Understory palms are not canopy palms writ small: Factors affecting Amazonian understory palms within riparian zones and across the landscape

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ABSTRACT

Understory palms are subject to different ecological pressures than those experienced by canopy palms, but most studies do not distinguish between understory and canopy palms, or include only canopy palms. Much of the variation in the taxonomic composition of understory palms in the Amazon is concentrated in riparian zones. However, abiotic characteristics of the riparian zone that influence this variation are underexplored or have been modeled only through additive relationships. Our objectives were to determine (1) if the abundance of understory palms is related to the abundance of canopy palms, (2) how topographic and soil variables, and their interactions, affect variation in composition of understory-palm assemblages across the entire landscape, which includes riparian and non-riparian zones, and (3) how understory-palm assemblages vary in species composition along streams as a result of variation in abiotic factors and their interactions within the riparian zone. We sampled 40 riparian areas and analyzed the data in combination with existing data from 72 non-riparian plots. Plots (250 m × 4 m) were distributed across 64 km^2 of a *terra-firme* forest (Reserva Ducke) covering two major drainage basins that differ in topography and soil characteristics. Abundances of understory and canopy palms have opposite relationships to the same environmental variables and, therefore, should not be treated as a single group. In addition, interactions among environmental factors at the mesoscale (entire landscape) and at the local scale (riparian zone), generate compositional turnover even among sites with only subtle environmental differences. Stream discharge and soil structure are among the first variables to be affected by human occupation of riparian zones, which indicates that a better understanding of interactions between environmental predictors and a landscape approach will be necessary to conserve Amazonian understory palms.

1. Introduction

Palms (Arecaceae) play an important role in the structure and dynamics of the Amazon rainforest due to their high abundance and interaction with vertebrates and invertebrates (Henderson et al., 1995; Kahn and de Castro, 1985; Küchmeister et al., 1998), and palms are more abundant in the Neotropics than in other tropical forests (Muscarella et al., 2020). Some species are also widely used by humans for food and construction, and thus have economic value (Shepard et al., 2020; Kahn, 1991). Studies on palm distribution and assemblage

composition at a variety of spatial scales in the Amazon have found relationships with soil and topographic characteristics related to drainage, water availability and soil nutrients (Costa et al., 2015; Eiserhardt et al., 2011; Svenning, 1999). However, although it is necessary to consider all forest strata to understand composition patterns in the Amazon (Draper et al., 2021), many studies have treated palms as a homogeneous group, without dividing them into understory and canopy species (e.g., Rodrigues et al., 2014; Schietti et al., 2014).

Based on their size, Amazonian forest palms can be divided into two major groups: canopy species with stems usually reaching more than 8 m

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in height, and understory species with stems shorter than 8 m in height (Costa et al., 2009). Palms in the Amazon have been reported to occur at higher densities on poorly structured soils associated with shallow water tables, such as in riparian zones (de Castilho et al., 2006; Peres, 1994). However, these conclusions do not distinguish between canopy and understory palms, or are based only on canopy palms. Thus, it is unclear whether these generalizations also apply to understory palms, which are subject to different ecological pressures than those experienced by canopy palms due to lesser rooting depths and reduced light availability in the understory (Kahn and de Castro, 1985). For example, Ma et al. (2015) found that palms occurring in lower strata of tropical forests have higher carbon-gain efficiency due to an evolutionary strategy enabling adaptation to shady environments, but they did not distinguish between canopy and understory palms.

Natural events, such as flooding, may be more pronounced in areas with restricted drainage and hydromorphic soils (Kahn, 1987), but different combinations of topographic and edaphic factors can affect water availability for plants. Therefore, it is unlikely that the effects of topographic and soil components on plant responses are simple additive combinations (Emilio et al., 2013; Hladik and Alber, 2014; Munson et al., 2016). Interactions among environmental factors are strongly scale-dependent (Balslev et al., 2011), and this could generate different niche compartments (Wright, 2002) and influence palm assemblage composition.

Interactions among watersheds, topography and soil characteristics (Costa et al., 2005), and distance from water courses and light availability (Paixão, 2012), affect the composition of understory plants. Distance from water courses is associated with large variation in floristic composition in areas close to streams (Costa et al., 2009; Schietti et al., 2014), indicating that unknown factors or interactions among factors that have not been studied affect floristic composition.

Studies of community ecology in the Amazon have generally included few riparian zones (e.g., Drucker et al., 2008; Fraga et al., 2013; Normand et al., 2006). Organisms of riparian zones may respond to subtle changes in local gradients, such as water retention in the soil and flooding regime (Drucker et al., 2008; Pazin et al., 2006). One of the few studies of the effects of environmental variables on understory-palm assemblages in the Amazonian found a large effect of proximity to water courses on floristic composition (Costa et al., 2009). However, the distribution of some terrestrial plant species is also regulated by factors that vary along streams because larger streams are usually associated with longer flooding and anoxic conditions in their associated riparian forests (Riis et al., 2001). In addition, plots used in the study by Costa et al. (2009) followed the altitudinal contours, so individual plots could include areas close to and far from streams, which reduces the chances of recording many riparian-zone species. The inclusion of riparian zones increases the amplitude of the gradients generally studied and is necessary to identify factors affecting understory-palm assemblage composition that have little effect in areas far from streams.

In Reserva Ducke, located on the outskirts of Manaus, Central Amazonia, riparian zones are distributed across two major watersheds that have different topographic profiles ("V" or "U" shaped valleys) and are separated by a central plateau, which can limit the dispersal of species even without large variations in soil characteristics (Costa et al., 2005). Thus, it is likely that the effects of variables associated with the riparian zone on floristic composition differ between watersheds.

