

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA - INPA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

**PALMEIRAS DE SUB-BOSQUE NÃO SÃO PALMEIRAS DE DOSSEL ESCRITAS
EM PEQUENAS: FATORES QUE AFETAM AS PALMEIRAS DO SUB-BOSQUE
AMAZÔNICO DENTRO DAS ZONAS RIPÁRIAS E EM TODA A PAISAGEM**

MARIANE RODRIGUES GUEDES

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Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do título de mestre em Biologia (Ecologia).

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ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 30 dias do mês de Agosto do ano de 2021, às 09h00min, por videoconferência. Reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: a Dra. **Thaise Emilio Lopes de Sousa**, da Universidade Estadual de Campinas - UNICAMP, a Dra. **Cíntia Gomes de Freitas**, da Universidade Federal do Paraná - UFPR e a Dra. **Flávia Delgado Santana**, do Instituto Nacional de Pesquisas da Amazônia - INPA, tendo como suplentes o Dr. Fabricio Beggiano Baccaro, do Instituto Nacional de Pesquisas da Amazônia - INPA, e o Dr. Jefferson da Cruz, da Universidade Federal do Amazonas - UFAM, sob a presidência da orientadora, a fim de proceder à arguição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** da **MARIANE RODRIGUES GUEDES**, intitulado: “**COMPLEXAS INTERAÇÕES ABIÓTICAS ESTRUTURAM ASSEMBLEIAS DE PALMEIRAS DE SUB- BOSQUE EM ZONAS RIPÁRIAS DE UMA FLORESTA DE TERRA FIRME DA AMAZÔNIA CENTRAL**”, orientada pela Dra. Juliana Hipólito de Sousa, do Instituto Nacional de Pesquisas da Amazônia – INPA e co-orientada pelo Dr. William Ernest Magnusson, do Instituto Nacional de Pesquisas da Amazônia - INPA.

Após a exposição, o(a) discente foi arguido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

APROVADO (A) REPROVADO (A)
 POR UNANIMIDADE POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

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Sinopse:

Estudamos a relação entre a abundância de palmeiras de sub-bosque e palmeiras de dossel; e o efeito de gradientes ambientais e suas interações sobre a composição de palmeiras de sub-bosque ao longo de toda a paisagem da Reserva Ducke que inclui áreas ripárias e não ripárias e somente em áreas ripárias.

Palavras-chave: Ecologia de comunidade; Gradiente ambiental; Interações abióticas; Formas de vida; Matas ciliares; Floresta tropical

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Resumo

As palmeiras de sub-bosque estão sujeitas a pressões ecológicas diferentes daquelas experimentadas pelas palmeiras de dossel, mas a maioria dos estudos não distingue entre as palmeiras de sub-bosque e as palmeiras de dossel, ou inclui apenas as palmeiras de dossel. Grande parte da variação na composição taxonômica das palmeiras de sub-bosque na Amazônia concentra-se nas zonas ripárias. No entanto, as características abióticas da zona ripária que influenciam esta variação são pouco exploradas ou foram modeladas apenas por meio de relações aditivas. Nossos objetivos foram determinar (1) se a abundância de palmeiras de sub-bosque está relacionada à abundância de palmeiras de dossel, (2) como as variáveis topográficas e de solo, e suas interações, afetam a variação na composição das assembleias de palmeiras de sub-bosque em toda a paisagem, que inclui zonas ripárias e não ripárias e (3) como as assembleias de palmeiras de sub-bosque variam na composição de espécies ao longo dos riachos como resultado da variação nos fatores abióticos e suas interações dentro da zona ripária. Nós amostramos 40 áreas ripárias e analisamos os dados em combinação com dados existentes de 72 parcelas não ripárias. Parcelas (250 m × 4 m) foram distribuídas em 64 km² de uma floresta de terra-firme (Reserva Ducke) cobrindo duas grandes bacias de drenagem que diferem na topografia e nas características do solo. A abundância de palmeiras de sub-bosque e palmeiras de dossel têm relações opostas com as mesmas variáveis ambientais e, portanto, não devem ser tratadas como um único grupo. Além disso, as interações entre os fatores ambientais na mesoescala (paisagem inteira) e na escala local (zona ripária), geram *turnover* composicional mesmo entre locais com apenas diferenças ambientais sutis. A vazão dos riachos e a estrutura do solo estão entre as primeiras variáveis a serem afetadas pela ocupação humana das zonas ripárias, o que indica que um melhor entendimento das interações entre os preditores ambientais e uma abordagem da paisagem serão necessários para conservar as palmeiras do sub-bosque amazônico.

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 km² 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.

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Introdução

Palmeiras (Arecaceae) desempenham um papel importante na estrutura e dinâmica da floresta amazônica devido à sua alta abundância e interação com vertebrados e invertebrados (Henderson et al., 1995; Kahn e de Castro, 1985; Küchmeister et al., 1998). Além disso, as palmeiras são mais abundantes nos Neotrópicos do que em outras florestas tropicais (Muscarella et al., 2020). Algumas espécies também são amplamente utilizadas por humanos para alimentação e construção e, portanto, têm valor econômico (Shepard et al., 2020; Kahn, 1991). Estudos sobre a distribuição de palmeiras e composição da assembleia em uma variedade de escalas espaciais na Amazônia encontraram relações com o solo e características topográficas relacionadas à drenagem, disponibilidade de água e nutrientes do solo (Costa et al., 2015; Eiserhardt et al., 2011; Svenning, 1999). No entanto, embora seja necessário considerar todos os estratos florestais para entender os padrões da composição de espécies na Amazônia (Draper et al., 2021), muitos estudos trataram as palmeiras como um grupo homogêneo (ex, Rodrigues et al., 2014; Schietti et al., 2014).

Com base em seu tamanho, as palmeiras da floresta amazônica podem ser divididas em dois grupos principais: dossel e sub-bosque (Kahn, 1986). Foi relatado que as palmeiras na Amazônia ocorrem em densidades mais altas em solos mal estruturados associados a lençóis freáticos rasos, como em zonas ripárias (Castilho et al., 2006; Peres, 1994). No entanto, essas conclusões não distinguem entre palmeiras de dossel e sub-bosque, ou se baseiam apenas nas palmeiras de dossel. Assim, não está claro se essas generalizações também se aplicam a palmeiras de sub-bosque, que estão sujeitas a pressões ecológicas diferentes daquelas experimentadas por palmeiras de dossel devido à menor profundidade de enraizamento e reduzida disponibilidade de luz no sub-bosque (Kahn e de Castro, 1985). Por exemplo, Ma et al. (2015) descobriram que palmeiras que ocorrem em estratos inferiores de florestas tropicais têm maior eficiência de ganho de carbono devido a uma estratégia evolutiva que permite a adaptação a ambientes sombreados, mas não distinguem entre palmeiras de dossel e sub-bosque.

As inundações podem ser mais pronunciadas em áreas com drenagem restrita e solos hidromórficos (Kahn, 1987), mas diferentes combinações de fatores topográficos e edáficos podem afetar a disponibilidade de água para as plantas. Portanto, é improvável que os efeitos dos componentes topográficos e do solo nas respostas das plantas sejam combinações aditivas simples (Emilio et al., 2013; Hladik e Alber, 2014; Munson et al., 2016). As interações entre os fatores ambientais são fortemente dependentes da escala (Balslev et al., 2011), e isso pode gerar

diferentes compartimentos de nicho (Wright, 2002) e influenciar a composição da assembleia de palmeiras.

