



Original article

Topographic separation of two sympatric palms in the central Amazon – does dispersal play a role?

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ABSTRACT

Despite broadly overlapping geographic distributions in the central Amazon basin, two congeneric palm species (*Attalea attaleoides* and *Attalea microcarpa*) have topographically separated distributions on a local scale in Reserva Ducke near Manaus. Our aim here was to determine if this local scale separation can be linked to (1) seedling stage specialization to different habitat conditions of the two species, and/or (2) environmentally-controlled seed dispersal. We assessed the role of these potential drivers by mapping the local distribution of the two species over a 25-km² grid and testing for correlation to seed removal and seed germination patterns using seed sowing experiments. 360 seeds of each species were sown in 30 uniformly distributed plots (12 seeds of each species in each plot), and seed removal and germination were subsequently monitored. Adult populations of the two species showed opposite distribution patterns linked to topography. However, there was little evidence for specialization to different habitat conditions at the seedling stage: after 11 months, 26.1% of seeds of *A. microcarpa* had germinated along the entire topographic gradient, albeit with a tendency toward higher germination in more inclined areas. For *A. attaleoides*, only 2.2% seeds had germinated, and again along the entire topographic gradient. In contrast, there was evidence for environmentally-controlled seed dispersal: for both species, seed removal was higher in flat areas. Presence of adults did not affect germination or seed removal. Our results suggest that topographically differentiated distributions of *A. attaleoides* and *A. microcarpa* may be reinforced by steep slope avoidance by their seed dispersers. A direct environmental control mechanism remains to be identified to explain the consistent topographic associations, but our results show that this mechanism does not work at the seed germination stage.

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1. Introduction

A core question in ecology is what limits species distributions. For plants, the most important driving mechanisms that have been proposed are i) environmental control, which leads species to specialize on particular habitats (e.g., Whittaker, 1956), and ii) neutral population processes, with distributions being determined by dispersal limitation and chance (Hubbell, 2001). Both mechanisms affect plant species distributions in tropical forests (Tuomisto et al., 2003; Vormisto et al., 2004a), and it has been suggested that they contribute to maintaining these forests' high species diversity (e.g., Svenning, 1999; Clark et al., 1999; Hubbell, 2001; Fine et al., 2006; Yavitt and Wright, 2008).

Topography is one important environmental feature that controls local- and landscape-level distributions of tropical forest

plant species, such as ferns (e.g., Jones et al., 2006; Zuquim et al., 2009), trees (e.g., Clark et al., 1999; Valencia et al., 2004), and palms (Kahn and Castro, 1985; Svenning, 1999; Svenning and Balslev, 1998; Svenning et al., 2009; Costa et al., 2009). The importance of topography probably reflects the integration of multiple environmental gradients of direct importance for plants, e.g., soil conditions, hydrology, and forest structure and dynamics (Svenning, 2001b). For example, in the central Amazon basin, topography is a major determinant of the physical and chemical characteristics of topsoil (Mertens, 2004), with local altitudinal gradients strongly correlated with clay content (Lucas and Chauvel, 1992). In this same region, topography also produces gradients in soil water availability (Hodnett et al., 1997). These topography-linked environmental patterns may drive plant distributions in tropical forest, and palm species distributions have been linked to hydrological gradients (Kahn and Castro, 1985; Kahn, 1987; Costa et al., 2009) and soil nutrients and drainage (Clark et al., 1995; Vormisto et al., 2004b; Montufar and Pintaud, 2006; Poulsen et al., 2006).

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There is also evidence that plant species distribution patterns in tropical forests may be driven by dispersal, and the limited efficiency of seed dispersal in tropical trees has been recognized for decades (Ashton, 1969). Dispersal limitation may prevent species from establishing in suitable sites (Hubbell, 1999; Wright, 2002) and thus generate clumped distribution patterns unrelated to environmental conditions (i.e., neutral effects). However, dispersal may also generate distribution patterns that are spatially correlated with environmental conditions. Notably, animal behavior may introduce environmentally related spatial heterogeneity in seed dispersal patterns due to environmental preferences of the disperser species (Svenning, 2001a). Animal movement and behavior are shaped by many factors such as seasonal flooding (Bodmer, 1990), canopy structure (Schupp and Frost, 1989), fruit availability and topographic preferences (Salas, 1996). Palm dispersal may thus be indirectly affected by environmental features in a non-random way, through their effects on the distributions and behavior of seed dispersers (Eiserhardt et al., 2011; Svenning, 2001a). Environment can also act as a barrier to dispersal (Wiens and Graham, 2005), and dispersal modes can restrict species to certain environments; e.g., water-dispersed seeds will not be moved beyond bottomlands even if they are able to germinate in the uplands.

