Instituto Nacional de Pesquisas da Amazônia – INPA

Programa de Pós-Graduação em Ecologia

Controles ambientais e bióticos da dinâmica de plântulas em uma floresta de terra-firme da Amazônia central

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Manaus, Amazonas

Novembro, 2012

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

Manaus, Amazonas

Novembro, 2012

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Avaliador	Instituição de origem	Parecer
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B238 Barbosa, Carlos Eduardo de Araújo
Controles ambientais e bióticos da dinâmica de plântulas em uma floresta de terra firme da Amazônia Central / Carlos Eduardo de Araújo Barbosa. --- Manaus : [s.n.], 2012.
xvi, 113 f. : il.

Tese (doutorado) --- INPA, Manaus, 2012.
Orientadora : Flávia Regina Capellotto Costa
Área de Concentração: Ecologia

1. Plântulas. 2. Plântulas – Controle ambiental. 3. Plântulas – Controle biótico. 4. Plântulas – Floresta de terra firme – Amazônia. I. Título.

CDD 19. ed. 574.52642

Sinopse: Foram investigados a relação de eventos de seca com a mortalidade de plântulas e sua interação com diferentes tipos de solo. A distribuição de plântulas e adultos de algumas espécies de árvores e palmeiras foi avaliada, buscando-se encontrar se as espécies estavam espacialmente restritas a algum trecho do gradiente de argila no solo, e em qual estágio ontogenético essa restrição ocorria. Finalmente foram investigados mecanismos envolvidos na formação de padrões de distribuição de genótipos na população de uma espécie comum na Amazônia em diferentes estágios de desenvolvimento, com o uso de ferramentas moleculares. A similaridade genética entre indivíduos vizinhos foi calculada para diferentes classes de tamanho de plantas e em diferentes ambientes, buscando entender o papel de filtros bióticos e abióticos na formação de padrões de parentesco na população.

Palavras-chave: plântulas, Teoria de Janzen-Connell, mortalidade, gradiente edáfico, pluviosidade, sazonalidade, Amazônia central, Reserva Ducke.

Agradecimentos

Agradeço à minha família, pelo apoio na escolha da profissão e compreensão de todas as consequências dessa escolha, entre elas morar em uma ilha a um país de distância. Que toda essa saudade tenha valido a pena.

Agradeço a meus amigos de longa data que me fazem companhia desde a graduação, Pedro Ivo, Waleska, Renato José, Sílvia, Kaká, Annelise, entre muitos na colônia londrinense estabelecida na Amazônia, com os quais migrei para o norte em busca de conhecimento e um bocado de aventuras. Aos grandes amigos que fiz na Amazônia, muitos deles colegas de profissão e companheiros nos intermináveis campos na Ducke. Flávio Rogério, a quem tive o prazer de iniciar nos campos Amazônicos e que sempre esteve presente em diversos campos, nos presenteando com piadas, papos cabeça e muita estória de pescador. Aos amigos e colegas de disciplinas na Ecologia.

À Cíntia Maria, amiga, irmã maninha, com quem enfrentei muita ladeira, tempestade, mosquitos e outras pragas (geralmente tudo junto), com quem cozinhei muita gororoba em campo e de quem escutei muita reclamação, queixas mil, e que se mostrou uma pessoa imune àquela vontade que se tem de esganar alguém. Com ela era só alegria, mesmo quando me tirava do sério. Na loucura do fim de tudo, quando achei por muitas vezes que o não tinha mais jeito, foi quem me botou no caminho diversas vezes.

À Manú, que resistiu à loucura crescente nos meses finais de tese. De quem também me afastei por um longo tempo, quando fui morar a um continente de distância, e que teve a paciência e tranquilidade pra vencer as saudades.

À Flávia Costa, parteira intelectual, que não desistiu de mim, nem mesmo quando o rebento estava virado com o cordão enrolado no pescoço. Não demorei a perceber que tinha escolhido a orientadora certa, de quem tenho muito orgulho e a quem sou muito grato por toda a atenção e paciência despendida. Devo muito, não nego, pago quando os supercomputadores da NASA calcularem a conta.

À família vegetal, pela companhia e suporte, em especial à Thaíse pelos insights explosivos capazes de dar novos rumos aos pensamentos e à Priscila, pelos infindáveis momentos de descontração.

