Too rare for non-timber resource harvest? Meso-scale composition and distribution of arborescent palms in an Amazonian sustainable-use forest

Short title: Meso-scale patterns of neotropical arborescent palms

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Highlights

- The occurrence, density and biomass of adult arborescent palms were measured in a National Forest in the eastern Brazilian Amazon.
- Commercially important arborescent palms were rare.
- Density and biomass were related to hydrographic and topographic variables.
- Subsidised agroforestry practices are required to facilitate the commercialization of palm NTFPs.

Abstract

Arborescent palms can provide an important source of non-timber forest products (NTFPs) within tropical forest REDD+ frameworks. To identify the NTFP potential of arborescent palms, we examined meso-scale patterns of abundance and distribution within a sustainable-use protected area in the eastern Brazilian Amazon. To understand the environmental correlates of observed patterns we evaluated the effects of topography, hydrography and geographic space on the presence, density and biomass of adult arborescent palms. Adult palms were sampled in 30 (250 x 20 m) plots systematically distributed within a 25-km^2 grid. Topographic and hydrographic variables were derived from a remotely sensed digital elevation model. Spatial correlations in the explanatory and response variables were examined using Mantel tests and GLMs. To test for evidence of dispersal limitation, semi-variograms were used to examine spatial patterns in GLM residuals. Adult arborescent palms were rare occurring in only 12 of the 30 plots. In total, we recorded 118 individuals from six species (*Bactris maraja*, *Euterpe oleracea*, *Iriartella setigera*, *Oenocarpus bacaba*, *Oenocarpus bataua and Oenocarpus minor*). This corresponded to a mean live aboveground biomass per plot of 0.85 Mg ha^{-1} (range: 0 – 28.1 Mg ha^{-1}). Hydrographic and topographic variables suggest that environmental conditions are suitable for *E. oleracea*, an economically important species. The presence, biomass, and density of palms were uncorrelated with geographic distances among plots. The hydrographic model significantly explained variation in palm presence and biomass, whereas density was only explained by the topographic model. Our findings indicate that arborescent palms are currently too rare to be efficiently harvested as NTFPs in the study area. Yet, comparisons with published estimates suggest that there is significant potential for agroforestry to facilitate the commercialization of palm NTFPs for community based extractive activities.

Keywords: Arecaceae; Arecoideae; biomass; canopy palm; meso-scale distribution; palm community

1 Introduction

Commercialisation of non-timber forest products (NTFPs) can contribute to the sustainable management of tropical forests. NTFPs are widely recognised as key components of REDD+ management frameworks and a variety of socio-economic action plans associated with much political will. For example, from January 2012 to December 2013, the Brazilian government invested approximately US$4.4 million in subsidizing NTFPs from community-based extractive activities (Brazil, 2015). These investments facilitated national commercialization of arborescent palm NTFPs by semi-subsistence extractive households, including açaí (*Euterpe* spp.) fruit, pulp, and palm heart (Brazil, 2015). However, there remains much uncertainty regarding the inclusion of palm NTFPs within forest management plans particularly across poorly studied parts of rural Amazonia.

Brazil has become a world leading example in the development and implementation of management options to reduce deforestation in the Amazon. Yet, the effective management of the 1.6 million km^2 of protected areas in the Brazilian Amazon that allow some form of human use remains a global and national challenge (Peres, 2011). Since 2006, the Brazilian government has been granting the private sector the right to manage public forests for the extraction of timber and non-timber products (Law No. 11.284). Although such use can contribute to the erosion of protectionist ideals (de Marques and Peres, 2015), the sustainable use of timber and non-timber products is widely recognised as a key national biodiversity management strategy enabling the integration of socio-economic and biodiversity conservation objectives (Brazil, 2015). With much of the ~1.6 million km^2 sustainable-use protected acreage occupied by sparsely settled human populations [densities < 4 inhabitants/km^2, (Norris and Michalski, 2013)] the commercialization of palm NTFPs is a rapidly expanding opportunity for community-based agroforestry and forest resource management across Amazonia.

The rural population density across the Brazilian Amazon has generally remained stable or has increased ((IBGE, 2010), see supplemental material in Norris and Michalski (2013)). Additionally, with the stricter controls on deforestation in large farms, the relative contribution of small-scale (<100 ha) rural farmers for the remaining deforestation in Brazil has also increased in comparison to that of large (>2,500 ha) landowners (Godar et al., 2014). As in much of the tropics, agroforestry is playing an

increasingly important role as a replacement to slash and burn practices across rural

35   Amazonia (Lasco et al., 2014; Schneider et al., 2015; Reed et al., 2016). NTFPs represent a key component of these agroforestry management practices (Lasco et al., 2014; Brazil, 2015), generating R$935.8 million, or 5.1% of the total Brazilian primary forest production in 2011 (Brazil, 2015).

       Arborescent palms are an important source of both food and income across the

40   Neotropics (Smith, 2015) and account for over 50% of the total NTFP commercial revenue in Brazil (Brazil, 2015). Palm NTFPs comprise a key part of priority production chains that can strengthen local production arrangements (Brazil, 2015). Depending on local culture and socio-economics, NTFP extraction of palms can range from simple collection in natural forest to intense cultivation (Richards, 1993; Muñiz-Miret et al.,

45   1996; Weinstein and Moegenburg, 2004; Benjamin Freitas et al., 2015; Smith, 2015; Steele et al., 2015). For example, Mauritia palm (*Mauritia flexuosa*) and açaí (*Euterpe oleracea*) are the two most valuable wild fruit species across Amazonia (Smith, 2015). The açaí production chain alone is estimated to generate over US$ 1 billion in net revenues annually (Brondízio, 2008). Understanding the spatial structure of arborescent

50   palm species richness, density, and biomass is therefore of direct interest to socio-economic stakeholders, and political decision-makers (Millennium Ecosystem Assessment, 2006).

