







# Anthropogenic disturbance of tropical forests threatens pollination services to açai palm in the Amazon river delta

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## Funding information

Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 400435/2014-4; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: 15/2014, CNPq (Pesquisador Produtividade - 306904/2016-0)

Handling Editor: Ainhoa Magrath

## Abstract

1. The açai palm *Euterpe oleracea* Mart. in the Amazon river delta has seen rapid expansion to meet increased demand for its fruit. This has been achieved by transforming lowland forest habitats (floodplains) into simplified agroforests and intensive plantation in upland areas. As açai palm makes an important contribution to the economy and food security of local communities, identifying management approaches that support biodiversity and ecosystem processes that underpin fruit production on açai farms is essential.
2. We compared flower-visitor communities and açai fruit production in floodplain forests and upland plantations, across gradients of local management intensity (i.e. açai density per ha) and surrounding forest cover. The relative contribution of biotic pollination and degree of pollen limitation were assessed using insect exclusion and hand-pollination experiments.
3. We found that açai flower visitors are highly diverse (c. 200 distinct taxa) and had variable responses to disturbance. Bee visitation was higher in floodplains and positively related to surrounding forest cover, but other flower visitors, including specialised curculionid beetles, were unresponsive to changes in surrounding forest cover. However, intensive management practices (i.e. high açai palm densities) in floodplains and uplands had contrasting effects on flower-visitor communities, with flower-visitor richness being lower on intensively managed floodplain farms and ant densities being higher on intensive upland farms.
4. Pollination experiments revealed açai palm to be highly dependent on biotic pollination. Fruit set in open-pollinated inflorescences was positively related to flower-visitor richness and specialised curculionid beetle visitation, whereas the presence of ants on inflorescences had a negative effect.
5. *Synthesis and applications.* Our study shows that pollinators are essential for açai fruit production, but that intensive farming practices have eroded the relationship between surrounding forest cover and ecosystem function in floodplains

(i.e. conversion of native forest into simplified agroforests) and increased the frequency of antagonistic interactions in uplands (e.g. high ant densities). These findings underline the value of extensive management practices, such as the maintenance of other tree species within farms and adjacent unmanaged forest patches, to ensure the long-term sustainability of açai fruit production in the Amazon river delta.

#### KEYWORDS

açai, Amazon rainforest, Amazon river, biodiversity, ecological intensification, ecosystem services, *Euterpe oleracea*, flower-visitor community, palm, pollinators

## 1 | INTRODUCTION

Tropical forests harbour much of Earth's remaining biodiversity, provide innumerable products and ecosystem services for local communities and play an essential role in global carbon and hydrological cycles (Foley et al., 2005). However, as a result of increased demand for food, energy, timber and other agricultural products, anthropogenic disturbance is putting these vital ecosystems under pressure (Laurance, Sayer, & Cassman, 2014).

Major drivers of tropical biodiversity loss include not only a reduction in overall forest cover, particularly through agricultural expansion (Laurance et al., 2014), but also human activities within forests, such as selective logging, fire and hunting (Barlow et al., 2016). While primary forests are irreplaceable in terms of biodiversity (Gibson et al., 2011), human-modified tropical landscapes can retain high value for species conservation and the delivery of ecosystem services, but only with appropriate (i.e. evidence-based), active management of human activities (Melo, Arroyo-Rodríguez, Fahrig, Martínez-Ramos, & Tabarelli, 2013).

Tidal floodplain forests (*várzeas*) cover an estimated 400,000 km<sup>2</sup> of the Amazon basin (Junk et al., 2011) and have a long history of human disturbance (e.g. hunting, extractive harvest, swidden agriculture; Lu et al., 2010). However, the recent surge in demand for the antioxidant-rich fruits of the açai palm (*Euterpe oleracea* Mart.) has led to rapid expansion in forest areas being managed for high fruit production (Brondízio, 2008). Much of this activity is concentrated in the Brazilian state of Pará, where over 1 million tonnes of fruit are produced and sold each year, generating US\$ 149 million for the Brazilian economy, and representing nearly a third (31%) of national income derived from non-timber forest products (NTFPs; IBGE, 2015). These "forest farms," where autochthonous palm stands are enriched by selective removal of other tree species, were initially seen as an example of how NTFPs can be used to promote forest conservation whilst providing income for local communities (Peters, Balick, Kahn, & Anderson, 1989). However, more recent analyses have revealed that the diversity of tree species, structural complexity and ecological integrity of floodplains have declined severely in areas under intensive management (Freitas, Vieira, Albernaz, Magalhães, & Lees, 2015; Weinstein & Moegenburg, 2004). At the same time, açai is increasingly grown in large plantations in cleared upland (*terra firme*) areas (Homma, Nogueira, de Menezes, de Carvalho, & Nicoli, 2014). Expansion of

upland farms has been identified by regional planning agencies as key to improving socioeconomic conditions within the state (PARÁ 2030). However, the impacts of different farming practices on biodiversity and ecosystem processes that underpin açai fruit production, such as pollination, remain poorly understood (Giannini et al., 2015).

Pollination by animal vectors is essential for reproduction in the vast majority of flowering plant species (Ollerton, Winfree, & Tarrant, 2011) and has a recognised importance for productivity in a huge number of crop species throughout the world (Garibaldi et al., 2016). Previous studies have suggested that Euterpeinae palms have "entomophilous" or generalised pollination strategies, as inflorescences lack clear morphological or physiological adaptations to a single pollinator taxon, and are visited by a large number of insect species, including bees, beetles, flies, wasps and ants (Kuchmeister, Silberbauer-Gottsberger, & Gottsberger, 1997; Listabarth, 2001). Such diversity may confer substantial resilience if losses of environmentally sensitive pollinator species are compensated for by more robust species (i.e. ecological redundancy; Larsen, Williams, & Kremen, 2005). For example, many tropical bees are sensitive to forest disturbance, as they rely on mature trees for nest sites and year-round provision of pollen and nectar for larval and adult nutrition and have limited dispersal (Brosi, Daily, & Ehrlich, 2007; Ferreira et al., 2015). In contrast, other insects, such as habitat generalists with non-flower feeding larvae (e.g. flies, wasps; Rader et al., 2016), or curculionid beetles (Coleoptera: Curculionidae) that specialise on palm inflorescences (i.e. larval and adult food, adult mating and oviposition site; Silberbauer-Gottsberger, 1990) may be less dependent on forest habitats. However, if important pollinators are also environmentally sensitive, then pollination services may be at risk from intensive management practices. Improving our understanding on the effects of anthropogenic disturbance on ecosystem processes that underpin açai fruit production is essential for the development of management strategies that protect both tropical biodiversity and the livelihoods of local communities in the Amazon river delta.