Drivers of plant species distribution linked to environmental conditions have often been seen as alternatives to drivers linked to dispersal, but as discussed above they may also interact. In the case of palms, a recent review stated that different drivers may act at different scales; the effects of dispersal limitation are expected at all scales, whereas environmental filters act differently all the way from local to global scales (Eiserhardt et al., 2011). At continental and regional scales, the most important environmental drivers of palm species distributions are amount and seasonality of precipitation; at landscape scales, they are topography, soil, and vegetation structure (such as canopy heterogeneity); at local scales, hydrology is often a major driver (Svenning, 2001b; Vormisto et al., 2004b; Poulsen et al., 2006; Costa et al., 2009; Eiserhardt et al., 2011). Dispersal limitation influences palm community composition and distribution patterns at all scales (Eiserhardt et al., 2011). Earlier studies have shown that palm seedlings are clumped around the parent (Svenning, 2001a) and that when palm seeds are taken by dispersers they are often moved only a few meters from the parent plant (e.g., Fragoso, 1997; Pimentel and Tabarelli, 2004; Almeida and Galetti, 2007). Although the random component of dispersal limitation is well documented, it remains poorly understood how dispersal is limited by the environment, and to what extent environmental constraints on dispersal affect species-environment relationships (but see Fragoso, 1997).

Attalea includes 27 species according to Henderson (1995), but the genus is being revised and a current estimate is that it has 35 species (Henderson, personal communication). *Attalea attaleoides* and *Attalea microcarpa* are both monoecious palms with short, subterranean stems and pinnate leaves with regularly arranged pinnae (Table 1 and Table 2). Closely related species are expected to share many ecological features (Webb et al., 2002; Feeley, 2003) and the evolution of niche differentiation between them remains an active area of research (Ackerly et al., 2006). For instance, according to Diamond (1975) co-occurrence rule, closely related species are unlikely to co-occur at small scales. In accordance with that, Svenning (1999) suggested that palms of similar growth form will show antagonistic microhabitat association. This appears to be the case in the two species that we focused on in this study. *A. attaleoides* and *A. microcarpa* are sympatric across most of their ranges (Henderson, 1995; Lorenzi et al., 2010), but at the landscape and local scale, more

Table 1

Reproductive traits, possible pollinators and dispersers, and other characteristics of *Attalea attaleoides* and *A. microcarpa*.

Characteristics	<i>A. attaleoides</i>	<i>A. microcarpa</i>
Inflorescence position	Interfoliar ^{a,b}	Interfoliar ^a
Rachis length (cm)	15–20 ^a	20–50 ^a
Staminate rachillae (no., length in cm)	90, 5–7 ^a	58–73, 3–9 ^a
Staminate flowers (mm)	10–14 ^a	7–10 ^a
Stamens (number) mm	Straight (6) 5–6 ^a	Curled (9–15) ^a ; 8–12 ^b
Anthers	Straight	Coiled and twisted ^{a,b}
Pistillate rachillae (cm)	1 ^a	1–6 ^a
Pistillate flowers (cm)	2 ^a	1.5–2 ^a ; 1.7–2.2 ^b
Pistil (mm)	–	3.5 ^b
Free petals (mm)	Yes 11–12 ^a	Yes 7–9 ^a
Fruits	Ovoid with elongate apex ^{a,b}	Ovoid or obovoid ^a ; Elongate ^b
Fruit length (cm)	4.5–5.5 ^{a,b}	3.5–4 ^{a,c}
Fruit width (cm)	2–2.5 ^{a,b}	2–3 ^{a,c}
Mesocarp	Dry and fibrous ^b	Dry and fibrous ^b
Endocarp fibers	Few or absent ^a	Thin with or without ^a
Seeds per fruit	2–3 ^a	1–3 ^a ; Often one ^b
Germination	Difficult ^b	Difficult and slow ^b

^a Henderson (1995).

^b Lorenzi et al., (2010).

^c Glassman (1999).

specifically in the *terra firme* forests north of Manaus, they are restricted to different habitats. *A. attaleoides* occurs on upland plateaus and less abundantly on slopes, whereas *A. microcarpa* is confined to bottomlands (Costa et al., 2009). In forests south of Manaus, where the landscape is predominantly composed of bottomlands, *A. attaleoides* is absent, while *A. microcarpa* is widespread (Emilio, pers. comm).

Environmental factors such as hydrology and soil conditions could directly separate these two sympatric species along the landscape and local scale topographic gradient, e.g., via physiological effects. However, topography could alternatively shape *Attalea* seed dispersers' behavior, creating topographically non-random patterns of seed distribution. As with other species, neutral dispersal processes may additionally affect their distributions, but are unlikely to account for their consistent topographic associations. To test these alternate driving mechanisms we designed a sowing experiment to answer the following specific questions:

- (1) Is seed germination related to the presence and abundance of adults or to the proportion of fruiting individuals? To assess whether dispersal limitation was neutral or environmentally determined we assumed that if a transplanted seed germinated in a site where an adult was not present, then the absence of adults could be due to dispersal limitation, which would involve neutral processes, or to environmental control in later phases of development. If transplanted seeds did not germinate in a site where adults were absent, then this absence could be due to environmental control in the seed phase, i.e., niche processes.
- (2) Is seed germination related to topography? If so, then physiological effects on seed germination could drive *Attalea*-topography relationships.
- (3) Is seed removal related to the presence and abundance of adults or to the proportion of fruiting individuals? If one of these is true, this would reinforce a mechanism of density-dependent predation.
- (4) Is seed removal related to topography? If so, this would offer a mechanism whereby disperser behavior could generate or strengthen *Attalea*-topography relationships.

