Forest Ecology and Management 619 (2026) 124066

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Palm assembly dynamics and its relationship with topography in terra firme forest in the Central Amazon

Paulo Rodrigues de Melo Neto [a,c,*], Milla de Freitas Oliveira [b,c], Ocírio de Sousa Pereira [c], Aldicir Osni Scariot [d], Andrew James Henderson [e], Manoel Augusto Whitaker Pacheco [1], José Luís Campana Camargo [c,f]

[a] Brazilian Agricultural Research Corporation (Embrapa Western Amazon), PO Box 319, Manaus, AM 69010-970, Brazil
[b] Ecology Graduate Program, National Institute for Amazonian Research (INPA), Manaus, AM, Brazil
[c] Biological Dynamics of Forest Fragments Project (BDFFP), National Institute for Amazonian Research (INPA), PO Box 478, Manaus, AM 69067-375, Brazil
[d] Brazilian Agricultural Research Corporation (Embrapa – Cenargen), PO BOX 2372, Brasília, DF 70770-900, Brazil
[e] New York Botanical Garden (NYBG), New York, NY – 10458, USA
[f] Coordination of Biodiversity, National Institute for Amazonian Research (INPA), PO Box 478, Manaus, AM 69067-375, Brazil

ARTICLE INFO

Keywords:
Arecaceae
BDFFP
Community ecology
Directional changes
Forest dynamics
Tropical rainforest

ABSTRACT

In recent years, studies have reported changes in the structure of different taxonomic groups in tropical forests without any apparent environmental disturbances. Changes in forest phytosociology, climate change, or even stochastic variation may be responsible for the observed results. Factors such as topography may mitigate or amplify these effects. We analyzed the long-term dynamics of an assembly of palm species in a 10-ha permanent plot within a continuous, mature forest in the Central Amazon. A previous census was conducted in 1990. As previously, all newly found adult palms were marked, identified, and classified by forest strata. Thus, we evaluated assembly dynamics overall and by strata, considering abundance, composition, and beta diversity. All parameters were contrasted with topography. We recorded 33 palm species, three more species than in 1990, and an impressive increase in abundance. Even with 1/3 of mortality, the net increase of the assembly was almost 50%, revealing a dramatic change in density from around 650 to almost 1000 adult palms per hectare. Mortality among the sub-canopy palm trees was more pronounced than for other strata. Meanwhile, the forest's understory presented the highest diversity. Species gain over time drove changes in the assemblage composition. Regarding topography, elevation influenced species distribution, while slope affected understory and assemblage dynamics. Thus, changes in the palm assemblage showed that even in forests considered preserved, certain groups are undergoing structural changes, which may be related to internal assemblage factors or external drivers, such as climate change and stochastic effects.

1. Introduction

Long-term studies in undisturbed tropical forests have recorded changes in the composition and function of different taxonomic groups (Costa et al., 2020; Laurance et al., 2014; Brice et al., 2019). At broad temporal scales, even small local changes in demographic rates can alter the balance between gains and losses of local species, thereby altering community composition (Brice et al., 2019; Esquivel-Muelbert et al., 2019). In the Amazon, records of structural and compositional changes in some groups, such as trees and lianas, have been observed in continuous, mature forests without anthropogenic disturbance (Laurance et al., 2014; Costa et al., 2020).

A close look at factors such as topography and soil types can reveal differences in species responses, even among congeneric species (Gleason, 1926; Esquivel-Muelbert et al., 2019; Piovesan et al., 2022). Therefore, data from long-term series in permanent plots can provide qualitative information at the species level. Precise taxonomic identification is also fundamental, given the high biological diversity in tropical forests. However, a taxonomically diverse group, apparently easily identifiable and occupying practically all forest strata and various

* Corresponding author at: Brazilian Agricultural Research Corporation (Embrapa Western Amazon), PO Box 319, Manaus, AM 69010-970, Brazil.
E-mail address: paulorodrigues.melo@embrapa.br (P.R. Melo Neto).
[1] In memorian

https://doi.org/10.1016/j.foreco.2026.124066
Received 2 April 2026; Received in revised form 23 June 2026; Accepted 29 June 2026
Available online 16 July 2026

topographic levels, is the palm family (Arecaceae), making it attractive to assess how environmental variables may affect species within the same group.

Palms have a wide distribution and are abundant and diverse, mostly in tropical zones. In the Amazon Basin, palms exhibit higher diversity and density, particularly in the western region (Scariot, 1996; Alvez-Valles et al., 2018). They are essential to the taxonomic, functional, structural, and ecological relationships within various Amazonian ecosystems (Kahn and Castro, 1985; Vormisto, 2002; Souza et al., 2020). Also, palms are a fundamental food source for native fauna and people (Peres, 2000).

Given the multiple importance of palms, one of the most abundant organisms in the Amazon Forest, it is relevant to understand how their assembly is structured. Such information may provide crucial clues about the group's importance in the Amazonian forestry system (Ter Steege et al., 2013; Olivares et al., 2017).

However, considering the assembly itself, examining how some environmental factors, such as topography, may contribute to the structure of the palm assembly is essential. Topographic gradients are strongly associated with hydromorphic variations in soil, a source of environmental heterogeneity that influences palm assembly composition and structure (Kahn and Castro, 1985; Vormisto, 2002; Browne and Karubian, 2016). For instance, heavy rain can lead to stream overflow even in upland forests, flooding adjacent areas. Variation in terrain elevation within small-scale gradients controls the length during which plants are subject to inundation, leading to differential mortality among species less tolerant to flooding (Pacheco, 2001).

In general, the valleys of Central Amazon upland forests are characterized by narrow streamside areas (Kahn and Castro, 1985; Costa et al., 2020), where palms are a prominent part of the forest structure, composing the canopy and understory (Kahn and Castro, 1985). Nevertheless, in higher-elevation areas with well-drained soils, known as plateaus, or on the slopes between plateaus and valleys, most palms are in the understory, and only a few reach the canopy or subcanopy (Vormisto, 2002; Clark et al., 1995).

Most studies on palm assemblies focus on how environmental and ecological factors affect the distribution of adult individuals (Rodrigues et al., 2014). Only a few studies have monitored palms over extended periods. In this context, we identified a unique opportunity to assess how the abundance and species composition of a palm assemblage and its vertical strata vary over time, and which factors (e.g., topography) may affect these parameters over long periods.

Therefore, this study aimed to evaluate how, after 30 years, the structure and composition of a palm assembly in a pristine terra firme (no-flooded) forest in the Central Amazon may change, and how these changes may be related to the position of the palm species within the forest vertical profile. Also, how the terrain's topography may affect the assembly. Specifically, we asked: 1) Have there been changes in phytosociological parameters (abundance and density) and composition (number of species and evenness) for the assembly as a whole and the forests' strata (understory, mid-story, or sub-canopy)?; and 2) How are the palm assembly configured in terms of the position of individuals in a topographic gradient, for the assembly as a whole, but also considering the forests strata (understory, mid-story, or sub-canopy)?

We hypothesized that the palm assembly must have changed over time, at least in its structure, but not necessarily in its composition. As for large trees facing extreme climatic events, we anticipate that arborescent palms in the sub-canopy or canopy should also present higher mortality. In contrast, understory palms may be favored by greater light penetration into the forest understory following increased tree mortality and gap formation. Changes in the light regime may promote higher reproduction, consequently higher fruit and seed production, and, in turn, seedling establishment and population growth.

Moreover, we expect that most species will be restricted to specific portions of the topographic gradient. Considering the assemblage as a whole, we expect greater variation in palm dynamics within valleys, in terms of beta diversity (abundance and composition), whereas greater stability should be observed on plateaus and slopes. In this scenario, topography is expected to be more strongly associated with understory palms, given their predominance in valleys.

2. Materials and methods

2.1. Study area

The study was conducted at the Km 41 reserve (02º 24' S and 59º 44' W), one of the study sites of the Biological Dynamics of Forest Fragments Project (ARIE BDFFP) (Fig. 1). The reserve covers 10,000 ha of continuous forest, part of a much larger forest continuum (Bierregaard et al., 1992). According to the Köppen-Geiger classification, the climate is type Am and Af, both humid tropical and monsoonal (Kottek et al., 2006). There is a rainy season from November to May, and a well-defined drier season, with up to 100 mm per month, from June to October. The average annual temperature is 26.7 ºC, and annual precipitation ranges from 1900 to 2500 mm (Laurance et al., 2010).

The terrain consists of small plateaus characterized by elevated, flat surfaces, often with long, gentle slopes that end in steep connections to narrow valleys where small first-order streams flow. A dense drainage network crisscrosses the region (Laurance et al., 2010; Pacheco, 1999). The terrain's elevation ranges from 40 to 100 m above sea level (Fig. 2).