By comparing flower-visitor communities and fruit production on floodplain and upland farms, and across gradients of local management intensity and surrounding forest cover, we evaluate how local farming practices and landscape structure affect açai flower-visitor communities (Objective 1) and how flower-visitor communities influence pollination and açai fruit production (Objective 2). We expect that floodplain farms, which resemble simplified patches of native

forest habitat (i.e. intermixed with other tree species, high canopy cover) embedded within a network of unmanaged forest areas, would support more diverse and abundant flower-visitor communities than upland plantations that are predominant in more degraded landscapes (i.e. low surrounding forest cover). However, impacts on fruit production would be determined by the sensitivity of pollinator species to local management practices and surrounding forest cover.

## 2 | MATERIALS AND METHODS

The study was conducted in 2016 (January–June) in the Amazon estuary region, Pará state, Brazil (1°27'S, 48°30'W). The landscape is characterised by large tracts of humid tropical rainforest and agricultural land uses (e.g. pasture and field crops) and lowland areas (floodplains) that tidally inundate (Weinstein & Moegenburg, 2004). Nine floodplain forests and nine upland farms being managed for açai fruit production were selected for study (Figure 1). Where possible, we selected upland farms near to floodplain farms and that bordered an adjacent forest fragment to minimise differences in local conditions and landscape structure (e.g. isolation from forest) between farm types, although overall forest cover was higher in floodplains (Figure 1; Table S1).

Current state guidelines for best practice propose an upper limit of 400 açai clumps (whole plants) per hectare (Secretaria de Estado de Meio Ambiente do Pará [SEMA], Brasil, 2014), but many areas already far exceed these recommendations (Freitas et al., 2015). On each farm, clump densities were estimated in 10 × 10 m plots established around six individuals whose inflorescences were used in flower-visitor surveys (1–2 plots per farm, see Section 2.2 for details). In each plot, we estimated canopy cover based on five photographs (plot corners and centre) taken using a smartphone camera with an external hemispherical lens in the programme “Gap Light Analysis Mobile App” (Tichý, 2016). Surrounding landscape composition was evaluated at 500 m and 1 km radii from the centre of each farm and measured based on 2016 satellite images from Google Earth Pro (scale 1:10,000) in ArcGIS 10.1 (ESRI, Redland, CA, USA). Forest cover was the dominant land use at either spatial scale and was negatively correlated with other land uses (Table S2). Farms were separated by at least 600 m; a distance that was considered sufficient to deal with scale-dependent responses of tropical pollinator communities to changes in landscape structure (<500 m; Brosi et al., 2007; Ferreira et al., 2015). All statistical analyses and model validation procedures were performed in R version 3.1.3 (R Core Team, 2015).

### 2.1 | Study species

Açai (*E. oleracea* Mart.) is a tall, slender, multistemmed palm and is naturally abundant in lowland forests of South and Central America (Henderson, Galeano, & Bernal, 1995). It produces inflorescences throughout the year but flowering peaks during the wet season (December to April; Oliveira, 2002). The inflorescences contain many

thousands of small, unisex flowers placed in triads (2:1 male to female flowers), spread along the flowering branches (rachilla; Figure S1). Anthesis is diurnal and strongly protandrous, with daily pulses of short-lived male flowers for the first 10–14 days, followed by the much shorter female phase (3–5 days; Oliveira, 2002).

