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Açaí palm intensification reorganizes woody plant assemblages at multiple spatial scales in an Amazonian estuarine forest

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Abstract

The exploitation of nontimber forest products has been proposed as a sustainable way to exploit tropical forests, but such an opportunity remains to be examined case-by-case. We examine the impact of the intensification of the açaí palm (*Euterpe oleracea*) management for fruit production via increments in palm clumps/stems density on the woody plant assemblages (adult and regenerating) in an estuarine forest landscape in the eastern Amazon region, Brazil. Across 30 forest stands açaí stem density correlated negatively with stem density and taxonomic diversity considering both adult and regenerating woody plant assemblages, but it posed a positive effect on beta diversity via species turnover. Soil fertility and forest stand accessibility played a complementary role. Moreover, açaí clump density affected the abundance of particular woody plant species, including a set of species declining before the 400-açaí clump density threshold imposed by current regulation. Accordingly, açaí clump density influenced the taxonomic organization of woody plant assemblages at the landscape spatial level. Finally, it is worth mentioning a group of 105 species, which were recorded across the regenerating assemblages but not in the adult assemblages. Among them, a large number of small-statured woody plant species typical from the forest understory (i.e., the shade-tolerant assemblage), such as those from *Miconia*, *Piper*, *Bactris*, *Annona* and *Geonoma* genera. As intensification is still spreading it can be considered a threat to the integrity of the Amazon estuarine forest and thus questions the ecological sustainability through which the current Amazonian “black gold” is now produced.

KEYWORDS

Amazon rainforest, beta diversity, chronic anthropogenic disturbance, *Euterpe oleracea*, forest management, land use and cover, nontimber forest products

1 | INTRODUCTION

Tropical forests provide a wide range of ecosystem services considered essential for sustainability at multiple spatial and temporal scales (Bonan, 2008). Such benefits of nature for people include climate regulation, carbon sequestration and storage, biomass production, water

supply and purification, pollination, and biodiversity persistence (Decocq et al., 2016; Giannini et al., 2020; Liang et al., 2016; Mori et al., 2017; Thompson et al., 2011); moreover, the livelihood of millions of people from uncountable ethnic groups and traditional populations (i.e., a tropical forest cultural heritage) relies on forest products for subsistence and commercial activities in small and local markets

(Shackleton & De Vos, 2022). Forest products offer support for a wide range of necessities, from firewood to building materials and bushmeat (Naughton-Treves et al., 2007). Such a forest-dependent socio-economy is still the predominant reality across both humid and dry tropical forests globally (Shackleton & De Vos, 2022); however, ecosystem services by tropical forests and their biological and cultural heritage are threatened by the conversion of old-growth forests for more economically profitable land use, such as the production of international commodities (e.g., soybean, beef, palm oil) and forest degradation by intense logging, hunting, and fire (Barlow et al., 2016). As human populations continue to grow, particularly across tropical countries (Bar-On et al., 2018), pressure on tropical forest lands and products is likely to escalate, largely limiting the achievement of the Global Sustainable Goals.

In this context, the exploitation of nontimber forest products (NTFP; e.g., edible fruits, oil, latex, fiber, cultural artifacts, and medicines) represents an opportunity for a forest-based economy to be able to guarantee forest persistence, better life conditions for traditional populations and regional socioeconomic development; i.e., win-win strategies (Hernández-Barrios et al., 2014; Ruiz Pérez & Arnold, 1996). Indeed, a review of the sustainability of NTFP harvesting states that a majority of practices is considered ecologically and economically sustainable (Stanley et al., 2012). It is important to mention that NTFPs fulfill multiple functions in supporting human well-being via five mechanisms: (1) direct household consumption for many of the world's poorest people (and less poor too) (Saha & Sundriyal, 2012), with this consumption reaching 60% of total household income (Babulo et al., 2009); (2) income generation for many households as additional or primary cash generation (Babulo et al., 2009) reaching over 90% of total income (Bista & Webb, 2006); (3) provide a safety net, or insurance, for use in times of misfortune (drought, death of a breadwinner in the household) (Shackleton & De Vos, 2022); (4) some NTFPs play extensive and important roles in local cultures and spirituality (Shackleton & De Vos, 2022) and, (5) the use of NTFPs by local households represents a cash saving (Shackleton et al., 2007).

In the Amazon region, particularly in the eastern, the açai palm fruits (*Euterpe oleracea* Mart.) have been historically consumed by traditional populations to produce a beverage adopted as a staple food (Brondizio, 2008). Nowadays, a myriad of food-related products based on the açai fruit pulps are already present from South America to Australia as part of a global market (Yamaguchi et al., 2015). Fruit pulp demand continues to grow, leading to an intensification of fruit production via immense increments in açai palm density across natural stands managed by traditional populations, particularly in the Amazon estuarine forest, i.e., the core area of açai consumption and production (IBGE, 2021). To artificially increment palm density, the forest is subjected to frequent selective thinning of undesirable plant species, from large shrubs to emergent trees, as it reduces competition for space and light (Anderson, 1988). Intensification can increment natural açai density by many folds (from 20 to over 1000 clumps per hectare; Freitas et al., 2015) and is able to promote a complete forest replacement by açai mono-specific stands, particularly close to households (Anderson, 1988). Intensification has been recognized to cause

a decline in tree species (>15 DBH) density and richness at the forest stand level, i.e., alpha diversity (Freitas et al., 2015, 2021); however, it is reasonable to expect that intensification effects on tree assemblages are widespread, which include a decline on beta diversity, impact tree recruitment, and the understory assemblages composed by large shrubs and small-statured trees and palms since all this forest components are exposed to the selective thinning (Anderson, 1988; Tregidgo et al., 2020).

Here we examine the impact of the açai intensification (i.e., increment in the açai clump and stem density) on woody plant assemblages in an estuarine-forest landscape historically devoted to açai exploitation in the eastern Amazon region (Pará state, Brazil). Adult plants (trees, palms, and lianas) and regenerating assemblages covering contrasting conditions relative to açai density, soil attributes, and forest stand accessibility were described considering a large set of community-level attributes. Precisely, we tested the following hypothesis: açai density negatively affects the attributes (plant density, species richness, and taxonomic beta diversity and composition) of both adult and regenerating woody plant assemblages, while other variables play a minor role. Our findings update our comprehension of the açai effects on plant assemblages, question the current regulation in support of sustainable açai fruit production, indicate the required investigation while they question the basic assumption that the extraction of NTFP is naturally sustainable as it operates as a species assembly force producing impoverished assemblages.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was conducted in the state of Pará, Brazil, within three protected areas: (1) Amazonian Urban Wildlife Refuge (REVIS, 6.367.27 ha; six forest stands), (2) Combú Island Environmental Protection Area/Combú Island Extractive Reserve (APA/PAE, 1.597.2 ha; 22 forest stands) and (3) Island Grande Extractive Reserve (PAE, 922.835.7 ha; two forest stands). These three protected areas are part of an ecological corridor in the metropolitan region of Belém, the capital of the state of Pará (Figure 1; Figure S1). Flat and alluvial lands dominate the landscapes, which are exposed to both seasonal and tide-driven floodings (Silva & Jardim, 2016). Hydromorphic soils with a high clay content predominate. The climate is humid tropical, with a mean annual temperature of 27°C and an average annual rainfall of 2000 mm without the occurrence of dry months (Lau & Jardim, 2013). A tidal floodplain evergreen forest exclusively exposed to an estuarine tide regime (i.e., short-term floodings occurring daily by tides) covers the region, and thereby, it has been referred to as an estuarine forest (see Freitas et al., 2021). The tree and palm species flora are dominated by Fabaceae, Euphorbiaceae, and Arecaceae families, with the large tree *Ceiba pentandra* and the açai palm as typical elements (Lau & Jardim, 2013). Açai is a canopy, light-demanding palm species (15 to 30 m high) that occurs naturally in this forest (ter Steege et al., 2013). Biogeographically, this estuarine forest belongs to the

