Instituto Nacional de Pesquisas da Amazônia – INPA

Programa de Pós-Graduação em Ecologia

# Reprodução, distribuição e padrões de co-ocorrência em uma comunidade de palmeiras na Amazônia central: Uma abordagem teórica e experimental

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Manaus, Amazonas

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# Reprodução, distribuição e padrões de co-ocorrência em uma comunidade de palmeiras na Amazônia central: Uma abordagem teórica e experimental

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**Sinopse:**

A fim de contribuir no entendimento de grandes questões ecológicas que abordam comunidades e fatores responsáveis pela distribuição das espécies, esse estudo usou como modelo as palmeiras. Foram investigados aspectos como produção de frutos e relações filogenéticas entre as espécies da comunidade com o intuito de identificar os padrões e os mecanismos que regulam a ocorrência das espécies. Para isso usou-se uma abordagem de gradientes ambientais. Além do mais, foi realizado um experimento de semeadura em campo para investigar mais profundamente tais fatores que afetam a distribuição de duas espécies em particular.

**Palavras-chave**: Arecaceae, limitação de distribuição, gradientes ecológicos, frutificação, filogenia.

‘Anything seen from some distance seems perfect and homogeneous, approaching the point of view we took the risk and the challenge of seeing a confusion of detail whose interpretation goes beyond intelligence and creativity. Ecologists of the local community are people of immense courage.’

Dedico esse trabalho a todos aos bravos ecólogos que tentam achar padrão no caos, principalmente à Flávia Costa e Cristian Dambros, dois malucos que vêem coisas que ninguém mais vê.

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# Resumo

Uma das maiores preocupações da ecologia de comunidades é determinar quais fatores afetam a distribuição e co-ocorrência de espécies. Partindo do pressuposto da produção de frutos como sendo o último passo do estabelecimento efetivo dos indivíduos, usamos duas abordagens: gradientes ambientais e experimental, e com o auxílio de ferramentas filogenéticas procuramos determinar quais mecanismos influenciam a distribuição das palmeiras em uma floresta de terra firme na Amazônia Central. Foram amostradas 30 parcelas padrão de 1 ha do delineamento estabelecido pelo PPBio localizadas na Reserva Florestal Adolpho Ducke, onde todos os indivíduos de nove espécies de palmeiras foram marcados, contados e identificados,. Mensalmente, a presença de frutos em todos os indivíduos marcados foi monitorada e para pelo menos dois indivíduos focais por espécie por parcela ainda a quantidade de frutos foi contada. Adicionalmente, foram usados dados de 72 parcelas, incluindo as 30 amostradas neste estudo para análises das relações filogenéticas, desta vez de toda a comunidade de palmeiras. Um experimento de semeadura com duas espécies de *Attalea* em 30 parcelas foi conduzido para detrminar quais fatores controla a distribuição dessas duas espécies. De forma geral, as espécies de palmeiras monitoradas apresentam algum grau de restrição de sua distribuição ao longo do gradiente de conteúdo de argila no solo, sendo os indivíduos reprodutivos mais restritos. A produção de frutos da maioria das nove espécies de palmeiras foi condicionada à disponibilidade de água e nutrientes no solo, embora algumas espécies frutifiquem independente da posição que ocupam no gradiente. De maneira geral não foi encontrada estrutura filogenética na comunidade de palmeiras local. Os caracteres morfológicos/reprodutivos analisados não são conservados, mas sim lábeis e não estão organizados espacialmente, embora nos baixios haja uma organização com indivíduos mais parecidos ocorrendo juntos. Finalmente, as espécies de *Attalea* semeadas germinaram independentemente da posição no gradiente topográfico sugerindo que a limitação de dispersão é mais importante do que ao controle ambiental nesta fase do desenvolvimento. Estes resultados trazem conclusões importantes acerca dos fatores responsáveis pela distribuição das palmeiras mostrando que informações que não levam em consideração a produção de frutos, nem as relações filogenéticas entre as espécies podem levar a conclusões equivocadas.

**Title:** Main drivers controlling reproduction, distribution and co-occurrence patterns in a palm community in a *terra firme* Forest at central Amazonia: A theoretical and experimental approach

## Abstract

One of the main concerns of community ecology is to determine which factors affect species distribution. Starting from the premise that fruit production is the last step of true establishment, we match environmental gradients and the experimental approaches with help from phylogenetic tools to bring light into the mechanisms influencing palm distribution patterns in a terra firme forest in central Amazonia. We sampled 30 PPBio standardized plots of 1 ha each at Ducke Reserve near Manaus, where every individual from nine species was identified, marked and counted. Every month, marked palms were monitored for fruit presence and some focal individuals had their fruits counted. Besides, we used data from the whole palm community available in a data set from 72 plots in the same area to analyze the phylogenetic community structure. Additionally, we conducted a seed-sowing experiment with two species of *Attalea* in 30 plots. Overall, most of nine species monitored presented some degree of restriction in at least one developmental phase along the clay content gradient, with fruiting individuals more restricted. Even so, some species produce fruits regardless of the gradient position such as *Euterpe precatoria*, *Iriartela setigera* and *Oenocarpus minor*. We did not find phylogenetic structure in the local palm community. Additionally, the morphologic/reproductive traits were not conservative, but labile and not spatially structured. However, in bottomlands more similar individuals co-occur more than expected by chance. Finally, the sowed seeds of *Attalea* did germinate regardless of the gradient position showing a distribution pattern more related to dispersal limitation than to environmental control. These results suggest important conclusions about the factors affecting the palm distribution showing that information that do not consider fruit production and species relatedness may lead to biased conclusions compromising choise of a appropriate site for conservation purposes.

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## Introdução geral

A ecologia se baseia na observação e descrição de padrões naturais e no poder de decisão advindo da capacidade de prever eventos baseada na relação entre fenômenos naturais. Os principais questionamentos baseados na observação destes padrões podem ser exemplificados em perguntas como: quais os fatores que controlam a distribuição das espécies? Quais fatores afetam a riqueza, abundância e composição de espécies? Baseada nessas duas perguntas gerais várias hipóteses foram postuladas, entre elas a hipótese de Janzen e Connell (Janzen, 1970; Connell, 1971) que delineia algumas conclusões a respeito dos mecanismos que controlam o estabelecimento inicial e consequentemente, o padrão de distribuição das espécies. Além do mais, lança a primeira luz sobre como a relação de parentesco entre os indivíduos pode influenciar o arranjo espacial dos mesmos dentro da comunidade. Muitos trabalhos testaram as previsões de Janzen e Connell obtendo resultados diferenciados, mas na maioria das vezes, corroborando a hipótese de que a chance de uma plântula ser consumida e/ou parasitada é maior quanto mais perto da planta mãe (e.g. Augspurger, 1984; Cintra 1997a,b; Cintra e Horna, 1997; Cintra e Terborgh, 2000).

Por outro lado, estudos descrevendo os padrões de ocorrência e abundância dos indivíduos (e.g. MacArthur e Wilson; 1963), a base da ecologia de comunidades, começaram a ser relacionados com características ambientais dando forma à teoria dos gradientes ambientais (Whittaker, 1956). Contudo, nem a germinação, nem o estabelecimento inicial das plântulas, nem a ocorrência dos adultos em qualquer ponto do gradiente ambiental, pode garantir que a planta esteja efetivamente estabelecida. Estabelecimento efetivo significa que a planta é hábil em contribuir com a manuteção da população produzindo frutos e sementes irão ser dispersados e colonizar novas áreas. Outra importante hipótese que foi levantada a partir da observação de representantes de populações de plantas que ocorriam em locais onde aparentemente sua adaptação é baixa é a hipótese do efeito de massa (Shmida e Wilson, 1985). Segundo essa hipótese a área de distribuição de uma espécie pode ser ampliada por individuos que dispersam para áreas periféricas (sumidouros) onde as condições não permitem a reprodução de modo que o estabelecimento nesta área não é auto suficiente e depende de colonizações eventuais vindas das áreas onde as plantas reproduzem (fonte). Assim, estudar quais fatores afetam a produção de frutos é de extrema importância na determinação das áreas de distribuição efetiva das espécies. Alguns estudos se concentraram na descrição dos padrões espaciais e temporais da produção de frutos (Chapman *et al.,* 2005; Adler e Lambert, 2008), outros associaram a frutificação a fatores ambientais como precipitação (Ruiz e Alencar, 2004) e luminosidade (Svenning, 2000). Outro estudo relacionaram a produção de frutos com características do próprio individuo, como tamanho (Gross 1981), que tem um componente relacionado à qualidade do ambiente, número e tamanho das folhas, além de posição espacial (Piñero e Sarukhan, 1982), tamanho da copa (Sarukhan *et al*., 1984; Oyama, 1990) e tipo de crescimento (e mudança na forma da folha) no caso de *Geonoma congesta* (Chazdon, 1992). Porém, relacionar a produção de frutos com a posição espacial ou a ambientes classificados de maneira arbitrária não abordam a questão de adaptação local tão efetivamente quanto por meio de estudos relacionando a produção de frutos à gradientes ambientais.

A hipótese dos gradientes ambientais resultou da observação da substituição na ocorrência das espécies ao longo de uma gradiente de variação altitudinal (Whittaker, 1956). Os principais gradientes encontrados na Amazônia Central estão relacionados à topografia e às características associadas ao solo, como por exemplo granulometria (Lucas e Chauvel, 1992). Ao longo do gradiente topográfico os solos argilosos, predominantes nas áreas mais altas, vão sendo substituidos por solos com cada vez menos argila e mais areia nas áreas mais baixas (Chauvel *et al.*, 1987). Essa substituição tem implicações cruciais para as plantas, principalmente porque o tamanho e a natureza das partículas do solo afetam a captação de nutrientes pelas raizes das plantas, além da disponibilidade de água (Lambers *et al.*, 2008). Por estar sob um solo muito antigo, proveniente da Formação Alter do Chão (Ribeiro *et al.*, 1995; Hoorn e Wesswlingh,. 2010), as florestas de terra firme na Amazônia central enfrentam uma forte limitação de fósforo (Mcgroddy *et al.*, 2004). O fósforo é um nutriente extremamente importante, juntamente com os cátions trocáveis para o vigor, crescimento e amadurecimento de frutos (Brady, 1974). Outro gradiente importante relacionado à topografia, é o da disponibilidade de água. Áreas mais altas (platôs) têm o lençol freático mais profundo do que as áreas de baixio, onde a água pode até aflorar. As partículas de argila se aderem firmemente às moléculas de água diminuindo a sua disponibilidade, principalmente nos períodos mais secos. Mesmo nos trópicos úmidos, a tolerância à seca e ao encharcamento sazonal do solo limita a distribuição das espécies (Wright, 1991; Engelbrecht *et al.*, 2002).

Recentemente cresceu a proeocupação em incorporar fatores históricos nos estudos ecológicos (Webb *et al.*, 2002). Os fatores históricos interagem com os fatores ecológicos para moldar a distribuição das espécies e a composição das comunidades. Desta forma, a evolução dos caracteres e as relações entre as espécies passou a ser uma preocupação recorrente nos estudos sobre os fatores que governam a co-ocorrência de espécies na comunidade, uma vez que ajudam a entender o processo de formação das comunidade (Webb *et al.*, 2002; Wiens e Graham, 2005). Historicamente, predominava a Teoria do Nicho (Hutchinson, 1957; Soberón, 2007), baseada na visão de que a identidade das espécies e suas relações ecológicas (não filogenéticas), como, por exemplo competição, predação, além de adaptação ambiental (Tilman, 1994) eram as principais forças moldadoras das comunidades. Posteriormente, a Teoria Neutra passou a questionar a importância das diferenças entre as espécies e enfatizar que, na verdade, as espécies são similares na capacidade competitiva e que a capacidade de dispersão regulada pelo acaso seria mais importante na formação das comunidades (Bell, 2001; Hubbell 2001). Muitas das mais proeminentes hipóteses e teorias ecológicas estão relacionadas com a primeira ou a segunda visão, como a hipótese do efeito de massa e de abundancia/colonização de MacArthur e Wilson (abordagem neutra) e as hipóteses de competição/predação de Janzen e Connell (abordagem de nicho). Assim, os processos neutros e de nicho parecem interagir, mas sua importância é fortemente dependente da escala de estudo (McGill, 2010).

Adicionando o componente filogenético à complexidade das regras de assembléia e assumindo a premissa de que as espécies mais próximas são mais parecidas (Princípio do conservatismo de Nicho – ver Blomberg *et al.*, 2003 e Losos, 2008 para uma discussão completa), espécies mais próximas filogeneticamente tendem a ocorrer juntas no ambiente (Webb *et al.*, 2002, Cavender-Bares *et al.*, 2004). Por outro lado, espécies mais distantes filogeneticamente ocorrem mais dispersas do que o esperado ao acaso (Webb et al., 2002, Cavender-Bares et al., 2004). Novamente, a escala de estudo é importante na interpretação desses padrões. Em escalas maiores, onde as diferenças entre os ambientes são mais marcantes, as espécies mais próximas e por isso mais parecidas são 'filtradas' pelo ambiente e co-ocorrem mais do que o esperado ao acaso. Esse grupo de espécies mais relacionados é organizado diferentemente em escalas menores por processos de nicho (Teoria da similaridade limitante – McArthur e Levins, 1967; Huston, 1979; Ricklefs, 1987) que postulam que espécies muito parecidas não vão ocorrer juntas por causa da forte competição e por processos neutros, que envolvem a capacidade de ocupar todos os locais disponíveis. Contudo, há evidências de que a premissa da conservação de nicho não deve ser assumida (Losos, 2008) o que pode mudar drasticamente as conclusões sobre estrutura filogenética das comunidades. Vários exemplos na literatura mostram que espécies mais próximas filogeneticamente podem ser mais distantes morfologica/ecologicamente apresentando caracteres evolutivamente lábeis (Losos, 2000; Blomberg *et al.*, 2003; Cavender-Bares *et al.*, 2004; Silvertown *et al.*, 2006a,b).

As palmeiras constituem um dos elementos mais conspícuos das florestas tropicais (Kahn e Castro, 1985). São consideradas 'recursos-chave' porque produzem frutos o ano todo, ao contrário das outras espécies (Terborgh, 1986). Além do mais, o grupo possui uma filogenia datada, resolvida ao nível de gênero (Couvreur *et al.*, 2011) e constitui um modelo útil para entender o processo de formação das comunidades, devido a sua grande área de distribuição. Alguns gradientes ambientais mais importantes são conhecidos por influenciar alguns aspectos da ecologia das palmeiras como a fertilidade do solo e a disponibilidade de água afetando a riqueza (Bjorholm *et al*,. 2005; Bjorholm *et al.*, 2006; Kristiansen *et al.*, 2011), a distribuição (Svenning, 2001b), a similaridade da comunidade (Andersen *et al.*, 2010) e a composição da comunidade (Vormisto *et al.* 2004). A topografia, que está relacionada com esses aspectos do solo mencionados acima (e.g. Svenning, 2001b) parece exercer um papel importante no controle da distribuição das palmeiras na escala local e da paisagem (Kahn e Castro, 1985; Svenning, 1999; Svenning e Balslev, 1998; Svenning *et al.*, 2009, Costa *et al.*, 2009), como vemos no caso de duas espécies de *Attalea* que ocorrem em posições distintas ao longo do gradiente topográfico.

A distribuição de abundância das espécies de palmeiras na Reserva Ducke mostram um padrão interessante para algumas espécies, destacando-se as espécies "acaules" de *Attalea*. Das duas espécies inventáriadas, uma ocorre exclusivamente no baixio, *Attalea microcarpa* Spruce e a outra, *Attalea attaleoides* Mart. ocorre no platô e chega algumas vezes a áreas mais baixas seguindo terrenos mais inclinados. A limitação de dispersão pode evitar que as espécies ocorram em locais propícios (Hubbell, 1999; Wright, 2002). A dispersão pode também gerar um padrão de distribuição agrupado não relacionado às condições ambientais ou ligadas ao ambiente, mas pela preferência dos agentes dispersores a determinados locais. De fato, os dispersores podem causar heterogeneidade espacial nos padrões de dispersão de sementes (Svenning, 2001b) e seu movimento pode ser afetado, por exemplo, por inundações sazonais (Bodmer, 1990), estrutura da copa das árvores (Schupp and Frost, 1989), disponibilidade de frutos e topografia (Salas, 1996). Então, o ambiente pode afetar a distribuição das sementes através do comportamento dos dispersores (Svenning, 2001a; Eiserhardt et al. 2011) e também pode agir como barreira (Wiens and Graham, 2005). A fim de entender o que determina o padrão de distribuição de *Attalea attaleoides* e *Attalea microcarpa*, foi conduzido um experimento de semeadura em campo. A abordagem experimental em trabalhos de ecologia em campo, apesar das dificuldades em controlar as variáveis, é crucial para descrever as relações diretas entre as variáveis estudadas.

Partindo do pressuposto da produção de frutos como sendo a última fronteira do estabelecimento efetivo dos indivíduos, utilizamos as abordagens de gradientes ambientais e experimental e com o auxílio de ferramentas filogenéticas procuramos determinar os mecanismos que influenciam a distribuição das palmeiras em uma floresta de terra firme na Amazônia Central. Esta tese está organizada em três capítulos, escritos em formato de artigos que serão submetidos para revistas científicas de alto impacto.

## Objetivo geral

Determinar os fatores que afetam a reprodução e a distribuição de nove espécies de palmeiras em uma floresta de terra firme na Amazônia Central.

## Objetivos específicos

(1) Determinar se as espécies estão restritas ao longo do gradiente de teor de argila no solo.

(2) Determinar o ponto de quebra que divide as distribuições, caso haja restrição.

(3) Determinar quais gradientes ambientais podem afetar a produção de frutos (e.g. proporção de indivíduos frutificando e média de frutos por indivíduo).

(4) Determinar se species mais próximas filogeneticamente co-ocorrem mais do que o esperado ao acaso.

(5) Determinar se os caracteres morfológicos/reprodutivos são conservados nas espécies da comunidade local.

(6) Determinar se a relação filogenética muda ao longo do gradiente de argila assim como a abundância dos indivíduos.

(7) Determinar se há estrutura espacial na distribuição das características morfológicas e ecológicas.

(8) Determinar se a germinação de sementes de *Attalea attaleoides* e *Attalea microcarpa* está relacionada com a presença e a abundância de adultos na parcela.

(9) Determinar se a germinação e a remoção de sementes de *Attalea attaleoides* e *Attalea microcarpa* está relacionada com a topografia.

# Capítulo 1

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Freitas, C.G., Costa, F.R.C. & Cintra, R. Restriction limits and main drivers of fruit production in palm species along environmental gradients at mesoscale in Central Amazonia. Manuscrito em preparação para o *Journal of Ecology*

# Restriction limits and main drivers of fruit production in palm species along environmental gradients in Central Amazonia

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Headline: Palm fruit production in environment gradients…

## Summary

1. Adult individuals of *Attalea attaleoides*, *Attalea microcarpa*, *Oenocarpus bacaba* and *Oenocarpus bataua* occur in sites where they do not reproduce, indicating a possible mass effect;

2. Most of the studied palms had some degree of habitat restriction. Along the clay content gradient *Attalea attaleoides*, *Attalea microcarpa* and *Oenocarpus bacaba* are restricted to different degrees in each development phase, e.g. the entire population having a wider area than adults and adults more widely distributed than fruiting individuals;

3. *Oenocarpus bataua* and *Socratea exorrhiza* are restricted only at the potential adult and reproductive stages, whereas *Euterpe precatoria*, *Iriartela setigera* and *Oenocarpus minor* occur and fruit along the whole gradient;

4. Water availability and exchangeable bases are limiting in the ability to produce fruits and in the amount of fruits produced (e.g. proportion of individuals fruiting and mean of fruits produced per individual);

5. Synthesis: Some palm species are restricted along the soil clay content gradient, if not in all stages, at some developmental stages, showing that the effective size of the population is smaller than shown in typical species abundance/gradient studies. In spite of some species fruiting regardless of their position along the ecological gradients, the lack of studies relating fruit production to environment condition can lead to biased decisions in terms of conservation planning.

**Key-words:** Arecaceae, cation exchangeable bases, fructification, landscape scale, species distribution limits, water availability.

## Introduction

In tropical rain forests, there has been a gap between studies of plant distribution and plant reproduction at spatial scales higher than sample plots. Most studies do not include information on the reproductive status of individuals, and if so, they mostly focus on how local environmental and ecological factors may affect flower or fruit/seed production. We argue that a link of these two approaches is crucial to progress the knowledge in plant community ecology and management.

Many studies in plant ecology have focused on the factors affecting plant establishment, mainly after Janzen and Connell set up their theory (Janzen 1970; Connell 1971; Augspurger 1983; Clark & Clark 1994; Cintra 1997a,b; Cintra & Horna 1997; Hammond & Brown 1998; Cintra & Terborgh 2000). In spite of the inspiring and extremely important conclusions from those studies, most took as establishment simply the attainment of some developmental phase after seedlings, what cannot be considered establishment from the point of view of the population. Also, the great majority of studies on species distribution and habitat associations do not discriminate the patterns of each species' developmental stage, and the association of species to the environment is evaluated only for the entire population. However, plants are expected to change their needs and tolerances as they grow (Brady 1974), so, habitat associations and restrictions may not be the same at each stage. Comita *et al.* (2007) showed these differences in association at the seedling or higher plant stages, but still the critical phase of plant maturity was not considered separately, and therefore the conclusions about species restrictions or associations are limited. The presence of adult-sized plants in a given site does not guarantee they will contribute seeds to promote a possible increace in the population, and parts of the population may be only sinks. An evaluation of the distribution of reproductive plants is therefore a key to understand the real limits to the distribution of species and the real impact of habitat restrictions in communities.

Mass effects may extend the distributional range of a species even at small scales (Shmida & Wilson 1985) and blur our perception of the factors affecting the success of a population. In management and conservation, knowing which environments support viable populations is vital. However, many decisions are made on distributional ranges derived from niche modeling of species occurrence, and occurrences do not necessarily indicate the status of individuals. We show here that distributions derived from the relationship between the entire population and the environment will generally overestimate the ranges of distribution of a viable population.