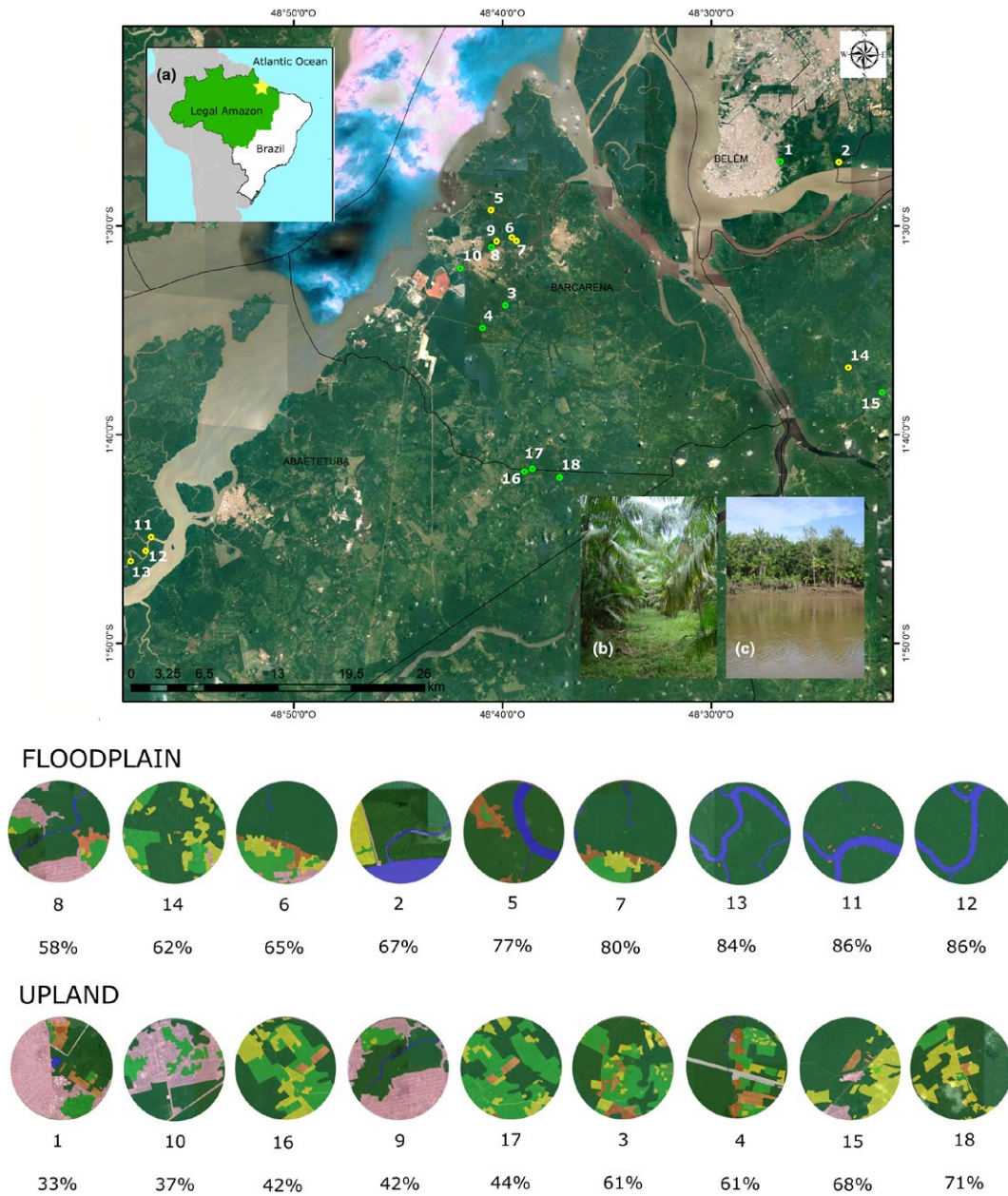
### 2.2 | Flower-visitor surveys

To identify açai flower visitors, visual surveys were carried out during peak flowering periods (January–May). On each farm, three inflorescences in each sexual phase were selected, but heavily shaded, deformed or damaged inflorescences were avoided. As flower-visitor activity was high, in each inflorescence, observations focused on five rachillae, on which the number of open flowers was counted. Temperature (°C) and cloud cover (oktas) estimates were taken prior to and immediately after each observation. Visual surveys (10 min, plus an additional 10 min for species collection) were repeated three times: 08:00–10:30 hr (male anthesis); 10:30–13:00 hr (dehiscing of anthers) and 13:00–16:00 hr (male flower abscission). Female flowers opened soon after 09:00 hr and remain receptive for up to 48 hr (Oliveira, 2002).

Visit frequencies were generated by combining data from visual surveys and collections (see *Insect sampling*, Appendix S1) before converting these data into visit rates (visits/open flowers/10 min), to account for effects of flower densities on insect counts. Individual flower-visitor taxa were then divided into the following three functional groups based on a priori expectations about açai pollination:

1. *Specialised curculionid beetles*. As many curculionid beetles that are specialised on palm inflorescences are small (<2 mm) and inconspicuous (Listabarth, 2001), visitation was recorded as a binomial variable (presence/absence) based on both surveys and collected individuals.
2. *Unspecialised visitors*. Palm inflorescences are also visited by many unspecialised taxa (e.g. bees, flies, wasps, other beetles; Kuchmeister et al., 1997; Listabarth, 2001). To assess the contribution of these species, we included their summed visit rate in models. As bees dominated flower-visitor communities, we also separated this group into bees and “non-bees.”
3. *Ants*. As a group, ants are not considered as effective pollinators of *Euterpe* species because of self-incompatibility mechanisms (Kuchmeister et al., 1997). However, ants may indirectly affect pollination by changing behaviour of other visitors (Philpott, Uno, & Maldonado, 2006). Ants were scored as a binomial variable (presence/absence) based on surveys and collections.

As pollinators must visit both sexual morphs of inflorescences to facilitate pollen transfer, we also calculated (1) richness of taxa that visited both sexual phases (“shared visitors”) based on surveys of all farms and (2) the degree of overlap in species composition (i.e. biotic similarity) of flower-visitor communities between sexual morphs on individual farms. Similarity was estimated using Jaccard index (presence/absence data) to account for the large differences in abundance among visitor taxa.



**FIGURE 1** Study region (inset—a, in relation to South America), division of Pará state municipalities, and study site locations (upland plantations = green circles; floodplain forests = yellow circles). Landscapes represent land use cover at 1 km radii and percentage forest cover (dark green) at each of 18 study sites. Photos provide examples of an upland plantation (b) and managed floodplain forest farm (c) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

### 2.3 | Pollination services and açai fruit production

To quantify effects of biotic pollination on fruit production, seven inflorescences prior to female anthesis and on unrelated plants were selected on each farm and divided among three treatments: (1) insect exclusion (i.e. abiotic pollination; three inflorescences), (2) open pollination (i.e. abiotic + biotic pollination; three inflorescences) and (3) hand pollination (1 inflorescence). For the insect exclusion treatment, the number of unopened female flowers on two rachillae was counted before one rachilla was covered by a wind and rain permeable mesh bag (clear plastic, 75 × 40 cm, mesh size 1 × 1 mm). Bags were left on throughout flowering before being removed in June

to count developing fruits. On open inflorescences, three rachillae were marked and flowers counted. On hand-pollinated inflorescences, six rachillae were tagged and female flowers on three were hand pollinated by contacting the stigma with freshly dehisced anthers of male flowers collected from an unrelated plant.

### 2.4 | Objective 1: To understand how farming practices and landscape structure affect açai flower-visitor communities

To test effects of local farming practice and landscape structure on flower-visitor communities, we first selected which landscape

variable (forest cover at 500 m or 1 km radius) best explained the variability of each flower-visitor variable. To do that we compared models with each landscape metric and selected the one with the lowest Akaike information criterion (AIC). We then ran models for each flower-visitor community variable, with farm type (floodplain or upland), local management intensity (low or high açai clump density per ha), inflorescence height, canopy cover and forest cover included as predictor variables, whilst accounting for effects of biotic (sexual phase, flowering intensity—proportion of stems in bloom per plot) and abiotic (temperature, cloud cover) variables. All two-way interactions between farm type, management intensity and forest cover were included in models. Visit rates of unspecialised visitors (summed, bees and non-bees) were square root transformed and analysed using linear mixed-effects models (LMMs) in the R package “lme4” (Bates, Mächler, Bolker, & Walker, 2015), with inflorescences nested within farms to account for our hierarchical design with repeated measures. Specialised curculionid visitation and ant presence/absence were modelled using generalized linear mixed-effects models (GLMMs) with binomial errors with the same random effect structure as visit rate models; and flower-visitor richness was analysed using a generalised linear model with Poisson-distributed errors.

