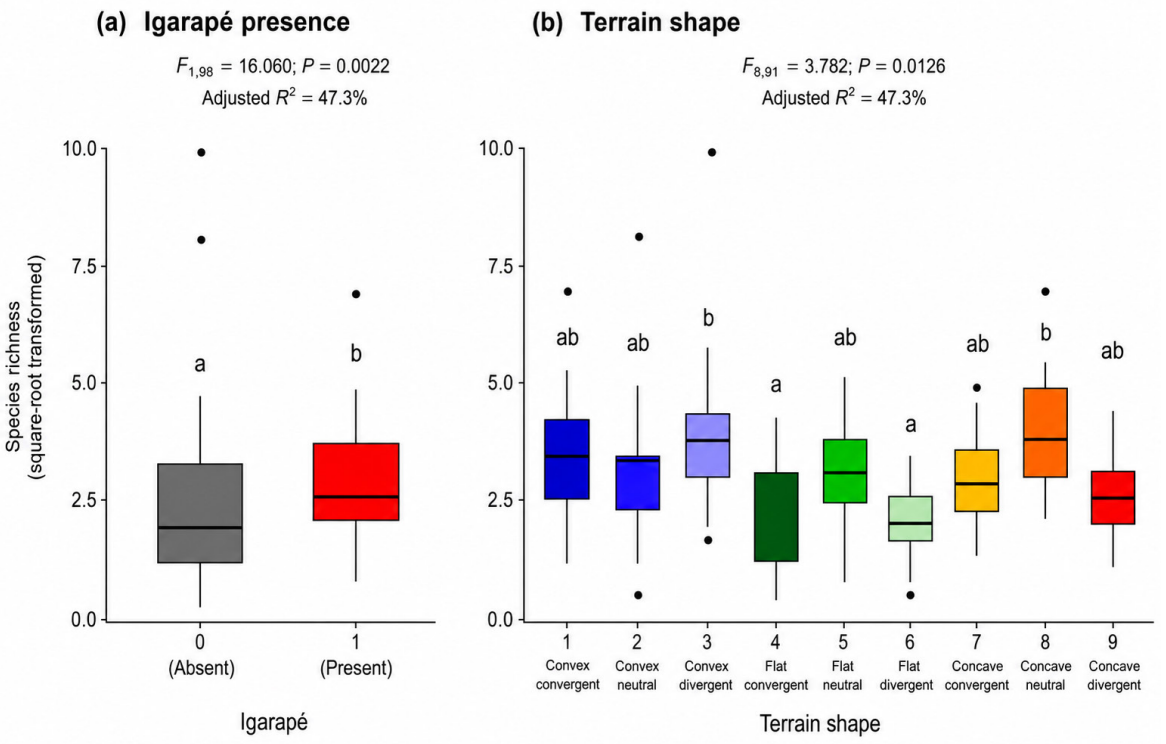

Figure 5. Effects of igarapé presence and terrain shape on Arecaceae species richness in the Riozinho do Anfrísio Extractive Reserve, Eastern Amazon, Pará, Brazil. Boxes represent the interquartile range (IQR), whiskers extend to 1.5 × IQR, thick horizontal lines indicate the median, and dots represent outliers. Groups followed by the same letters do not differ significantly from each other (ANOVA followed by Tukey's post hoc test, α = 0.05).

Table 2. Summary of the Bayesian regression models explaining the distribution of the six most abundant Arecaceae species in the Riozinho do Anfrísio Extractive Reserve, Iriri River Valley, Eastern Amazon, Pará, Brazil. Predictors were NDVI (continuous), terrain shape (categorical), and igarapé presence (binary). A positive sign under "Potential effects" indicates higher abundance or probability of species occurrence, whereas a negative sign indicates lower abundance or probability of occurrence.

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 gynacanthum	Logistic	NDVI, Shape	NDVI (-), Shape6 (-), Shape8 (+)	0.24
Astrocaryum aculeatum	Logistic	NDVI, Shape	NDVI (+), Shape6 (-), Shape7 (-)	0.18

Habitat characteristics related to abundant species

Among the six most abundant palm species, *Attalea speciosa* showed the strongest associations with the measured environmental variables. Its expected abundance decreased with increasing NDVI and was lower in plots containing igarapés, indicating a preference for areas with lower vegetation greenness and away from streams (Bayesian R^2 = 0.36; Suppl. material 1: table S7).