Excluding the effect of pollen limitation, the variation in plant fecundity can be influenced by spatial differences in the availability of light, water and nutrients. Therefore, plants have to share resources between growth, reserves, and breeding (Chapin *et al*. 1990), and those estabilished in sites with more resources available are better able to reproduce more effectively. Plant fruit production has been associated before with a critical size, and the length of time needed to achieve critical size is strongly dependent on environmental conditions (Gross 1981). Fruit production was also associated with leaf area and spatial location (Piñero & Sarukhan 1982) and crown height in *Astrocaryum mexicanum* (Sarukhan *et al*. 1984), and *Chamaedorea tepejilote* (Oyama 1990), and is suggested to be linked with growth form (change in leaf morphology) in *Geonoma congesta* (Chazdon 1992).

Water availability is the factor that most strongly limits terrestrial plant production (Lambers, Chapin III & Pons 2008) and affects nutrient uptake. Tolerance to drought is an important trait constraining the distribution of tropical plants (Wright 1991; Engelbrecht *et al.*

2002). In spite of the higher precipitation levels in humid tropical region, the amount of rain can be variable enough to cause extreme drought periods that affect plants (Tobin *et al.* 1999). However, in bottomlands and first slopes, the tree root can reach the water table and in the wet season those areas can be waterlogged (Nobre *et al*. 2011). Tolerance to waterlogging may prevent non-tolerant species to occur in bottomlands, though the tolerance to the alternance of extreme conditions i.g. flooding and the subsequent dry season seems to be the main factor shaping the communities (Lopez and Kursar, 1999; 2003). Many plants in the humid tropical region, and especially palms, have a superficial root system. The root system of *Bactris gasipaes* Kunth, for instance, is only 0.4 m deep (Ramos *et al.* 2009). This may be linked to the superficial distribution of nutrients in the topsoil (Jobbágy & Jackson 2001). Besides, the terra firme forests in Central Amazonia, based on old soils originated from Alter do Chão formation (Ribeiro *et al.* 1995; Hoorn & Wesswlingh. 2010) are known to be nutrient limited (see Mcgroddy *et al.* 2004). Therefore, the way roots interact with the soil to uptake nutrients and water may shape the distribution of the effective population able to reproduce.

Little attention has been given to how environment affects palm fruit production (but see Chapman *et al.* 2005 and Ruiz & Alencar 2004). Kahn & Castro (1985) had already linked fruit production of *Euterpe precatoria* and *Oenocarpus bacaba* to hidrology showing that juvenil life stage had a wider distribution area than reproductive adults. Palms are one of the most conspicuous and important tropical forest elements (Kahn & Castro 1985), considered a key resource to frugivorous animals due to their year-round fruit production (Terborgh 1986). They are also important resources for human populations in the Amazon. Given this importance, we chose nine palm species as study models to understand how fruit production may be linked to the environment at a mesoscale, and how our perception of aspecies' habitat restrictions changes when different life-stages are examined. Our main hypotheses were: (1) Mainly restricted species, fruiting individuals will occurs in a more restricted area than the entire population across a given gradient. (2) Fruit production (e.g. proportion of individuals fruiting and mean of fruits produced per individual) is limited by environmental condition and this limitation is species specific.

## Materials and methods

### Study site

This study was conducted in Adolpho Ducke Forest Reserve (RFAD) from the National Institute of Amazonian Research (INPA), 26 km north from Manaus (02°55’S/59°59’W, Fig. 1). The reserve has 10,000 ha (10 x 10 km) covered by terra firme tropical rain forest. The canopy is 30-37 m high and in the understory *Atrocaryum* spp. and *Attalea* spp. palms are abundant (Ribeiro *et al.* 1999). The mean temperature is 26°C, the relative humidity varies from 77 to 88 % and the annual precipitation varies between 1750 and 2500 mm. The soil is derived from Tertiary marine sediments of the Alter do Chão formation and constitutes a gradient, from clayey ferralsols in the high and flat areas (uplands) (Quesada *et al.* 2011), becoming sandier in slopes toward bottomlands until they are almost pure sand in the lower areas (bottomlands). The clay soils are mainly ferralsols and the sandy soils are podzols. There is a concomitant change in soil drainage, from well drained on the plateaus, poorly drained slopes and waterlogged bottomlands (Kahn & Castro, 1985). Waterlogged soils penetrate upslope, reaching about 8m vertical height above the nearest stream (Nobre *et al*. 2011). This soil gradient is thought to be an important driver of tree and palm community structure (Castilho *et al.* 2006, Costa *et al.* 2009, Kahn & Castro, 1985).

### The palm species

Nine palm species were selected based on their abundance and economical potential. All the genera are classified within the subfamily Arecoideae, but grouped in four tribes according to Dransfield *et al*. (2008): Iriarteeae (*Iriartella setigera* (Mart.) H Wendl. and *Socratea exorrhiza* (Mart.) H. Wendland); Euterpeae (*Euterpe precatoria* Mart., *Oenocarpus* *bacaba* Mart., *O. bataua* Mart. and *O. minor* Mart.); Geonomateae (*Geonoma aspidiifolia* (Barb. Rodr.) Wess. Boer); Cocoseae (*Attalea attaleoides* Mart. and *A. microcarpa* Spruce). According to Dransfield *et al.* (2008) all genera included in this study are monoecious. This is crucial because we can be sure that a plant that never produced fruits is not actually a male plant. The palms were identified using recent palm treatments such as Henderson 1995, Ribeiro *et al.* 1999 and Emilio 2008 (computer based interactive key). Plants were classified as potential adults according to their height or by the number of leaves in the case of acaulescent palms following potential reproductive height in specialized literature (Henderson 1995; Lorenzi 2010): *Attalea attaleoides* (8 leaves), *A. microcarpa* (6 leaves), *Euterpe precatoria* (10 m), *Geonoma aspidiifolia* (1 m), *Iriartella setigera* (3 m), *Oenocarpus bacaba* (10 m), *O. bataua* (18 m), *O. minor* (3 m), *Socratea exorrhiza* (15 m). In addition, we consulted the expertise of palm specialists and local inhabitants and went on a field trip to explore in detail the variability of heights in reproductive palms.

## Sampling design and data collection

In the reserve there is a grid of regularly spaced (1 km) north-south and east-west trails covering a total area of 64 km$^2$. The grid was established and is maintained by PELD-Brazil (Long Duration Ecological Research Project) and PPBio (Biodiversity Research Program) a partnership of INPA with MCT-Brazil (Science and Technology Ministry). Seventy-two permanent plots were sistematically distributed over this grid, of which 30 are the standard permanent PPBio plots. Each plot is 250 m long, with variable width depending on taxa or life stage and are 1 km distant from each other. The plots follow altitudinal contour, that minimize the internal variation in soil properties which tend to be correlated with altitude and have a central 1 m wide corridor for transit, which allows the researchers to access the plots causing minimal disturbance.

Palms for this study were sampled in two diffent ways; first, counts of the entire population of each species (including young at least 1 m tall to potential adults) were done in a 4 m wide strip, along the 250 m of each plot, by J.-L. Guillaumet (see Costa *et al.* 2009). Second, by Freitas CG in the 30 PPBio standard plots where potential adult individuals were counted and monitored in a 40 m wide strip in each 250 m-plots. From August 2008 to January 2009 all potential adults of the nine palm species cited above were identified, marked with sequential numerical tags and located with an X,Y coordinate system. Every month, from May 2009 to October 2010 all individuals were monitored for the presence of fruits. We also counted the number of fruits in at least two focal individuals, distant 1at least 00 m from each other, of each species in each plot. For small and acaulescent palms we pulled aside the bunch to see all the fruits. For tall palms a field assistant climbed the palm or a neighboring tree and counted directly all the fruits without cutting the bunch. The counting of fruits in tall individuals was limited by the raining season because the trunks were too wet to be climbed.

Altitude, clay content, nutrient content (exchangeable bases and phosphorus), and inclination were taken from a database available at the PPBio site (http://ppbio.inpa.gov.br/Port/inventarios/ducke/pterrestre/). The distance to the nearest stream and a metric describing the height of the terrain above the nearest drainage (hereafter called HAND) were calculated by Juliana Schietti in 2010. The distance to the nearest stream was derived from a hydrographic map as the distance, in meters, between the central point of the plot and the nearest watercourse. The central point of the plot was mapped with a GPS based on 10 points georeferenced along the central longest axis of the plot. HAND values were produced following the algorithm developed by Rennó *et al.* (2008) and based on

SRTM-DEM (Shuttle Radar Topography Mission – Digital Elevation Model) data. The model's starting point for first-order streams was defined as 30 pixels (24 ha) of land area furnishing runoff to that point. This choice was validated in the field.

Altitude of each plot was obtained by a professional surveyor, with a theodolite. The terrain slope was measured with a clinometer at six equidistant points (at each 50 m) along the main length of the plot, and averaged for the entire plot. At these six points soil samples were taken at a depth of 0–5 cm and bulked to produce a composite sample for each plot. Before analysis, samples were cleaned of roots, air-dried and sieved through a 2-mm sieve. Soil's chemical properties were analyzed at the Soil Laboratory of EMBRAPA-Manaus (Mertens 2004). The sum of exchangeable bases (Ca++, Mg++, K+), hereafter called bases, did not include $Na^+$ because it was too low, bellow the spectrometer detection level.

Data analysis

Two groups of analysis were done to understand how palm reproduction is limited by environmental factors, (1) restriction analysis and (2) Regression Models. The first is based on plant occurrences, and examines how the environment filters each species through its development. Since this analysis is based on presences and absences, it is designed to capture only strong patterns of restriction. The second is based on abundances, and examines subtleties of how the environment affects the abundance of reproductive individuals or the number of fruits per plant.

Palms were assigned to three population stages: 1) entire population, including young to potential adult individuals; 2) potential adults only and 3) reproductive adults. The entire population stage is a heterogeneous group including mainly young life stages, though we did not take size measurements. A comparison between Costa et al. 2009 data and those collected by the first author shows that around 90% of the entire population individuals were juvenile plants.

(1) Restriction Analysis. We tested whether the entire population of each species was restricted along the main ecological gradients, and if futher restriction limits are found for each developmental stage. The test examines whether occurrences are more restricted to some portion of the gradient than expected by chance using a statistic to access habitat specificity that is independent of the number of sites occupied (Kinupp & Magnusson 2005). The mean and the standard deviation of the value of the environmental gradient for those plots occupied by the species or stage are determined. The expectancy is that a restricted species have a smaller deviation than would be found if the same number of occupied sites was randomly distributed along the entire environmental gradient. To determine the variation in environmental gradient expected to be found in occupied sites when the null hypothesis (no habitat specificity) is true, we used a resampling procedure. Using the number of sites occupied by a species (N), we randomly sampled all the surveyed sites (i.e. along the entire environmental gradient) and determined the standard deviations of soil clay content in the sample. This process was repeated 1000 times for each life stage and each species separately (non hierarchical model using only on variable – clay content). The proportion of standard deviations in the 1000 random samples that were equal to, or less than, the observed standard deviation was used to test the null hypothesis of no habitat restriction for each species and for each stage. Restriction analysis was done for the clay content gradient, which is related to topography and is the most general gradient in the area (Costa *et al.* 2005). Statistical calculations followed Kinupp & Magnusson (2005), and the implementation in R was done by Victor L. Landeiro. If any life stage in each species was restricted, a regression tree was used

to find the break point (restriction limit) dividing that life stage of a given species into the two most homogeneous groups (occurrences and absences) based on the environmental gradient. Regression trees were implemented with the mrpart package in R (Therneau & Atkinson 2000).

(2) Regression Models. The metrics describing reproduction were the proportion of fruiting individuals per plot, calculated as the ratio between fruiting individuals and the abundance of potential adults (hereafter called adults) for each species in each plot. We calculated the mean of fruits per plot using data from the two focal individuals we used for fruit counts. For this, we used only the first bunch we saw with fruits in the field.

We used Cleveland dot-plots to search for outliers, and pair-plots and the Variance Inflation Factor (VIF) to look for correlations among the independent variables - altitude, soil clay content, soil nutrients content (phosphorus and exchangeable bases), distance to the nearest stream, HAND (height above the nearest drainage) and terrain inclination. After correlation analysis we excluded altitude, distance to the nearest stream and clay content for being highly correlated with HAND, which we believe is a better proxy for the proximate factors (water availability and tolerance to the waterlogging) affecting reproduction.

Simple or multiple regressions were used to determine the environmental effects on proportion of individuals fruiting and mean fruits per individual. A model selection was run for each species, retaining only significant variables. We chose a backward selection approach and AIC values resulting in specific models depending on each species, but initial models always included exchangeable bases, phosphorus, inclination and height above the nearest drainage (HAND). GLM (binary or Poisson), quantile or ordinary LM regressions were chosen according to the distributions of the response variables. When overdispersion was detected, we applied a correction in the standard errors using a quasi-Poisson or a Negative Binomial model (Zuur *et al*. 2009). GLM models do not provide a $R^2$ value, so we used the percentage of the null deviance minus the residual deviance divided by null deviance to calculate the amount of deviance in the response variable that is explained by the predictor (Zuur *et al*. 2009).

When the response variable had a distribution in which the upper boundary changed along the predictor we fitted a Quantile Regression model. We chose Quantile Regression because very often there are factors not measured that could affect the reproduction in an uneven way along the environmental gradient, causing heteroscedasticity, a common pattern in ecological data (Cade & Noon 2003). In those cases a model based on the mean of the response variable would have a weak predictive power and might hide an important ecological relationship.

All the analyses were performed in the R statistic environment (R Development Core Team 2010) with the packages Hmisc 3.8-3 (Harrell 2010), MASS (Venables & Ripley 2002), Vegan (Oksanen *et al.* 2011), quantreg (Koenker 2011) and functions developed by C.S. Dambros).

## Results

A total of 2988 adult individuals from the nine species were found and tagged (Appendix 1). Most species (six out of nine) had a clear restriction in occurrence along the clay content gradient, and the restriction tended to become stronger through palm development stages. *Attalea attaleoides*, *Attalea microcarpa* and *Oenocarpus bacaba* were restricted at every population stage (Fig. 2). We could not find a significant restriction for *Attalea attaloides* adults, although the pattern is clear in the graphic (Fig. 2a) and the restrictions in the entire population and in the fruiting individuals levels reinforce this possibility.

*Oenocarpus bataua* and *Socratea exorrhiza* were restricted only at the adult and reproductive levels (Table 2, Fig. 2d). Congeneric species pairs were restricted to opposite ends of the soil gradient, *Attalea attaleoides* and *Oenocarpus bacaba* to the clayey end of the gradient, and *Attalea microcarpa* and *Oenocarpus bataua* to the sandy end. At the population level, which represents mostly the juveniles, there was a large overlap in distributions of these species pairs, especially for the *Oenocarpus*. However, adults and reproductive plants were more restricted than juveniles, and show little overlap (Fig 2).

*Geonoma aspidiifolia*, *Euterpe precatoria*, *Iriartela setigera* and *Oenocarpus minor* were not restricted to any part of the clay gradient, and also fruited regardless of the environmental condition, except for adults of *Geonoma aspidiifolia*. Overall, the point between 5 and 10% of clay seems to be a break point in the ecological response of many groups in the Ducke Reserve (F.R.C Costa, pers. comm). For a complete description of the restriction limits, including the break points between presence and absence and p values see Table 1.

Within the environmental regions (defined by soil texture) to which species occurrences were restricted, we asked if the proportion of fruiting individuals and the mean number of fruits/individual were related to other environmental predictors (bases, inclination, HAND and phosphorus). Details on the models are shown in Table 2 and 3.

Using quantile regression we are able to describe the complex relationship between HAND and the proportion of individuals fruiting for *Atallea attaleoides*. HAND sets the upper boundary of the distribution. The greater the distance the plant is from the water table, the higher the potential to produce fruits. Very likely other variables besides HAND are influencing fruit production at higher HAND values for this species (Fig. 3a). There is also a slight positive effect of HAND in the proportion of individuals fruiting of *Oenocarpus bacaba* ($R^2$=0.14; $p_w$=0.22; $p_h$=0.08, Fig. 3c). The mean fruit production of *Attalea attaleoides* was negatively associated with the soil exchangeable bases (Fig 3b; ED =0.78; p=0.001, Fig. 3d) and that of *Oenocarpus bacaba* was negatively associated with HAND, although there was no statistical support for this last relationship. There was an overall tendency to less fruiting individuals of *Iriartella setigera* in plots with higher amounts of exchangeable bases (Fig. 3e) and tendency of less fruits produced in plots with higher HAND values, although this last relationship had no statistical support (Fig. 3f). In this case HAND and exchangeable bases both seem to have a weak negative effect on *Iriartella setigera* fruit production, while these two variables have strongly antagonistic effects in *Attalea attaleoides*.

*Attalea microcarpa* produced fruits only in a small range of its occurrence within the bottomlands, as shown by the restriction analysis. There was no detectable influence of a finer environmental filter on the number of fruiting plants, although there was a tendency for less fruits in more inclined areas. *Oenocarpus bataua* also produced fruits well everywhere it occurs. Inside the range of bottomlands to which adults are restricted, variations in other environmental factors do not influence the proportion of individuals fruiting, nor the amount of fruits produced (Tables 2 and 3). *Socratea exohrriza* seems to produce fruits everywhere, although there was a weak tendency for a positive effect of exchangeable bases on the amount of fruits produced (Tables 2 and 3). Since it is a rare species in the area and we had few plots with reproductive plants, this conclusion should be taken with caution.

There was a slightly positive effect of exchangeable bases on the proportion of individuals fruiting of *Euterpe precatoria* ($R^2$=0.35; $p_w$=0.13; $p_b$=0.06). There were too few plots with data for the amount of fruits produced by this species. *Geonoma aspidiifolia* also produces fruits everywhere, but low numbers of fruits at higher HAND values (ED =0.38; p=0.02). The proportion of individuals fruiting of *Oenocarpus minor* is not related to any environmental variable, however terrain inclination strongly influences the amount of fruits produced, with less fruits in more inclined areas (ED=0.19; p=0.02).

## Discussion

The literature is filled with examples of how environmental gradients affect the abundance and distribution of tropical plant species (e.g. Tuomisto & Poulsen 1996; Kinnup & Magnusson 2005; Costa *et al.* 2005), especially palms (Svenning 2001; Vormisto *et al.* 2004; Normand *et al.* 2006; Costa *et al.* 2009; Andersen *et al.* 2010). However, it is expected that the relationships between plants and environment may change with plant development stage (Nogueira *et al*. 2011), so relationships at the entire population level may not be a good indicator of species' realized niches. The greatest majority of the studies addressing how species are restricted along topographic or soil gradients are based on the entire population, or more commonly on a sample of the population starting with the saplings (e.g. Clark *et al.* 1998; Valencia *et al.* 2004; Gunatilleke *et al.* 2006; John *et al.* 2006). Since in any population, most of the individuals are in the younger stages, the conclusions regarding species restrictions must refer mostly to the patterns given by those young plants. Here we have shown that data on the distribution at the population level is not enough to understand the real distribution limits of a species, since the established population, given by the individuals able to produce seeds, is generally more restricted. Therefore, the levels of habitat association reported in previous studies do not reflect habitat specialization and overestimate species' local distributions (see Harms *et al.* 2001).

Most palm species at our site showed a strongly restricted distribution pattern across the main environmental gradient in the region, with reproductive individuals occurring in more restricted conditions than their conspecific non-reproductive adults and the mostly juvenile population. Also, for those palms with limited distributions in the clay content gradient, there are more fine scale factors affecting the fruit production and reinforcing even more the limitation pattern.

Not only do some species not reproduce everywhere, but the amount of fruits is limited in particular sites. Some species (*Euterpe precatoria, Iriartela setigera* and *Oenocarpus minor*) are not limited at the entire population and adult levels, and may be considered generalists within our landscape. Nonetheless, for these apparently non-restricted adult palms, nutrients, water availability and terrain inclination did limit their mean number of fruits. Palms which did not respond to soil nutrients, such as *Oenocarpus bataua*, can probably use the nutrients accumulated in the litter beneath them, which can be higher than anywhere else (Chauvel *et al.* 1987; Facelli & Picket 1991). The distribution of fruiting individual reveals a local mass effect along both, the water availability and the nutrient gradients. The water availability gradient may also represent a waterlogging gradient. In the bottomlands and first slopes the water table can emerge periodically (Nobre *et al*. 2011), which can prevent non-tolerant species to ocuppy these areas. Comparing species from periodically and non-periodically flooded areas there are no differences in many parameters including seedling growth and mortality (Lopez and Kursar, 1999; 2003). Instead, the stress condition of periodically flooding followed by a dry season may be more important for community assembly (Lopez and Kursar 2003), but maybe not for fruiting. The difference in performance according to environmental conditions and suggests, mainly in the case of *Attalea attaleoides* and *Oenocarpus bacaba* a fundamental niche smaller than the realized niche, at the considered scale.

The most striking finding was that even within a tropical forest area in Central Amazonia, water availability and tolerance to waterlogging can be a factor ruling which plants are going to produce fruits. Height above the drainage, which can be considered a proxy for soil water availability and soil drainage along with exchangeable bases, was the main determinant of fruit production as a whole. In *Attalea attaleoides* and *Oenocarpus* *bacaba* the proportion of fruiting individuals increased with HAND, being higher in areas far from the water table, whereas *Geonoma aspidiifolia* had the opposite pattern. *Attalea microcarpa*, *Oenocarpus bataua* and *Socratea exorhiza* had their reproductive individuals restricted to the sandy areas, which are close to the water table (low HAND values). These patterns may be associated with the ability to tolerate drought, which is a strong constraint in tropical forests (Wright 1991; Engelbrecht *et al.* 2002). Water availability is the factor that most strongly limits terrestrial plant production (Lambers, Chapin III & Pons 2008) and has been long thought to be the main driver in palm distribution, richness and diversity at local, regional (Eiserhardt *et al.* 2011; Kristiansen *et al.* 2011) and continental scales (Bjorholm *et al.* 2005). At mesoscale, the distribution of these species and other palms has been associated to hydrology, most specifically with the tolerance to waterlogging (Kahn & Castro 1995), but we have shown that this relationship extends beyond the population distribution until the fruit production. Although ecophysiological studies of palms, besides cultivated ones, are still lacking, responses of trees may be similar and indicate the strategies behind topographic specialization. Baltzer *et al.* (2005) showed that plant species restricted to ridges of humid tropical forest had lower stomatal conductance and higher efficiency in water use than plants restricted to valleys. A higher stomatal control is useful in preventing drought stress, but may restrict growth, leading to a lower competitive advantage. Therefore, stomatal behavior – open and freely transpiring or more closed, may be behind the opposite behaviors of bottomland sandy or upland clayey specialists.