Abiotic conditions between plateaus and valleys vary, with a pedological gradient (Fig. 2). The soil is clayey on plateaus and on rare occasions experiences temporary flooding in some terrain depressions, mainly at the end of the rainy season. Canopy light penetration is generally less intense and depends on canopy openings created by fallen trees (Pacheco, 2001). In valleys, soil is sandier, with, on average, higher water potential and a higher phosphorus concentration. Areas adjacent to streams are generally flooded after heavy rains, and the canopy is more open, allowing high-intensity light penetration (Pacheco, 1999). A dense terra firme forest type characterizes the vegetation, and the forest vertical profile can be classified into five strata: understory, mid-story, sub-canopy, canopy, ranging from 25 to 35 m, and emergent trees reaching up to 45 m (Albiero-Júnior et al., 2021). The forests of Central Amazon are among the most biodiverse in the world. In the permanent plots of the BDFFP, ca. 280 spp. per ha of trees (DBH $>$10 cm) were recorded (Laurance et al., 2017), along with about 160 spp. per ha of lianas (stems $\geq$ 2 cm diameter) (Piovesan et al., 2022) and ca. 30 palm spp. per ha (considering only adults; this study), dominated by stemless palms (Scariot, 1999).

2.2. Palm census

In the late 1980s, a 100-ha permanent plot (1000 x 1000 m) was established in the Km 41 reserve to study the ecology and systematics of the Lecythidaceae family, half was designed to study the Sapotaceae family, and a 10-ha strip (1000 $\times$100 m) was designated to study the Arecaceae family. Within the plot, a grid with stakes every 20 m was established, and thus, a 20 x 20 m area was used as a sample unit (see Mori and Becker 1991).

Concomitantly, a meticulous topographic survey was realized in the area, and elevation data were recorded every 5 m (Garcia, 2000). Thus, the terrain elevation was calculated as the average of the 25 points observed in each sample unit (20 x 20 m), and the slope was obtained from the elevation at the four corners of the area. The percentage elevation difference between these points was estimated, and the arctangent of this slope percentage was then calculated, yielding the slope in degrees.

A botanical inventory of palms was conducted in 1988 and 1989 (Henderson et al., 2000; Pacheco, 2001). All adult palms were located, mapped, identified, and uniquely numbered with aluminum tags placed on each individual (Garcia, 2000). In 2020, after 30 years, we conducted a new palm census in the area. No disturbances or degradation, such as

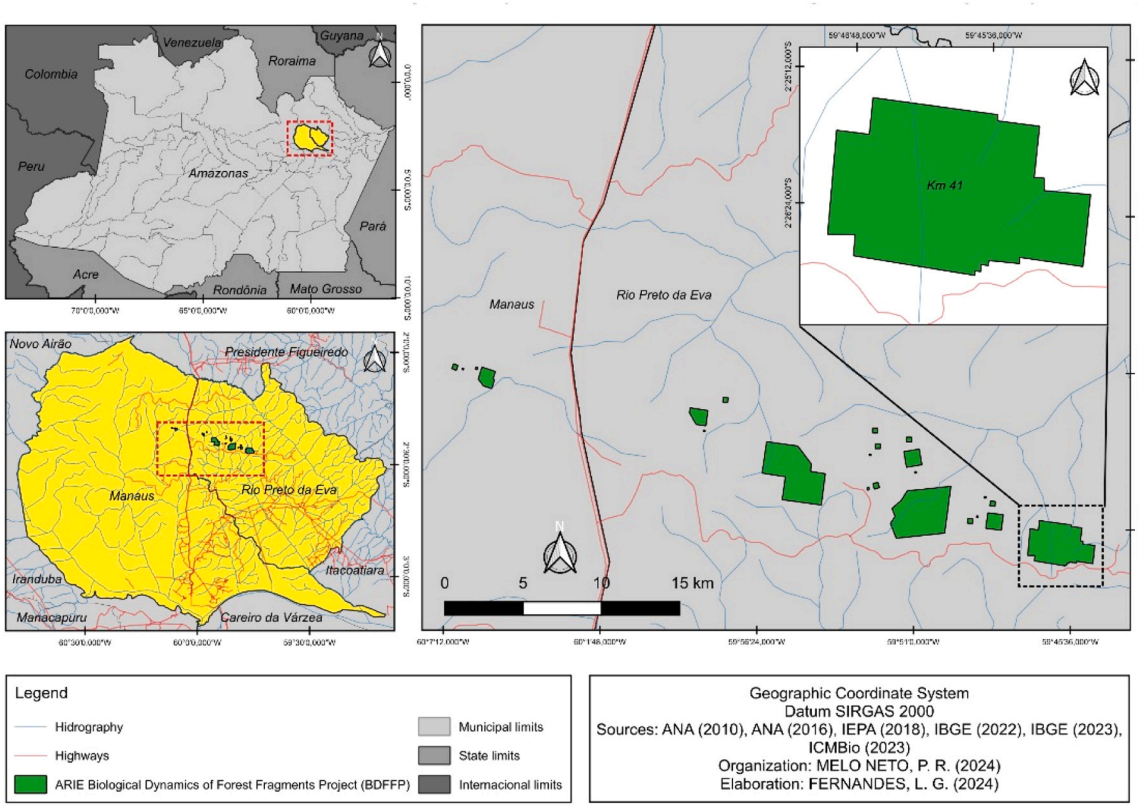

Fig. 1. Location map of the permanent plot in the KM 41 Reserve (BDFFP-INPA) in terra firme forest type in Central Amazon, approximately 100 km North of Manaus. On the top right is the state of Amazonas in northern Brazil, with a yellow distinction corresponding to the municipality of Manaus. On the bottom right, in yellow, is a map of Manaus municipality showing the ARIE BDFFP. *Map lines delineate study areas and do not necessarily depict accepted national boundaries.*

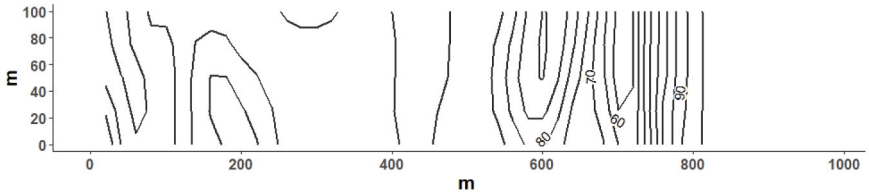

Fig. 2. Topographic map (contour lines at each 10 m) of the permanent plot of 10 ha (1000 ×100 m), where a palm assembly was surveyed in 1990 and 2020 in the Km 41 Reserve (BDFFP-INPA), upland forest in Central Amazon, Brazil. The contour lines shown at 10 m intervals are the true altitude above sea level.

fires, deforestation, selective logging, or hunting, were recorded in the area in the last decades within the census.

Systematically, many of the marked adult palms in the first census were found, but we also marked, mapped, and identified new founders' adult individuals. We considered adult palms by directly observing flowers or fruits or by examining old reproductive scars. We also relied on the skills of O. S. Pereira, who participated in the first census for taxonomic identification. With rare exceptions, the identification reached a specific level.

The taxonomic classification of palms was also verified through field guides, taxonomic reviews, and specialized websites. Notable references include field guides for the Arecaceae family (Henderson et al., 1995; Ribeiro et al., 1999) and reviews for some species from specific genera, such as *Astrocaryum* (Kahn, 2000), *Bactris* (Henderson, 2000), *Desmoncus* (Henderson, 2011), *Geonoma* (Henderson, 2011b), and *Euterpe* (Henderson and Galeano, 1996) were consulted.

For species with multiple stems, we considered each clump as an individual. When clumps were separated by more than 1 m and showed no apparent connection, we considered them distinct individuals. Palms were classified into three groups based on their position in the vertical forest profile: understory (0–2 m height), mid-story (2–8 m), and sub-canopy (> 8 m) species, considering that each stratum has distinct abiotic conditions, mainly light, temperature, and air humidity (Chazdon, 1986). The maximum height of each palm was obtained through field observations and information gathered from the literature, considering their support structure (stemless, short stem, long stem, or arboreal) (Kahn and Castro, 1985). Liana-like palm species, *Desmoncus polyacanthos* and *D. mitis*, were understory species, as we observed that most of their presence in this position in the vertical forest profile.

2.3. Data analysis

For analytical purposes, we adopted the sampling unit of 20 x 20 m, totaling 250 continuous sub-plots. In this study, we focused mainly on density and abundance parameters, considering density as the number of individuals per sample unit and abundance as the total absolute number of individuals in the population of each species, either per sample unit or stratum. Two variables were used to represent topography: mean elevation (m) and slope (degrees).

Subspecies in the inventory were treated as specific taxa for the

analyses (Browne and Karubian, 2016). The exception was *Bactris hirta* individuals classified according to vegetative characteristics into *B. hirta* var. *hirta* and *B. hirta* var. *spruceanum* in the second inventory (Henderson, 2000). Because such a taxonomic distinction was not included in the first inventory, it was not included in the data analysis.