Interações entre bacias hidrográficas, topografia e características do solo (Costa et al., 2005), distância dos cursos d'água e disponibilidade de luz (Paixão, 2012), afetam a composição das plantas do sub-bosque. A distância dos cursos d'água está associada a grande variação na composição florística em áreas próximas aos riachos (Costa et al., 2009; Schiatti et al., 2014), indicando que fatores desconhecidos ou interações entre fatores não estudados afetam a composição florística.

Estudos de ecologia de comunidades na Amazônia geralmente incluem poucas zonas ripárias (por exemplo, Drucker et al., 2008; Fraga et al., 2013; Normand et al., 2006). Organismos de zonas ripárias podem responder a mudanças sutis nos gradientes locais, como retenção de água no solo e regime de inundação (Drucker et al., 2008; Pazin et al., 2006). Um dos poucos estudos sobre os efeitos das variáveis ambientais nas assembleias de palmeiras de sub-bosque na Amazônia encontrou um grande efeito da proximidade de cursos d'água na composição florística (Costa et al., 2009). No entanto, a distribuição de algumas espécies de plantas terrestres também é regulada por fatores que variam ao longo dos riachos, porque riachos maiores geralmente estão associados a inundações mais longas e a condições anóxicas em suas matas ciliares associadas (Riis et al., 2001). Além disso, as plotagens utilizadas no estudo de Costa et al. (2009) seguiram os contornos altitudinais, então parcelas individuais poderiam incluir áreas próximas e distantes de riachos, o que reduz as chances de registro de muitas espécies das zonas ripárias. A inclusão de zonas ripárias aumenta a amplitude dos gradientes geralmente estudados e é necessária para identificar fatores que afetam a composição da assembleia de palmeiras de sub-bosque que têm pouco efeito em áreas distantes de riachos.

Na Reserva Ducke, localizada nos arredores de Manaus, Amazônia Central, as zonas ripárias estão distribuídas em duas grandes bacias hidrográficas que possuem diferentes perfis topográficos (vales em forma de “V” ou “U”) e são separadas por um platô central, que pode limitar a dispersão de espécies mesmo sem grandes variações nas características do solo (Costa et al., 2005). Assim, é provável que os efeitos das variáveis associadas à zona ripária na composição florística difiram entre as bacias hidrográficas.

Hipóteses

Com base em estudos anteriores de palmeiras do dossel e outros táxons de plantas, a zona ripária provavelmente representa um habitat discreto para palmeiras de sub-bosque, mas a falta de estudos que se concentraram nas zonas ripárias limita nossa capacidade de determinar a magnitude ou mesmo a direção de tais efeitos. Portanto, investigamos as seguintes hipóteses: (1) A abundância de palmeiras de sub-bosque está relacionada com a abundância de palmeiras de dossel, (2) as variáveis topográficas e de solo e suas interações afetam positivamente a variação na composição das assembleias de sub-bosque-palmeiras em toda a paisagem, que inclui zonas ripárias e não ripárias, e (3) as assembleias palmeiras de sub-bosque variam na composição de espécies ao longo dos riachos como resultado da variação nos fatores abióticos e suas interações dentro da zona ripária.

Capítulo 1

Guedes, M. Falen, L. Pereira, O. S. Lima, A. P. de Castilho, C.V. Jorge, R. F. Magnusson W. E. Hipólito, J. Understory palms are not canopy palms writ small: factors affecting Amazonian understory palms within riparian zones and across the landscape. Submetido e em revisão na revista Forest Ecology and Management.

1 **1. Introduction**

2 Palms (Arecaceae) play an important role in the structure and dynamics of the Amazon
3 rainforest due to their high abundance and interaction with vertebrates and invertebrates
4 (Henderson et al., 1995; Kahn and de Castro, 1985; K uchmeister et al., 1998), and palms are
5 more abundant in the Neotropics than in other tropical forests (Muscarella et al., 2020). Some
6 species are also widely used by humans for food and construction, and thus have economic
7 value (Shepard et al., 2020; Kahn, 1991). Studies on palm distribution and assemblage
8 composition at a variety of spatial scales in the Amazon have found relationships with soil and
9 topographic characteristics related to drainage, water availability and soil nutrients (Costa et
10 al., 2015; Eiserhardt et al., 2011; Svenning, 1999). However, although it is necessary to consider
11 all forest strata to understand composition patterns in the Amazon (Draper et al., 2021), many
12 studies have treated palms as a homogeneous group (e.g., Rodrigues et al., 2014; Schietti et al.,
13 2014).

14 Based on their size, Amazonian forest palms can be divided into two major groups:
15 canopy and understory (Kahn, 1986). Palms in the Amazon have been reported to occur at
16 higher densities on poorly structured soils associated with shallow water tables, such as in
17 riparian zones (Castilho et al., 2006; Peres, 1994). However, these conclusions do not
18 distinguish between canopy and understory palms, or are based only on canopy palms. Thus, it
19 is unclear whether these generalizations also apply to understory palms, which are subject to
20 different ecological pressures than those experienced by canopy palms due to lesser rooting
21 depths and reduced light availability in the understory (Kahn and de Castro, 1985). For
22 example, Ma et al. (2015) found that palms occurring in lower strata of tropical forests have
23 higher carbon gain efficiency due an evolutionary strategy enabling the adaptation to shady
24 environments, but they did not distinguish between canopy and understory palms.

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

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

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

50 studied and is necessary to identify factors affecting understory-palm assemblage composition
51 that have little effect in areas far from streams.