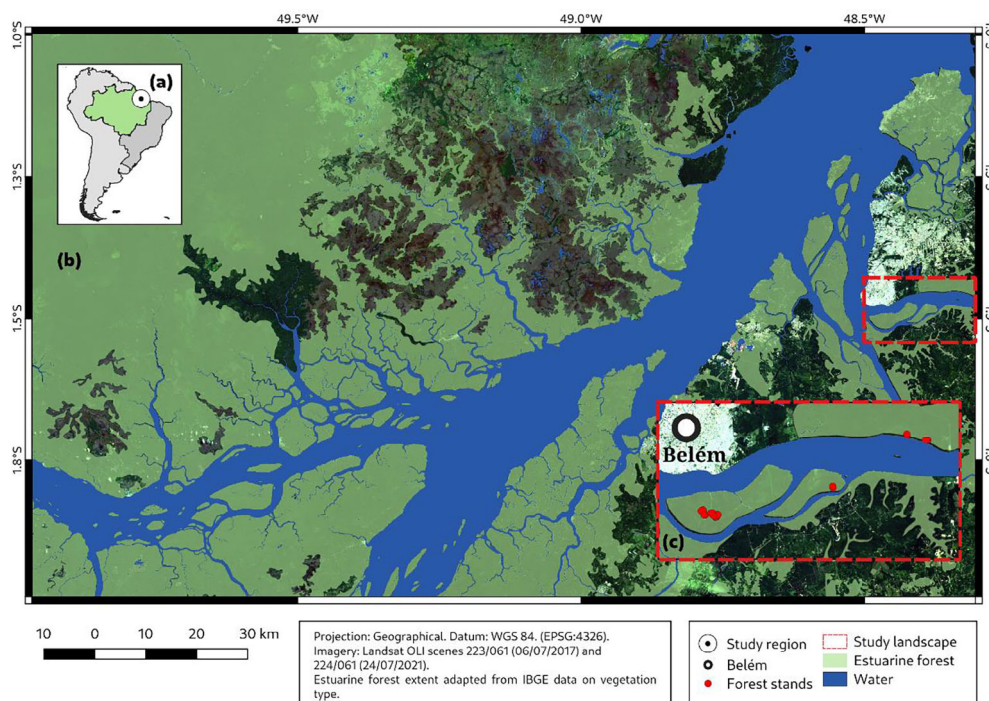


FIGURE 1 Location of the study area in the Amazon forest, northern region of Brazil (a), with emphasis on the estuarine forest (b), and details of the 30 forest stands studied (c). [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/for.24903)]

Belém Area of Species Endemism (BAE sensu Cracraft, 1985) and together with the surrounding estuarine forests, constitutes the core area of açaí fruit production in the Amazon region (IBGE, 2021).

These protected areas have long been inhabited by traditional populations (i.e., riverine people or caboclos), with livelihood or familiar-based economic supported by forest extractivism and slash-and-burn agriculture; agroforestry by agro-extractivist communities (Brondízio, 2008; Brondízio et al., 2002). Rubber latex (from *Hevea brasiliensis*), annatto (from *Bixa orellana*), cocoa (from *Theobroma cacao*), açaí (from *E. oleracea*), and valuable timber species (e.g., *Virola surinamensis*) are traditionally exploited (Anderson et al., 1985). Açaí has been managed for domestic consumption but also for commercial purposes, leading to an artificial increment in clump and stem density via practices such as the elimination of undesirable woody plant species but also the spare of useful ones (Tregidgo et al., 2020). Such an intensification gained speed in the 80s, and it is still in process across our focal landscapes (Freitas et al., 2021).

2.2 | Woody plant assemblages

We recorded all adult woody individuals (i.e., trees, palms, and lianas) with the circumference at breast height (CBH) ≥ 15 cm in 30 plots, 20 m \times 20 m (0.04 ha), and across three landscapes. Within these plots, two subplots of 4 m \times 4 m (0.0008 ha) were established to sample the regenerating plant assemblage (up to 4 m). Adults were recorded once, while regenerating individuals were recorded monthly; however, only 20 plots (out of 30) contained information for the regenerating assemblage because they were accessible for eight consecutive months (July 2019–February 2020), assuming that water dynamics can interfere with plant recruitment (Parolin et al., 2004). It

is important to note that the location of the subplots was different in each sampling month. All species collected were identified to the lowest possible taxonomic level with the aid of parataxonomists and taxonomists and by checking specimens at the regional herbarium, João Murça Pires Herbarium. Vouchers are available at the same herbarium and the Laboratory of Plant Ecology, both at the Museu Paraense Emílio Goeldi, Brazil. These plots were disposed into açaí management gradient (i.e., number of açaí clumps or stems per ha; 25–1125 clumps per ha or 25–3575 stems per ha). We considered the forest stands with ≤ 400 clumps per ha as exposed to nonintensive management and those with ≥ 400 clumps per ha as intensive management (EMBRAPA, 2015; Queiroz & Mochiutti, 2001). Stand selection was based on semi-structured interviews with the local population, with special attention to land use. We acknowledge that (1) plots were relatively small due to limited mobility across the floodplains, and (2) the best control for the effects of açaí intensification refers to landscapes covered by pristine old-growth forests rather than human-modified landscapes as we adopted here in the lack of such condition; however, both plot size and number permitted us to record over 14,000 plants and document some of the effects of açaí intensification even across landscapes historically devoted to açaí consumption/management (Brondízio, 2008); i.e., increments on clumps and stem density.