Ao Paul Fine por todo o auxílio oferecido desde o início do doutorado, passando por dezenas de cartas e memorandos e documentos assinados, encaminhados, extraviados, sem nunca ter perdido a paciência no longo processo para a obtenção do visto. A todo o apoio concedido em seu laboratório e posteriormente no desenvolvimento de um estimulante artigo. A toda a equipe do *Fine lab*, Felipe, Chris, Tracey, Krista e Jenny que me receberam de braços abertos.

À Ana Almeida, Carol Sardinha e Ângela Ribeiro, pelo companheirismo e amizade no estranho estrangeiro. Novamente à Ângela pelas conversas que mudaram o rumo do meu trabalho e pela eterna disposição em ajudar.

Agradeço ao INPA pela estrutura logística e apoio na execução dessa tese. Ao Programa de Pós-Graduação em Biologia (Ecologia) pelas disciplinas, estrutura logística, administrativa, incluindo à coordenação e às secretárias Beverly e Rosi. Ao Programa de Pesquisas em Biodiversidade pela estrutura física que apoiou este estudo.

Agradeço ao Renato, único ganhador do troféu “Melhor Estagiário do Mundo” por dois anos consecutivos, oferecido pela Associação dos Doutorandos Desesperados. Aos demais estagiários/amigos/colegas que fizeram o campo e o manejo do enorme volume de dados possível, Leka, Carol, Paola, Denise e Vanessa. Agradeço à Naza por toda a competência nos campos e pelo eterno bom humor. Era sempre um prazer estar ao lado dela. E aos colegas mateiros, sem os quais nada disso seria viável.

Agradeço ao CNPq pela concessão da bolsa de doutorado e à CAPES pela concessão da bolsa sanduíche e ao CNPq pelo financiamento de dois projetos que permitiram que esse trabalho fosse realizado. Ao Dr. Bruce Walker Nelson por auxiliar no envio da proposta de financiamento ao CNPq.

Resumo

A transição de plântulas para estágios mais avançados de desenvolvimento é um momento crucial na definição da distribuição de plantas nos trópicos. Dessa forma faz-se necessário compreender os mecanismos envolvidos neste estágio de vida. Assim como na distribuição de plantas adultas, características do solo têm grande influência no estabelecimento de plântulas, mas com diferente intensidade. Este estudo aborda de três formas distintas o papel da granulometria do solo no estabelecimento de plântulas de espécies amazônicas. (1) Para avaliar como a sazonalidade interage com a textura do solo influenciando o estabelecimento de plântulas, a mortalidade e recrutamento de plântulas foram monitorados em 30 parcelas ao longo do gradiente ambiental durante duas estações chuvosas e três estações secas. O atraso nos efeitos da chuva na mortalidade de plântulas foi acessado a partir da comparação da série temporal de chuva com as séries temporais de mortalidade e recrutamento por meio de correlação cruzada e regressões múltiplas com *lags* de valores de chuva. Encontramos que seca extrema tem grande efeito na mortalidade de plântulas e que seus efeitos continuam durante a estação chuvosa subsequente. Os efeitos negativos da seca na sobrevivência das plântulas em solos argilosos foram observados um mês após o final das chuvas. No entanto a influência da falta de chuva na sobrevivência de plântulas em solos arenosos foi mais imediata, indicando que os baixios são mais vulneráveis ao stress hídrico. Esta pode ser uma das razões para a composição de plantas nos baixios ter um alto *turnover* com relação aos platôs e vertentes. (2) Ao observar a distribuição de árvores adultas e plântulas ao longo do gradiente de argila no solo foi possível descrever padrões de restrição de espécies a diferentes porções do gradiente edáfico. A maioria das espécies restritas só apresentou essa condição no estágio adulto, sugerindo uma contração do habitat com o avanço dos estágios de vida. Duas espécies foram restritas apenas quando plântulas, o que pode indicar assincronia temporal e/ou espacial na frutificação ao longo do gradiente. (3) Buscando evidências de efeitos de denso-dependência no estabelecimento de plântulas, foi descrita a estrutura genética de uma população de *Protium subserratum,* uma espécie de árvore comum na Amazônia. Plântulas espacialmente próximas umas das outras tenderam a ser mais similares geneticamente, e essa similaridade diminuiu conforme a distância entre as plântulas aumentava e o estágio ontogenético avançava. No entanto arvoretas e adultos não seguiram essa tendência, e a similaridade entre indivíduos vizinhos nessa classe de tamanho foi alta. Isso sugere um balanço compensatório entre os efeitos negativos de estar próximo de um adulto conspecífico (por exemplo a herbivoria) e as vantagens de estar em um local favorável ao estabelecimento. Também encontramos que plântulas em solos argilosos eram mais relacionadas umas com as outras do que as plântulas em solos arenosos, sugerindo que os efeitos de denso-dependência que mantém a diversidade da comunidade arbórea podem interagir com características ambientais.