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

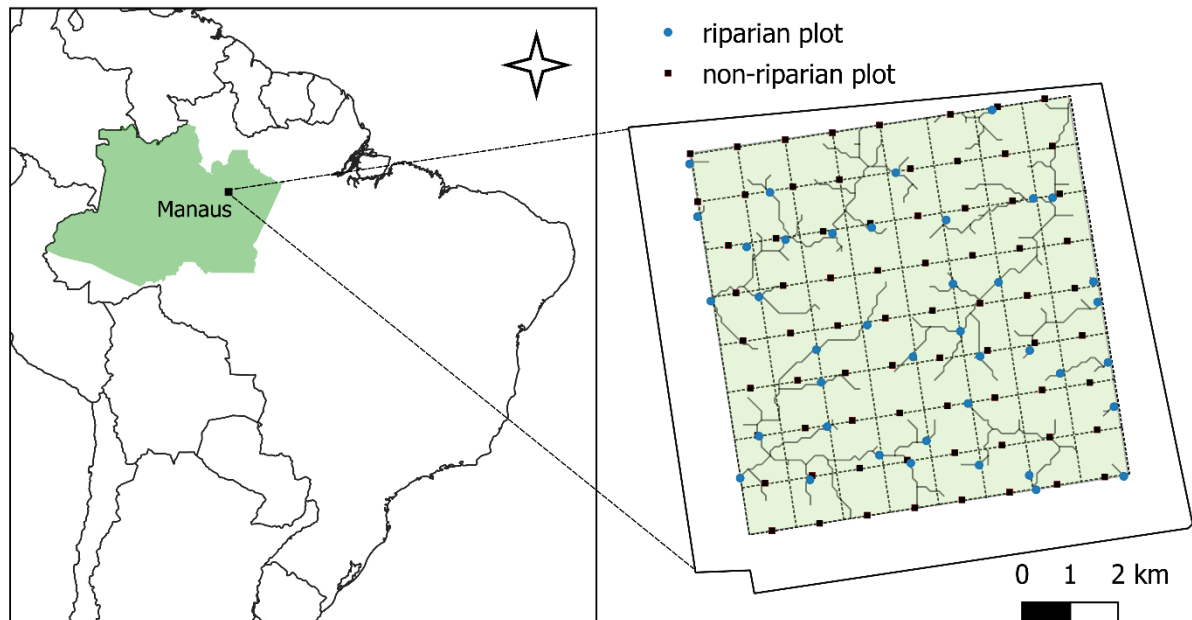
58 Based on previous studies of canopy palms and other plant taxa, the riparian zone is
59 likely to represent a discrete habitat for understory palms, but the lack of studies that have
60 focused on riparian zones limits our ability to determine the magnitude or even direction of
61 such effects. Therefore, we investigated the following hypotheses: (1) The abundance of
62 understory palms is related to the abundance of canopy palms, (2) topographic and soil variables
63 and their interactions positively affect variation in composition of understory-palm assemblages
64 across the entire landscape, which includes riparian and non-riparian zones, and (3) understory-
65 palm assemblages vary in species composition along streams as a result of variation in abiotic
66 factors and their interactions within the riparian zone.

67 **2. Materials and Methods**

68 *2.1. Study site*

69 We conducted the study over a 64-km² trail system within Reserva Ducke (2°55'
70 47.80'' S; 59°58' 30.34'' W). The reserve covers a 100 km² forest remnant on the outskirts of
71 Manaus, Amazonas State, Brazil (Fig. 1). Although Manaus has reached the southern and
72 western limits of the reserve, Reserva Ducke is still connected to continuous forest on the
73 eastern side. The reserve is covered by evergreen *terra-firme* tropical rain forest with a closed

74 canopy that reaches 30–37 m high. The understory is characterized by an abundance of
 75 acaulescent palms (Ribeiro et al., 1999). The mean annual temperature from 1966 to 2016 was
 76 around 26 °C and mean annual rainfall was around 2,572 mm (Esteban et al., 2021).



77

78 Fig.1. Map showing the study area located in Amazonas State in central Brazilian Amazonia
 79 and the grid system in Reserva Florestal Adolpho Ducke, Manaus, Amazonas, Brazil, with 40
 80 riparian plots (blue circles) and 72 non-riparian plots (black squares); black lines represent
 81 streams.

82 Soils in Reserva Ducke are derived from tertiary fluvio-lacustrine deposits from the
 83 Alter do Chão formation (Sombroek, 2000). They are mostly clayey oxisols on the ridges;
 84 podzols on the valley slopes; and spodosols when close to small streams. Soils near streams are
 85 almost permanently waterlogged during the rainy season between November and June (Bravard
 86 and Righi, 1989; Chauvel et al., 1987). In general, Reserva Ducke soils are acidic and poor in
 87 nutrients, such as phosphorus, calcium and potassium (Chauvel et al., 1987). The topography
 88 of Reserva Ducke is undulating/hilly, with altitude ranging from 40 to 140 m (Ribeiro et al.,
 89 1999). The reserve has a dense drainage network with two main watersheds separated by a

90 central ridge; the streams from the eastern watershed flow to tributaries of the Amazon River
91 and those in the western watershed flow to the Negro River (Mendonça et al., 2005).

92 2.2. *Sampling design*

93 2.2.1 *Riparian plots*

94 The data for understory-palm assemblages in riparian plots were collected between
95 October 2019 and December 2020 in 40 plots distributed over the 64 km² grid following the
96 RAPELD method (Magnusson et al., 2005, 2013). These 250 m × 4 m (1,000 m²) plots were at
97 least 300 m apart and included streams of first, second, and third order in the two watersheds
98 (Rodrigues, 2006). We established the plots to comprehensively cover the two watersheds
99 where streams crossed the trail system. Most plots were located along narrow first- and second-
100 order streams (n = 29), but eleven plots were beside third-order streams. Riparian RAPELD
101 plots have a 250 m long center line that follows the stream bank (in the direction mouth to
102 source) divided in 10 m linear segments and a minimum distance between the stream margin
103 and the nearest point on the center line of each 10-m segment of 1.5 m; therefore, they are close
104 to the stream along their entire lengths. Data on canopy-palm abundance in the riparian plots
105 were collected in the same way as for understory palms. Because they follow the stream margin,
106 RAPELD plots of the same length have slight differences in area. The area of each plot was
107 calculated using the R codes available in the PPBio website
108 (<https://ppbio.inpa.gov.br/analises/area>) and the average size difference among riparian plots
109 was 1% (~10 m²).

110 2.2.2 *Non-riparian plots*

111 The data for understory-palm assemblages of the non-riparian plots were provided by
112 authors of the study by (Costa et al., 2009). These data were collected in January and February
113 2003, 16 years before the riparian plots. This temporal difference between non-riparian and

114 riparian plots can generate changes in vegetation. However, well-conserved forests (e.g.
115 Reserva Ducke) are less susceptible to changes in productivity. Olivares et al. (2016), for
116 example, demonstrated that the structure and composition of a palm community in a protected
117 western Amazon Forest remained stable for over 17 years.

118 We used 72 non-riparian plots uniformly distributed over the 64 km² grid following the
119 RAPELD method (Magnusson et al., 2005, 2013). These 250-m × 4-m plots were at least 1 km
120 apart, and established following the altitudinal contours. As soil properties are closely related
121 to altitude in Reserva Ducke (Chauvel et al., 1987), this reduces within-plot variation in soil
122 characteristics and hence vegetation (Costa et al., 2009). The data for canopy-palm abundance
123 in the non-riparian plots were collected in the same way as for understory palms from a previous
124 study (Castilho et al., 2006). Because they follow the altitudinal contours, RAPELD plots of
125 the same length have slight differences in area. The average size difference among non-riparian
126 plots was 3% (~73 m²) and between riparian and non-riparian plots was 2% (~24 m²).

127 2.3. *Palm assemblages*

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

138 2.4. Environmental variables

139 The topographic variables used in this study were the terrain slope measured in degrees
140 and the height above the nearest drainage in meters (HAND). The slope of riparian and non-
141 riparian plots was measured with a clinometer perpendicular to the main axis of the plot at every
142 50 m, and summarized as averages of the six measurements per plot. Height above nearest
143 drainage is estimated from digital elevation models that give the altitude of the plot and the
144 nearest drainage channel. HAND is directly correlated with the gravitational potential of soil
145 water. The gravitational potential of water is a component of the soil's water potential, which
146 reflects the difficulty of plants in extracting water from the soil or avoiding excess water. High
147 HAND values mean high gravitational potential (high vertical drainage potential) and low
148 HAND values mean low gravitational potential (low vertical drainage potential) and proximity
149 to the water table (Nobre et al., 2011). HAND measurements for riparian and non-riparian plots
150 were obtained using the HAND algorithm (Rennó et al., 2008) in a Digital Elevation Model
151 (DEM, 90 m grain) with a minimum contribution area of 0.41 km². HAND and slope data for
152 non-riparian plots were provided by the authors of previous studies (Costa et al., 2009; Schietti
153 et al., 2014). Thus, we used the same methodology to obtain data from riparian plots.