Table 2
Results for ANOVA and multiple regression models showing the response variables in the column headings (G = germination, R = removal and PxA = presence/absence) and the study species in the rows. No germination data are shown for *A. attaleoides* because of low germination rates. Data shown for adult abundance and number of adults fruiting are with outliers removed. *P* values are provided for the entire model and for each variable included in the model.

Species	PxA individuals in the plot		Abundance of adults ^a		Number of adults fruiting ^a		Model [*]	
	G	R	G	R	G	R	G	R
<i>A. attaleoides</i>	–	$F = 0.14,$ $P = 0.70$	–	$R^2 = 0.03,$ $P = 0.31$	–	$R^2 = 0.03;$ $P = 0.29$	–	$R^2 = 0.31; P = 0.006$
<i>A. microcarpa</i>	$F = 0.08,$ $P = 0.77$	$F = 1.84,$ $P = 0.18$	$R^2 = 0.02,$ $P = 0.44$	$R^2 = 0;$ $P = 0.68$	$R^2 = 0.00,$ $P = 0.88$	$R^2 = 0.01;$ $P = 0.52$	$R^2 = 0.19;$ $P_w = 0.06;$ $P_i = 0.08$	$R^2 = 0.09; P_w = 0.24;$ $P_i = 0.16$

^a Does not include an outlier plot with more than 250 individuals of *A. microcarpa*. For ANOVA test the $Df = 1,28$ for all models. $P_w = p$ value for the whole model, $P_i = p$ value for slope.

^{*} Model including environmental variables.

2. Material and methods

2.1. Study site

The study was conducted in the Reserva Florestal Adolpho Ducke of the Instituto Nacional de Pesquisas da Amazônia, located 26 km northwest of Manaus, Brazil (02°55'S; 59°59'W, Fig. 1). The reserve covers 10,000 ha (10 × 10 km) of *terra firme* tropical rain forest. The canopy is 30–37 m high and the understory is dominated by *Astrocaryum* and *Attalea* palms (Ribeiro et al., 1999). Mean annual temperature in the area is 26 °C and air humidity ranges from 77 to 88%. Mean annual rainfall is 2362 mm and the dry season is from July to October; September is the driest month (Marques-Filho et al., 1981). Soils vary along a gradient from clayey latosols in the uplands to increasingly sandier soils at lower elevations, until almost only sand is found in the bottomlands. The vegetation in the area is mainly *terra firme* forest, with some intermingled patches of white sand forest.

The Reserva Ducke has a grid of regularly (1 km) spaced north-south and east-west running trails covering a total area of 25 km². Within the gridded area, the PPBio program (Research Program in Biodiversity) of the Brazilian Ministry of Science and Technology has established a set of 30 plots, each one 250 m long and 40 m wide. These plots are not rectangular but rather aligned so that the long axis of each plot follows a local altitudinal contour, thus minimizing altitudinal variation within plots. The main gradient within the area is topographic, with elevation varying between 46.7 m and 105.1 m above sea level.

2.2. Data collection and experimental design

Abundance of the two species (*A. attaleoides*, *A. microcarpa*) was determined for each plot by J.-L. Guillaumet (Fig. 2). Seeds of both species were collected from infructescences still attached to palms within the grid and close to the plots, but never inside them. We collected 360 viable seeds of each species that were randomized in

