

Intensification of açai palm management largely impoverishes tree assemblages in the Amazon estuarine forest

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ABSTRACT

The exploitation of non-timber forest products has been encouraged in order to reconcile economic uses, biodiversity conservation and the provision of ecosystem services. In this paper we investigate how increments on the açai palm density (*Euterpe oleracea*) via forest management change tree assemblages across 47 plots in the Amazon estuarine forest (Brazil). Assemblage attributes were confronted to açai clump density, soil fertility, canopy openness and elevation. Both tree species density and richness were negatively affected by açai, but species richness was also affected by tree abundance. Species-accumulation curves also indicated higher alpha and beta diversity across low-intensity forest patches with high-intensity patches lacking half of the tree species. A small set of species dominated forest patches, but açai density did not correlate with the abundance of valuable species. Explanatory variables, including açai density, explained a small fraction of the variation on the functional profile of tree assemblages, but functional richness was reduced by a half across forest stands exceeding 600 açai clumps per ha. Our results suggest that açai intensification alters the structure of woody plant assemblages in estuarine forest. Tree abundance and species richness consistently declines as açai clump density increases, with some forest stands being dominated by açai and almost lacking any tree species. Accordingly, landscapes dominated by high-intensity forest stands are largely impoverished in terms of understory, canopy and emergent tree species. These findings question the current legal regulations and thresholds adopted for açai management, while alert for potential disasters caused by poorly-regulated extractions of NTFPs.

1. Introduction

Tropical forests represent a crucial resource for global sustainability by offering a wide range of ecosystem services, from climate regulation to supporting traditional populations. Unfortunately, the opportunity cost exhibited by standing forest has resulted in forest clearance and alternative land uses (Bawa, 2004; Coomes et al., 2008; Ros-Tonen, 2000). In this context, the extraction of non-timber forest products (NTFPs) has been advocated as an important strategy for: (1) the sustainable use of tropical forests (Nepstad and Schwartzman, 1992); (2) poverty alleviation, particularly for forest-dependent people (Pandey et al., 2016); (3) provision of forest-related key ecosystem services such

as climatic regulation (Nadkarni and Kuehl, 2013), and part of the global cultural heritage (Shackleton et al., 2018); i.e. a potential win-win situation (Uma Shaanker et al., 2004). In fact, NTFPs encompass a variety of products (e.g. fruits, seeds, palm hearts, oils, raw materials) supporting both household subsistence (including food security) but also for local and global markets (Ahenkan and Boon, 2011; Ingram and Schure, 2010). Apparently convincing examples of win-win situations are already documented in the literature (Hernández-Barrios et al., 2015; Stanley et al., 2012).

However, there has been an increasing number of studies reporting negative ecological impacts posed by extraction of NTFPs (Ahenkan and Boon, 2011; Upreti, 2017). The unsustainable harvesting of target

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species, leading to demographic changes (e.g. aging structure) population decline or even local extirpation are commonly reported (Gaoue et al., 2014, 2013; Ticktin, 2004; Ticktin et al., 2012). Changes in species composition and species richness, forest structure/biomass and soil nutrients have also been reported as consequences of NTFP extraction (Ndangalasi et al., 2007; Ruwanza and Shackleton, 2017; Trauernicht and Ticktin, 2005). Such impacts on multiple ecological levels (from population to ecosystem) bring into question the sustainability of such practices (Belcher and Rui, 2005; Morsello et al., 2012; Ticktin, 2015).

In fact, negative ecological impacts should be expected since NTFP harvesting varies from simple extractivism (i.e. gathering from the wild) through intense management and even cultivation via agroforestry systems (Ticktin and Shackleton, 2011). In the case of plant-related NTFP, management practices (e.g. coppicing, weeding, vegetation removal) are intended to benefit the target species by increasing their abundance and/or productivity, but frequently they alter forest structure, biomass and microclimate with cascading effects on other levels of ecological organization and processes, such as forest regeneration (Trauernicht and Ticktin, 2005; Uma Shaanker et al., 2004). As management intensifies to increase yields, impacts are likely to increase too (Hernández-Barrios et al., 2015; Shackleton et al., 2011). Overharvesting and management intensification apparently represent a common path for NTFP use, when regulation is lacking or the establishment of best practices is limited (Wilsey and Radachowsky, 2007).

The fruits of the açai palm (*Euterpe oleracea* Mart) and its fresh beverage (i.e. the açai wine) represent a traditional staple food and an important income source for riverine populations of the Amazon (Brondízio, 2008). This multi-stemmed canopy palm occurs naturally across tide-driven floodplain or estuarine forests (i.e. palm forest) and has been traditionally managed via practices such as forest thinning to eliminate competitors (Anderson, 1988). In recent decades, açai-based food products have reached global markets (e.g. energetic drinks, ice creams and fresh creams) and contributed to an economic boom in açai producing communities (IBGE, 2020). Although intensification started in the 1960s, açai has now achieved the status of a forest-based Amazonian commodity. Around 1% of Amazonian estuarine floodplain forests (2193 km²) is now devoted to açai, producing 126,027 tons of fruits per year and more than \$ 200 million of income annually (IBGE, 2020). To attend such an increasing demand for fresh fruits, açai stands are becoming increasingly denser through active management, i.e. açai intensification (Brondízio et al., 1994; Freitas et al., 2015; Weinstein and Moegenburg, 2004). We refer to stands that can reach over 1000 clumps per hectare, at the expense of forest structure, particularly in terms of tree species assemblages (Freitas et al., 2015). To avoid negative ecological impacts from intensification, including local tree species impoverishment (Freitas et al., 2015; Weinstein and Moegenburg, 2004) and reductions in pollination services (Campbell et al., 2018), a state regulation suggests a maximum of 400 clumps per hectare (Brasil, 2014). However, the extent to which açai intensification negatively impacts estuarine forests is yet to be elucidated.