154 The soil variables used in this study were the proportional sand content (greater range
155 of variation compared to clay content) to represent the soil structure, and the sum of
156 exchangeable bases in soil to represent the chemical aspects of soil-sampling locations. Soil
157 samples were taken at 10 cm depth for riparian plots and at 5 cm depth for non-riparian plots at
158 every 50 m along the plot center line, and the soil samples from each plot were mixed and
159 cleaned of roots, producing a composite sample. Although the depths differed because the data
160 were already collected, both depths can be considered as superficial soil samples (Jobbágy and
161 Jackson, 2001). Soil sand content in riparian plots was obtained through the pipette method
162 (Claessen et al., 1997). For the non-riparian plots, soil samples were air-dried and sieved

163 through a 2 mm mesh sieve. The analysis of soil texture of all plots was carried out in the
164 Thematic Soil and Plants Laboratory (LTSP) at INPA, as well as the chemical analyses to
165 calculate the content of exchangeable soil bases (including Ca^{+2} , Mg^{+2} , K^{+}) of riparian plots that
166 followed standardized methods (for details, see dos Santos et al., 2009). Chemical analyses of
167 the soil of the non-riparian plots were carried out at the EMBRAPA-Manaus Soil Laboratory
168 using the same protocol. The soil data for riparian plots and non-riparian plots were obtained
169 from previous studies (Costa et al., 2005; Jorge et al., 2016).

170 We used stream discharge (m^3/s) to represent the physical characteristics of streams.
171 Stream discharge is related to the overflow of water from the stream to the banks. Low discharge
172 values mean less overflow (lower water level at the stream banks) and high discharge values
173 mean higher overflow values (higher water level at the stream banks) that result in more severe
174 flooding and, consequently, longer submersion time for riparian vegetation (Junk et al., 2011;
175 Zhu et al., 2021). Stream discharge was estimated only for riparian plots, where the vegetation
176 is very close to the streams. At each of the slope- and soil-collection points, the width, depth
177 and water velocity in the stream were measured. The average of six measurements per plot for
178 each variable was used to characterize each plot. Stream width was measured from one margin
179 to the other perpendicular to stream direction and depth was measured using a wood pole along
180 a transect established from one margin to the other, divided every 10 cm. Thus, for each point,
181 we had several depth values that were summarized in a single average value. Flow speed (m^3/s)
182 was estimated by launching a silicon ball (0.5 g) in the middle of the watercourse and recording
183 the time it took to travel one meter. These measures were used in the formula $Q = A \times V$, where
184 Q = discharge; V = average flow speed; A = average width (m) x average depth (m), to estimate
185 the average stream discharge (m^3/s). These data were available from a previous study (Jorge et
186 al., 2016).

187 2.5. Data analysis

188 We investigated whether the abundance of understory palms is related to the abundance
 189 of canopy palms (hypothesis 1) with a GLM (Generalized Linear Model, *glm* function of the
 190 “MASS” R package) that allowed us to use the most appropriate distribution for our dataset
 191 (Venables and Ripley, 2002). Thus, Model 1 = *Abundance of understory-palm assemblage* ~
 192 *Abundance of canopy-palm assemblage*, family = Binomial negative.

193 We investigated whether the topographic and soil variables and their interactions
 194 positively affect variation in composition of understory-palm assemblages across the entire
 195 landscape, which includes riparian and non-riparian zones (hypothesis 2) and whether the
 196 understory-palm assemblages vary in species composition along streams as a result of variation
 197 in abiotic factors and their interactions within the riparian zone (hypothesis 3) using interactive
 198 multivariate GLMs for both hypothesis. For hypothesis 2, we analyzed in the same model the
 199 influence of all combinations of predictors common to the entire landscape dataset (riparian
 200 plots and non-riparian plots) on the response variable (Multivariate species composition of the
 201 entire landscape dataset) using a negative binomial distribution. Thus, Model 2 = *Composition*
 202 *of understory-palm assemblage* ~ *Watershed* + *HAND* + *Slope* + *Sand content* + *Base content*
 203 + *Watershed * HAND* + *Watershed * Slope* + *Watershed * Sand content* + *Watershed * Base*
 204 *content* + *HAND * Slope* + *HAND * Sand content* + *HAND * Base content* + *Slope * Sand*
 205 *content* + *Slope * Base content* + *Sand content * Base content*, family= "Negative binomial".

206 For hypothesis 3, we analyzed in the same model the influence of all combinations of
 207 predictors for riparian plots on the response variable (Multivariate species composition of
 208 riparian plots) also using a negative binomial distribution. In riparian plots, we did not use
 209 HAND, which is not relevant as we analyzed only plots very close to the stream. Thus, Model
 210 3 = *Composition of understory-palm assemblage* ~ *Watershed* + *Stream discharge* + *Slope* +
 211 *Sand content* + *Base content* + *Watershed * Stream discharge* + *Watershed * Slope* + *Watershed*

212 * *Sand content* + *Watershed* * *Base content* + *Stream discharge* * *Slope* + *Stream discharge* *
213 *Sand content* + *Stream discharge* * *Base Content* + *Slope* * *Sand content* + *Slope* * *Base content*
214 + *Sand content* * *Base content*, family= "Negative binomial". For the interactive multivariate
215 GLMs used to investigate hypothesis 2 and 3, we used the *manyglm* function of the “mvabund”
216 R package (Wang et al., 2021) that uses 'pit-trap' bootstrapping to resample the residuals of the
217 abundance of each species, calculates the probabilities of each species using the Wald test
218 statistic and combines these probabilities into a single probability to represent the community
219 (Wang et al., 2012). The *manyglm* function takes into account the mean-variance relationship
220 and consequently does not confound the effects of location and dispersion, as occurs in analyses
221 based on distance, such as NMDS, PCoA and RDA (Warton et al., 2012).

222 It is difficult to illustrate the patterns obtained by the *manyglm* analysis, since the
223 response variable used in this analysis has multiple dimensions. Therefore, to illustrate the
224 species composition in a single dimension for the entire landscape dataset (hypothesis 2) and
225 only for riparian plots (hypothesis 3), we used latent-variable coefficients from a model-based
226 Bayesian ordination implemented in the “boral” package. Latent variables (variables that are
227 not directly observed, but inferred through a mathematical model about other variables that are
228 directly measured) allow inferences about the multiple dimensions of species composition in
229 only one dimension, facilitating visualization of species composition. However, the latent
230 variables do not present all the information contained in the multidimensional species
231 composition (Hui et al., 2015). Thus, we use the univariate species composition indicated by
232 the latent variable coefficients only to illustrate the results that were obtained using the
233 multivariate species composition. For an illustration of the results equivalent to the multivariate
234 GLM, we used the univariate species composition as the response variable, and all
235 combinations of predictors, common to the entire landscape data set (same predictor variables

236 as in the multivariate GLM) and only for riparian plots, in a univariate GLM. This allowed us
237 to visualize the results through partial graphics of the univariate GLM.

