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RESEARCH ARTICLE

Açaí palm management disturbs seed rain and soil seed bank of an Amazonian estuarine forest

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Abstract

The exploitation of non-timber forest products has been proposed as a sustainable way to exploit tropical forests, but such an opportunity remains to be proved. Here, we examine the impact of intensive açaí palm (*Euterpe oleracea*) management on the seed rain and soil seed bank in an estuarine forest landscape with a long history of forest management by locals in the Amazon region. Seed rain (100 80 cm^2 collectors) and soil seed bank (100 30 cm^2 samples) were monitored through a year across 20 forest stands, covering a gradient of açaí stem density (50–3575 açaí stems per ha). Seed rain and bank were dominated by açaí seeds (85.5%–85.8%) and by excluding them, seed rain and bank were low density and species poor, capturing a tiny subset from the local (17.91%–19.40%) and landscape woody flora (11.82%–14.55%). Moreover, autochthonous and vertebrated-dispersed predominated as well as those from tree species considered useful by locals. Overall, açaí stem density positively affected açaí seed abundance in the seed rain and negatively affected seed pools in the bank in relation to abundance of seeds and vertebrated dispersed, while adult tree species richness and density and accessibility to forest stands were associated with more diversified seed pools. Thereby, forest stands are exposed to different levels of açaí management (high vs. low intensity) supported taxonomically distinct seed pools. Our results suggest that açaí intensification disturbs seed rain and soil seed bank with potential impacts on forest regeneration and the forest integrity standards required to consider açaí fruit production as sustainable according to current legislation.

KEYWORDS
Amazon, estuarine forest, forest regeneration, non-timber forest products, sustainability

INTRODUCTION

Tropical forests are responsible for providing essential ecosystem services at both local and global scales (Hawes et al., 2020). These services include carbon sequestration and storage, climate regulation, maintenance of soil fertility, biodiversity conservation and support for the livelihoods of thousands of traditional forest-dependent populations across the tropics (Fearnside, 2015; Hawes et al., 2020). However, the provision of these ecosystem services is threatened by the replacement of forests by other forms of land use (e.g., agriculture and livestock) or forest degradation in response to other disturbances such as selective logging and exploitation of non-timber forest products (NTFPs) (Brockerhoff et al., 2017; Chazdon, 2003); as well as climate change (Senior et al., 2017). Accordingly, the loss and degradation of tropical forests, including the elimination of traditional human cultures, have attracted the attention of scientists and decision-makers across the globe (Pandit et al., 2020). Indeed, the exploitation or sustainable use of tropical forests is one of the great scientific, technological, political and economic challenges of this century.

In this context, the exploitation of NTFPs has been put forward as a way to reconcile employment and income, conservation of biological diversity and the provision of essential ecosystem services as forest integrity is maintained (Ticktin, 2004). However, this new conservation paradigm becoming increasingly controversial in the context of tropical forests, not only from the point of view of the economic viability and its potential for poverty reduction among traditional populations that are reliant on extractivism (e.g., fruits, fibres, resins) but also due to the impacts on biological diversity at different levels of ecological organization; i.e., ecological sustainability (Arnold & Pérez, 1996; Gaoue et al., 2016; Illukpitiya & Yanagida, 2010). There is evidence that exploitation of NTFPs can lead to the collapse of exploited plant populations from direct exploitation of resins, fruits, leaves, seeds, among other products (Ticktin, 2004). Changes in the structure of plant communities (i.e., reduction in the abundance of individuals and richness of tree species) and in the physical structure of the forest have also been reported as direct and indirect results of management practices associated with the exploitation of NTFPs (Freitas et al., 2021, 2015; Trauernicht & Ticktin, 2005).

The exploitation of NTFPs may be associated with hunting, elimination of plants without economic value, increases in the density of exploited plants, among other practices (Trauernicht & Ticktin, 2005). These practices, either directly (e.g., elimination of large trees) or indirectly (e.g., changes in light regime and microclimate) can alter the regeneration process and the successional pathway of the forest and, consequently, the provision of key ecosystem services. Namely, we refer to changes in the seed rain and soil seed bank, two fundamental mechanisms of tropical forest regeneration, with direct impacts on the tree assemblage structure (Baider et al., 2001; Chalermsri et al., 2020; Menezes et al., 2019; Shahabuddin & Prasad, 2004). Potential impacts the exploitation of NTFPs on forest regeneration and dynamics remains poorly explored as most studies has focused on the target plant populations and the viability of such exploitation (Hernández-Barrios et al., 2015).

The exploitation of the fruits of the açaí palm (*Euterpe oleracea* Mart.) in the Amazon estuarine forests (i.e., the Amazonian "black gold") offers an interesting opportunity to investigate the impact of this practice on forest regeneration and the taxonomic and functional composition of the remaining forests, with plausible impacts in the maintenance of ecosystem services and sustainability (both economic and ecological). Fruits from this native palm are the most important cash crop in the Amazon estuary and a staple food for local riverine populations (Brondízio et al., 2002), but also a commodity in the global market devoted to energetic and health drinks (Freitas et al., 2021). Traditionally, the açaí palm density is increased (i.e., stem and clump density) by eliminating competing vegetation, including much of the trees (i.e., understory, canopy, emergent trees) to increase the amount of light and decrease competition with other species, while açaí naturally emerged seedling/saplings are spared/favoured (Anderson et al., 1995; Freitas et al., 2015). Açaí traditional management also includes the retention or even the cultivation of other economically valuable species such as cocoa (*Theobroma cacao* L.) and timber species (Freitas et al., 2015).

Açaí-dominated forests have lower biomass and lower canopy/foliar cover due to reduction on tree density (i.e., decline of local seed production), with implications on the light regime and microclimate conditions (Freitas et al., 2021, 2015). These changes facilitate some life forms such as light-demanding herbaceous plants (Braga & Jardim, 2019), but also the recruitment of light-demanding species such as the açaí palm (Arango et al., 2010; Damasco et al., 2022), with a positive response particularly among young palms (Ramírez et al., 2015). All of these factors may affect the seed rain and soil seed bank, both taxonomically and functionally, potentially leading to alternative successional trajectory as açaí management intensifies. As an international commodity (Freitas et al., 2015), the açaí fruit production is a model capable of spreading the discussion about the exploration of NTFPs and the integrity of tropical forests. It has been already proposed and regulated that a forest stand managed for açaí production (i.e., açaizal) should contain per hectare (1) a maximum of 400 clumps with five stems per clump, (2) 50 individuals from other palm species (20 adult and 30 young) and (3) a minimum of 200 broadleaved trees, 40 of which large (>45 in DBH), 40 medium (20–45 cm in DBH) and 120 small-statured (5–20 cm in DBH). This number of plants should guarantee a high production of açaí fruits and hearts of palm, with a minimal change in biodiversity (Mochiutti et al., 2002). However, several producers along the Amazon estuary do not seem to be following the plan and the regulation (Freitas et al., 2021, 2015).