Title: Environmental and biotic drivers of seedling dynamics in a terra firme forest in Central Amazon

Abstract

The transition of seedlings to advanced development stages is probably the most important bottleneck defining plant distribution in the tropics. Thus there is a need to better understand the mechanisms acting at this life stage. As with adult distribution, edaphic features greatly influence seedling establishment, but with different strength. This study comprises three different approaches on seedling establishment along a clay soil gradient. (1) In order to evaluate how seasonality interacts with soil texture in influencing seedling establishment, seedling mortality and recruitment were monitored at 30 plots along the environmental gradient, during two rainy seasons and three dry seasons. The time needed for rainfall decrease to affect seedling mortality was assessed by comparing the time series of rainfall with the time series of seedling mortality and recruitment with cross-correlation analysis and multiple lagged-regressions. We found that the effects of the extreme dry season on seedling mortality continued into the rainy season. Drought effects had a delay of approximately 1 month in seedlings of clay soils and an immediate effect on seedlings in sandy soil, indicating that this environment is more vulnerable to drought stress. That may be one of the reasons the plant composition in the valleys (always with sandy soils at Ducke) has a higher turnover than on the plateaus and slope. (2) Observing adult trees and seedlings distribution across a topo-edaphic gradients it was possible to describe patterns of restriction of species to different portions of the environmental gradient. Most of the species were restricted at the adult stage, suggesting a contraction of the suitable habitat as ontogenetic development proceeds. Two species were restricted only during seedling stage, which might indicate temporal and/or spatially fruiting asynchrony across the soil gradient. (3) Searching for evidence of density-dependent effects on seedling establishment, the genetic structure of a tree species population was estimated, and the changes of the structure across different stages of development was assessed. Seedlings spatially close to each other tend to be more genetically similar, but the similarity decreased as distance was augmented and as the plant grew older, but juveniles and adults did not follow that trend, as relatedness values were higher among neighboring individuals in this size class. That suggests a trade-off between the negative effects of being near closely-related adults (e.g. Herbivore and pathogen attack) and the advantage of being in a site favorable to establishment. We also found young seedlings in clay soils (slope and plateau) were more related to each other than were seedlings in sandy soils (valley), suggesting that the outcomes of conspecific negative density-dependent effects that maintain tree community diversity may interact with environmental features.

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Introdução geral

Um dos grandes objetivos da ecologia vegetal continua sendo a compreensão dos fatores determinantes da distribuição de plantas nos trópicos, assim como a determinação da parcela de influência de fatores estocásticos, interações bióticas e propriedades do ambiente na composição final das comunidades (Diamond 1975). No entanto, a vasta maioria de estudos sobre o tema foca nos estágios finais de desenvolvimento das plantas, avaliando a composição da comunidade com base na distribuição de indivíduos adultos. Considerando que os processos envolvidos na mortalidade de plantas em estágios iniciais de desenvolvimento podem influenciar desproporcionalmente a estrutura das comunidades (Clark et al. 2007), entender os determinantes da distribuição de plântulas no sub-bosque de florestas influencia diretamente o modo de interpretar a distribuição de espécies e composição das comunidades.

Assim como os indivíduos adultos, plântulas respondem à fatores bióticos e abióticos, mas são de maneira geral muito mais sensíveis a eles. A emergência e estabelecimento de plântulas são influenciados, entre outros fatores, pela camada de serrapilheira (Molofsky & Augspurger 1992, Donath & Eckstein 2012), pela quantidade de luz que atinge o sub-bosque (Augspurger 1984), por patógenos e/ou herbivoria (Bell et al. 2006, Alvarez-Loayza & Terborgh 2011, Packer & Clay 2000), pela disponibilidade de água no ambiente (Slot & Poorter 2007, Engelbrecht et al. 2005, Brenes-Arguedas et al. 2009, Tyree et al. 2003) e fatores associados com a variação topo-edáfica (Comita & Engelbrecht 2009). As variáveis que representam o solo e a topografia relacionam-se, direta ou indiretamente, a outras variáveis ambientais e por isso têm sido usadas como características ambientais preditivas da distribuição de plantas em várias florestas tropicais (Tuomisto & Ruokolainen 1993, Tuomisto et al. 2003, Bohlman et al. 2008).