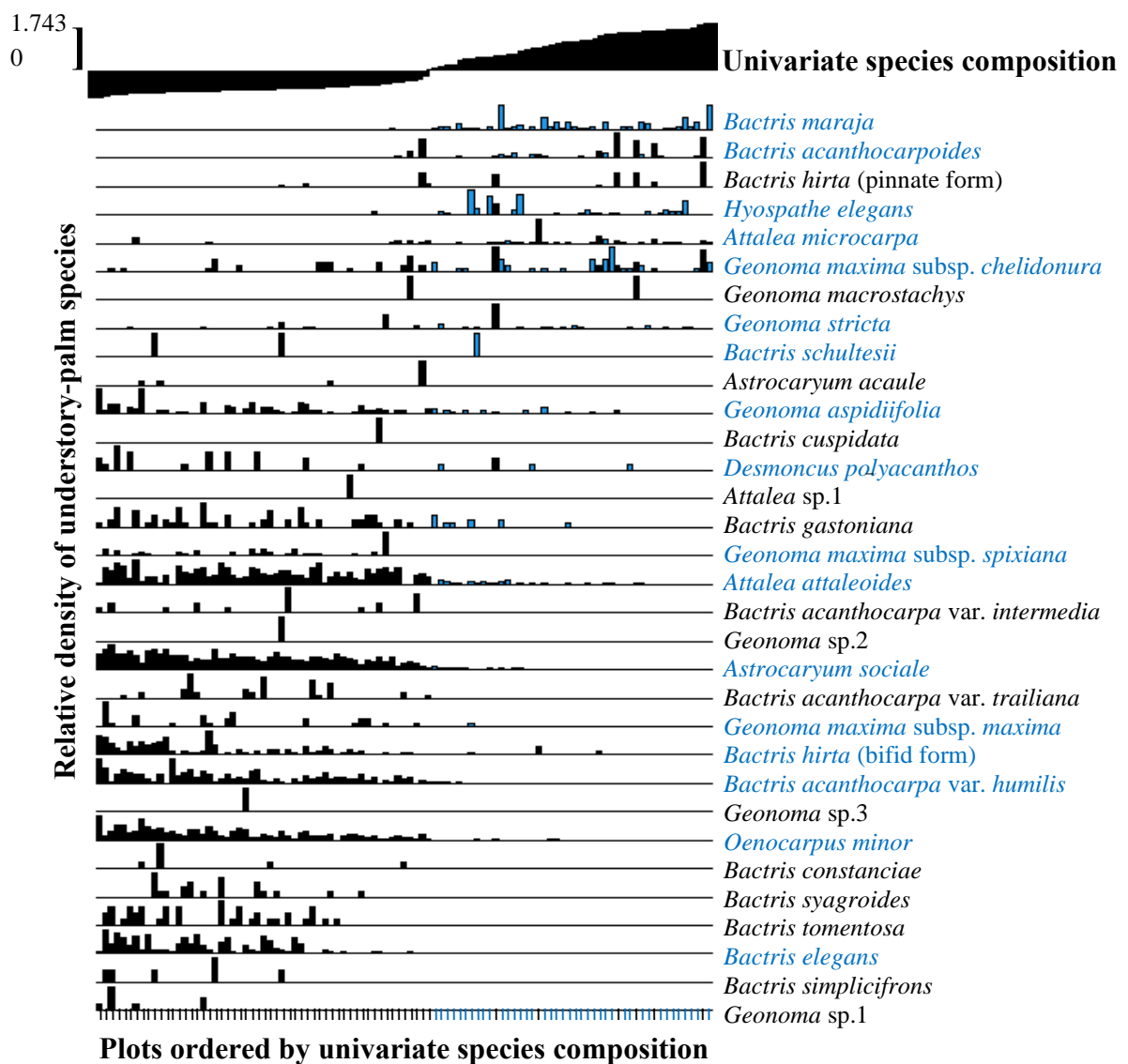
238 We measured multicollinearity between predictors with the VIF (Variance Inflation
239 Factor) through the *vif* function of the “usdm” package (Naimi et al., 2013). A VIF greater than
240 10 is a signal that the model has a collinearity problem (Dormann et al., 2012). All predictors
241 used for the entire data set (riparian and non-riparian plots) and considering only riparian plots
242 had $VIF < 4$, indicating that multicollinearity was unlikely to affect our conclusions. We used
243 the *APE* package to test spatial autocorrelation (Paradis et al., 2004). To remove possible
244 problems caused by spatial autocorrelation (Landeiro and Magnusson, 2011), we excluded a
245 riparian plot that was in the same stream as another riparian plot and 10 plots from non-riparian
246 plots less than 300 m away from riparian plots. Thus, we used 39 riparian plots and 62 non-
247 riparian plots, totaling 101 parcels for the entire dataset/landscape. Analyses were run in R
248 version 4.0.5 (R Development Core Team, 2021).

249 **3. Results**

250 *3.1. Palm assemblages*

251 We found 32 understory-palms species of which four were morphospecies, in a total of
252 12,486 understory-palm individuals across the entire landscape (Fig. 2). The varieties and
253 subspecies of *Bactris acanthocarpa*, *Geonoma maxima* and the two morphological forms of
254 *Bactris hirta* (bifid or pinnate form) were counted separately and considered as different
255 botanical entities in the analyses. Eighteen species were found in the riparian areas, with a total
256 of 976 individuals. Four species had only one record in riparian areas and were excluded from
257 the analysis considering only riparian areas to reduce the effect of noise generated by the
258 inclusion of rare species (Cao, Y; Larsen, DP; Thorne, 2001). All 32 understory-palm species
259 were found in the non-riparian areas (11,510 individuals). We found seven canopy-palm species

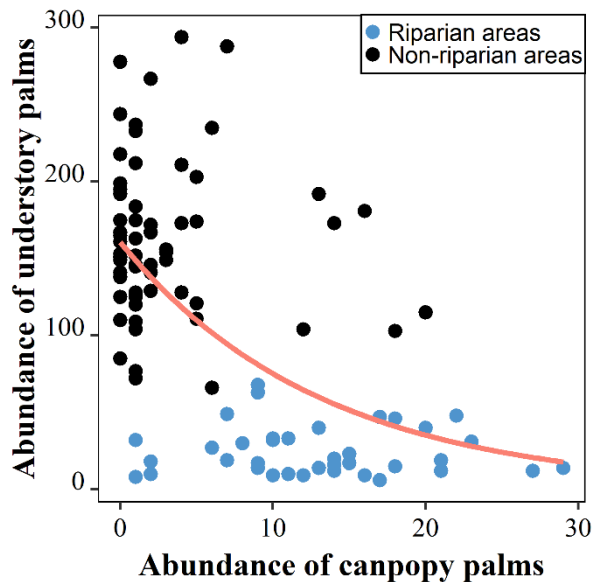
260 (*Astrocaryum murumuru*, *Attalea maripa*, *Euterpe precatoria*, *Mauritia flexuosa*, *Oenocarpus*
 261 *bacaba*, *Oenocarpus bataua* and *Socratea exorrhiza*) and two morphospecies, in a total of 715
 262 individuals across the entire landscape. Four species were found in the riparian areas, with 512
 263 individuals and all canopy-palm species were found in the non-riparian areas, with 203
 264 individuals. There was a significant negative relationship between the abundance of
 265 understory palms and canopy palms across the entire landscape (Hypothesis 1; $z = -7.259$,
 266 degrees of freedom = 99, $p < 0.001$; Fig. 3).