This paper examines the extent to which açai intensification alters the structure and functional profile of tree assemblages at local and landscape spatial scale by examining 47 estuarine forest stands in the Amazon region (Pará-Brazil). We refer to changes in a wide spectrum of community-level attributes from tree density to functional composition and diversity considering forest stands covering a wide range of açai density. We considered three sources of impacts on tree assemblages, which are associated with açai management and intensification: (1) reduction in tree stem density imposed by thinning operations, (2) selection/persistence of commercially-valuable tree species, and (3) environmental filtering associated with the increment in açai density (i.e. açai intensification). Thus, we identified commercially-valuable tree species and selected traits associated with strategies of plant resource use (e.g. water, light and nutrients). Changes in the functional profiles reflect forces controlling species assembly potential changes in the ability of forests to deliver key ecosystem services, such as carbon

sequestration. Our patterns we uncovered are discussed in the light of current debate on açai sustainability. We also examine current legal regulations on açai palm exploitation in the Amazon estuary region.

2. Material and methods

2.1. Study area

Our focal region consisted of a 376,000-km² polygon in eastern Amazonia, in the state of Pará, Brazil (1°27'S, 48°30'W; Fig. 1). This region is covered by upland forest (*terra firme*), estuarine forests and mangroves along river banks, particularly the Pará, Guamá and Tocantins rivers, and floodplain areas (*várzea*) of the Marajó Island (Junk et al., 2015; Fig. 1). This is the core region of açai production/harvesting in the Amazon region (IBGE, 2020). Soils are predominantly humic-gley soils, with pH ranging from 4.5 to 5.5, fertility ranging from intermediate to high, an intermediate organic matter content and a relatively high cation exchange capacity (Falesi and Silva, 1999). The weather is hot and humid (Af, Köpen Group, 2018), with a mean monthly temperature of 26 °C, and monthly rainfall ranging from 110 mm to 612 mm (Instituto Nacional de Meteorologia - INMET, 2017). Land use and forest exploitation by humans dates back to pre-Columbian times through collection of forest products (including açai fruits by indigenous populations (Levis et al., 2017). Europeans arrived in the 16th century and gradually settled on the Amazon estuary, adopting subsistence agriculture and exploitation of timber and NTFP such as açai palm fruit, rubber, cocoa, palm hearts via extractivism or agroforest systems; i.e. the riverine or the estuarine caboclo culture (Anderson, 1988; Vogt et al., 2015; Levis et al., 2017).

Açai is a light-demanding multi-stemmed (clumped) palm species that occurs naturally in, and represent a dominant physiognomic component of Amazonian estuarine forests (ter Steege et al., 2013). Although açai is not restricted to this forest type, the traditional açai fruit consumption (as a staple food) and fruit production/harvesting for market is concentrated to households (10 ha in average) in estuarine forests. Açai fruits are gathering from wild populations as well as from intensely management forests and even from agroforestry systems where açai palms are planted (Brondízio, 2008). Here, intensification is used to describe the increment in açai clump density via forest thinning in order to eliminate competitors (Anderson, 1988; Anderson et al., 1995). This can include forest patches supporting few clumps (Almeida et al., 2004) up to açai monodominant forests (Belcher, 2003; Freitas et al., 2015).

2.2. Sampling design

Forty-seven sites were selected in the focal region in order to cover as much as possible the variation of açai clump density, from forest patches supporting natural populations (Almeida et al., 2004; Grossmann et al., 2004; Weinstein and Moegenburg, 2004) up to highly intensified forest stands (> 1000 clumps ha⁻¹). Tree assemblages (stems ≥5 cm DBH) were surveyed in one 0.1-ha plot (100 m × 10 m) per site. Thirty six of the 47 plots were sampled in a previous study on tree taxonomic diversity (Freitas et al., 2015).

Tree species were surveyed between April and June 2016. Species identification was carried out by parataxonomists and by comparing samples with specimens deposited in the Museu Paraense Emílio Goeldi herbaria (MG herbaria, Belém, Pará state, Brazil). Finally, we considered as low-intensity açai management the presence of ≤200 clumps per hectare (16 forest patches), a maximum that can naturally occur across estuarine forest stands (Freitas et al., 2015; Grossmann et al., 2004; Queiroz and Machado, 2008). Accordingly, those 31 forest patches supporting >200 clumps/ha were considered to be exposed to high-intensity açai management (Fig. 2). This threshold was adopted to highlight the magnitude of tree assemblage changes as açai management intensified beyond the abundance found in natural populations.