The mean number of fruits produced per individual of *Oenocarpus bacaba*, *Oenocarpus minor*, *Iriartela setigera* and *Geonoma aspidiifolia* responded negatively to exchangeable bases and HAND (only a weak tendency in *O. bacaba*), meaning that in better drained areas those species produced a significant amount of fruits. Again this seems to be related to extreme condition related to drought and waterlogging tolerance, which is striking in the case of the later since it is apparently widespread in the area and was only restricted at the adult level. The fact that some species responded positively and some negatively to the height above the nearest drainage mean that this tolerance to drought or tolerance to waterlogging is a good functional trait to separate species in trait functional space (see McGill et al 2006) and should be investigated deeply.

We expected that fruit production would be positively associated with soil nutrients, as has been previously shown for some palm species (Castro *et al.* 2007) and on the basis of classical studies on plant production. However, some species had higher fruit production in the less fertile plots. Exchangeable bases and water availability (represented by HAND) were somewhat correlated (r=0.5, p= 0.005), so that higher fertility sites are far from the water table. The model selection for these species retained bases as the best predictor of reproduction or fruit set, but this does not necessarily mean that this is the causal factor. From the other analyses performed here, we believe that water availability (or the tolerance to waterlogging) is the real causal factor of the fruit production patterns.

Although *Attalea attaleoides* had its reproductive adults restricted to the upland drier sites, fruit production was higher in the less fertile/wetter parts of these uplands. This suggests that the factors affecting establishment of mature adult plants may not be the same as those controlling the reproductive effort at the landscape scale, even though our samples are not large enough to provide strong evidence to this statement.

Studies on leaf harvest in palms show that generally fruit production is negatively affected when plants lose leaves (Zuidema *et al.* 2007, Martínez-Ramos *et al.* 2009, Lopez-Toledo 2011) and some studies have shown that the probability of reproduction or the reproductive effort is related to plant size in palms (Oyama 1990, Chazdon 1992, Cunningham 1997, Mendoza & Franco 1998). Plants that cannot keep a positive photosynthetic balance may therefore not be able to allocate resources to reproduction, since a trade-off between investments in vegetative growth and reproduction is expected (Chapin *et al.* 1990). Plants outside their preferred environment may face strong competition and, though able to survive, may not be able to maintain a positive resource balance in order to invest in reproduction. Brum (2011) has shown that leaves of two of the palms studied here (*Oenocarpus bataua* and *Oenocarpus bacaba*) were larger in the environment where we have found higher reproduction, which rise the possibility of a size controlled in reproduction. Our results suggest that only a smaller part of the area of occurrence of each species at the landscape is in fact favorable to the growth and accumulation of enough reserves that can be invested in reproduction.

Most studies of plant reproduction do not consider how reproduction is affected by environmental features at landscape scales (but see Castro *et al.* 2007), which is crucial to understand realized niches and therefore to be able to correctly manage and conserve species. Studies on the environmental effects on reproduction have been mostly on the effects of local features, such as light or the density of potential competitors in the neighborhood (Cunningham 1997, Rodriguez-Buritica 2005, Svenning 2002). Although it is important to understand these local effects to manage species for non timber forest products, understanding limitations on reproduction at the landscape scale is crucial to the conservation of species, since much of the area actually occupied by a species may represent sink habitat that is unable to sustain a population without the contribution of immigrating individuals (Tyre *et al.* 2001). This is mainly important regarding preservation of forest up to certain distance of streams or roads, since conservation planning of larger areas will hopefully include the entire environmental gradient.

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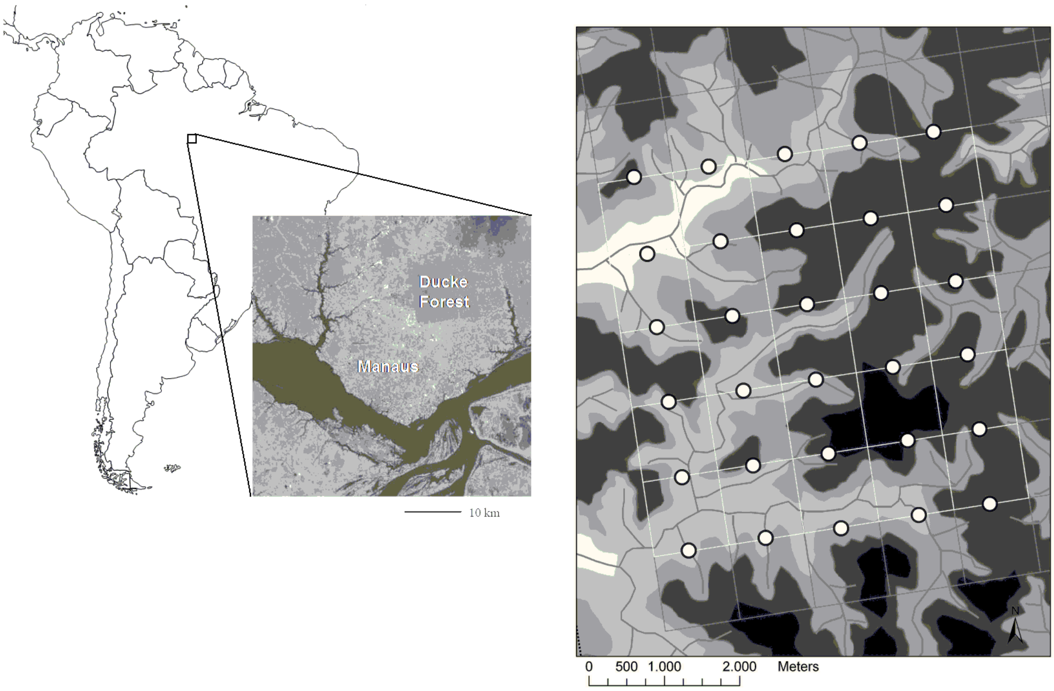

Fig. 1 The Central Amazon basin, indicating the position of the study site in the Reserva Ducke 30 km from Manaus. To the right the PPBio grid where the study was performed.

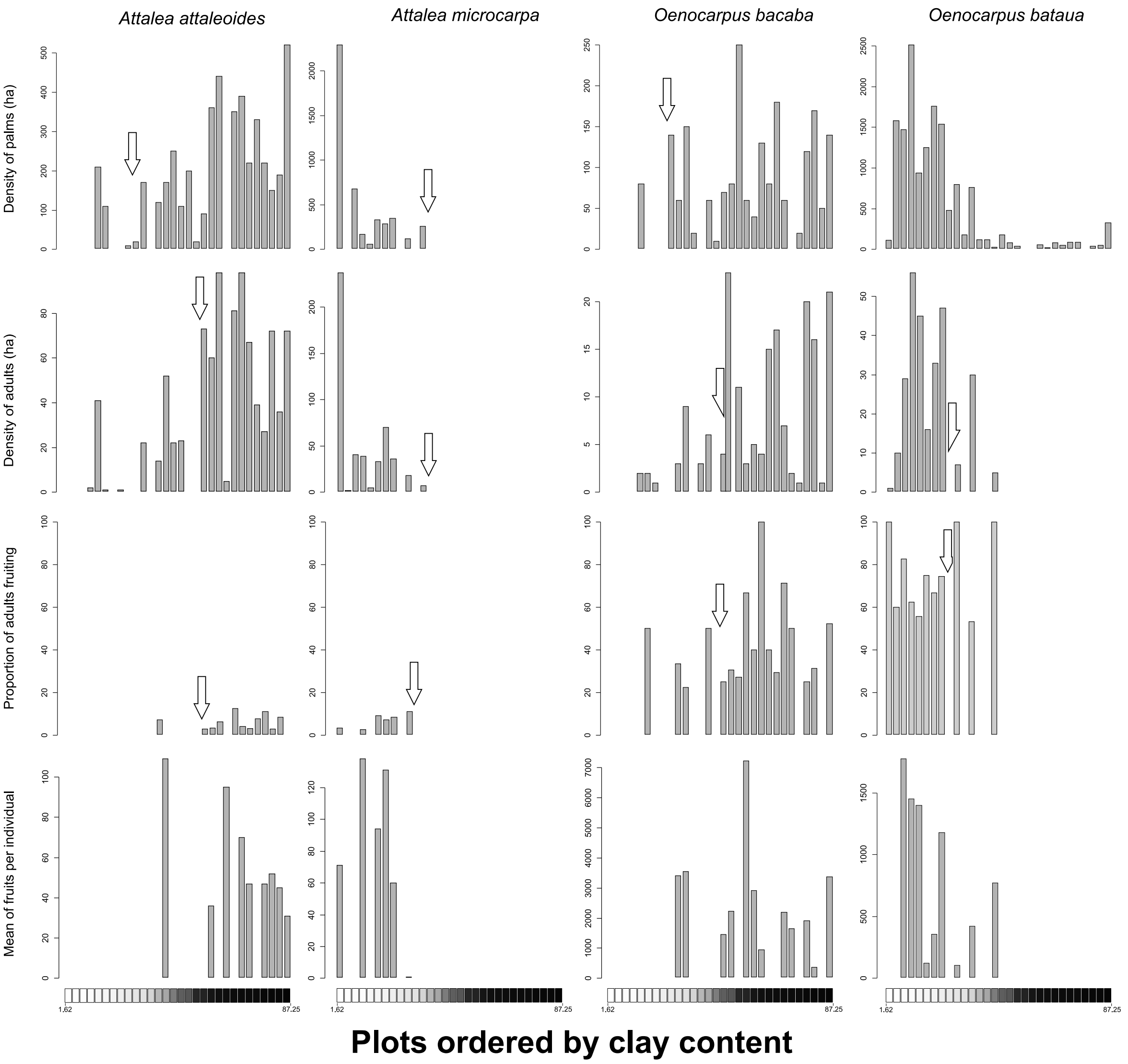

Fig. 2 Distribution of the life stages of four palm species along the soil clay content gradient in a terra firme forest at Reserva Ducke, Manaus, Brazil. Each palm species is represented by 4 panels: entire population, potential adults, proportion of individuals fruiting and mean of fruits per plot. For *Attalea attaleoides*, entire population (limit between homogeneous presence and absence = found at 4% of clay; p=0.008), adults (no restriction) and reproductive individuals (limit=67% of clay; p=0.000). For *Attalea microcarpa*, entire population (limit=12%; p= 0.000), adults (limit=12%; p=0.000) and reproductive individuals (limit=6%; p=0.000). For *Oenocarpus bacaba*, entire population (limit=4%; p=0.003), adults

(limit=37%; p=0.008) and reproductive individuals (limit=37%; p=0.003). For *Oenocarpus bataua*, entire population (no restriction), adults (limit=4%; p=0.000) and reproductive individuals (limit=4%; p=0.000).

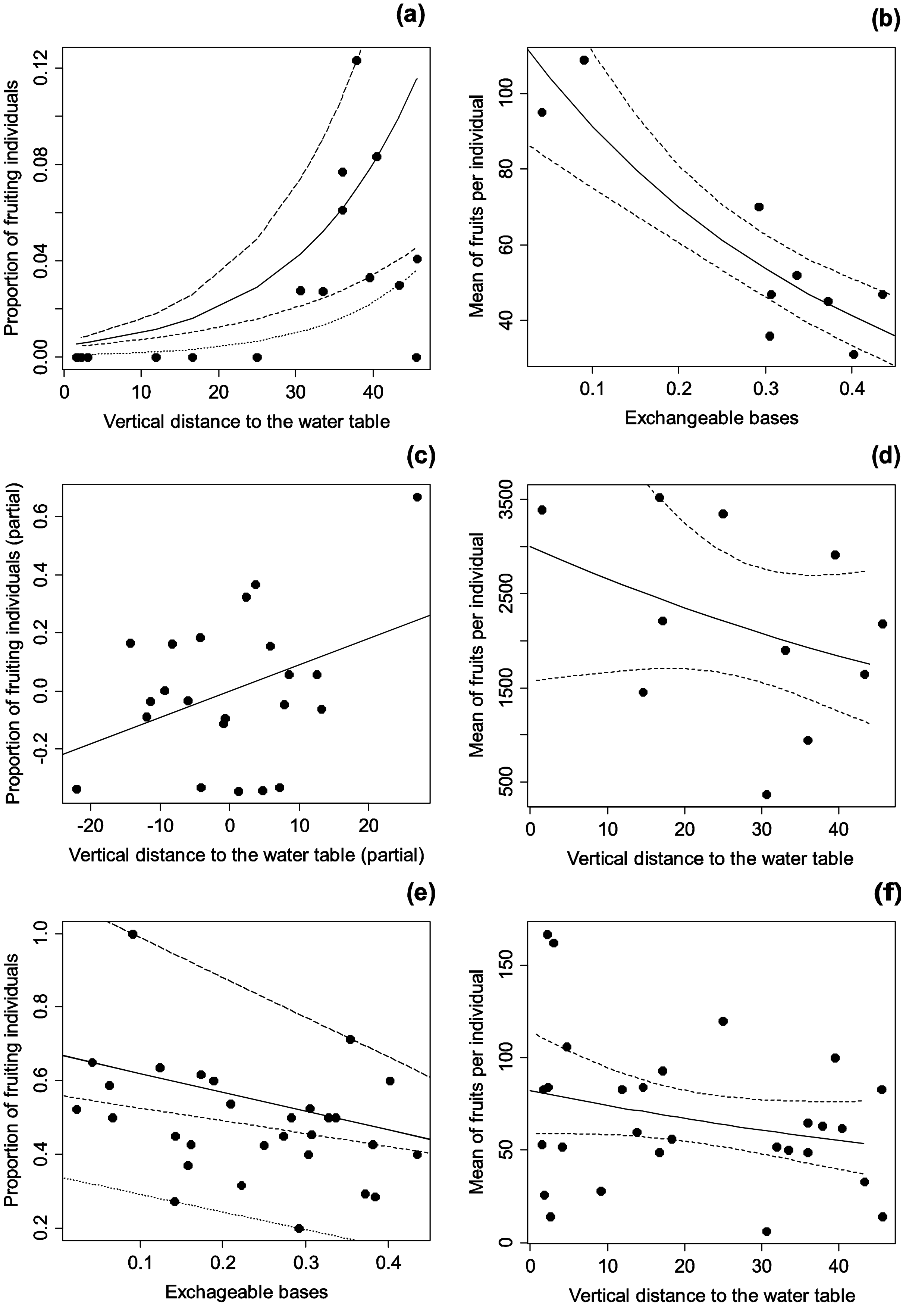
(a)
Proportion of fruiting individuals
0.00
0.04
0.08
0.12
0
10
20
30
40
Vertical distance to the water table
(b)
Mean of fruits per individual
40
60
80
100
0.1
0.2
0.3
0.4
Exchangeable bases
(c)
Proportion of fruiting individuals (partial)
-0.2
0.0
0.2
0.4
0.6
-20
-10
0
10
20
Vertical distance to the water table (partial)
(d)
Mean of fruits per individual
500
1500
2500
3500
0
10
20
30
40
Vertical distance to the water table
(e)
Proportion of fruiting individuals
0.2
0.4
0.6
0.8
1.0
0.1
0.2
0.3
0.4
Exchageable bases
(f)
Mean of fruits per individual
0
50
100
150
0
10
20
30
40
Vertical distance to the water table

Fig. 3. Response of *Attalea attaleoides* fruiting production according to environmental gradients. (a) Quantile regression model for proportion of individuals fruiting, including the 95th quantile (long dashed line), 75th quantile (solid line), 50th quantile (dashed line) and 25th quantile (dotted line), (b) GLM model with Poisson distribution (quasipoisson adjustment) showing the relationship between exchangeable bases and mean of fruits per individual of *Attalea attaleoides* (ED=0.78; p=0.001). Response of *Oenocarpus bacaba* fruiting production according to environmental gradients. (c) Linear multiple regression model showing the effect of HAND (partial, excluding influence of exchangeable bases) in the proportion of individuals fruiting ($R^2$=0.14; $p_w$=0.22; $p_h$=0.08). (d) Mean of fruits produced per individual (not significant). Response of *Iriartela setigera* fruiting production according to environmental gradients. (e) Quantile regression model for proportion of individuals fruiting, including the 95th quantile (long dashed line), 75th quantile (solid line), 50th quantile (dashed line) and 25th quantile (dotted line). (f). Mean of fruits produced per individual (not significant).

Table 1. Results from restriction limit function using clay content data for the entire population, adults and only fruiting individuals.

| | Population | | Adults | | Fruiting adults | |
|---|---|---|---|---|---|---|
| Species | *p* | BP* | *P* | BP | *P* | BP |
| *Attalea attaleoides* | 0.008 | 4.27 | 0.183 | 67.4 | 0.000 | 67.43 |
| *Attalea microcarpa* | 0.000 | 12.43 | 0.000 | 12.43 | 0.000 | 6.15 |
| *Euterpe precatoria* | 0.784 | - | 0.595 | - | 0.694 | - |
| *Geonoma aspidiifolia* | 0.116 | - | 0.000 | 4.27 | 0.096 | - |
| *Iriartella setigera* | 0.391 | - | 0.969 | - | 0.959 | - |
| *Oenocarpus bataua* | 0.445 | - | 0.000 | 4.27 | 0.000 | 4.27 |
| *Oenocarpus bacaba* | 0.003 | 4.27 | 0.008 | 37.40 | 0.003 | 37.40 |
| *Oenocarpus minor* | 0.075 | - | 0.262 | - | 0.082 | - |
| *Socratea exorrhiza* | 0.331 | - | 0.002 | 4.27 | 0.002 | 4.27 |

*Break point where the group splits up.

Table 2. Final models for the proportion of adults fruiting after backward model selection.

| Species | Variables retained in the Model | Model type | Distribution | Sample size | p* | $R^2$ |
|---|---|---|---|---|---|---|
| *Attalea attaleoides* | HAND | Non-linear quantile | Binomial | 16 | - | - |
| *Attalea microcarpa* | Phosphorus | OLS | Normal | 11 | 0.23 | 0.15 |
| *Euterpe precatoria* | Bases+inclination | OLS | Normal | 12 | 0.13/0.06<br>Bases (+) | 0.35 |
| *Geonoma aspidiifolia* | HAND | OLS | Normal | 23 | 0.25 | 0.06 |
| *Iriartela setigera* | Bases | Linear quantile | Normal | 29 | - | - |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Oenocarpus bataua* | Phosphorus +Inclination | OLS | Normal | 11 | 0.66 | 0.09 |
| *Oenocarpus bacaba* | HAND+bases | OLS | Normal | 22 | 0.14/0.08 (HAND) | 0.22 |
| *Oenocarpus minor* | Bases | OLS | Normal | 25 | 0.61 | 0.01 |
| *Socratea exorrhiza* | Bases+inclination | OLS | Normal | 11 | 0.15 | 0.37 |

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* Double p values mean the p value for the whole model/the p value for the significant variable, the sign between parentheses means the direction of the relation for those variables which we do not show graphically.

Table 3. Final models for the mean amount of fruits per individual after backward model selection.

| Species | Variables retained in the Model | Model type | Distribution | Sample size | DE | *p* |
|---|---|---|---|---|---|---|
| *Attalea attaleoides* | Bases | GLM | Poisson (quasi) | 9 | 78 | 0.001 |
| *Attalea microcarpa* | * | GLM | * | 6 | - | - |
| *Euterpe precatoria* | * | GLM | * | 4 | - | - |
| *Geonoma aspidiifolia* | HAND | GLM | Poisson (quasi) | 13 | 38 | 0.02 (-) |
| *Iriartela setigera* | HAND+bases | GLM | Negative binomial | 28 | 7.2 | 0.14 |
| *Oenocarpus bataua* | HAND | GLM | Negative | 9 | 10 | 0.29 |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
|  |  |  | binomial |  |  |  |
| *Oenocarpus bacaba* | HAND | GLM | Negative binomial | 11 | 15 | 0.17 |
| *Oenocarpus minor* | Phosphorus+Inclination | GLM | Negative binomial | 20 | 19 | 0.02**(-) |
| *Socratea exorrhiza* | Bases | GLM | Negative binomial | 8 | 45 | 0.02 |

*Not analyzed due to lack of sample units, ** probability associated with inclination. The sign between parentheses means the direction of the relation for those variables which we do not show graphically.

Appendix 1

Appendix 1. Numbers of individuals in each population stage and mean fruit production in 30 1 ha-plots of terra firme Forest at Reserva Ducke.

| Species | Population | Adults | Reproductive adults | Individuals with fruits counted | Mean number of fruits per species |
|---|---|---|---|---|---|
| *Attalea attaleoides* | 4650 | 906 | 38 | 22 | 59.11 |
| *Attalea microcarpa* | 4570 | 489 | 22 | 17 | 82.5 |
| *Euterpe precatoria* | 320 | 41 | 23 | 5 | 1713 |
| *Geonoma aspidiifolia* | 1910 | 173 | 44 | 35 | 14 |
| *Iriartella setigera* | 4120 | 590 | 286 | 134 | 67.75 |
| *Oenocarpus bataua* | 14770 | 279 | 188 | 20 | 842.55 |
| *Oenocarpus bacaba* | 1970 | 176 | 64 | 21 | 2590.83 |

| | | | | | |
|---|---|---|---|---|---|
| *Oenocarpus minor* | 3840 | 296 | 83 | 33 | 68.8 |
| *Socratea exorrhiza* | 230 | 38 | 21 | 11 | 440.75 |
| Total | 36940 | 2988 | 769 | 298 | 653.25 |

# Capítulo 2

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Freitas, C.G., Dambros, C.S., Eiserhardt, W.L., Costa, F.R.C., Svenning, J.C. & Balslev, H. Trait And Phylogenetic Structure Of Palms In Central Amazon: Neutral And Non-Neutral Processes Are Environment Dependent. Manuscrito em Preparação para a *Biotropica*

# Trait and Phylogenetic Structure of Palms in the Central Amazon: Neutral and Non-Neutral Processes are Environment Dependent (4087 words)

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Abstract (231 words)

One of the most important questions in community ecology is whether species distributions are controlled by neutral or niche-based processes such as competition and environmental control. Addressing evolutionary history of traits and spatial distribution of species makes it possible to disentangle the role of different processes that govern community assembly. To determine the roles of these processes, we compared the observed palm phylogenetic community structure from 72 plots distributed in 64 km$^2$ against assemblages generated by null models. We also analyzed whether morphological traits are labile or conserved along the phylogeny, accounting for spatial structure of morphological traits in each plot. We found an overall neutral phylogenetic structure, but closely related species are more clumped than expected by chance in the bottomlands. We did not find evidence of niche conservatism, which means that close relatives are not more similar than the expected under Brownian motion evolution. However, we found a strong negative correlation between phylogenetic community structure and spatial trait structure for most traits — i.e. plots with the most closely related species have overdispersed traits. Our study suggests that phylogenetic clumping in the bottomlands could be the result of competition between distant relatives with similar traits. In accordance with previous expectations, our results support the idea of a more relaxed community structure in tropical forests, with competition being more important between distant relatives with similar traits. However, a strong phylogenetic signal in a few plots deserves further investigation.