267

268 Fig. 2. Distribution of understory-palm species across the entire landscape, which includes
 269 riparian (blue bars) and non-riparian zones (black bars) in Reserva Ducke, Manaus, Amazonas,

270 Brazil, in relation to plots ordered by univariate composition of understory-palm assemblages
 271 (latent-variable coefficients based on a model-based Bayesian ordination). All species listed
 272 were found in non-riparian areas and in blue the subgroup found in riparian areas.



273

274 Fig. 3. Relationship between the abundance of understory and canopy palms in riparian (39
 275 blue points) and non-riparian areas (62 black points) in Reserva Ducke, Manaus, Amazonas,
 276 Brazil. The salmon-colored line represents the non-linear trend.

277 3.2. Environmental variables

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

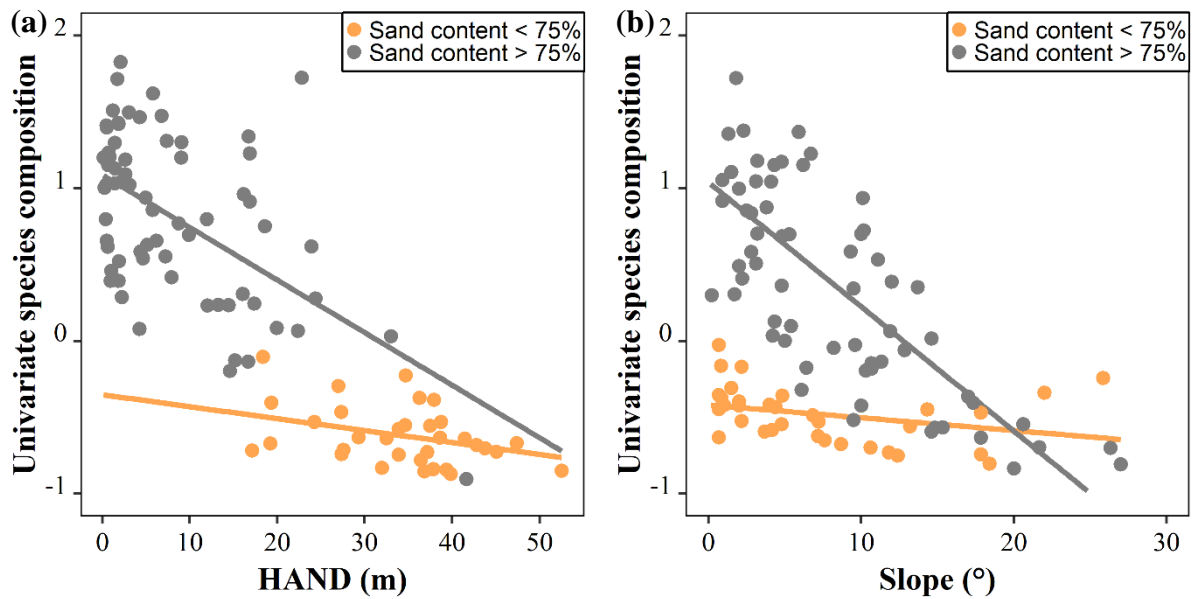
287 using a reduced number of variables produced similar results (supplementary material Table
288 S3).

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

292 Table 1. Influence of environmental predictors on the multivariate composition of understory-
293 palm assemblages across the entire landscape in Reserva Ducke, Manaus, Amazonas, Brazil.

294 Values in bold indicate $p < 0.05$ and “*” indicates the interaction among predictors.

Environmental variables	Wald	p
Model	33.10	0.035
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



295

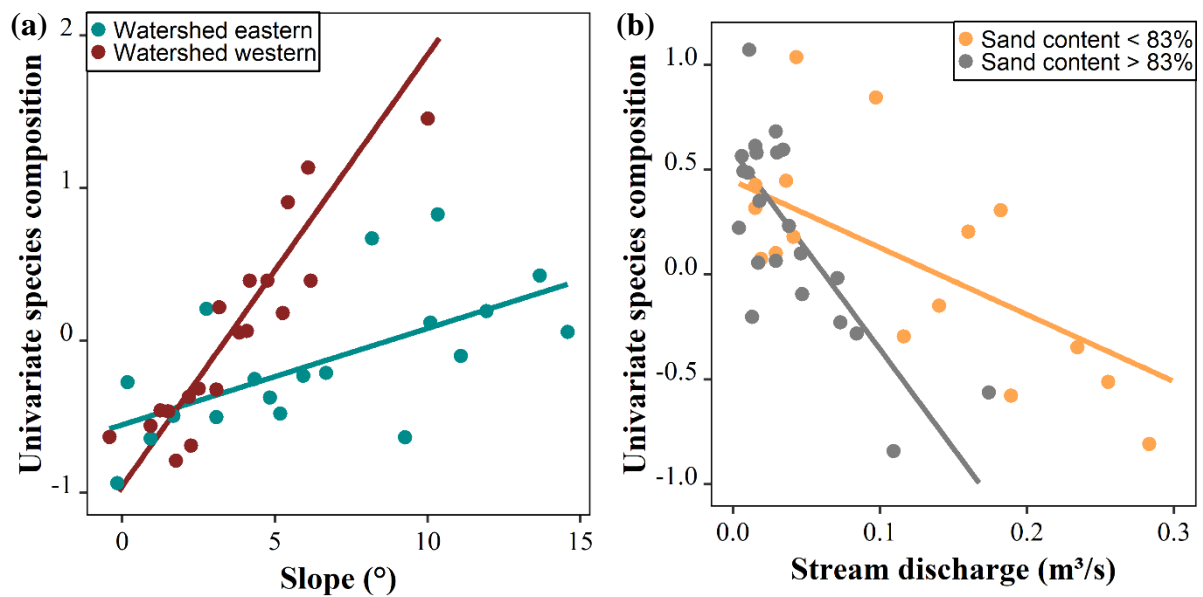
296 Fig. 4. Partial plots of the effects of the interaction among environmental predictors on the
 297 univariate composition of understory-palm assemblages (latent-variable coefficients based on
 298 a model-based Bayesian ordination) across the entire landscape in Reserva Ducke, Manaus,
 299 Amazonas, Brazil. The effect of the interaction between HAND and soil sand content (a) and
 300 the effect of the interaction between slope and soil sand content on understory-palm
 301 composition (b). We categorized the sand content as being above or below the median to
 302 visualize the interaction.