Based on previous studies of canopy palms and other plant taxa, the riparian zone is likely to represent a distinct habitat for understory palms, but the lack of studies that have focused on riparian zones in the Amazon limits our ability to determine the magnitude or even direction of such effects. Therefore, we investigated the following hypotheses: (1) The abundance of understory palms is related to the abundance of canopy palms, (2) topographic and soil variables and their interactions affect variation in composition of understory-palm assemblages across the entire landscape, which includes riparian and non-riparian zones, and (3) understory-palm assemblages vary in species composition along

streams as a result of variation in abiotic factors and their interactions within the riparian zone.

2. Materials and methods

2.1. Study site

We conducted the study over a 64 km^2 trail system within Reserva Ducke (2°55′ 47.80′′ S; 59°58′ 30.34′′ W). The reserve covers a 100 km^2 forest remnant on the outskirts of Manaus, Amazonas State, Brazil (Fig. 1). Although Manaus has reached the southern and western limits of the reserve, Reserva Ducke is still connected to continuous forest on the eastern side. The reserve is covered by evergreen *terra-firme* tropical rain forest with a closed canopy that reaches 30–37 m high. The understory is characterized by an abundance of acaulescent palms (Ribeiro et al., 1999). The mean annual temperature from 1966 to 2016 was around 26 °C and mean annual rainfall was around 2572 mm (Esteban et al., 2021).

Soils in Reserva Ducke are derived from tertiary fluvio-lacustrine deposits from the Alter do Chão formation (Sombroek, 2000). They are mostly clayey oxisols on the ridges; podzols on the valley slopes; and spodosols when close to small streams. Soils near streams are almost permanently waterlogged during the rainy season between November and June (Bravard and Righi, 1989; Chauvel et al., 1987). In general, Reserva Ducke soils are acidic and poor in nutrients, such as phosphorus, calcium and potassium (Chauvel et al., 1987). The topography of Reserva Ducke is undulating/hilly, with altitude ranging from 40 to 140 m (Ribeiro et al., 1999). The reserve has a dense drainage network with two main watersheds separated by a central ridge; the streams from the eastern watershed flow to tributaries of the Amazon River and those in the western watershed flow to the Negro River (Mendonça et al., 2005).

2.2. Sampling design

2.2.1. Riparian plots

The data for understory-palm assemblages in riparian plots were collected between October 2019 and December 2020 in 40 plots distributed over the 64 km^2 grid (Fig. 1) following the RAPELD method (Magnusson et al., 2005; 2013). These 250 m × 4 m (1000 m^2) plots were at least 300 m apart and included streams of first, second, and third order in the two watersheds (Rodrigues, 2006). We established the plots to comprehensively cover the two watersheds where streams crossed the trail system. Most plots were located along narrow first- and second-order streams (n = 29), but eleven plots were beside third-order streams. Riparian RAPELD plots have a 250 m long center line that follows the stream bank (in the direction mouth to source) divided in 10 m linear segments and a minimum distance between the stream margin and the nearest point on the center line of each 10-m segment of 1.5 m; therefore, they are close to the stream along their entire lengths. Data on canopy-palm abundance in the riparian plots were collected in the same way as for understory palms. Because they follow the stream margin, RAPELD plots of the same length have slight differences in area. The area of each plot was calculated using the R codes available in the PPBio website (https://ppbio.inpa.gov.br/analises/area) and the average size difference among riparian plots was 1% (~10 m^2).

2.2.2. Non-riparian plots

The data for understory-palm assemblages of the non-riparian plots were provided by authors of the study by (Costa et al., 2009). These data were collected in January and February 2003, 16 years before the riparian plots. This temporal difference between non-riparian and riparian plots can generate changes in vegetation. However, well-conserved forests (e.g. Reserva Ducke) are less susceptible to changes in productivity, and Olivares et al. (2016) demonstrated that the structure and composition of a palm community in a protected western Amazon Forest remained stable for over 17 years.
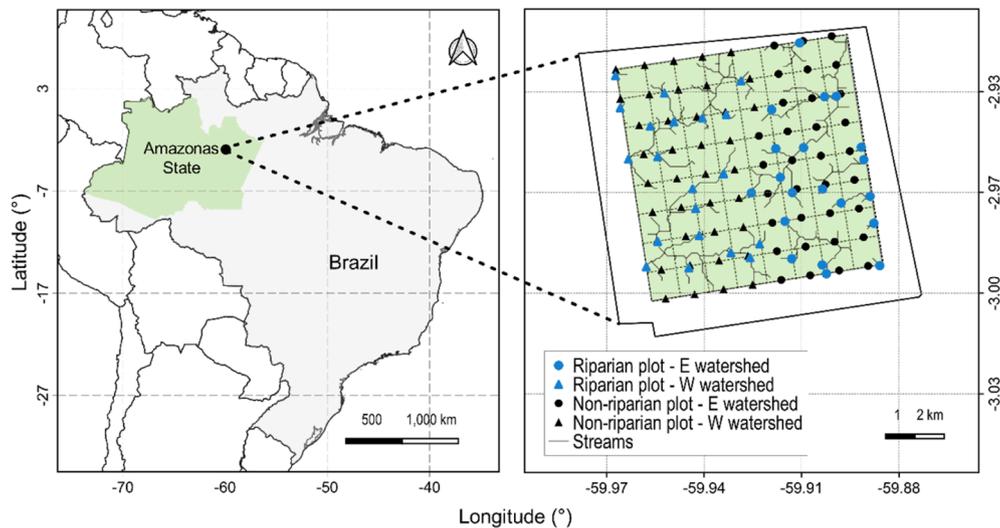
Fig. 1. Map showing the study area located in Amazonas State in central Brazilian Amazonia and the grid system in Reserva Florestal Adolpho Ducke, Manaus, Amazonas, Brazil. Geographic coordinate system, datum WGS84. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

We used 72 non-riparian plots uniformly distributed over the 64 km^2 grid (Fig. 1) following the RAPELD method (Magnusson et al., 2005; 2013). These 250-m × 4-m plots were at least 1 km apart, and established following the altitudinal contours. As soil properties are closely related to altitude in Reserva Ducke (Chauvel et al., 1987), this reduces within-plot variation in soil characteristics and hence vegetation change (Costa et al., 2009). The data for canopy-palm abundance in the non-riparian plots were collected in the same way as for understory palms from a previous study (de Castilho et al., 2006). Because they follow the altitudinal contours, RAPELD plots of the same length have slight differences in area. The average size difference among non-riparian plots was 3% (~73 m^2) and between riparian and non-riparian plots was 2% (~24 m^2).

