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Açaí management intensification impoverishes Amazonian avian assemblages in estuarine forests

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ABSTRACT

Non-timber forest product (NTFP) exploitation has emerged as an alternative to deforestation in human-modified landscapes, but their overexploitation can also reduce biodiversity if it leads to chronic habitat degradation. This study investigates the effects of management intensification on the taxonomic and functional diversity of bird assemblages in Amazonian floodplain forests. The management is directed at enhancing açaí palm (*Euterpe oleracea* Mart.) density for fruit production in the estuarine floodplains of Pará, Brazil. We explored community change across a gradient of açaí palm density ranging from 11 to 1430 clumps.ha^{-1} and we used multimodel inference to assess its effects on the richness, abundance, and functional attributes of bird guilds. We found that increasing açaí density was negatively correlated with species richness at local and landscape scales, leading to shifts in richness and composition especially negatively impacting insectivores and 'forest dependent species', whilst only a few species benefitted from intensification, such as *Pitangus sulphuratus*. These changes in avian community structure associated with açaí management intensification indicate that demand for this NTFP is driving ecological degradation of Amazon estuarine forests at local and landscape scales. Our findings underscore the need to regulate açaí management intensity to safeguard estuarine forest biodiversity.

1. Introduction

Tropical forests provide irreplaceable ecosystem services of both local and global relevance, including climate regulation, biodiversity conservation and support for human wellbeing (Haines-Young and Potschin, 2018; IPCC, 2023). Beyond their ecological role, these forests are central to global carbon cycling, since they are responsible for removing nearly one-third of the CO_2 emitted annually to the atmosphere (Friedlingstein et al., 2019), while their forest products support the livelihood of countless traditional communities (Mohamad, 2023). Despite their critical role in facilitating achievement of the sustainable development goals, tropical forests continue to experience habitat loss, fragmentation and degradation driven by a combination of microclimatic and ecological edge effects, selective logging, severe and wildfires exacerbated by climate change (Lapola et al., 2023). In this context, the climate crisis is only one of many factors highlighting the urgent need to promote sustainable tropical forest use that reconciles socioeconomic development, biodiversity conservation, and ecosystem service provision goals (IPCC, 2023; Steel et al., 2023).

Over recent decades, several strategies have been proposed to secure the future of tropical forests and the cultural systems they support (Metzker et al., 2012; Nadkarni and Kuehl, 2013). Seeking a way to harmonize socioeconomic and ecological goals, a key approach has been the community-based management of Non-Timber Forest Products (NTFPs, Gaoue and Ticktin, 2008; Nadkarni and Kuehl, 2013). Recent frameworks have incorporated additional key concepts such as

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biocultural restoration (Pradhan and Ormsby, 2020; Shackleton et al., 2018), food security (Ahenkan and Boon, 2011; Zimmerer, 2013) and the bioeconomy (de Assis Costa et al., 2022; Rosenfeld et al., 2024; Vieira et al., 2024). However, the sustainability of NTFP exploitation must be considered on a case-by-case and long-term ecological basis. This is particularly important when global markets are involved, since increases in demand can trigger unsustainable extraction and ecological degradation, (de Mello et al., 2020; Ferreira et al., 2024), in a transition toward overexploitation, increasing vulnerability for the whole socio-ecological system (Nugraha et al., 2024; Pandey et al., 2022; Singh et al., 2021). Although NTFP harvesting is generally less damaging than other productive models that may result in total habitat loss and fragmentation, there remain questions over the potential for managed forests to continue delivering key ecosystem services and supporting forest-associated biodiversity in the long-term (de Mello et al., 2020; Mandle et al., 2013; Shackleton et al., 2018; Ticktin, 2004).

The açaí palm (*Euterpe oleracea* Mart.) is native to Amazonian floodplain forests and naturally abundant in estuarine forests (sensu Freitas et al., 2015). Its fruits are a culturally and economically important non-timber forest products (NTFP) with a long history of use as a daily staple food for traditional riverine communities in the Amazon estuary (Brondízio, 2008; Laurindo et al., 2023; dos S Tavares et al., 2020). Over the last two decades, açaí has expanded from a regional product to a national and international commodity, marketed as a "superfood" with associated nutritional and health claims, and sold mainly in the form of ice cream and energetic beverages (Magrach and Sanz, 2020). The accelerated expansion of this emerging global market has driven a substantial demand for the fruit (dos S Tavares et al., 2020). Annual harvests in the Brazilian state of Pará (the epicenter of açaí extractivism) have reached one million tons and the national revenue exceed US$1 billion, representing 38% of Brazil's total income from non-timber forest products (IBGE, 2022).

Although current legislation in Pará limits açaí management in natural forests to a maximum of 400 clump.ha^{-1} (Brasil, 2014), demand driven intensification has become widespread. This intensification is characterized by managed increases in palm clump density and selective removal of other trees and shrubs to favor the light-demanding açaí stems and facilitate manual fruit collection (Freitas et al., 2015; Homma et al., 2006; Weinstein and Moegenburg, 2004). Such management practices convert structurally complex and diverse forests into simplified stands dominated by palms, with up to 1000 clumps.ha^{-1} (compared to a natural density of about a 100 clumps.ha^{-1}) and sharp declines in basal area and stem density of other tree species (Barros et al., 2023; Freitas et al., 2015, 2021, 2025). Intensified management can lead to a 70% decline in tree species richness, with no evidence that any other tree species in the estuarine forest benefit from this process (Freitas et al., 2021, 2025).

While the ecological effects of açaí intensification impacts have been documented for plant communities, the consequences for animal communities remain largely unexplored (Moegenburg and Levey, 2003, 2002, Menon et al., 2019). Although the regional sensitivity of Amazonian birds to habitat changes is well stablished for terra firme forests (e.g. Moura et al., 2013), there are no landscape-scale assessments of their responses to floodplain forests management intensification. This knowledge gap is particularly relevant because (1) the ecology of the Amazonian estuarine region remains poorly investigated (Capurucho et al., 2024), and (2) many floodplain species often have narrow geographic ranges, making them especially vulnerable to habitat loss and degradation (Bird et al., 2012).

Here, we investigate the functional and taxonomic responses of avian assemblages to increasing intensity of açaí management across a gradient of açaí clump density ranging from 11 to 1430 clumps.ha^{-1} at both local and landscape scales. We classified bird species into functional groups related to habitat preference, trophic niche and assessed community-level scores under varying intensity of forest management. Additionally, we evaluated landscape effects of forest cover on bird community structure for the first time in this ecosystem type. Considering that bird communities become impoverished in other monocultural palm systems such as oil palm plantations (e.g. Bohada-Murillo et al., 2020; Lees et al., 2015)' we expected to find similarly taxonomically and functionally depauperate assemblages in intensively managed açaí landscapes. We interpret our findings within the framework of community assembly in human-modified landscapes (Filgueiras et al., 2021) and discuss their implications for açaí fruit production as NTFP model aimed at promoting sustainable forest use rather than contributing to forest degradation.