Here, we assess whether intensification of açaí management (i.e., increments in açaí stems and clumps) affects the structure and composition of the seed rain and soil seed bank in a traditional landscape covered by an estuarine forest devoted to açaí fruit production in the Amazon region (Ilha do Combú, Pará). We examined the role açaí stem density (50–3575 per ha), tree species richness and density, flooding level and accessibility to forest stands play in determining seed abundance, species richness but also the taxonomic and functional composition of woody flora (i.e., trees, palms, lianas) in the seed rain and soil seed bank across 20 forest stands immersed into a human-modified landscape with a long tradition of forest exploitation and management by traditional riverine communities. We expected a negative influence of açaí stem and clump density on the attributes of these mechanisms of forest regeneration. Our findings are examined in the context of forest regeneration, integrity and the challenge to produce açaí fruits traditionally but also as a sustainable NTFP.

MATERIALS AND METHODS

Study area

The study was carried out in the Combú Island Environmental Protection Area (1°25′31″ S; 48°25′37″ W) in the eastern Amazon region, Brazil (Figure S1). This 15 km^2 estuarine island bordered by inland area stretches over a flat and low-altitude terrain, which is exposed to a tidal regime and the consequent flooding events occurring regularly through the year (Maués et al., 2011). The soil is of the Low Humid Glei type, with a high percentage of silt and clay and a lower proportion of sand (Jardim et al., 2007). The region has a hot and humid tropical climate, with an average annual rainfall of 2500 mm and an average temperature of 27°C. The rainiest period is from December to May (with an average rainfall of 12.42 and 14.76 mm in the period of this study, respectively) and the least rainy period is from June to November (with an average rainfall of 8.29 and 8.35 mm in the period of this study, respectively) (Cavalcante et al., 2017; Inmet, 2021).

FIGURE 1 A managed stand of estuarine forest with the presence of açaí palms (a, b), a forest stands under intensive açaí management (c), a forest stand under non-intensive açaí management (d), a forest stand flooded during the high tide (e), a traditional house during the low tide (f), and a barochoric seed of tree species *Swartzia racemosa* Benth (g), Ilha do Combú in the northeast Amazon region, Brazil.

The natural vegetation refers to an evergreen estuarine forest through which açaí occurs naturally and it managed (Figure 1). The forest is periodically flooded by tides with a flooding regime by tide height. Overall, tides impose short-lasting flooding events (up to 12 h), not exceeding 2.6 m (the highest tide) with a minimal frequency of once a month during the highest tide as informed by locals. In March–April equinox occur the most intensive floods, which coincides with the high-water levels of the rainy season (Anderson & Ioris, 1992). During this time, the entire flood plain is inundated when the tide-driven floods peak at the full and new moons (Anderson & Ioris, 1992). This flooding regime contrast to that imposed to seasonally flooded forest, which experience once a year a long-last event of flooding, with waterlogging lasting a period of 4–9 months a year (see Junk et al., 2015, 2010).

Forest is dominated by typical tree species from Amazon floodplain forests such *E. oleracea* (Arecaceae), *Pterocarpus santalinoides* (Fabaceae) and *Hura crepitans* (Euphorbiaceae) (Lau & Jardim, 2013), with the presence of palm trees and trees of high-commercial value, such as *E. oleracea* (Arecaceae), *Virola surinamensis* (Myristicaceae), *Carapa guianensis* (Meliaceae), *Hevea brasiliensis* (Euphorbiaceae) and *Symphonia globulifera* (Clusiaceae). Fabaceae and Arecaceae are the most species-rich woody plant families (Lau & Jardim, 2013). Combú Island has historically been inhabited by traditional populations (i.e., caboclos and riverine populations; Ioris & Anderson, 1993) as it is surrounded easily accessed and lays close to urban settlements. Locals have intensively exploited rubber, timber, bushmeat and other forest products in addition to forest enrichment with cocoa tree and açaí palm tree (Magalhães et al., 2015). Currently, the island is inhabited by approximately 1500 people (~350 families) whose livelihoods are based on fishing, extracting forest resources, and raising ducks and pigs, while other residents providing services and entertainment to tourists, including riverside bars and restaurants, ecotourism activities and transportation to and from the island (IdeflorBio, 2014). It is worth mention that a considerable proportion of açaí fruit production comes from such fluvial islands formed via silt sediments discharged by large river courses (e.g., Tocantins, Amazon, Guamá) in the estuarine area, which is considered the historical/colonial Amazon region since Portuguese founded Belem in 1616; i.e., cultural landscapes (Brondízio et al., 1994).

Seed rain and soil seed bank of woody species

We selected 20 forest stands and set one plot per stand forest (20 m × 20 m; 0.04 ha; distance between 50 and 120 m from each other). Across the plots all stems with a DBH ≥15 cm were recorded. The 67 woody plant species recorded in these 20 plots were referred here as local flora (Table S1), while other 110 species recorded across 31 plots (MF Barros unpublished data) are referred in the text as the landscape level (Table S2). In order to infer about the taxonomic and ecological coverage by seed rain and soil seed bank, we also compiled a check list of woody plant species, particularly trees species DBH ≥10 cm, inhabiting the Amazon estuarine forest via published articles; here referred as regional flora (MF Barros and collaborators unpublished data). It was an exhaustive search and although this checklist does not contain all species inhabiting the estuarine forest the 793 (only 11 species (less than 1%) were shared with seed rain and soil seed bank; in both cases, approximately 1.5% were shared, 14 and 15 species, respectively) valid names permitted us to obtain a taxonomic and ecological profile of this flora.

The 20 plots were chosen to cover a local gradient in terms of density of açaí clumps (50–3575 stems per ha). Here we considered plots with ≤400 clumps per ha as exposed to low-intensity management (six plots) and those with ≥400 clumps per ha exposed to high-intensity management (14 plots) based on the management threshold already proposed (Mochiutti et al., 2002; Embrapa, 2015). Four hundreds açaí clumps per hectare represents the maximum density recommended by the Pará's state regulation relative to açaí management in native forests (Mochiutti et al., 2002; Embrapa, 2015). Although this threshold is ecologically questionable (see Freitas et al., 2021), it represents the guideline to be attended by açaí producers and then its impact and effectivity must be continuously verified, including potential impacts on the forest regeneration mechanisms such as seed rain and soil seed bank.

Seed rain and soil seed bank from woody plant species were recorded every 2 months during a period of 1 year to capture the arrival of seeds in the rainy (December to May 2019) and the least rainy seasons (June to November 2020). We acknowledge that a 1-year period may not be enough to record all woody species inhabiting our focal landscape via seeds arriving in our selected stands. However, 1 year would be representative in terms of seed density and seed functional profile; i.e., relative contribution of seeds into ecological groups relative to dispersal syndrome, growth form, seed mass, origin and utility. Seed monitoring was limited to 1-year period due to logistic limitations imposed to flooded terrains, and thereby, it is possible that we failed to capture potential species bearing supra-annual reproduction, particularly tree species, in which such strategy has been documented (Haugaasen & Peres, 2005). However, a 1-year monitoring has been successfully adopted for describe seed rain across tropical forests (see Alvarez-Buylla & Martínez-Ramos, 1990; Holl, 1999; Melo et al., 2006; Myster, 2015; Reid et al., 2015).