2.3 | Soil attributes and forest stand accessibility as explanatory variables

Soil attributes can also affect woody plant assemblage attributes (Baldeck et al., 2013; Lu et al., 2002). To address soil attributes at each forest stand, we collected five samples of topsoil (up to 20 cm deep)

per stand and then pooled them into a single sample per forest stand. These soil samples were analyzed by a private laboratory (EMBRAPA; *Empresa Brasileira de Pesquisa Agropecuária*) following the Brazilian protocol for agricultural analyses (EMBRAPA, 1997). Later, soil attributes were combined to create a single soil fertility index (sensu Lu et al., 2002): $SF = [Ca + Mg + K - \log(1 + Al)] * OM + 5$, where SF = Soil Fertility, Ca = Calcium ($cmolc\ dm^{-3}$), Mg = Magnesium ($cmolc\ dm^{-3}$), K = Potassium ($cmolc\ dm^{-3}$), Al = Aluminium ($cmolc\ dm^{-3}$), and MO = Organic Matter ($g\ kg^{-1}$).

We calculated the distance (m) of each plot to the main river (Rio Guamá), the nearest human settlements, and the closest bore arms of the river (i.e., small drainage channels). These four Geo information collapsed, resulting in a main axis with 69% explanatory power, adopting the method of principal component analysis (PCA). Accessibility in this study represents a measure of chronic anthropogenic disturbance (i.e., consumption of forest products) as adopted by Hawes et al. (2012) and Arnan et al. (2018) and can potentially affect woody plant assemblages in addition to açai intensification.

2.4 | Data analysis

Collinearity between açai stems density, soil fertility and accessibility (i.e., explanatory variables) was checked using the variation inflation factor (VIF) via *car* package (Fox & Weisberg, 2019); as they were not collinear (VIF values <2; açai stem density = 1.34, soil fertility = 1.30 and accessibility = 1.05), all of them were included in the subsequent analyses (Jou et al., 2014; Legendre & Legendre, 1998). It is important to mention that we consider both açai clump density and açai stem density in different analyses. We decided to use açai stems density because we consider it a more accurate variable as compared to açai clump density (see Freitas et al., 2021), as açai clumps can support one or several stems. The explanatory-variable effects on the attributes of woody plant assemblage were assessed using generalized linear models (GLMs) from the *stats* package. For the GLMs, binomial negative distribution was used for the count variable (density), and Gaussian distribution was used for continuous data ($q = 0$, $q = 1$, $q = 2$, and NMDS1) (Venables & Smith, 2018). Residues were checked via *DHARMa* (Hartih, 2022) and *hnp* (Moral et al., 2017) packages, while under/overdispersion was checked by dividing the residual deviance by the degrees of freedom. Here, NMDS axis 1 was used as a proxy for woody species' taxonomic composition.

We calculate taxonomic beta diversity and its components based on a pairwise method. Both Sorensen (presence) and Bray-Curtis (abundance) dissimilarity coefficients were used to calculate the total beta diversity, turnover, balanced variation, nestedness, and abundance gradient using the *betapart* package (Baselga, 2016). To understand how açai clump density affects woody plant-assemblage beta diversity, clump density was adopted as an environmental distance matrix, which was in contrast to diversity scores. In this context, Euclidean distance was used as a pairwise index for each site, and a Pearson Partial Mantel test with 999 permutations was run with a third spatial distance matrix. The environmental, spatial and Pearson

Partial Mantel test were performed using a *vegan* package (Oksanen et al., 2019).

To examine how açai clump density influences species abundance, positively (increasing the abundance) or negatively (reducing the abundance), a TITAN test was adopted via *TITAN2* package (Baker & King, 2010). Finally, to exam the taxonomic organization of both adult and regenerating assemblages and their response to açai density, we applied a nonmetric multidimensional scaling (NMDS) followed by ANOSIM (Oksanen et al., 2019) based on Bray-Curtis dissimilarity matrices using the *vegan* package.

3 | RESULTS

A total of 1169 adult woody plants from 109 species and 34 families were recorded across all the 30 estuarine forest stands (Table S1), including 13.125 açai clumps and 40.000 açai stems. Trees dominated adult assemblages by accounting for 92.59% of all species and 52.52% of the individuals by excluding açai clumps/stems. Stem density and species richness achieving 563.3 ± 298.1 and 18.6 ± 9.3 per $400\ m^2$ (mean \pm SD) as açai clumps were excluded from adult assemblages. More than half of the species (55.04%) were considered rare (i.e., one or two individuals across the 30 forest stands). In fact, woody plants assemblages were dominated by few species, with the 10 most abundant species representing nearly 70% of individuals (Figure S2). Woody plants density varied from 75 to 1125 and it was reduced by half as açai stems density increased up to 3575 (density: $x^2 = 5.87$, $p = 0.01$; Figure 2a). The same occurred with species richness ($q = 0$: $x^2 = 7.22$, $p = <0.01$; Figure 2c) and typical species ($q = 1$: $x^2 = 5.26$, $p = 0.02$; Figure 2e). Only dominant species ($q = 2$) were not related to açai stems ($x^2 = 2.07$, $p = 0.14$; Figure 2g). These same variables were positively related to accessibility (density: $x^2 = 5.70$, $p = 0.01$ [Figure 2b]; $q = 0$: $x^2 = 10.63$, $p = <0.01$ [Figure 2d]; $q = 1$: $x^2 = 12.67$, $p = <0.01$ [Figure 2f] and $q = 2$: $x^2 = 9.23$, $p = <0.01$ [Figure 2h]). None of the response variables were correlated with soil fertility (Table 1).

Moving to the regenerating assemblages, 13,378 individuals were record from 168 species and 46 families across the 20 forest stands (Table S2). By excluding açai clumps, trees also dominated the regenerating assemblages; 92.26% of all species and 76.55% of the individuals. Stem density and species richness achieved 343.8 ± 108.4 and 48.4 ± 17.4 per $16\ m^2$ respectively by excluding açai clumps/stems. Similar to the adult tree assemblages, many species (36.3%) were considered rare across the 20 forest stands with regenerating assemblages dominated by few species, i.e., the 10 most abundant species also representing nearly 70% of individuals (Figure S3). Plant density across regenerating assemblages varied from 170 to 568.1 and it was positively related with soil fertility (density: $x^2 = 8.19$, $p = <0.01$; Figure 3b). In fact, plant density doubled in more fertile forest stands. On the other hand, açai stem density negatively affected species richness ($q = 0$: $x^2 = 4.21$, $p = 0.04$; Figure 3c), typical species ($q = 1$: $x^2 = 16.02$, $p = <0.01$; Figure 3e) and dominant species ($q = 1$: $x^2 = 18.36$, $p = <0.01$; Figure 3g). By considering the extremes açai