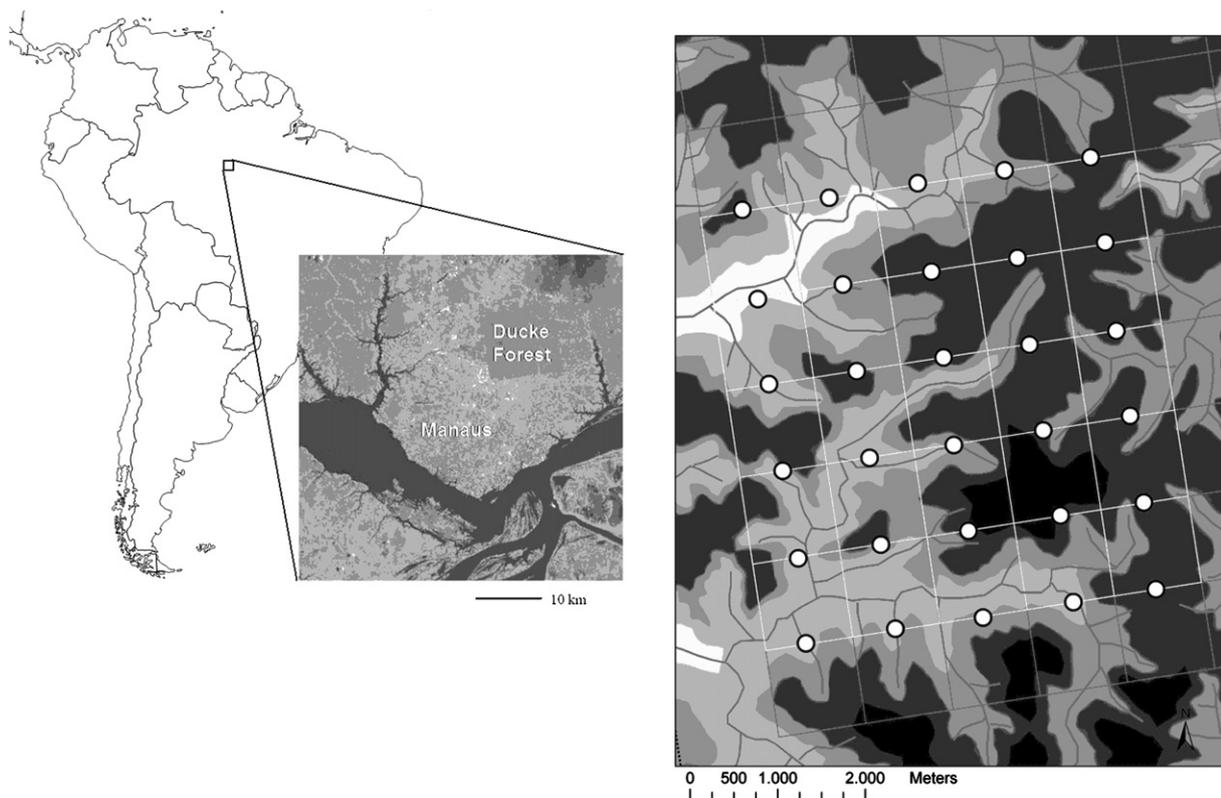


Fig. 1. The central Amazon basin, indicating the position of our study site in reserva Ducke, 30 km from Manaus, Brazil. The gridded map on the right shows the PPBio grid where the study was carried out.

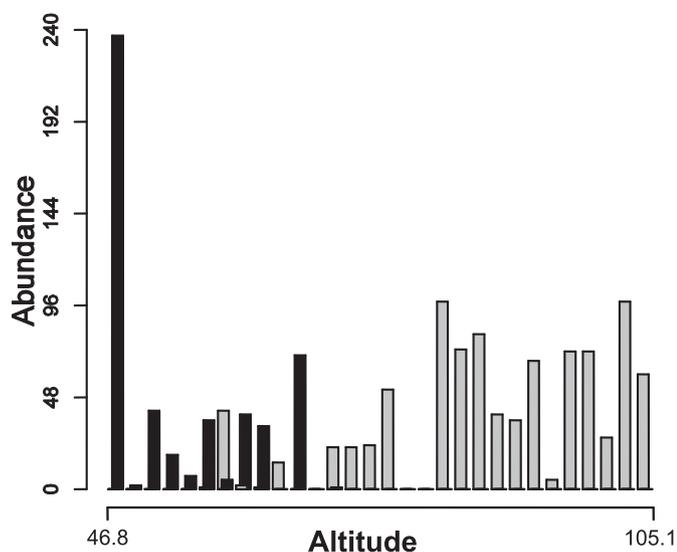


Fig. 2. Abundance of adult *Attalea attaleoides* (gray) and *A. microcarpa* (black) along the topographic gradient in 30 plots in the reserva Adolpho Ducke. The plots are ranked by altitude.

relation to sowing them in plots. Seed viability was tested by placing seeds in water; those that floated were discarded. We then sowed 12 seeds each of *A. attaleoides* and *A. microcarpa* in separate 1 m² subplots in each of the 30 plots. The subplots were always placed halfway along the 250-m plot central axis (i.e., at 125 m) and to the left of it when walking from the start of the central axis. The seeds were placed in three parallel rows of four seeds and buried 2–3 cm below the soil surface so they could be relocated without using any mark that could attract predators. Although we did not have information about how deep seeds of the two investigated species are buried under natural circumstances, we knew that 74% of one-leaf seedlings of *Attalea oleifera* were buried 1–3 cm below the surface (Pimentel and Tabarelli, 2004). Based on that information, our burial depth of 2–3 cm below the soil surface would seem to provide a good escape from predation.

Sowing was done in April 2009 for *A. microcarpa* and in January 2010 for *A. attaleoides*. Non-spiny cocosoid palms such as *Attalea* have been reported to have a long dormancy of 312–475 days (Wagner, 1982), although this may be an overestimate as these palms have remote germination, which initially takes place underground (Henderson, 2002). After sowing the seeds, we monitored germination and removal by predators every month by digging up seeds and re-burying them until germination, which we defined as when the primary root appeared. Germinated seeds were left in the plots and observed again after nine months. After nine months, more than 20% of *A. microcarpa* seeds and only one *A. attaleoides* seed had germinated. For this reason, we made an additional observation one year after sowing. A seed was considered to have been removed by seed dispersers or predators when it could not be relocated. The proportion of germinated seeds was calculated as the ratio of germinated seeds to sowed seeds minus removed seeds. The proportion of removed seeds was calculated as the ratio between removed and sowed seeds.