## Resumo

Uma das questões mais importantes da ecologia de comunidades é se a distribuição das espécies é controlada por processos neutros ou de nicho, como competição e controle ambiental. Usando a história evolutiva das características relevantes e a distribuição espacial das espécies é possível distinguir entre os diferentes processos que governam a formação das comunidades. Para determinar o papel desses processos, nós comparamos a estrutura filogenética da comunidade de palmeiras de 72 parcelas distribuídas em 64 km2 com assembléias geradas por modelos nulos. Nós também analisamos se os caracteres morfológicos são lábeis ou conservadas ao longo da filogenia e se há estrutura espacial nas características morfológicas em cada parcela. De modo geral, nós achamos uma estrutura neutra na comunidade de palmeiras. Contudo, nos baixios espécies mais próximas filogeneticamente estão mais agrupadas. Nós não encontramos evidência de conservatismo de nicho o que significa que espécies mais próximas filogeneticamente não são mais similares que o esperado usando um modelo Browniano. Nós encontramos  uma forte correlação entre a estrutura filogenética da comunidade e a estrutura espacial das características para a maioria das características – i.e. parcelas com espécies mais proximamente relacionadas tiveram características agrupadas. De acordo com nossas expectativas prévias, nossos resultados corroboram a ideia de uma estrutura da comunidade menos estruturada nas florestas tropicais, com a competição sendo mais importante entre as espécies mais distantes com características similares. Contudo, um forte sinal filogenético em algumas parcelas merece mais atenção.

*Key words*: Competition; environmental filtering; limiting similarity; niche; null models; Tropical forest.

DRIVERS OF COMMUNITY ASSEMBLY AND THEIR ASSOCIATION WITH ECOLOGICAL PROCESSES such as competition and dispersion have interested ecologists for decades. The discussion of whether species are assembled according to niche (e.g. Tilman 1994) or neutral processes (Bell 2001, Hubbell 2001) remains important, and more recently arose again the consensus that not only current factors are responsible for the assembly process. Hence, historical components have been incorporated in community ecology studies (Webb *et al.* 2002). Knowing the phylogenetic relationship between species in a community can help us to understand the community assembly process (Webb *et al.* 2002, Wiens & Graham 2005), but the applicability of this phylogenetic approach to smaller scales has only been explored to a limited extent. Nevertheless, historical processes do contribute to contemporary patterns of biodiversity even at the local scale (Brown *et al.* 2000, Stevens 2006) and contribute to the framework in which the assembly processes work. We used a phylogenetic approach, ecological gradients and analysis of traits to better understand the assembly of a palm community at local to landscape scales.

Different neutral and niche-based processes can structure biological communities and these processes depend on geographical scale (McGill 2010) but also on environmental heterogeneity and species traits. At larger spatial scales, species can be adapted to different environments where groups of species show different responses along environmental gradients, and therefore the environmental heterogeneity *per se* can prevent species from existing in places in which they are not adapted (environmental filtering, e.g. Webb *et al.* 2002, Cavender-Bares *et al.* 2004). At smaller scales, those groups of species already environmentally filtered may be prevented to co-occur by competitive exclusion or ecological displacement (assuming no dispersal limitation) (McArthur & Levins 1967, Huston 1979, Ricklefs 1987).

Niche-based processes can lead to co-occurrence of similar species or to their overdispersion, depending on which processes are acting (Cadotte *et al.* 2009) and the way in which species' traits evolve also has strong implications for the interpretation of phylogenetic community structure. Since Darwin's time, the niche conservatism premise has been assumed, but only few recent studies have accounted for the problems arising from this assumption and there is growing evidence that it is not always true (Losos 2008). The niche conservatism is defined as the tendency of a close related species being more ecologically similar than expected under solely Brownian motion evolution, which will prevent new species or its decendants to ocuppie another niche (Wiens and Graham, 2005; Losos, 2008). So, traits can be conserved, which means that close related species are more similar than expected by chance, indicating niche conservatism, or traits can be labile and close related species are less similar than expected by chance (Blomberg et al 2003; Losos, 2008). An alternative approach to compare trait evolution and spatial phylogenetic structure is to measure the spatial distribution of traits directly. If traits are clustered in space, then similar species can share the same environment and limiting similarity may not be the main mechanism acting to prevent similar species to co-exist.

Palms are a very conspicuous element in tropical forests systems and their phylogeny is well resolved to the genus level, being therefore a useful model to understand community assembly processes. These features allowed us to test for neutrality, competition or environmental filtering in this group using a phylogenetic approach. There is also a vast literature of palm traits and it is easy to measure and estimate the important traits that could potentially create fitness differences between individuals of different species and guide the assembly process.

Edaphic variation is known to be one of the main gradients determining the structure and composition of plant communities in the tropics, from local to regional scales (Tuomisto *et al.* 1995, Svenning 2001, Tuomisto *et al.* 2003, Costa *et al.* 2005). Specifically, topography is a powerful predictor of plant community structure in the central Amazon basin (Costa *et al.* 2005, 2009; Kinupp & Magnusson 2005, Zuquim *et al.* 2009). However, despite the large evidence of environmental influence on species turnover, there is little attempt to understand the processes that cause such distribution or even test if a niche-based process can sort the palm species into the landscape.

Here we studied assembly mechanisms in a landscape scale palm community using a phylogenetic approach. The main objectives were to determine the co-occurrence pattern of close relatives and whether neutral or niche-based processes of environmental filtering and competition rule the phylogenetic palm community structure at this local to intermediate scale. We measured the phylogenetic community structure of 39 species in 72 small plots in Reserva Ducke, located near Manaus in the Central Amazon basin and determined whether close relatives are clumped or overdispersed in space. We also determined if the species traits are conserved along the phylogenetic tree and if these traits are spatially organized. Within this framework, we asked the following specific questions: (1) Do close relatives co-occur more or less than expected by chance at the local scale? (2) Do species have traits conserved at local community scale? (3) Does phylogenetic relatedness change along the most important environmental gradients following the same pattern of species composition? And, (4) is there any spatial pattern of grouping or overdispersion in trait distributions?

## **METHODS** (1348 words)

ECOLOGICAL DATA.–Our study was performed in the Adolpho Ducke Forest Reserve, a well preserved forest of 10,000 ha. The canopy is 30–37 m high and *Astrocaryum* and *Attalea* palms dominated the understory (Ribeiro *et al.* 1999). The annual mean temperature is 26°C, the relative humidity varies from 77–88% and the annual precipitation varies between 1750 and 2500 mm. Soil types are associated with topography; clayey soils (mainly ferralsols) in the higher areas (Quesada *et al.* 2011) grade to podzolic sandy soils in the lower areas and this gradient is an important driver of tree- and palm-community structure (Castilho *et al.* 2006, Costa *et al.* 2009). The reserve has a 64 km$^2$ grid with trails from the PELD-Brazil program (Long Duration Ecological Research) and PPBio (the Brazilian Biodiversity Research Program of the Science and Technology Ministry). 72 plots are systematically distributed at 1 km intervals over the grid (Fig. 1). Plots are 250 m long, following the terrain altitudinal contour, and the plot width is variable depending on the taxa being sampled. For palms, plots were 250 x 4 m. In each plot all palms > 1 m high were counted and identified in 2003 (Costa *et al.* 2009). The standardized sampling design used in this study was originally established to avoid environmental variation inside each plot and suited us to investigate changes in phylogenetic community structure while keeping constant the environmental variation and spatial scale.

The topographic variables, originally measured by a professional surveyor team, are available at the PPBio website (http://ppbio.inpa.gov.br/). Altitude was measured using a theodolite at the beginning of each plot. Inclination was measured with a clinometer every 50 m along the plot's longest axis. In the same points, soil was sampled at 0–5 cm depth from a 30 x 30 cm area, mixed to get a compound sample, and clay content and chemical properties were 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 in the grid and its nearest drainage (Rennó *et al.* 2008). HAND was calculated for Reserve Ducke, calibrated in the field and averaged for each plot based on the 250 m central line (Schietti, *unpubl.* data).

PHYLOGENETIC DATA.–We constructed one tree for the 39 taxa identified to the species level by Jean-Louis Guillaumet and reported in Costa *et al.* (2009). We excluded three botanical entities they had identified to the variety level or only to the genus level. The tree was constructed based on a dated phylogeny by Couvreur *et al.* (2011). Polytomies and dating estimates were solved partially with the help of specialized bibliography (Baker *et al.* 2009 and Couvreur *et al.* 2011, for the family until genus level; Roncal *et al.* 2011, for *Geonoma*; and Eiserhardt *et al.* 2011, for *Bactris*) and using a function to randomly sort out ten *Bactris* species for which the position within the *Bactris* clade is unknown (function developed by Eiserhardt, W.L). We use this tree in the phylogenetic structure community analysis.

PHYLOGENETIC COMMUNITY STRUCTURE.–We used two approaches to access the phylogenetic structure for each plot, following Webb (2000) and Webb *et al.* (2002): the Net Relatedness Index (NRI) and the Nearest Taxon Index (NTI). Both indices are calculated based on differences between the observed community and 999 random communities generated by a null model. For each observed and null community we measured the Mean Pairwise Distance (MPD) and the Mean Nearest Neighbor Distance (MNND) to calculate NRI and NTI, respectively. Positive scores in both cases indicate phylogenetic clustering in a plot and that close relatives co-occur more than expected by chance and negative scores mean phylogenetic overdispersion and that close relatives co-occur less than expected. To summarize the general effect in the whole area we used a two-tailed one-sample t-test based on the mean and variance of NRI and NTI across all 72 plots.

We performed this analysis for the whole community (39 taxa) considering two monophyletic groups within our local community (*e.g.* Arecoideae [Areceae plus Geonomateae - *Euterpe, Oenocarpus*, *Hyospathe* and *Geonoma*] and Cocoseae [Cocoeae–*Syagrus, Bactris, Astrocaryum, Desmoncus* and *Attalea*]). Hereafter we will refer to Arecoideae and Cocoseae to facilitate the discussion. We excluded *Mauritia, Mauritiela* and *Iriartella, Socratea* from the group analysis due to the small number of species representing these two major groups i.e, Tribe Lepidocaryeae, Subtribe Mauritiinae and Tribe Iriarteeae, respectively, and also because they are much more ancient than the other major groups. We also used presence/absence and abundance data only for this specific analysis.

Additionally, we used the nodesig function from the Phylocom program (Webb *et al.* 2008) to determine if any specific clade is phylogenetically structured and the pattern is being obscured in the analysis considering the whole community (Parra *et al.* 2010). We also calculated the Phylogenetic Species Variability (PSV) index (Helmus *et al.* 2007). The results using nodesig and PSV were similar. We do not show the results obtained for PSV, which are available in the supplementary material.

PHYLOGENETIC RELATEDNESS ALONG ENVIRONMENTAL GRADIENTS.–To determine if the phylogenetic relatedness between species co-occurring in each plot changes with environmental gradients we used Linear Regression to fit the relationship between NRI and NTI and two gradients known to be most representative of the reserve; soil texture (represented by clay content) and the height of the terrain above the nearest drainage (HAND).

SPECIES TRAITS AND NICHE CONSERVATISM.–We compiled data on morphological and reproductive traits for palms (Table S1) from the literature (*e.g.* Henderson 1995, Dransfield *et al.* 2008). We used only traits available for all species (palm height, number of leaves, presence of spines, inflorescence position, pinnae arrangement, length of the staminate flower, length of the pistilate flower, petal length, fruit length, fruit weight and number of seeds). As a measure of ecological traits, we used the response of palms to important environmental gradients by measuring the mean abundance of each species in its range of distribution along each gradient and the regression coefficient from the relationship between the abundance of each species and all environmental gradients separately (see Gómez *et al.* 2010, Helmus *et al.* 2007). To determine if traits are conserved or labile we used the k statistics of Blomberg *et al.* (2003) and to determine its significance we calculated the variance in each trait for all species considered in the phylogenetic tree and compared that with the variance calculated from random communities (Blomberg *et al.* 2003). Values of k greater than zero and smaller than one indicate trait lability and *k* values greater than one indicate trait conservatism, assuming Brownian motion as a model of evolution of traits. Tests of phylogenetic signal in traits were performed using the multiPhylosignal function (Kembel *et al.* 2009) in the R program (R Development core team 2011). We performed the analysis considering the whole community and the monophyletic groups mentioned above separately.

SPATIAL STRUCTURE OF TRAITS.–To determine if traits are clumped in the environment without accounting for species relatedness we tested for the spatial structure of the morphological/reproductive traits using the Phylocom program (Webb *et al.* 2008). We followed Rabosky *et al.* (2007) where the standardized effect size of the variance (SES) in each trait is counted to compare the observed grouping of characteristics within 1000 random species assemblages. The SES values were compared among the plots using a two-tailed one-sample t-test to test if the SES values of all plots are greater or lesser then zero. Values significantly greater than zero indicate trait clumping and were assumed indicative of environmental filtering.

NULL MODEL.–To create the null species assemblages we used the constrained model and the Swap algorithm proposed by Gotelli and Entsminger (2003), which randomize the real community keeping the number of species and the frequency of occurrence in each site fixed. The Swap algorithm replaces in the original matrix the combination of (0,1)(1,0) by (1,0)(0,1) and the combination of (1,0)(0,1) by (0,1)(1,0), thus, randomizing but keeping the row and column sums fixed (fixed number of species in each plot and fixed number of occurrences for each species). The randomizations were performed by 1000 swaps (iterations), with each subsequent null community generated by checkerboard swapping the previous matrix 999 times.

## **RESULTS** (451 words)

PHYLOGENETIC COMMUNITY STRUCTURE.–The overall phylogenetic structure of the palm community at the 66 km$^2$ scale of Reserva Ducke was close to random. Although some plots had a clumped or overdispersed pattern, on average close relatives are randomly distributed in the community and our results did not change when using presence/absence ($t$=0.29, $P$=0.79; $t$=-0.36, $P$=0.71) or abundance weighted data ($t$=1.49, $P$=0.14; $t$=-0.98, $P$=0.32) for the most common phylogenetic structure indexes) (Fig. 3). The same pattern was found when Arecoideae and Cocoseae were analyzed separately.

However, the species relatedness indices (NRI) were weakly related with two of the most important ecological gradients in the area, HAND and soil clay content (HAND: $R^2$ = 0.20; $P$

= 0.0001 and clay: $R^2 = 0.26$; $P = 0.0001$). Plots in the bottomland sandy soils had phylogenetically more closely related species than expected by chance, and this phylogenetic pattern disappeared for HAND values greater than 10 m and soil clay contents higher than 5% (Fig. 4). The pattern is the same, but less evident for NTI (HAND: $R^2 = 0.12$; $P = 0.002$ and clay: $R^2 = 0.07$; $P = 0.02$).

SPECIES TRAITS AND NICHE CONSERVATISM.–We found phylogenetic signal in some traits as stated below. Presence of spines in the community as a whole (Table 1) and height, presence of spines, length of pistillate flowers and petal length in Cocoae (Table 3) were conserved according to the k statistic. This means that closely related species are more similar than expected under Brownian motion evolution. However, most traits were labile indicating general absence of niche conservatism in trait evolution (Table 1; Table 2; Table 3). Regarding the ecological traits, only the position of species along the soil Mg content gradient had a phylogenetic signal for the whole palm group (Table 1) and Mg and Ca++ showed signal for Cocoseae (Table 3). However these traits were labile and did not show phylogenetic niche conservatism that could be stronger than if these traits had evolved by Brownian motion evolution.

SPATIAL STRUCTURE OF TRAITS.–Although in some plots species traits were significantly clumped (six out of 72 in relation to fruit traits and height; SES>2) and in some plots the present species had different traits (overdispersed traits; two out of 72 in relation to presence of spines; SES<2), on average the morphological/reproductive traits were not spatially organized, considering either presence/absence or abundance data. However, for almost all traits, spatial structure is negatively correlated with NRI and NTI. This means that when there is phylogenetic clumping there is also trait overdispersion (close relatives are clumped and have different traits) and *vice-versa* so these results agree with our previous expectations based on phylogenetic structure (NRI and NTI) and analysis of trait evolution.

## **DISCUSSION** (1511 words)

PHYLOGENETIC COMMUNITY STRUCTURE.–Assuming niche conservatism, communities are expected to shift from phylogenetic clustering to overdispersion with decreasing spatial scales (Cavender-Bares *et al.* 2009, Webb *et al.* 2002, Goméz *et al.* 2010) and this is strongly dependent on taxa inclusiveness (Cavender-Bares *et al.* 2006). We found a random phylogenetic structure at the plot level, i.e., contrary to the expectations for local scales. The overall phylogenetic structure of the palm community is not significantly different from the null expectation, although some plots had clumped or overdispersed patterns. This pattern may arise from random colonization or diffuse competition. A local site colonized randomly from the regional pool of species (Hubbell 2001, Bell 2001) is consistent with findings of dispersal limitation for palms found in experiments performed in the same area (Freitas *et al.*, 2012). Also, diffuse competition, which is thought to exist among plants and birds in tropical environments (Huston 1979, Wright 2002, Goméz *et al.* 2010) and the high genotypic variability in plants (Hamrich *et al.* 1979), including palms (Enguiart 1992), can facilitate coexistence (Booth & Grime 2003).

High genotypic variability associated with plasticity and adaptation to local heterogeneity (Hamrick *et al.* 1979) can lead to a random phylogenetic structure of the palm community because species can occur throughout the entire ecological gradient regardless of their phylogenetic relationships. However, in spite of the difficulties of disentangling the importance of niche and neutral processes at local scale (John *et al.* 2007, Karst *et al.* 2005) and keeping in mind that these results could be due to the rarefied community sample (Losos 2008) we believe that the species relatedness plays a minor role in assembling our community and maybe the caracteres analysed are assemble neutraly since we did not find any spatial structure in traits. Also, since most of traits analysed are labile, and therefore, the premise of conservatism is not true, we believe that our results for phylogenetic community structure are not compromised by our rarefied sample of the entire Arecaceae clade, though we are aware that our result may be sensitive to community composition.

Phylogenetic structure depends on the evolution of species traits and the intensity of the influence of these traits in species distribution across environmental gradients (Cavender-Bares *et al.* 2006). Despite the absence of spatial structure in traits, which means that there is no phenotypical aggregation in any part of the ecological gradient, phylogenetic relatedness was associated with the vertical distance to the water (HAND) and soil clay content. Communities in bottomlands were phylogeneticaly aggregated, while communities far from the watercourses were essentially random assemblages from the phylogenetic pool. In spite of being considered a unit in terms of vegetation, within *terra-firme* forest there are at least four different habitats that respond mostly to the topographical/soil gradient (Ribeiro *et al.* 1999, Costa *et al.* 2005). Also, *terra firme* was always thought to be an upland, well drained area, but there are, in some cases, more than 40 % are swampy bottomlands, which the importance canot be ignored (Nobre *et al.* 2011). In the central Amazon basin, many studies have documented a significant association between abundance of species and changes in community composition along topographic gradients at the meso-scale (Costa *et al.*2005, Costa *et al.* 2009, Drucker *et al.* 2005, Castilho *et al.* 2006, Braga-Neto *et al.* 2008). Considering the premise of niche conservatism we should expect that the clustering patterns found in bottomlands is due to environmental filtering. However, the traits we measured were not conserved (see below), and the closely related species were not more morphologically similar than expected, so this pattern in the bottomlands suggests instead, that competition may lead closely related species with dissimilar traits to co-occur in the bottomlands, even if most plots did not show a significant pattern of phylogenetic clustering (SES<2). Another possibility is that the traits we measured are not related to the tolerance to wet environments and in fact, bottomlands filter those species by some other physiological water-tolerance traits.

SPECIES TRAITS AND NICHE CONSERVATISM.–Considering the local scale of our study and the niche conservatism premise, we expected an overdispersed pattern of phylogenetic community structure controlled by limiting similarity and competition between close relatives according to previous studies (*e.g* McArthur & Levins 1967, Webb *et al.* 2002, Cavender-Bares *et al.* 2006, Kembel & Hubbell 2006). Recent studies have shown that niche conservatism is not a rule in many morphological traits and, instead of assuming it we should test for it (Losos 2008, Wiens 2010). Overall, the traits for the whole community showed a phylogenetic signal with most traits being labile as has been shown previously for meadow communities (Silvertown *et al.* 2006). In our study, Arecoideae presented a weak phylogenetic signal with no morphological traits conserved and only two being labile. For Cocoseae we found the opposite situation with strong phylogenetical signal and with four conserved traits, although the majority of traits are labile. Among ecological traits, the response to magnesium and calcium soil content was labile for Cocoseae, just the same pattern of the whole community. Trait lability means that close relatives are not more similar than expected under Brownian motion evolution (Blomberg *et al.* 2003, Losos 2008). Indeed, traits that define the α niche (as proposed by Pickett & Bazzaz (1978), based on Whittaker's alpha diversity concept, which means the traits that possibly define the species distribution at local scale) are supposed to be more labile to permit species to co-occur (Silvertown *et al.* 2006). According to our findings, due to the lability of the traits might have be a weaken competition between close relatives in bottomlands allowing they to co-occur at this geographic.

Studies restricted to species from a single community are likely to present little or no phylogenetic signal (Losos 2008). Although measures of trait conservatism are influenced by taxon sampling (Cavender-Bares *et al.* 2006), spatial scale and how the community is defined, our results can explain why the phylogenetic relationship between species does not contribute to the palm community assembly at least for the whole community and Cocoseae, which presented most labile traits. Competition can facilitate co-existence in the sense that under competitive pressure species with labile traits can co-exist, however competition does not force trits to be labile (Silvertown *et al.* 2006). Lack of phylogenetic signal is sufficient to indicate that phylogenetic niche conservatism does not occur (Losos 2008). Detection of phylogenetic signal depends on sample size, power of the statistical test, accuracy and choice of the phylogenetic tree, accuracy of trait data and degree of phylogenetic inclusiveness (Blomberg *et al.* 2003, Losos 2008). Here specificaly, we are analyzing together the phylogenetic structure and the traits, which make the influence of temporal and spatial scale less important than the phylogenetic sampling scale. Working with only parts of the entire Arecaceae clade can also mask the real pattern.