2.3. Palm assemblages

We considered understory palms to be those with subterranean stems or with aerial stems < 8 m tall. Maximum species sizes were obtained from Kahn and de Granville (1992), Ribeiro et al. (1999), Balslev et al. (2011) and field observations. We used the same protocol to record understory-palm species in non-riparian and riparian plots. Every palm rooted inside the plot with leaf height ≥ 1 m was recorded and identified according to Ribeiro et al. (1999) and Henderson et al. (1995). We included modifications in the classification of *Astrocaryum* suggested by Kahn (2001). For species that may have more than one stem, we considered each clump as a different individual. As the density of these species is not high in the study area, in most cases it was possible to distinguish different individuals. We considered canopy-palm species as those in which adults have aerial stems ≥ 8 m high and dbh ≥ 10 cm.

2.4. Environmental variables

The topographic variables used in this study were the terrain slope measured in degrees and the height above the nearest drainage in meters (HAND). The slope of riparian and non-riparian plots was measured with a clinometer perpendicular to the main axis of the plot at every 50 m, and summarized as means of the six measurements per plot. Height above nearest drainage was estimated from digital elevation models that give the altitude of the plot and the nearest drainage channel. HAND is directly correlated with the gravitational potential of soil water. The gravitational potential of water is a component of the soil's water potential, which reflects the difficulty of plants in extracting water from

the soil or avoiding excess water. High HAND values mean high gravitational potential (high vertical drainage potential) and low HAND values mean low gravitational potential (low vertical drainage potential) and proximity to the water table (Nobre et al., 2011). HAND measurements for riparian and non-riparian plots were obtained using the HAND algorithm (Rennó et al., 2008) in a Digital Elevation Model (DEM, 90 m grain) with a minimum contribution area of 0.41 km^2. HAND and slope data for non-riparian plots were provided by the authors of previous studies (Costa et al., 2009; Schietti et al., 2014). We used the same methodology to obtain data from riparian plots.

The soil variables used in this study were the proportional sand content (greater range of variation compared to clay content) to represent the soil structure, and the sum of exchangeable bases in soil to represent the chemical aspects of soil-sampling locations. Soil samples were taken at 10 cm depth for riparian plots and at 5 cm depth for non-riparian plots at every 50 m along the plot center line, and the soil samples from each plot were mixed and cleaned of roots, producing a composite sample. Although the depths differed because the data were already collected, both depths can be considered as superficial soil samples (Jobbágy and Jackson, 2001). Soil sand content in riparian plots was obtained through the pipette method (Claessen et al., 1997). For the non-riparian plots, soil samples were air-dried and sieved through a 2 mm mesh sieve. The analysis of soil texture of all plots was carried out in the Thematic Soil and Plants Laboratory (LTSP) at INPA, as well as the chemical analyses to calculate the content of exchangeable soil bases (Ca^{+2}, Mg^{+2}, K^+) of riparian plots that followed standardized methods (for details, see dos Santos et al., 2009). Chemical analyses of the soil of the non-riparian plots were carried out at the EMBRAPA-Manaus Soil Laboratory using the same protocol. The soil data for riparian plots and non-riparian plots were obtained from previous studies (Costa et al., 2005; Jorge et al., 2016).

We used stream discharge (m^3/s) to represent the physical characteristics of streams. Stream discharge is related to the overflow of water from the stream to the banks. Low discharge values mean less overflow (lower water level at the stream banks) and high discharge values mean higher overflow values (higher water level at the stream banks) that result in more severe flooding and, consequently, longer submersion time for riparian vegetation (Junk et al., 2011; Zhu et al., 2021). Stream discharge was estimated only for riparian plots, where the vegetation is very close to the streams. At each of the slope- and soil-collection points, the width, depth and water velocity in the stream were measured. The average of six measurements per plot for each variable was used to

characterize each plot. Stream width was measured from one margin to the other perpendicular to stream direction and depth was measured using a wooden pole along a transect established from one margin to the other, divided every 10 cm. Thus, for each point, we had several depth values that were summarized in a single mean value. Flow speed (m^3/s) was estimated by launching a silicon ball (0.5 g) in the middle of the watercourse and recording the time it took to travel one meter. These measures were used in the formula $Q = A \times V$, where Q = discharge; V = mean flow speed; A = mean width (m) × average depth (m), to estimate the mean stream discharge (m^3/s). These data were available from a previous study (Jorge et al., 2016).

2.5. Data analysis

We investigated whether the abundance of understory palms is related to the abundance of canopy palms (hypothesis 1) with a GLM (Generalized Linear Model, *glm* function of the "MASS" R package) that allowed us to select the most appropriate distribution for our dataset (Venables and Ripley, 2002) according to the Akaike Information Criterion (AIC; Sakamoto et al., 1986). Thus, Model 1 = *Abundance of understory-palm assemblage ~ Abundance of canopy-palm assemblage,* family = Negative binomial.