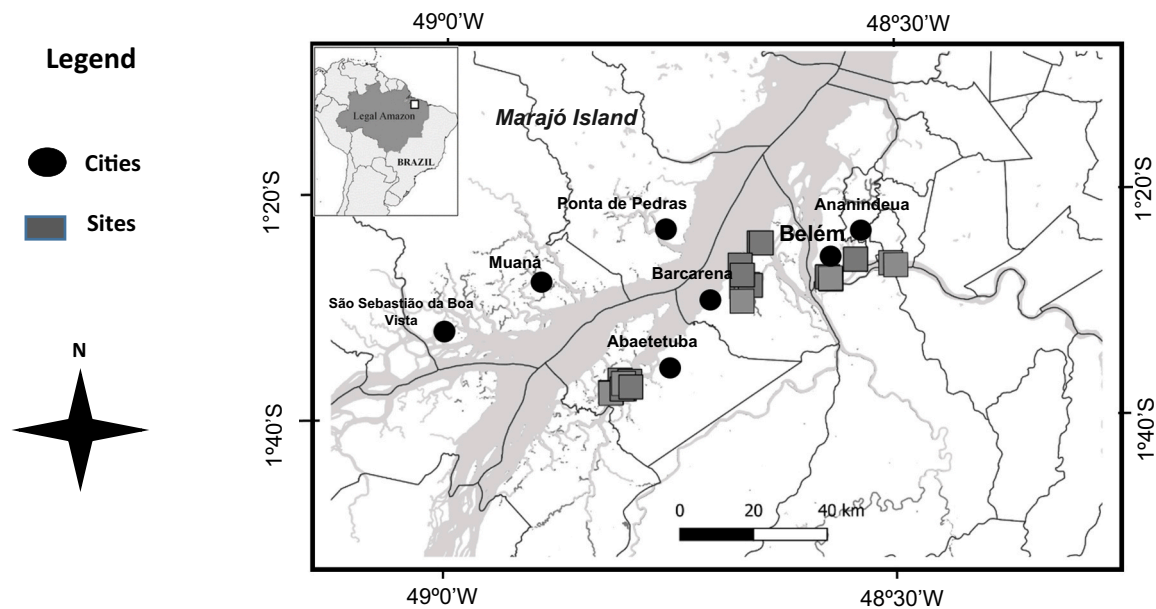


Fig. 1. Location of the study area in the Amazon estuarine region, Brazil. Please note that most research sites are overlapped due to map spatial scale.



Fig. 2. Estuarine forest stands experiencing low-intensity açai management (A), and high intensity management (B). Note açai palm individuals in B. Photos: A courtesy of Maria F. Barros.

2.3. Explanatory variables

As tree assemblage structure usually responds to physical and biotic forces (Parolin, 2012), we assessed four predictor variables within each plot: (i) açai clump density (clumps/ha); (ii) canopy openness; (iii) elevation (meters above sea level), and (iv) soil fertility; see Freitas et al. (2015) for further details. Briefly, canopy openness was measured by taking 30 hemispherical photographs within each plot with a digital camera and fisheye lens. Pictures were taken one meter above ground level, between 8:00 and 10:00 am. Canopy openness was estimated by the *Hemiphot.R* script (Steege, 2018). Elevation, taken here as a proxy for flooding intensity, was estimated at plot level by randomly selecting 10 points within each plot and obtaining an average value through Quickbird satellite imagery available in Google Earth™ (version 7.3) (Google, 2017).

Soil collection followed the protocol of Pinho et al. (2017): three samples per plot were collected and pooled into a single sample. Soil analysis was carried out by the Soil Laboratory of Embrapa Amazônia Oriental, Belém, which followed the Brazilian protocol for agronomic analysis (Embrapa, 1997). Soil attributes related to fertility were log-

transformed to normalize and standardize the distribution to zero mean and unit variance. Then, a principal component analysis (PCA) was performed to produce orthogonal axes to be used in the explanatory Akaike models. The first two axes of the PCA explained 43.4% and 24.6% of the variation in the dataset, respectively (Table S1, Fig. S1, Supplementary Material). Soil aluminum content was negatively related to açai clump density, and the other soil attributes increased in more intensively managed forest patches. In other words, patches exposed to high-intensity management exhibited greater fertility as compared to those exposed to low management. Thus, the first PCA axis reflected a gradient of infertility.

2.4. Ecological traits and functional diversity metrics

First, we assessed the completeness of plant inventories with the sample coverage estimator proposed by Chao and Jost (2012), with the *iNEXT* package for R (Chao et al., 2016). Sample coverage was very high (97%), suggesting that plant inventories accurately represented the plant species richness across forest patches (Chao and Jost, 2012). We then selected three to 27 stems (mean = 5.3 stems) per plant species (n

= 120 species) distributed across the plots to measure eight functional traits associated with life history strategies and one associated with natural flood disturbance: (i) maximum plant height (Hmax henceforth; m); (ii) stem specific density (SSD; mg/mm³); (iii) specific leaf area (SLA; mm²/mg); (iv) leaf dry matter content (LDMC; mg/g); (v) leaf thickness (Lth; mm); (vi) stomatal density (N_est; n/μm²); (vii) stomatal area (Area_est; μm²); and (viii) seed mass (g). Maximum plant height is associated with competitive ability and dispersal (Díaz et al., 2016), and was measured using the highest part of the leaf exposed to the sun. Stem specific density is negatively associated with growth potential and positively associated with longevity (Pérez-Harguindeguy et al., 2013). We collected a segment from five branches per plant which were then dried at 70 °C for 72 h. We then obtained the SSD for each segment by dividing its dry weight by its volume when fresh. Specific leaf area, leaf dry matter content and leaf thickness reflect adaptive conditions of plants to energy demand and water balance, and correlate with resource use strategies and with the trade-off between photosynthetic potential and nitrogen acquisition and herbivory (Díaz et al., 2016; Pérez-Harguindeguy et al., 2013; Wright et al., 2004). To estimate these traits, we collected at least three whole branches per stem, and five leaves per branch, avoiding leaves with apparent physical damage (e.g. herbivory). Stomatal density and area are associated with water transportation in the xylem, and with water loss by evapotranspiration and stomatal conductance (Parolin et al., 2010). These two variables were measured from surface impressions of the mid-blade abaxial leaf surface with instant dry glue, and then checked with a microscope using a millimeter slide (Segatto et al., 2004). Finally, seed mass reflects dispersion syndromes and is associated with a trade-off between seedling survival and colonization ability (Díaz et al., 2016; Pérez-Harguindeguy et al., 2013). Information on seed mass was obtained from the literature (Lorenzi, 2002, 2009; Lorenzi, 2008; Wittmann et al., 2010).