Seed rain was collected using 5 screen collectors (80 cm × 80 cm) with a 1.0 mm mesh in each plot (four at the ends of the plot and one central), giving a total of 100 collectors in our 20 plots (adapted from Terborgh et al., 2011). Within each plot, seed collectors were placed at least 5 m apart each other (a rare situation associated with collectors at the ends of the plot and the central one) and 150 cm above soil level; considering the entry of water into the plots (an important variable in floodplain forests) so that the seeds are not in direct contact with the water, preventing deterioration or predation (Terborgh et al., 2011). The samples were sorted, separating leaves, twigs and flowers from the seeds, which were stored in paper bags. Seeds were identified to the lowest taxonomic level possible by a parataxonomist of the Museu Paraense Emílio Goeldi and other specialists with the aid of specimens stored in the João Murça Pires Herbarium. Finally, the abundance of each species was then recorded, and trait measurements were taken. Useful species were acknowledged by locals, but they have also been referred in the literature (see literature by A. Anderson and collaborators).

To estimate the soil seed bank, we collected the litter and soil at five random points within each plot, giving a total of 100 samples per sampling; resulting in 600 soil samples after 1-year period. A 30 cm × 30 cm wooden template was used to demarcate the collection area, after which the litter was discarded, and the topsoil layer (first 10 cm) was collected with the help of a spade. An auger was used to collect soil in flooded plots (adapted from Lau & Jardim, 2014). Samples were sieved, separating the soil, branches and pieces of root from the seeds, which were stored in paper bags. Intact seeds were identified taxonomically as referred earlier. Lastly, seed rain and soil seed bank floras were taxonomically compared to the woody flora (DBH ≥15 cm) from the 20 plots (i.e., local flora) and the landscape level as already mentioned. As intact seeds were not tested for viability, our figures represent the maximum recruitment potential supported by these two mechanisms of forest regeneration (see Trindade et al., 2020) as a substantial proportion of intact seeds can consist of unviable seeds (Bezerra et al., 2022).

Functional and ecological groups

The woody plant species collected as intact seeds were classified into functional and ecological groups as follows: (1) primary dispersal syndrome: vertebrate-dispersed, hydrochoric, auto/ballistic-dispersed or anemochoric (Roosmalen, 1985); (2) growth/life form: tree, palm or liana; (3) seed mass by weighting trapped seeds in the lab; (4) origin: allochthonous as seeds without adults in the forest stand or autochthonous as seeds with adults in the forest stand and (5) useful by locals such as a source of wood, food, cosmetics production or medicine; unmeasured information about the species was obtained through specialized literature (Felizardo et al., 2015; Nascimento & Silva, 2005). By these procedures, we obtained the percentual of species and seeds into these ecological groups plus the total seed mass by vertebrate-dispersed species for each forest stand excluding the açaí seeds. Here, we consider the total seed mass as complementary measure for seed rain impact and relevance on the forest regeneration process. Few seeds were not assigned to a functional and ecological group as they were not assigned into a genus or family (see Tables S3 and S4). Seed classification was carried out to permit insights relative to potential drivers and ecological impacts from disrupted seed rain and seed bank associated with the intensification of açaí management.

Flooding and human accessibility to forest stands

To verify the influence of flooding (cm) on the seed rain and soil seed bank, 1.50 m rulers made of PVC pipe were installed in the centre of each plot. Starting at 30 cm (the part buried in the soil), the rulers were marked every 5 cm for 1 m above the ground. Measurements were taken on 4 occasions throughout 2020: March 11, at 13 h:01, April 10, at 13 h:40, May 8, at 12 h:45 and September 19, at 12 h:38; these months and times were chosen as they corresponded to the highest recorded flooding for the Port of Belém 2020 (Centro de Hidrografia da Marinha do Brasil, 2020). At least in floodplain forests (i.e., seasonal flooding), flooding level (i.e., water depth) has been considered to affect seed deposition on the ground and seed dispersal (Moegenburg & Levey, 2002).

Human accessibility (m) to forest stands and plots was estimated using a geographic information system. We calculated the distance of the plots to the main river (i.e., the Guamá river), the nearest human settlements (residents' houses) and nearest drainage channels used by people to access açaí stands. These stand location variables were collapsed via an ordination with principal component analysis (PCA), resulting in a principal axis with 69% explanatory power to be used further as an explanatory variable. Accessibility in this study represents a proxy of chronic anthropogenic disturbance (i.e., consumption of forest products) as adopted and proposed by Arnan et al. (2018), but also the stand access to locals and the frequency to which stands receive management operations or planting of useful tree species. It is part of the riverine culture to keep high-density açaí forest stands close to the householdings (Loris & Anderson, 1993). Finally, we also considered adult tree species richness and tree density across forest stands as explanatory variables as it is expected to affect the abundance of açaí seeds, seed rain and seed bank attributes.

Data analysis

Collinearity between our continuous explanatory variables: açaí stem density, adult tree species richness, tree density, flooding level and accessibility to forest stands was checked using the variation inflation factor (VIF) via *car* package (Fox & Weisberg, 2019). They were not collinear (VIF values <4; açaí stem density = 3.72, tree species richness = 1.33, tree density = 2.68, flooding = 1.36, and accessibility = 1.36), so all were included in the subsequent analyses (Legendre & Legendre, 1998; Jou et al., 2014). We consider açaí stem density as more accurate variable as compared to açaí clump density (see Freitas et al., 2021) as açaí clumps can support one or several stems. The explanatory-variable effects on the attributes of seed assemblages were assessed using generalized linear models (GLMs) from the *stats* package. It is important to mention that one single model was applied for each response variable. For the GLMs, the Quasipoisson distribution was used for count variable (seed abundance, açaí seed abundance and species richness), Gaussian distribution for continuous data (seed mass by vertebrate-dispersed species) and Binomial and Quasibinomial distribution for percentage data (life form and utility) (Venables & Smith, 2018). Residues were checked via *DHARMa* (Hartih, 2022) and *hnp* (Moral et al., 2017) packages, while under and overdispersion were checked dividing the residual deviance by the degrees of freedom.

It is important to mention that except for the açaí seed abundance as a response variable, açaí seeds were removed from the other response variable as the study was focused on the attributes of seed rain and soil seed bank, particularly seed abundance and species richness considering the whole woody flora as they drive forest regeneration and integrity. Açaí seed abundance, although probably correlated with açaí stem and clump density (our main explanatory variable), deserves to be quantified as it can result into açaí seedlings competing with other woody plant species across the seedling banks of managed forest stands. To verify the taxonomic organization of seed rain and seed bank across forest stands, we adopted a non-metric multidimensional scaling (NMDS) based on the Bray–Curtis dissimilarity, followed by ANOSIM (Oksanen et al., 2015) using the *vegan* package. Further, we adopted the Envfit procedure (Oksanen et al., 2015) to investigate the explanatory variable-effects on the NMDS taxonomic organization using the *vegan* package as well. In both cases, forest stands were assigned to two categories recognized by current legislation: low-intensity management (≤400 açaí clumps per ha) versus high-intensity management (≥400 açaí clumps per ha). Species-level responses to açaí stem density was also examined to investigate the extent to which management affect forest regeneration. Finally, to examine sample coverage for each plot, we used protocol on number of individuals-based using the *iNEXT* package (Hsieh et al., 2016). All the analyses were performed in the R environment (R Development Core Team, 2019).