All predictors were scaled and centred using z-scores to allow comparison of regression coefficients. To avoid collinearity, we excluded all models including predictors with correlation coefficients greater than .5 and set a maximum of five parameters to avoid overfitting. Accordingly, farm type and forest cover (always higher in floodplains) were never included in the same model (Table S1). Best models were selected by comparing AIC from all possible combinations of included predictors using the dredge function included in R package “MuMIn” (Barton, 2015). As we had multiple models with similar explanatory power (i.e. similar Akaike weights), we calculated the average model based on selected models ( $\Delta\text{AIC} < 2$ ). Whenever a variable was not included in the model, we assumed that its estimate was zero (Grueber, Nakagawa, Laws, & Jamieson, 2011). We tested significance of included interactions by comparing models with and without terms using likelihood ratio tests (LRT). To check for effects of spatial autocorrelation, residuals of best models fitted with restricted maximum likelihood were tested using Moran’s I in the R package “ape” (Paradis, Claude, & Strimmer, 2004).

## 2.5 | Objective 2: To understand how flower-visitor communities influence pollination services and açai fruit production

Effect of pollination treatment on fruit set (i.e. proportion of flowers developing into fruit) was assessed using a binomial GLMM. Random effects nested inflorescences within farms. Significance of pollination treatment was tested using LRTs and significant differences between treatment levels assessed using post hoc tests (“Tukey”) in the R package “multcomp” (Herberich, Sikorski, & Hothorn, 2010) with corrected p-values for multiple testing (Holm–Bonferroni). Fruit set in additional control rachillae did not differ significantly from the open treatment and are not presented in the main text (Figure S2).

To evaluate effects of flower-visitor communities (visitor abundance, overall flower-visitor richness, shared visitor richness and similarity) on fruit set, we used binomial GLMMs with individual inflorescences nested within farms included as random effects. As models using data pooled across sexual phases did not differ from the null model, we used mean (visitor abundance) and summed (richness) values from each sexual phase as predictors. To test effects of ants on other flower visitors, we included all two-way interactions between ants and other groups, and to test species interaction effects (e.g. Greenleaf & Kremen, 2006), we included interactions between richness and visitor groups. Lastly, to validate connectivity between effects of anthropogenic disturbance on pollinators and pollinators on fruit set, effects of farming practices and landscape structure on fruit set were analysed using binomial GLMMs (Table S6, Figure S3).

## 3 | RESULTS

### 3.1 | Açai flower-visitor communities

A total of 9,635 flower visits and 2,157 insects from 194 taxa were observed or collected on açai inflorescences, including bees, flies, wasps, ants and beetles (specialised and unspecialised taxa; Table 1; Table S3 for species details). Trigonid bees (Apidae: Meliponini: *Trigona* spp.) were the most abundant visitor group (29.1% of total visits) and beetles the most diverse (51 taxa). Male inflorescences attracted a higher number of visitor taxa than female inflorescences, while 102 taxa were collected on both sexual phases (Table 1; Figure 2).

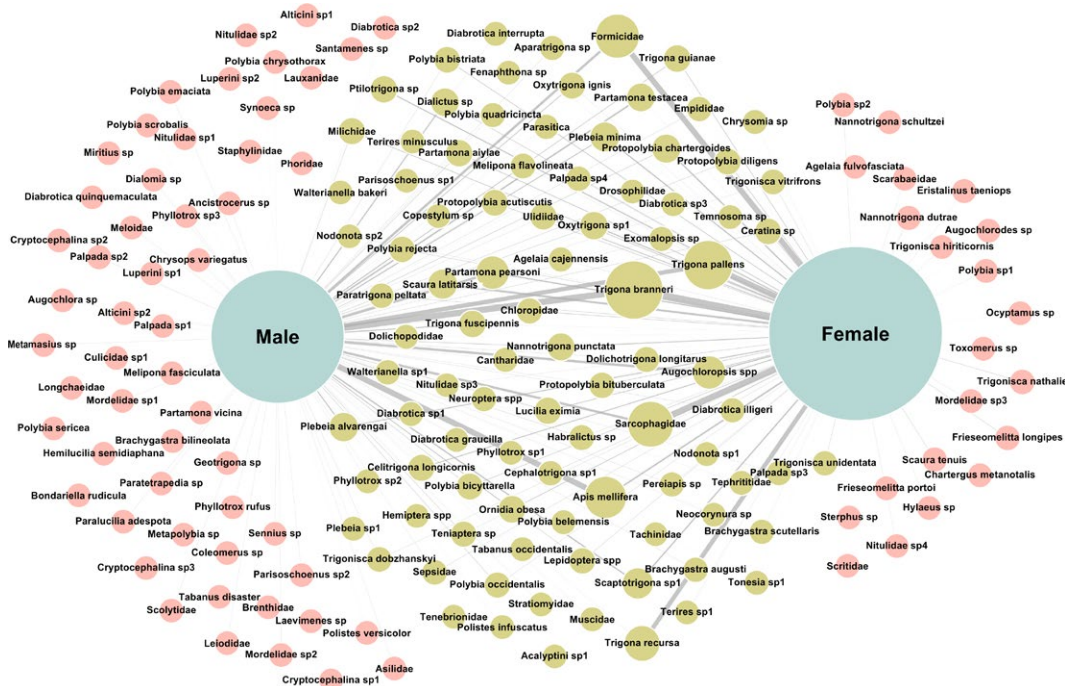
### 3.2 | Effect of farming practices and landscape structure on açai flower-visitor communities