       Palms have myriad growth forms (from small shrubs to tall canopy trees) and are widespread and highly abundant across Amazonia (Terborgh and Andresen, 1998;

55   Balslev et al., 2011; ter Steege et al., 2013). For example, *Euterpe* is the most abundant tree genus across the entire Amazon, and *Euterpe precatoria* and *E. oleracea* are the most and seventh most abundant hyperdominant tree species, respectively (Ter Steege et al., 2013). Arborescent palms also represent a dominant proportion of tree basal area and biomass in central and western Amazon forests (Vormisto et al., 2004; Emilio et

60   al., 2014), but they appear to be less dominant in eastern Amazonia, including areas of the Guianan Shield (Terborgh and Andresen, 1998). Yet even when palms are less dominant and/or less abundant, they can still provide a disproportionate contribution to forest and cultural dynamics due to extended fruiting seasons and high levels of fruit production (Peres, 2000; Link and De Luna, 2004; Cámara-Leret et al., 2014). For

65   example, a study from the eastern Amazon showed that five arborescent palm species (including *E. oleracea*) were the most important of 27 known palm species for local extractive communities living in and around protected areas (Araújo and Lopes, 2012).

Previous studies suggest that arborescent palm communities are likely to change as a consequence of extraction (Steele et al., 2015), land-use change (Brum et al., 2008; Eiserhardt et al., 2011) and global warming (Bjorholm et al., 2005; Eiserhardt et al., 2011). Studying determinants of palm community structure and diversity is therefore central to Neotropical forest ecology and management.

Studies have documented broad (biogeographic, e.g. (Göldel et al., 2015)) and local (<1 km^2) scale patterns in arborescent palms (Balslev et al., 2011). The principal findings documenting ecological patterns in Neotropical palms come from western and central Amazonia (Balslev et al., 2011; Emilio et al., 2014). Most ecological studies form the eastern Amazon focus on economically important arborescent palms in tidal and floodplain forests (e.g. Benjamin Freitas et al., 2015). There is strong evidence for water-related climatic factors as the primary determinant of broad-scale patterns in the regional to continental scale distribution of palm species (Bjorholm et al., 2005; Bjorholm et al., 2006; Göldel et al., 2015). At more local scales, the composition of arborescent palms is known to change across hydrological and topographic gradients (Kahn and de Castro, 1985; Balslev et al., 2011). Despite this understanding, the low sampling representativeness and lack of studies across vast swathes of the Amazon basin limit our ability to inform the effective management of commercially important palm NTFPs. Here we examine meso-scale patterns of arborescent palms in a 25-km^2 lowland forest plot of eastern Brazilian Amazonia. Specifically we examine the composition and spatial distribution of palm species within the 25-km^2 study area, and ask (1) to what extent does topography, hydrography and space influence the occupancy, density and biomass of arborescent palms; (2) whether the species distribution and density of palms are primarily affected by topography or hydrography; and (3) what is the potential of arborescent palms to provide economically viable NTFPs in the study area.

2 Material and Methods

Ethics Statement

Fieldwork was conducted under research permit number IBAMA/SISBIO 47859-1 to DN, issued by the Brazilian Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio).

2.1 Study area

This study was conducted in the Amapá National Forest (Floresta Nacional do Amapá – hereafter, ANF), a sustainable-use protected area of approximately 412,000 ha, centered in the state of Amapá, in north-eastern Brazilian Amazonia (0°55'29''N, 51°35'45''W, Fig. 1). The ANF is located on the pre-Cambrian Guianan shield craton at the base of the Tumucumaque Uplands. The regional climate is hot and humid, with annual rainfall ranging from 2,300 mm to 2,900 mm (Oliveira et al., 2010). During the wettest months (February, March and April), rainfall may exceed 500 mm/month. The dry season (September to November) is characterized by a maximum precipitation below 250 mm/month (Oliveira et al., 2010).

The ANF consists of continuous tropical rainforest vegetation, predominantly never-flooded closed canopy "terra firme" forest (ICMBIO, 2014). Canopy trees within the ANF typically reach a height of 25-35 m interspersed with emergents reaching up to 50m (ICMBIO, 2014). Based on 14.7 ha of floristic inventories conducted across the ANF (Pereira et al., 2008; ICMBIO, 2014), the 10 most common tree families (accounting for > 60% of individuals with ≥ 10cm DBH) were Annonaceae, Apocynaceae, Burseraceae, Chrysobalanaceae, Combretaceae, Fabaceae, Lauraceae, Lecythidaceae, Moraceae, Sapotaceae, which follows the expected pattern for the region (Terborgh and Andresen, 1998; ter Steege et al., 2000; ter Steege et al., 2013). Surveys have recorded 45 commercially valuable timber species within the ANF, with standing commercial timber volume estimates ranging from 21.4 to 52.7 m³/ha (ICMBIO, 2014). Considering selective and reduced impact logging activities typically harvest 20 to 30 m³/ha in Amazonian forests (Asner et al., 2005; Sist and Ferreira, 2007), these standing volumes are borderline for sustainable commercial exploitation. Such standing volumes combined with the remoteness of the site means there is no short-term expectation (i.e. within the next 5 - 10 years) for the commercial exploitation of timber species within the ANF.