We investigated whether the topographic and soil variables and their interactions affect variation in composition of understory-palm assemblages across the entire landscape, which includes riparian and non-riparian zones (hypothesis 2) and whether the understory-palm assemblages vary in species composition along streams as a result of variation in abiotic factors and their interactions within the riparian zone (hypothesis 3) using interactive multivariate GLMs. For the interactive multivariate GLMs used to investigate hypotheses 2 and 3, we used the *manyglm* function of the "mvabund" R package (Wang et al., 2021) that uses 'pit-trap' bootstrapping to resample the residuals of the abundance of each species, calculates the probabilities of each species using the Wald test statistic and combines these probabilities into a single probability to represent the effects of the predictor variables on the multivariate species composition (Wang et al., 2012). The *manyglm* function takes into account the mean–variance relationship and consequently does not confound the effects of location and dispersion, as occurs in analyses based on distance, such as NMDS, PCoA and RDA (Warton et al., 2012).

For hypothesis 2, we analyzed in the same model the influence of all combinations of predictors common to the entire landscape dataset (riparian plots and non-riparian plots) on the response variable (Multivariate species composition indicated by a list of species with their respective abundances across the entire landscape dataset) using a negative binomial distribution. Thus, Model 2 = *Multivariate composition of understory-palm assemblage ~ Watershed + HAND + Slope + Sand content + Base content + Watershed * HAND + Watershed * Slope + Watershed * Sand content + Watershed * Base content + HAND * Slope + HAND * Sand content + HAND * Base content + Slope * Sand content + Slope * Base content + Sand content * Base content,* family = Negative binomial.

For hypothesis 3, we analyzed in the same model the influence of all combinations of predictors for riparian plots on the response variable (Multivariate species composition of riparian plots) also using a negative binomial distribution. In riparian plots, we did not use HAND, which is not relevant as we analyzed only plots very close to the stream. Thus, Model 3 = *Multivariate composition of understory-palm assemblage ~ Watershed + Stream discharge + Slope + Sand content + Base content + Watershed * Stream discharge + Watershed * Slope + Watershed * Sand content + Watershed * Base content + Stream discharge * Slope + Stream discharge * Sand content + Stream discharge * Base Content + Slope * Sand content + Slope * Base content + Sand content * Base content,* family = Negative binomial.

It is difficult to illustrate the patterns obtained by the manyglm analysis, since the response variable used in this analysis has multiple

dimensions. Therefore, to illustrate the species composition in a single dimension for the entire landscape dataset (hypothesis 2) and only for riparian plots (hypothesis 3), we used latent-variable coefficients from a model-based Bayesian ordination implemented in the "boral" package (Hui et al., 2015). Latent variables (variables that are not directly observed, but inferred through a mathematical model about other variables that are directly measured) allow inferences about the multiple dimensions of species composition in only one dimension, facilitating visualization of species composition (Hui et al., 2015). However, the latent variables do not represent all the information contained in the multidimensional species composition (Hui et al., 2015). Thus, we use the univariate species composition indicated by the latent variable coefficients only to illustrate the results that were obtained using the multivariate species composition. For an illustration of the results equivalent to the multivariate GLM, we used the univariate species composition as the response variable, and all combinations of predictors, common to the entire landscape data set (same predictor variables as in the multivariate GLM) and only for riparian plots, in univariate GLM. This allowed us to visualize the results through partial graphics of the univariate GLM.

We measured multicollinearity between predictors with the VIF (Variance Inflation Factor) through the *vif* function of the "usdm" package (Naimi et al., 2013). A VIF greater than 10 is a signal that the model has a collinearity problem (Dormann et al., 2012). All predictors used for the entire data set (riparian and non-riparian plots) and considering only riparian plots had VIF < 4, indicating that multicollinearity was unlikely to affect our conclusions. We used the APE package to test spatial autocorrelation (Paradis et al., 2004). There was significant autocorrelation using the entire data set and in the analyses restricted to riparian plots. To remove possible problems caused by spatial autocorrelation (Landeiro and Magnusson, 2011) in the analyses involving the entire data set, we excluded a riparian plot that was in the same stream as another riparian plot and 10 plots from non-riparian plots < 300 m away from riparian plots. Statistical models using the reduced data set did not show significant autocorrelation. Thus, we used 39 riparian plots and 62 non-riparian plots, totaling 101 plots for the entire landscape dataset. Analyses were run in R version 4.0.5 (R Development Core Team, 2021).

3. Results

3.1. Palm assemblages

We found 32 understory-palm species of which four were morpho-species, in a total of 12,486 understory-palm individuals across the entire landscape (Fig. 2). The varieties and subspecies of *Bactris acanthocarpa* Mart., *Geonoma maxima* (Poit.) Kunth, and the two morphological forms of *Bactris hirta* Mart. (bifid or pinnate form) were counted separately and considered as different botanical entities in the analyses. Eighteen species were found in the riparian areas, with a total of 976 individuals. Four species had only one record in riparian areas and were excluded from the analysis considering only riparian areas to reduce the effect of noise generated by the inclusion of rare species (Cao and Larsen, 2001). All 32 understory-palm species were found in the non-riparian areas (11,510 individuals).