Topographic data collected by a professional surveying team (<http://ppbio.inpa.gov.br/>) were obtained from PPBio. Altitude was measured using a theodolite at the 0-m mark at the beginning of each plot. Slope was measured with a clinometer every 50 m along the plots' long axis. At the same points, soil was sampled at 0–5 cm depth from a 30 × 30 cm area, mixed to create a compound sample, and clay content and chemical properties analyzed in INPA's Plant and Soil Thematic Laboratory. Height above nearest drainage

(HAND) is a quantitative topographic descriptor based on a digital elevation model (SRTM-DEM) that measures vertical height difference between a specific point on the landscape and its nearest drainage (Rennó et al., 2008). HAND was calculated for Reserva Ducke, calibrated in the field, and averaged for each plot with values calculated based on the 250-m central long axis (Schiatti, unpublished data).

2.3. Data analysis

The numbers of germinated seeds and removed seeds were used as response variables in one-way ANOVA type III (function `Anova` in the R package `car`: Fox and Weisberg, 2011) and compared between plots with and without adults (as a measure of habitat suitability) and to control for conspecific density- or distance effects. Type III sums of squares were used, as they allow for unbalanced sample sizes (Zahn, 2009). We tested the effects of adult abundance, the proportion of individuals fruiting, and environmental factors on the proportion of germinated seeds and the proportion of removed seeds using linear regression models. Response variables were arcsine transformed for proportion data to fit a linear model. We used Cleveland dot-plots to check for outliers, and pairwise correlations and Variance Inflation Factors (VIFs) to check for multicollinearity among predictors. All non-correlated variables were used in a preliminary model (altitude, HAND, phosphorus, exchangeable bases and slope), which was subjected to a stepwise function in order to select the best model for each response variable. Regardless of species, slope and phosphorus were the explanatory variables retained for germination data, and altitude and slope for removal data. All analyses were performed in the R statistical environment (R Development Core Team, 2010).

3. Results

3.1. Germination

Of the 360 sowed *A. attaleoides* seeds, only 8 (2.2%) germinated, and therefore we did not test their relationships with adults or the environment. For *A. microcarpa*, 94 seeds (26.1%) germinated and their numbers did not differ between sites with or without adults ($F_{1,28} = 0.08$, $P = 0.77$). Furthermore, the proportion of germinated *A. microcarpa* seeds was neither related to the abundance of adults nor to the number of individuals fruiting at the site ($R^2 = 0.02$, $P = 0.44$, and $R^2 = 0.00$, $P = 0.88$, respectively).

The pattern of seed germination along the topographic gradient is shown in Fig. 3. Seeds of *A. microcarpa* germinated along the entire topographic gradient, with a slight tendency for higher germination in more inclined plots (Fig. 4a, $R^2 = 0.19$; $P = 0.06$ for the complete model (with phosphorus and slope). Although only a very limited number of *A. attaleoides* seeds germinated, the four plots in which seeds did germinate were in different parts of the slope gradient (2, 4.84, 10 and 10.17°; mean plot slope values range between 0.7 and 26.66, with just three values above 15°) (Fig. 3).

3.2. Seed removal

The number of removed *A. attaleoides* and *A. microcarpa* seeds did not differ between plots with or without adults ($F_{1,28} = 0.14$, $P = 0.70$; $F_{1,28} = 1.84$, $P = 0.18$, respectively). Furthermore, the proportion of removed *A. attaleoides* seeds was not related to adult abundance or to the number of individuals fruiting at the site ($R^2 = 0.03$, $P = 0.31$; $R^2 = 0.03$; $P = 0.29$). The proportion of *A. microcarpa* seeds removed was positively related both to adult abundance ($R^2 = 0.13$, $P = 0.05$) and to the proportion of individuals fruiting ($R^2 = 0.12$; $P = 0.06$), but this result was influenced by one