We then used all these traits to assess the functional structure of tree assemblages by using three complementary approaches: (1) trait variation at species level; (2) community-weighted mean (CWM), weighted according to species local abundance; and (3) functional diversity indices that have been widely used in previous studies (Mouillot et al., 2013; van der Plas et al., 2017). The CWM was calculated according to Garnier et al. (2004). We used functional richness (FRic) and functional dispersion (FDis) to estimate functional diversity. All functional structure analyses were done using the *FD* package (Laliberté et al., 2015) in R (R Development Core Team, 2017). Both FRic and FDis are not independent from species richness (Carmona et al., 2019, 2017), but this relationship can be controlled by means of null models. Thus, we estimated standardized effect size for FRic and FDis (SES.Fric and SES.FDis, respectively) and tested for significant deviation between observed and random communities. SES was calculated as follows: $SES = (FD_{obs} - FD_{null})/FDSD$; where FD_{obs} is the FD value observed in each plot, while FD_{null} and $FDSD$ are the mean and standard deviation, respectively, of the null distribution of FD values generated for each assemblage; i.e. a null distribution without considering species relative abundance (Gotelli and Graves, 1996). SES values below zero indicate that the trait distribution patterns are more convergent than expected by chance, while positive values reflect a more divergent trait distribution than expected by chance.

2.5. Data analysis

To examine the role of explanatory variables in the structure of tree assemblages we adopted two complementary approaches by considering açai density as a descriptive, categorical variable (low vs. high intensity) and a continuous variable as well. Elevation, fertility and canopy openness were treated as continuous variables. When considering our explanatory variables as continuous, we adopted information-theoretic and multi-model inference to assess the relative effect of each predictor on each response variable (Burnham and Anderson, 2002). All predictors were scaled and centered using *z-scores* to allow for a comparison

of regression coefficients. To avoid collinearity, we excluded all models whose predictors had correlation coefficients greater than 0.5 through the *max.r* function in the *dredge* package (Jaffé, 2016). Thus, we generated models representing all combinations of explanatory variables with Akaike information criterion corrected for small samples (AICc) and mean parameter estimates weighted by the Akaike weights (w_i). The sum of Akaike weights ($\sum w_i$) of all models is 1.0, and the set of models for which $\sum w_i$ is 0.95 represents a set that has 95% probability of containing the true best model (Burnham and Anderson, 2002). We compared the averages of the adjustment percentages of the most plausible models ($\Delta AIC < 2$) weighted by the null model as a quality adjustment index, in which the model differs from that expected by chance. A given explanatory variable was considered important for a given response variable if the following three criteria were met: (i) it showed a relatively high sum of Akaike weights (i.e., considering each candidate model in which it appeared); and (ii) the model-averaged unconditional variance was lower than the model-averaged parameter estimate; and (iii) the complete model showed a high percentage of explained deviance (i.e., high goodness-of-fit; Crawley, 2013). All models were generated using the *dredge* function in the *MuMIn* package (Barton, 2018) for R version 3.4.1 (R Development Core Team, 2017).

3. Results

A total of 2405 individuals from 120 tree species were recorded across the 47 plots, most of them canopy tree species (Table S2, supplementary material). Tree density ranged from 3 to 131 individuals per ha (56 ± 35 ; mean \pm SD), while species richness ranged from 2 to 30 species per hectare (13 ± 8). Tree density and species richness were influenced by a group of variables including açai density, soil fertility, elevation and canopy openness (Table S3, Fig. 3a, 3b). Furthermore, tree density and species richness were negatively correlated with acai management, with intensively-managed forest patches retaining only a small fraction of the stems and species in forest stands submitted to low management intensities (Fig. 4a, 4b). Species richness was particularly affected by acai management intensity but also negatively affected by tree abundance.

Thus, forest patches submitted to low management (16 plots) supported a much more diverse flora. Although our sampling effort was not sufficient to capture the whole assemblage of trees, species-accumulation curves indicated higher alpha and beta diversity across low-intensity forest patches (Fig. 5). In fact, high-intensity patches lacked half of the flora recorded across all plots, including species across all ecological groups; i.e. understorey, canopy and emergent tree species (Table S2). Moving to species dominance, a small set of tree species dominated forest patches, such as the cocoa tree species (*Theobroma cacao* L.) dominating both low and high intensity forest patches; 11% vs. 17% of all stems, respectively (Fig. 6a, 6b). Note that in the estuarine forest cocoa currently occurs as cultivated or spontaneously. However, açai clump density did not affect the relative abundance of useful/valuable tree species (Table S3, Fig. S2).

Moving to the functional dimension of tree assemblages, high-management forest stands captured the same spectrum of trait variation or diversity as compared to low management forest stands (Fig. S3) when considering species composition alone; i.e. the same plant strategies were present across both types of forest stands. However, when considering species abundance, forest stands differed in terms of community-level functional composition (CWM) due to the influences of several environmental variables, including açai clump density. Our explanatory variables explained a relatively small fraction of the variation (19–26.6%) in stem specific density, leaf dry matter content and stomata area. More specifically, stem density was mainly affected by elevation (a positive correlation) and negatively by fertility (Fig. 7a, Table S3), while leaf dry matter content was negatively affected by soil fertility (Fig. 7b). Stomata area was particularly affected by canopy openness and elevation (Fig. 76c); negatively in both cases. The other