We found seven canopy-palm species (*Astrocaryum murumuru* Mart., *Attalea maripa* Mart., *Euterpe precatoria* Mart., *Mauritia flexuosa* L.f., *Oenocarpus bacaba* Mart., *Oenocarpus bataua* Mart. and *Socratea exorrhiza* (Mart.) H.Wendl.) and two morphospecies, in a total of 715 individuals across the entire landscape. Four species were found in the riparian areas, with 512 individuals and all canopy-palm species were found in the non-riparian areas, with 203 individuals. There was strong evidence for a negative relationship between the abundance of understory palms and canopy palms across the entire landscape (Hypothesis 1; z = -7.259, degrees of freedom = 99, p < 0.001; Fig. 3), but the evidence was weak for this relationship within riparian (z = -0.188, p = 0.851) or
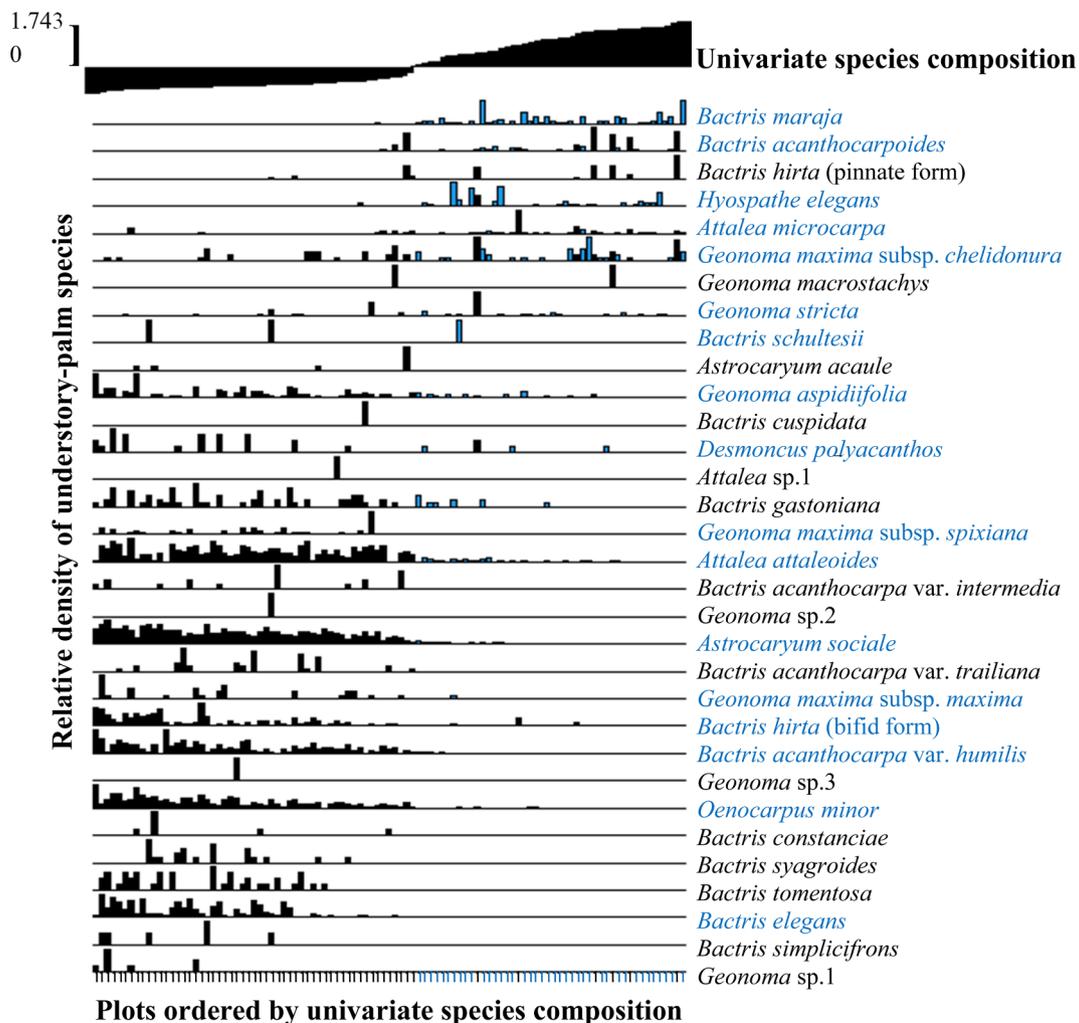
Fig. 2. Distribution of understory-palm species across the entire landscape, which includes riparian (blue bars) and non-riparian zones (black bars) in Reserva Ducke, Manaus, Amazonas, Brazil, in relation to plots ordered by univariate composition of understory-palm assemblages (latent-variable coefficients based on a model-based Bayesian ordination). All species listed were found in non-riparian areas and the subgroup found in riparian areas is in blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

non-riparian areas (z = -0.565, p = 0.572).

3.2. Environmental variables

Topographic and soil variables and their interactions affected variation in composition of understory-palm assemblages across the entire landscape (Hypothesis 2; Table 1; Fig. 4) and the abiotic factors and their interactions affected variation in understory-palm assemblages along streams within the riparian zone (Hypothesis 3; Table 2; Fig. 5). The multivariate species composition revealed patterns similar to those obtained using univariate species composition, with some exceptions (e. g., interaction between watershed and sand content in riparian zone; see supplementary material Table S1 and Table S2). The small number of samples in relation to the number of parameters estimated to test hypothesis 3 (overfitting) did not affect our conclusions as analyses using a reduced number of variables produced similar results (supplementary material Table S3).

Although the watersheds differed in mean slope (6.55° western; 4°eastern) and mean sand content (85% western; 78% eastern), watershed affected understory-palm composition only for comparisons among riparian plots (Table 2).

4. Discussion

Understory and canopy palms are recognized as separate groups by palm specialists, mainly based on characteristics of the support structures (Balslev et al., 2011; Kahn, 1986). We identified several environmental variables that may explain those differences. and potentially provide information for management actions and forest conservation.

4.1. The abundance of understory palms is related to the abundance of canopy palms

The abundances of understory and canopy palms show opposite patterns in riparian and non-riparian areas. Two alternative hypothesis may help to explain those patterns: environmental filtering (Keddy, 1992) or one group could be negatively affecting the other. We believe that the first is more likely. Because if the second were true, we would expect understory and canopy palms to be negatively correlated within riparian and non-riparian areas, and we found no such evidence. Both groups are mainly dispersed by birds, so we think it unlikely that their distributions are limited by seed dispersal.