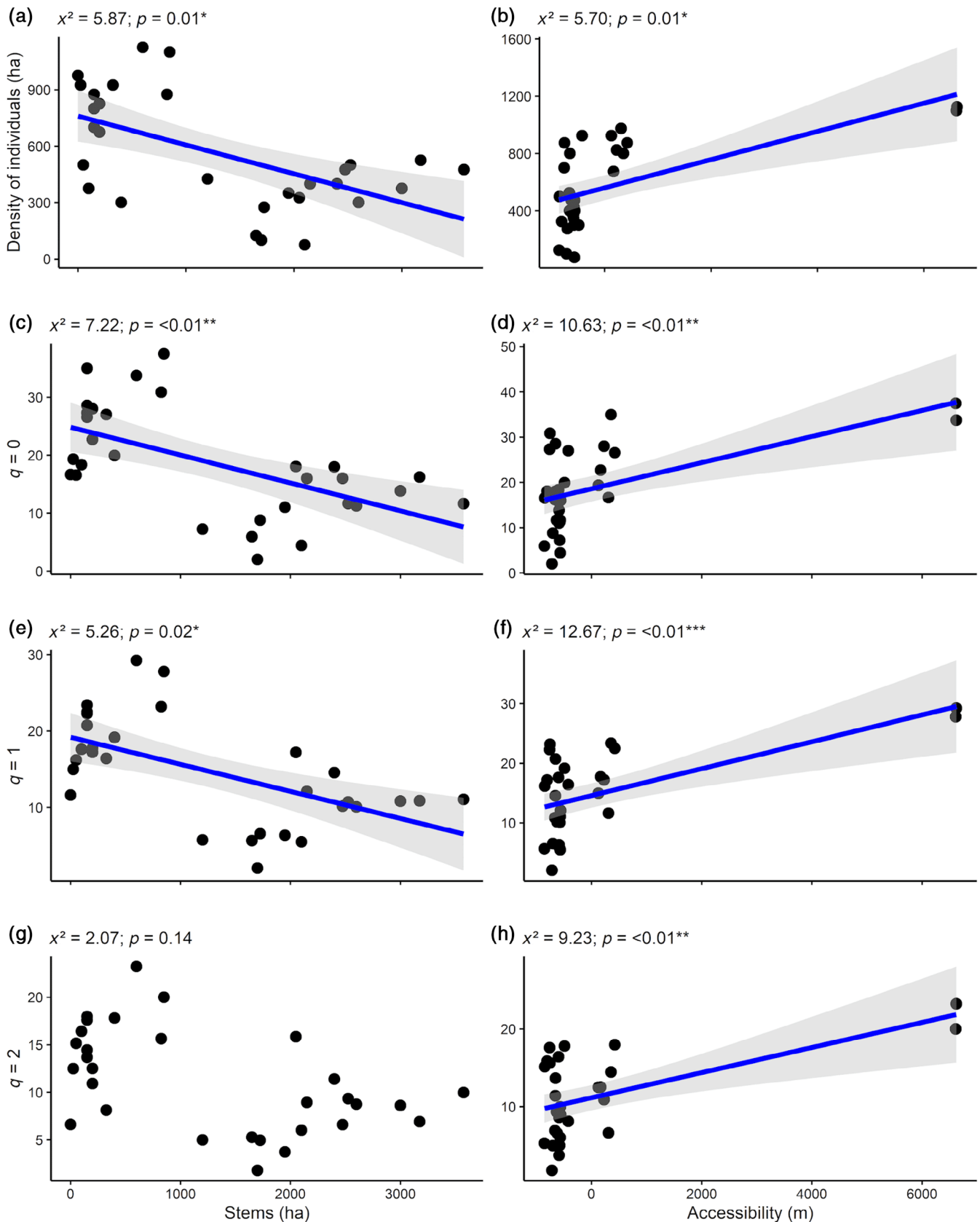


FIGURE 2 Relationship between explanatory variables (stems (ha) and accessibility (m)) and response variables (density of individuals (ha), species richness ($q = 0$), typical species ($q = 1$) and rare species ($q = 2$)) in relation to adult woody assemblages of an Amazonian estuarine forest. $^*p < 0.05$; $^{**}p < 0.001$; $^{***}p < 0.0001$. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/for.2903)]

TABLE 1 Results of generalized linear models between explanatory variables (stems (ha), soil fertility and accessibility (m)) and response variables (density of individuals (ha), species richness ($q = 0$), typical species ($q = 1$), rare species ($q = 2$) and NMDS1) in 30 forest stands in the Amazon estuarine region, Brazil.

	Stems (ha)	Soil fertility	Accessibility (m)	r^2
Adult woody assemblages				
Density	$\chi^2 = 5.87$ $p = \mathbf{0.01^*(-)}$	0.02 0.86	5.70 0.01^*(+)	0.63
$q = 0$	$\chi^2 = 7.22$ $p = \mathbf{<0.01^{**}(-)}$	<0.01 0.93	10.63 <0.01^{**}(+)	0.53
$q = 1$	$\chi^2 = 5.26$ $p = \mathbf{0.02^*(-)}$	0.63 0.42	12.67 <0.01^{***}(+)	0.56
$q = 2$	$\chi^2 = 2.07$ $p = 0.14$	1.54 0.21	9.23 <0.01^{**}(+)	0.48
NMDS1	$\chi^2 = 14.83$ $p = \mathbf{<0.01^{***}(-)}$	0.76 0.38	3.06 0.07	0.61
Regenerating assemblages				
Density	$\chi^2 = <0.01$ $p = 0.94$	8.19 <0.01^{**}(-)	3.00 0.08	0.64
$q = 0$	$\chi^2 = 4.21$ $p = \mathbf{0.04^*(-)}$	0.01 0.90	0.78 0.37	0.32
$q = 1$	$\chi^2 = 16.02$ $p = \mathbf{<0.01^{***}(-)}$	0.90 0.34	0.61 0.43	0.65
$q = 2$	$\chi^2 = 18.36$ $p = \mathbf{<0.01^{***}(-)}$	1.44 0.22	0.09 0.75	0.68
NMDS1	$\chi^2 = 37.57$ $p = \mathbf{<0.01^{***}(-)}$	3.70 0.05	0.02 0.87	0.81

Note: Significant ($p < 0.05$) results are in bold. Positive signal indicate significant positive relationships, whereas negative signal indicate the opposite trend. * $p < 0.05$; ** $p < 0.001$; *** $p < 0.0001$.

stem density, species richness, typical and dominant species dropped by almost half. None of the woody plant assemblage attributes correlated with accessibility (Table 1).

Açaí clump density positively affected beta diversity (i.e., pairwise dissimilarity) across adult woody plant assemblages by considering both incidence and abundance-based dissimilarity with taxonomic beta-diversity being represented more by turnover (Figure 4b) and balanced variation (Figure 4e) than nestedness (Figure 4c) and abundance gradient (Figure 4f; Table 2). In contrast, açaí clump density did not affect beta diversity across regenerating forest stands (Figure 5; Table 2), but it was geographical distance (Table 2).