The distributions of *Geonoma baculifera* and *Euterpe oleracea* were both positively associated with the presence of igarapés, exhibiting substantially higher expected abundance in riparian plots (Bayesian R^2 = 0.46 and 0.50, respectively; Suppl. material 1: tables S9, S10). Although both models included NDVI, its estimated effects were uncertain because the 95% credible intervals overlapped zero.

For *Euterpe longibracteata*, terrain shape showed stronger associations than NDVI, with higher expected abundance in specific topographic positions, whereas the effect of NDVI remained uncertain because its credible interval overlapped zero (Bayesian R^2 = 0.46; Suppl. material 1: table S8).

Models for *Astrocaryum gynacanthum* and *A. aculeatum* showed comparatively low explanatory power (Bayesian R^2 = 0.24 and 0.18, respectively) and broad credible intervals, indicating substantial uncertainty in the estimated environmental associations (Suppl. material 1: tables S11, S12). Detailed model outputs are provided in Suppl. material 1: tables S7–S12, and the strongest associations identified by the Bayesian models are illustrated in Fig. 6.

Discussion

Our survey revealed the marked dominance of *Attalea speciosa* in the palm community of the Iriri River Valley, reaching an average density of 52.7 individuals ha^{-1} and local densities of up to 270 adult individuals ha^{-1} within a single sampling plot. This species was consistently associated with lower NDVI values, indicating a greater occurrence in relatively more open forest patches along the surveyed transect, consistent with previous studies showing that large arborescent *Attalea* species are frequently associated with more open forest structures and natural disturbance regimes (Salm et al. 2005). Although the present study did not directly evaluate the mechanisms underlying this distribution, the high local abundance of *A. speciosa* may reflect a combination of environmental conditions and the historical land-use legacy previously documented for this region.