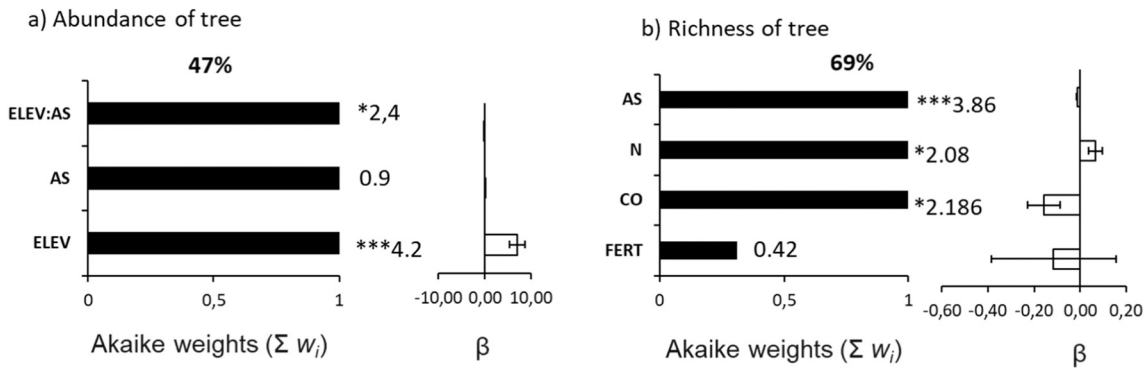


Fig. 3. Best models generated to explain the abundance of tree species (a) and richness of trees species (b) across 47 forest patches in the Amazon estuarine region, Brazil. The sum of Akaike weights (Σw_i) shows the importance of each variable (black bars, panels in the left side) and their respective z-scores value. Panels on the right side indicate the values of model-averaged parameter estimates (β) and unconditional variance of information-theoretic based model selection and multi-model inference. Codes of significance of p -values: 0 ‘***’, 0.001 ‘**’ and 0.01 ‘*’.

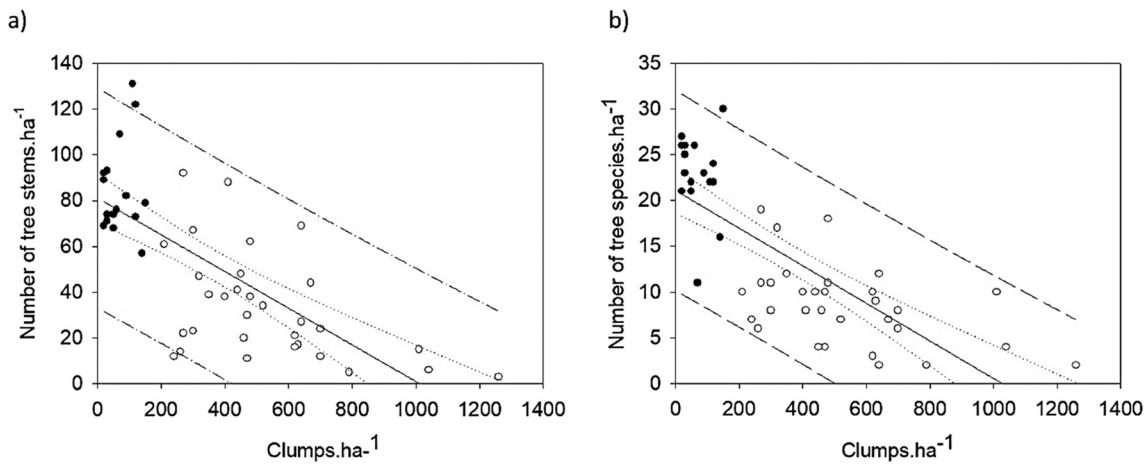


Fig. 4. Scatter plot of the density of açai (clumps per hectare) and its relationship with tree density (a, stems per hectare) and number of tree species (b) across 47 forest patches in the Amazon estuarine region, Brazil. Black circles indicate areas of low açai management and white circles represent areas of high management. Dashed line: 95% prediction band; dotted line: 95% confidence band.

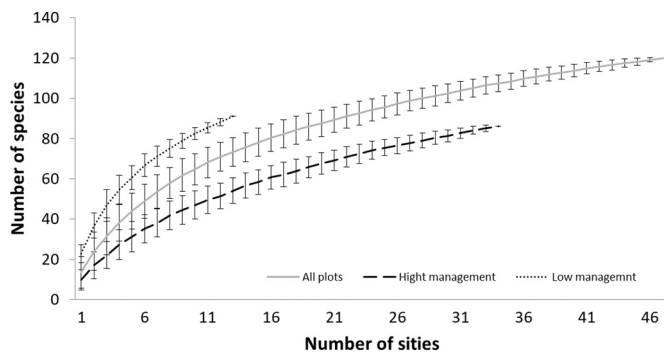


Fig. 5. Species accumulation curve for plots with low-intensity açai management, high-intensity management and for all plots across 47 forest patches in the Amazon estuarine region, Brazil.

traits were influenced to a lesser extent by the explanatory variables adopted here (i.e. < 15% of the whole variation), including açai density (Fig. 7e, 7f, 7g, 7h).

Moving to functional diversity, açai exhibited a major role as compared to other environmental variables such as soil fertility and canopy openness. Namely, açai density slightly increased the dispersal dimension of functional diversity (SES.FDis), while largely reducing

functional richness (SES.FR_{ic}, Table S3, Fig. S4). In fact, over 600 clumps of açai per ha led to functional richness dropping by half (Fig. 8).

4. Discussion

Our results suggest that açai intensification alters the structure of woody plant assemblages in Amazonian estuarine forests, particularly tree abundance, species richness (at both local and landscape level) and patterns of species dominance. Tree abundance and species richness consistently declines as açai clump density increases, with some forest stands being dominated by açai and exhibiting a clear lack tree species. Accordingly, landscapes dominated by high-intensity forest stands are impoverished in terms of understorey, canopy and emergent tree species. Moreover, estuarine forests tend to be dominated by a small set of valuable species regardless of açai clump density, but low-intensity stands retain many other species without utility for local householders, such as *Taralea oppositifolia* Aubl., *Ormosia coutinhoi* Ducke and *Swartzia polyphylla* DC.