None of the tested flower-visitor community variables exhibited significant spatial autocorrelation, and therefore, all farms were considered spatially independent (Table S4). Visitation by specialised curculionid beetles was unaffected by either local management (e.g. farm type, açai clump density) or surrounding forest cover (Table 2; additional models Table S5). In contrast, visitation by unspecialised taxa (e.g. bees, flies, wasps, non-curculionid beetles), ant presence and overall flower-visitor richness on inflorescences were explained by the interaction between farm type and local management intensity (Table 2; LRT of models including interaction: unspecialised visitors: LRT = 6.67,  $df = 1$ ,  $p = .009$ ; ants: LRT = 10.53,  $df = 1$ ,  $p = .001$ ; flower-visitor richness: LRT = 15.77,  $df = 1$ ,  $p < .001$ ). Unspecialised visitor abundance and flower-visitor richness were markedly lower on floodplain farms under intensive management compared to extensively managed floodplains, whereas parameter estimates on upland farms were similar between different management intensities (Figure 3a). In contrast, ant densities were much higher on upland farms under intensive management compared to all other farms (Figure 3b). Separation of unspecialised taxa into bees and non-bees revealed that bee visitation was higher on floodplain farms and positively related to surrounding forest cover (Table 2; Figure 3c,d), whereas non-bee visitation was unaffected by farm type or landscape

**TABLE 1** Taxonomic groups of flower visitors, functional group, percentage of total visits, percentage of flower-visitor surveys where the presence was recorded (curculionid beetles and ants only), number of taxa collected on male inflorescences (inf.), female inflorescences, both sexual phases (shared) and overall total. For species details, see Table S3

Visitor taxa	Functional group	Visits (%)	Surveys (%)	No. taxa			
				Male inf.	Female inf.	Shared	Total
Coleoptera							
Curculionidae	Specialised	0.5	21.0	14	7	7	14
Non-Curculionidae	Unspecialised	1.9	—	33	19	15	37
Diptera	Unspecialised	16.7	—	32	24	20	36
Hymenoptera							
Apoidea	Unspecialised	63.7	—	38	45	35	48
Formicidae	—	7.1	55.0	18	18	10	26
Vespoidea	Unspecialised	9.1	—	25	19	15	29
Other <sup>a</sup>	Unspecialised	1.0	—	4	4	—	4
Total		100.0		164	136	102	194

<sup>a</sup>Other taxa include flower visitors identified only to order/superfamily (Hemiptera, Lepidoptera, Neuroptera and Parasitica (Hymenoptera)). These taxa were excluded from the shared visitor count.



**FIGURE 2** Summed flower-visitor communities of açai palm inflorescences in different sexual phases from 18 farms in the Amazon river delta. Node size represents total number of interactions (visits) and edge width (grey bars) the relative abundance of each insect taxa on male and female inflorescences. Yellow nodes = insect taxa recorded on both sexual phases (shared visitors), Red nodes = taxa collected on a single sexual phase. For brevity, ants (26 taxa) are presented together ("Formicidae"; see Table S3 for species details) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

structure (Table 2). However, high collinearity between farm type and forest cover limited our capacity to distinguish their individual effects on bee visitation to açai inflorescences. Bee abundance was also positively related to temperature and flowering intensity had negative effects on visitation by non-bee insects (Table 2). Lastly, specialised curculionid beetles were three times more abundant on male inflorescences (Table 2).

### 3.3 | Effect of flower-visitor communities on açai fruit production

The effect of pollination treatment on fruit set was highly significant (LRT = 41.86,  $df = 2$ ,  $p < .001$ ; Figure 4a). Bagged inflorescences set very few fruit compared to other treatments (bagged vs. open:  $z = -6.1$ ,  $p < .001$ ; bagged vs. hand:  $z = -6.97$ ,  $p < .001$ ). Fruit set

**TABLE 2** Effects of farming practice (Farm: floodplain or upland, Açai: Açai clump density per ha (low or high), CC: Canopy cover %, Ht: Height (m) of inflorescence), landscape structure (Forest cover) and abiotic/biotic variables (SP: sexual phase, FI: Flowering intensity—proportion of adult stems in flower per plot, Temp.: Temperature (°C), CLC: Cloud cover (oktas)) on flower-visitor communities in açai palm. For each component of the community (visitation rate of specialised visitors (curculionid beetles), unspecialised visitors (bees, flies, wasps and non-curculionid beetles together), unspecialised bees, unspecialised non-bees and ants; richness of flower visitors), the first four selected models ( $\Delta AIC < 2$ ; see Table S5 for additional models), average model (where more than one model was selected) and importance values (*w*) of all included predictors are presented. Model coefficients presented in bold show predictors with 95% confidence intervals that did not cross zero (confidence intervals presented in Figure 3). The scale of forest cover measurements that was most important to visitors varied (see notes below table)

Response variable	Farming practice				Landscape		Abiotic/Biotic factors					AIC	$\Delta AIC$	Weight
	Farm	Açai	CC	Ht	Farm × Açai	For.	SP	FI	Temp.	CLC				
<b>Specialised visitors<sup>a</sup></b>														
Model 1						-0.893	<b>1.496</b>					306.1	0.0	0.12
Model 2						-0.915	<b>1.508</b>			0.41		306.8	0.7	0.09
Model 3		-0.440				-0.836	<b>1.498</b>					307.2	1.1	0.07
Model 4	0.853	-0.820					<b>1.510</b>			0.571		307.4	1.3	0.06
Avg. model	0.210	-0.219	-0.013	0.002		-0.445	<b>1.501</b>		-0.002	0.166		—	—	—
<i>w</i>	0.25	0.35	0.06	0.05		0.57	<b>1.00</b>		0.05	0.36		—	—	—
<b>Unspecialised visitors<sup>b</sup></b>														
Model 1	-0.037	-0.002			<b>0.154</b>				<b>0.034</b>			-533.8	0.0	0.32
Model 2	-0.037	-0.002			<b>0.153</b>		0.010		<b>0.034</b>			-532.4	1.4	0.16
Model 3	-0.039	0.001		-0.008	<b>0.153</b>				<b>0.033</b>			-532.0	1.8	0.13
Model 4	-0.036	-0.003			<b>0.150</b>				<b>0.034</b>	0.01		-532.0	1.8	0.13
Avg. model	-0.038	-0.002	-0.0004	-0.001	<b>0.151</b>		0.002	-0.002	<b>0.034</b>	0.001		—	—	—
<i>w</i>	1.00	1.00	0.12	0.13	1.00		0.16	0.13	1.00	0.13		—	—	—
<b>Unspecialised bees<sup>b</sup></b>														
Model 1	<b>-0.057</b>						0.020		<b>0.060</b>			-632.3	0.0	0.13
Model 2						<b>0.055</b>	0.020		<b>0.060</b>			-632.0	0.3	0.11
Model 3	<b>-0.056</b>	0.001			<b>0.092</b>		0.020		<b>0.058</b>			-631.9	0.5	0.11
Model 4	<b>-0.060</b>			-0.014			0.019		<b>0.059</b>			-631.3	1.0	0.08
Avg. model	-0.041	0.0002	0.0001	-0.003	0.013	0.016	0.014	-0.002	<b>0.060</b>	-0.0003		—	—	—
<i>w</i>	0.71	0.21	0.05	0.19	0.17	0.29	0.75	0.10	1.00	0.05		—	—	—
<b>Unspecialised non-bees<sup>a</sup></b>														
Model 1			-0.028						<b>-0.045</b>	0.017		-696.7	0.0	0.20
Model 2			<b>-0.030</b>						<b>-0.049</b>			-695.8	0.9	0.12
Model 3									<b>-0.039</b>	0.018		-695.4	1.3	0.10
Model 4		-0.011	-0.026						<b>-0.047</b>	0.017		-695.2	1.5	0.09
Avg. model	-0.001	-0.003	0.022	0.0001	0.008		-0.001	-0.044	-0.0001	0.015		—	—	—
<i>w</i>	0.18	0.20	0.79	0.09	0.10		0.09	1.00	0.08	0.86		—	—	—