Although the ANF was created in 1989, the management plan was only recently completed and published in 2014 (ICMBIO, 2014). According to Brazilian law (Law No. 9.985/2000) the key objective of sustainable-use areas is the sustainable and multiple uses of native forest resources. One of the objectives of the ANF identified in the management plan is the economic and long-term sustainable use of timber and nontimber forest products (specifically *E. oleracea*). ANF currently experiences low levels of anthropogenic perturbations (there has been no mechanised logging within the boundaries

of ANF), largely because only eight families live along the reserve border, there are no major access roads, and the nearest town is located 46 km away by river (Norris and Michalski, 2013). The exploitation of NTFPs in the ANF is incipient with an association of 21 local smallholders informally (i.e. lacking commercial production chains) harvesting açaí fruits and producing soap from native tree oilseed extracts (e.g. *Carapa guianensis* and *Copaifera langsdorffii*).
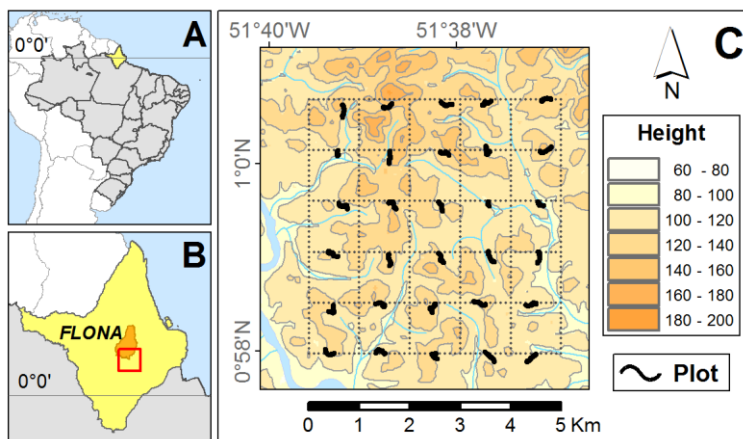

Fig 1. Location of the study region in the Amapá National Forest (ANF), State of Amapá, north-eastern Brazilian Amazon. (A) State of Amapá in Brazil. (B) Location of ANF within Amapá. (C) Elevation (20-m) contours across the grid system (dotted lines) and nonlinear plots placed along topographic contours (solid black lines) where palm surveys were conducted.

2.2 Sampling / Data collection

Palm surveys were conducted within a 25 km^2 area delimited by a series of 5 km linear transects that form a survey "grid" (Fig. 1). This grid was established as part of the Brazilian Program for Biodiversity Research ["Programa de Pesquisa em Biodiversidade" – hereafter PPBio, (Magnusson et al., 2013)]. Within the grid a total of 30 regularly spaced sample plots were established at 1-km intervals (Fig. 1). This regular arrangement and sample size of 30 plots has been shown to be adequate for capturing variation in meso-scale species diversity responses across lowland Amazonia (Norris et al., 2014).

Palm surveys were conducted during September 2015 in 30 plots of 20 x 250 m that follow altitudinal contours to minimise the internal variation in both altitude and correlated covariates such as soil type (Magnusson et al., 2005; Magnusson et al., 2013).

If plots were rectangular this would represent a plot area of 0.5 ha (250 x 20m) and a total survey area of 15 ha. However, due to the nonlinear plots, the total survey area was 18.3 ha (mean plot area $\pm$ SD = 0.61 $\pm$ 0.09 ha). The sample grid and plots are located within areas of lowland (50 – 150 m.a.s.l) evergreen *terra firme* forest or dense ombrophilous rainforest following the Brazilian "universal" vegetation classification system (Veloso et al., 1991). The soil is predominantly low-fertility oxisols, including a mix of red, yellow and red-yellow latosols following the Brazilian soil classification system (Eswaran et al., 2002; ICMBIO, 2014)).

All adult arborescent palms with DBH $\geq$ 10 cm (at 1.3m above ground level) were tagged, measured and identified within the 30 plots. The total and stem height of all individuals were estimated visually by previously trained observers. The identity of all palms considered here could easily be determined in situ following field guides (Henderson et al., 1995; de Andrade Miranda, 2001) and identification keys (Kahn, 1990; Rocha and Silva, 2005). Mature fruits of all species were also collected for confirmation by a botanist from the Amapá State Scientific Research and Technology Institute (Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá, IEPA) with more than 20 years of experience in palm species identification.

Explanatory variables

We obtained three topographic and three hydrographic explanatory variables from the SRTM digital elevation model (90-m resolution, version 2 "void filled", downloaded from http://earthexplorer.usgs.gov/). These six explanatory variables were selected, based on findings from previous studies (Terborgh and Andresen, 1998; de Castilho et al., 2006; Poulsen et al., 2006; Costa et al., 2009; Eiserhardt et al., 2011; Göldel et al., 2015; Salm et al., 2015). Topographic variables were selected to represent the form and shape of land surface: slope, aspect and terrain ruggedness. Hydrographic variables represented the spatial distribution of waterbodies and associated features, which are important for plant-soil interactions (e.g. surface inflow, surface moisture content): height above the network drainage (HAND), distance to the nearest stream, and distance to the nearest river.

All topographic and hydrographic variables were calculated using standard GIS procedures (Norris et al., 2014; Michalski et al., 2015). GIS processing was carried out using SAGA (System for Automated Geoscientific Analyses) (http://www.saga-

gis.org/en/index.html) and Quantum GIS (http://www.qgis.org/en/site/). All variables were weakly correlated (Pearson r ≤ 0.69) and as they represent distinct ecological components were retained in subsequent analyses.