Forest stands supported a functionally conservative flora, as indicated by high average values of leaf dry matter content, thick leaves and relatively heavy seeds (Díaz et al., 2016; Lebrija-Trejos et al., 2010; Wright et al., 2009). Interestingly, açai intensification played a minor role in the functional profile of forest stands, regardless of reduction in tree species richness. Soil fertility, flooding regime and canopy openness (a proxy for light availability) appeared to exhibit the greatest influent

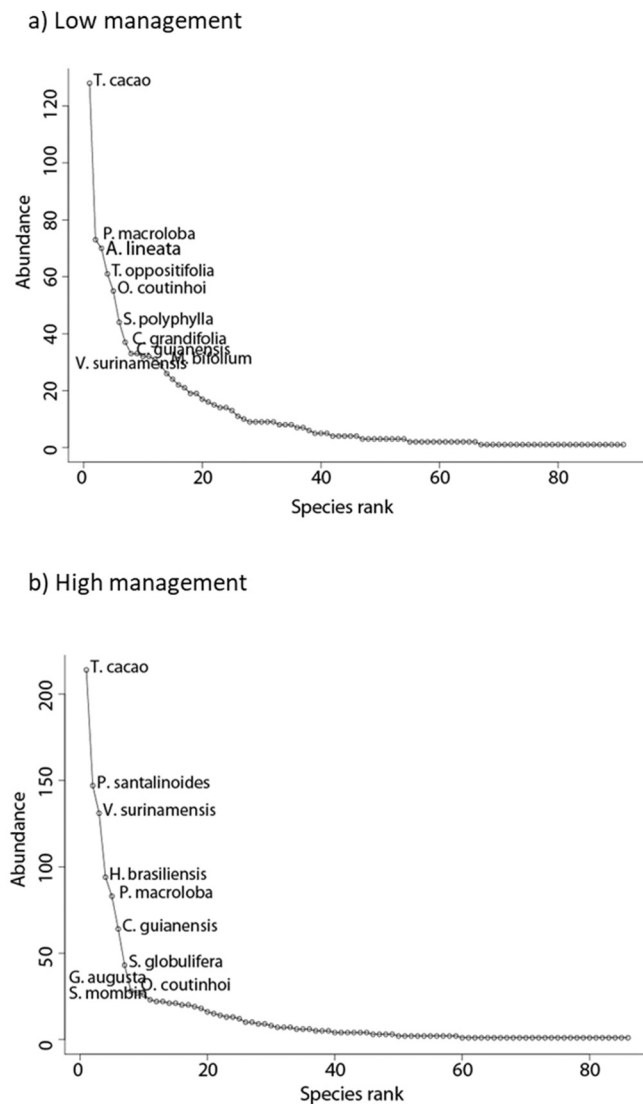


Fig. 6. Rank species curve for forest patches with low-intensity management (a) and high-intensity management (b) across 47 forest patches in the Amazon estuarine region, Brazil. Trees of commercial value as timber and non-timber forest products are highlighted.

on functional composition. Collectively, drier and more open forest stands with low açai densities and less fertile soils tended to support more functionally conservative tree assemblages with higher functional richness. Despite the small impact on functional composition, açai intensifications reduced the functional richness of forest stands, which is consistent with the drastic species impoverishment experienced by high-intensity forest stands.

Our findings reinforce the notion that açai intensification reduces tree species richness at local scale, as previously documented by Freitas et al. (2015), who examined a subset of the forest stands examined here (36 of our 47 forest stands). However, here we have demonstrated that tree species reduction takes place in parallel with decreases in tree abundance, suggesting that recruitment failure and/or elimination of standing trees are the main drivers of community-level species impoverishment. In other words, we show that açai intensification results in a collapse of the forest physical structure (from 130 to 3 stems ≥ 5 DBH/ha), leading to species impoverishment. Furthermore, our species accumulation curves (Fig. 4) show there has been a substantial reduction in beta diversity, or species richness at landscape scale. We also confirm the prevalence of useful or commercially-valuable tree species across all

forest stands (Freitas et al., 2015), which, in terms of relative abundance, were not affected by açai intensification. Such species are native with a spontaneous occurrence but actively selected to persist in the forest; i.e. some individuals are spared during forest-understorey cleaning operations. This is consistent with our observation that the cocoa tree species can dominate, or be completely absent in both low- and high-intensity management stands.

These findings are consistent with the way the estuarine forests have been historically exploited. In fact, the estuarine forests of the Amazon have a long history of management by local populations (i.e. riverine families or “caboclos”), starting with the arrival of Europeans in the 16th century, particularly the Portuguese (Bronzizio, 2008; Barros and Uhl, 1999). Estuarine forests are managed to provide both commercial and subsistence products, from crops to forest products, including timber, firewood, fruits and bushmeat (Rankin, 1985; Zarin et al., 2001). Briefly, traditional forest management includes the elimination of undesirable plant species, the introduction of native/exotic species of interest and their proliferation, particularly close to households (Anderson, 1988; Anderson et al., 1995; Scoles, 2009). Tree elimination (i.e. forest thinning/clearing) intend to reduce açai competition for space and light is well documented (Homma et al., 2006; Weinstein and Moegenburg, 2004). Accordingly, forest stands with human-induced increments in the abundance of useful/valuable plant species, but also lacking over-exploited species (valuable timber species such as *Virola surinamensis* author), have emerged before contemporary açai intensification. However, the close relationship we have uncovered between tree species abundance and açai clump density reinforces the notion that it is currently the major force leading to community-level tree species impoverishment, with impacts on understorey, canopy and emergent tree species.