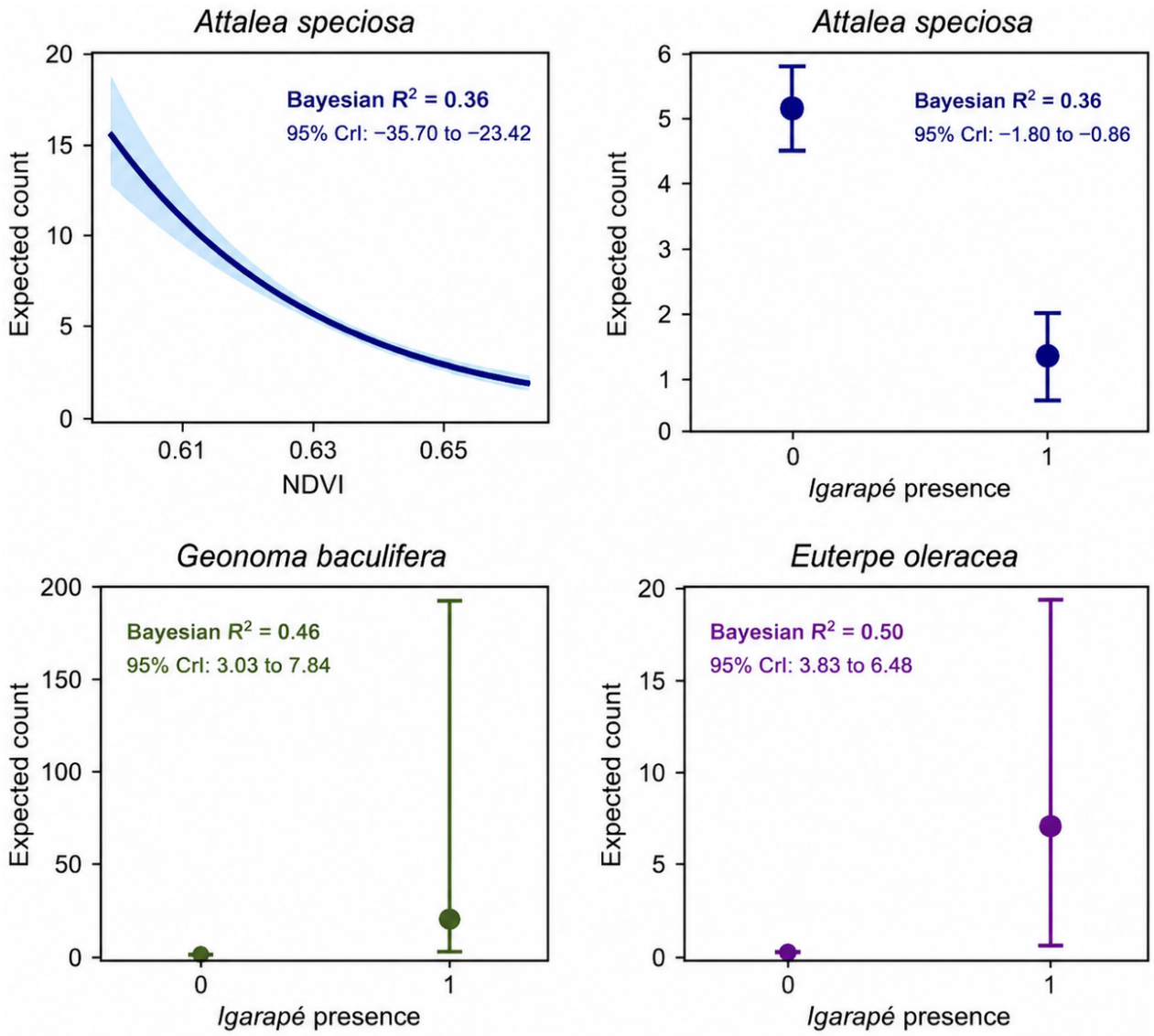

Figure 6. Marginal effects of Bayesian regression models showing the four strongest palm–environment associations identified in the Riozinho do Anfrísio Extractive Reserve, Iriri River Valley, Eastern Amazon, Pará, Brazil. Panels show the effects of NDVI and igarapé presence on the expected abundance of *Attalea speciosa*, and the effects of igarapé presence on the expected abundance of *Geonoma baculifera* and *Euterpe oleracea*. Shaded areas represent 95% credible intervals. In interval graphs, bars indicate credible intervals and dots represent posterior means.

The high abundance of *Attalea speciosa* in the study area may reflect multiple, non-exclusive drivers shaping forest composition. This interpretation is supported by the species' high density, a species widely recognized for its ecological and economic importance and valued for numerous industrial applications (Lima et al. 2024). The association of *A. speciosa* with lower NDVI values suggests a preference for relatively more open forest patches, consistent with disturbance-driven environments shaped by both natural and anthropogenic processes. A similar pattern has been reported in the neighboring RESEX Rio Iriri, on the opposite bank of the Iriri River, where *A. speciosa* was also hyperdominant and associated with historical forest disturbance (Smith 2015). In that area, archaeological evidence indicates that this disturbance dates to Indigenous occupation during the eighteenth century, suggesting that the present-day dominance of the species may reflect a long-term anthropogenic legacy rather than recent extractive

activities by the beiradeiros, whose resource use is regulated within the reserve (Balée et al. 2020). In the present study area, however, the relative contributions of natural disturbance regimes and historical human influence remain uncertain, and both may have contributed to the current dominance of the species.

Palm richness in RESEX Riozinho, with 17 identified species and one additional morphospecies identified to genus level, was higher than in the two other areas previously surveyed along the eastern margin of the Xingu Basin. At the Kayapó Indigenous Territory, approximately 400 km southwest of RESEX Riozinho, ten Arecaceae species were recorded (Salm et al. 2007), whereas eleven species were found near the city of Altamira, Pará (Salm et al. 2015). This pattern is consistent with the broader westward increase in palm diversity observed across Amazonia, which has been associated with large-scale environmental gradients, particularly increasing rainfall toward central and western Amazonia (Alvez-Valles et al. 2018; Muscarella et al. 2020). Nevertheless, the richness documented at RESEX Riozinho reinforces the importance of surveying remote and poorly sampled regions to improve our understanding of palm diversity patterns across Amazonia.