195   2.3 Data analysis

All statistical analyses were undertaken within the R language and environment for statistical computing (R Core Team, 2015), using base functions and functions available in the following packages: *geoR* (Ribeiro Jr and Diggle, 2015), *ggplot2* (Wickham, 2009), *raster* (Hijmans, 2015), *sp* (Pebesma and Bivand, 2005), *tweedie* (Dunn, 2014)

200   and *vegan* (Oksanen et al., 2015).

To estimate the number of species in the 25-km^2 area we obtained the extrapolated species richness using the second-order jackknife estimator. Given the cross-sectional anatomy and crown architecture of arborescent palms, live tree aboveground dry biomass (AGB) of all individuals was calculated from genus-specific

205   allometric equations, which provide improved AGB estimates compared with standard models developed on the basis of dicot trees [(Goodman et al., 2013), Supplemental Material S1]. A family level model was used for *Iriartella setigera* and *Bactris maraja* as genus level models were unavailable [(Goodman et al., 2013); Supplemental Material S1]. We calculated the density and biomass of individuals per species and per plot.

210   Biomass and density values were expressed per hectare.

We tested for spatial auto-correlation of response and explanatory variables with Mantel tests. We calculated association matrices of independent variables as the difference in the value of the variable between plots. We used the Euclidean Distance coefficient to calculate the geographic distance matrix.

215   We used Generalized Linear Models (GLMs) to explore how topography and hydrography explained the variation in the presence (Binomial error distribution family), and density and biomass (both modelled with Tweedie error distribution family) of arborescent palms. Semi-variograms were used to test for spatial pattern in the GLM residuals.

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3 Results

3.1 Species composition

We recorded a total of 118 arborescent palms within the 30 nonlinear plots, providing an overall density of 6.5 ind. ha^{-1}. These included six species representing four genera (Table 1), all in the Arecoideae subfamily (Dransfield et al., 2005). We obtained an extrapolated species richness value of 11. Overall the plots contained an average of 0.5 species. Although some species were relatively common, half of the species recorded were represented by a single individual (Table 1).

E. oleracea was the most abundant species, accounting for 89% of all palms sampled. The dominance of *E. oleracea* largely resulted from a single riparian plot (i.e. permanently inundated plot along a perennial river) where 83% (n=98) of all individuals were recorded. This riparian plot ("permanent swamp forest", *sensu* Kahn and Granville 1992) was identified as an outlier and excluded from subsequent GLM analysis due to the stark differences in environmental characteristics.

Table 1. Density and biomass of arborescent palms in a 25-km^2 grid of lowland Amazonian terra firme forest.

Tribe / Species[a]	Growth form[b]	Inds. (inds.ha^{-1})	Plots	Plot Density (inds.ha^{-1})[c]	Plot Biomass (Mg.ha^{-1})[c]
Cocoseae					
Bactris maraja	Medium-sized	1 (0.05)	1	1.6	0.01
Euterpeae					
Euterpe oleracea	Large tall-stemmed	106 (5.80)	3	91.1 (7.5-255.5)	9.96 (0.56-28.07)
Oenocarpus bacaba	Large tall-stemmed	6 (0.33)	5	1.9 (1.4-3.2)	0.65 (0.28-1.15)
Oenocarpus bataua	Large tall-stemmed	3 (0.16)	3	1.6 (1.5-1.6)	0.58 (0.42-0.80)
Oenocarpus minor	Small	1 (0.05)	1	1.5	1.11
Iriarteeae					
Iriartella setigera	Small	1 (0.05)	1	1.8	0.12

[a] Taxonomy follows Dransfield et al. (2005)

[b] Growth form classification following Balslev et al. (2011)

[c] Values considering only the plots where the species was present (range in parenthesis).

3.2 Occupancy, density and biomass

Adult arborescent palms were recorded in only 12 of the 30 plots and only two plots contained more than one species (2 species in both cases, Fig. 2). From the total of 118 individual palms we calculated an overall live aboveground biomass of 15.63 Mg, resulting in a mean biomass of 0.85 Mg ha^{-1} for the 18.3 ha cumulative plot area. Summing values from all species the median plot biomass was 0.11 Mg ha^{-1} (95% quantiles for 30 plots: 0 - 1.27 Mg ha^{-1}).