We compared inventories to assess possible phytosociological changes and changes in the palm assembly's composition. We evaluated total abundance between the two inventories with a paired *t*-test and the number of species per sample unit between inventories with the Wilcoxon test (data distributions were not normal and the samples were paired).

In addition to the total abundance of the assembly, we assessed, using the Wilcoxon test, whether there was a difference in the abundance of each species between the inventories. Only species with more than ten individuals in both inventories were considered to ensure robustness in the analysis. Thus, the species *Desmoncus mitis*, *Geonoma maxima* subsp. *chelidonura*, *G. maxima* subsp. *maxima* and *Oenocarpus bataua* were excluded from the analyses. Species registered only in the second census, were also not considered.

Beta diversity between inventories was assessed using the Temporal Beta Diversity Index (TBI), which measures dissimilarity in abundance and total number of species for each sample unit across both periods (Legendre, 2019). TBI ranges from 0, where the community composition is precisely the same in both periods, to 1, where the composition is entirely different, with no sharing of species (abundance per species). For this analysis, abundance data were used.

Dissimilarity (β) was calculated as the percentage difference using the Bray-Curtis index (Brice et al., 2019), which allows statistical evaluation of diversity change at each sample unit. TBI values are randomly sampled through permutation (9999 times), and Holm's correction (Holm, 1979) was applied to generate adjusted *p*-values. Additionally, it enables decomposition of the generated dissimilarity into components of species losses or gains. Calculations and graphics were performed using the adespatial package in R (Dray et al., 2019).

The same analyses were conducted for each forest stratum; both understory and mid-story units had representatives in all of 250 sample units, whereas for sub-canopy species, 25 sample units had no palm trees. This configuration did not affect the TBI analysis, as the comparison was made pairwise between the diversity of each sample unit in 1990 and 2020 (Legendre and Condit, 2019).

An individual was considered dead if their presence in the first inventory (1990) was not confirmed in the second (2020). Meanwhile, mature palms entering the second inventory were considered new individuals. Rates were calculated per hectare over the 30-year time interval.

A species ordination was performed based on abundance across sample units' mean elevation and slope to determine whether populations and the palm assembly are structured along the topographic gradient. The method used for ordering was the weighted average species abundance from the 2020 inventory, accounting for the addition of new individuals.

A Generalized Linear Model (GLM) was used to evaluate whether topography affects the dynamics of vertical strata and the palm assembly. In all models, the dependent variable was TBI values, and the predictors mean elevation (m) and slope (in degrees). For the general assembly, the gamma distribution provided the best fit to the data, while for the strata, the Gaussian distribution provided the best fit; the choice of the best distributions was based on the Akaike Information Criterion (AIC). Adjustments and distribution selection were performed using the stats package. The multicollinearity of the models' predictor variables was evaluated using the Variance Inflation Factor (VIF), and all VIF values were below 2, indicating that multicollinearity did not affect parameter estimates. The ape package was used to evaluate spatial autocorrelation using Moran's Index statistics, and the results indicated that the response variables showed no spatial structure ($p = 0.59$). The results of the GLMs were presented through graphs of the partial effects of each predictor using the *ggeffects* package (Lüdecke, 2018). The statistical software R was used for all analyses and the production of graphs (R Core Team, 2023).

3. Results

3.1. Phytosociological characteristics of palms

In 1990, 6535 adult palms were recorded. Surprisingly, in 2020, there was a global adult palm increase of 47%, totaling an inventory of 9595 individuals (Fig. 3), 46% corresponded to survivors and 54% were new registrations. Over this 30-year interval, there was a positive balance between new individuals' entries (5185; 79% of the total abundance in 1990) and even the impressive mortality of 1/3 (32.5% or 2125 adult individuals) in the assemblage. There was a significant difference in abundance between inventories ($t = 21.76$, df $= 249$, $p < 0.0001$; paired *t*-test).

The average density of palms in 1990 was 653.5 ($\pm$ 188.4) ind. per ha; in 2020, it was nearly one-third higher, at 959.5 ($\pm$ 296) ind. per ha. Thus, we revealed that Central Amazon terra firme forests could be considered a "forest of palms," as in some cases, we surprisingly recorded $>$ 1000 adult palms in just 1 ha.

3.2. Species composition

In total, 11 genera were recorded throughout the inventory, with *Bactris* having the highest number of species, 14 spp. (42%), accounting for 38.9% of the total assembly abundance in 2020. *Geonoma* was the second highest in the number of species, with six spp. (18.2%), which represents only 9% of the abundance in the 2020 inventory. Six genera had only one species in the inventory (supplementary material, Table S1).

Over 30 years, there was an increase in the number of species, from 30 to 33 spp. (10%), with the addition of two rare species in the region, *Bactris schultesii* and *Geonoma macrostaschys*, having just one individual each, and finally, *Bactris oligocarpa*, with a density of 6.7 ind. per ha (supplementary material, Table S1). The average species density per sample unit was 9.3 ($\pm$ 2.2 spp. per sample unit) in 1990 and 11.5 ($\pm$ 2.6 spp. per sample unit) in 2020 (V = 1731, df = 249, $p < 0.05$; Wilcoxon test).

Of the 30 species recorded in the first inventory, 25 showed an increase in abundance in 2020 (Fig. 4). The other five species showed a slight decrease in abundance, indicating stable populations. The most common species in 1990 was *Astrocaryum sociale*, with 1937 individuals, which increased by almost 1/3, totaling 2598 individuals in 2020. However, its relative abundance decreased from 30% to 27%, indicating that other species (e.g., *B. hirta*) had a proportionally higher increase in abundance. This result was observed for the three most abundant species: *A. sociale*, *Attalea attaleoides*, and *Bactris acanthocarpa* var. *exscapa*, representing 55.6% of the total relative abundance in the first inventory, but dropped to 51.2% in 2020 (Supplementary material, Table S1). Notably, *Bactris constanciae* recorded no mortality in 30 years and practically doubled its population.

3.3. Temporal variation in palm diversity

Across most of the area, there was an increase in beta diversity (89.2%), driven by a combination of abundance and the number of species. Conversely, a negative change was recorded in another 9.2% of the area, while in only 1.6% of the area, no change was observed. Overall, the mean difference between gains and losses was positive (0.18), with high statistical significance ($t = 21.32$, $p = 0.00001$; paired *t*-test), indicating and confirming the dominance of species gain in the assembly (Fig. 5A) (further details in Supplementary material, Table S2).

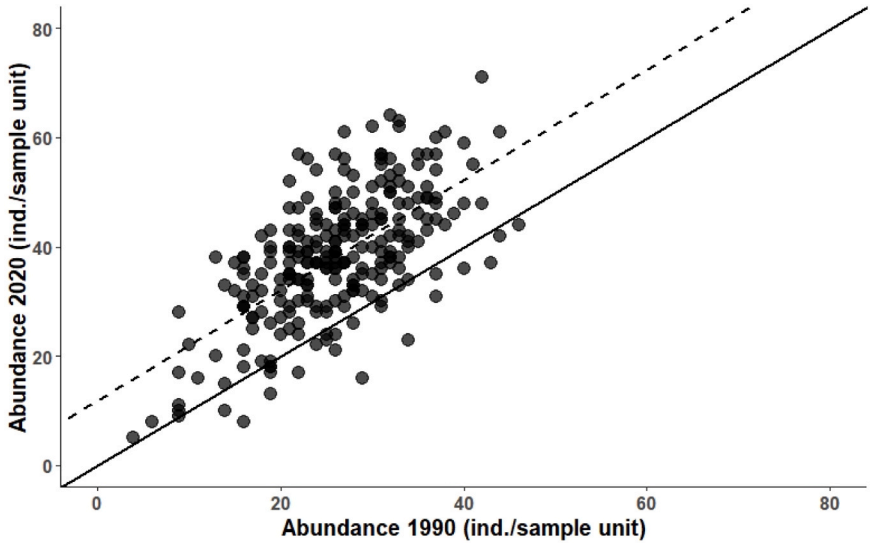

Fig. 3. Comparison of palm abundance (ind./20x20m plot) between 1990 and 2020 in a 10-ha permanent plot in the Km 41 Reserve (BDFFP-INPA) on terra firme forest in Central Amazon. Each point represents the abundance of a sample unit (s.u., n = 250) in 1990 and 2020. The solid theoretical line would represent equal abundance between the two inventories. The dashed line represents the fit of a linear regression between palm abundance for the two periods.