2. Material and methods

2.1. Study area

The study was conducted across forest stands distributed over 376,000 km^2 of the Amazon estuarine region (1°270 S, 48°300 W, Fig. 1, Table S4.). Sampling localities encompassed portions of the municipalities of Belém, Barcarena, Abaetetuba and Igarapé Mirí in the state of Pará, Brazil. The estuarine region consists of flat lands up to 20 m a.s.l., with fertile gley soils formed by riverine sediment deposition (Falesi and da Silva, 1999). The dominant soil type in this ecosystem covers about 54,260 km^2 within the Legal Amazon (IBGE, 2023), with a mean elevation of 8 m (±6 m, Google, 2025).

The mean annual rainfall is 2500 mm, with maximum daily precipitation reaching 410 mm during the wettest months (January to May) and around 30 mm during the driest period (June to December). Most of the floodplain area was originally covered by evergreen forest subject to tidal regimes driven by the estuary, hence the designation Amazonian estuarine forests. This vegetation type is distinct from mangroves, which occur in more saline, marine-influenced environments (Junk et al., 2011; Lima and Tourinho, 1996).

Amazonian estuarine forests are structurally complex, well-developed three-strata forests dominated by trees belonging to the Fabaceae, Malvaceae, Arecaceae, Chrysobalanaceae and Meliaceae families (Freitas et al., 2015). The dense understorey is composed mainly by shrubs and small trees, mostly from the Piperaceae, Melastomataceae, Rubiaceae and Areacaceae families (Barros et al., 2023). The açaí palm is a light-demanding canopy species that occurs naturally and represents a typical component of this forest, coexisting with emergent trees such as the giant sumaúma (*Ceiba pentandra*, Barros et al., 2023).

Historically, the Amazon estuarine forest has undergone successive cycles of logging, cocoa and rubber exploitation and became home to traditional communities that rely on forest resources for both subsistence and commercial uses (i.e. caboclos or riverine people (Brondízio, 2008; Barros and Uhl, 1999). The exploitation of açaí fruits represents the most recent cycle of forest use, and the Amazon estuarine floodplain is now the epicenter of both Brazilian and global açaí production., Within this region, the state of Pará alone accounts for 85% of the country's total output (IBGE, 2022), with most production occurring in smallholder landholdings (Brondízio, 2008). Intensification began in the 1980s, when natural populations of fewer than 100 clumps.ha^{-1} were actively managed toward higher densities, in some cases, replacing forest areas by monospecific açaí stands (Anderson, 1988; Weinstein and Moegenburg, 2004).

2.2. Bird surveys

We sampled birds at 36 stands along single 300-m transects, spaced at least 1 km apart, covering a gradient of açaí clump density from 11 to 1430 clumps.ha^{-1}. Although habitat context ('fluvial-tidal island' vs. 'mainland' stands) was not a primary focus of this study, it was included as an explanatory variable to account for potential effects of insularity on bird assemblages. In order to assess whether current legislation defining management intensity thresholds (Brasil, 2014) is sufficient to

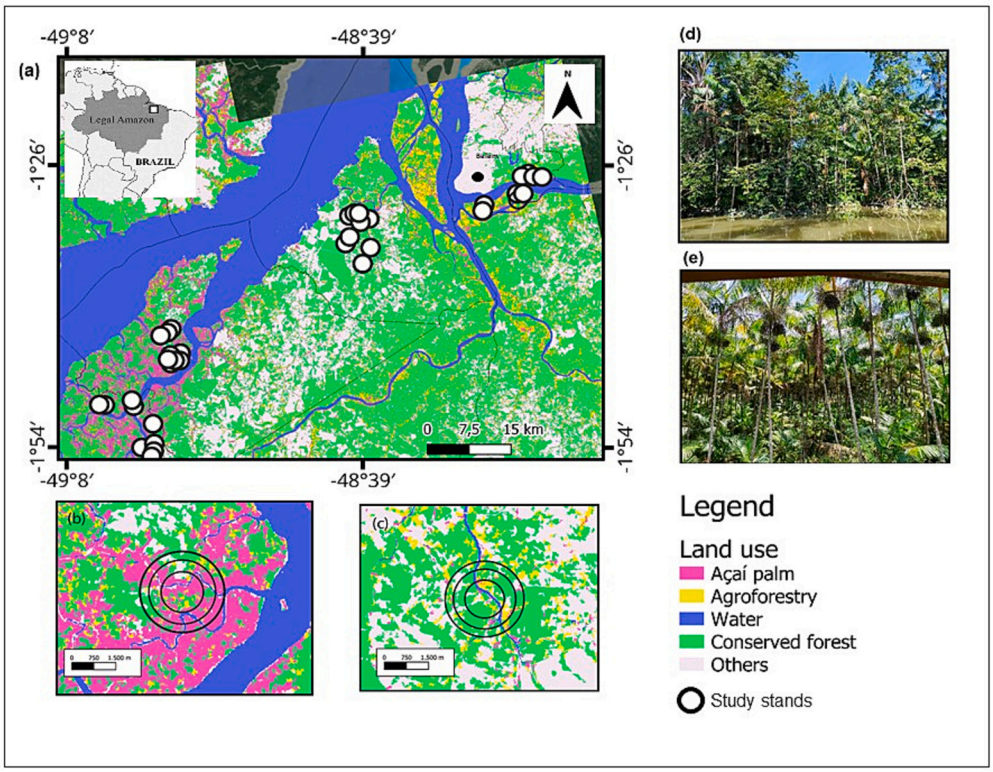

Fig. 1. Study region and study stands; maps showing the location of estuarine floodplain forests in the Belém region of Pará state, Brazil (a). The study region is a mosaic of floodplain forest subject to intensive açaí management (high-intensity managed forest stands, b and e) and natural vegetation types (low-intensity managed forest stands, c and d). In this region we sampled birds at 36 stands (white circles in a) which were distributed in five dominant land uses: forests managed for açaí, agroforestry, open water, conserved forest and other land use types. Around each stand we also quantified landscape-level habitat extent inside three buffer widths (radii 797 m, 1561 m and 1595 m) that were centered on our 10 m × 150 m sampling stands stratified by açaí density. The landscape profile of each sampling locality is shown in Fig. S3.

maintain the ecological integrity of this forest, 16 stands managed at fewer than 400 clumps.ha^{-1} were classified as "low-intensity managed forest stands" and 20 stands managed at more than 400 clumps.ha^{-1} were considered "high-intensity managed forest stands".