None of the three responses were correlated with geographic distances among plots (Mantel tests: P=0.88, P=0.38 and P=0.35, for occupancy, biomass and density, respectively), which was also confirmed by visual inspection of the mapped values (Fig. 2). There was no significant correlation between the geographic distances among plots and any of the six explanatory variables (Mantel test: P≥0.33).
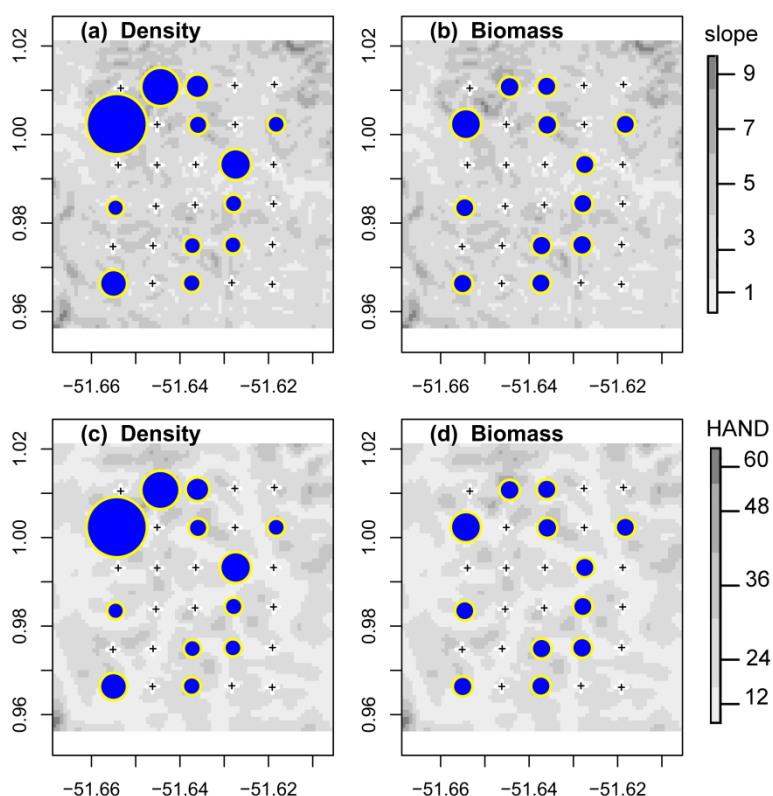
Fig 2: Spatial patterns in arborescent palm density and biomass. Location of the 30 plots are shown with size of blue spheres proportional to palm density (left panels) and biomass values (right panels). Crosses denote locations of plots with no arborescent palms. Mapped values of the most important topographic and hydrographic variables

shown as grey shaded background for slope (panels (a) and (b)) and height above the
network drainage (panels (c) and (d)).

Palm density varied more than palm biomass between plots (Fig. 2). Plot-wise
differences in the biomass of arborescent palms were only weakly explained by
topography and hydrography (Table 2). Presence and biomass were best explained by
hydrographic variables (Table 2), with both responses increasing significantly with
HAND elevation above the landscape drainage (Table 2, Fig. 3). Variation in density
was most strongly explained by topography, with significant negative and positive
relationships with slope and terrain ruggedness respectively (Table 2). None of the
unexplained variation (model residuals) was related to the geographic distance among
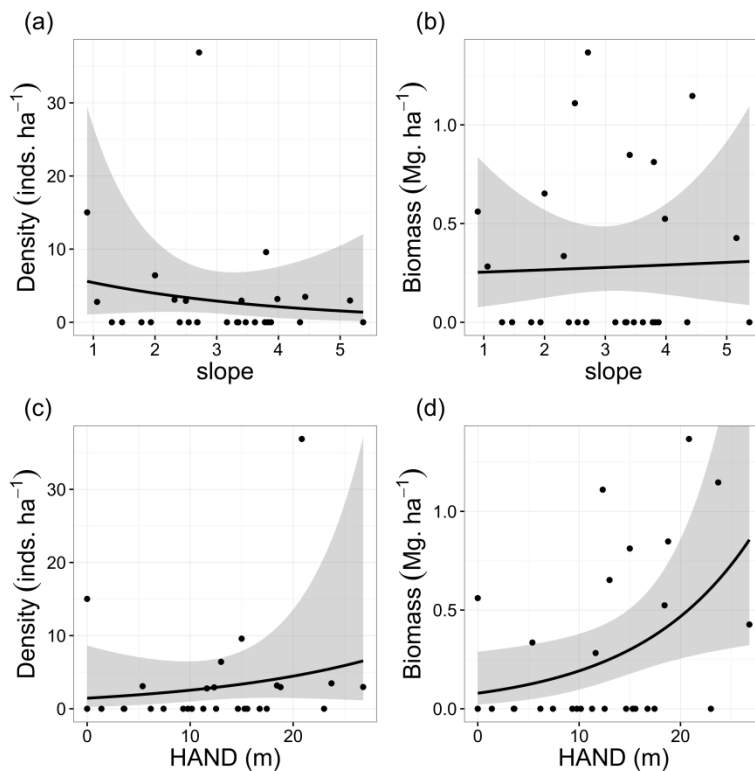plots (Supplemental Material S2).

Fig 3: Relationship between arborescent palm density and biomass and slope and height
above the network drainage (HAND). Solid dots show values from 29 lowland terra
firme plots in Amapá National Forest, Brazil. Solid line shows trend with grey shading
showing 95% confidence intervals from GLMs (Tweedie error distribution).

Table 2. Variation in arborescent palm distribution in relation to topography and hydrography. Results from GLMs used to explain the variation in occupancy, density and biomass of arborescent palms recoded from 29 lowland terra firme forest plots in Amapá National Forest, Brazil.

Model	Presence		Density		Biomass	
	[a]Est (SE)	Rank[c]	[a]Est (SE)	Rank[c]	[a]Est (SE)	Rank[c]
Model 1 - Topography						
Intercept	-0.50 (0.39)		0.87 (0.35)		-1.31 (0.29)	
Slope	0.12 (0.55)	3	**-0.90 (0.49)***	1	-0.01 (0.41)	3
Aspect	0.18 (0.39)	2	0.17 (0.32)	3	0.23 (0.28)	1
TRI	-0.32 (0.57)	1	**0.74 (0.41)***	2	-0.11 (0.38)	2
AIC	45.9		111.3		54.3	
[b] Dev. expl	1.5		**17.3***		2.6	
Model 2 - Hydrography						
Intercept	-0.56 (0.41)		0.94 (0.43)		-1.51 (0.31)	
HAND	**0.83 (0.55)***	1	0.31 (0.49)	2	**0.66 (0.33)***	1
Dist. river	0.20 (0.41)	2	0.43 (0.43)	1	0.23 (0.28)	2
Dist. creek	-0.08 (0.52)	3	0.18 (0.50)	3	-0.09 (0.35)	3
AIC	42.5		113.0		50.1	
[b] Dev. expl	**10.3***		11.2		**20.3***	

Significant models in bold, significance codes: '*' 0.01, '**' 0.05

[a] Standardized regression coefficient and associated standard error (SE).