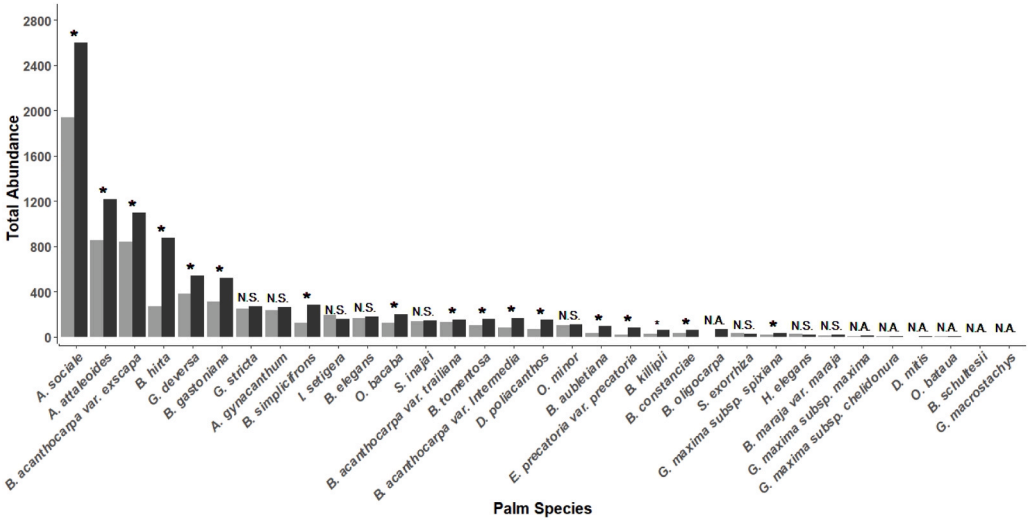

Fig. 4. Variation in abundance after 30 years (1990–2020) of palm species recorded in a 10-ha permanent plot in the Km 41 Reserve (BDFFP-INPA) on terra firme forest in the Central Amazon. The species are organized according to their abundance in 2020. The gray bars represent the total abundance of species in 1990, and the black bars represent the total abundance in 2020. * Indicates a significant difference ($p < 0.05$; Wilcoxon test) in abundance between inventories; N.S. indicates no significance; N.A. indicates that the species was not evaluated.

3.4. Forestry vertical profile of the assembly

The highest abundance and number of palm species were recorded in the understory, with 4664 individuals of 12 spp. in 1990 and 6689 individuals of 14 spp. in 2020, an increase of 43% in individuals and 17% in species (Table 1), including the three most abundant species (*Astrocaryum sociale*, *Attalea attaleoides*, and *Bactris acanthocarpa* var. *exscapa*) which represented over 50% of the total abundance of the assembly. In the mid-story, there were 12 spp. in 1990 and 13 in 2020. Arborescent palms (sub-canopy), had general abundance was 420 palms in 1990 and 578 in 2020, corresponding to only six spp. in both inventories (Supplementary material, Table S1).

The TBI analysis for the strata demonstrated that the understory and mid-story exhibited a changing pattern congruent with the overall assembly, where most sample units showed a shift in composition driven by species gains (89.6% for the understory and 77.6% for the mid-story). Few sample units experienced a loss of diversity (6.4% for the understory and 13.6% for the mid-story), and less than 10% of the sample units in both strata showed no changes of any kind (Fig. 5B-5C) (further details in Supplementary material, Table S2).

Fewer sample units (n = 225) were occupied by sub-canopy palm trees, indicating that the arboreal palms were not distributed throughout the study area. However, as in the understory and midstory, most sample units showed increased beta diversity (51.6%) for arboreal palms. In comparison, approximately 1/4 of the sample units (24%) experienced a negative change, and a few (14.4%) showed no alteration (Fig. 5D).

3.5. Species arrangement based on topography

The elevation gradient of the terrain appears to define the distribution of species into three groups (Fig. 6A): 1) A distribution of species more associated with lower areas of the terrain (valleys), primarily

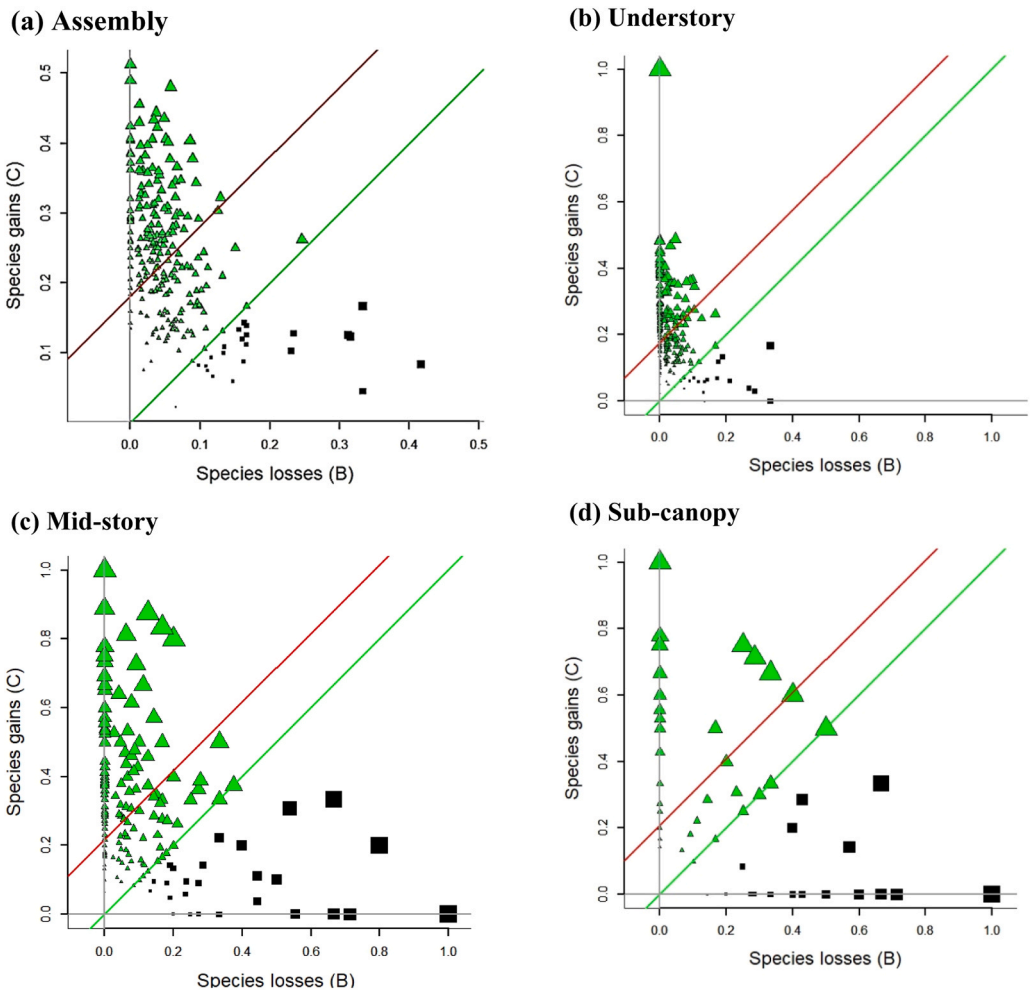

Fig. 5. Gains and losses of species in palm assembly (a) and the three forest strata: Understory (n = 250) (b); Mid-story (n = 250) (c); Sub-canopy (n = 225) (d), according to TBI analysis between inventories (1990 and 2020) in a 10-ha permanent plot at km 41 reserve (BDFFP-INPA) on terra firme forest in Central Amazon. The points represent sample units (20 x 20 m), with triangles indicating species gain and squares indicating species loss. The sizes of the symbols are proportional to the change in beta diversity in the sample units. The bigger the symbols, the greater the changes. The green line represents a theoretical position where species gain and loss would be equal. The red line, parallel to the green line and passing through the centroid of all points, indicates that, on average, species gain dominated over species loss.

Table 1
The absolute and relative number of species (in %), palm abundance in 1990 and 2020, and abundance change (in %), recruitment, and mortality of palms (in %) for three strata and the overall palm assembly in a 10-ha permanent plot at km 41 reserve (BDFFP-INPA) on terra firme forest in Central Amazon.

Forest Stratum	# spp. (%) 1990	# spp. (%) 2020	Abund. 1990 (%)	Abund. 2020 (%)	Abund. change (%)	Recruitment (%)	Mortality (%)
Understory	12 (40)	14 (42.4)	4664 (71.4)	6689 (69.7)	+43.4	3210 (68.8)	1185 (25.4)
Mid-story	12 (40)	13 (39.4)	1451 (22.2)	2328 (24.3)	+60.4	1524 (105)	647 (44.6)
Sub-canopy	6 (20)	6 (18.2)	420 (6.4)	578 (6.0)	+37.6	451 (107.4)	293 (69.8)
Assembly	30 (100)	33 (100)	6535 (100)	9595 (100)	+46.8	5185 (79.3)	2125 (32.5)

composed of *Bactris maraja* var. *maraja*, *Hyospathe elegans*, *Socratea exorrhiza*, and *Oenocarpus bataua*. 2) A second group, with few species, is more associated with plateaus, such as *Desmoncus mitis* and *Geonoma maxima* subsp. *chelidonura*. 3) A larger group of species that did not exhibited a direct association with the topographic gradient of the terrain and were distributed across the entire elevation gradient. This group also includes species such as *Astrocaryum sociale*, *Bactris simplicifrons*, and *Geonoma deversa*, which showed a slight increase in abundance in higher, flatter areas, but without a clear pattern along the slope gradient (Fig. 6B).