(Continues)

TABLE 2 (Continued)

Response variable	Farming practice				Landscape		Abiotic/Biotic factors				AIC	ΔAIC	Weight
	Farm	Açaí	CC	Ht	Farm × Açaí	For.	SP	FI	Temp.	CLC			
Ant presence <sup>a</sup>													
Model 1	1.024	0.805		-0.539	2.924		-0.518				398.5	1.7	0.30
Richness <sup>c</sup>													
Model 1	-0.130	-0.490			0.590						136.19	0.00	1.00

<sup>a</sup>Forest cover included at 1 km radius.

<sup>b</sup>Forest cover included at 500 m radius.

<sup>c</sup>Model selected using AICc scores (Akaike Information Criterion corrected for small sample sizes). AIC, Akaike Information Criterion; Wgt, Model weight.

on open inflorescences was on average four times that on bagged inflorescences, but hand-pollinated inflorescences set on average 30% more fruit than open inflorescences (open vs. hand:  $z = -2.52$ ,  $p = .029$ , Figure 4a).

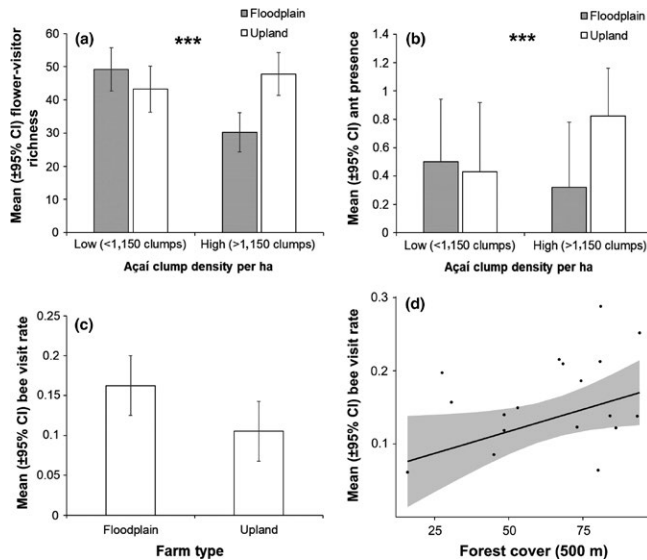
Fruit set on open inflorescences was positively related to shared visitor richness (i.e. insect taxa recorded on both sexual phases) and specialised curculionid beetle abundance on male inflorescences (Table 3; Figure 4b,c). Separate analyses of direct effects of landscape variables and farm management on fruit set confirmed that management practices that affect pollinator diversity affected açai production, showing positive effects of forest cover within 500 m radii on fruit production, but only on farms under extensive management (Table S6, Figure S4). Fruit set was also negatively related to ant presence on male inflorescences (Table 3; Figures 4d), and selected models included a positive interaction between ants and curculionids (Table 3), but the effect of this interaction was not significant (LRT = 3.32,  $df = 1$ ,  $p = .069$ ). In summary, pollinator diversity and specialised curculionid beetles underpinned pollination services in açai.

## 4 | DISCUSSION

Anthropogenic disturbance of tropical forests threatens not only biodiversity but also the vital ecosystem services that forests provide for local communities (Laurance et al., 2014). Here, we show that pollination services of an important Amazonian crop are dependent on a diverse set of insect pollinators. Our results show that intensive management practices have impoverished pollinator communities in floodplains and increased the frequency of antagonistic interactions on inflorescences in upland plantations (e.g. high ant densities). We discuss the implications of our findings for the long-term sustainability of açai fruit production in the Amazon river delta.

### 4.1 | Objective 1: To understand how farming practices and landscape structure affect açai flower-visitor communities

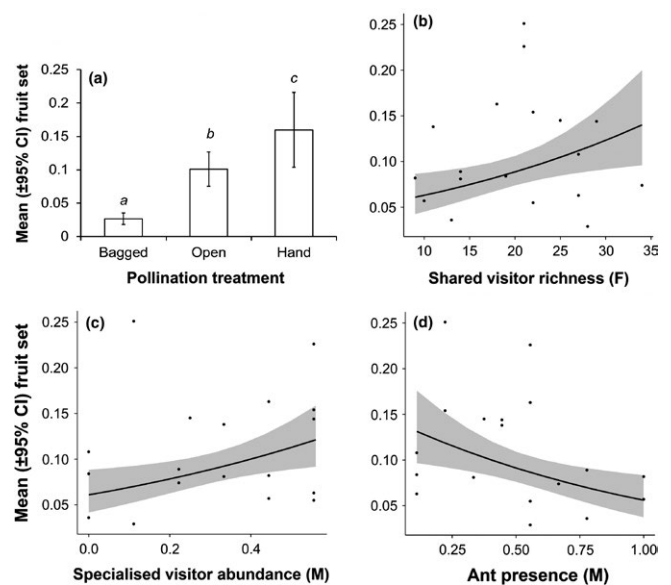
Flower visitors showed distinct responses to disturbance. Unspecialised flower visitors (e.g. bees, flies, wasps, non-curculionid beetles) were markedly less abundant in floodplains under intensive management (i.e. high açai clump density) compared to extensively managed floodplains. In contrast, specialised curculionid beetles were unaffected by farming practices and even showed a negative trend with forest cover. Separation of unspecialised visitors revealed that bees, but not other taxa, were more abundant in floodplains, where forest cover was greater. As many tropical bees have limited dispersal and require access to a range of different plant-provided resources (e.g. pollen, nectar, resins; Brosi et al., 2007), high forest cover and the presence of other tree species in floodplains probably ensured both greater "spill-over" from unmanaged areas (Kennedy et al., 2013) and higher densities of stingless bees nesting within farms compared to upland farms. Thus, further loss of forest cover is likely to have