Birds were recorded at three point-count stations located along each 300 m transects: at 0, 150 and 300 m. Point counts were recorded with a Zoom H1 voice recorder and lasted 15 min per station. Surveys were carried out during two field campaigns (August–November 2016 and July–October 2019), and all birds seen or heard within a 75 m radius from each point were recorded (following Moura et al., 2013). This sampling period aligns with the fruiting phenology of *E. oleracea*, which extends from July to December in Amazonian estuarine floodplain forests and standardizes avian habitat use (Freitas et al., 2015; Weinstein and Moegenburg, 2004). Each transect was surveyed eight times: four times in the morning (between 0600 and 0800) and four times in the afternoon (between 1600 and 1800) on alternate days, ensuring that the surveys were repeated an each plot at different times (Bibby et al., 2000).

The mean survey time per stand was 6 (± 0:23) hours and the overall sampling effort resulted in 127 h of auditory and visual observations across the 36 stands. Point-count surveys were conducted by Raphel Vasconcelos Nunes and Danielson Aleixo. The avian taxonomy follows the Comitê Brasileiro de Registros Ornitológicos – CBRO, list of bird species (Pacheco et al., 2021). All species records were pooled at the transect level to obtain incidence per transect (i.e., transect-level frequency of occurrence, Cavarzere et al., 2012) which was used as a proxy for abundance. This approach was adopted because accurate counts of individuals are often unreliable in tropical forests, where detectability varies across taxa (Robinson et al., 2018). Challenges such as flocking behavior, overlapping vocalizations, and cryptic species make it difficult to distinguish individuals from auditory data. Therefore, we used incidence data, which provides a more robust and standardized measure at the community level.

2.3. Structure of bird assemblages

In order to assess the completeness of the bird surveys, we applied the sample coverage estimator proposed by Chao and Jost (2012) and compared observed and expected richness and abundance values using rarefaction curves, in addition to extrapolations for richness, abundance and common species using the R package iNEXT (Fig. 2, Chao et al., 2016). For this, we adopted species richness (S), Shannon's exponential entropy (q = 1, or typical species) and the inverse of Simpson's concentration (q = 2, or dominant species) as different measures of bird diversity based on Hill numbers of order *q* (Chao et al., 2010). The q = 1 measure (Q1, exponential of Shannon entropy) reflects the effective number of typical species, scaling with relative abundance, while the q = 2 measure (Q2, Simpson's inverse index) estimates the effective number of dominant species, down weighting rare ones (Chao et al., 2014). These analyses were conducted using the Alpha Diversity function in the *entropart* package 1.6–12 in R (Marcon and Hérault, 2015; R Core Team, 2025).

All bird species were assigned to functional groups based on habitat preference, trophic niche and foraging behavior using trait data from Tobias et al. (2022; Table S1, supplementary materials). Habitat was classified as: (a) forest (tall, closed-canopy tree-dominated vegetation, including palm forests), (b) grassland (open landscapes dominated by grasses and herbs, with few or no trees.), (c) human-modified habitats (including intensive agriculture), (d) shrubland (low-stature, bushy habitats), and (e) woodland (medium-stature tree-dominated habitats,

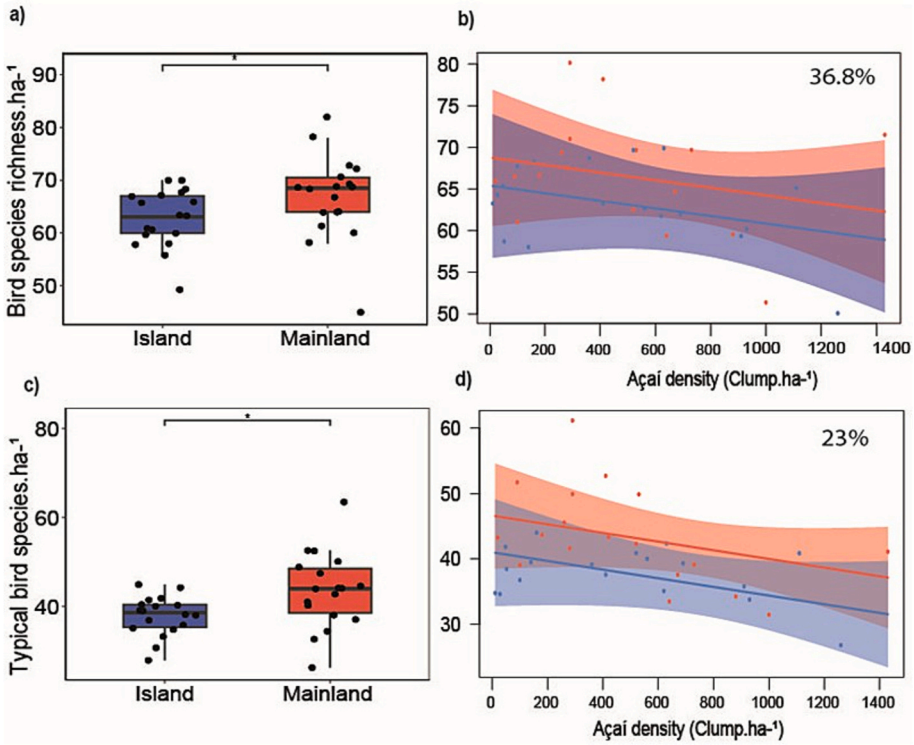

Fig. 2. Fitted models of the predictor variables included in the best models (according to Table S5 supplementary material) for two avian response variables: avian species richness.ha^{-1} (a and b), typical bird species.ha^{-1} (c and d). The figure presents two components: boxplots on left panels showing the distribution of values across habitat types (blue = fluvial-tidal island, red = mainland), with individual data points overlaid and quartiles clearly represented. Statistical significance between groups is indicated above the boxplots. Right panels showing the fitted models evaluating the effect of the focal predictor (açaí density) on the response variable. These panels display observed values (colored dots), estimated marginal means (colored lines), and 95% confidence intervals (shaded areas), using the same colour scheme for habitat type. The goodness-of-fit of each model is indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

including riparian woodlands and forest edges) (Table S1, supplementary material).