303 Table 2. Influence of environmental predictors on the multivariate composition of understory-
 304 palm assemblages in riparian areas in eastern and western watersheds of Reserva Ducke,
 305 Manaus, Amazonas, Brazil. Values in bold indicate $p < 0.05$ and “*” indicates the interaction
 306 among predictors.

Environmental variables	Wald	p
Model	17.77	0.581
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

307



308

309 Fig. 5. Partial plots of the effects of the interactions between environmental predictors on the
 310 univariate composition of understory-palm assemblages (latent-variable coefficients based on
 311 a model-based Bayesian ordination) in riparian areas of Reserva Ducke, Manaus, Amazonas,
 312 Brazil. The effect of the interaction between slope and watershed (a) and the effect of the
 313 interaction between stream discharge and soil sand content on understory-palm composition
 314 (b). We categorized the sand content as above or below the median to visualize the interaction.

315 4. Discussion

316 Understory and canopy palms are recognized as functionally separate groups within
 317 palms, and we identified several variables that explained differences among those groups that
 318 could provide information for the conservation of forests.

319 4.1. *The abundance of understory palms is related to the abundance of canopy palms*

320 The negative relationship between the abundances of understory and canopy palms is
321 primarily because of the opposite patterns of abundance of these groups in riparian and non-
322 riparian areas, which suggests the process of environmental filtering (Keddy, 1992).
323 Morphological characteristics related to individual survival and performance change according
324 to environmental conditions (Violle et al., 2007). Understory and canopy palms differ in relation
325 to their support structures, which result in differences in physical resistance to disturbance
326 (Barry Tomlinson and Huggett, 2012). The understory palms had thinner trunks than the canopy
327 palms. Balslev et al. (2011) suggested that the ability to remain submerged during floods favors
328 species with large trunks which in turn would lead to a disadvantage for smaller species in
329 American palm communities. Thus, environmental filtering due to flooding is likely to act at
330 different intensities on understory and canopy palms.

331 Areas close to watercourses are subject to short and unpredictable flood pulses due to
332 local rain events (Junk et al., 2011), resulting in long-term waterlogging of soils, while deep
333 flooding occurs only for short periods. Tall-stemmed palms are abundant in these areas (Kahn
334 and de Castro, 1985), suggesting that this growth form has an ecological advantage in flooded
335 habitats, possibly due to the more open canopy structure associated with flooding (Svenning,
336 2000). In contrast, small palms are underrepresented in flooded areas. This pattern suggests that
337 the stressful conditions imposed by floods can negatively affect the occurrence of palm species
338 with less robust support structures, such as understory species (Kahn and de Castro, 1985). In
339 the present study, one of the most abundant understory-palm species in riparian areas, *Bactris*
340 *maraja*, has larger and thicker stems than other understory palms. This species is apparently not
341 inhibited by anoxic conditions, and it is frequently found close to streams (Balslev et al., 2011;
342 Ribeiro et al., 1999).

343 4.2. *Topographic and soil variables and their interactions positively affect variation in*
344 *composition of understory-palm assemblages across the entire landscape*

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

353 The effect of topographic and soil conditions in determining species distributions has
354 been reported in studies at both local (Pansini et al., 2016; Pearson and Dawson, 2013;
355 Svenning, 1999), and wide scales (Eiserhardt et al., 2011; Muscarella et al., 2020). The
356 distributions of twenty-five species of palms from tropical forests were related to environmental
357 factors associated with water (Blach-Overgaard et al., 2010) and many palm species appear to
358 be intolerant of flooding (Eiserhardt et al., 2011; Losos, 1995; Pacheco, 2001). Palms of Central
359 Amazonian are generally associated with poorly drained soils with high sand content in areas
360 close to streams (Kahn, 1987). Plants that occur in seasonally flooded areas have been shown
361 to have a number of highly specialized adaptations to this habitat (Parolin, 2009) and Normand
362 et al. (2006) demonstrated that forests on paleo-riparian terraces and forests located on
363 unflooded terraces and in geographically close floodplains in the Peruvian Amazon have clear
364 differences in palm-species composition. However, areas close to streams with greater slope
365 are less subject to waterlogging, which may allow some non-riparian species to occur near
366 streams (Drucker et al., 2008; Gregory et al., 1991). Thus, interactions among environmental

367 predictors may provide far more potential niches for palm species than simple additive
368 conceptual (Wright, 2002) or statistical models (Eiserhardt et al., 2011) might suggest.

369 Although we found that the composition of understory palms is influenced by soil
370 fertility, as did Costa et al. (2009), this variable explained little variation in the distribution of
371 species. This may be because of the small range of variation in fertility, which could prevent
372 the differentiation of the species composition along this gradient (MacArthur, 1958). The range
373 of variation we found was small ($0.04 - 0.58 \text{ cmol.kg}^{-1}$) in relation to studies that found
374 exchangeable base content to be a significant predictor of plant composition at wider scales
375 (e.g. Jones et al., 2006; Vormisto et al., 2004). There was also weak evidence that the influence
376 of exchangeable soil bases on the composition of understory palms depends on slope. The
377 variation of the exchangeable-bases content of the soil was smaller in less inclined places (0.141
378 $- 0.517 \text{ cmol.kg}^{-1}$) and greater in more inclined places ($0.041 - 0.576 \text{ cmol.kg}^{-1}$). Thus,
379 different portions of the slope gradient could provide qualitatively different conditions for palm
380 species.

381 *4.3. Understory-palm assemblages vary in species composition along streams as a result of* 382 *variation in abiotic factors and their interactions within the riparian zone*

383 Differences between watersheds were found only for comparisons among riparian plots.
384 Within the riparian zone, there was no evidence of an effect of fertility, and this is likely because
385 the variation in base content within the riparian zone was less than across the entire landscape
386 for non-riparian areas of Reserva Ducke Costa et al. (2009), and other studies carried out on
387 broader scales (e.g. Jones et al., 2006; Vormisto et al., 2004).

388 Other variables found to be significant across the landscape (sand content, slope and
389 HAND) probably reflect similar processes occurring along streams within the riparian zone.
390 HAND reflects distance to the nearest drainage, and being close to a drainage (riparian zone)

391 indicates that the plot could be affected by discharge from the stream, whereas non-riparian
392 plots, by definition, have discharge = zero. Within the riparian zone, increased discharge
393 implies more intense flooding and the need for stronger support structures.

394 The differences in the variation of soil-texture gradients in Reserva Ducke are subtle in
395 relation to the sudden changes in soil composition found in some areas, such as the transitions
396 between clay and white sands (Tuomisto et al., 1995). However, Tuomisto et al. (2003), showed
397 that subtle changes in soil texture generated compositional discontinuities in plants assemblages
398 in a long transect (43 km) crossing what was considered a superficially uniform closed-canopy
399 non-inundated forest in Peru. In addition, in a local-scale (extent = 5–500 m) analysis of palm
400 assemblages in paleo-riverine terrace forests in Peru (Normand et al., 2006), soil moisture
401 explained more compositional variation than other measured environmental variables. Soil
402 moisture can vary over short distances between complete water logging and relatively dry
403 conditions (Kahn and de Castro, 1985), depending on topographic position relative to the water
404 table, soil drainage qualities, and flooding regime.