**FIGURE 3** Effect of farm management and landscape on açai flower-visitor community. We detected effects of farm type (floodplain and upland farms) and management intensities (low or high clump density per ha) on (a) flower-visitor richness and (b) ant presence on inflorescences; (c) farm type on bee visitation (Bee Model 1, Table 2) and (b) forest cover within 500 m on bee visit rate (Bee Model 2, Table 2). Solid regression lines (d) represent an important detrended main effect in best models (confidence intervals do not cross zero), grey ribbons (d) and error bars (a–c) show 95% confidence intervals (CI), and asterisks show level of significance reported in likelihood ratio tests of models with and without interaction term (see Table 2 and main text for details)

negative effects on bee visitation to açai palm, but this was not possible to test in our study region where all floodplains had high forest cover. In contrast, other insects, including curculionid beetles, may be less dependent on forest habitats (Rader et al., 2016; Silberbauer-Gottsberger, 1990) and may even be favoured under intensive management practices (e.g. ants). Separation of taxa into functional groups would help clarify which species are affected by disturbance and traits that determine environmental sensitivity (e.g. body size, nesting requirements, diet breadth; Lichtenberg, Mendenhall, & Brosi, 2017).

Overall flower-visitor richness was also lower in intensively managed floodplains compared to other farms, suggesting that intensive practices in floodplains had important negative effects on flower-visitor communities. Changes in local habitat quality (e.g. floral resource availability) can have important effects on pollinators (Kennedy et al., 2013), and lower abundance and richness of flower visitors in intensively managed floodplains could imply that insects responded to disturbance at relatively fine spatial scales. However, clump densities in floodplains were equivalent to those in upland farms, and it is highly unlikely that upland plantations represented better quality habitats for pollinating insects than floodplains, as evidenced by patterns in bee abundance. Instead, lower richness in intensive floodplains probably reflects a wider disturbance of the surrounding forest areas, that is, conversion of native forest into açai-dominated stands. Over time, this process has created large patches of heavily simplified habitat that offers few resources for forest-dependent species, despite little change



**FIGURE 4** Effect of pollination treatment and flower visitor community on açai fruit production (fruit set). We detected effects of (a) pollination treatment; (b) shared flower-visitor richness (i.e. insect taxa recorded on both sexual phases) on female (F) inflorescences; (c) specialised curculionid visitor abundance on male (M) inflorescences and (d) ant presence on male inflorescences on fruit set. Solid regression lines represent an important detrended main effect in best models (confidence intervals do not cross zero), ribbons and error bars show 95% confidence intervals (CI), and letters represent significant differences between treatment levels. See main text and Table 3 (Model 1) for model details

in overall vegetation cover (Freitas et al., 2015; Moegenburg & Levey, 2002). In contrast, clump densities on upland farms are less likely to be related to any wider trend in adjacent forests as many farms were established in already cleared land parcels that are distinct from surrounding land uses. To test this, future research must distinguish between enriched areas and natural forest stands.

## 4.2 | Objective 2: To understand how flower-visitor communities influence pollination services and açai fruit production

Pollination experiments revealed that açai is highly dependent on insect visitors for fruit set and that pollination was an important limiting factor on fruit yield. Over half of all insect taxa visited both sexual phases, which is important for pollen transfer in dichogamous or dioecious plants (Greenleaf & Kremen, 2006). Moreover, positive effects of flower-visitor communities (richness and specialised beetle abundance) were strengthened by the exclusion of taxa recorded only on male or female inflorescences. Thus, we confirmed that açai is pollinated not only by a diverse range of insects, including specialised curculionid beetles, but also by unspecialised bees, beetles, flies and wasps (Kuchmeister et al., 1997; Listbarth, 2001).

High species diversity in tropical regions may confer substantial resilience to ecosystem processes against environmental change, due to high levels of redundancy among interacting species (Larsen et al.,

**TABLE 3** Effect of different flower visitors on fruit production (fruit set) in açai palm. Flower-visitor community variables included the abundance of specialised curculionid beetles (SV) and unspecialised visitors (bees, flies, wasps and non-curculionid beetles; UV), ant presence, shared visitor richness (SVR) and overall visitor richness (VR). Flower-visitor community variables were measured on male inflorescences (M) and on female inflorescences (F). All selected models ( $\Delta AIC < 2$ ), average model (Avg. Mod.) and importance values ( $w$ ) are presented. Model coefficients ( $\pm 95\%$  confidence interval) presented in bold show predictors with confidence intervals that did not cross zero

Model no.	SV (M)	UV (M)	UV (F)	Ants (M)	Ants (F)	Ants $\times$ SV (M)	SVR (F)	VR (F)	VR (M)	AIC	$\Delta AIC$	Weight
Model 1	<b>0.526</b>			<b>-0.566</b>		0.758	<b>0.522</b>			1208.1	0.0	0.27
Model 2	<b>0.539</b>		-0.268	<b>-0.513</b>		<b>0.819</b>	<b>0.617</b>			1208.5	0.4	0.22
Model 3		<b>-0.511</b>		<b>-0.458</b>			<b>0.648</b>		0.374	1209.3	1.2	0.15
Model 4	<b>0.390</b>			<b>-0.584</b>			<b>0.519</b>			1209.4	1.3	0.14
Model 5	<b>0.545</b>			<b>-0.510</b>		0.767		<b>0.437</b>		1209.8	1.7	0.12
Model 6	<b>0.525</b>			<b>-0.558</b>	-0.025	0.759	<b>0.532</b>			1210.1	2.0	0.10
Avg. model	0.433	-0.077	-0.060	<b>-0.533</b>	-0.002	0.553	0.502	0.051	0.056	—	—	—
$w$	0.85	0.15	0.22	1.00	0.10	0.71	0.88	0.12	0.15	—	—	—

AIC, Akaike Information Criterion; Wgt, Model weight.