3.6. Palm assembly dynamics and topography

The slope of the terrain negatively affected the Temporal Beta Diversity (TBI) of the understory stratum and the palm assembly. In contrast, the elevation parameter did not affect TBI at any of the levels evaluated (Supplementary material, Table S3 and Fig. S1). Upon conducting a more detailed assessment, exploring a direct relationship between slope and TBI of the assembly (Fig. 7C), it was observed that TBI values varied significantly up to a 40° slope. However, beyond this point, TBI values tended to decrease, indicating that excessively steep terrain leads to lower beta diversity in the palm assembly.

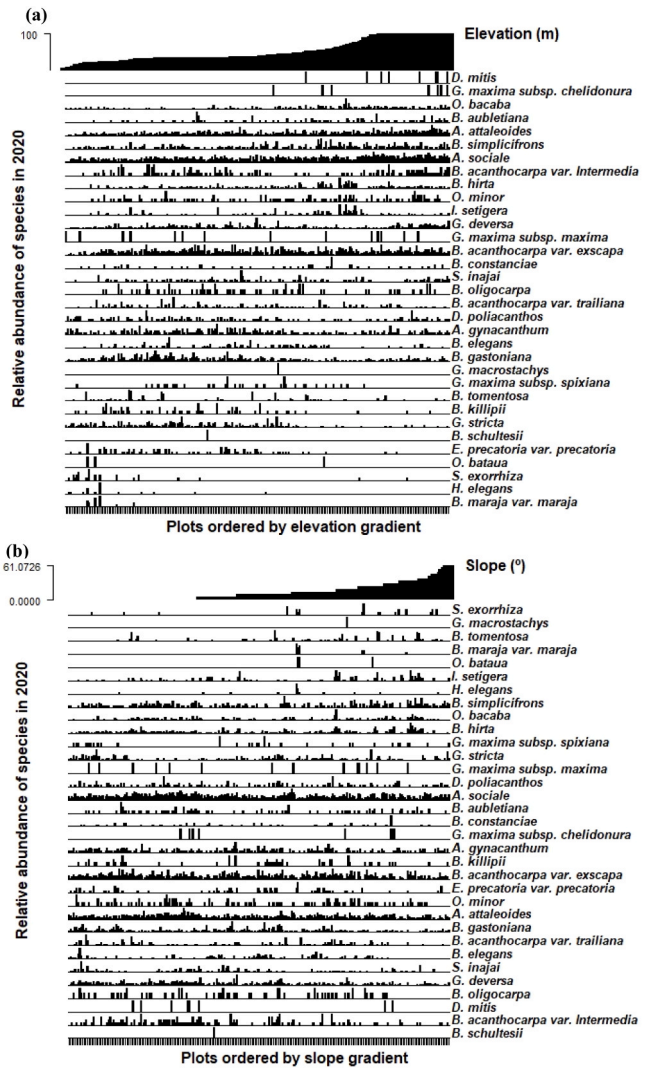

Fig. 6. Based on the topographic elevation gradient (m), palm species are ordered by relative abundance (a). Species ordering concerning the slope of the terrain (°) and (b) in the 10-ha permanent plot of the km 41 reserve (BDFFP-INPA) on continuous terra firme forest in Central Amazon. In Figures (a) and (b), the values in the upper left part of the graph represent the range of the predictor variable.

4. Discussion

We analyzed the structure of a palm assembly and examined changes over a 30-year interval. This is likely the broadest and most enduring survey to date for this important taxonomic group, typical of tropical forests. The study's novelty extends to its findings as well. To our knowledge, there is few information on the lifespan of palms (Jansen et al., 2012; Otárola and Avalos, 2014), especially for native and non-domesticated species in the Amazon.

Within this context, we can highlight two points. First, the 30 palm species were recorded as reproductive for at least 30 years, although this does not indicate their total lifespan or the time to reach adulthood, it demonstrates that these palm trees have a long reproductive period. Second, most species showed low mortality, especially understory palms, which represented over 40% of species in both inventories. Most populations increased their number of individuals during the period evaluated, except *Iriartella setigera*, *Socratea exorrhiza*, *Hyospathe elegans*, *Geonoma maxima* subsp. *chelidonura*, and *Oenocarpus bataua*. However, even these species had individuals surviving for at least 30 years.

4.1. Phytosociological characteristics of palms

The 2020 inventory revealed two key findings: a significant increase in palm abundance, due to high recruitment and low mortality; and the notable survival of many palms for over 30 years despite recurring extreme climatic events and the occurrence of blowdowns not too far from the study area. Contrary to expectations of higher mortality under such conditions, these results demonstrate the palm assemblage's high resilience, especially in understory palms. Additionally, the area maintains a high adult palm density (~ 1000 ind. per ha).

The Neotropics are among the global hotspots for palm diversity (Muscarella et al., 2020). We documented a high number of palm species characteristic of Central Amazonia, particularly in continuous terra firme forests (Kahn and Castro, 1985; Balslev et al., 2011; Guedes et al., 2022). Only three species were added to our list between inventories, but the average occurrence of palm species per sample unit also rose. This pattern indicates that individuals from species not previously found in these sample units colonized them.

In the Central Amazon, Rodrigues et al. (2014) observed that canopy opening influenced the composition of an adult palm assembly. The abundance of adult palm individuals is low in areas with higher tree density. Although palms are adapted to low-light conditions (Ma et al., 2015), resources such as water and nutrients may become less available with high tree density (Rodrigues et al., 2014).

Extreme climatic events in the region over recent decades have increased mortality among canopy trees (Espinoza et al., 2019; Toledo et al., 2012). Consequently, this may have created more suitable environmental niches for palm establishment due to greater light availability and reduced competition for nutrients, especially benefiting understory species, which showed the largest absolute increase in population. Additionally, palms generally do not face limitations in mesoscale dispersal capacity.

In this context, these new spatial niches provide suitable conditions for palm establishment, enabling palms to reach them. This may explain the significant increase in species abundance and the spread of species across sample units. This result highlights the importance of a large, well-preserved continuous forest reserve. Conversely, a study conducted by Oliveira *et al.* (unpublished results), a few km apart, recorded a decline in the abundance and number of palm species due to forest fragmentation.

However, in a 17-year study monitoring a palm assembly in the Western Amazon, Olivares et al. (2017) did not corroborate the hypothesis above. They found no difference in the abundance or species composition of palms over the observed period. Nor were large climatic oscillations observed in the region. Thus, palm assemblies in the Central Amazon are likely undergoing changes in their natural dynamics guided by climatic oscillation. This pattern has also been documented for other taxonomic groups, such as lianas, in the same study area (Laurance et al., 2014).

4.2. Species composition

Species with fewer individuals or that were rare in 1990 increased their populations at proportionally higher rates. For example, *Bactris constanciae* and *Desmoncus mitis* experienced no deaths. Recruitment almost doubled the former's population, while the latter's population increased eightfold.

Some species showed high resilience after 30 years. For instance, local disturbances did not affect *Astrocaryum sociale*, the most abundant species in both inventories. After 20 years, the species' size structure in unlogged sites was like that in selectively logged sites, as reported by Higashikawa et al. (2019).