SPATIAL STRUCTURE OF MORPHOLOGICAL TRAITS.–Overall, species distributions are not related to the traits of table S1, which means that the phenotypes are not significantly organized in space. This is compatible with the prediction of neutral models (Hubbell 2001). Indeed, local and regional assembly factors seem to work together in tropical areas building a random trait distribution at least in local frog communities (Algar *et al.* 2011). However, in our palm community a plot–plot comparison shows a tendency to overdispersion in traits in plots with phylogenetic clustering and *vice versa*. Every time we get a positive value of NRI/NTI in phylogenetic structure analysis we get a negative value of 1-SES in spatial trait analysis and vice-versa, but few of these relationships are statistically significant. These results are in accordance with the conclusion that competition possibly is promoting dissimilar species (close relatives) to co-occur in bottomlands. As close relatives tend to have different traits, they can co-occur without competing, while competition is acting in distantly related species that share some traits.

In conclusion, the absence of a non-random phylogenetic pattern does not mean that there is no mechanism acting in the community phylogenetic assembly (Peres-Neto *et al.* 2001). The phylogenetic approach was a tool to determine the mechanism of community assembly and is not our intention to make any evolutionary inferences. However, even in a local community, the assembly process can be influenced by the way traits evolve (Webb *et al.* 2002, Cavender-Bares *et al.* 2004). We found that our local palm community is neutral in its phylogenetic assembly. Looking ahead, we encourage local scale researchers to test the prevision that at the local scale palms are assembled randomly regarding phylogenetic relatedness. Additionally to the phylogenetic random community we found the most important traits are labile and that besides there is no spatial structure in traits within bottomlands. Due to the multidimensional nature of the niche it is virtually impossible to know if we tested the most important traits in terms of conservativeness, lability, spatial structure or even promoting competition between species by limiting similarity. This shows that evolutionary processes help the ecological constraints to shape the community structure mostly in bottomlands, however it makes the assumption that our palm community at local scale is neutral in most places and that the phylogenetic structure depends on environmental conditions *per se* i.e bottomlands, not just environmental variability i.e environmental grandient.

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TABLE S1. *Traits used in trait conservatism analysis compiled from specialized literature.*

| | Stems category | Height (m) | Number of leaves | Presence of spines | Inflorescence position | Pinnae shape | Staminate flowers (mm) | Pistillate flowers (cm) | Length of petals (mm) | Fruits length (cm) | Fruits width (cm) | Number of seeds |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Astrocaryum acaule* | 2 | 1 | 7 | 2 | 1 | 2 | 4 | 1 | 3 | 3 | 2 | 1 |
| *Astrocaryum ferrugineum* | 3 | 4 | 11 | 2 | 1 | 1 | 3 | 1 | 2 | 5 | 3 | 1 |
| *Astrocaryum gynacanthum* | 4 | 4 | 10 | 2 | 1 | 1 | 3 | 1 | 1 | 3 | 1 | 1 |
| *Astrocaryum sociale* | 3 | 1 | 10 | 2 | 1 | 1 | 3 | 1 | 3 | 5 | 3 | 1 |
| *Attalea attaleoides* | 1 | NA | 10 | 1 | 1 | 1 | 12 | 2 | 12 | 5 | 2 | 3 |
| *Attalea maripa* | 3 | 12 | 16 | 1 | 1 | 2 | 12 | 2 | 10 | 5 | 3 | 3 |
| *Attalea microcarpa* | 1 | NA | 11 | 1 | 1 | 1 | 9 | 2 | 8 | 4 | 3 | 2 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Bactris acanthocarpa intermedia* | 3 | 1 | 8 | 2 | 1 | 2 | 1 | 0 | 3 | 1 | 1 | 1 |
| *Bactris acanthocarpa humilis* | 3 | 1 | 5 | 2 | 1 | 2 | 3 | 0 | 0 | 1 | 1 | 1 |
| *Bactris acanthocarpa var trailiana* | 5 | 6 | 9 | 2 | 1 | 3 | 3 | 0 | 3 | 1 | 1 | 1 |
| *Bactris acanthocarpoides* | 4 | 3 | 12 | 2 | 1 | 2 | 3 | 1 | 3 | 1 | 1 | 1 |
| *Bactris constanciae* | 4 | 3 | 7 | 2 | 1 | 2 | NA | 1 | 5 | 2 | 2 | 1 |
| *Bactris cuspidata* | 4 | 1 | 5 | 2 | 1 | 2 | NA | 0 | 2 | 1 | 1 | 1 |
| *Bactris elegans* | 4 | 3 | 10 | 2 | 1 | 1 | 5 | 0 | 5 | 1 | 1 | 1 |
| *Bactris gastoniana* | 5 | 0 | 6 | 2 | 1 | 2 | 10 | NA | NA | 2 | 1 | 1 |
| *Bactris hirta bifida* | 5 | 2 | 5 | 2 | 2 | 4 | 4 | 0 | 3 | 1 | 1 | 1 |
| *Bactris hirta pinada* | 5 | 2 | 5 | 2 | 2 | 2 | 4 | 0 | 3 | 1 | 1 | 1 |
| *Bactris maraja* var. *maraja* | 5 | 4 | 7 | 2 | 1 | 5 | 4 | 0 | 3 | 1 | 1 | 1 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Bactris schultesii* | 5 | 1 | 7 | 2 | 1 | 5 | 4 | 0 | 4 | 1 | 1 | 1 |
| *Bactris simplicifrons* | 5 | 1 | 7 | 2 | 1 | 5 | 4 | 0 | 4 | 1 | 1 | 1 |
| *Bactris syagroides* | 4 | 1 | 7 | 2 | 1 | 1 | NA | NA | NA | 1 | 1 | 1 |
| *Bactris tomentosa* | 4 | 2 | 11 | 2 | 1 | 2 | 6 | 0 | 4 | 2 | 2 | 1 |
| *Desmoncus polyacanthos* | 6 | 9 | 22 | 2 | 1 | 6 | 5 | 0 | 5 | 2 | 1 | 1 |
| *Euterpe precatoria* | 3 | 15 | 15 | 1 | 1 | 1 | 5 | 0 | 4 | 1 | 1 | 1 |
| *Geonoma aspidifolia* | 4 | 2 | 10 | 1 | 1 | 1 | 5 | 1 | 4 | 1 | 1 | 1 |
| *Geonoma macrostachys* | 5 | 0 | 9 | 1 | 1 | 5 | 5 | 0 | 5 | 1 | 1 | 1 |
| *Geonoma maxima* var. *chelinodura* | 4 | 4 | 3 | 1 | 2 | 5 | 5 | 1 | 2 | 1 | 1 | 1 |
| *Geonoma maxima maxima* | 7 | 3 | 12 | 1 | 3 | 1 | 5 | 1 | 2 | 0 | 1 | 1 |
| *Geonoma maxima spixiana* | 7 | 4 | 12 | 1 | 1 | 1 | 5 | 1 | 2 | 1 | 1 | 1 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Geonoma stricta* | 7 | 2 | 10 | 1 | 4 | 3 | 4 | 0 | 4 | 1 | 1 | 1 |
| *Hyospathe elegans* | 4 | 5 | 8 | 1 | 5 | 1 | 6 | 0 | 2 | 2 | 1 | 1 |
| *Iriartella setigera* | 4 | 8 | 7 | 2 | 4 | 3 | 3 | 0 | 1 | 2 | 1 | 1 |
| *Mauritia flexuosa* | 3 | 14 | 14 | 2 | 1 | 7 | 0 | 1 | 1 | 5 | 4 | 1 |
| *Mauritiella aculeata* | 4 | 6 | 7 | 2 | 1 | 7 | 6 | NA | 5 | 5 | 4 | 1 |
| *Oenocarpus bacaba* | 3 | 15 | 13 | 1 | 5 | 2 | 5 | 0 | 3 | 1 | 1 | 1 |
| *Oenocarpus bataua* | 3 | 15 | 15 | 1 | 5 | 1 | 6 | 1 | 4 | 4 | 2 | 1 |
| *Oenocarpus minor* | 4 | 5 | 9 | 1 | 5 | 1 | 4 | 1 | 5 | 2 | 1 | 1 |
| *Socratea exorrhiza* | 3 | 20 | 7 | 2 | 4 | 3 | 11 | 1 | 4 | 3 | 2 | 1 |
| *Syagrus inajai* | 7 | 9 | 12 | 1 | 1 | 2 | 8 | 1 | 7 | 4 | 3 | 1 |

TABLE 1. *Bloomberg's k for morphological and ecological traits analysis considering all species. Ecological traits followed Helmus* et al. *(2007).*

| | K | Variance (Obs) | Variance (Null) | *P* | Z |
|---|---|---|---|---|---|
| Morphological traits | | | | | |
| Stems | 0.204 | 0.149 | 0.555 | **0.023** | -0.812 |
| Height (m) | 0.545 | 1.085 | 6.699 | **0.002** | -0.875 |
| N leaves | 0.179 | 1.083 | 3.431 | **0.058** | -0.735 |
| Spines | 5.170 | 0.001 | 0.061 | **0.001** | -1.513 |
| Inflorescence position | 0.485 | 0.059 | 0.523 | **0.001** | -0.979 |
| Pinnae shape | 0.084 | 0.891 | 0.851 | 0.670 | 0.056 |
| Staminate flowers (mm) | 0.030 | 3.443 | 1.889 | 0.835 | 0.840 |
| Pistillate flowers (cm) | 0.674 | 0.004 | 0.019 | **0.001** | -2.606 |
| Petals (mm) | 0.539 | 0.141 | 0.552 | **0.001** | -2.459 |
| Fruits length (cm) | 0.266 | 0.159 | 0.533 | **0.038** | -0.892 |
| Fruits width (cm) | 0.380 | 0.054 | 0.224 | **0.013** | -0.863 |
| Seeds | 0.237 | 0.007 | 0.032 | 0.157 | -0.448 |
| Ecological traits | | | | | |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| Altitude (m) | 0.026 | 0.003 | 0.001 | 0.873 | 1.164 |
| Near distance (m) | 0.112 | 2.23E-05 | 4.05E-05 | 0.518 | -0.416 |
| meanHAND50 | 0.048 | 0.002 | 0.002 | 0.766 | 0.103 |
| Soil clay content | 0.044 | 0.003 | 0.002 | 0.790 | 0.190 |
| Inclination | 0.127 | 3.01E-05 | 7.06E-05 | 0.300 | -0.599 |
| K (mg/dm$^3$) | 0.098 | 0.000 | 0.000 | 0.455 | -0.445 |
| Na (mg/dm$^3$) | 0.051 | 0.000 | 0.000 | 0.765 | 0.167 |
| Ca (mol/dm$^3$) | 0.185 | 0.000 | 0.000 | 0.075 | -0.670 |
| Mg (mol/dm$^3$) | 0.275 | 0.000 | 0.001 | **0.010** | -0.885 |
| Bases | 0.042 | 0.000 | 0.000 | 0.762 | 0.327 |

TABLE 2. *Bloomberg's k for morphological and ecological traits analysis considering Arecoidae species. Ecological traits followed Helmus* et al. *(2007).*

| | K | Variance (Obs) | Variance (Null) | *P* | Z |
|---|---|---|---|---|---|
| Morphological traits | | | | | |
| Stems | 0.345 | 0.273 | 0.372 | 0.222 | -0.800 |
| Height (m) | 0.419 | 2.698 | 4.550 | 0.110 | -1.169 |
| N leaves | 0.196 | 2.004 | 1.586 | 0.792 | 0.709 |
| Inflorescence position | 0.524 | 0.223 | 0.473 | **0.046** | -1.612 |
| Pinnae shape | 0.256 | 0.350 | 0.366 | 0.502 | -0.116 |
| Staminate flowers (mm) | 0.144 | 0.119 | 0.064 | 0.976 | 2.458 |
| Pistillate flowers (cm) | 0.805 | 0.000 | 0.002 | **0.001** | -1.757 |
| Petals (mm) | 0.432 | 0.090 | 0.155 | **0.097** | -1.228 |
| Fruits length (cm) | 0.259 | 0.102 | 0.106 | 0.498 | -0.107 |
| Fruits width (cm) | 0.369 | 0.025 | 0.037 | 0.253 | -0.785 |
| Ecological traits | | | | | |
| Altitude (m) | 0.154 | 0.002 | 0.001 | 0.912 | 1.485 |
| Near distance (m) | 0.306 | 1.31E-05 | 1.59E-05 | 0.356 | -0.464 |
| meanHAND50 | 0.138 | 0.002 | 0.001 | 0.911 | 1.759 |

| | | | | | |
|---|---|---|---|---|---|
| Soil clay content | 0.133 | 0.003 | 0.002 | 0.941 | 1.859 |
| Inclination | 0.269 | 2.93E-05 | 2.92E-05 | 0.551 | 0.011 |
| K (mg/dm$^3$) | 0.235 | 0.000 | 0.000 | 0.607 | 0.268 |
| Na (mg/dm$^3$) | 0.298 | 4.40E-05 | 5.28E-05 | 0.386 | -0.407 |
| Ca (mol/dm$^3$) | 0.277 | 0.000 | 0.001 | 0.452 | -0.252 |
| Mg (mol/dm$^3$) | 0.439 | 0.000 | 0.000 | 0.103 | -1.228 |
| Bases | 0.215 | 0.000 | 0.000 | 0.694 | 0.482 |

TABLE 3. *Bloomberg's k for morphological and ecological traits analysis considering Cocoae species. Ecological traits followed Helmus* et al. *(2007).*

| | K | Variance (Obs) | Variance (Null) | *P* | Z |
|---|---|---|---|---|---|
| Morphological traits | | | | | |
| Stems | 0.418 | 0.137 | 0.766 | **0.011** | -0.848 |
| Height (m) | 1.303 | 0.451 | 3.552 | **0.003** | -0.723 |
| N leaves | 0.569 | 0.960 | 5.179 | **0.012** | -0.629 |
| Spines | 10.66 | 0.001 | 0.057 | **0.001** | -0.916 |
| Inflorescence position | 0.874 | 0.003 | 0.031 | **0.016** | -0.567 |
| Pinnae shape | 0.046 | 1.347 | 0.870 | 0.702 | 0.549 |
| Staminate flowers (mm) | 0.055 | 6.017 | 4.224 | 0.742 | 0.400 |
| Pistillate flowers (cm) | 1.473 | 0.006 | 0.030 | **0.001** | -2.589 |
| Petals (mm) | 1.635 | 0.182 | 0.877 | **0.001** | -2.408 |
| Fruits length (cm) | 0.370 | 0.220 | 0.846 | 0.094 | -0.849 |
| Fruits width (cm) | 0.281 | 0.077 | 0.255 | 0.143 | -0.749 |
| Seeds | 0.544 | 0.012 | 0.070 | 0.113 | -0.540 |
| Ecological traits | | | | | |
| Altitude (m) | 0.034 | 0.005 | 0.002 | 0.832 | 1.066 |

| | | | | | |
|---|---|---|---|---|---|
| Near distance (m) | 0.134 | 3.00E-05 | 5.32E-05 | 0.604 | -0.407 |
| meanHAND50 | 0.080 | 0.003 | 0.003 | 0.725 | -0.007 |
| Soil clay content | 0.073 | 0.004 | 0.003 | 0.732 | 0.093 |
| Inclination | 0.256 | 3.86E-05 | 0.000 | 0.240 | -0.648 |
| K (mg/dm$^3$) | 0.149 | 0.000 | 0.000 | 0.487 | -0.393 |
| Na (mg/dm$^3$) | 0.075 | 0.000 | 0.000 | 0.711 | 0.054 |
| Ca (mol/dm$^3$) | 0.456 | 5.78E-05 | 0.000 | **0.017** | -0.626 |
| Mg (mol/dm$^3$) | 0.365 | 0.000 | 0.001 | 0.070 | -0.692 |
| Bases | 0.055 | 0.000 | 0.000 | 0.771 | 0.383 |

Figure legends (one page)

Figure 1. The central Amazon basin, indicating the position of the study site in the Reserva Ducke 30 km from Manaus. To the right the PPBio grid where the study was performed.

Figure 2. Topology of the palm local community phylogeny in a 64 $km^2$ terra firme forest at Reserva Ducke, Manaus, Brazil.

Figure 3. Nearest Relatedness Index and Neartest Taxon Index for presence-absence and abundance data for the local palm community in a 64 $Km^2$ terra firme forest at Reserva Ducke, Manaus, Brazil.

Figure 4. Standardized size effect from the Nearest Relatedness Index against the main environmental gradients, HAND (height above the nearest drainage) and soil clay content for a local palm community in a 64 $km^2$ terra firme forest at Reserva Ducke, Manaus, Brazil. Filled dots represent bottomland areas classified by less than 5 m of HAND and less than 10 % of soil clay content.

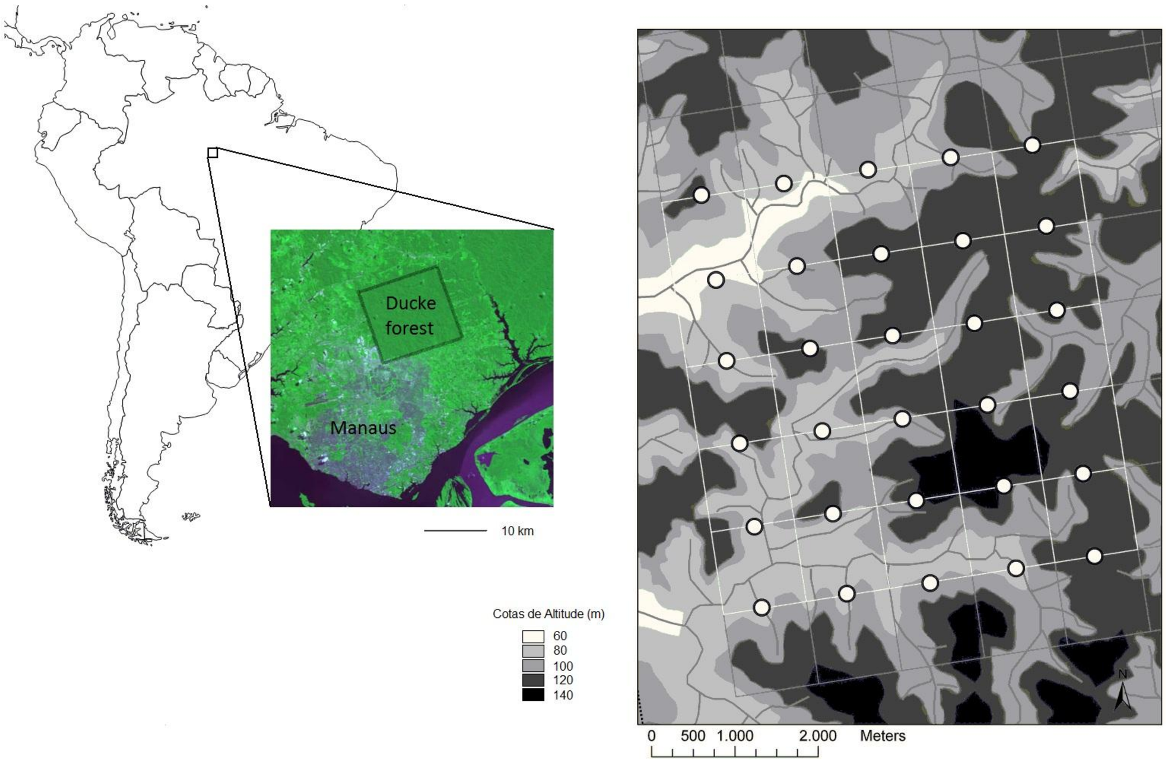

Ducke forest
Manaus
10 km
Cotas de Altitude (m)
60
80
100
120
140
0
500
1.000
2.000
Meters
N

Fig 1.

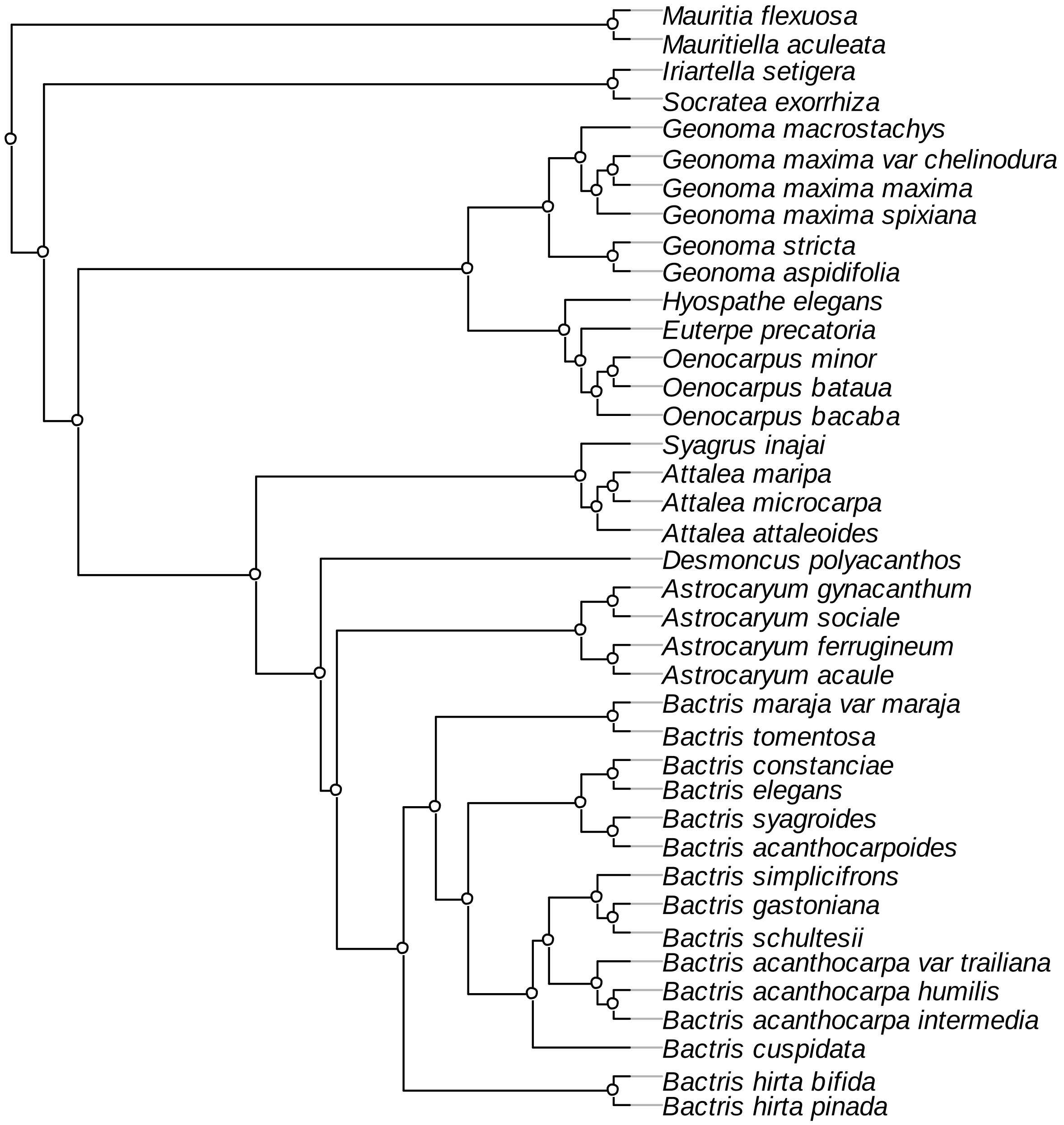

Mauritia flexuosa
Mauritiella aculeata
Iriartella setigera
Socratea exorrhiza
Geonoma macrostachys
Geonoma maxima var chelinodura
Geonoma maxima maxima
Geonoma maxima spixiana
Geonoma stricta
Geonoma aspidifolia
Hyospathe elegans
Euterpe precatoria
Oenocarpus minor
Oenocarpus bataua
Oenocarpus bacaba
Syagrus inajai
Attalea maripa
Attalea microcarpa
Attalea attaleoides
Desmoncus polyacanthos
Astrocaryum gynacanthum
Astrocaryum sociale
Astrocaryum ferrugineum
Astrocaryum acaule
Bactris maraja var maraja
Bactris tomentosa
Bactris constanciae
Bactris elegans
Bactris syagroides
Bactris acanthocarpoides
Bactris simplicifrons
Bactris gastoniana
Bactris schultesii
Bactris acanthocarpa var trailiana
Bactris acanthocarpa humilis
Bactris acanthocarpa intermedia
Bactris cuspidata
Bactris hirta bifida
Bactris hirta pinada

Fig 2.