Morphological characteristics related to individual survival and performance change according to environmental conditions (Violle et al., 2007). Understory and canopy palms differ in relation to their support structures, which result in differences in physical resistance to
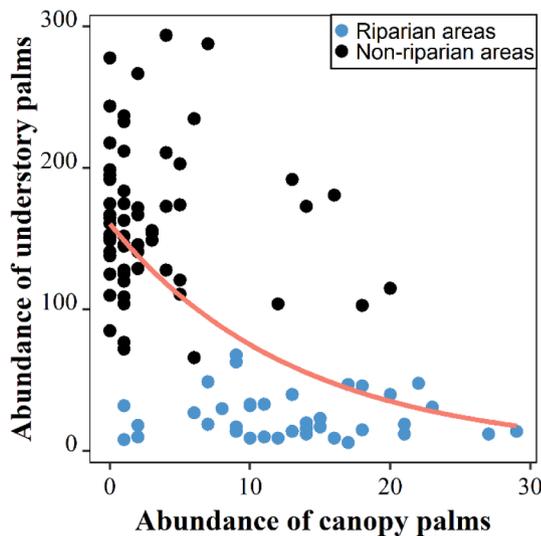
Fig. 3. Relationship between the abundance of understory and canopy palms in riparian (39 blue points) and non-riparian areas (62 black points) in Reserva Ducke, Manaus, Amazonas, Brazil. The salmon-colored line represents the non-linear trend. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Influence of environmental predictors on the multivariate composition of understory-palm assemblages across the entire landscape in Reserva Ducke, Manaus, Amazonas, Brazil. Values in bold indicate evidence of the effect of environmental variables on the composition of understory palms at alpha = 0.05. For full model, Wald = 33.1, p = 0.035. An asterisk (*) indicates interactions among variables.

Environmental variables	Wald	p
Watershed	5.457	0.420
HAND	6.158	0.171
Slope	6.531	0.143
Sand content	8.984	**0.003**
Base content	8.016	**0.001**
Watershed * HAND	5.068	0.610
Watershed * Slope	6.014	0.233
Watershed * Sand content	5.856	0.277
Watershed * Base content	6.083	0.207
HAND * Slope	6.136	0.265
HAND * Sand content	8.958	**0.002**
HAND * Base content	6.847	0.091
Slope * Sand content	7.938	**0.001**
Slope * Base content	7.498	0.057
Sand content * Base content	6.704	0.131

disturbance (Tomlinson and Huggett, 2012). Understory palms have thinner trunks than canopy palms. Balslev et al. (2011) suggested that the ability to remain submerged during floods favors species with large trunks which would lead to a disadvantage for smaller species in American palm communities. Thus, environmental filtering due to flooding is likely to act at different intensities on understory and canopy palms.

Areas close to watercourses are subject to short and unpredictable flood pulses due to local rain events (Junk et al., 2011), resulting in long-term waterlogging of soils, while deep flooding occurs only for short periods. Large palms are more abundant in these areas (Kahn and de Castro, 1985), suggesting that this growth form has an ecological advantage in flooded habitats, possibly due to the more open canopy structure associated with flooding (Svenning, 2000). In contrast, small palms are underrepresented in flooded areas. This pattern suggests that the stressful conditions imposed by floods can negatively affect the occurrence of palm species with less robust support structures, such as

understory species (Kahn and de Castro, 1985). In the present study, one of the most abundant understory-palm species in riparian areas, *Bactris maraja,* has larger and thicker stems than other understory palms. This species is apparently not inhibited by anoxic conditions, and it is frequently found close to streams (Balslev et al., 2011; Ribeiro et al., 1999).

4.2. Topographic and soil variables and their interactions affect variation in composition of understory-palm assemblages across the entire landscape

The effects of distance above the nearest drainage (HAND) and slope on understory-palm composition were more pronounced on sandy soils. Hydromorphic sandy soils in riparian areas have higher levels of flooding and more anoxic conditions (Chauvel et al., 1987) because drainage is limited and water remains in the superficial layers (Damaceno et al., 2020). Sandy soils are also generally poorly structured, making it difficult for roots to support plants (Emilio et al., 2013). Thus, seasonal water-table fluctuations that lead to frequent flooding in valleys can generate turnover in plant species composition in these areas, and this has been related to higher stem mortality and recruitment in forests across the Amazon basin (Phillips et al., 1994).

Our results indicate that interactions among the effects of water-table depth, soils and slope may result in many more distinct habitats than the simple effects of this number of variables would suggest. Distance to the water table (HAND) and slope only had strong effects on species composition of understory palms on soils with high (>75%) sand content. The effect of topographic and soil conditions in determining species distributions has been reported in studies at both local (Pansini et al., 2016; Pearson and Dawson, 2013; Svenning, 1999), and wide scales (Eiserhardt et al., 2011; Muscarella et al., 2020). The distributions of twenty-five species of palms from tropical forests were related to environmental factors associated with water (Blach-Overgaard et al., 2010) and many palm species appear to be intolerant of flooding (Eiserhardt et al., 2011; Losos, 1995; Pacheco, 2001). Palms of Central Amazonia are generally associated with poorly drained soils with high sand content in areas close to streams (Kahn, 1987). Plants that occur in seasonally flooded areas have been shown to have a number of highly specialized adaptations to this habitat (Parolin, 2009) and Normand et al. (2006) demonstrated that forests on paleo-riparian terraces and forests located on unflooded terraces and in geographically close floodplains in the Peruvian Amazon have clear differences in palm-species composition. However, areas close to streams with greater slope are less subject to waterlogging, which may allow some non-riparian species to occur near streams (Drucker et al., 2008; Gregory et al., 1991). Thus, interactions among environmental predictors may provide far more potential niches for palm species than simple additive conceptual (Wright, 2002) or statistical models (Eiserhardt et al., 2011) might suggest.