RESULTS

Seed rain

A total of 5005 seeds were obtained between November 2019 and September 2020, of which 4879 belonged to 11 families, 16 genera and 16 species; only 126 seeds (2.5%) were unidentified even to genus or family level (Table S3). Açaí accounting for 4282 seeds, i.e., the vast majority of all seeds (85.5%), while the majority of the other species exhibited a negligible contribution (Figure S2). By polling all seeds that arrived through a year across the 20 forest stands, including açaí seeds, seed rain was low density; it ranged from 1.7 to 16.8 seed m^2/year (8.1 ± 4.6; mean ± standard deviation). Excluding açaí seeds, the number of accumulated seeds was almost negligible even elapsed a year as it varied between 0.06 and 5.0 seeds per m^2/year (1.1 ± 1.2 seeds). Seven forest stands (35% of the total) received less than 10 seeds over the 12 months by excluding açaí seeds; i.e., a negligible seed rain. In addition, only 32 seeds (29.4%; from 5 species) were considered allochthonous, with more than half of forest stands lacking allochthonous seeds during the 12-month period. All allochthonous seeds arrived between November and January (transition for the rainy season); i.e., a large spatio-temporal gap in seed arrival by excluding açaí seeds. It is important to mention that the sample coverage of all plots ranged from 66% to 100% (with 15 of the 20 plots ranging between 90% and 100%), indicating that we recorded a substantial portion of the flora attending seed rain.

Trees and palms dominated seed rain (84 ± 27% of all seeds) as did vertebrated-dispersed seeds across the stands (49 ± 26%); lianas contributed little and seed rain lacked shrub species. Moreover, more than half of vertebrate-dispersed species exhibited light or moderately-heavy seeds (<2 g) associated with gut dispersal such as *Virola surinamensis* (1.6 g) and *Spondia mombin* (1.8 g; Table S3). Accordingly, accumulated seed mass from vertebrated-dispersed species (excluding açaí seeds) varied between

TABLE 1 Generalized linear models of the seed rain examining the relationships among the explanatory variables (açaí stem density, tree species richness, tree density, flooding (cm), and accessibility (m)) and the seed rain attributes (seed abundance, açaí seed abundance, species richness and the percentual of species and seeds within functional groups plus total seed mass (g) by vertebrate-dispersed species across 20 forest stands of an estuarine forest, Ilha do Combú, the Amazon northeast region, Brazil.

Seed rain		Açaí stem density	Tree species richness	Tree density	Flooding	Access	r^2
Seed abundance	x^2	0.52	2.40	0.17	0.92	0.02	0.38
	p	0.46	0.12	0.67	0.33	0.87	
Açaí seed abundance	x^2	11.85	6.58	2.85	2.71	0.02	0.58
	p	<**0.01*****(+)	**0.01***(−)	0.09	0.09	0.86	
Species richness	x^2	0.11	0.03	0.78	1.09	0.40	0.15
	p	0.73	0.85	0.37	0.29	0.52	
Vertebrate-dispersed species	x^2	0.71	0.64	0.64	0.00	0.46	0.17
	p	0.39	0.42	0.42	0.99	0.49	
Vertebrate-dispersed seeds	x^2	0.24	0.70	0.00	0.17	0.78	0.14
	p	0.61	0.40	0.96	0.67	0.37	
Tree species	x^2	0.18	1.16	0.22	0.16	0.37	0.25
	p	0.66	0.28	0.63	0.68	0.53	
Tree seeds	x^2	0.01	2.03	7.94	0.53	8.14	0.28
	p	0.89	0.15	<**0.01****(−)	0.46	<**0.01****(+)	
Useful species	x^2	0.14	5.21	0.27	0.01	0.10	0.37
	p	0.70	**0.02***(−)	0.59	0.89	0.74	
Seeds from useful species	x^2	0.00	4.10	0.00	0.08	1.44	0.49
	p	0.96	**0.04***(−)	0.97	0.76	0.22	
Seed mass	x^2	0.09	1.23	0.38	0.54	0.07	0.22
	p	0.76	0.26	0.53	0.45	0.78	

Note: Only the significant relationships are shown in bold. Positive and negative signs indicate significant positive and negative relationships, respectively.
*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$.

0.01 and 6.8 g of seeds m^2/year across forest stands (1.18 g ± 1.75 m^2/year), with a more than a half of forest stands accumulating less than 1 g of seeds per m^2/year. Finally, useful tree species (83.3% all species) and their seeds dominated seed rain across forest stands: 67 ± 39% of all seeds with two useful tree species (*V. surinamensis* and *S. mombin*) dominating seed rain.

Regarding explanatory variables, the abundance of açaí stems positively affected the of açaí seed abundance ($X^2 = 11.85$, $p = <0.01$), while adult tree species richness correlated negatively with (1) açaí seed abundance ($X^2 = 6.58$, $p = 0.01$), and (2) the relative contribution of useful species ($X^2 = 5.21$, $p = 0.02$) and their seeds ($X^2 = 4.10$, $p = 0.04$). Tree density negatively affected the contribution of seeds from tree species ($X^2 = 7.94$, $p = <0.01$), but this life form correlated positively to accessibility ($X^2 = 8.14$, $p = <0.01$, Table 1). Moving to the temporal dimension, seed capture/m^2 was higher in November/2019 (23.4 seeds/m^2; a total of 1497 seeds) and September/2020 (23.6 seeds/m^2; a total of 1511 seeds); i.e., the least rainy period. July/2020 (the beginning of the least rainy period), was the month with the lowest seed capture/m^2 (4.9 seeds/m^2; a total of 312 seeds; Figure 2a) and species (a total of five species; Figure 2b), but açaí dominated seed rain (>95% of all seeds) through the year.

Non-metric multidimensional scaling made evident (1) a segregation between intensive and non-intensive açaí management seed pools, and (2) greater taxonomic distinction between non-intensive management forest stands compared with the intensive management stands (Figure 3). This distinction was confirmed by the ANOSIM test ($r = 0.61$