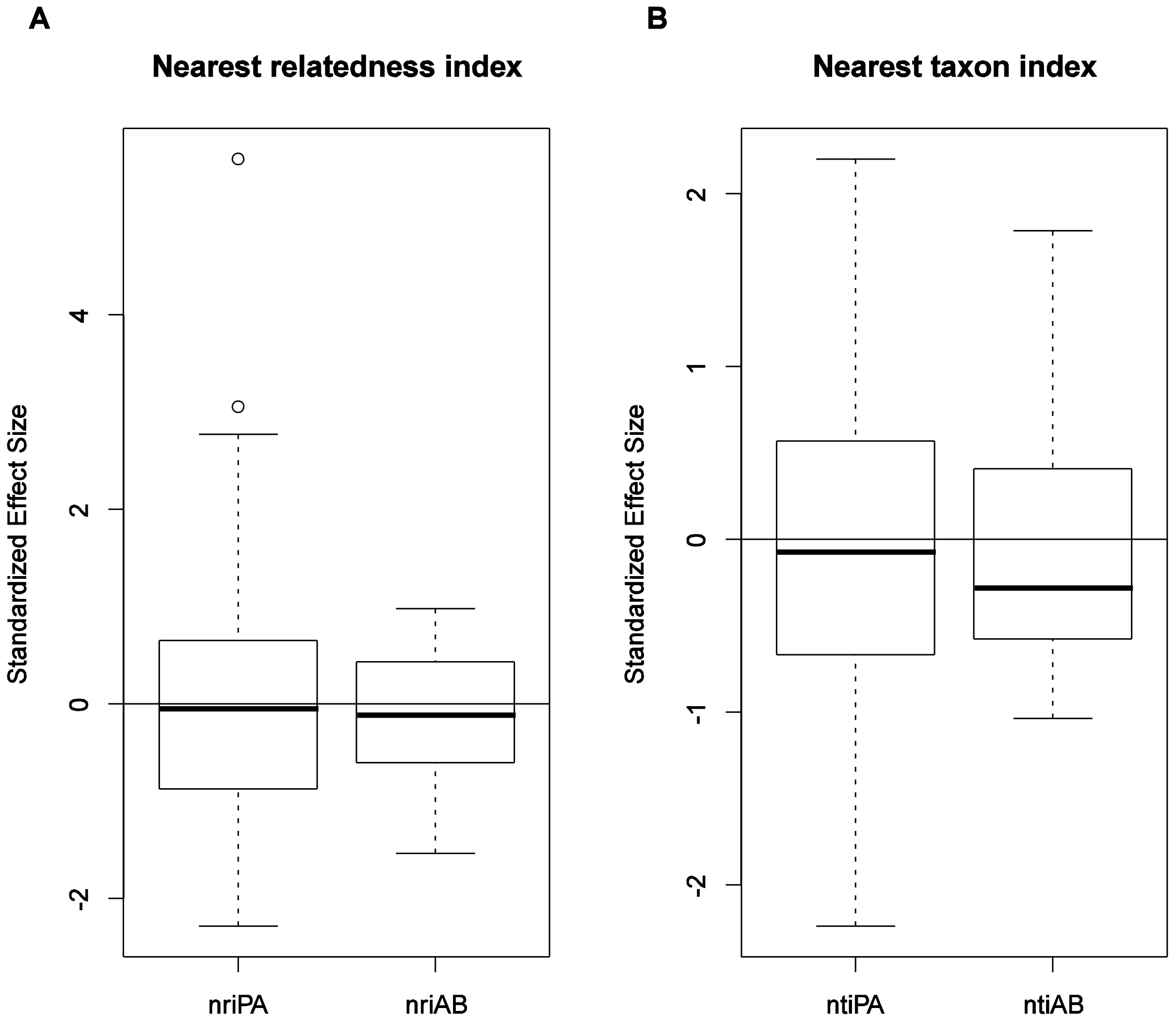
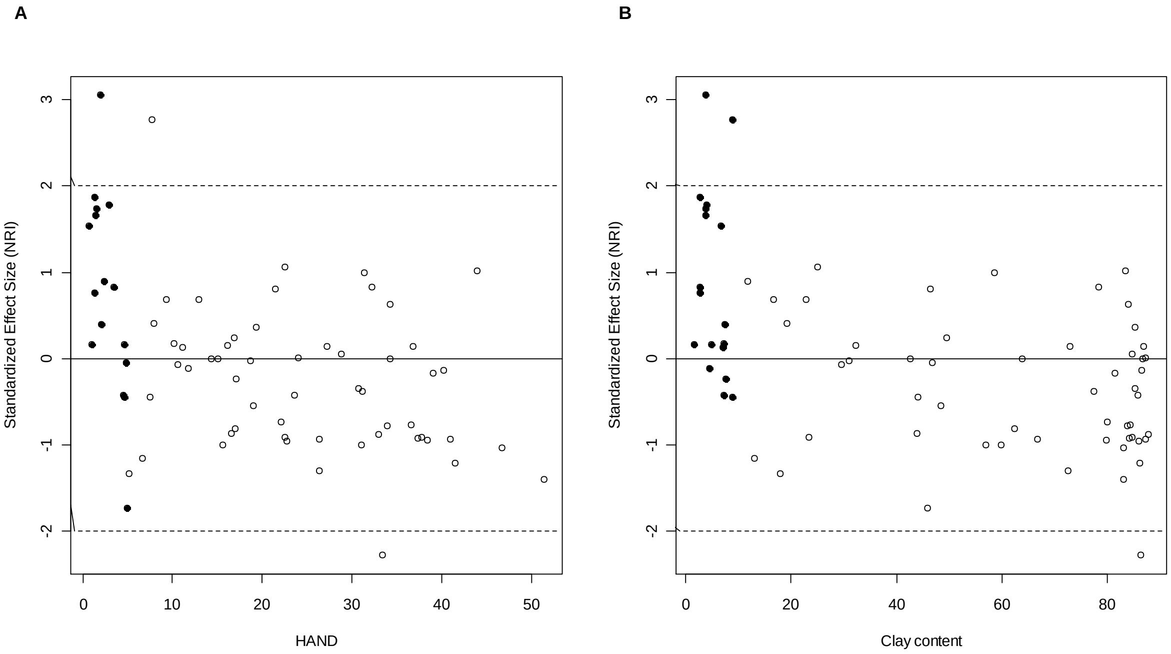

A
Nearest relatedness index
Standardized Effect Size
-2
0
2
4
nriPA
nriAB
B
Nearest taxon index
Standardized Effect Size
-2
-1
0
1
2
ntiPA
ntiAB

Fig 3.

616

617

618



619

620 Fig 4.

621

# Capítulo 3

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Freitas, C.G., Costa, F.R.C., Svenning, J.C. & Balslev, H. Topographic separation of two sympatric palms in the central Amazon – does dispersal play a role? Aceito pela *Acta Oecologica*

# 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, two congeneric palm species (*Attalea attaleoides* Mart. and *A. microcarpa* Spruce) have topographically separated distributions at local scales in the central Amazon basin. Our aim here was to determine if this local-scale separation can be linked to (1) seedling-stage environmental specialization of the two species, and/or (2) environmentally-controlled seed dispersal patterns. We assessed the role of these potential drivers by mapping the local distribution of the two species and testing for correlation to seed removal and seed germination patterns using seed sowing experiments. Twelve seeds of each species were added to each of 30 plots uniformly distributed over a 25-km$^2$ grid, and seed removal and seed germination were subsequently monitored. There was little evidence for environmental specialization at the seedling stage: after 11 months only 2.2 % of *A. attaleoides* seeds had germinated, but along the entire topographic gradient. Seeds of *A. microcarpa* germinated along the entire topographic gradient, but with a tendency towards more inclined areas. In contrast, there was evidence for environmentally-controlled seed dispersal patterns: 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 of 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.

## Keywords

*Attalea*; Arecaceae; endozoochory; seed germination; spatial ecology; tropical forest

## 1. **Introduction**

A core question in ecology is what limits species distributions. For plants, the most important driving mechanism that has been proposed is environmental control, leading to species' habitat specialization (e.g., Whittaker, 1956), and non-equilibrium population processes, with distributions being determined by dispersal limitation and chance (Hubbell, 2001). Both mechanisms appear to 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 the high species diversity of these forests (e.g., Svenning, 1999; Clark et al., 1999; Hubbell, 2001; Fine et al., 2006; Yavitt and Wright, 2008).

Topographic conditions constitute an important environmental control of local- and landscape 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 and Balslev, 1998; Svenning, 1999; 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 physical and chemical characteristics of top soil (Mertens, 2004), with local altitudinal gradients strongly correlating with clay content (Lucas and Chauvel, 1992). At the same time, topography also produces gradients in soil water availability (Hodnett et al. 1997) and root zone waterlogging (Nobre et al. 2011) in this region. All of these topography linked environmental patterns may drive plant distribution in tropical forest, and for, palms, 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).

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

Drivers of plant species distribution linked to environmental conditions have often been seen as alternatives to those linked to dispersal, but it now seems clear that the two processes are not just complementary, but that they may even interact. Different drivers may act at different scales, and the effects of dispersal limitation are expected at local scales, while environmental filters act from global to local scales. At large scales, the distribution of palms is controlled mostly by amount and seasonality of precipitation; at landscape scales by topography, soil, and vegetation structure (such as canopy heterogeneity), and at local scales also by hydrology (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 the distribution patterns at all scales (Eiserhardt et al., 2011). Earlier studies have shown that palm seedlings are clumped around the parent (Svenning, 2001a) and other studies have shown, that when palm seeds are taken by dispersers they are often removed only a few meters away 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 explored how dispersal is limited by the environment, and to what extent such constraints on dispersal may affect species-environment relationships.

*Attalea* includes approximately 27 species according to Henderson (1995) but Pintaud (2008), in a review of the genus, showed that there is a consensus for the validity of only 20 species. *Attalea attaleoides* and *A. microcarpa* are both monoecious palms with short, subterranean stems, and pinnate leaves with the pinnae regularly arranged (Table 1). Closely related species are expected to share many ecological features (Webb et al., 2002; Feeley, 2003) and the evolution of niche differentiation between them is being discussed extensively (Ackerly et al., 2006). For instance, according to Diamond’s (1975) co-occurrence rule, closely related species are unlikely to co-occur at small scales, and in line 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 focus on in this study. *Attalea attaleoides* and *A. microcarpa* are sympatric in most of their range of occurrence (Henderson, 1995; Lorenzi, 2010), but at meso and local scale, more specifically in the *terra firme* forests north of Manaus, they are restricted to different habitats: *Attalea attaleoides* occurs in the upland plateaus and less abundantly on the slopes, whereas *A. microcarpa* is confined to the bottomlands (Costa et al., 2009). In the forests to the south of Manaus, in which most of the environment can be considered as bottomlands, *A. attaleoides* is absent, while *A. microcarpa* is widespread, except in places where floods are frequent (Emilio, *pers. comm*).

We propose that a mixture of meso- and local scales processes (e.g., topography, soil condition and dispersal) separate these two sympatric species along a topographic gradient. First, some mechanism linked to environmental control of dispersers' behavior shapes non-random dispersal limitation in seeds and second, an edaphic control prevents seedlings that could reach areas outside the adults' distribution range to establish. Keeping this scenario in mind we ask why these two sympatric species' distributions do not overlap at the meso-scale and we designed a sowing experiment to answer especially if this pattern is related to niche or neutral processes. Specifically we ask:

(1) Is seed germination related to presence and abundance of adults or to the proportion of individuals fruiting? To access the role of dispersal limitation and environmental control we stated that if a transplanted seed germinates in a site where the adult is not present, 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 do not germinate in a site where adults are absent, this absence could be due to environmental control in the seed phase, i.e., niche processes and local adaptation.

(2) Are seed germination and seed removal related to topography? If yes, one could expect that seed germination will reflect the adult distribution pattern and removal will inversely reflect adult distribution.

## 2. Material and methods

## 2.1 Study site

The study was conducted in Reserva Florestal Adolpho Ducke of the Instituto Nacional de Pesquisas da Amazônia, located 26 km north-west of Manaus (02°55'S; 59°59'W, Fig. 1). The reserve covers 10,000 hectares (10 x 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). The mean annual temperature in the area is 26°C and humidity ranges from 77–88%. The mean annual rainfall is 2362 mm with a dry season from July to October, September being the driest month (Marques-Filho et al., 1981). Soils vary along a gradient from clayey latosols in the uplands towards sandier soils as inclination increases, 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 km$^2$. Within the gridded area, there is a set of 30 plots, each one 250 m long, with variable width depending on taxa being studied, and following altitudinal contours which minimize the internal variation of altitude of each plot. The main gradient within the area is the topography which varies between 46.7 meters and 105.1 meters above sea level. The plots are managed by PPBio program (Research Program in Biodiversity) of the Brazilian Ministry of Science and Technology.

## 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 the plants within the grid and always close to the plots, but never inside them. We collected all seeds that we found in order to obtain at least 360 and brought them to the camp where they were randomized in relation to plots. No viable seeds (those that floated on water) were discarded. We then sowed 12 seeds of *A. attaleoides* and 12 seeds of *A. microcarpa* in two 1 m$^2$ subplots in each of the 30 plots. The subplots were always placed half way along the 250 m plot base line, on the 125 m. The seeds were sowed 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 seed consumers. Although we had no information about how deep the 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). Compared to this, 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 January, 2010 for *A. attaleoides*. Non spiny Cocosoids, such as *Attaleas*, may have a long dormancy of 312–475 days (Wagner, 1982); although this time may be an overestimate given that these palms have remote germination, a kind of germination which takes place underground at the beginning of the germination process (Henderson 2002). So, after the sowing process, we monitored germination and removal by seed consumers, every month until the seeds germinated, which we took as when the primary root appeared (digging up seeds and reburying). Germinated seeds were left in the plots and observed again after nine months. After nine months, more than 20 % of the seeds of *A. microcarpa* and only one seed of *A. attaloides* had germinated. So we made an additional observation one year after sowing. A seed was considered removed by seed consumers when it could not be found. 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.

The topographic variables were made available by PPBio and had originally been measured by a professional surveyor team (http://ppbio.inpa.gov.br/). Altitude was measured using a theodolite in the zero mark at the beginning of each plot. The inclination was measured using a clinometer every 50 m along the plot baseline. At the same points, soil was sampled at 0–5 cm depth from a 30 x 30 cm area, mixed to get a compound sample, and clay content and chemical properties were analyzed at 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 in the landscape and its nearest drainage (Rennó et al. 2008). HAND was calculated for Reserve Ducke, calibrated in the field and averaged for each plot based on the 250 m central line (Schietti, 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, 2011) and compared between plots with and without adults (as a measure of habitat suitability and to control for conspecific density- or distance effects). Anova type III refers to type III sums of squares for unbalanced samples so that the analysis controls for sample size (Zahn, 2009). We tested the effects of abundance of adults, 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 search for outliers and Pair plots and the Variance Inflation Factor (VIF) to look for correlations among the explanatory variables, altitude, clay content, HAND, inclination and nutrient content, this given by the amount of phosphorus and exchangeable bases. All non-correlated variables were used in a complete model, which was subjected to a stepwise function in order to select the best model for each response variable. Inclination and phosphorus were the explanatory variables retained for *A. microcarpa*, and altitude and inclination for *A. attaleoides*. All analyses were performed in the R statistical environment (R Development Core Team, 2010).

## 3. Results

*Germination* — Of 360 sowed seeds of *Attalea attaleoides*, only 8 (2.2%) germinated, and therefore we did not test their relationships with adults or environment. For *Attalea 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 *A. microcarpa* germinated seeds was not 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 seed germination pattern along the topographical gradient is shown in Fig. 3. Seeds of *Attalea 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; and $P = 0.08$ for inclination). Although there was only a very limited number of germinated seeds of *Attalea attaleoides*, the four plots in which seeds did germinate were in different parts of the inclination gradient (2, 4.8, 10 and 10.2°, where the range of variation in the mean plot values are between 0.7 and 26.7, with just three values above 15°). For the plots where *A. attaleoides* did germinate see asterisks in Fig. 3.

*Removal* — the number of removed seeds of *A. attaleoides* and *A. microcarpa* 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 seeds of *A. attaleoides* was not related to the abundance of adults 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 removed seeds of *A. microcarpa*, was positively related both to the abundance of adults ($R^2$ = 0.13, $P$ =0.05) and to the proportion of individuals fruiting ($R^2$ = 0.12; $P$ =0.06), but this result is influenced by one 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 abundance of adults and for proportion of individuals fruiting respectively).

The seed removal pattern along the topographical gradient is shown in Fig. 3. The proportion of removed seeds of *Attalea attaleoides* was higher in less inclined plots (Fig. 4b, open dots; $R^2$ = 0.31; $P$ = 0.006). We also found a higher proportion of removed seeds of *A. microcarpa* in less inclined plots; however this result is not statistically significant (Fig. 4b, filled dots; $R^2$ = 0.09; $P$ = 0.24 for the complete model; and $P$ = 0.16 for inclination). For the full results including non significant ones see Table 2.

## 4. Discussion

*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 adult of *A. microcarpa* in the uplands. These results suggest that its distribution may be governed by dispersal limitation, so seeds under natural conditions do not reach the uplands. Indeed, Svenning (2001a) attributed the clumping pattern in some Andean palms to recruitment limitation due to restricted seed dispersal. A set of factors contribute to this, including seed size, which limits the distance a seed can be carried, size of the disperser, digestive characteristics, habitat preference of the disperser, 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 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, 1991).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 (Bodmer, 1991; Quiroga-Castro and Roldán, 2001), which moves over very long distances, prefers low and moist areas (Bodmer, 1991; Salas, 1996), and their latrines are located mostly in wet areas (Fragoso, 1997; Quiroga-Castro and Roldán, 2001) just like our bottomlands. Even if the maximum elevation difference within the grid is 58 meters, and the maximum difference between adjacent high and low sample plots is only 43 meters, the mean inclination of slopes is 26° (maximum inclination is 48°), therefore it is possible that such topographic features prevent dispersers from moving seeds from the bottomlands to the uplands. A second possible explanation for the absence of adult *A. microcarpa* in the uplands is related to environmental control in the seedling phase. Similar transplantation experiments conducted in central Amazonia with the clay (*Oenocarpus bacaba*) and sandy soil (*Socratea exorrhiza*) specialists showed that the sand-specialist germinated well along the entire gradient (Pacheco, 2001), in the same way as *A. microcarpa* did in our experiment. That study also found that the impact of herbivores on seedlings was similar in both species, but protection against herbivory reduced mortality only in the clay-specialist. This supports the idea of a trade-off between growth-defense against herbivores in pairs of closely related species in the same clay/sand scenario proposed by Fine et al., (2004, 2006). Based on the growth/defense trade-off idea we may infer that *A. microcarpa*, as a sand-specialist, can be eliminated from the uplands (assuming they reach it) by edaphic conditions more than any other biological constraint. However, this remains to be tested for our two species.

Considering the germination and removal patterns and the pattern of distribution of adults, we infer that dispersers are most important and environmental mechanisms are secondary at germination phase contributing in keeping *A. microcarpa* in bottomlands. For *A. attaleoides* the seeds were heavily removed and germinated in only four plots, but since these four plots were located along the entire topographic gradient, we cannot conclude about any difference in germination patterns with altitude between the two species.

Compared to literature germination rate for non-spiny Cocosoids species (37%) in green house conditions (Wagner, 1982), we consider our germination rate (26%) reasonable. Dormancy, very common in non-spiny Cocosoids may cause this low germination rate, but as the germination was consistent along the whole gradient, we believe that this does not affect our main conclusion that an environmental filter at the germination stage is not the first barrier to the distribution of *Attalea attaleoides* and *Attalea microcarpa*. It is possible that seeds germinating later could be restricted to some part of the gradient, owing to genetic variability promoting adaptations to different environments. We recommend that future germination experiments, mostly in this species, should take longer to address this possibility.

*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 where there was higher abundance of adults, but this pattern was due to an outlier. Some studies found the opposite, i.e., that there was more predation by herbivores in areas of higher abundance of reproductive adults (DeSteven and Putz, 1984; Forget, 1992) and Janzen (1975) found similar seed predation in riparian sites and hilltops, such as ours. Our removal data reinforce our idea about dispersal limitation; if the seed is available it will be removed independently of adults, but not independently of the topographic condition.