The Redundancy Analysis (RDA) indicated that variation in palm community composition was associated with NDVI, altitude, and distance to streams, although these variables together accounted for only 17.8% of the observed variation between plots. Plots containing igarapés tended to occur at lower elevations and exhibited lower NDVI values, reflecting the environmental characteristics of these riparian habitats. These findings partially support our hypothesis that local environmental heterogeneity promotes spatial variation in palm diversity by creating habitats with differing environmental suitability for palm species. As predicted, palm community composition varied along local hydrographic, topographic, and forest-structure gradients, indicating that environmental heterogeneity contributes to shaping species distribution within the surveyed landscape. The relatively low proportion of explained variation suggests that additional environmental factors not evaluated in this study, such as edaphic properties, disturbance history, or other sources of local environmental heterogeneity, may also contribute to the observed spatial variation in palm community composition. Similar patterns have been reported for Amazonian forests at broader spatial scales. For example, in a study of tree diversity across 2,046 plots throughout Amazonia, location and forest type explained approximately 70% of the variation in floristic composition, whereas a model including only environmental variables, such as cumulative water deficit, tree density, and temperature, explained 47% of the variation in tree species richness in terra firme forests (ter Steege et al. 2023). Together, these findings indicate that local environmental gradients account for only part of the observed spatial variation in palm community composition, highlighting the complexity of ecological processes operating in Amazonian forests.

The influence of topography and hydrography on arborescent palms is well established (Svenning et al. 2009; Salm et al. 2015), and edaphic factors are associated with Arecaceae community structure through soil macronutrient availability (Cámara-Leret et al. 2017). Soil physical properties affect basal area, with palms dominating weakly structured soils, whereas other trees are more affected by species turnover and rainfall (Emilio et al. 2014). Topography influences soil composition through altitude, exposure, slope, and terrain shape, affecting erosion, organic carbon, and macronutrient availability, which have been associated with patterns of species distribution (Måren et al. 2015). In our study,

palm community composition was associated with NDVI, altitude, and distance to streams, whereas species richness showed stronger associations with the presence of igarapés and terrain shape. The concentration of plots containing igarapés at lower elevations and lower NDVI values further highlights the importance of local hydrographic heterogeneity in structuring palm communities along the surveyed transect. Together, these results partially support our hypothesis that local environmental heterogeneity promotes spatial variation in palm diversity by creating habitats differing in environmental suitability for palm species. These findings are consistent with previous studies showing that several Amazonian palm species are closely associated with riparian habitats and seasonally wet environments (Kahn and Castro 1985; Salm et al. 2015).

Species richness was not significantly associated with NDVI, altitude, or distance to streams, but was significantly associated with igarapé presence and terrain shape. The stronger association with field-recorded igarapés than with HydroSHEDS-derived stream distance suggests that small watercourses recorded during fieldwork better represent local hydrographic conditions than remotely sensed perennial streams (Lehner et al. 2008). Plots containing igarapés exhibited higher species richness, with *Geonoma baculifera* and *Euterpe oleracea* being particularly associated with these habitats. In contrast, flat, water-convergent terrains exhibited lower richness, whereas concave, water-divergent and convex, water-neutral terrains supported higher richness. These patterns are consistent with previous studies showing that many Amazonian palm species are associated with riparian habitats and local topographic variation, although responses differ among species according to their ecological requirements (Kahn and de Granville 1992; Muscarella et al. 2020).

At the Iriri site, *Geonoma baculifera* formed dense clusters, reaching local densities of up to 630 individuals ha^{-1}, similar to those reported for seasonally flooded sandy soils throughout the eastern Amazon, where densities may exceed 700 individuals ha^{-1} (Kahn and de Granville 1992). *Euterpe oleracea* was also locally abundant, reaching densities of up to 280 individuals ha^{-1}, consistent with its recognition as one of the hyperdominant palm species in Amazonian forests (ter Steege et al. 2013). Two widespread palms of the Xingu River Basin, *Socratea exorrhiza* and *Oenocarpus bataua* (Salm et al. 2007, 2015), were also recorded in RESEX Riozinho. *Socratea exorrhiza* is well known for its adaptation to seasonally flooded soils through its characteristic stilt roots, giving rise to the common name "walking palm" (Kahn and de Granville 1992; Smith 2015), whereas *O. bataua* is widely distributed in seasonally flooded forests up to 1,400 m elevation and has long been associated with Indigenous management and dispersal (Kahn et al. 1988; Smith 2015). Although both species rank among the most abundant trees in Amazonia (ter Steege et al. 2013), they occurred at comparatively low abundance in the present study, indicating that their regional dominance is not necessarily reflected at the local scale. Finally, the occurrence of *Iriartea deltoidea* in the study area extends the documented distribution of the species within the eastern Amazon and further highlights the importance of floristic surveys in remote and poorly sampled regions of Pará. Given that *I. deltoidea* is among the most abundant Amazonian tree species, despite having been recorded in relatively few floristic inventories (ter Steege et al. 2013, 2023), its occurrence emphasizes the value of continued botanical inventories for improving our understanding of species distributions across the Amazon.