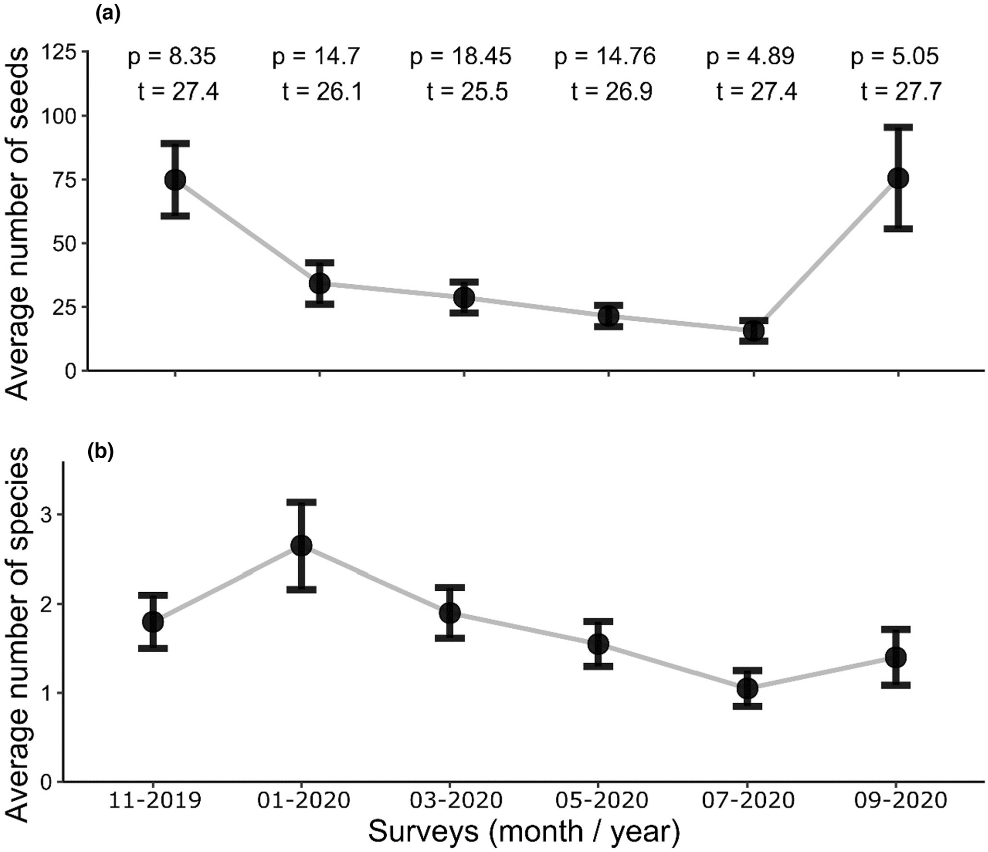

FIGURE 2 The number of seeds/m^2 and average seed number of woody species (trees, palms, and lianas) in the seed rain from 20 forest stands, Ilha do Combú in the northeast Amazon region, Brazil. $p = -$ average precipitation (mm); $t = -$ average temperature (°C).

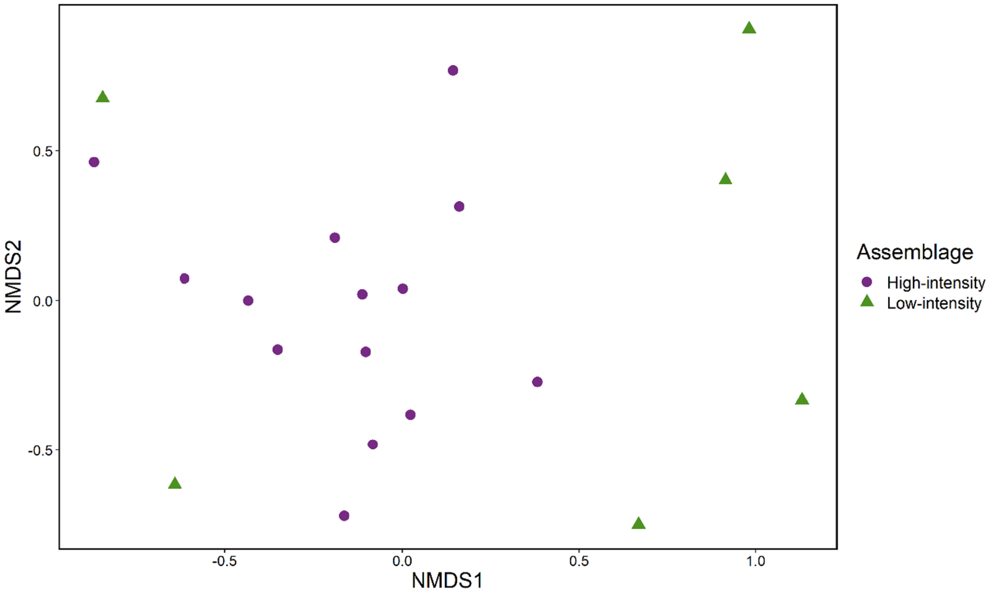

FIGURE 3 The taxonomic ordination of the seed rain assemblages from 20 forest stands via a non-metric multidimensional scaling (NMDS) considering intensive (≥400 clumps/ha) and non-intensive (<400 clumps/ha) açaí management, Ilha do Combú in the northeast Amazon region, Brazil. Stress = 0.17.

and $p = <0.01$). NMDS followed by Envfit indicated that açaí management intensity ($r^2 = 0.43$, $p = <0.01$) and plot spatial location affected seed rain taxonomic composition (Mantel test, $r = 0.64$; $p = <0.01$). Consistent with the taxonomic segregation exhibited by seed pools, several species had their relative abundance/occurrence correlated with açaí stem density (Figure S3). Finally, the seed rain though a whole year captured less than 20% of the species presented in both local and landscape-level flora.

Soil seed bank

A total of 862 seeds were obtained with 844 assigned to 13 families, 19 genera and 17 woody plant species; 18 seeds (2.08%) were not identified (Table S4). Açaí dominant the bank with 740 seeds (85.8%), while other species contributed with few seeds (Figure S4). By pooling all seeds from the 20 forest stands, seed density ranged from 0.01 to 0.28 seeds m^2/month (1.3 ± 1.1 seeds; mean ± standard deviation), including açaí seeds. By excluding açaí seeds, soil seed bank density declined drastically: 0.06–0.19 seeds per m^2/month (0.2 ± 0.1 m^2/month), with only nine seeds (across six stands) classified as allochthonous; i.e., a large spatio-temporal lack of intact seeds in the bank by excluding açaí seeds. In fact, 95.9% of all seeds were classified as autochthonous. Finally, about sample coverage of all plots ranged from 41% to 100% (with seven plots ranging between 90% and 100%), indicating that we recorded a reasonable portion of the flora attending seed rain.

Across forest stands, seeds from tree species (88% ± 31%), vertebrate dispersed (57% ± 41%) and those from useful species (69% ± 37%) dominated soil seed bank by excluding açaí seeds. Moving to the explanatory

TABLE 2 Generalized linear models of the soil seed bank examining the relationships among the explanatory variables (açaí stem density, tree species richness, tree density, flooding (cm), and accessibility (m)) and the soil seed bank attributes (seed abundance, açaí seed abundance, species richness, and the percentual of species and seeds within functional groups plus total seed mass (g) by vertebrate-dispersed species across 20 forest stands of an estuarine forest, Ilha do Combú, the Amazon northeast region, Brazil.

Seed bank		Açaí stem density	Tree species richness	Tree density	Flooding	Access	r^2
Seed abundance	x^2	4.11	1.11	11.50	2.53	0.68	0.67
	p	**0.04***(–)	0.29	**<0.01*****(+)	0.11	0.40	
Açaí seed abundance		1.71	9.83	0.00	1.16	0.36	0.37
		0.18	**<0.01****(–)	0.98	0.28	0.54	
Species richness	x^2	0.38	0.00	0.08	0.06	0.17	0.09
	p	0.53	0.97	0.77	0.79	0.67	
Vertebrate-dispersed species	x^2	2.32	1.39	0.97	0.96	0.02	0.11
	p	0.12	0.23	0.32	0.32	0.87	
Vertebrate-dispersed seeds	x^2	3.86	4.86	3.05	1.02	0.07	0.43
	p	**0.04***(–)	**0.02***(–)	0.08	0.31	0.78	
Tree species	x^2	1.71	0.00	0.00	0.00	0.00	0.32
	p	0.19	1.00	1.00	1.00	1.00	
Tree seeds	x^2	2.98	2.36	0.61	1.51	0.60	0.26
	p	0.08	0.12	0.43	0.21	0.43	
Useful species	x^2	1.00	0.48	0.32	0.57	0.06	0.16
	p	0.31	0.48	0.56	0.44	0.79	
Seeds from useful species	x^2	0.80	6.75	0.07	1.33	0.25	0.38
	p	0.36	<**0.01****(–)	0.78	0.24	0.61	
Seed mass	x^2	1.39	5.87	1.56	0.01	0.29	0.32
	p	0.23	**0.01***(–)	0.21	0.90	0.58	

Note: Only the significant relationships are shown in bold. Positive and negative signs indicate significant positive and negative relationships, respectively.
$^*p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$.