Trophic niches were categorized as aquatic predator, frugivore, granivore, invertivore, nectarivore and omnivore following Wilman et al. (2014). Foraging behavior was classified as aerial, arboreal or terrestrial according to the species' predominant locomotion mode while foraging (Tobias et al., 2022). To evaluate functional composition, we calculated community-weighted means (CWM) for the selected traits using the functcomp function from the FD package (Laliberté et al., 2015; Lavorel et al., 2008; R Core Team, 2025).

2.4. Local and landscape attributes

Our explanatory variables captured environmental variation at both local and landscape spatial scales. The density of açaí clumps served as the local-scale variable. The plots were distributed along an açaí management gradient, defined by the number of clumps per hectare, ranging from 11 to 1430 clumps.ha^{-1} (Freitas et al., 2015; Grossmann et al., 2004), while landscape-scale variables were derived from a digital land-use and land-cover map of estuarine floodplain forests (see Campbell et al., 2022 for details). Our land use classification comprises five dominant classes: forests managed for açaí, agroforestry, open water, conserved forest, and other land use types. Since this raster map (30 m resolution) integrates multiple land-use and land-cover (LULC) data layers, we hereafter refer to it as the LULC dataset. From this LULC we used 249 validation points to achieve an accuracy of 78% for global accuracy and a Kappa coefficient of 74% which is robust enough for the purposes of this study (Hudson and Ramm, 1987). These landscape variables represented habitat composition and configuration, including: percentage of forest cover (%FC), percentage of total open areas (%OA), percentage of open areas containing only açaí clusters (%OA.açaí) and patch density (PD) were adopted as landscape variables. Our measure of %FC entailed: total other forest vegetation / total buffer area * 100, whilst %OA was: total pasture + water + exposed soil + intensive açaí / total buffer area * 100, and %OA.açaí represented: total intensive açaí / total buffer area * 100. We also assessed habitat fragmentation effects (PD) within the "low-intensity managed forest stands" class within each buffer, using the share index (SI). This fragmentation index has been adopted as a measure of landscape configuration given by: $S = A_t^2 / \sum_{i=1}^{n} A_i^2$, where A*t* where is the area covered by forest in the landscape and A*i* is the area of the forest fragment *i* (Jaeger, 2000).These variables have been considered to structure bird assemblages across multiple spatial scales (e.g. Carrara et al., 2015; Smith et al., 2011).

We measured our landscape variables around each transect using the landscape composition approach (sensu Fahrig, 2013), with the amount of forest habitat evaluated in three buffer width radii of 797 m, 1561 m and 1595 m (200 ha, 500 ha and 800 ha, respectively, Fig. 1, b and c, Fig. S2). Landscapes did not overlap, except in one case (spatial overlap of 45% between two landscapes at the 500 ha scale). It is considered that habitat patterns such as landscape heterogeneity, landscape fragmentation, and habitat connectivity are the main factors affecting bird diversity at the landscape scales, so four indices typically used to assess habitat availability were used: percentage of forest cover (%FC), percentage of total open areas (%OA), percentage of open areas containing only açaí clusters (%OA.açaí) and patch density (PD). To determine the spatial scale between habitat variables and diversity indices, we compared R^2 values for three buffer sizes considering the transect in the center of the plot: 200, 500 and 800 ha (Jackson and Fahrig, 2015). We adopted this procedure in order to identify in advance the radius that best predicted the variation in the response variables using linear

regressions with the R package *vegan* (version 1.4–2, spatial scale sensu Holland et al., 2004; R Core Team, 2025; Jackson and Fahrig, 2015, Table S6).

2.5. Data analysis

We tested the effects of local (açaí clump density) and landscape (LULC) variables on community diversity (S, Q1 and Q2) and functional traits (CWM below). Differences in community composition between control and managed stands were evaluated using non-metric multidimensional scaling (NMDS) ordination using the metaNMDS function in the *vegan* package and Bray-Curtis dissimilarity (R Core Team, 2025). Spatial autocorrelation was assessed through MANTEL and PERMANOVA tests between distance matrices (Table S2, supplementary materials). The Mantel test was used to compare geographical distance and composition matrices, with the former obtained using a Distance Matrix Computation with the *as.dist* function in the *stats* package (version 3.6.2) and the dissimilarity for species composition obtained from the Bray-Curtis distance with the *vegdist* function in the *vegan* package (version 1.4–2).

Since spatial effect influenced bird composition, plots were categorized by habitat context (fluvial-tidal island vs. mainland) and included as a fixed factor in model selection (Burnham and Anderson, 2002). Compositional dissimilarity was further compared with Euclidean distance matrices for habitat context, treatment and LULC variables (%OA, %AO.açaí, %FC and PD) using PERMANOVA (*adonis2,* vegan v. 1.4–2), and with non-categorical effect variables (%OA, %FC and PD) by means of a Mantel Test, using the Euclidean distance (*vegdist, vegan* 1.4–2).

We found that the between-plot distance affected species composition (Mantel, $R^2 = 0.24$; $p < 0.001$), indicating that the 36 stands were not spatially independent. Thus, Models with significant spatial autocorrelation (Moran's I p-value <0.05) and a multicollinearity structure (max.$r > 0.5$) were excluded during the model dredging process (Table S3, Jaffé, 2016). To further control for predictor redundancy, variance inflation factors (VIF) were calculated using the car package (Fox and Weisberg, 2019). This procedure was conducted for each response variable, as landscape predictors were evaluated at their respective scales of effect (Jackson and Fahrig, 2015; Table S6, supplementary materials). Among the 18 models, only one (Habitat grassland) showed collinearity (VIFs >4).

In order to assess the possible contribution of plot location on either fluvial islands or the nearby continent due to varying species pools, the categorical variable (fluvial-tidal island or mainland) was included among the effect variables (habitat context as treatment in addition to clumps.ha^{-1} and LULC such as OA, AO.açaí, FC and PD, Table S4, supplementary material). All predictors were scaled and centered using z-scores to allow a comparison of regression coefficients i. When spatial autocorrelation was detected by the Mantel test, the residuals of the models were used to assess whether spatial distribution patterns were random or clustered using the Moran's I Autocorrelation Index with the Moran I function in the *ape* package (version 5.7–1, Table S3, supplementary materials). Moran's I coefficient was non-significant ($p > 0.05$) for all response groups (Table S3, supplementary material), indicating no spatial autocorrelation in any of the response variables.