The entry of only one individual of *Bactris schultisii* and *Geonoma maxima* subsp. *chelidonura* in the 2020 inventory is likely due to the mass effect (Andersen et al., 2009). Meanwhile, *Bactris oligocarpa*, which was not recorded in 1990 (Henderson, 2000), had an abundance of 67

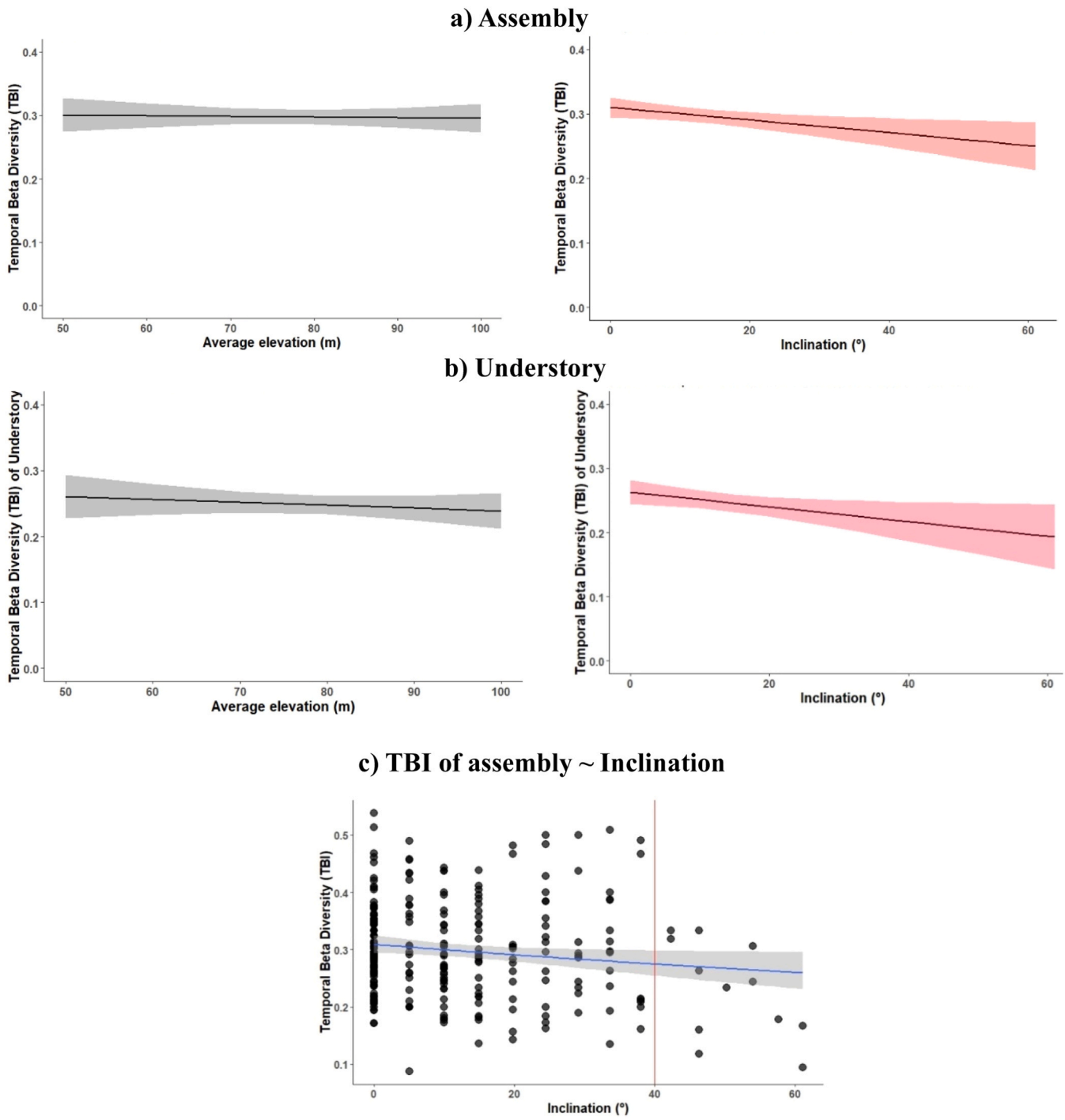

Fig. 7. Partial effects of terrain elevation (m) (column 1) and partial effects of terrain slope (°) (column 2) on Temporal Beta Diversity (TBI) of assembly (a) and understory (b). Values were obtained through the Generalized Linear Model (GLM); the direct relationship between TBI of the assembly and slope (°) (c) in the palm assembly in a 10-ha permanent plot at the Km 41 Reserve (BDFFP-INPA) on continuous terra firme forest in the Central Amazon. Figures marked in red indicate statistical significance ($p < 0.05$), and in Figure (c), the additional vertical red line indicates the point at which the slope negatively affects TBI. The complete statistical results for the models can be found in the Supplementary Material (Table S3).

individuals in 2020. This suggests an expansion of its local occurrence area through consistent colonization. In a study on the effects of forest fragmentation in the same region, Scariot (1999) also did not record the presence of *B. oligocarpa* in continuous forests, but only in 10-ha forest fragments. This indicates that the species' distribution is likely highly clustered.

4.3. Temporal variation in palm beta diversity

Temporal Beta Diversity (TBI) results showed high dissimilarity between sampling intervals for both strata and the entire assembly, driven by the gain of species in the sample units. This indicates that overall conditions are becoming more favorable for the palm family, not just for a particular subgroup.

These results partially support the central hypothesis, but more

evidence is needed to infer if this dynamic pattern is typical of palm assembly in mature forests of the Central Amazon. Including to assess whether demographic rates may require correction due to recruitment and mortality events occurring between census intervals (Lewis et al., 2004).

4.4. Vertical assembly profile

Most palms and species are found in the forest understory, including the most common species. The mid-story has a similar number of species but far fewer individuals. The sub-canopy has the fewest palms and species in both intervals. This is not surprising, as this pattern is already recorded in other palm groups in the Central Amazon (Kahn and Castro, 1985; Guedes et al., 2022).

The high number of palms in the understory likely comes from their strong photosynthetic ability and adaptations to shade (Ma et al., 2015; Souza Júnior, 2019). Medium- to large-sized palms can alter several features of nearby sites. They block sunlight and cause a thicker layer of litterfall. This makes it harder for new plants to sprout and grow. As a result, fewer seedlings are established, and growth and survival are reduced (Farriz-Lopez et al., 2004; Wang and Augspurger, 2004). These results likely apply to palms with big leaves, such as *Astrocaryum sociale* and *Attalea attaleoides*, which are very locally common. When these palms are more common, they can shape the forest's structure.

4.5. Species arrangement on topography

The distribution of species abundance across the evaluated topographic gradients (elevation and slope) revealed that only elevation affected species abundance. In contrast, the slope did not yield a random species-abundance distribution. This occurs because it becomes a non-reliable predictor when the slope is zero, as in valleys and plateaus.

Three species-composition groups of palms were observed along the elevation gradient: species more associated with valleys, species more linked to plateaus, and species distributed approximately equally across the entire gradient. This pattern has been previously documented in other assemblies in the Central Amazon (Kahn and Castro, 1985; Rodrigues et al., 2014; Guedes et al., 2022).

The species associated with valleys included arborescent palms such as *Socratea exorrhiza*, *Oenocarpus bataua*, and *B. maraja* var. *maraja*, although belonging to a genus predominantly composed of understory species, have characteristics that enable them to thrive in environments with higher water availability, such as larger and thicker stems than those of other understory species. These characteristics are also present in arborescent species that inhabit these environments (Balslev et al., 2011; Guedes et al., 2022). The absence of *Mauritia flexuosa* and the presence of a few individuals of *Oenocarpus bataua* in the inventory, both common arborescent palms present along streams and flooded areas in the Central Amazon (Melo et al., 2020), was because the flooded areas of the valleys represented only about 3% of the total study area (Pacheco, 2001).

Most species occurred throughout the evaluated elevation gradient, contrary to the initial prediction that most species would have a restricted distribution. Rodrigues et al. (2014) demonstrated that elevation-based partitioning of the environmental niche has little influence on the composition of the palm assembly. However, as emphasized by the same author, such results should be approached with caution, as a given biological or environmental resource may have different importance across palm species, making it difficult to identify a key factor for each species.

4.6. Palm assembly structure and topography

Unlike reported for species distribution, terrain slope proved more relevant, showing a negative relationship with understory and assembly structure. This fact reinforces that the assemblage is strongly influenced by understory palm patterns. Furthermore, the understory is the only stratum with a remarkable presence across the topographic gradient, though it is more concentrated on the plateaus. The mid-story species are distributed across the entire topography gradient; however, they are primarily low in abundance, whereas the sub-canopy species do not occur throughout the area.

The low diversity in steepy areas is probably due to factors affecting seedling establishment, such as reduced seed dispersal; seed fixation, since most palm seeds are elliptical, ovoid, or spherical; and rooting, which is difficult because of the shallow soil (Zona and Henderson, 1989; Brewer, 2001; Guedes et al., 2022). Areas with less steep slopes show the most significant variation in TBI values, indicating that temporal variation in species composition is affected by topography and other factors. On the other hand, the greater the slope, the lower the dynamics of the palm assembly tend to be.

Despite the analysis showing that elevation did not affect temporal beta diversity in the assembly, this topographic factor must still be addressed. As Souza et al. (2020) demonstrated, in areas with shallower water tables, usually in valleys, palms do not experience high mortality rates during dry events, and recruitment can even be higher.

The low representation of bottom-of-valley areas (~3%) in this study (Pacheco, 1999) may explain the decreased influence on beta diversity, as these environments are more dynamic due to their abiotic characteristics, such as regular flooding (Schietti et al., 2014). Such characteristics were expected to directly affect the palm assembly, either through mortality or indirectly through the high tree mortality in these environments (Toledo et al., 2012). Additionally, those areas are colonized by a group of palm species with dynamics different from those in other environments (as reported in this study).

Considering this set of factors, it is impossible to confirm or refute the initial hypothesis that valley palm assemblies would be more dynamic than plateau assemblies. Long-term monitoring across broader altitudinal gradients, while accounting for equivalent areas for each terrain type, may elucidate how topography affects the diversity of the palm assembly.