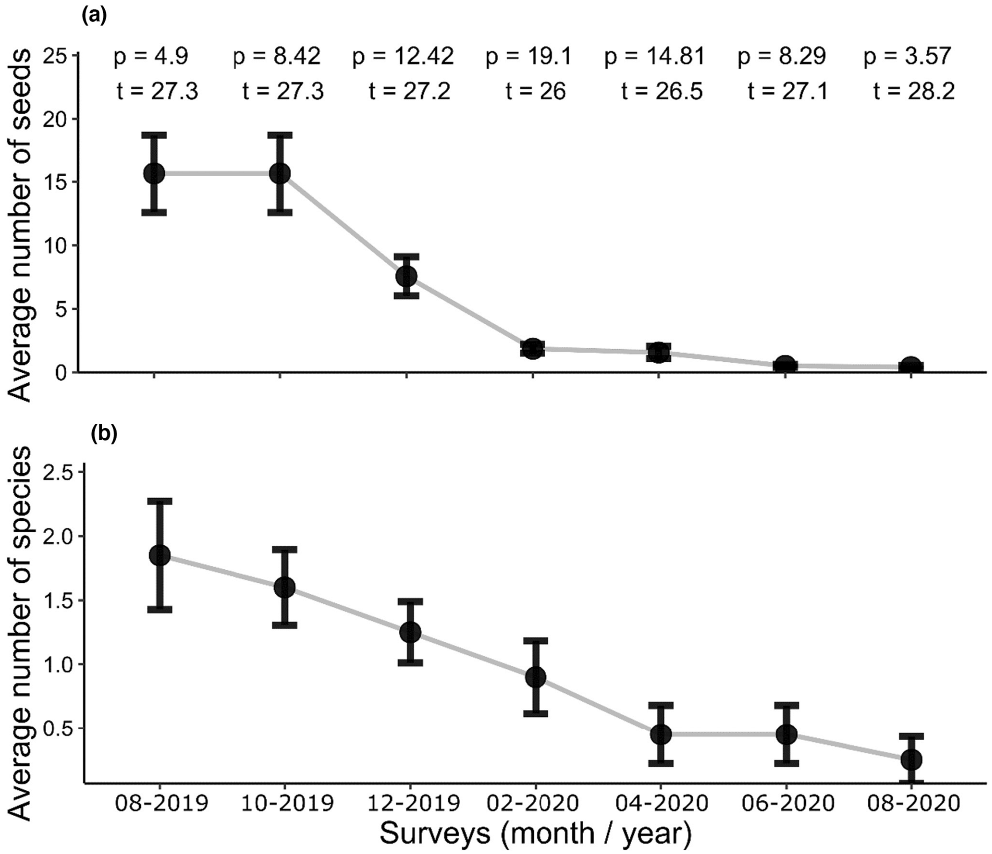

FIGURE 4 The number of seeds/m^2 and average seed number of woody species (trees, palms, and lianas) in the soil seed bank from 20 forest stands, Ilha do Combú in the northeast Amazon region, Brazil. p = average precipitation (mm); t = average temperature (°C).

variables, seed abundance ($X^2 = 4.11$, $p = 0.04$) and percentual of vertebrate-dispersed seeds ($X^2 = 3.86$, $p = 0.04$) correlated negatively with the abundance of açaí palm stems. Tree species richness negatively affected açaí seed abundance ($X^2 = 9.83$, $p = <0.01$), percentual of vertebrate-dispersed seeds ($X^2 = 4.86$, $p = 0.02$), percentual of useful seeds ($X^2 = 6.75$, $p = <0.01$) and accumulated seed mass ($X^2 = 5.87$, $p = 0.01$). Finally, tree density was positively related to seed abundance ($X^2 = 11.50$, $p = <0.01$, Table 2). In relation to temporal dimension, August/2019 (4.9 seeds/m^2; 315 seeds) and October/2019 (4.9 seeds/m^2; 312 seeds) exhibited the highest abundance of seeds and tree species richness (Figure 4), but açaí dominated the seed bank along the year as it did regarding seed rain.

The NMDS ordination indicated a taxonomic segregation of seed bank between forest stands exposed to intensive vs. non-intensive açaí management (Figure S5). This pattern was confirmed by an ANOSIM test ($r = 0.61$ and $p = <0.01$), while Envfit indicated no influence from açaí management intensity and the other explanatory variables on the taxonomic composition of seed bank. However, a Mantel's test indicated a significant relationship ($r = 0.69$; $p = <0.01$) between taxonomic similarity patterns in the soil seed bank and plot location. Finally, some species did appear to respond to açaí management (Figure 5) and similar to the seed rain, soil seed bank captured less than 20% of species recorded in both local and landscape-level flora.

DISCUSSION

Our results suggest that the estuarine forest historically managed by traditional populations supports seed rain and soil seed bank dominated

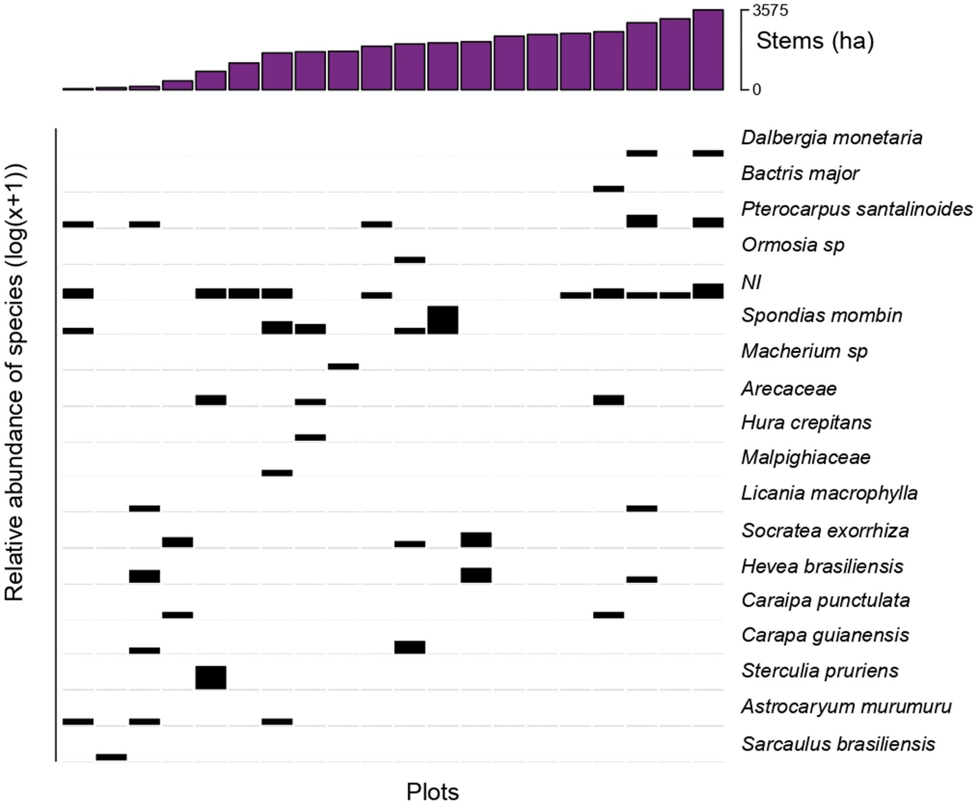

FIGURE 5 Tree species ordination according to the seed abundance in seed bank and açaí stem density across 20 estuarine forest stands, Ilha do Combú in the northeast Amazon region, Brazil.