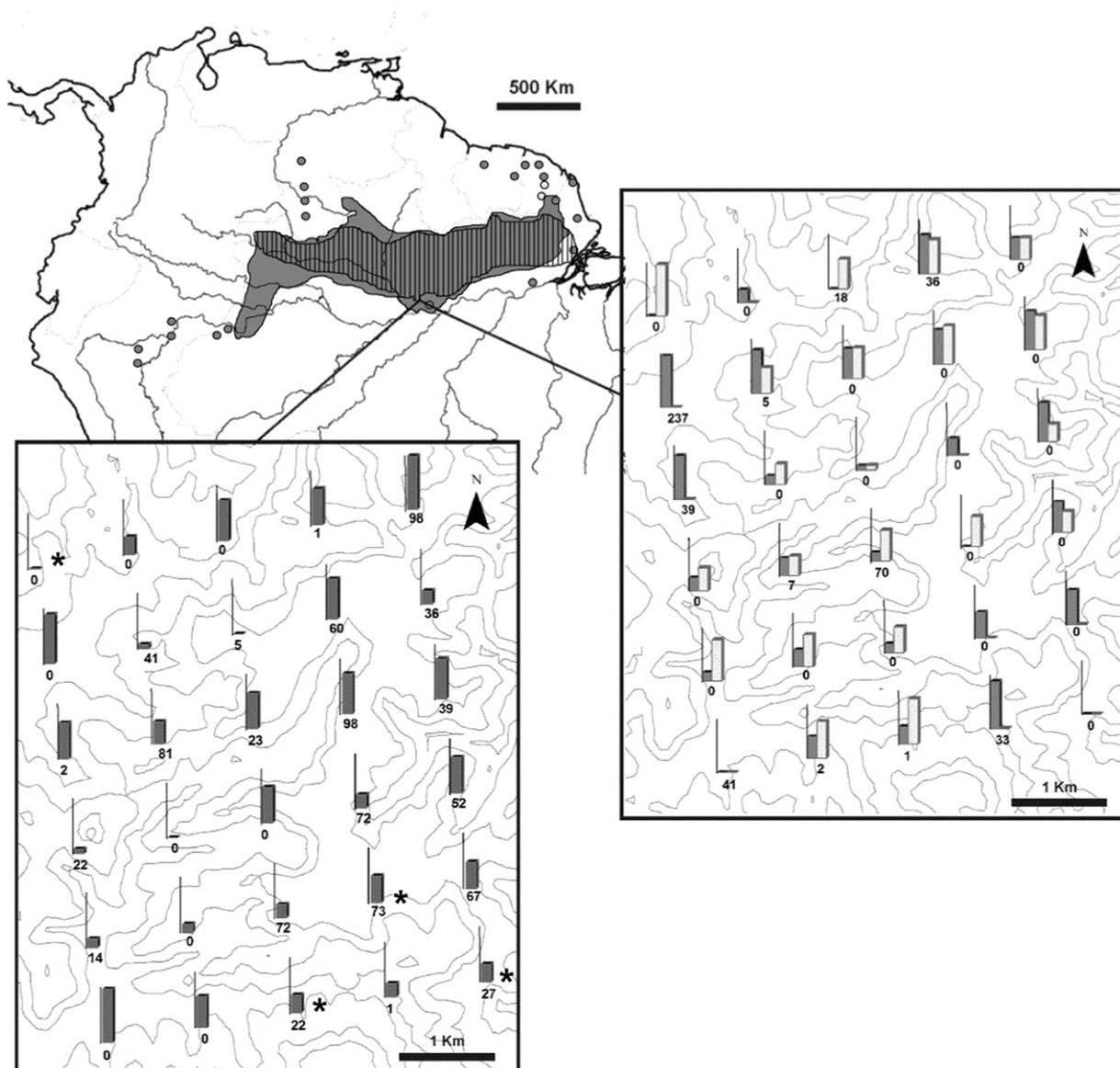


Fig. 3. A map of the overall distributions of *Attalea attaleoides* and *A. microcarpa*. Circles represent the species' distributions in the Amazon according to Henderson (1995) in light gray for *A. attaleoides* and dark gray for *A. microcarpa*. Shaded areas are the distribution in Brazil according to Lorenzi et al. (2010), with the vertical lines indicating *A. attaleoides* and the solid color *A. microcarpa*. The details show local abundance of adults (numbers under bars). The proportions of seeds removed are shown in dark gray and the proportions of seeds germinated are shown in light gray in the right panel for *A. microcarpa* and in the left panel for *A. attaleoides*. Plots where *A. attaleoides* germinated are marked with asterisks.

outlier plot that had more than 250 individuals of *A. microcarpa*. Repeating the analyses without this outlier produced non-significant results ($R^2 = 0$; $P = 0.68$ and $R^2 = 0.01$; $P = 0.52$ for adult abundance and for proportion of individuals fruiting respectively).

The proportion of removed *A. attaleoides* seeds was higher in less inclined plots (Fig. 4b; $R^2 = 0.31$; $P = 0.006$). The proportion of removed *A. microcarpa* seeds also tended to be higher in less inclined plots, albeit not statistically significantly so (Fig. 4b; $R^2 = 0.09$; $P = 0.24$ for the complete model).

4. Discussion

4.1. Germination

Seeds of *A. microcarpa* germinated along the entire topographic gradient – and did so independently of adult presence/

absence or abundance – raising the question of what causes the absence of adults of *A. microcarpa* in the uplands. These results suggest that the species' distribution may be governed by dispersal limitation, which prevents seeds from reaching the uplands under natural conditions. A number of other studies have also found evidence for dispersal-constraints on local- and landscape scale distributions of other palms in the tribe *Cocoseae* as palm that belong to other tribes (e.g., Svenning, 2001a; Charles-Dominique et al., 2003; Eiserhardt et al., 2011). Various factors may contribute to this, including seed size, which limits the distance a seed can be carried, size of the disperser, digestive characteristics, habitat preference, feeding behavior (Jordano, 2000), and distance that a disperser can move (Fragoso, 1997; Boll et al., 2005). There are no specific studies of the dispersal of *A. microcarpa* (see Table 3 for possible dispersers and Table 4 for traits of the possible dispersers), but common dispersers of other palm species include tapirs, deers, peccaries, agoutis and