Although we found that the composition of understory palms is influenced by soil fertility (base content), as did Costa et al. (2009), the range of variation we found was small (0.04 – 0.58 cmol.kg^{-1}) in relation to studies that found exchangeable base content to be a significant predictor of plant composition at wider scales (e.g. Jones et al., 2006; Vormisto et al., 2004), which reported ranges values at least 3 times greater than ours. The small variation could prevent major changes in species composition along this gradient (MacArthur, 1958). There was also weak evidence that the influence of exchangeable soil bases on the composition of understory palms depends on slope. The variation of the exchangeable-bases content of the soil was smaller in less inclined places (0.141 – 0.517 cmol kg^{-1}) and greater in more inclined places (0.041 – 0.576 cmol kg^{-1}). Thus, different portions of the slope gradient could provide qualitatively different conditions for palm species.
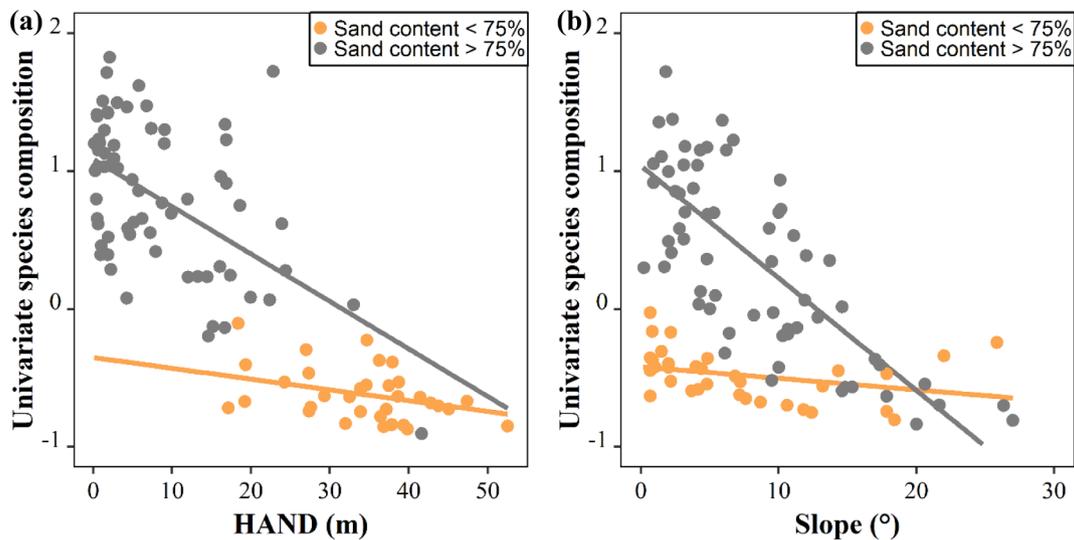
Fig. 4. Partial plots of the effects of the interaction of HAND and soil sand content (a) and slope and soil sand content (b) on the univariate composition of understory palms. Data was collected in riparian and non-riparian zones at Reserva Duke, Manaus, Brazil. We categorized the sand content as being above or below the median to visualize the interaction.

Table 2

Influence of environmental predictors on the multivariate composition of understory-palm assemblages in riparian areas of Reserva Ducke, Manaus, Amazonas, Brazil. Values in bold indicate evidence of the effect of environmental variables on the composition of understory palms at alpha = 0.05. For full model, Wald = 17.77, p = 0.581. An asterisk (*) indicates interactions among variables.

Environmental variables	Wald	p
Watershed	6.045	**0.018**
Stream discharge	7.259	**0.007**
Slope	5.845	0.069
Sand content	5.182	0.162
Base content	5.164	0.179
Watershed * Stream discharge	4.305	0.250
Watershed * Slope	6.177	**0.013**
Watershed * Sand content	6.731	**0.004**
Watershed * Base content	4.757	0.230
Stream discharge * Slope	4.800	0.307
Stream discharge * Sand content	7.052	**0.001**
Stream discharge * Base content	3.962	0.515
Slope * Sand content	5.449	0.116
Slope * Base content	2.669	0.949
Sand content * Base content	5.376	0.187

4.3. Understory-palm assemblages vary in species composition along streams as a result of variation in abiotic factors and their interactions within the riparian zone

Differences between watersheds were found only for comparisons among riparian areas. This may be related to the proximity of the riparian plots to the watercourse, where they are more subject to the effects caused by the characteristics of the basins ("V" or "U" shaped valleys). In contrast, evidence of fertility effects (base content) was found only across the entire landscape. This is likely because the variation in base content within the riparian zone was small in relation to that found across the landscape and for non-riparian areas of Reserva Ducke (Costa et al. 2009), and in other studies carried out on broader scales (e.g. Jones et al., 2006; Vormisto et al., 2004).

Other interactions among variables found to have strong effects across the landscape (sand content, slope and HAND) probably reflect similar processes occurring along streams within the riparian zone. HAND reflects distance to the nearest drainage, and being close to a drainage (riparian zone) indicates that the plot could be affected by

discharge from the stream, whereas non-riparian plots, by definition, have discharge = zero. Within the riparian zone, increased discharge implies more intense flooding and the need for stronger support structures.