by seeds of the açaí palm (>85% of the seeds), although açaí fruits are regularly collected by locals. Moreover, seed rain and bank occur through extremely low density and species-poor assemblages with allochthonous seed pools/assemblages considered inexpressive. Seed pools are dominated by tree species, vertebrate-dispersed and those bearing relatively light (<27.99 g) and medium-sized seeds. Both the seed rain and soil seed bank have a seasonal character (peaking in the dry season), with large spatio-temporal gaps in seed supply for forest regeneration by excluding açaí seeds. Moreover, species exploited by local populations, such as *V. surinamensis* and *C. guianensis* predominate. Considering short periods, such a year, seed rain and soil seed bank contain a small proportion of the local and landscape-level woody flora. Overall, seed rain and bank result from a combination of adult plant assemblage attributes, including açaí stem and clump density, but also adult tree species richness and tree density. Forest stand accessibility and flooding level appear to play a minor role on seed pools. Although some of our findings were highly expected (such as the correlation between açaí seeds and açaí clump density) they have ecological relevance in the context of forest regeneration dynamics as discussed further.

Most studies on the impact by the exploitation of NTFP in tropical forests is focused on the exploited species (Muler et al., 2014; Peres & Lake, 2003). There is a much smaller number of studies assessing community-level impacts of NTFP extraction, and very few studies addressing ecosystem-level issues such as regeneration mechanisms (see Trauernicht & Ticktin, 2005). This is particularly true for the estuarine forest exposed to the açaí management since there is no a single record for seed rain and seed bank although this forest represents the core habitat for açaí-fruit collection and intensification in the Amazon region (Tregidgo et al., 2020). In fact, information on seed rain bank is even scarce for the Amazonian floodplain forests one of the most investigated flooded forests globally (see Wittmann et al., 2010). In this context, forest stands managed for açaí support seed rain and bank from woody plant species with both similarities and contrasts as compared to unmanaged floodplain forests, at least qualitatively. First, most of tree species refers to those with primary seed-dispersal by vertebrates (i.e., gut-dispersal), although some species bear seeds that might be able to float; i.e., secondarily dispersed by water (Parolin et al., 2013, 2004). Others may be dispersed by mammal/birds and fishes (i.e., ichthyochory), particularly those species small seeds (Anderson et al., 2011, 2009), while others exhibit devices directly associated to hydrochory such as air-containing or spongy tissues (Barbosa & Montag, 2017; Wittmann et al., 2007). In both habitats (i.e., estuarine and floodplain forests), species bearing medium-sized (<1.5 cm length) and relatively light seeds (<2 g) predominate (Parolin, 2000). Finally, as suggested by the proportion of allochthonous seeds we documented in our focal landscape (29.4%), seed dispersal limitation is frequent (Terborgh et al., 2019).

Indeed, our literature-based checklist relative to tree species inhabiting the Amazon estuarine forests (as referred earlier) has revealed the presence of hundreds of species bearing attributes associated with vertebrate-dispersed species including gut-dispersal by medium-sized or even large vertebrates such as those belonging to Sapotaceae, Chrysobalanaceae, Myristicaceae, Annonaceae and Fabaceae, including those into *Pouteria*, *Licania*, *Virola*, *Anonna* and *Inga* just to mention a few genera (see Roosmalen, 1985). This clearly suggest the presence of a flora adapted to active seed dispersal by vertebrates such as primates, large rodents and large-gaped birds, which in many cases are responsible for long-distance seed dispersal such as the *Virola* species (Russo et al., 2006). In which extent, complementary vectors (i.e., fishes and water) are able to guarantee effective seed dispersal is still to be revealed, although we documented the presence of buoyant seeds and those exhibiting the hydrochloric syndrome (see Parolin, 2000; Parolin et al., 2004). However, hydrochory is always downstream, with upstream forests relaying on either vertebrates or wind to be receive allochthonous seeds (Parolin et al., 2013).

However, in contrast to the few findings from the Amazon floodplain forests, we documented a species poor and low-density seed assemblages with a lack of floating seed banks (sensu Parolin et al., 2010), seed patches (Antunes et al., 2019), seed piles associated with primate/bat sleeping sites (Russo & Augspurger, 2004), latrine with seeds by tapirs (Tobler et al., 2010) or even seedling carpets (Barnett et al., 2012; Antunes et al., 2019), with exception of those by açaí seeds/seedlings. Although floodplain forests may support less dense seed rain as compared with *terra firme* forests (see Myster, 2015), hundreds of seeds from dozens of woody plants species are likely to achieve any tropical forest stand (Aud & Ferraz, 2012; de la Peña-Domene et al., 2017; Jesus et al., 2012; Melo et al., 2006; Sousa et al., 2017; Terborgh et al., 2011). Even in a scenario of seed limitation it was recorded 148 seeds per m^2 year 1, among them 63 intact seeds with 13 seeds from tree species (Terborgh et al., 2019). Considering both floodplain and *terra firme* old-growth forests, we probably recorded the lowest scores ever reported in the literature by not considering açaí seeds; i.e., the managed species (Chapla & Campos, 2011; Jara-Guerrero et al., 2020; Myster, 2014, 2015; Terborgh et al., 2019). This is also valid for the accumulated seed mass by vertebrate-dispersed species we documented (see Parolin et al., 2010). Moreover, a single palm species dominates seed rain and seed bank through both seasons but with a peak during the dry season across all stands. It implies an unseasonal seed rain and bank, largely reducing the high spatiotemporal heterogeneity, which is typical from seed rain across floodplain forests (Terborgh et al., 2019; Menezes et al., 2019). As we monitored seed rain and bank for a year, long-term monitoring is welcome, but there is no reason to believe that we assessed an idiosyncratic reproductive period or failed to document high density, species rich and functionally diverse seed assemblages in the case it occurs in our focal landscape. In fact, our sampling effort achieved a reasonable taxonomic coverage by the seed assemblages, up to 100% across several forest stands.