The Bayesian analyses further highlighted differences in the associations between the dominant palm species and local environmental characteristics along the surveyed transect, reinforcing the ecological heterogeneity of the study area (Svenning 1999). *Attalea speciosa* showed the strongest association with plots with lower NDVI values and located away from igarapés, whereas *Euterpe longibracteata* was more frequently associated with less dense forest and flat water-neutral or convex water-convergent terrain. In contrast, *Geonoma baculifera* and *Euterpe oleracea* were consistently associated with plots containing igarapés, reflecting their affinity for riparian environments. Associations involving *Astrocaryum gynacanthum* and *A. aculeatum* were less consistent, with broad credible intervals and lower explanatory power, and should therefore be interpreted cautiously. These findings corroborate our prediction that dominant palm species would exhibit species-specific associations with local environmental variables, reflecting differences in habitat preference. Overall, these results agree with previous studies showing that Amazonian palm species differ markedly in their associations with local environmental heterogeneity, particularly in relation to hydrographic conditions and topographic variation (Svenning 1999; Kahn and de Granville 1992; Salm et al. 2015). In addition, recent evidence indicates that palms exhibit substantial functional variation, with differences in specific leaf area (SLA) between understory and canopy species and changes in SLA with plant size, reflecting differences in resource-use strategies (Avalos et al. 2025). These functional differences may contribute to the ability of palm species to occupy contrasting environmental conditions and may help explain the species-specific associations with local environmental gradients observed in our study.

These associations are consistent with the habitat preferences previously reported for these species (Kahn and de Granville 1992; Smith 2015) and provide additional information on their local distribution in a poorly sampled region of the eastern Amazon. The high abundance of palms documented in this study, particularly the marked dominance of *Attalea speciosa*, is also consistent with the prediction of Dalagnol et al. (2022) that the Iriri River region would harbor high densities of large arborescent palms. This information may contribute to future ecological studies, restoration initiatives, and agroforestry projects involving native palms. Because several palm species have been proposed as indicators or surrogates of biodiversity (Svenning et al. 2009; Menger et al. 2024), describing their local environmental associations may also improve their application in conservation planning, although further studies with replicated sampling designs are needed to confirm species-specific habitat requirements (Ritter et al. 2019).

Conclusions

This study provides the first characterization of a palm community in a remote sector of the Iriri River Valley, documenting high palm richness and abundance in a region that has remained poorly sampled. Palm community composition was associated with local environmental heterogeneity, particularly variation in NDVI, altitude, and proximity to igarapés, whereas species richness showed stronger associations with local hydrographic and terrain characteristics. Together, these findings partially support our hypothesis that local environmental heterogeneity promotes spatial variation in palm diversity by creating habitats differing in environmental suitability for palm species. As predicted, environ-

mental heterogeneity influenced palm community composition and the distribution of dominant species, whereas species richness responded primarily to hydrographic and topographic characteristics. Because these patterns were documented along a single continuous transect, they should be interpreted as spatial associations within the surveyed landscape rather than as general ecological relationships for the eastern Amazon. Nevertheless, this inventory provides an important floristic baseline for one of the least-studied regions of Pará and highlights the value of additional botanical surveys and replicated ecological studies to improve our understanding of palm diversity and distribution across Amazonia.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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Author contributions

Rodolfo Salm conceived the ideas; Rodolfo Salm, Dilaílson Araújo de Souza, Angelino Pereira de Oliveira Jr collected the data used in this manuscript; Karin Elisabeth von Schmalz performed the analyses; Cássio Cardoso Pereira and Karin Elisabeth von Schmalz made the figures; Cássio Cardoso Pereira led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

Supplementary material 1

Supplementary tables and figures

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