The influence of stream discharge on the composition of understory palms depended on the soil sand content. Sandy/poorly structured soils can enhance the effects of flooding on the banks of streams, generating higher water levels and greater mechanical instability for plant rooting (Emilio et al., 2013). When there are changes in flow, total annual discharge and depth to groundwater, communities may shift in predictable ways according to traits associated with water acquisition, such as root morphology (Merritt et al., 2010). During periods of low discharge in most streams, the exposed active channel is colonized by herbs, and shrub and tree seedlings. Frequent flooding in this area discourages the establishment of terrestrial vegetation, both through surface erosion and the physiological effects of periodic flooding (Gregory et al., 1991). Merritt et al. (2010) demonstrated that the flow regime exerts selective pressures on riparian vegetation and that widespread modification of flow regimes by humans resulted in extensive alteration of riparian-vegetation communities. In the present study, most understory-palm species only or mainly occur away from streams, and those that occur in the riparian zone tend to occur in areas with lower stream discharge and less sandy soils. This may be because the impact of flooding on palm distributions is mainly related to inhibition of seed germination and seedling survival (Braz et al., 2015; Losos, 1995; Pacheco, 2001; Svenning, 2001). Thus, the differentiation of the palm-assemblage composition along subtle variations of interacting environmental gradients indicates strong niche partitioning among species (Emilio et al., 2013).

There was a strong effect of watershed on understory-palm composition in the riparian zone, and the effect of slope on the composition of riparian understory-palm species differed between watersheds. Some species were dominant in or restricted to one of the watersheds. Watershed is a descriptive geographic category rather than an ecological variable, so other factors, such as historical or mass effects (Shmida and Wilson, 1985), may be involved. Therefore, management plans should not assume homogeneity in the distribution of understory palms in Reserva Ducke, especially in riparian zones.

Brazilian environmental legislation gives special protection to riparian areas (Brasil, 1998), but few understory-palm species are restricted to, or even more abundant in, riparian areas. The conservation of most species requires maintenance of extensive areas of upland
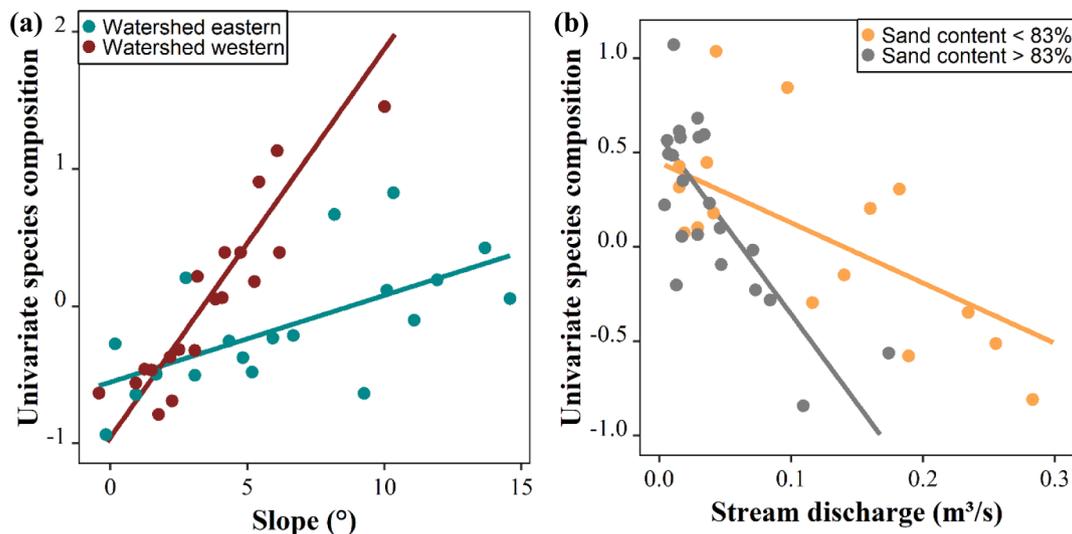
Fig. 5. Partial plots of the effects of the interaction of slope and watershed (a) and stream discharge and soil sand content (b) on the univariate composition of understory palms. Data was collected in riparian zones at Reserva Duke, Manaus, Brazil. We categorized the sand content as above or below the median to visualize the interaction.

forests. Where this is not possible, a broad range of soil, slope and stream-discharge conditions will have to be included to maximize the number of species to be protected.

5. Conclusions

Our study demonstrates that conclusions based on studies of canopy palms, such as that they occur more frequently on poorly structured soils in areas with a superficial water table, do not apply to understory palms. Although our results are specific to the Reserva Ducke, this is likely to be the situation in other Amazonian regions, especially when there are differences (e.g., soil conditions) related to the abundance of understory and canopy individuals at local scale. In our study site, understory palms are more abundant in areas with well-structured soil (low sand content, mean = 50%) and deep-water table (high HAND, mean = 22 m). In addition, interactions among environmental factors at the mesoscale (entire landscape), and at the local scale (riparian zone), generate compositional turnover among sites. This suggests that these interactions can generate niches for species and that modeling species/ environment relationships through simple additive relationships may not reveal the ecological complexity of these interactions. Stream discharge and soil structure are among the first variables to be affected by human occupation of riparian zones, which indicates that a better understanding of interactions between environmental predictors and a landscape approach will be necessary to conserve Amazonian understory palms, especially if they are limited to permanent-protection areas around streams. Management and conservation actions must consider those differences in order to be effective, otherwise we risk losing important components of natural ecosystems.

CRediT authorship contribution statement

Mariane Guedes: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration. **Lourdes Falen:** Investigation, Project administration, Writing – review & editing. **Ocirio S. Pereira:** Investigation, Writing – review & editing. **Albertina P. Lima:** Investigation, Writing – review & editing. **Carolina V. de Castilho:** Investigation, Writing – review & editing. **Rafael F. Jorge:** Investigation, Writing – review & editing. **William E. Magnusson:** Conceptualization, Methodology, Formal analysis, Resources, Writing – original draft, Writing – review & editing, Supervision, Funding acquisition. **Juliana Hipólito:** Conceptualization, Writing – review & editing, Supervision.

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.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi. org/10.1016/j.foreco.2022.120054.

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