[b] Model deviance explained (%)

[c] Ranked variable importance based on z ("Presence") or t ("Density" and "Biomass") test probability values.

3.3 Species distribution and density

Only three species occurred in more than one plot (*O. bacaba, O. bataua* and *E. oleracea*; Fig. 3). *Oenocarpus bacaba* was the most widely distributed species, but was only recorded in 17% of the plots (Table 1, Fig. 4). Although only present in five plots this species was recorded across the entire topographic and hydrographic gradient

examined (Fig. 4). With a density of 255.5 stems ha^{-1}, *E. oleracea* was most abundant in the flooded plot (Table 1), but this species was also absent from three other unflooded plots with the same HAND value (Fig. 4). *E. oleracea* was also recorded at plots with higher HAND values (Fig. 4). *Oenocarpus bataua* was found in plots with greater HAND and slope values (Fig. 4).
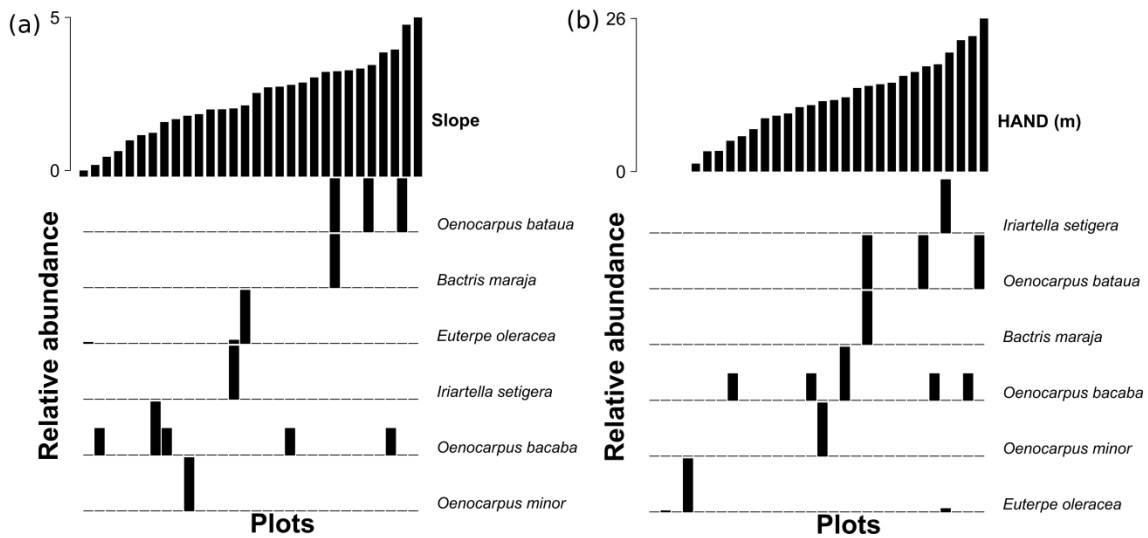
Fig. 4. Direct ordination of arborescent palm species abundance data in 30 lowland Amazonian terra firme forest plots, showing species abundances in relation to gradients in slope (a) and height above the network drainage (b). Plots (x-axes) are ordered left to right from lowest to highest slope and HAND values. Bars indicate relative abundance in a given plot within species but are not comparable between species because the number of individuals varied among species (Table 1). Values of the y-axis in the top bar plots represent the range of gradient values.

4 Discussion

4.1 Species composition

Our study region has a relatively high species richness of palms (Bjorholm et al., 2006; Göldel et al., 2015), with the Arecoideae showing a strong mid-domain effect whereby

species richness peaks around the equator (Bjorholm et al., 2006). We recorded six

315 arborescent palm species from 18 ha (0.18 km^2) of forest. Findings from previous studies show that we could expect as many as 25 or more caulescent ("stemmed") palms within a 101 x 101 km (10,201 km^2) area (supplementary figure S1a in Göldel et al. 2015). Although stemmed palms is the most common growth form in the Arecaceae (Göldel et al., 2015), most stemmed species are classified as "understory" palm,

320 whereas arborescent canopy and subcanopy palms are typically less species-rich in lowland Amazonia (Kahn and de Castro, 1985; Costa et al., 2009). For example, in central Amazonia, only five of a total of 32 palm species recorded from 1.2 ha were arborescent (Kahn and de Castro, 1985). A study from this same region recorded 11 species of "canopy" palms (typically > 8m) from a total of 38 species in 7.2 ha (Costa et

325 al., 2009). In contrast, studies in the Guianan Shield (NW Guyana) reported very low numbers of palms (e.g. 4.6 trees/hectare) (Davis and Richards, 1934; Kahn and Granville, 1992). Our estimated and observed species richness values are therefore within the expected range considering the location and overall size of our study area.

We obtained an estimate of 11 arborescent palm species from our survey of

330 thirty 250 x 20 m plots within the 25-km^2 grid, suggesting that several species remain undetected. Previous studies report *Attalea* sp. and *Astrocaryum* sp. as commonly found arborescent palms from lowland forests in central and western Amazonia. Species from these genera provide commercially marketable NTFPs (Smith, 2015), and have been reported from studies across the Guianan Shield (Smith, 2015). Therefore, it seems

335 likely that *Attalea* sp. and *Astrocaryum* sp. do occur within the ANF. However, our survey suggests that these species are likely to be rare across the area and do not represent a source of commercially viable NTFPs.