O presente estudo foi realizado na Reserva Ducke, próximo à cidade de Manaus, na Amazônia central. A Reserva Ducke compreende uma área de 100 km^2 com grande variação topo-edáfica o que, como consequência, confere à esta área uma grande heterogeneidade ambiental. Um dos traços mais marcantes nesta floresta é a grande variação na relação argila/areia nos solos, compreendendo um gradiente de textura do solo completo, que muda gradativamente com a altitude de solos extremamente arenosos (2% de argila) para solos com alto teor de argila (90%). Essa configuração permitiu o desenvolvimento de uma série de estudos quanto à distribuição de plantas (i.e., Costa et al. 2005, 2009, Kinupp & Magnusson 2005, Freitas 2012). Um grande facilitador para o desenvolvimento de estudos ecológicos na Reserva foi a publicação do Guia de Campo para a identificação da Flora da Reserva Ducke (Ribeiro et al. 1999). No entanto a falta de conhecimento taxonômico das espécies amazônicas em estágios iniciais de desenvolvimento é provavelmente uma das razões para o pouco conhecimento sobre a ecologia de plântulas na Amazônia brasileira.

Este estudo se propõe a avaliar o processo de estabelecimento de plântulas abordando alguns mecanismos responsáveis pela filtragem ambiental e suas interações com propriedades edáficas. Um dos fatores mais importantes para a sobrevivência das plântulas é a disponibilidade de água (Engelbrecht et al. 2005), que em determinadas situações pode ter mais peso para as plântulas do que fatores como a herbivoria (Brenes-Arguedas et al. 2009). Uma vez que a textura do solo influencia diretamente a capacidade de reter umidade e disponibilizar água para as plantas, é plausível esperar que ao longo de um gradiente de conteúdo de argila no solo a comunidade de plântulas responda à seca de forma diferente. Trabalhos como o de Comita & Engelbrecht (2009), que abordaram explicitamente o gradiente edáfico associado à disponibilidade de água na análise de mortalidade de plântulas, encontraram que plântulas respondem de forma diferente a eventos de seca de acordo com o solo onde estão estabelecidas. No entanto a variação nos solos da Ilha de Barro Colorado, local onde o estudo foi realizado, não é tão grande quanto à variação nos solos da Amazônia Central, o que dificulta a comparação de dados entre as áreas.

Além dos efeitos de fatores abióticos (como a água), o estabelecimento de plântulas pode ser afetado por inimigos naturais (Alvarez-Loayza & Terborgh 2011). Neste caso, a tendência é que o sucesso no estabelecimento das plântulas seja positivamente relacionado à distância que a plântula foi dispersa do adulto materno. Esta é uma das previsões da teoria de Janzen-Connell (Janzen 1970, Connell 1971), proposta há décadas atrás e corroborada por uma série de estudos (e.g., Augspurger & Kelly 1984, Harms et al. 2000, Wills et al. 2006, Alvarez-Loayza & Terborgh 2011), mas que ainda é objeto de debate na comunidade científica (Hyatt et al. 2003). Um ponto de discussão é o *tradeoff* entre a desvantagem de uma plântula de estar próxima à planta-mãe, e consequentemente sofrer com a transferência de patógenos e/ou herbívoros (Alvarez-Loayza & Terborgh 2011), mas ao mesmo tempo desfrutar de um microhabitat com as características ideais para o desenvolvimento até o estágio adulto (Poorter 2007).

Neste estudo abordamos os efeitos de denso-dependência com o uso de ferramentas moleculares para avaliar mudanças na similaridade genética entre indivíduos em diferentes estágios de vida de uma espécie de árvore que é comum em praticamente toda a Amazônia. A mudança nos padrões de similaridade genética entre indivíduos de uma população de plantas ao longo do desenvolvimento ontogenético pode ser interpretada como um reflexo de efeitos de denso-dependência (competição, herbivoria, etc.) Atuando na distribuição e densidade de plântulas de idades similares. Abordagens similares foram realizadas, buscando entender como a denso-dependência atua na distribuição das plantas e de suas proles por meio de análise da estrutura genética em pequena escala (Steinitz et al. 2011, Zhou & Chen 2010). No entanto estudos similares são raros em ambientes tropicais, e não há trabalhos que relacionam de forma explícita o efeito de denso-dependencia em padrões de similaridade genética a gradientes ambientais, como foi realizado neste estudo.