Our findings also indicate that the functional profile of estuarine forests respond to a set of variables, particularly soil fertility through its impact on leaf dry matter content. Açai also plays a role in functional structure by slightly altering leaf dry matter content and reducing functional richness as it becomes more abundant. Lower leaf dry matter content implies a slight transition from acquisitive to conservative plant strategies (Carreño-Rocabado et al., 2016; Craine, 2009; Wright et al., 2004), as forest stands support more açai and less canopy cover, particularly across more fertile soils and stand that experience less flooding. In fact, the occurrence of a relatively conservative flora with little response to açai intensification suggests that poor soils (i.e. pH and phosphor content), high salinity and tide regime (two flooding periods every 24 h) impose severe environmental filters, as has been documented in other tropical forest across the globe that experience flooding (Assis et al., 2014; Cattanio et al., 2002; Parolin, 2000). Reduced functional diversity with açai intensification is expected, considering the profound tree species impoverishment that high-intensity forest stands experience. However, the impoverishment we documented was greater than expected, even after accounting for the effect of species richness through null models. This suggests that açai intensification acts as a filter on the range of trait values that are found in the most intensified plots. When these results are considered together, they suggest that the functional structure of estuarine forests relative to foliar economic spectrum appears to be relatively resistant (i.e. the overall structure persists). Although açai intensification slightly favored more acquisitive strategies, its main effect was to eliminate species with extreme functional strategies, thus reducing functional richness and leading to functionally impoverished communities. Similar effects of management intensification have previously been described in a number of systems and organisms, including grasslands (Carmona et al., 2015), agricultural landscapes (Guerrero et al., 2014; Hevia et al., 2016) and rainforests (Martello et al., 2018). However, to our knowledge, this is the first time that these effects have been reported in relation to açai intensification.

Tropical forests usually respond to human disturbances, including chronic human disturbance. One such example is that of the proliferation of disturbance-adapted species (both native and exotic) with

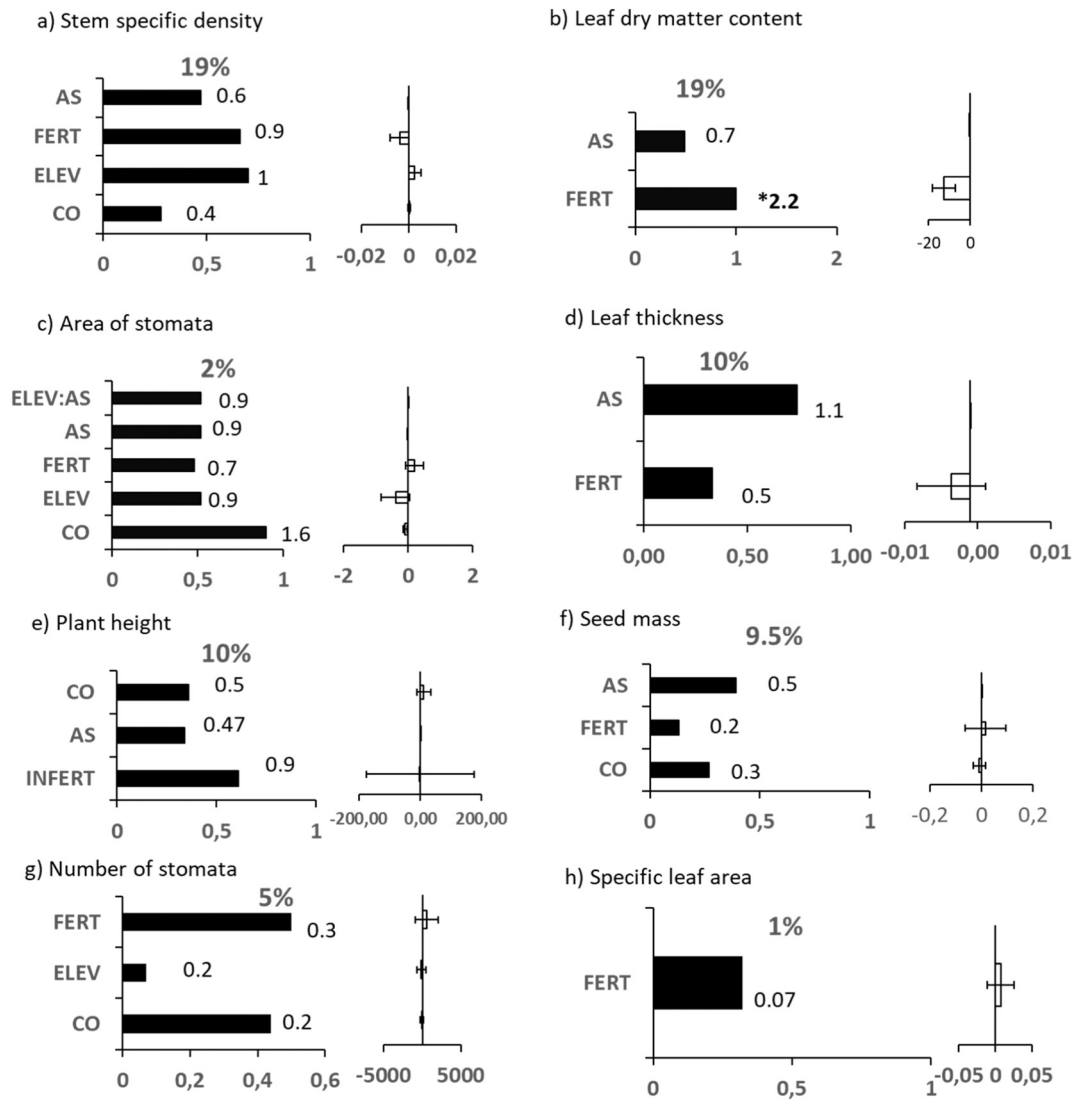


Fig. 7. Best models generated to explain community-weighted means (CWM) of functional traits across 47 forest patches in the Amazon estuarine region, Brazil. The sum of Akaike weights (Σw_i) shows the importance of each variable (black bars, panels in the left side) and their respective z-scores. The mean percentage of deviance explained by the most parsimonious models for each response variable is included as a proxy of goodness-of-fit. Panels on the right side indicate the values of model-averaged parameter estimates (β) and unconditional variance of information-theoretic based model selection and multi-model inference. *P*-values: 0 ‘***’, 0.001 ‘**’ and 0.01 ‘*’.

tangible impacts on the functional structure of tree assemblages as a result of NTFP exploitation (Leitão et al., 2016). In many situations, proliferation, to some extent, compensates for the extirpation of sensitive species (Mouillot et al., 2013). Intense environmental filtering (i.e. acid/saline soils and daily flooding) plus regular and severe thinning limit this possibility in the case of açai intensification. Moreover, the species impoverishment of forest stands due to açai intensification is likely to alter the functional structure of the remaining forest, considering other dimensions such as plant phenology, pollination and seed dispersal ecology, plant stature and regeneration to mention a few attributes (Brockerhoff et al., 2017).