5. Conclusions

We found a significant increase in the abundance of adult palms, directly associated with low mortality and high recruitment for most species. This results in a group pattern rather than being guided by a few species. The species composition was little altered during the evaluated interval, and the species expanded their distribution across the area, indicating the emergence of suitable environmental niches for palms.

Most palm species and abundance occur in the understory. Meanwhile, the sub-canopy species exhibited similar recruitment and mortality, possibly due to intrinsic biological conditions of species in this stratum based on their morphology. Topography was a relevant factor in species distribution along elevation gradients and in assembly dynamics, particularly on terrain with slopes exceeding 40 °.

The present study features the longest interval between samplings for palms in the Amazon. The unique results regarding assembly structure and palm lifespan underscore the significance of long-term monitoring, as carried out in the BDFFP. Only through long-term studies can we monitor crucial aspects of organism ecology, such as lifespan and the interaction between long-term assembly structure and topographic factors. In this context, preserving large, forested areas is essential to assess this information without interference from local anthropogenic factors.

However, inventories assessing palm assembly with shorter sampling intervals are also necessary. In a scenario where extreme climatic events are expected to become more frequent, monitoring may help determine whether the observed influence of climate oscillations and other aspects in a more minimalistic way led to a significant increase in assembly abundance or whether it results from a natural long-term fluctuation in palm dynamics.

CRediT authorship contribution statement

Paulo Rodrigues de Melo Neto: Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ocírio de Sousa Pereira:** Writing – review & editing, Project administration, Methodology, Investigation, Data curation. **Milla de Freitas Oliveira:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Data curation, Conceptualization. **Andrew James Henderson:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition, Data curation. **Aldicir Osni Scariot:** Writing – review & editing, Methodology, Investigation, Data curation. **José Luís Campana Camargo:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Manoel Augusto Whitaker Pacheco:** Writing – review & editing, Methodology, Investigation, Data curation.

Funding

P. R. Melo Neto received a scholarship from the Brazilian Coordination of Support for Higher Education Personnel (CAPES). M. F. Oliveira received a scholarship from the Amazonas State Research Support Foundation (FAPEAM), and both authors enrolled in the Ecology Graduate Program at INPA. We thank the Thomas Lovejoy Field Research Support Program for funding the fieldwork. Also, we thank the Biological Dynamics of Forest Fragments Project (BDFFP) for logistical support and the partnership between INPA/BDFFP and ICMBio for co-managing the BDFFP Conservation Unit.

Declaration of Competing Interest

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

Acknowledgements

Special acknowledgment goes to Manoel (Manolo) Augusto Withaker Pacheco (*in memoriam*), one of the pioneers in collecting data on palms in the Central Amazon, and to the team of palms who collected and provided the data from the 1990 census. This article is number 891 of the BDFFP Technical Series.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.124066.

Data Availability

Data available in the BDFFP repository.

References

Albiero-Júnior, A., Venegas-González, A., Camargo, J.L.C., Roig, F.A., Tomazello-Filho, M., 2021. Amazon forest fragmentation and edge effects temporarily favored understory and midstory tree growth. Trees 35, 2059–2068. ⟨https://doi.org/10.1007/s0068-021-02172-1⟩.

Alvez-Valles, C.M., Balslev, H., Carvalho, F.A., Garcia-Villacorta, R., Grandez, C., Menini Neto, L., 2018. Endemism and conservation of amazon palms. Biodivers. Conserv. 27, 765–784. https://doi.org/10.1007/s10531-017-1463-0.

Andersen, K.M., Turner, B.L., Dalling, J.W., 2009. Soil-based habit partitioning in understorey palms in lower montane tropical forests. J. Biogeogr. 37, 278–292. https://doi.org/10.1111/j.1365-2699.2009.02192.x.

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

Bierregaard, R.O., Lovejoy, T.E., Kapos, V., Santos, A.A., Hutchings, R.W., 1992. The biological dynamics of tropical rainforest fragments. BioScience 42, 859–866. https://doi.org/10.2307/1312085.

Brewer, S.W., 2001. Predation and dispersal of large and small seeds of a tropical palm. Oikos 92, 245–255.

Brice, M.-H., Cazelles, K., Legendre, P., Fortin, M.-J., 2019. Disturbances amplify tree Community responses to climate change in the temperate-boreal ecotone. Glob. Ecol. Biogeogr. 00, 1–14. https://doi.org/10.1111/geb.12971.

Browne, L., Karubian, J., 2016. Diversity of palm communities at different spatial scales in a recently fragmented tropical landscape. Bot. J. Linn. Soc. 182, 451–464. https://doi.org/10.1111/boj.12384.

Chazdon, R.L., 1986. Light variation and carbon gain in rain forest understorey palms. J. Ecol. 74, 995–1012. https://doi.org/10.2307/2260229.

Clark, D.A., Clark, D.B., Sandoval, R.M., Castro Vinicio, M.C., 1995. Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. Ecology 76, 2581–2594. https://doi.org/10.2307/2265829.

Costa, F.C., Zuanon, J.A.S., Baccaro, F.B., Almeida, J.S., Menger, J.S., Souza, J.L.P., Borba, G.C., Esteban, E.J.L., Bertin, V.M., Gerolamo, C.S., Nogueira, A., Castilho, C. V., 2020. Effects of climate change on central Amazonian forests: a two decades synthesis of monitoring tropical biodiversity. Oecologia Aust. 24, 317–335. https://doi.org/10.4257/oeco.2020.2402.07.

Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guénard, G., Jombart, T., Larocque, G., Legendre, P., Madi, N., Wagner, H.H., & Siberchicot, A. (2019). *adespatial*: Multivariate multiscale spatial analysis. R package version 0.3-3. Retrieved from ⟨https://cran.r⟩-project.org/package=adespatial.

Espinoza, J.C., Ronchail, J., Marengo, J.A., Segura, H., 2019. Constrating North-South changes in Amazon wet-day and dry-day frequency and related atmospheric features (1981-2017). Clim. Dyn. 52, 5413–5430. https://doi.org/10.1007/s00382-018-4462-2.

Esquivel-Muelbert, A., Baker, T.R., Dexter, K.G., Lewis, S.L., Brienen, R.J.W., Feldpausch, T.R., et al., 2019. Compositional response of Amazon forests to climate change. Glob. Change Biol. 25, 39–56. https://doi.org/10.1111/gcb.14413.

Farriz-Lopez, K., Denslow, J.S., Moser, B., Passmore, H., 2004. Influence of a common palm, *Oenocarpus mapora*, on seedling establishment in a tropical moist forest in Panama. J. Trop. Ecol. 20, 429–438. https://doi.org/10.1017/S0266467404001531.

Garcia, J.P.M., 2000. A geomorfologia como instrumento de identificação de unidades físiconaturais em florestas úmidas. PhD Thesis, Universidade de São Paulo, São Paulo.

Gleason, H.A., 1926. The individualistic concept of the plant association. Bull. Torre Bot. Club 53, 7–26. https://doi.org/10.2307/2479933.

Guedes, M., Falen, L., Pereira, O.S., Lima, A.P., Castilho, C.V., Jorge, R.F., Magnusson, W. E., Hipólito, J., 2022. Understory palms are not canopy palms writ small: factors affecting Amazonian understory palms within riparian zones and cross the landscape. For. Ecol. Manag. 509. https://doi.org/10.2139/ssrn.3967980.

Henderson, A., 2000. *Bactris* (Palmae). Flora Neotrop. 79, 1–181. ⟨https://www.jstor.org/stable/4393⟩.

Henderson, A., 2011b. A revision of *Geonoma* (Arecaceae). Phytotaxa 17, 1–127.

Henderson, A., 2011. A revision of *Desmoncus* (Arecaceae). Phytotaxa 35, 1–88. https://doi.org/10.11646/phytotaxa.35.1.1.

Henderson, A., Galeano, G., 1996. *Euterpe*, *Prestoea*, and *Neonicholsonia* (Palmae). Flora Neotrop. 72, 1–89.

Henderson, A., Galeano, G., Bernal, R., 1995. Field Guide to the Palms of the Americas. Princeton University Press, USA (New Jersey).

Henderson, A., Fisher, B., Scariot, A., Pacheco, M.A.W., Pardini, R., 2000. Flowering phenology of a palm Community in a central Amazon Forest. Britonia 52, 149–159. https://doi.org/10.2307/2666506.

Higashikawa, E.M., Brasil, M.M.O., Magnusson, W.E., 2019. A 30-year study of the effects of seletive logging on a stem-less palm (*Astrocaryum sociale*) in a central-Amazon forest. For. Ecol. Manag. 432, 607–611. https://doi.org/10.1016/j.foreco.2018.10.003.