The açaí clump density, moreover, affected the abundance of particular woody plant species positively and but also negatively considering both adult and regenerating woody plant assemblages: 11 species from adult (Figure 6a) and six species in the case of regenerating assemblages (Figure 6b). It is worth mentioning that with the exception to *Quararibea guianensis* (Malvaceae) and *Astrocaryum murumuru* (Arecaceae), this team of species declined before the 400-açaí clump density threshold (Figure 6a); moreover, all woody species that responded positively to increments in açaí clump density occurred widespread across forest stands. Accordingly, açaí clump density

influenced the taxonomic organization of both adult ($\chi^2 = 14.83$, $p = <0.01$; Table 1) and regenerating woody plant assemblages ($\chi^2 = 37.57$, $p = <0.01$; Table 1). Finally, adult and regenerating plant assemblages exhibited distinct taxonomic composition (ANOSIM: $R = 0.93$, $p = <0.01$; Figure S4) by sharing 45 species ($\cong 17\%$) of the whole flora. It is worth mentioning a group of 105 species, which were recorded across the regenerating assemblages but not in the adult woody plant assemblages. Among them, a large number of small-statured woody plant species typical from the forest understory (i.e., the shade-tolerant flora) such as those from *Miconia*, *Piper*, *Baccharis*, *Annona*, and *Geonoma* genera.

4 | DISCUSSION

Our results suggest that açaí clump and stem density (i.e., a measure of açaí management intensification) reorganize woody plant assemblages in the estuarine forest landscapes devoted to açaí fruit production. Açaí intensification reduces the density and alpha taxonomic diversity of both adult woody plant assemblages inhabiting the forest canopy and the emergent layer, but also of those assemblages

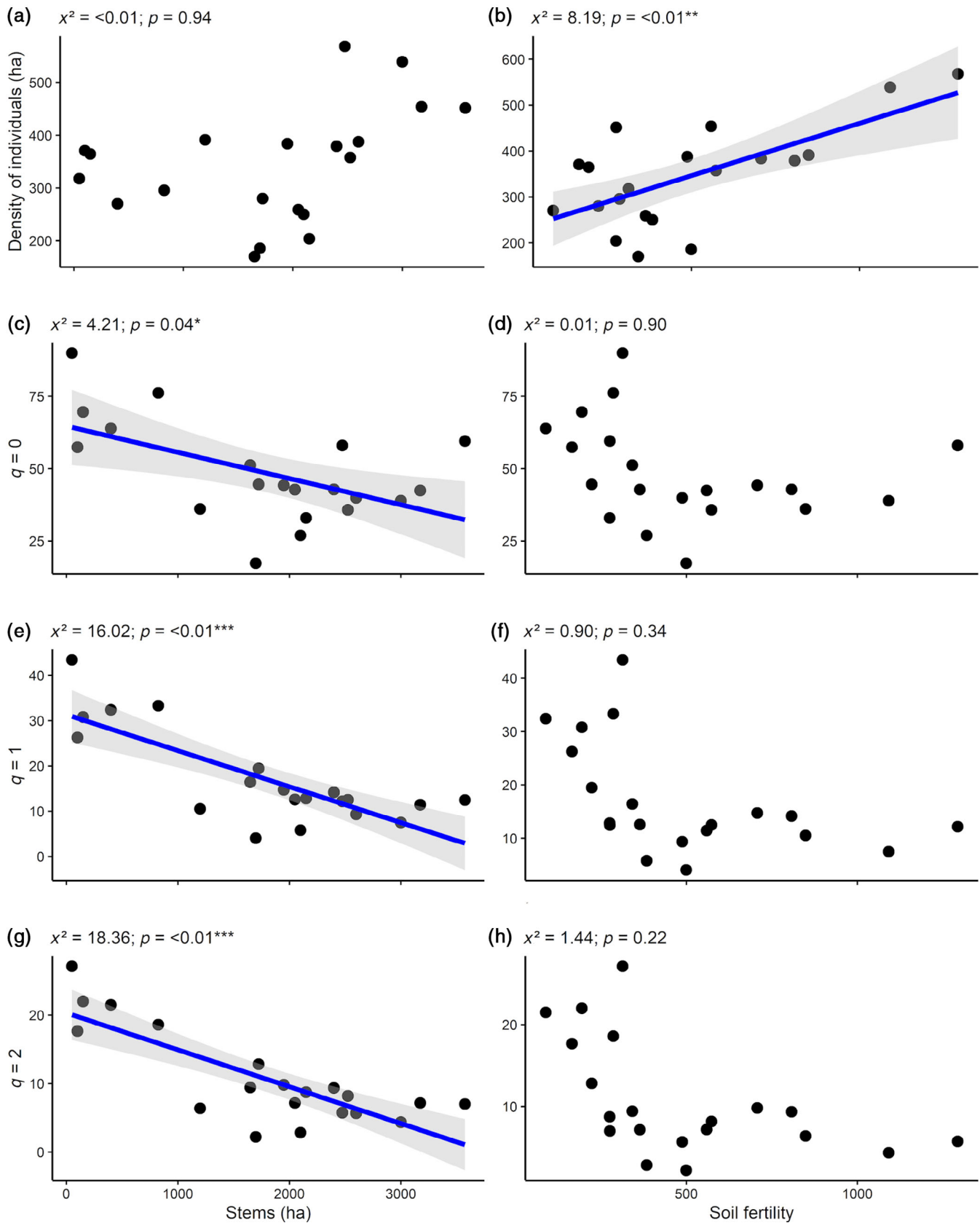


FIGURE 3 Relationship between explanatory variables (stems (ha) and soil fertility and response variables (density of individuals (ha), species richness ($q = 0$), typical species ($q = 1$) and rare species ($q = 2$)) in relation to regenerating assemblages of an Amazonian estuarine forest.

* $p < 0.05$; ** $p < 0.001$; *** $p < 0.0001$. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/for.2903)]