We then generated models representing all combinations of explanatory variables with Akaike's information criterion corrected for small samples (AICc) combining average parameter estimates weighted by the Akaike weights (wi). From the sum of the Akaike weights ($\sum$wi) of all models (1.0) and the set of models for which $\sum$wi is 0.95 we assume that these represent a set that has 95% probability of containing the true best model (Burnham and Anderson, 2002). In this study, we compared the mean fit percentages of the complete model, weighted by the null model, as an index of fit quality. This comparison was made using the residuals of these models relative to variance deviation. For a given explanatory variable to be considered an important predictor for a given response variable, four criteria had to be met: 1) subsets of models with max.r less than 0.6 would be non-collinear; 2) relatively high sum of Akaike weights (considering each candidate model in which it appeared); 3) average unconditional variance of the model lower than the estimate of the average model parameter; 4) the complete model would have to have a high percentage of explained deviation (i.e. high quality of fit, Crawley, 2013). All models were generated using the dredge function in the Mumin package (Barton, 2018) for R version 4.5.1 (R Core Team, 2025).

To examine species abundance responses to açaí clump density, a Threshold Indicator Taxa Analysis (TITAN) test was implemented using the *TITAN2* package using 5000 bootstrap resamples to estimate the accuracy of the change points (Baker and King, 2010). Only indicator taxa with purity and reliability values $\geq$0.95 were considered, ensuring that only the most consistent responses were retained for interpretation. The results for winning and losing birds were cross-validated using simple generalized linear models (GLMs) with Spearman's correlation and FDR correction. Additionally, Pearson correlations were performed in *vegan* to assess direct relationship between species abundance and açaí clump density gradients (R Core Team, 2025).

3. Results

3.1. General description

A total of 3580 individual bird detections (99 ± 15 per stand) were obtained during 127 h of point counts (6:21 ± 0:23) conducted across 36 stands spanning the gradient of açaí clump density. These detections comprised 145 species belonging to 43 families and 116 genera (Table S7). The most species-rich families were Tyrannidae (19 spp.), Thraupidae (12 spp.), Thamnophilidae (10 spp.) and Psittacidae (9 spp.). Sample completeness averaged 83% ± 5% for low-intensity managed forest stands and 85% ± 3% for high-intensity managed forest stands, indicating that the survey adequately captured patterns of local bird species richness (Table S4, supplementary materials).

3.2. Species richness and beta diversity

Açaí clump density was a strong predictor of bird species richness (Fig. 2a-b) and the number of typical species across both fluvial-tidal island and mainland stands (Fig. 2c-d; Pseudo R^2: 36%–23%, respectively, Table S5, supplementary materials). We found that species richness declined by 28% and the abundance of typical species by 48% along the intensification gradient. Moreover, low-intensity managed forest stands contained 83% of the total species (68.3 ± 5.21 species per stand), whereas high-intensity managed forest stands supported 80% (62 ± 7.3). Low-intensity managed forest stands also hosted more typical species (43.9 ± 7 across all stands) compared to high-intensity managed forest stands (38.1 ± 6.5, Fig. 2d, Table S5). We found that the sample completeness estimator (coverage) did not vary with açaí density, moreover beta diversity was higher in low-intensity managed forest stands for both typical and dominant species (Q1 and Q2, Fig. 3b and c, respectively).

3.3. Bird guild composition

Considering all forest stands, the bird fauna was dominated by invertivorous, forest-dwelling and arboreal species (Fig. S2). Our predictor variables (Açaí clump density, forest cover, open areas with açaí and total open areas) explained a significant portion of the variation in guild structure (Pseudo R^2: 26%–50%) (Fig. 4, Table S5).

Açaí clump density, the local-scale variable, was the main driver shaping community functional traits. It showed positive correlations with community-weighted means (CWM) trait values of shrubland (16.7%) and woodland 16.3%) species assemblages (Table S5 and S6). Conversely, açaí management intensity correlated negatively with forest-associated (−23%), terrestrial (−23%) and invertivorous (−6.7%)

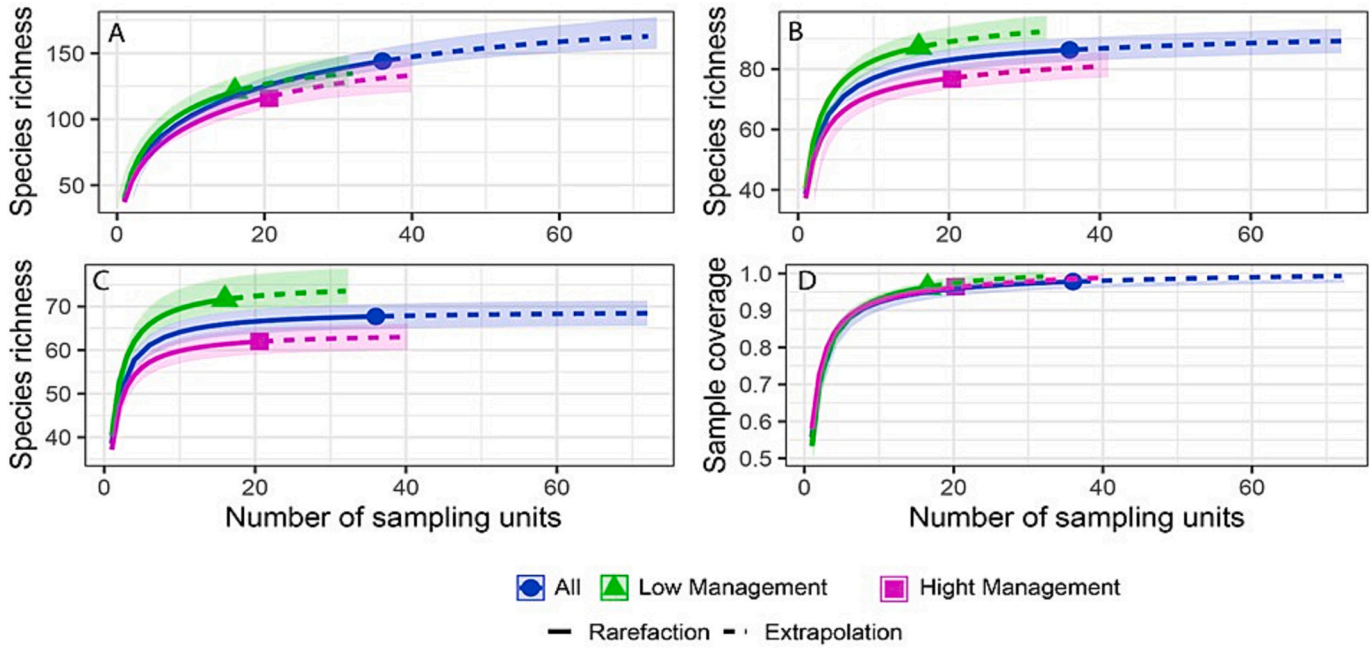

Fig. 3. Species accumulation curve and extrapolation to Hill order numbers q = 0 (A, species richness), q = 1 (B, typical species). q = 2 (C, dominant species) and for sample coverage (D) in estuarine floodplain forest under 400 clumps.ha^{-1} (low-intensity managed forest stands) and over 400 clumps.ha^{-1} (high-intensity managed forest stands) according to legislation in the Amazon region, Brazil.