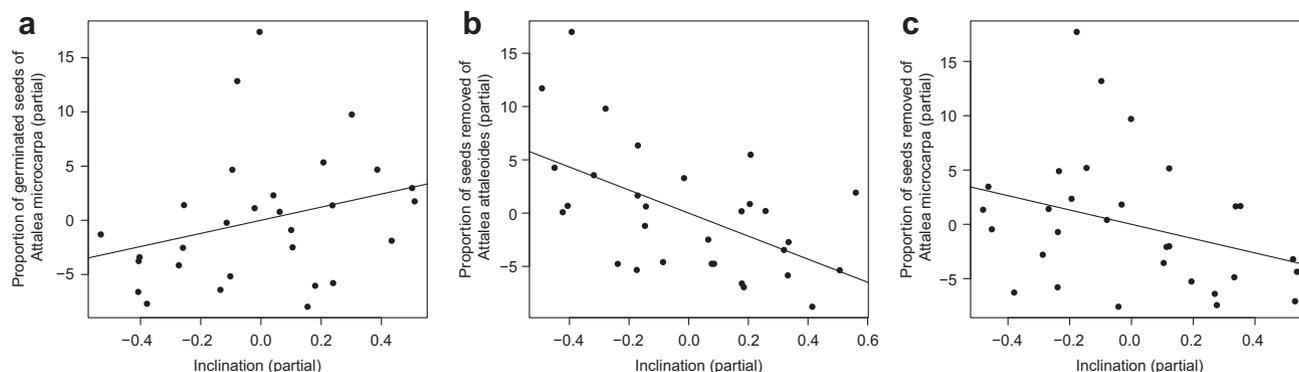


Fig. 4. Partial regressions showing the proportion of germinated *Attalea microcarpa* seeds (a), the proportion of removed *Attalea attaleoides* seeds (b), and the proportion of removed *A. microcarpa* seeds (c) against slope in 30 plots in a 25 km² terra firme area at reserva Forestal Adolpho Ducke in central Amazonia. The partial effects of slope exclude the effects of other variables included in each model. The values can be negative and are the residuals resulting from the multiple regression model, but slope data in the area ranges between 0.66 and 26.33.

squirrels (Smythe, 1989; Galetti et al., 1992; Quiroga-Castro and Roldán, 2001; Wyatt and Silman, 2004; Pimentel and Tabarelli, 2004). Intrinsic behavior of these animals can generate micro-environmental heterogeneity (Svenning, 2001b; Forget, 1992). The small rat, *Heteromys desmarestianus*, which disperses *Astrocaryum mexicanum* seeds, is 4.5 times more abundant in flat areas than on slopes (Klinger and Rejmánek, 2010). The tapir, an effective palm seed disperser (Quiroga-Castro and Roldán, 2001; Bodmer, 1991) which moves over very long distances, prefers low and moist areas (Bodmer, 1991; Salas, 1996), and tapir latrines are mostly located in wet areas (Quiroga-Castro and Roldán, 2001; Fragoso, 1997) like the bottomlands at our study plots in Reserva Ducke. While the maximum elevation difference within the grid is just 58 m, and the maximum difference between adjacent high and low sample plots is just 43 m, the mean inclination of slopes is 26° (maximum slope is 48°), and these slopes could prevent dispersers from moving seeds from the bottomlands to the uplands. The altitudinal difference in itself may not be a problem, but potential dispersers may have difficulties navigating steep slopes even if these are short. A second possible explanation for the absence of adult *A. microcarpa* in the uplands is related to environmental control in the seedling phase. Similar transplant experiments conducted in central Amazonia with a clay-soil specialist palm (*Oenocarpus bacaba*) and a sandy soil specialist palm (*Socratea exorrhiza*) showed that the sand-specialist germinated well along the entire gradient (Pacheco, 2001), just as *A. microcarpa* did in our experiment. That study also found that the impact of herbivores on seedlings was similar in both species, but that protection against herbivory reduced mortality only in the clay-specialist. This supports the idea of

a trade-off between growth and defense against herbivores in pairs of closely related species in the same clay/sand scenario proposed by Fine et al. (2004, 2006). Such a process could also account for the mismatch between the germination results and the spatial distribution of *A. microcarpa*, but this remains to be tested.

Considering the germination and removal patterns and the adult distribution patterns, we infer that dispersers are the most important factor keeping *A. microcarpa* in bottomlands and that, environmental mechanisms are of secondary importance. For *A. attaleoides* the seeds were heavily removed, and germinated in only four plots. However, since these four plots were located along the entire topographic gradient, we cannot make conclusions about differences in germination patterns with altitude between the two species. While not conclusive, the findings for *A. attaleoides* are at least qualitatively similar to those for *A. microcarpa*, i.e., with no clear topographic constraint on germination.

Compared to reported germination rates for other non-spiny cocosoid palms (37%) under green house conditions (Wagner, 1982), our germination rate of 26% appears reasonable. Dormancy, which is very common in non-spiny cocosoid palms, may cause this low germination rate, but as the germination did not vary along the gradient, we believe that this does not affect our conclusion with respect to the topographic gradient.

4.2. Seed removal

Seed removal in *A. attaleoides* was not related to presence or abundance of adults or to the proportion of adults fruiting in the plot. For *A. microcarpa* we found that more seeds were removed in

Table 3
Ecological and reproductive traits of *Attalea attaleoides* and *A. microcarpa*.