4.2 Occupancy, biomass and density

340 Our occupancy, biomass and density values are generally lower than those reported from other regions in central and western Amazonia (Kahn and de Castro, 1985; Terborgh and Andresen, 1998; ter Steege et al., 2000; de Castilho et al., 2006; Costa et al., 2009; Goodman et al., 2013). Previous studies provide live tree aboveground dry biomass estimates of 434 Mg ha^{-1} (95% CI: 293.9–763.4 Mg ha^{-1}) from 45 permanent

345 tropical forest plots in the Guianan Shield (Feldpausch et al., 2012). Based on our plotwise mean estimate, adult arborescent palms represented <0.2% (0.85/434 Mg ha^{-1})

of the total aboveground biomass. However, considering the maximum biomass value obtained from the plot dominated by *E. oleracea* (28.07 Mg ha^{-1}) then arborescent palms represented up to 10% of the overall biomass (28.07/293.9 Mg ha^{-1}).

350   The distribution and density of arborescent palm species is often locally clustered and unpredictable (Kahn and Granville, 1992; Eiserhardt et al., 2011; Göldel et al., 2015) . The density of canopy palms in Amazonian terra firme forests may range from low (< 40 individuals per ha) to more than 200 individuals per ha in oligarchic or monotypic forests (Kahn and Granville, 1992; Peres, 1994; Benjamin Freitas et al.,

355 2015). The weak explanatory power of our GLMs for occupancy, biomass and density of adult arborescent palms is therefore to be expected. There are several alternate non-mutually exclusive explanations for the observed patterns. Firstly, palms were rare in our study plots and modelling rare species is notoriously challenging. Although our findings generally agree with those of previous studies, much unexplained variation in

360 the GLMs remain. Secondly, we did not consider edaphic factors, which have been shown to be important drivers of arborescent palm species composition (Costa et al., 2009) and biomass (de Castilho et al., 2006). However, topography and hydrography are strongly related to meso-scale soil characteristics in lowland Amazonia. Indeed elevation is so strongly correlated with soil characteristics that their effects cannot be

365 easily separated (de Castilho et al., 2006; Poulsen et al., 2006; Costa et al., 2009), leading to the conclusion that topography is an adequate proxy for meso-scale soil properties (de Castilho et al., 2006; Costa et al., 2009). As such we believe soil properties are unlikely to provide additional insights beyond those provided by our topographic and hydrological covariates.

370   Dispersal limitation has been proposed to explain unpredictable patterns in arborescent palm density and diversity (Svenning, 2001; Bjorholm et al., 2005). Yet, we found no obvious spatial structure in meso-scale palm distribution. No correlation was found between any of the responses and the geographic distance among plots. When combined with the fact that, when controlling for topographic and hydrological effects,

375 there was no association with spatial distance, we conclude that meso-scale dispersal limitation does not operate in our study area. Indeed the relatively pristine forest status of the Amapá National Forest ensures the presence of a full complement of vertebrate dispersers including tapir, large primates and scatter-hoarding rodents [(Michalski et al., 2015), D. Norris, pers. obs.].

380   Foraging behaviour of vertebrate frugivores induces complex, non-random patterns of palm species distribution at local and landscape scales (Fragoso, 1997; Sezen et al., 2009). For example, dispersal effects are evident at local scales in the distance decay of floristic similarity and are also suggested to be responsible for large fractions of unexplained variation at this scale (Normand et al., 2006). Considering the

385   importance of such biotic and abiotic interactions, the unexplained variation in palm occupancy, density, and biomass is therefore unsurprising and supports findings from previous studies (Eiserhardt et al., 2011).

4.3 Species distribution and density

390   The three most common arborescent palms at ANF are early successional species that have been recorded across a range of environmental gradients (Peres, 1994; Henderson et al., 1995; Svenning, 1999; Pacheco, 2001; Brum et al., 2008; Ter Steege et al., 2013). Both species of *Oenocarpus* (*O. bacaba* and *O. bataua*) are widely distributed throughout Neotropical evergreen forests on both sides of the Andes (Henderson et al.,

395   1995; Smith, 2015). We recorded both species in upland plots above 5 m from the drainage network, with most individuals recorded at higher elevation plots (HAND > 10 m). Previous studies show that inundation inhibits germination in *O. bacaba* (Pacheco, 2001). This finding may explain the increased abundance of this species on plateau and slope ridges compared to lowland areas (i.e. < 5m above stream level) (Pacheco, 2001).

400   In contrast *O. bataua* has been recorded from terra firme forests in the western Amazon (Vormisto et al., 2004) and in floodplain areas in central Amazon (Kahn and de Castro, 1985).

        Previous studies show that *O. bataua* can be 20-fold more abundant than *O. bacaba* across both wet and dry forests in western South America (Amazon, Chocó and

405   montane forest habitats) (Cámara-Leret et al., 2014). In contrast, *O. bacaba* dominates well drained terra firme forests in the central Amazon but was absent from floodplain areas where *O. bataua* dominates (Kahn and de Castro, 1985). In the ANF both species were rare compared with the results from these previous studies and were never recorded in the same plot. Although there are methodological differences (such as the

410   minimum DBH cut-off) previous studies report density values that are substantially (3 – 10 fold) greater than those at ANF. For example the mean stem density of large (>10 cm

DBH) *O. bacaba* was 5 ind. ha^{-1} within 21 central Amazon terra firme forest plots of 1 ha each (Brum et al., 2008).