The practical implication of our findings is that the açai regulation (the normative instruction n° 09/2014) stimulating açai clump density to not surpass the threshold of 400 clumps ha^{-1} and preserving 250 dicotyledonous ha^{-1} is not enough to guarantee the persistence of the diverse estuarine flora, locally or at landscape level when stands are reduced to below threshold levels. Here, tree stem density explained 50% of the variation in tree species richness, and when tree density was below 60 stems/ha, at least one third of tree species were lost. A minimum number of tree stems should be targeted not only for the sake of the

tree flora, but also because tree species, particularly large trees, respond to substantial proportion of the ecosystem services provided by tropical forests, including biodiversity persistence through several taxa (Campbell et al., 2018; Freitas et al., 2015; Pinho et al., 2020). Açai production has already achieved an economic boom (>US\$290 million/year), with global markets for açai still expanding (açai-related products are available in many wealth countries). In this context, it is not unlikely that a vast portion of the diverse estuarine forest (up to 30 species per ha) will move towards quasi-monomodominant açai forests with few plant species (Freitas et al., 2015; Tagore et al., 2018). It cannot be denied, however, that, demand for açai has benefited local populations and the regional economy, while helping riverine culture to persist by improving the livelihoods of local populations (Brondízio, 2008; Vogt et al., 2015). Although rural local populations are not responsible for açai industrial processing (it is done in urban areas), locals benefit from the açai market by providing mature fruits (the raw material) in addition to consume an açai-fruit beverage daily as a staple food (i.e. forest-depend people experiencing increased income). Such unique culture is part of the Amazon legacy and is worthy of preservation, serving as an example of tropical forest sustainable use, despite it becoming clear that açai

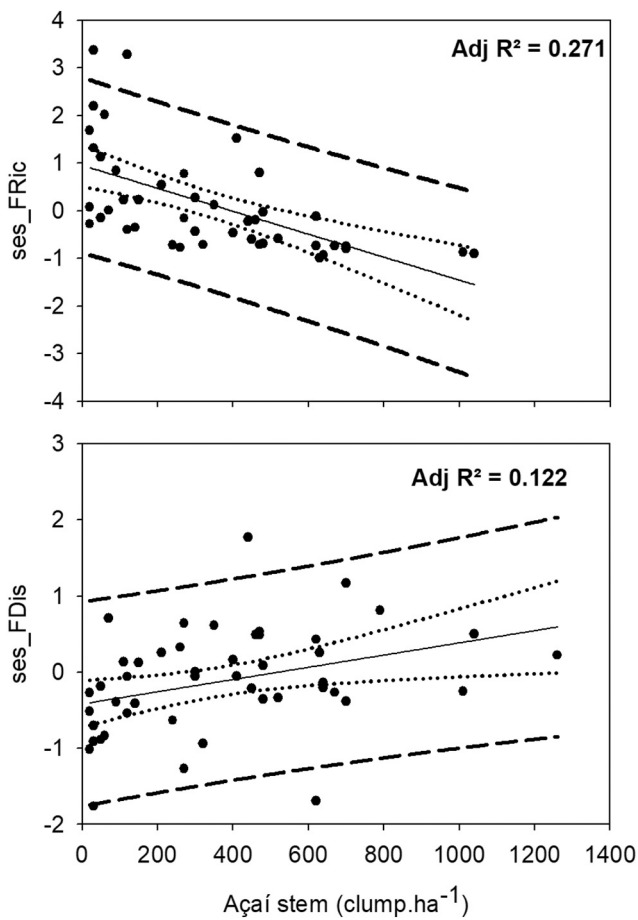


Fig. 8. Scatter plot of the standard effect size of the functional richness (SES.Fric) (a) and functional dispersion (SES.FDis) (b) and its relationship with açai across 47 forest patches in the Amazon estuarine region, Brazil. We indicate plots with less than 200 stems per hectare with white circles, to represent a parameter with low-intensity management (see, Freitas et al., 2015), while black triangles indicate plots with different levels of açai management intensity.

represents both a key opportunity and a threat. Without the persistence of a diverse forest and their multiple benefits, the whole socio-ecological system become vulnerable, like any local economy supported by a monoculture of an international commodity (Shackleton, 2015).

5. Conclusions

In synthesis, NTFPs have been advocated as an effective instrument for the sustainable use of tropical forests and a better life for local/traditional communities (Shackleton et al., 2011). The exploitation of NTFPs, however, represents a form of chronic human disturbance, with potential negative impacts from population level to ecosystem integrity, which should not be neglected. Açai intensification for enhancing fruit yield represents a complete reorganization of estuarine forests, with conspicuous reductions in stem abundance, tree species richness and functional diversity. Such an “industrialization” of NTFP represents a potential risk not only for the estuarine forest, but also for other ecosystems from which NTFP gain global markets and a commodity status. Further studies should investigate and quantify the cascading effects on the wider ecology and ecosystem services that are promoted by changes in forest structure, as well as in tree species richness and functional impoverishment.

CRedit authorship contribution statement

Madson Freitas: Data collection, Data analysis, Writing & Review.
 José Magalhães: Data analysis.
 Carlos Carmona: Data analysis.
 Victor Arroyo-Rodriguez: Data analysis, Methodology.
 Ima Vieira: Conceptualization, Writing & Review.
 Marcelo Tabarelli: Conceptualization, Writing & Review.

Declaration of competing interest

All authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109251>.

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