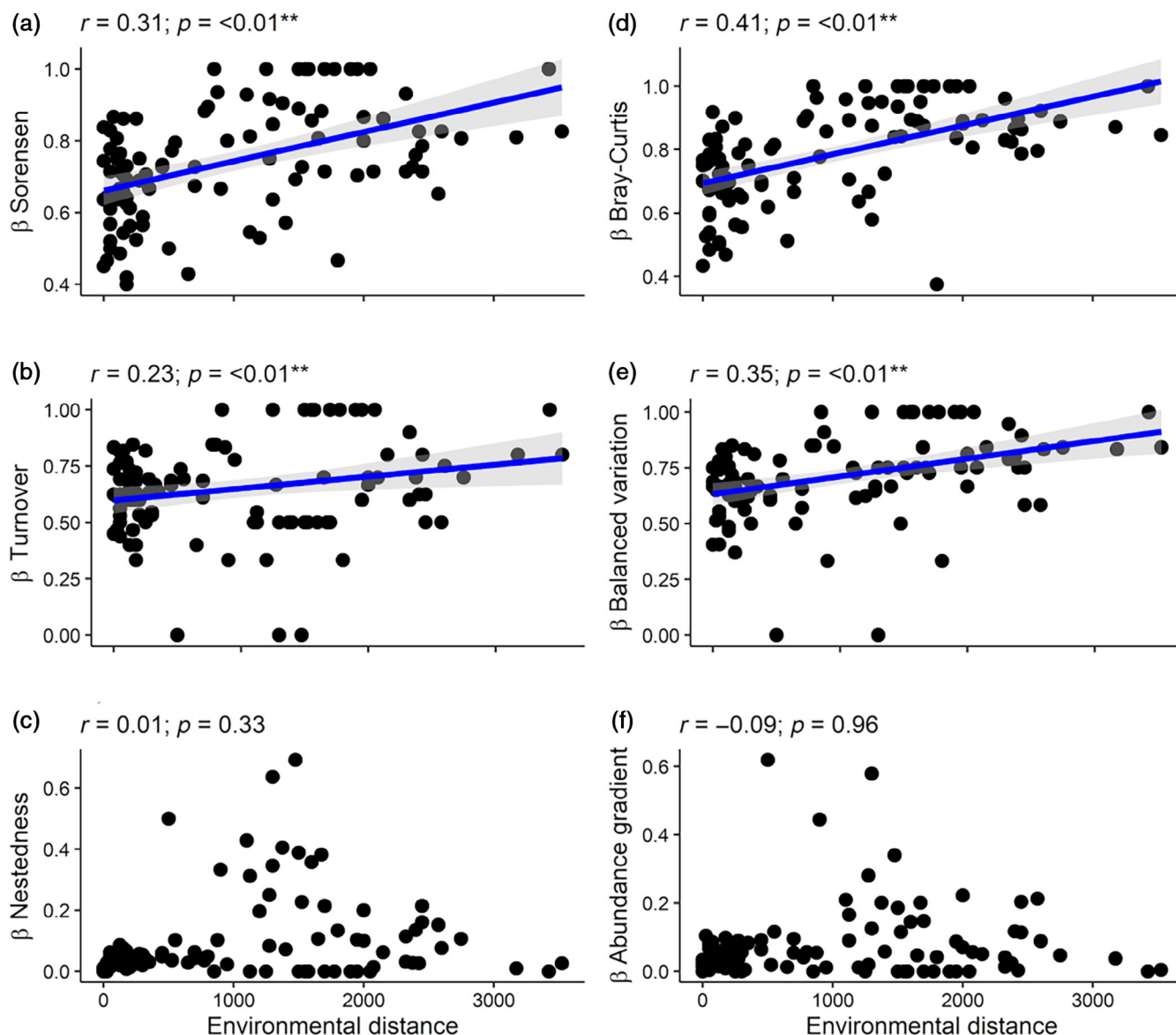


FIGURE 4 Relationship between biotic dissimilarity and environmental distance (açaí clump density) using incidence (a–c) and abundance (d–f) in relation to adult woody assemblages of an Amazonian estuarine forest. Total dissimilarity (β Sorensen and β Bray-Curtis) and its components (β Turnover, β Nestedness, β Balanced Variation, and β Abundance gradients). Both determination coefficients (r) and significance (p) for each relationship are shown. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/1365-3113.12025)]

inhabiting the forest understory. We refer to assemblages by small-statured tree species, palms, and large shrubs. In fact, such understory assemblage appears to be much more diverse than canopy and emergent assemblages, as they combine individuals from species occurring across all forest vertical habitats. On the other hand, açaí intensification appears to increment taxonomic beta diversity, particularly due to species turnover in response to the reduction in alpha diversity and increasing levels of rarity as açaí density increases. The estuarine forest also supports an ecologically diverse team of sensitive species (from large trees to shrubs), which decline before the regulatory threshold of 400-açaí clumps ha, while a reduced number of species respond positively. Accordingly, açaí intensification reorganizes plant assemblages taxonomically but also ecologically toward impoverished

species sets, probably including the assemblages responsible for forest regeneration and structural integrity (i.e., saplings from the canopy and emergent tree species).

Our findings reinforce the notion that açaí intensification promotes the establishment of low-density and impoverished adult tree assemblages, which become taxonomically distinct as açaí density increases, as already documented (Freitas et al., 2015, 2021); however, we offer evidence suggesting that species loss among adult tree assemblages occurs across forest stands still supporting relatively low-density açaí stands; species loss occurs as soon as intensification starts to alter açaí abundance (Figure 2; Table 1). On the other hand, few species respond positively to açaí intensification (Figure 6a,b); i.e., more losers than winners sensu Tabarelli et al. (2012).

TABLE 2 Partial Mantel results (Pearson method) showing the relationship between woody assemblages dissimilarity (taxonomic) and environmental distance (açai clumps by ha) of an Amazonian estuarine forest, Brazil.

	Ydis	Xdis	Zdis	Mantel <i>r</i>	Significance
Adult woody assemblages					
Incidence	Sorensen	Geo	Env	0.12	0.10
		Env	Geo	0.31	<0.01**
	Turnover	Geo	Env	0.09	0.16
		Env	Geo	0.23	<0.01**
	Nestdness	Geo	Env	−<0.01	0.47
		Env	Geo	0.01	0.33
Abundance	Bray-Curtis	Geo	Env	0.10	0.11
		Env	Geo	0.41	<0.01**
	Balanced variation	Geo	Env	0.05	0.20
		Env	Geo	0.35	<0.01**
	Abundance gradient	Geo	Env	0.02	0.32
		Env	Geo	−0.09	0.96
Regenerating assemblages					
Incidence	Sorensen	Geo	Env	0.41	<0.01**
		Env	Geo	−<0.02	0.57
	Turnover	Geo	Env	0.17	0.08
		Env	Geo	−<0.02	0.57
	Nestdness	Geo	Env	0.21	0.08
		Env	Geo	−<0.01	0.43
Abundance	Bray-Curtis	Geo	Env	0.74	<0.01**
		Env	Geo	−0.05	0.70
	Balanced variation	Geo	Env	0.72	<0.01**
		Env	Geo	−0.05	0.72
	Abundance gradient	Geo	Env	−0.26	1
		Env	Geo	0.02	0.40

Note: The significance of the statistic is evaluated by permuting (999 permutations) rows and columns of the explanatory dissimilarity matrix (xdis), using partial correlation conditioned on a third matrix (zdis). Significant ($p < 0.05$) results are in bold. A positive signal indicates significant positive relationships, whereas a negative signal indicates the opposite trend. * $p < 0.05$; ** $p < 0.001$; *** $p < 0.0001$.

Furthermore, our findings indicate the occurrence of a diverse woody plant assemblage inhabiting forest understory, which combines saplings from canopy tree species, but also a variety of large shrubs, small-statured trees, and palm species (Table S2), i.e., a typical understory assemblage across tropical forests (Gentry & Emmons, 1987; Whitmore, 1984). This neglected forest component in açai-related studies, but not necessarily less diverse than the canopy woody assemblage, appears to be negatively affected by açai intensification, and thus, calls attention to other forest components being impacted by açai intensification. In fact, a reasonable portion of the Amazonian woody plant flora consists of shrubs, small-statured trees, and palms inhabiting forest understory by being shade-tolerant species; i.e., the whole life-cycle in the shaded forest understory (Bloor & Grubb, 2003). The few estimates available report a minimum of 16% of tree species flora belonging to this ecological group in the Amazon region (Assis & Wittmann, 2011); however, by considering herbs, shrubs and small palms, the understory flowering species flora is expected to achieve over 20% of all species (see Costa &

Magnusson, 2002). Unfortunately, there is little information about the Amazon estuarine forest, even for the tree flora, although this unique forest represents the core area of açai production and intensification (Brondizio, 2008) and an ecologically unique component of an area of species endemism considering an immense number of taxa, from insects to primates (Moraes et al., 2020; Silva et al., 2022).