These findings from our estuarine managed forest contrast to the idea that (1) floodplain forests in the Amazon region do not form seed bank as seeds start germinating shortly after flood-water recede (Kubitzki and Ziburski, 1994; Wittmann et al., 2007), and (2) seed rain occurs during the rainy/flooding period/aquatic phase (Hawes and Peres, 2016; Haugaasen and Peres, 2005; Parolin and Wittmann, 2010). In fact, such a year-round dominance by a single light-demanding species (i.e., the açaí palm species) across both seed rain and bank is likely to occur at (1) early-successional stages, (2) forest edges, (3) restored forest stands (Holl, 1999; Melo et al., 2006; Reid et al., 2015).

According to our expectations, açaí stem and clump density but also adult tree species richness and tree density affected most of seed rain and bank attributes, including a taxonomic organization associated to levels of açaí management; low intense and intensively managed. Although we did not explicitly examine the underlying mechanisms, the nature of açaí-managed forest stands offers reasonable explanations for our “disrupted” seed rain and bank. Açaí-managed forest stands are likely to produce over a 1 million açaí fruits per ha (Oliveira et al., 2000), part of it saturating seed rain and soil seed bank along the year as documented here; i.e., the uncollected seeds. Moreover, forest stand management also eliminates undesirable plants (particularly trees) in order to give açaí clumps more space and illuminated habitats, although desirable/useful species can be spared (Anderson et al., 1995). Accordingly, açaí intensification is negatively associated with tree species richness and abundance, in some cases leading to the establishment of monospecific stands; up to 1040 clumps per ha (Freitas et al., 2021, 2015). Note that almost half of our 20 plots exhibited less than 10 woody plant species, i.e., 50% of the species richness observed in the most species-rich plots with few açaí clumps. Reduced tree density not only results into lower seed production but also eliminates large trunks and buttress roots, which trap seeds while waters are receding towards major bays (Junk et al., 2010). Collectively, these processes are the best explanation for (1) the positive relationship between açaí stem density and açaí seeds but a negative impact from stem density on seed bank abundance and vertebrate-dispersed seeds, (2) the negative relationship between tree species richness and the contribution of useful tree species and açaí seeds in the seed pools, (3) a positive impact of tree density on the abundance of seeds in the bank and (4) the lack of shrub species in the seed pools. However, tree species richness apparently reduces the relative contribution vertebrates-dispersed species and their accumulated seed mass by vertebrate-dispersed species in the bank. This is consistent with the fact tree species richness is negatively related to the useful species, including the vertebrate-dispersed ones such as *V. surinamensis* and *S. globulifera*. Increased species richness might also be associated with the occurrence of abiotically dispersed species, such as *C. guianensis*. Accordingly, there is a clear taxonomic distinction between the seed pools achieving low intensively vs. intensively managed forest stands. Overall, there is a negative impact of açaí intensification on seed pools, while tree species abundance and species richness contribute for a more dense and diversified seed pools.

As a working hypothesis, we shall propose that landscapes rather than stands devoted to açaí production via intensification tend to supported depleted seed rain and soil seed bank as compared to unmanaged forest landscapes due to (1) low density and impoverished woody plant assemblages (see Freitas et al., 2021) causing reduced seed production, (2) protection of tree species of economic interest, such as cocoa (*T. cacao*), *ucuúba* (*V. surinamensis*) and *cupuaçu* (*T. grandiflorum*; Anderson et al., 1995; Tregidgo et al., 2020), (3) rapid/intense seed flow/runoff towards river channels as the tide penetrates freely across the forest stands lacking big trees and their logs and buttresses operating as seed traps (see Moegenburg and Levey, 2002) and (4) depauperated vertebrate fauna acting as seed dispersers in response to (a) historical bushmeat, (b) changes on forest structure and (c) high levels of seed-harvesting by locals. Particularly in the case of açaí, intensive seed-harvesting has been document to reduce seed dispersal by frugivores (Moegenburg and Levey, 2002), while açaí intensification been associated with pollination decline (Campbell et al., 2018).

Although in this moment we are not able to accurately estimate in which extent açaí intensification respond for such a disrupted/peculiar seed rain and bank, it is reasonable to propose that açaí-managed forest stands do not offer enough seeds from woody plant species required to guarantee the emergence of functionally diverse seedling banks required for regeneration dynamics of flooded forests and their plant communities structured according to flooding, light and predation gradients (see Lopez and Kursar, 2007; Parolin, 2002; Parolin et al., 2004; Terborgh et al., 2017). Moreover, tree seedlings emerging from the few seeds able to reach açaí-dominated forest stands are expected (1) to be outcompeted for the massive açaí seedling bank and by those seedlings from useful species plus the layer of herbs species associated to high-density açaí forest stands (Weinstein and Moegenburg, 2004), and/or (2) be suppressed by açaí dropped fronds as already documented by several arborescent palm species in tropical forests (Aguiar and Tabarelli, 2010; Farris-Lopes et al., 2004).

The practical implication from this situation is that it is unlikely that açaí-managed forest stands/landscapes will naturally achieve the standards posed by current regulations, a pre requisite to label açaí-based commodities as sustainable via the certification of açaí fruit production (see Damasco et al., 2022). We refer to forest stands supporting a minimum of 400 clumps/ha according to the current regulation (SEMAS, 2013). In response to an increasing global demand, açaí intensification shall continue to expand as transition from extractivism based on natural açaí populations (i.e., traditional forest management (Anderson et al., 1995)) towards açaí-dominated forests or even plantations/monospecific forest stands (see Freitas et al., 2021; Weinstein and Moegenburg, 2004). Açaí fruit production is the most lucrative NTFP from the Amazon region, a key asset for riverine populations and a potential global "case" of a sustainable NTFP already influencing the collection/cultivation of other native fruits (Damasco et al., 2022; Tregidgo et al., 2020; Sousa & Barros, 2018).

In this context, the Amazon estuarine forest currently responds for the bulk of açaí fruit production via familiar/small-holding production/extractivism with a trend of higher yields by a combination of stand intensification and a progressive encroachment of the entire estuarine forest; i.e., one of the most populated region in the Brazilian Amazon (IBGE, 2022). Reverting such a disturbing trend depends on a combination of initiatives including (1) improved governance in order to guarantee compliance with the current regulations, (2) education programs targeting both producers, consumers and the processing industry towards sustainable standards and (3) the establishment of protected areas into the last tracts of relatively preserved forests. Considering the ecological and economic impacts emerging from traditional açaí management (sustainable vs. unsustainable collection/cultivation), the hypotheses presented here should receive attention while research offers the basic biological/ecological standards to be achieved towards sustainable production/certification with the help of effective public policies and regulations.

AUTHOR CONTRIBUTIONS

Gabriele Silva: Data curation (lead); formal analysis (supporting); funding acquisition (supporting); investigation (equal); methodology (supporting); writing – original draft (lead); writing – review and editing (equal). **Marcelo Tabarelli:** Conceptualization (supporting); funding acquisition (supporting); investigation (supporting); methodology (supporting); supervision (supporting); validation (supporting); visualization (supporting); writing – review and editing (supporting). **Mário Jardim:** Conceptualization (supporting); investigation (supporting); methodology (supporting); supervision (equal); writing – review and editing (equal). **Eniel Cruz:** Data curation (equal); writing – review and editing (equal). **Maria Fabíola Barros:** Conceptualization (lead); data curation (supporting); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (lead); resources (supporting); supervision (lead); validation (lead); visualization (lead); writing – review and editing (lead).

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DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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