*Topography* — Seed removal of *A. attaleoides* was related to inclination, being lower in the more inclined areas. The tendency is the same for *A. microcarpa*, even if the relationship is not statistically significant. So, our results for seed removal of both species and for *A. microcarpa* germination suggest that recruitment may be higher in more inclined plots. This result agrees with Janzen (1975) who found similar seed predation in riparian sites and hilltops and with Klinger and Rejmánek (2010) who found the same pattern in *Astrocaryum mexicanum*, e.g., lower removal rates in slopes, but greater germination in flat areas conditional to disperser manipulation. Our removal data reinforce our previous assumption about preferences of seed dispersers/predators. But, even if dispersers hardly ever carry seeds throughout the entire gradient, they may occasionally do this. Therefore, it is expected that we would find seedlings of *A. microcarpa* outside of the known range of adults, even if dispersal limitation was the only process affecting its distribution. Since seeds are able to germinate along the entire topographic gradient, and seed removal is smaller in slopes, we should expect higher recruitment in slopes. This is not in accordance with the distribution pattern of adults, which are less abundant in slopes for *A. microcarpa* and not more abundant in slopes than in plateaus for *A. attaleoides*. Therefore, environmental filters presumably act after germination to set the pattern observed for adults. These filters may be linked to seed consumers, as suggested by Fine et al., (2004; 2006), but may also be a result of physiological constraints (Gibbons and Newberry, 2002).

## 5. Conclusion

Overall, our results suggest that distribution of the *Attalea attaleoides* and *A. microcarpa* is partially set by topographically constrained dispersal, probably mediated by disperser's behavior, and partially by more direct environmental control on local individual performance, mediated by filters associated to the topography. Disperser feeding preferences associated to certain habitats may create seed shadows restricted to these habitats and prevent ample dispersal of a species. We suggest that 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, and therefore the expectation is that herbivores or physiological constraints must limit their performance at later ontogenetic stages. Hence, all the factors described here seem to work together in confining *A. attaleoides* to the uplands and *A. microcarpa* to the bottomlands even if these two closely related species are sympatric in their overall distribution.

## 6. Acknowledgments

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Table 1. *Attalea attaleoides* and *A. microcarpa* reproductive traits, possible pollinators and dispersers and distribution at large and local scales.

| Characteristics | *A. attaleoides* | *A. microcarpa* |
|---|---|---|
| Inflorescences position | Interfoliar [a,b] | Interfoliar [a] |
| Rachis length (cm) | 15–20 [a] | 20–50 [a] |
| Staminate rachillae (no, length 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];<br>Elongate [b]; |
| Fruits length (cm) | 4.5–5.5 [a, b]; | 3.5–4 [a]; 3.7 [c] |
| Fruits width (cm) | 2–2.5 [a, b] | 2–3 [a]; 2.5 [c] |
| Mesocarp | Dry and fibrous [b] | Dry and fibrous [b] |
| Endocarp fibers | Few or absent [a] | Thin with or without [a] |
| Seeds | 2–3 [a] | 1–3[a]; Often one [b] |
| Germination | Difficult [b] | Difficult and slowly [b] |

[a] Henderson (1995); [b] Lorenzi (2010); [c] Glassman (1999).

Table 2. Results for ANOVA and Multiple Regression models.

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

* Without considering an outlier 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 inclination. PxA means presence and absence data. G and R means germination and removal, respectively.

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

| Species | Distribution | Habitat | Pollinators |
|---|---|---|---|
| *Attalea attaleoides* | French Guiana, Surinam and Brazil (Amapá e Amazonas) [a] | Higher areas and occasionally slopes (study area) [b]; low land rain forest on *terra firme*, rarely to 750 m elevation [a]; Campinarana (sandy soils) [c] | Beetle pollinated, most by *Mystrops* (Nitidulidae) and *Phyllotrox* (Curculionidae) [d] |
| *Attalea microcarpa* | Colombia, Venezuela, Guianas, Peru and Brazil (Amapá, Amazonas and Pará) [a] | Restricted to bottomlands (study area); low land 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, Nitidulidade and Staphylinidae)[e] |

[a] Henderson (1995); [b] Costa et al. (2009); [c] Lorenzi (2010); [d] Küchmeister et al (1998); [e] Küchmeister et al (1993).

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

| Possible dispersors [a] | Home range | Activity period [b] | Habit [c] |
|---|---|---|---|
| *Potos flavus* | 8–50 ha | Nocturnal | Arboreal |
| *Tapirus terrestris* | - | Mostly nocturnal, partially diurnal | Terrestrial (can negotiate almost vertical slippery hillsides) |
| *Tayassu tajacu* | 30–800 ha [c] | Diurnal | Terrestrial |
| *Odocoileus virginicus* | 229 ha [d] | Diurnal/nocturnal | Terrestrial |
| *Mazama americana* | - | Diurnal/nocturnal | Terrestrial |
| *Mazama gouazoubira* | - | Mostly diurnal | Terrestrial |
| *Dasyprocta leporine* | - | Diurnal | Terrestrial |
| *Sciurus spadiceus* | - | Diurnal | Terrestrial/Arboreal [e] |
| *Cebus apella* | 850 ha [f]; 180 ha [d] | Diurnal | Arboreal/Prefer areas bottomlands near streams [a] |
| *Saimiri sciureus* | 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 Rosemblum (1974).

Figure legends

**Fig. 1** The central Amazon basin, indicating the position of our study site in the Reserva Ducke 30 km from Manaus. To the right the PPBio grid where the study was performed

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

**Fig. 3** Large scale distribution of *Attalea attaleoides* and *A. microcarpa*. Circles are distribution in the Amazon according to Henderson (1995). Shades are the distribution in Brazil according to Lorenzi (2010); hatched shade for *A. attaleoides* and dark shade for *A. microcarpa*. The detail shows local abundance (numbers under bars). The proportions of seeds removed are represented in dark gray and the proportion of seeds germinated is represented in light gray in the top for *A. microcarpa* and in the bottom for *A. attaleoides*

**Fig. 4** Partial regressions showing the proportion of germinated seeds of *Attalea microcarpa* (A), the proportion of removed seeds of *Attalea attaleoides* (filled dots, solid line) and the proportion of removed seeds of *Attalea microcarpa* (open dots, dashed line) against inclination in 30 plots in a 25 km$^2$ *terra firme* area at Reserva Forestal Adolpho Ducke in Central Amazonia. The partial effects of inclination exclude the effects of other variables included in each model. The values can be negative since thay are the residuals from the multiple regression model but the inclination ranges between 0.7 and 26.3° in the area.

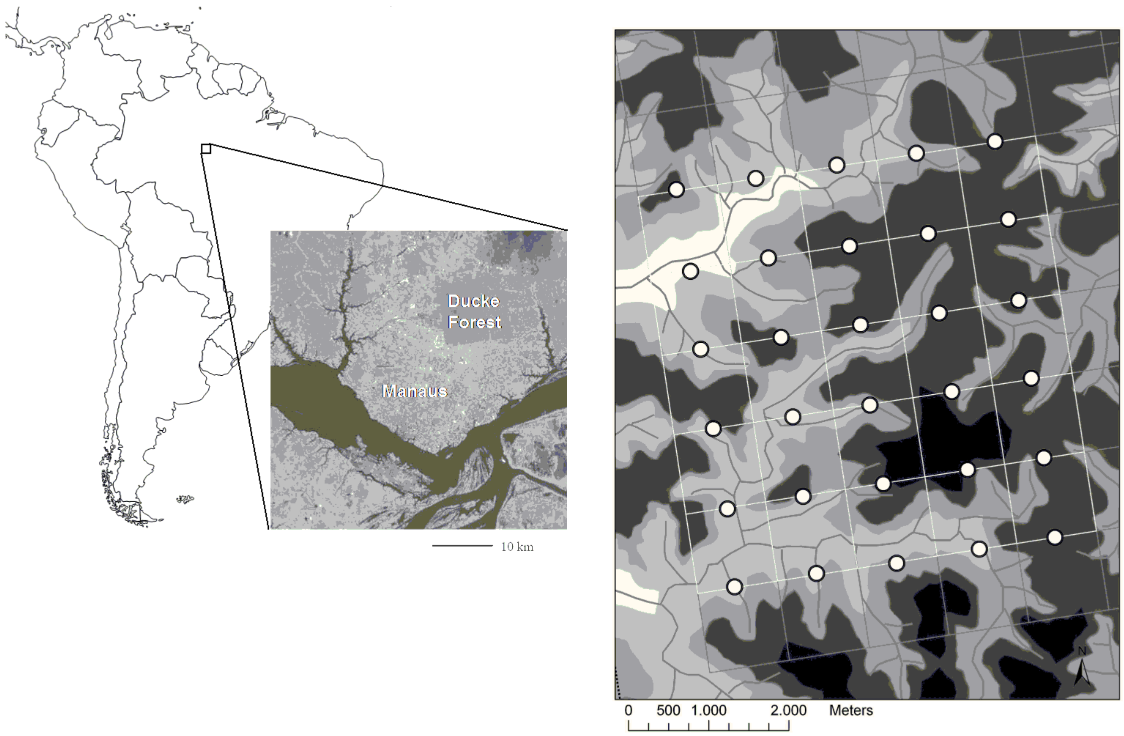


Fig 1.

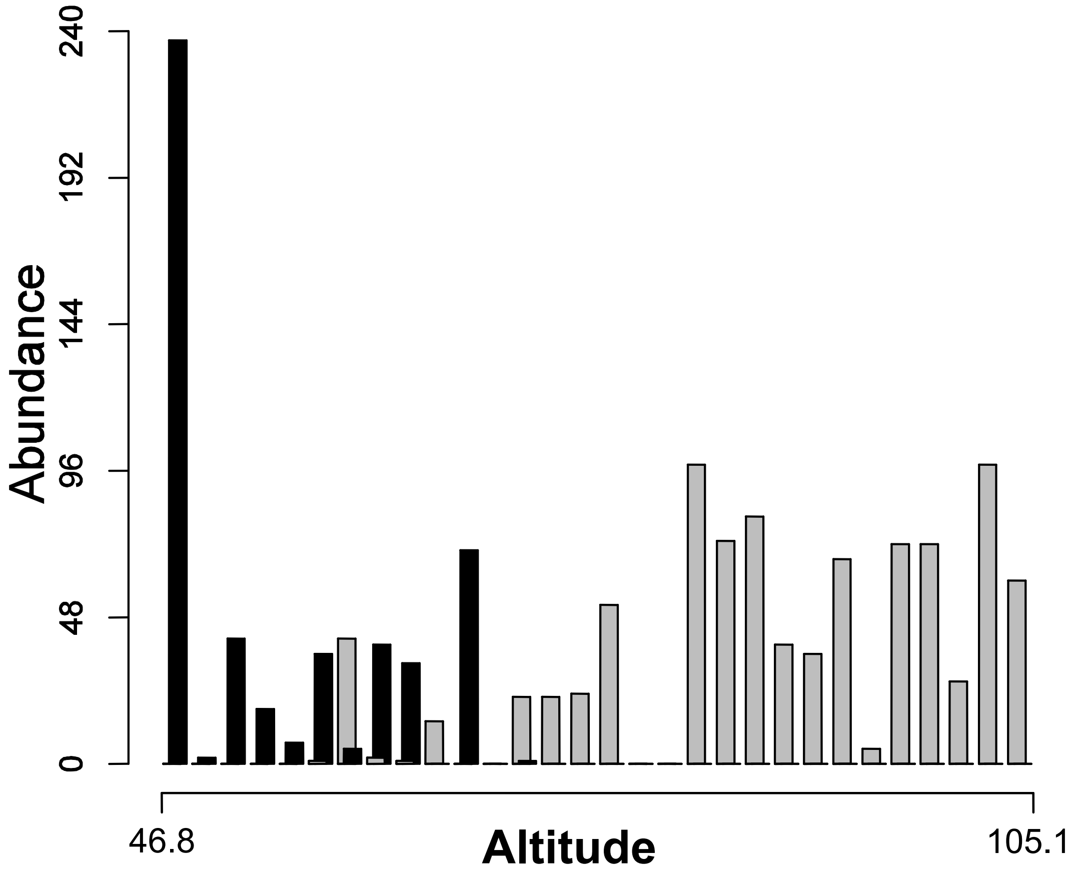
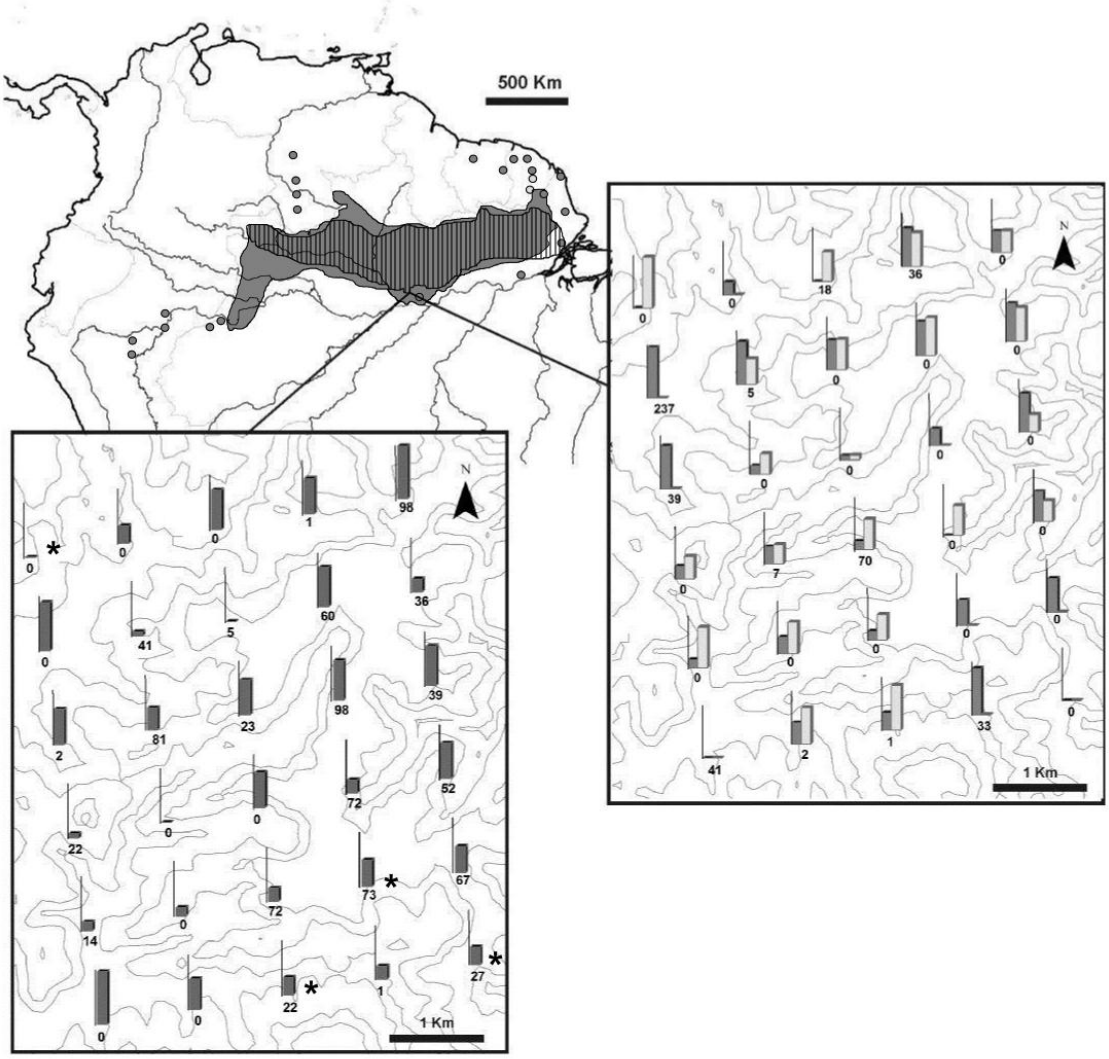


Fig 2.


500 Km
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237
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N
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41
5
60
36
2
81
23
98
39
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14
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72
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*
67
0
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22
*
1
27
*

Fig 3.

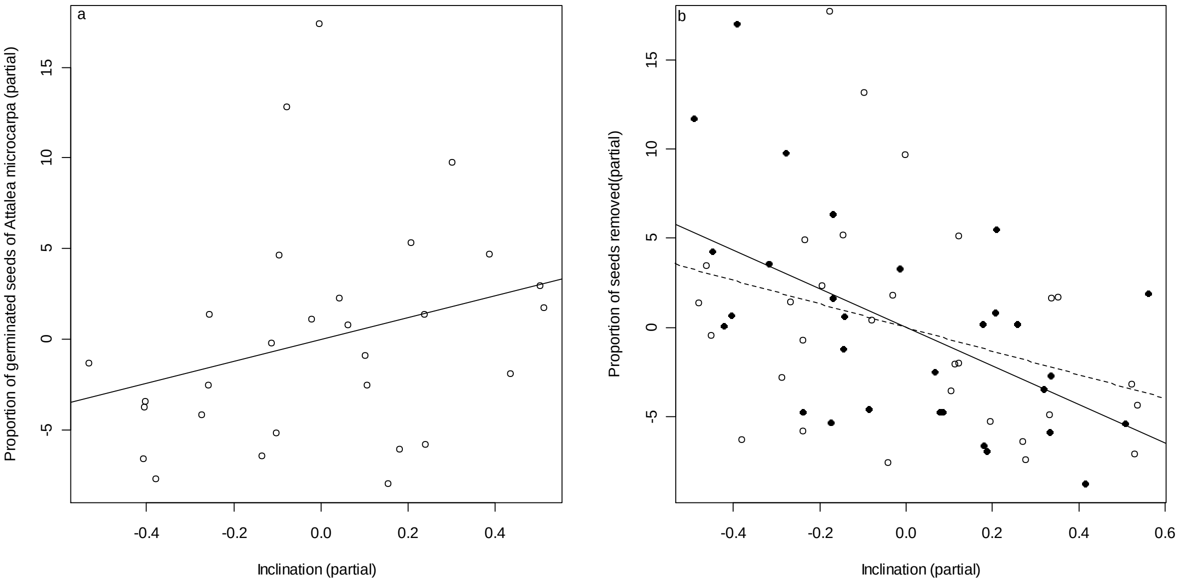
a
Proportion of germinated seeds of Attalea microcarpa (partial)
15
10
5
0
-5
-0.4
-0.2
0.0
0.2
0.4
Inclination (partial)
b
Proportion of seeds removed(partial)
15
10
5
0
-5
-0.4
-0.2
0.0
0.2
0.4
0.6
Inclination (partial)

Fig 4.

## Síntese

De maneira geral, a maioria das nove espécies de palmeiras monitoradas apresentou algum grau de restrição de sua distribuição ao longo do gradiente de conteúdo de argila considerando a fase do desevolvimento, com indivíduos frutificantes mais restritos. A produção de frutos da maioria das nove espécies de palmeiras está condicionada à disponibilidade de água e nutrientes no solo, embora algumas espécies frutifiquem independente da posição no gradiente. Adicionalmente, não foi encontrada estrutura filogenética na comunidade de palmeiras local. Além do mais, os caracteres morfológicos/reprodutivos analisados não são conservados, mas sim lábeis e não estão organizados espacialmente, embora nos baixios haja uma organização com indivíduos mais parecidos ocorrendo juntos. Finalmente, as sementes de *Attalea* germinaram independentemente da posição no gradiente topográfico mostrado uma distribuição mais ligada a limitação de dispersão do que ao controle ambiental nesta fase do desenvolvimento.

Muitos estudos sobre reprodução de plantas não abordam a questão de como a reprodução é afetada por características do ambiente nas escalas da paisagem. Essa abordagem é crucial para entender o nicho realizado e assim tomar decisões de conservação de forma correta. Embora seja importante entender quais fatores locais (e.g luz e relações com os vizinhos mais próximos) abordados em muitos trabalhos, entender as limitações da reprodução na escala da paisagem é crucial para a conservação das espécies, uma vez que grande parte da área ocupada pode representar áreas sumidouras onde os indivíduos presentes são incapazes de manter a população sem a contribuição de imigrantes.

No que diz respeito às relações filogenéticas entre as espécies, as palmeiras parecem organizadas de forma neutra, com a maioria dos caracteres analisados tendo evoluído de forma lábil ao longo do tempo. Além do mais, esses mesmo caracteres não estão organizados no espaço, com exceção nos baixios, onde os indivíduos mais parecidos ocorrem juntos, embora eles sejam mais distantes filogeneticamente. Isso mostra como os processos evolutivos ajudam a moldar a comunidade, principalmente nos baixios.

Quanto às duas espécies de *Attalea*, provavelmente a topografia e a habilidade dispersivas mediada pelo comportamento dos dispersores é responsável pela distribuição em áreas opostas do gradiente topográfico. Além do mais, um controle ambiental no desempenho local de cada espécie mediada por filtros ligados à topografia pode ajudar a explicar esse padrão. Todos esses fatores parecem constituir no primeiro passo para confinar *Attalea attaleoides* nos platôs e *Attalea microcarpa* nos baixios

Os baixios parecem ser um ambiente muito peculiar quanto a constituição de sua comunidade e quanto aos processos ecológicos. Há uma clara restrição das populações das palmeiras ao longo do gradiente de conteúdo de argila do solo dividindo as populaçãoes do baixio do resto do gradiente. Além do mais, a estrutura filogenética do baixio pode ser reconhecida com espécies mais próximas co-ocorrendo juntas enquanto que no resto do gradiente a estrutura parece aleatória. No baixio, então a comunidade de palmeiras parece bem melhor definida do que no restante do gradiente.