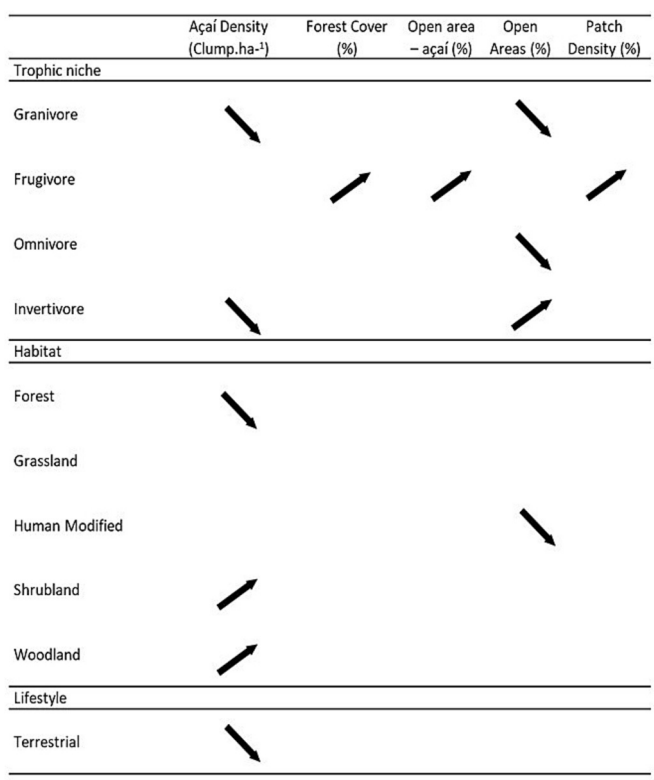

Fig. 4. Summary of the relationship between disturbance at the local level (açaí density) and at the landscape level (Forest Cover, Open Area with Açaí, General Open Area, and Patch Density) on the CWM of functional groups of bird species. Arrows pointing upward and downward indicate significant positive and negative relationships, respectively. Only significant relationships are shown; for detailed results, see supplementary material Table S4.

species groups. The surrounding habitat context also consistently influenced bird assemblage composition (Fig. 4, Table S5). The proportion of open habitats was negatively correlated with granivores (−12%, 800 ha), omnivores (−18%, 200 ha), and species associated with human modified environments (−9%, 200 ha, Table S5 and S6).

3.4. Taxonomic responses to disturbance gradients

Ordination analysis (Fig. 5, Table S2) revealed that both local- and landscape-level variables contributed to avian community composition, with significant differences between mainland and fluvial-tidal island stands (Pseudo-$F_{1,27} = 2.84$; $R^2 = 0.37$; $p = 0.001$, stress = 0.22 and two dimension). However, the test for homogeneity of multivariate dispersions (PERMDISP) was non-significant ($F = 1.69$; $p = 0.21$), suggesting that beta-diversity patterns were driven by compositional turnover rather than differences in group dispersion.

As expected, açaí clump density influenced bird community

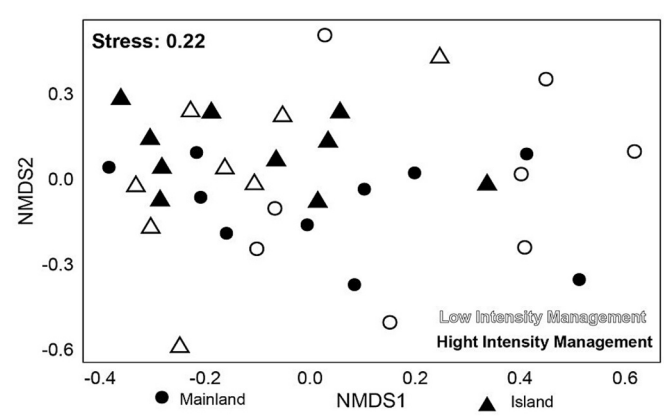

Fig. 5. Bird composition at two levels of açaí management intensity revealed by non-metric multidimensional scaling (nMDS) based on Bray-Curtis dissimilarity in managed and unmanaged forests in estuarine floodplain forest under 400 clumps.ha^{-1} (low-intensity managed forest stands) and over 400 clumps.ha^{-1} (high-intensity managed forest stands) according to legislation in the Amazon region, Brazil. Results of PERMANOVA: $R^2 = 0.03$. $p = 0.16$ for treatment and $R^2 = 0.3$. $p < 0.001$ for habitat context.

structure (Pseudo-$F_{1,27} = 1.03$; $R^2 = 0.02$; $p = 0.4$, nMDS stress = 0. 22), as did some landscape-scale variables. In particular, open area coverage around stands significantly contributed to species differentiation (Pseudo-$F_{1,27} = 2.07$; $R^2 = 0.05$; $p = 0.01$), whereas forest cover (%FC) and patch density (%PD) showed no significant effects (Table S2).

Several bird families were ubiquitous across both low- and high-intensity managed forest stands for example: at least one member of the Trochilidae, Dendrocolaptidae, Ramphastidae, Rhynchocyclidae, Tyrannidae, and Thraupidae were found in all stands. While members of the Accipitridae, Ardeidae, Caprimulgidae, Cathartidae, Furnariidae and Strigidae families were recorded exclusively in high-intensity managed forest stands, members of the Eurypygidae, Formicariidae, Galbulidae, Threskiornithidae and Xenopidae were recorded exclusively in low-intensity managed forest stands, with mean change points (50th percentile) ranging between 470 and 545 açaí clumps.ha^{-1} (95th–99th percentiles).

At the species level, *Pitangus sulphuratus* ($R^2 = 0.45$, $p = 0.05$), *Thraupis palmarum* ($R^2 = 0.38$, $p = 0.02$), *Polioptila plumbea* ($R^2 = 0.32$, $p = 0.05$) and *Coereba flaveola* ($R^2 = 0.31$, $p = 0.05$) were detected more frequently with increasing açaí clump density and were therefore classified as winner species along the intensification gradient. Conversely, *Phaethornis superciliosus* ($R^2 = -0.31$, $p = 0.05$) showed a strong negative relationship with açaí clump density and was classified as a loser species (Fig. 6).