Holm, S., 1979. A Simple Sequentially Rejective Multiple Test Procedure. Scand. J. Stat. 6, 65–70. ⟨http://www.jstor.org/stable/4615733⟩.

Jansen, M., Zuidema, P.A., Antes, N.P.R., Martinez-Ramos, M., 2012. Strong persistent growth differences govern individual performance and population dynamics in a tropical forest undestorey palm. J. Ecol. 100, 1224–1232. https://doi.org/10.1111/j.1365-2745.2012.02001.x.

Kahn, F., 2000. Two Amazonian palm species revalidated: *Astrocaryum forinosum* and *A. sociale*. Palms 45, 29–36.

Kahn, F., Castro, A., 1985. The palm community in a forest of Central Amazonia, Brazil. Biotropica 17, 210–216. https://doi.org/10.2307/2388221.

Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. World map of the Köppen-Geiser climate classification uptaded. Meteorol. Z. 15, 259–263. https://doi.org/10.1127/0941-2948/2006/0130.

Lüdecke, D., 2018. *ggeffects*: Tidy Data Frames of Marginal Effects from Regression Models. J. Open. Source Softw. 3, 772. https://doi.org/10.21105/joss.00772.

Laurance, S.G.W., Laurance, W.F., Andrade, A., Fearnside, P.M., Harms, K.E., Vicentini, A., Luizão, R.C.C., 2010. Influence of soils and topograghy on Amazonian tree diversity: a landscape-scale study. J. Veg. Soc. 21, 96–106. https://doi.org/10.1111/j.1654-1103.2009.01122.x.

Laurance, W.F., Andrade, A.S., Magrach, A., Camargo, J.L.C., Valsko, J.J., Campbell, M., Fearnside, P.M., Edwards, W., Lovejoy, T.E., Laurance, S.G.W., 2014. Long-term changes in liana abundance and forest dynamics in undisturbed Amazonian forests. Ecology 95, 1604–1611. https://doi.org/10.1890/13-1571.1.

Laurance, W.F., Camargo, J.L.C., Fearnside, P.M., Lovejoy, T.E., Williamson, G.B., Mesquita, R.C.G., Meyer, C.F.J., Bobrowiec, P.E.D., Laurance, S.G.W., 2017. An Amazonian rainforest and its fragments as a laboratory of global change. Biol. Rev. 93, 223–247. https://doi.org/10.1111/brv.12343.

Legendre, P., 2019. A temporal beta-diversity index to identify sites that have changed in exceptional ways in space-time surveys. Ecol. Evol. 9, 3500–3514. https://doi.org/10.1002/ece3.4984.

Legendre, P., Condit, R., 2019. Spatial and temporal analysis of beta diversity in the Barro Colorado Island forest dynamics plot, Panama. For. Ecosyst. 6 (7). https://doi.org/10.1186/s40663-019-0164-4.

Lewis, S.L., Phillips, O.L., Sheil, D., Vinceti, B., Baker, T.R., Brown, S., et al., 2004. Tropical forest tree mortality, recruitment and turnover rates: calculation, interpretation and comparison when census intervals vary. J. Ecol. 92 (6), 929–944. https://doi.org/10.1111/j.0022-0477.2004.00923.x.

Ma, R.-Y., Zhang, J.-L., Cavaleri, M.A., Sterck, F., Strijk, j S., Cao, K.-F., 2015. Convergent evolution towards high net carbon gain efficiency contributes to the shade tolerance of palms (Arecaceae). PLoS. ONE 10, e0140384. https://doi.org/10.1371/journal.pone.0140384.

Melo, W.A., Vieira, L.D., Novaes, E., Bacon, C.D., Collevatti, R.G., 2020. Selective sweeps lead to evolutionary sucess in an Amazonian hyperdominant palm. Front. Genet. 11, 596662. https://doi.org/10.3389/fgene.2020.596662.

Mori, S.A., Becker, P., 1991. Flooding affects survival of Lecythidaceae in *terra firme* forest near Manaus, Brazil. Biotropica 23, 87–90. https://doi.org/10.2307/2388692.

Muscarella, R., Emilio, T., Phillips, O.L., Lewis, S.L., Slik, F., et al., 2020. The global abundance of tree palms. Glob. Ecol. Biogeogr. 29, 1495–1514. https://doi.org/10.1111/geb.13123.

Olivares, I., Svenning, J.C., Bodegom, P.M.V., Valencia, R., Balslev, H., 2017. Stability in a changing world – palm community dynamics in the hyperdiverse western Amazon over 17 years. Glob. Change Biol. 23, 1232–1239. https://doi.org/10.1111/gcb.13494.

Otárola, M.F., Avalos, G., 2014. Demographic variation across successional stages and their effects on the population dynamics of the neotropical palm *Euterpe precatoria*. Am. J. Bot. 101, 1023–1028. https://doi.org/10.3732/ajb.1400089.

Pacheco, M.A.W., 1999. Spatial variation in abundance of tropical forest trees: the role of herbivores and abiotic factors. PhD thesis, University of Illinois, Chicago.

Pacheco, M.A.W., 2001. Effects of flooding and herbivores on variation in recruitment of palms between habits. J. Ecol. 89, 358–366. ⟨https://www.jstor.org/stable/3072281⟩.

Peres, C.A., 2000. Identifying keystone plant resources in tropical forests: the case of gums from Parkia pods. J. Trop. Ecol. 16, 287–317. https://doi.org/10.1017/S0266467400001413.

Piovesan, P.R.R., Burnham, R.J., Ferraz, I.D.K., Camargo, J.L.C., 2022. Species density diverges after forest fragmentation in lianescent *Machaerim* Pers. (Fabaceae) in Central Amazonia. For. Ecol. Manag. 519. https://doi.org/10.1016/j.foreco.2022.120335.

R Core Team. (2023). R: A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing*, Vienna, Austria. ⟨https://www.R-project.org/⟩.

Ribeiro, J.E.L.S., Hopkins, M.J.G., Vicentini, A., Sothers, C.A., Costa, M.A.S., Brito, J.M., Souza, M.M.A.D., et al., 1999. Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônia Central (1st ed). INPA-DFID, Manaus, Brasil.

Rodrigues, L.F., Cintra, R., Castilho, C.V., Pereira, O.S., Pimentel, T.P., 2014. Influences of forest structure and landscape features on spatial variation in species composition in a palm community in Central Amazonia. J. Trop. Ecol. 30, 565–578. https://doi.org/10.1017/S0266467414000431.

Scariot, A.O., 1996. The effects of rain forest fragmentation on the palm community in the Central Amazonia. PhD thesis, University of California, California.

Scariot, A.O., 1999. Forest fragmentation effects on palm diversity in central Amazonia. J. Ecol. 87, 66–76. ⟨https://www.jstor.org/stable/2648681⟩.

Schietti, J., Emilio, T., Rennó, C.D., Drucker, D.P., Costa, F.R.C., Nogueira, A., Baccaro, F. B., et al., 2014. Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. Plant. Ecol. & Divers. 7, 241–253. https://doi.org/10.1080/17550874.2013.783642.

Souza, T.S., Schietti, J., Souza, F.C., Esquivel-Muelbert, A., Ribeiro, I.O., Emílio, T., Pequeno, P.A.C., Phillips, O., Costa, F.R.C., 2020. Palms and trees resist extreme drought in Amazon forest with shallow water tables. J. Ecol. 00, 1–13. https://doi.org/10.1111/1365-2745.13377.

Souza Júnior, H.P., 2019. Estrutura funcional de uma comunidade de Palmeiras (Arecaceae) ao longo de gradientes ambientais em uma floresta da Amazônia Central. *Dissertation*, Master degree. Instituto Nacional de Pesquisas da Amazônia, Manaus.

Ter Steege, H., Pitman, N.C.A., Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E., et al., 2013. Hyperdominance in the amazonia tree flora. Science 342, 1243092. https://doi.org/10.1126/science.1243092.

Toledo, J.J., Magnusson, W.E., Castilho, C.V., Nascimento, H.E.M., 2012. Tree mode of death in Central Amazonia: effects of soil and topography on tree mortality associated with storm disturbances. For. Ecol. Manag. 263, 253–261. https://doi.org/10.1016/j.foreco.2011.09.017.

Vormisto, J., 2002. Palms as rainforest resources: how evenly are they distributed in Peruvian Amazonia? Biodivers. Conserv. 11, 1025–1045. https://doi.org/10.1023/A:1015873223350.

Wang, Y.H., Augspurger, C., 2004. Dwarf palms and cyclants strongly reduce Neotropical seedling recruitment. OIKOS 107, 619–633. ⟨https://ui.adsabs.harvard.edu/link_gateway/2004Oikos.107.619O/doi:10.1111/j.0030-1299.2004.13328.x⟩.

Zona, S., Henderson, A., 1989. A review of animal-mediated seed dispersal of palms. Selbyana 11, 6–21.