Although we did not explicitly address the baseline mechanisms driving the changes in plant assemblages, it has been argued that the elimination of undesirable trees in order to provide better microclimatic conditions and the space demand to increment clump density is the main driver for the impoverishment that tree assemblages experience as açai clump density increases (Freitas et al., 2015, 2021). Such forest thinning or coppicing is one of the prescribed management procedures in order to increment açai fruit productivity (Anderson, 1988), and to a large extent responds to a complete degradation of forest spatial structure and the impoverishment of tree assemblages, although it has never been experimentally tested. In this context, decreasing species richness and increasing rarity as açai density

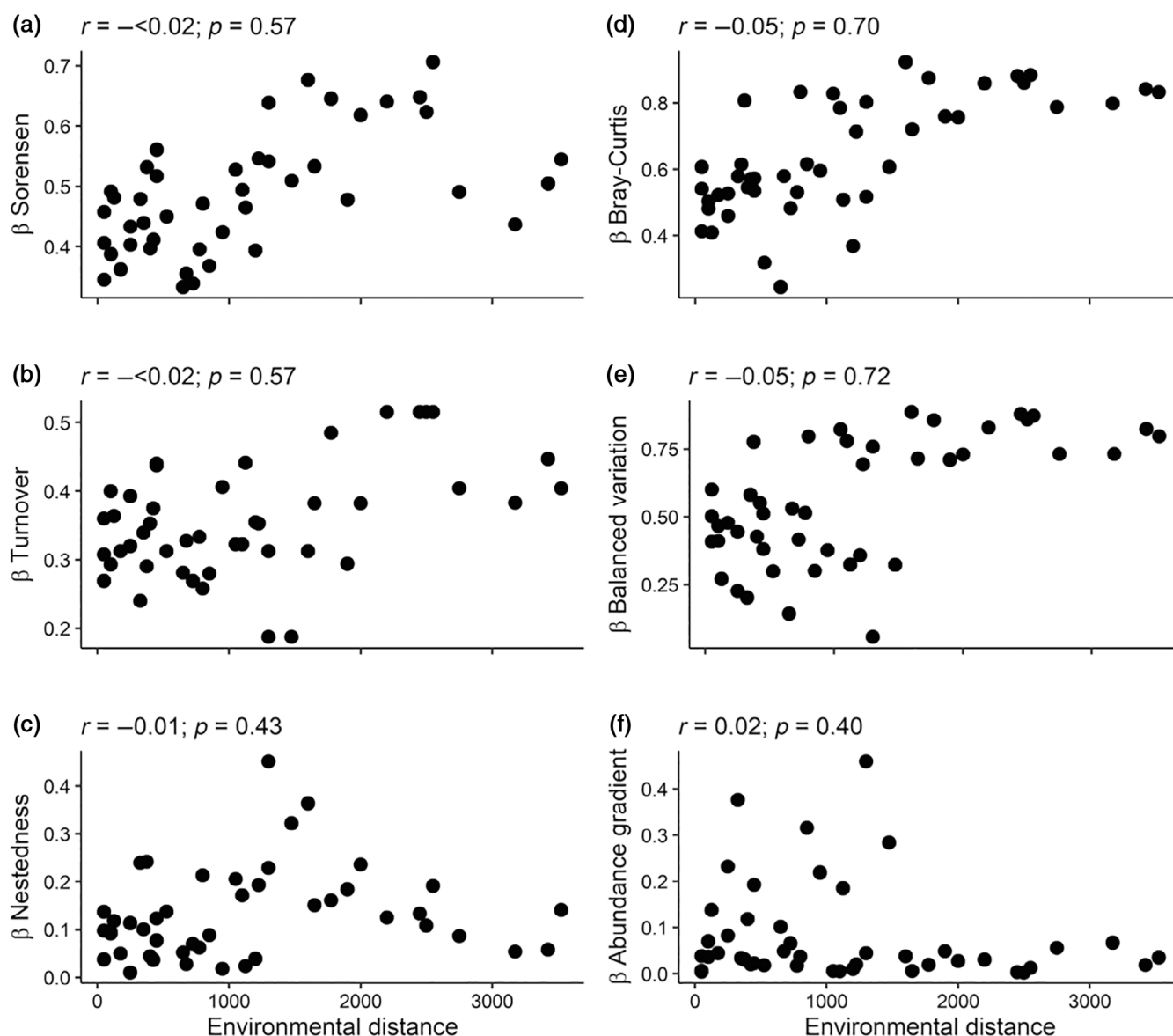


FIGURE 5 Relationship between biotic dissimilarity and environmental distance (açaí clump density) using incidence (a–c) and abundance (d–f) in relation to regenerating assemblages of an Amazonian estuarine forest. Total dissimilarity (β Sorensen and β Bray-Curtis) and its components (β Turnover, β Nestedness, β Balanced Variation, and β Abundance gradients). Both determination coefficients (r) and significance (p) for each relationship are shown.

increases is probably the mechanism behind higher beta diversity as intensification proceeds (see Figure 4), a similar phenomenon in response to habitat loss and fragmentation resulting in low gamma diversity as already documented; i.e., species richness at landscape/regional level (Sfair et al., 2016).

In fact, it is reasonable to propose that changes promoted by forest thinning in forest physical structure and woody plant assemblages will alter a myriad of processes, limiting further plant recruitment upon which thinning operations will occur; for example, elimination of large trees probably results into much more illuminated habitats filtering shade-tolerant species while favoring light demand such as sun-loving grasses and açaí recruitment (Pinho et al., 2020; Rutishauser et al., 2016). Similarly, the elimination of large buttressed trees,

including their large dead trunks over the ground, is likely to increase seed runoff during water descending (Junk et al., 2010). Increased runoff causing lower soil fertility is another potential effect of “açaização”, the local expression to describe intensification leading to the emergence of monospecific stands, which are not permitted according to current regulation but continue to proliferate (Freitas et al., 2021; Hiraoka, 1993). As we have documented here, soil fertility is associated with several community and ecosystem attributes across tropical forests, including density, species richness, forest productivity, and aboveground biomass, with cascading effects relative to support for herbivores/frugivores assemblages (Cleveland et al., 2011; Gentry & Emmons, 1987; Peres, 2008). It is interesting to note that forest stand accessibility was positively associated with adult species richness