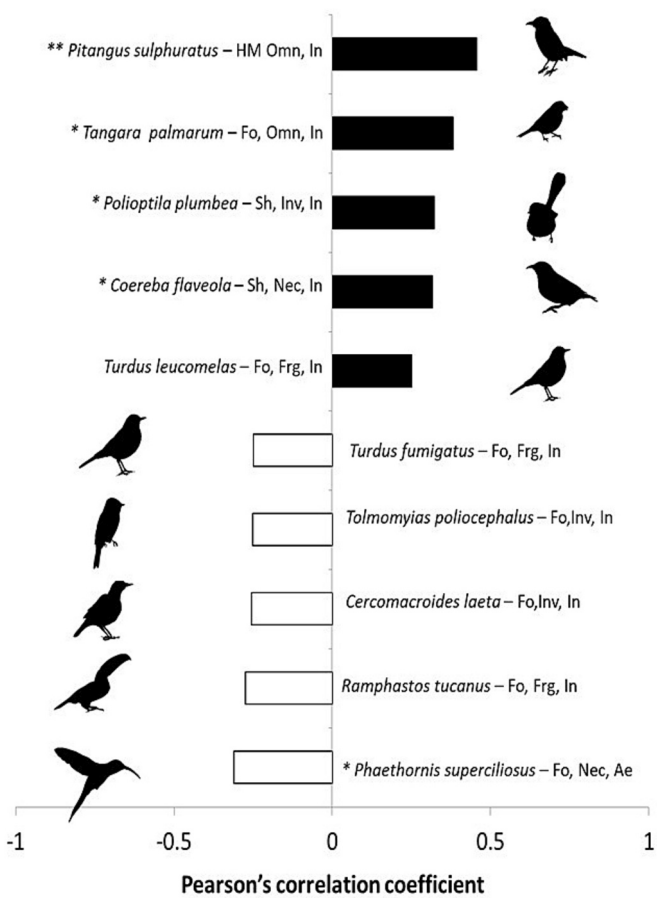

Fig. 6. Ten species (minimum $n = 50$ individuals/species) exhibiting significant abundance responses to açaí clump density, classified as either 'winners' (positive correlation) or 'losers' (negative correlation) under intensification scenarios. The functional groups are represented by acronyms (*$p \leq 0.05$, **$p \leq 0.01$): Habitats (Forest - Fo; grassland - Gr; human modif - Hm; shrubland - Sh; woodland - Wo), Trophic niche (aquatic predator - AP; frugivore - Frg; granivore - Grn; invertivore - Inv; nectarivore -Nec; omnivore - Omn) and Life style (aerial - Ae; arboreal - Ar; terrestrial – Ter, details in Table S1).

TITAN analysis further identified two species with significant and contrasting responses to disturbance (i.e. land-use changes and açaí clump density). *Phaethornis superciliosus* was classified as a negative indicator (*Z*-, IndVal = 51.6, $p < 0.05$, purity = 0.99), while *Pitangus sulphuratus* acted as a positive indicator (Z+, IndVal = 67.28, $p < 0.05$, purity = 0.99), increasing in abundance under disturbed conditions, including those resulting from açaí management intensification (Fig. 7, table S8 and S9). All results were validated using simple GLMs and Spearman correlation, confirming the winner and loser species (Table S9).

4. Discussion

Our study is the first to demonstrate that açaí palm management intensification reduces species richness at local and landscape scales, while altering the assemblages functionally and taxonomically. In contrast to tree species, a small set of birds respond positively to increasing açaí clump density (i.e. winner species), leading to assemblages with a higher contribution of frugivores. Depauperate assemblages emerged in response to increasing levels of disturbance (degradation and habitat loss) at both spatial scales, with forest loss resulting in an approximately one-third reduction in species richness along the intensification gradient.

Bird species were not randomly affected, some, such as *Phaethornis superciliosus, Ramphastos tucanus* and *Cercomacroides laeta* responded negatively to intensification, while *Pitangus sulphuratus*, *Thraupis palmarum*, *Polioptila plumbea* and *Coereba flaveola* showed positive responses (i.e. CWM scores). Such changes reflect the proliferation in species that occupy more open or non-forest habitats and the simultaneous loss of forest associated species (e.g. Moura et al., 2013; Lees et al., 2015). Disturbance thus promotes the emergence of impoverished and functionally altered assemblages (Moegenburg and Levey, 2002) while a small set of disturbance-adapted species (e.g. open-habitat specialists) thrive (Gray et al., 2007).

Interestingly, 35 bird species recorded by Lees and Moura (2017) in the urban environment of Belém were also detected in our survey. Notably, all four "winner species" identified in our study (*Pitangus sulphuratus, Coereba flaveola, Polioptila plumbea, and Thraupis palmarum*) were likewise common in the Belém assemblage, reinforcing their adaptability to human-modified or simplified habitats. Conversely, *Phaethornis superciliosus*, the main "loser species" under açaí management intensification, was unrecorded in the urban community. This suggests a convergent trajectory of community homogenization with urbanization and indicates an unfavorable trajectory for biodiversity retention should management intensification continue.

The collapse of the forest's physical structure associated with the increasing density of açaí clumps is probably the main driver of changes in bird assemblages. Açaí intensification is intrinsically linked to the elimination of undesirable vegetation (i.e. competing tree and shrubs) to favor the palms and facilitate manual fruit harvesting (Freitas et al., 2021, Freitas et al., 2015). These management practices result in a 52% decrease in stem density, a 28% reduction in stem volume and a 57% decline in tree species richness along the açaí gradient (20 to 1260 clumps.ha^{-1}, Freitas et al., 2021). Regular coppicing and weeding transform a once dense forest into a more open, derived woodland habitat with a canopy dominated by açaí palms and a few spared trees (Freitas et al., 2015; Weinstein and Moegenburg, 2004).