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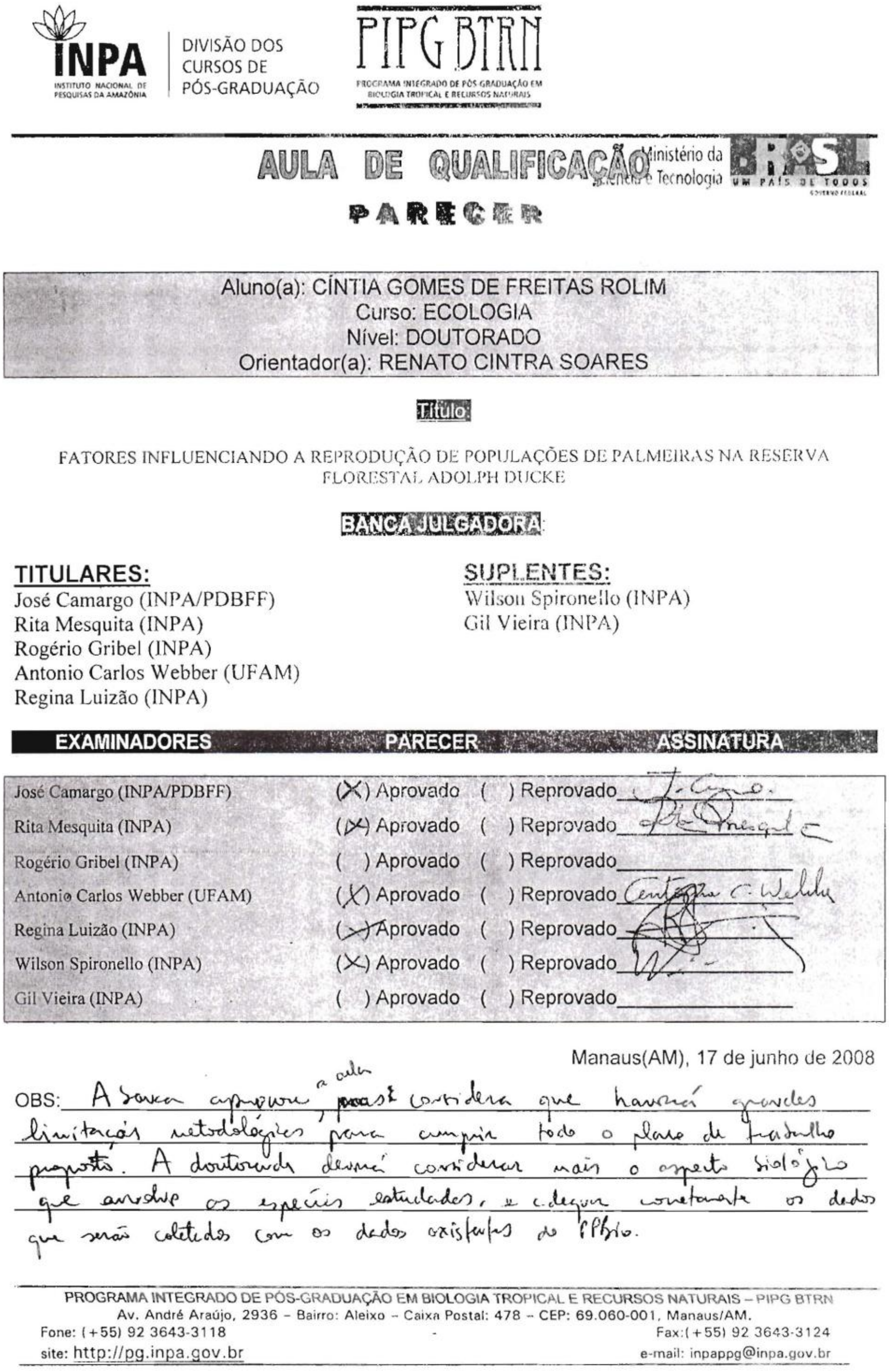
Apêndice 1 – Ata da aula de qualificação



INPA
INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA
DIVISÃO DOS CURSOS DE PÓS-GRADUAÇÃO

PIPG BTRN
PROGRAMA INTEGRADO DE PÓS-GRADUAÇÃO EM BIOLOGIA TROPICAL E RECURSOS NATURAIS

Ministério da Ciência e Tecnologia
BRASIL UM PAÍS DE TODOS
GOVERNO FEDERAL

**AULA DE QUALIFICAÇÃO**

**PARECER**

Aluno(a): CÍNTIA GOMES DE FREITAS ROLIM
Curso: ECOLOGIA
Nível: DOUTORADO
Orientador(a): RENATO CINTRA SOARES

**Título:**

FATORES INFLUENCIANDO A REPRODUÇÃO DE POPULAÇÕES DE PALMEIRAS NA RESERVA FLORESTAL ADOLPH DUCKE

**BANCA JULGADORA:**

| TITULARES: | SUPLENTES: |
|---|---|
| José Camargo (INPA/PDBFF) | Wilson Spironello (INPA) |
| Rita Mesquita (INPA) | Gil Vieira (INPA) |
| Rogério Gribel (INPA) | |
| Antonio Carlos Webber (UFAM) | |
| Regina Luizão (INPA) | |

| EXAMINADORES | PARECER | | ASSINATURA |
|---|---|---|---|
| José Camargo (INPA/PDBFF) | (X) Aprovado | ( ) Reprovado | |
| Rita Mesquita (INPA) | (X) Aprovado | ( ) Reprovado | |
| Rogério Gribel (INPA) | ( ) Aprovado | ( ) Reprovado | |
| Antonio Carlos Webber (UFAM) | (X) Aprovado | ( ) Reprovado | |
| Regina Luizão (INPA) | (X) Aprovado | ( ) Reprovado | |
| Wilson Spironello (INPA) | (X) Aprovado | ( ) Reprovado | |
| Gil Vieira (INPA) | ( ) Aprovado | ( ) Reprovado | |

Manaus(AM), 17 de junho de 2008

OBS: A banca aprovou a aula, mas considera que haverá grandes limitações metodológicas para cumprir todo o plano de trabalho proposto. A doutoranda deverá considerar mais o aspecto fisiológico que envolve as espécies estudadas, e conjugar corretamente os dados que serão coletados com os dados existentes do PPBio.

PROGRAMA INTEGRADO DE PÓS-GRADUAÇÃO EM BIOLOGIA TROPICAL E RECURSOS NATURAIS – PIPG BTRN
Av. André Araújo, 2936 – Bairro: Aleixo – Caixa Postal: 478 – CEP: 69.060-001, Manaus/AM.
Fone: (+55) 92 3643-3118 Fax:(+55) 92 3643-3124
site: http://pg.inpa.gov.br e-mail: inpappg@inpa.gov.br

# Apêndice 2 – Pareceres dos avaliadores do trabalho escrito

**Instituto Nacional de Pesquisas da Amazônia - INPA**
**Programa de Pós-graduação em Ecologia**

## Avaliação de tese de doutorado

Título: **Principais fatores que controlam a reprodução, distribuição e os padrões de co-ocorrência em uma comunidade de palmeiras em uma floresta de terra firme na Amazônia central: Uma abordagem teórica e experimental**

Aluno: **CINTIA GOMES DE FREITAS**

Orientador: **Renato Cintra** Co-orientador: **Flávia R. C. Costa**

Avaliador:

**Por favor, marque a alternativa que considerar mais apropriada para cada ítem abaixo, e marque seu parecer final no quadro abaixo**

| | Muito bom | Bom | Necessita revisão | Reprovado |
|---|---|---|---|---|
| Relevância do estudo | ( x ) | (  ) | (  ) | (  ) |
| Revisão bibliográfica | ( x ) | (  ) | (  ) | (  ) |
| Desenho amostral/experimental | ( x ) | (  ) | (  ) | (  ) |
| Metodologia | (  ) | ( x ) | (  ) | (  ) |
| Resultados | ( x ) | (  ) | (  ) | (  ) |
| Discussão e conclusões | (  ) | ( x ) | (  ) | (  ) |
| Formatação e estilo texto | ( x ) | (  ) | (  ) | (  ) |
| Potencial para publicação em periódico(s) indexado(s) | ( x ) | (  ) | (  ) | (  ) |

**PARECER FINAL**

( x ) **Aprovada** (indica que o avaliador aprova o trabalho sem correções ou com correções mínimas)

(  ) **Aprovada com correções** (indica que o avaliador aprova o trabalho com correções extensas, mas que não precisa retornar ao avaliador para reavaliação)

(  ) **Necessita revisão** (indica que há necessidade de reformulação do trabalho e que o avaliador quer reavaliar a nova versão antes de emitir uma decisão final)

(  ) **Reprovada** (indica que o trabalho não é adequado, nem com modificações substanciais)

Carolina V. de Castilho

**Boa Vista, 29/01/2012,** **Assinatura**

**Comentários e sugestões podem ser enviados como uma continuação desta ficha, como arquivo separado ou como anotações no texto impresso ou digital da tese. Por favor, envie a ficha assinada, bem como a cópia anotada da tese e/ou arquivo de comentários por e-mail para pgecologia@gmail.com e claudiakeller23@gmail.com ou por correio ao endereço abaixo. O envio por e-mail é preferível ao envio por correio. Uma cópia digital de sua assinatura será válida.**

**Endereço para envio de correspondência:**

**Claudia Keller**
**DCEC/CPEC/INPA**
**CP 478**
**69011-970 Manaus AM**
**Brazil**

**Instituto Nacional de Pesquisas da Amazônia - INPA**
**Graduate Program in Ecology**

# Referee evaluation sheet for PhD thesis

Title: **Main drivers controlling reproduction, distribution and co-occurrence patterns in a palm community in a *terra firme* Forest at central Amazonia: A theoretical and experimental approach**

Candidate: **CINTIA GOMES DE FREITAS**

Supervisor: **Renato Cintra** Co-supervisor: **Flávia R. C. Costa**

Examiner: **Kyle E. Harms**

**Please check one alternative for each of the following evaluation items, and check one alternative in the box below as your final evaluation decision.**

| | Excellent | Good | Satisfactory | Needs improvement | Not acceptable |
|---|---|---|---|---|---|
| Relevance of the study | ( ) | ( X ) | ( ) | ( ) | ( ) |
| Literature review | ( ) | ( X ) | ( ) | ( ) | ( ) |
| Sampling design | ( ) | ( X ) | ( ) | ( ) | ( ) |
| Methods/procedures | ( ) | ( X ) | ( ) | ( ) | ( ) |
| Results | ( ) | ( X ) | ( ) | ( ) | ( ) |
| Discussion/conclusions | ( ) | ( X ) | ( ) | ( ) | ( ) |
| Writing style and composition | ( ) | ( X ) | ( ) | ( ) | ( ) |
| Potential for publication in peer reviewed journal(s) | ( ) | ( X ) | ( ) | ( ) | ( ) |

FINAL EVALUATION

( X ) **Approved without or minimal changes**

( ) **Approved with changes** (no need for re-evaluation by this reviewer)

( ) **Potentially acceptable, conditional upon review of a corrected version** (The candidate must submit a new version of the thesis, taking into account the corrections asked for by the reviewer. This new version will be sent to the reviewer for a new evaluation only as acceptable or not acceptable)

( ) **Not acceptable** (This product is incompatible with the minimum requirements for this academic level)

Kyle E. Harms

**__Baton Rouge, LA, USA__, ____Dec. 19, 2011______, __Kyle E. Harms____________________**
**Place Date Signature**

**Additional comments and suggestions can be sent as an appendix to this sheet, as a separate file, and/or as comments added to the text of the thesis. Please, send the signed evaluation sheet, as well as the annotated thesis and/or separate comments by e-mail to pgecologia@gmail.com and claudiakeller23@gmail.com or by mail to the address below. E-mail is preferred. A scanned copy of your signature is acceptable.**

**Mailing address:**

**Claudia Keller**
**DCEC/CPEC/INPA**
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**69011-970 Manaus AM**
**Brazil**

**Instituto Nacional de Pesquisas da Amazônia - INPA**
**Graduate Program in Ecology**

# Referee evaluation sheet for PhD thesis

Title: **Main drivers controlling reproduction, distribution and co-occurrence patterns in a palm community in a *terra firme* Forest at central Amazonia: A theoretical and experimental approach**

Candidate: **CINTIA GOMES DE FREITAS**

Supervisor: **Renato Cintra** Co-supervisor: **Flávia R. C. Costa**

Examiner:

**Please check one alternative for each of the following evaluation items, and check one alternative in the box below as your final evaluation decision.**

| | Excellent | Good | Satisfactory | Needs improvement | Not acceptable |
|---|---|---|---|---|---|
| Relevance of the study | x | | | | |
| Literature review | x | | | | |
| Sampling design | | x | | | |
| Methods/procedures | | x | | | |
| Results | | | x | | |
| Discussion/conclusions | | x | | | |
| Writing style and composition | | | | x | |
| Potential for publication in peer reviewed journal s | | x | | | |

FINAL EVALUATION

**Approved without or minimal changes**

x **Approved with changes** no need for re-evaluation by this reviewer

**Potentially acceptable, conditional upon review of a corrected version** The candidate must submit a new version of the thesis, taking into account the corrections asked for by the reviewer. This new version will be sent to the reviewer for a new evaluation only as acceptable or not acceptable

**Not acceptable** This product is incompatible with the minimum requirements for this academic level

Aarhus, 6 January, Anders S Barfod
Place, Date, Signature

**Additional comments and suggestions can be sent as an appendix to this sheet, as a separate file, and/or as comments added to the text of the thesis. Please, send the signed evaluation sheet, as well as the annotated thesis and/or separate comments by e-mail to pgecologia@gmail.com and claudiakeller23@gmail.com or by mail to the address below. E-mail is preferred. A scanned copy of your signature is acceptable.**

**Mailing address:**

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**69011-970 Manaus AM**
**Brazil**

**Instituto Nacional de Pesquisas da Amazônia - INPA**
**Programa de Pós-graduação em Ecologia**

# Avaliação de tese de doutorado

Título: **Principais fatores que controlam a reprodução, distribuição e os padrões de co-ocorrência em uma comunidade de palmeiras em uma floresta de terra firme na Amazônia central: Uma abordagem teórica e experimental**

Aluno: **CINTIA GOMES DE FREITAS**

Orientador: **Renato Cintra** Co-orientador: **Flávia R. C. Costa**

Avaliador: **Mauro Galetti**

**Por favor, marque a alternativa que considerar mais apropriada para cada ítem abaixo, e marque seu parecer final no quadro abaixo**

| | Muito bom | Bom | Necessita revisão | Reprovado |
|---|---|---|---|---|
| Relevância do estudo | ( x ) | ( ) | ( ) | ( ) |
| Revisão bibliográfica | ( x ) | ( ) | ( ) | ( ) |
| Desenho amostral/experimental | ( x ) | ( ) | ( ) | ( ) |
| Metodologia | ( x ) | ( ) | ( ) | ( ) |
| Resultados | ( x ) | ( ) | ( ) | ( ) |
| Discussão e conclusões | ( x ) | ( ) | ( ) | ( ) |
| Formatação e estilo texto | ( x ) | ( ) | ( ) | ( ) |
| Potencial para publicação em periódico(s) indexado(s) | ( x ) | ( ) | ( ) | ( ) |

**PARECER FINAL**

( x ) **Aprovada** (indica que o avaliador aprova o trabalho sem correções ou com correções mínimas)

( ) **Aprovada com correções** (indica que o avaliador aprova o trabalho com correções extensas, mas que não precisa retornar ao avaliador para reavaliação)

( ) **Necessita revisão** (indica que há necessidade de reformulação do trabalho e que o avaliador quer reavaliar a nova versão antes de emitir uma decisão final)

( ) **Reprovada** (indica que o trabalho não é adequado, nem com modificações substanciais)

**Rio Claro 1/1/2012**

Galetti

**Local** **Data** **Assinatura**

**Comentários e sugestões podem ser enviados como uma continuação desta ficha, como arquivo separado ou como anotações no texto impresso ou digital da tese. Por favor, envie a ficha assinada, bem como a cópia anotada da tese e/ou arquivo de comentários por e-mail para**

pgecologia@gmail.com **e** claudiakeller23@gmail.com **ou por correio ao endereço abaixo. O envio por e-mail é preferível ao envio por correio. Uma cópia digital de sua assinatura será válida.**

**Endereço para envio de correspondência:**

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**Por favor, marque a alternativa que considerar mais apropriada para cada ítem abaixo, e marque seu parecer final no quadro abaixo**

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| Revisão bibliográfica | ( x ) | ( ) | ( ) | ( ) |
| Desenho amostral/experimental | ( x ) | ( ) | ( ) | ( ) |
| Metodologia | ( x ) | ( ) | ( ) | ( ) |
| Resultados | ( x ) | ( ) | ( ) | ( ) |
| Discussão e conclusões | ( x ) | ( ) | ( ) | ( ) |
| Formatação e estilo texto | ( x ) | ( ) | ( ) | ( ) |
| Potencial para publicação em periódico(s) indexado(s) | ( x ) | ( ) | ( ) | ( ) |

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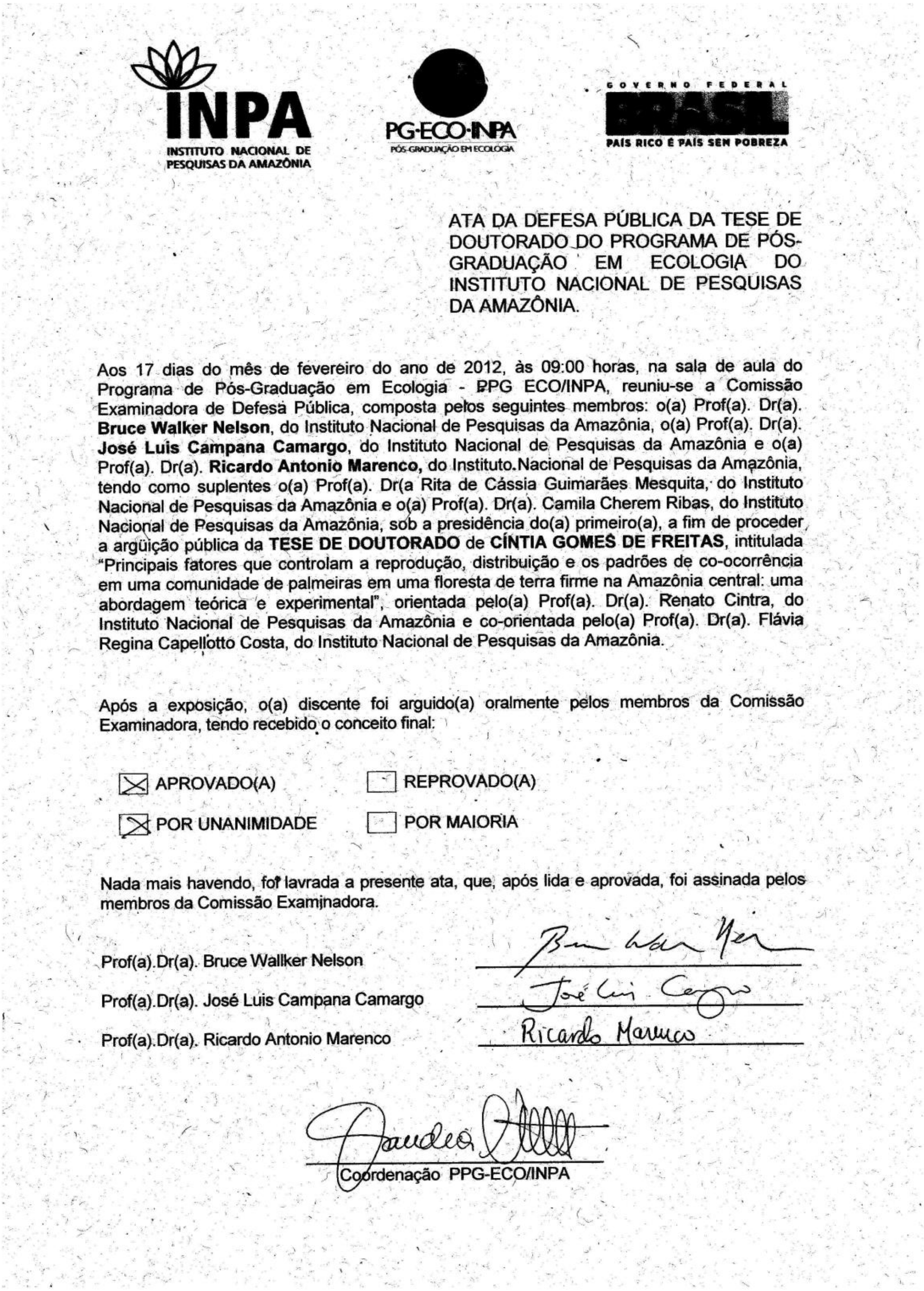
| | | |
|---|---|---|
| **Brasília, DF** | **31 de Janeiro de 2012,** | |
| **Local** | **Data** | **Assinatura** |

**Comentários e sugestões podem ser enviados como uma continuação desta ficha, como arquivo separado ou como anotações no texto impresso ou digital da tese. Por favor, envie a ficha assinada, bem como a cópia anotada da tese e/ou arquivo de comentários por e-mail para pgecologia@gmail.com e claudiakeller23@gmail.com ou por correio ao endereço abaixo. O envio por e-mail é preferível ao envio por correio. Uma cópia digital de sua assinatura será válida.**

Apêndice 3 Parecer dos avaliadores da defesa pública.



INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

PG-ECO-INPA
PÓS-GRADUAÇÃO EM ECOLOGIA

GOVERNO FEDERAL
BRASIL
PAÍS RICO É PAÍS SEM POBREZA

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

Aos 17 dias do mês de fevereiro do ano de 2012, às 09:00 horas, na sala de aula do Programa de Pós-Graduação em Ecologia - PPG ECO/INPA, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Bruce Walker Nelson**, do Instituto Nacional de Pesquisas da Amazônia, o(a) Prof(a). Dr(a). **José Luís Campana Camargo**, do Instituto Nacional de Pesquisas da Amazônia e o(a) Prof(a). Dr(a). **Ricardo Antonio Marenco,** do Instituto Nacional de Pesquisas da Amazônia, tendo como suplentes o(a) Prof(a). Dr(a Rita de Cássia Guimarães Mesquita, do Instituto Nacional de Pesquisas da Amazônia e o(a) Prof(a). Dr(a). Camila Cherem Ribas, do Instituto Nacional de Pesquisas da Amazônia, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública da **TESE DE DOUTORADO** de **CÍNTIA GOMES DE FREITAS**, intitulada "Principais fatores que controlam a reprodução, distribuição e os padrões de co-ocorrência em uma comunidade de palmeiras em uma floresta de terra firme na Amazônia central: uma abordagem teórica e experimental", orientada pelo(a) Prof(a). Dr(a). Renato Cintra, do Instituto Nacional de Pesquisas da Amazônia e co-orientada pelo(a) Prof(a). Dr(a). Flávia Regina Capellotto Costa, do Instituto Nacional de Pesquisas da Amazônia.

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.

Prof(a).Dr(a). Bruce Wallker Nelson ____________________

Prof(a).Dr(a). José Luis Campana Camargo José Luis ____________________

Prof(a).Dr(a). Ricardo Antonio Marenco Ricardo Marenco ____________________

____________________
Coordenação PPG-ECO/INPA