2005). Here, curculionid beetles, many of which complete their life cycle on palm inflorescences (Barfod, Hagen, & Borchsenius, 2011), were the only visitors that had a direct positive effect on fruit production. Previous studies have highlighted the importance of curculionids as pollinators of açai palm (Jardim & Macambira, 1996; Kuchmeister et al., 1997; Listabarth, 2001). However, we also found a strong positive effect of pollinator diversity, which was negatively affected by local management intensity in floodplains. This suggests that the presence of more robust species (e.g. curculionids, non-bee taxa) did not fully compensate for the loss of environmentally sensitive species (e.g. forest-dependent bee taxa).

Pollinator diversity may enhance pollination through several mechanisms, including increased spatiotemporal complementarity among pollinator species (Hoehn, Tschardt, Tylianakis, & Steffan-Dewenter, 2008). For example, whilst bees and flies are strictly diurnal flower visitors, many beetles remain active at night (Barfod et al., 2011). Alternatively, pollination may be stabilised by differences in species' responses to abiotic filters (e.g. Brittain, Kremen, & Klein, 2013). We found bees were more sensitive to temperature changes than other taxa. Therefore, "non-bee" taxa may help stabilise pollination services across frequent fluctuations in abiotic conditions (e.g. heavy rainfall; Rader et al., 2016). To address these uncertainties, studies should investigate differences (or lack of, i.e. redundancy) in pollinator efficiency, sample under different abiotic conditions and use a range of sampling methods (e.g. collect entire inflorescences to sample beetles; Dáttilo, Aguirre, Quesada, & Dirzo, 2015).

Pollinator diversity can also affect ecosystem function by interspecific interactions, where the efficacy of pollinators is altered in the presence of other species (Greenleaf & Kremen, 2006). As ants are unlikely to contribute to pollination directly due to their limited mobility, this could explain why ants had both negative and positive effects on fruit production. A previous study of the closely related *Euterpe precatoria* described ants not as pollinators but as predators of curculionid beetles (Kuchmeister et al., 1997). Therefore, ants may not only have negative effects on pollination by predation or interference

of pollinators but also have positive effects by encouraging beetles to move more frequently between inflorescences. Further studies (e.g. exclusion experiments) are required to disentangle the role of ants in açai pollination.

### 4.3 | Implications for sustainable farming practice in açai fruit production landscapes

Ecological intensification, increasing crop yields through improved ecological functioning, is a promising means to generate "win-win" scenarios for both local communities and biodiversity (Garibaldi et al., 2016). Here, we show that extensive farming practices (i.e. low açai densities) promoted high pollinator diversity and fruit yields on açai farms. By increasing fruit production per clump, such "pollinator-friendly" practices can reduce pressure on surrounding forests by diminishing the need to expand areas under production to increase overall yield. Nonetheless, even low levels of management in floodplains, such as those proposed by existing recommendations (SEMA, Brasil, 2014), can have deleterious effects on tree diversity and vegetation structure (Freitas et al., 2015), underlining the importance of undisturbed forest for species conservation (Barlow et al., 2016). Moreover, unmanaged forest areas may be crucial to ensure high "spill-over" of pollinators from the surrounding landscape, as evidenced by the positive effect of overall forest cover on fruit production in extensively managed farms. Thus, further research is required to identify the most effective spatial configuration of habitats for both biodiversity and açai fruit production.

An alternative solution in degraded landscapes is the use of managed pollinators. Pollination is rarely considered in management, although the use of stingless bee hives has been previously recommended (Venturieri, 2014). Several species observed here visiting inflorescences are also commonly kept by local beekeepers

(Jaffé et al., 2015), but remain largely untested as pollinators. Alternatively, the management of weevil populations, akin to oil palm (*Elaeis guineensis* Jacq.; Syed, Law, & Corley, 1982), could prove highly effective.

Alongside biodiversity, ensuring the long-term sustainability of açai production in floodplains is essential for the livelihoods of an estimated 25,000 people, many of whom live in isolated communities with few alternative means of employment (Lopes & Santana, 2005; Weinstein & Moegenburg, 2004). In contrast, many upland farms are located in periurban areas with better access to local markets and owned by large producers (Homma et al., 2014). Accordingly, technological solutions (e.g. pollinator introductions, irrigation, fertiliser) to yield deficits are probably best suited to upland farms, and the maintenance of diverse forest habitats, the best means in floodplains.

## ACKNOWLEDGEMENTS

The authors would like to thank all land owners and those who helped in the field. We thank the two anonymous referees whose comments greatly improved a previous version of this manuscript, and all specialists for their help in identifying insects, including R.R. Silva, J.N.A. Santos Jr., R. de Melo Valente, J.H. Viana and F.S. Carvalho Filho. We also thank Dr Adriano Venturieri for providing land cover maps. This work was funded by two grants received by A.J.C. from CNPq (Pesquisador Visitante – 400435/2014-4) and Capes/Embrapa (Edital no. 15/2014), and by C.M. from CNPq (Pesquisador Produtividade – 306904/2016-0).

## AUTHORS' CONTRIBUTIONS

A.J.C., C.M., M.M.M., M.A.B.F. and L.G.C. conceived the experimental design; A.J.C. collected and analysed data; B.T.C. led insect identification and identified all Apoidea; L.G.C., R.J. and T.C.G. assisted with data analyses; A.J.C. wrote initial draft of manuscript and all authors contributed to subsequent revisions and gave final approval for publication.

## DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.28m55> (Campbell et al., 2018).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** Campbell AJ, Carneiro LG, Maués MM, et al. Anthropogenic disturbance of tropical forests threatens pollination services to açaí palm in the Amazon river delta. *J Appl Ecol*. 2018;55:1725–1736. <https://doi.org/10.1111/1365-2664.13086>