Species	Distribution	Habitat	Pollinators
<i>Attalea attaleoides</i>	French Guiana, Surinam and Brazil (Amapá and Amazonas) ^a	Higher areas and occasionally slopes (study area) ^b ; lowland rain forest on terra firme, rarely to 750 m elevation ^a ; campinarana (sandy soils) ^c	Beetle pollinated, most by <i>Mystrops</i> (Nitidulidae) and <i>Phyllotrox</i> (Curculionidae) ^d
<i>Attalea microcarpa</i>	Colombia, Venezuela, Guianas, Peru and Brazil (Amapá, Amazonas and Pará) ^a	Restricted to bottomlands (study area); lowland rain forest; open low forest, or rocky places, usually on sandy soils. ^a Semi-open areas or wet areas in sandy soils in low altitudes ^c	Feeding and ovipositing (Curculionidae, Nitidulidae and Staphylinidae) ^e

^a Henderson (1995).

^b Costa et al. (2009).

^c Lorenzi et al. (2010).

^d K uchmeister et al. (1998).

^e K uchmeister et al. (1993).

Table 4List of possible dispersers of *Attalea attaleoides* and *A. microcarpa* in the reserva Ducke, including traits, home range, and habit.

Possible dispersers ^a	Home range	Activity period ^b	Habit ^c
<i>Potos flavus</i>	8–50 ha	Nocturnal	Arboreal
<i>Tapirus terrestris</i>	–	Mostly nocturnal, partially diurnal	Terrestrial
<i>Tayassu tajacu</i>	30–800 ha ^c	Diurnal	Terrestrial
<i>Odocoileus virginicus</i>	229 ha ^d	Diurnal/nocturnal	Terrestrial
<i>Mazama americana</i>	–	Diurnal/nocturnal	Terrestrial
<i>Mazama gouazoubira</i>	–	Mostly diurnal	Terrestrial
<i>Dasyprocta leporine</i>	–	Diurnal	Terrestrial
<i>Sciurus spadiceus</i>	–	Diurnal	Terrestrial/Arboreal ^e
<i>Cebus apella</i>	850 ha ^f ; 180 ha ^d	Diurnal	Arboreal/Prefer bottomlands areas near streams ^a
<i>Saimiri sciureus</i>	65 ha ^d	Diurnal ^g	

^a Mendes-Pontes et al., 2008.^b Emmons and Feer (1997).^c MacDonald (1984).^d Jones et al. (2009).^e Hershkovitz (1969).^f Gordo et al. (2008).^g Coe and Rosenblum (1974).

plots with higher abundance of adults, but this pattern was driven by a single plot with an extremely high density of *A. microcarpa*. Other studies of seed removal or predation in palms have found more clearly positive density-dependent patterns, i.e., with higher removal/predation in areas of higher adult abundance (DeSteven and Putz, 1984; Forget, 1992). Our results for seed removal reinforce the idea that dispersal limitation affects the occurrence of this palm; i.e., if seeds are available they will be removed independently of the presence of adults, but not independently of the topographic condition.

Removal of *A. attaleoides* seeds was highly related to slope, being lower in the more inclined areas. The tendency was the same for *A. microcarpa*, even if the relationship was not statistically significant. These patterns suggest that *Attalea* seed dispersers (mostly species that are also seed predators) are less active on steep slopes, which may constrain *Attalea* species to flatter areas due to limited seed input into steep areas. The lack of influence of topography on *Attalea* seed germination rates is consistent with this interpretation. In agreement with our findings, the cocosoid palm *A. mexicanum* also experienced lower seed removal rates on slopes in a Mexican rain forest (Klinger and Rejmánek, 2010). Slope avoidance by seed dispersers would act to reinforce the respective hill-top and bottomland associated distributions of the two studied *Attalea* species, but another factor is needed to explain how these consistent topographic associations arise in the first place, e.g., physiological constraints (Gibbons and Newbery, 2002) – post-germination, given our germination results – or predation-mediated effects (Fine et al., 2004, 2006).

5. Conclusion

Our results are consistent with the distributions of *A. attaleoides* and *A. microcarpa* on local- and landscape scales being partially set by topographically-constrained dispersal, mediated by disperser behavior, and partially by more direct environmental control on local individual performance, mediated by post-germination filters associated with topography. Notably, disperser avoidance of steep slopes may create seed shadows biased toward flatter habitats and thereby limit dispersal to and colonization of steep slopes. In our case, avoidance of steep slopes by seed dispersers may generate an absence of seeds of *A. microcarpa* in the uplands and of *A. attaleoides* in the lowlands. Furthermore, our germination data show that there is limited environmental control in the germination phase; hence, the environmental filters that must ultimately drive the consistent topographic associations of the two studied *Attalea* species must act at later ontogenetic stages. Our findings exemplify

how the important role of topography in local- and landscape-scale palm species distributions (Svenning, 1999, 2001b; Eiserhardt et al., 2011) may arise through complex interacting ecological processes.

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