Euterpe oleracea is known for its strong association with floodplain and tidal várzea forest areas (Muñiz-Miret et al., 1996; Weinstein and Moegenburg, 2004; Fortini and Carter, 2014), which are often exploited for the commercial management of the species (Weinstein and Moegenburg, 2004; Smith, 2015). We recorded *E. oleracea* both at and above the drainage network (0 – 20 m). The fact that this species occurs above the drainage network is consistent with other studies showing this species can occur in a variety of topographic and hydrographic conditions (Vedel-Sorensen et al., 2013). But as found for the two *Oenocarpus* species the density of *E. oleracea* in the ANF was much lower than those reported from central Amazon areas (Kahn and de Castro, 1985; Costa et al., 2009).

4.4 NTFP potential of arborescent palms

Economically viable densities of adult arborescent palms are likely to be orders of magnitude above the values we recorded at ANF. For example, in commercially managed floodplain areas, *E. oleracea* density ranges between 200 and 1000 stems ha^{-1} (Benjamin Freitas et al., 2015). Açaí production from semi-natural oligarchic palm stands arguably accrues the highest socio-economic value at local to national scales from any nontimber neotropical forest resource (Muñiz-Miret et al., 1996; Heckenberger et al., 2007; Cámara-Leret et al., 2014; Benjamin Freitas et al., 2015). In contrast the commercialization of *Oenocarpus* remains much less important locally, and we could not find any published reports from our region of NTFP trade of these species. Due to the overall rarity of arborescent palms at ANF, and the apparent lack of a local market for *Oenocarpus* sp., we focus on *E. oleracea* as the most viable palm NTFP option that could be harvested for either subsistence or cash.

Management of insufficiently dense resource populations may be required to boost stocks of commercially valuable NTFPs. Although recent studies highlight degradation of forest diversity within monodominant açaí stands (Weinstein and Moegenburg, 2004; Benjamin Freitas et al., 2015), the recommended açaí management practice for smallholders is agroforestry, in which areas with 200-400 açaí stems per ha can still retain 200 native forest trees ha^{-1} (Queiroz and Mochiutti, 2012). Adoption of agroforestry management practices reduces biodiversity impacts and increases açaí fruit

445   production. For example, these agroforestry mosaics can extend açaí fruiting periods from 3 to 7 months (Queiroz and Mochiutti, 2012), thereby significantly increasing NTFP productivity within smallholdings.

        A comparison of smallholder açaí and micro scale timber producing firms from around the Amazon estuary found that average start-up costs for clearing and planting 1

450   ha of açaí was US$948 (Fortini and Carter, 2014), compared to an annual revenue of US$1040 assuming the average açaí stand density. These authors also found that the financial break-even point based on açaí sales was relatively long at 8 years, largely because of the 3-5 years between planting and full production (Hiraoka, 1995; Fortini and Carter, 2014). If smallholder açaí production is deemed as an acceptable choice in

455   balancing conservation and local livelihoods in and around sustainable-use protected areas, then our findings suggest that subsidies and/or financial assistance will be needed to fund the start-up and management costs during pre-production years.

        The ANF management plan establishes a 26,208 ha zone for community-based extractive activities, including nontimber resources. Assuming that lowland areas

460   accessible within 2000 m of the main river and with HAND values below 1 m are likely suitable for commercial açaí agroforestry plantations, the results of our HAND model suggest that approximately 2,845 ha (11% of the 26,208 ha zone) is available for commercial açaí planting. Assuming an average yearly revenue of US$1040 per hectare (Fortini and Carter, 2014), this provides an estimate of US$ 2,958,800 per year from

465   commercial açaí production for the local residents in and around the ANF.

        There are a total of 8 families who live along the ANF border and a further 23 within 20 km (Norris and Michalski, 2013). It is estimated that 12.5 ha of permanent açaí cultivation would be required to provide the equivalent net present value of commercially valuable timber purchased by a sawmill (Fortini and Carter, 2014).

470   Therefore, allocating 12.5 ha for commercial production per family (smallholders typically manage between 10 and 20 ha in the region) would require a total area of 388 ha, thereby generating a mean gross annual revenue of US$ 13,000 per family. Although there are large uncertainties in these revenue estimates arising from a variety of economic, management and environmental challenges, a rural worker in Brazil earns

475   on average US$468 per month (IBGE, 2013) and in our study region, the principal earner from the families living around the ANF earns on average US$ 500 per month [(Norris and Michalski, 2013), 2012 exchange rate of US$1.00 to R$1.70]. Revenue

from the effective management and commercialisation of palm NTFPs can therefore represent significant opportunities that remain under-exploited.

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4.5 Conclusion

Based on our results, we conclude that hydrography and topography have direct but distinct effects of the occupancy, density and biomass of adult arborescent palms at ANF. Based on the findings from our ecological models, and the economic potential of

485 *E. oleracea* NTFPs, we consider that with appropriate management the proportional area designated for extractive activities within sustainable-use Amazonian forest reserves appears to be adequate to generate significant socio-economic benefits for the rural population. Our findings emphasize that management of arborescent palms within an extensively managed agroforestry context will be necessary to realise the full socio-

490 economic and conservation potential of sustainable–use protected areas. This is particularly important in the National Forests of Brazilian Amazonia, where market-competitive NTFP extractive activities can stave off the economic alternative of allocating much larger areas to corporate logging concessions, which are far more powerful agents of forest degradation.

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