405 The influence of stream discharge on the composition of understory palms differed
406 along the sand gradient. Sandy/poorly structured soils can enhance the effects of flooding on
407 the banks of streams, generating higher water levels and greater mechanical instability for plant
408 rooting (Emilio et al., 2013). When changes in flow permanence, total annual discharge and
409 depth to groundwater occur, communities may shift in predictable ways according to traits
410 associated with water acquisition, such as root morphology (Merritt et al., 2010). During
411 periods of low discharge in most streams, the exposed active channel is colonized by weeds and
412 shrub and tree seedlings. Frequent flooding in this area discourages the establishment of
413 terrestrial vegetation both through surface erosion and the physiological effects of periodic
414 flooding (Gregory et al., 1991). Merritt et al. (2010) demonstrated that the flow regime exerts
415 selective pressures on riparian vegetation and that widespread modification of flow regimes by

416 humans resulted in extensive alteration of riparian vegetation communities. In the present study,
417 most understory-palm species only or mainly occur away from streams, and those that occur in
418 the riparian zone tend to occur in areas with lower stream discharge and less sandy soils. This
419 is because the impact of flooding on palm distributions is mainly related to inhibition of seed
420 germination and seedling survival (Braz et al., 2015; Losos, 1995; Pacheco, 2001; Svenning,
421 2001). Thus, the differentiation of the palm-assemblage composition along subtle variations of
422 interacting environmental gradients indicates strong niche partitioning among species (Emilio
423 et al., 2013).

424 The differences in the composition of understory-palm species between watersheds
425 (some species dominant or even restricted to one of the watersheds) that could not be accounted
426 for by the environmental variables we measured indicate that other factors, such as historical
427 or mass effects (Shmida and Wilson, 1985), may be involved. Therefore, management plans
428 should not assume homogeneity in the distribution of understory palms in Reserva Ducke,
429 especially in riparian zones.

430 Brazilian environmental legislation gives special protection to riparian areas, but few
431 understory-palm species are restricted to, or even more abundant in, riparian areas. The
432 conservation of most species requires maintenance of extensive areas of upland forests. Where
433 this is not possible, a broad range of soil, slope and stream-discharge conditions will have to be
434 included to maximize the number of species to be protected.

435 **5. Conclusions**

436 Conclusions based on studies of canopy palms, such as that they occur more frequently
437 on poorly structured soils in areas with a superficial water table, do not apply to understory
438 palms. At least in Reserva Ducke, the numbers of individuals and species of understory palms
439 are greater in areas with well-structured soil (low sand content) and deep-water table. In
440 addition, interactions among environmental factors at the mesoscale (entire landscape), and at

441 the local scale (riparian zone), generate compositional turnover among sites with only subtle
442 environmental differences that filter understory-palm species. This suggests that these
443 interactions can generate new niches for species and that modeling species/environment
444 relationships through simple additive relationships may not reveal the ecological complexity of
445 these relationships. Stream discharge and soil structure are among the first variables to be
446 affected by human occupation of riparian zones, which indicates that a better understanding of
447 interactions between environmental predictors and a landscape approach will be necessary to
448 conserve Amazonian understory palms, especially if they are limited to permanent-protection
449 areas around streams.

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- 779

780 **Supplementary material**

781 Table S1. Influence of environmental predictors on the univariate composition of understory-
782 palm assemblages (latent-variable coefficients based on the model-based Bayesian ordination)
783 across the entire landscape in Reserva Ducke, Manaus, Amazonas, Brazil. Values in bold
784 indicate significant $p < 0.05$ and “*” indicates the interaction among predictors.

Environmental variables	<i>t</i>	<i>p</i>
Watershed	0.082	0.934
HAND	-0.317	0.752
Slope	-0.144	0.886
Sand content	1.008	0.316
Base content	-1.407	0.163
Watershed * HAND	-0.247	0.806
Watershed * Slope	-0.614	0.541

Watershed * Sand content	0.315	0.753
Watershed * Base content	-0.244	0.808
HAND * Slope	-0.092	0.927
HAND * Sand content	-1.912	0.059
HAND * Base content	0.664	0.509
Slope * Sand content	-1.821	0.072
Slope * Base content	1.131	0.261
Sand content * Base content	2.189	0.031

785

786 Table S2. Influence of environmental predictors on the univariate composition of understory-
787 palm assemblages (latent-variable coefficients based on the model-based Bayesian ordination)
788 in riparian areas in eastern and western watersheds of Reserva Ducke, Manaus, Amazonas,
789 Brazil. Values in bold indicate significant $p < 0.05$ and “*” indicates the interaction among
790 predictors.

Environmental variables	t	p
Watershed	0.656	0.518
Stream discharge	2.482	0.021
Slope	2.164	0.041
Sand content	1.544	0.136
Base content	0.997	0.329
Watershed * Stream discharge	-2.149	0.042
Watershed * Slope	2.596	0.016
Watershed * Sand content	-0.593	0.559
Watershed * Base content	-0.863	0.397
Stream discharge * Slope	-2.671	0.014
Stream discharge * Sand content	-1.888	0.072
Stream discharge * Base content	-1.480	0.152
Slope * Sand content	-1.761	0.092
Slope * Base content	-0.731	0.472
Sand content * Base content	-0.704	0.488

791

792 Table S3. Influence of environmental predictors on the multivariate composition of understory-
793 palm assemblages in riparian areas in eastern and western watersheds of Reserva Ducke,
794 Manaus, Amazonas, Brazil, without statistically non-significant ($p > 0.05$) interactions. Values
795 in bold indicate $p < 0.05$ and “*” indicates the interaction among predictors.

Environmental variables	Wald	p
Model	14.81	0.007
Watershed	5.436	0.035
Stream discharge	5.619	0.044
Slope	7.396	0.001
Sand content	4.712	0.219
Base content	3.953	0.505
Watershed * Slope	5.953	0.007
Watershed * Sand content	5.369	0.041
Stream discharge * Sand content	5.624	0.046

796

Conclusão

Conclusões baseadas em estudos de palmeiras de dossel, como a de que ocorrem mais frequentemente em solos mal estruturados em áreas com lençol freático superficial, não se aplicam a palmeiras de sub-bosque. Pelo menos na Reserva Ducke, o número de indivíduos e espécies de palmeiras do sub-bosque é maior em áreas com solo bem estruturado (baixo teor de areia) e lençol freático profundo. Além disso, as interações entre os fatores ambientais na mesoescala (paisagem inteira) e na escala local (zona ripária), geram mudanças composicionais entre locais com diferenças ambientais sutis que filtram as espécies de palmeiras sub-bosque. Isso sugere que essas interações podem gerar novos nichos para as espécies e que a modelagem das relações espécie/ambiente por meio de relações aditivas simples pode não revelar a complexidade ecológica dessas relações. A vazão dos riachos e a estrutura do solo estão entre as primeiras variáveis a serem afetadas pela ocupação humana das zonas ripárias, o que indica que um melhor entendimento das interações entre os preditores ambientais e uma abordagem da paisagem será necessário para conservar as palmeiras do sub-bosque amazônico, especialmente se forem limitadas a áreas de proteção permanente no entorno dos riachos.