The combined loss of a diverse shade-tolerant flora of shrubs and small tree species in the understorey, many of which bear small fleshy fruits, from families such as the Melastomataceae, Rubicaceae, Myrtaceae and Piperaceae, together with the loss of canopy and emergent tree species that provide large-seeded fruits (Freitas et al., 2015, 2021, 2025) is particularly detrimental to frugivores. Moreover, large trees also offer essential structural support for avian biodiversity, serving as nesting and foraging substrates (see Moura et al., 2016; Pinho et al., 2020) yet they are increasingly rare in intensively managed stands (Levis et al., 2017;

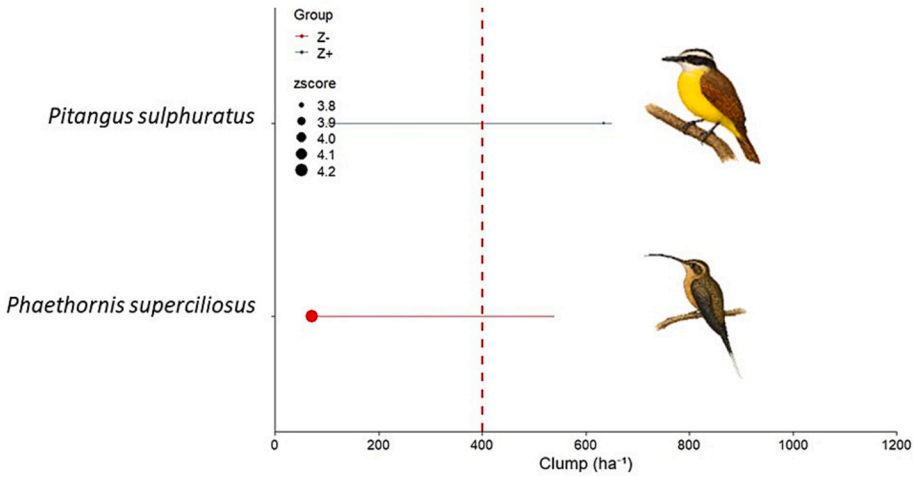

Fig. 7. Threshold Indicator Taxa ANalysis (TITAN) of the birds' response to açaí clump density across 36 forest stands of an Amazonian estuarine forest, Brazil. Horizontal lines overlapping each symbol represent 5th and 95th percentiles among 5000 bootstrap replicates. Only species affected negatively (left; reducing in abundance) and positively (right; increasing in abundance) are represented. The dashed red line represents the 400-açaí clump density threshold. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Freitas et al., 2025). At the same time, most açaí fruits - a food source for many large frugivores - are removed throughout the year (Moegenburg and Levey, 2003, Moegenburg and Levey, 2002).

Consequently, the increasing dominance of açaí palms at the expense of the old-growth flora leads to structural homogenization of forest habitats, depleting specialized microhabitats and reducing key resources such as food availability and nesting sites for forest-specialists (Leaver et al., 2019). Bird assemblages in tropical forests are vertically structured in response to microenvironmental conditions and food resources (Casas et al., 2016; Jayapal et al., 2009). It is therefore not surprising that stand-level forest degradation, combined with landscape-scale habitat loss, has negative effects on bird assemblages.

Moving to an applied context, our results provide empirical support to the current regulation (IN 09/2013, Brasil, 2014), which limits açaí fruit production through forest management to a maximum of 400 clumps.ha^{-1}. We unequivocally identified the forest-associated understorey hummingbird *Phaethornis superciliosus* as a species that declines sharply as açaí palm density approaches this threshold, with forest stands exceeding 400clumps.ha^{-1} supporting significantly fewer individuals (Fig. S4). However, empirical evidence has demonstrated that even this limit results in a 65% reduction in tree species richness and a 70% loss of plant functional diversity, revealing that intensification beyond 400 clumps.ha^{-1} is ecologically unsustainable (Barros et al., 2023; Freitas et al., 2025, Freitas et al., 2021, Freitas et al., 2015).

The açaí fruit market has already achieved annual revenues of US$2 billion (IBGE, 2022), and increasing demand is accelerating the transition from traditional extractivism led by local communities (land sharing) toward forest conversion for açaí monocultures (Freitas et al., 2025). The bioeconomy approach is likely to intensify industrial-scale exploitation, increasing forest degradation and leading to a consequent collapse of ecosystem services. This trend is particularly concerning because bioeconomic expansion has been promoted primarily as a greenhouse gas mitigation strategy, without adequately valuing or conserving biodiversity - especially the still unquantified diversity of most taxonomic groups, including birds and tree species endemic to this unique habitat (de Assis Costa et al., 2022). While such approaches yield economically promising outcomes, scholars advocate for an alternative bioeconomy model that prioritizes local markets, diversification, and scope economies through bottom-up arrangements (Vieira et al., 2024).

Evidence continues to accumulate suggesting that the ongoing transition from traditional exploitation of NTFP toward intensive management in response to market demands undermines any assumption of sustainability related to forest integrity, biodiversity persistence and provision of ecosystem services. Originally, the forests of the Amazon estuarine region covered 160,000 km^2 (Barthem et al., 2024), with a long history of exploitation for both subsistence and commercial purposes (logging, latex, cocoa). Their future integrity depends on the implementation of ambitious conservation programs that include the establishment of protected areas to safeguard biodiversity reservoirs (i.e. land sparing), the adoption of improved açaí management practices and strict law enforcement.

In the near future, as markets will probably become increasingly dominated by açaí produced in industrial plantations within *terra firme* areas, maintaining sustainable açaí from the estuarine forests, recognized as a cultural landscape, will be essential to ensure the persistence of this irreplaceable socioecological system.

5. Conclusion

Açaí intensification promotes the imporverishment of bird assemblages at both local and landscape scales, leading to taxonomic and functional impoverishment in which only a few species benefiting. Although NTFP extraction has been advocated as an effective strategy for sustainable tropical forest use, providing economic benefits to traditional populations while contributing to climate change mitigation, current açaí palm exploitation has shifted from traditional extractive practices to monoculture-oriented systems focused on yield maximization, representing an unsustainable production model of the so-called "Amazonian black gold". Therefore, açaí production must be incorporated into an ambitious initiative that integrates socioeconomic development with the maintenance of estuarine forest integrity, rather than becoming another example of degradation resulting from the overexploitation of NTFPs.

CRediT authorship contribution statement

Madson Antonio Benjamin Freitas: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Raphael Vasconcelos Nunes:** Writing – original draft, Visualization, Supervision, Software, Project administration, Data curation. **Maria Aparecida Lopes:** Visualization, Project administration, Investigation, Funding acquisition, Conceptualization. **Caio Crisley Moura Soares:** Methodology, Formal analysis, Data curation, Conceptualization. **Thiago Sanna Freire Silva:** Validation, Methodology, Formal analysis,

Data curation. **Ima Célia Guimarães Vieira:** Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Marcelo Tabarelli:** Writing – review & editing, Writing – original draft, Supervision, Software, Project administration, Methodology, Investigation, Conceptualization. **Alexander Charles Lees:** Validation, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization.

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Declaration of competing interest

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

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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.2026.111710.

Data availability

Data will be made available on request.

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