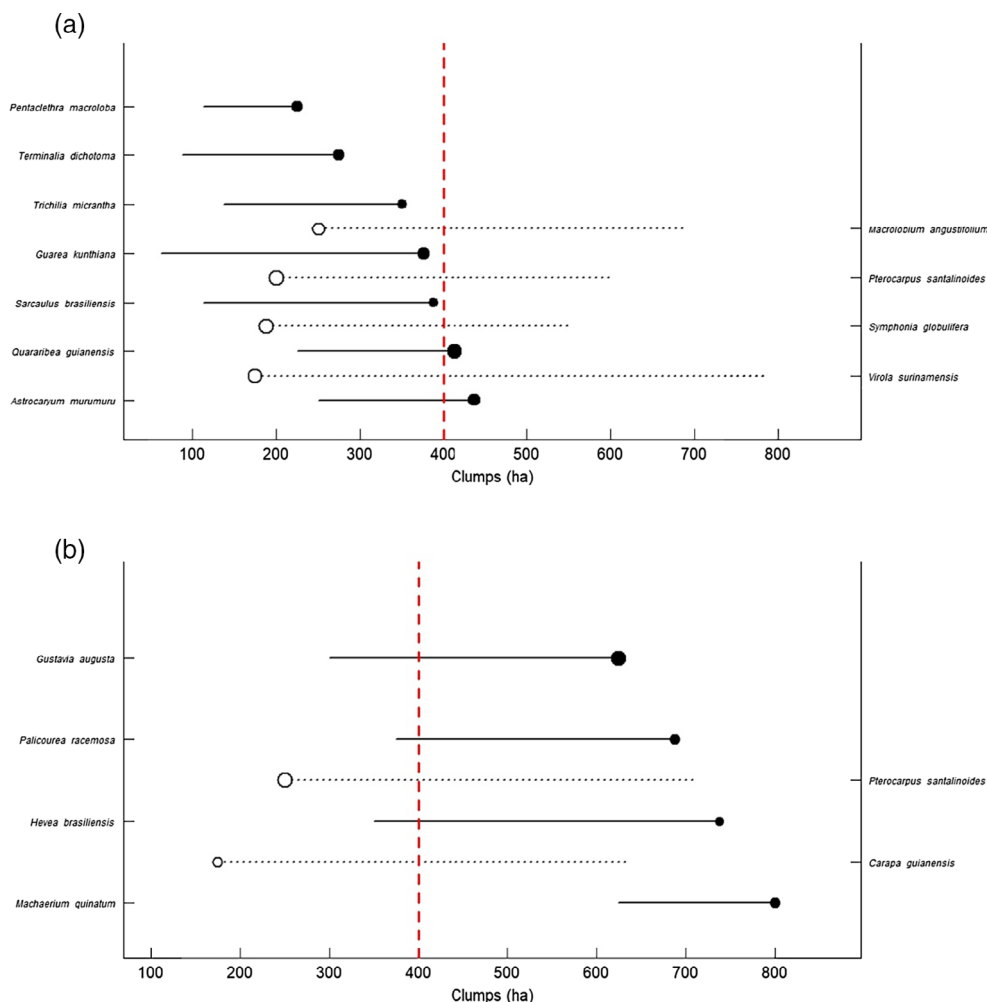


FIGURE 6 Threshold Indicator Taxa ANalysis (TITAN) of adult (a) and regenerating (b) woody assemblages response to açaí clump density across 30 forest stands of an Amazonian estuarine forest, Brazil. Horizontal lines overlapping each symbol represent 5th and 95th percentiles among 5000 bootstrap replicates. Only species affected negatively (left; reducing in abundance) and positively (right; increasing in abundance) are represented. The dashed red line represents the 400-açaí clump density threshold. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/for.2903)]

(Figure 2; Table 1). Such a priori unexpected result may, in fact, result from a higher number of useful species being spared close to households, such as *Theobroma cacao*, *H. brasiliensis*, *Spondias mombim*, *Mauritia flexuosa* (Nogueira et al., 2005; Tregidgo et al., 2020). Additionally, açaí dropped fronds may cover seedlings on the ground and reduce the recruitment of woody plant species as already documented for other palm species (Peters et al., 2004). Finally, there is evidence suggesting that açaí intensification disturbs plant pollination (Campbell et al., 2018) and seed dispersal by frugivorous vertebrates (Moegenburg & Levey, 2002). We refer to both abiotic and biotic changes affecting plant recruitment and then contributing to forest impoverishment as “managed forest/landscapes” experience the intensification trajectory.

In this context, the current regulation requiring a maximum of 400-açaí clumps per ha plus the persistence of 50 palm trees of other species and 200 trees hardwoods, 40 thick (>45 cm DBH), 40 medium (20 to 45 cm DBH) and 120 thin (5 to 20 cm DBH) is highly welcome (see Queiroz & Mochiutti, 2001); however, to acknowledge the açaí management as sustainable and then stimulate legislation compliance by riverine traditional producers, it is highly recommendable to examine in which extent these thresholds are able to guarantee forest integrity considering and all ecosystem services this forest provide,

from biodiversity persistence to the apportion of organic material (e.g., leaves, flowers, fruits, seeds) to a highly productive estuarine system (Sodré et al., 2011). Accordingly, it is required a reference ecosystem (sensu Suganuma & Durigan, 2015) as a baseline (probably landscapes still covered by old-growth forests) to investigate forest changes and responses to the whole package involving the açaí management as it involves more forest thinning and increments on açaí density.

It is true the estuarine forest has long been submitted to the extraction forest products, including management, to favor cocoa, rubber trees and açaí; i.e., a typical land-sharing approach (Green et al., 2005). Like in the past, such a “disturbed forest” currently experiencing açaí intensification continues to be exposed to a management exclusively restricted to açaí forestry/agricultural demands rather than a management able to guarantee both forest products and forest integrity. Such a broad perspective of forest management is likely to demand land-use zoning and the establishment of *strictu* sensu protected areas in addition to a more comprehensive and robust set of guidelines to manage açaí stands considering multiple spatial scales (e.g., land-sparing vs. land-sharing). This more ambitious approach remains neglected due to a lack of (1) a substantial research effort focused on the multiple impacts of açaí intensification (from

local to regional scales), such as the collapse of the understory flora, and (2) a detailed reference on the estuarine forest relative to patterns of species diversity, community organization, physical structure, and ecosystem functioning, including primary productivity and biomass.

In synthesis, we shall recognize that rather than the extension of the flooding period (Parolin & Junk, 2002), açaí intensification currently represents the major driver of plant species assembly and community organization operating across several floodplain forests. Applied, açaí intensification moves forward into a “blind context,” and thus, it can be considered a major threat to estuarine/floodplain forests, offering a disturbing message about the role played by NTFPs as an opportunity for sustainability. In fact, the “açaí case” informs us that NTFPs can only be sustainably extracted in the case appropriate public policies/regulations are incorporated to guarantee traditional low-impact forest management approaches rather than market-oriented management stimulating intensification.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the Appendix S1 of this article.

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SUPPORTING INFORMATION

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