Dessa forma o presente estudo visa contribuir para um entendimento mais completo dos fatores envolvidos na distribuição de plantas em florestas tropicais, em especial na Amazônia central, região na qual estudos sobre a distribuição de plantas e composição de comunidades raramente consideram os processos ligados aos estágios iniciais de desenvolvimento. Compreender como as plântulas respondem a variáveis climáticas estando em diferentes pontos de um gradiente hidro-edáfico permitirá a criação de modelos mais precisos que visem prever os padrões de distribuição de espécies na paisagem.

Objetivo geral

Avaliar o sucesso do estabelecimento de plântulas durante a fase inicial de desenvolvimento frente às variáveis ambientais de chuva e textura de solo e compreender o papel dos efeitos de denso-dependência na distribuição espacial de plântulas no sub-bosque de uma floresta na Amazônia central.

Objetivos específicos

1. Avaliar a mortalidade e recrutamento de plântulas em função do tipo de solo e da variação inter-anual da chuva, e a interação entre ambas variáveis ambientais.

2. Quantificar se existem efeitos retardados das estações chuvosas e secas na mortalidade de plântulas ao longo de um gradiente topo-edáfico e, caso existam, qual o tamanho do período de atuação destes efeitos.

3. Avaliar se há distribuição preferencial de espécies de árvores e palmeiras em sítios ao longo de um gradiente topo-edáfico e se essa restrição é diferente de acordo com o estágio ontogenético.

4. Quantificar o grau de similaridade genética em uma espécie de árvore comum na Amazônia e que está representada em todos os estágios ontogenéticos ao longo de um gradiente topo-edáfico, de forma a permitir avaliar a importância relativa dos estágios de vida e do hábitat na geração de padrões de denso-dependência.

Capítulo 1

Barbosa, C.E.A., Costa, F.R.C., Freitas, C.G. Seedling drought related mortality in an Amazon terra firme forest: the effects of seasonal rainfall variation and delayed response according to soil type. Manuscript in preparation for Biotropica.

Seedling drought related mortality in an Amazon terra firme forest: the effects of seasonal rainfall variation and delayed response according to soil type

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Received: ________________ Revision accepted: __________________

ABSTRACT (246 words)

The transition of seedlings to advanced developmental stages is probably the most important bottleneck defining plant distribution in the tropics. As seedlings are more vulnerable to hydric stress given their limited root system, their survival is highly affected by dry season length. There are plenty of studies describing seedling mortality as a function of drought, but the effects of soil features, responsible for controlling water availability to plants, have not been evaluated across a soil texture gradient long enough to encompass a large variety of soil types. We aimed to understand how seedling establishment limitation differs across sites with different soil texture at a Central Amazon forest and how this variability relates to the seasonal variation of rainfall. We monitored seedling mortality and recruitment at 30 plots with soil clay content ranging from 2 to 87%, and compared seedling mortality among two rainy seasons and three dry seasons. To assess seedling delayed response to rainfall we compared the time series of rainfall with the time series of seedling mortality and recruitment with cross-correlation analysis and multiple lagged-regressions. We found that the effects of an extreme dry season on seedling mortality continued in the rainy season. Drought effects had a delay of approximately 1 month in clayey soil seedlings and an immediate effect on sandy soil seedlings, indicating that this environment is more vulnerable to drought stress. That may be one of the reasons plant composition studies performed in the same site points to higher species turnover in the valleys when comparing to the plateaus and slope.

Key words: cross-correlation function (CCF), clay content, rainfall, season, seedling survival, soil texture, tropical forest.

THE FACT THAT HIGHER RAINFALL IN TROPICAL FORESTS OFTEN CORRELATES WITH HIGHER PLANT diversity (Gentry 1988, Pitman et al. 2002) is a good indicator of the ecological relevance of water availability for processes involving plant distribution. That is because the intensity and length of dry seasons (or drought events) can select species that will succeed at a given site according to their drought resistance (Tyree et al. 2003, Engelbrecht et al. 2005, Lloret et al. 2009). The water available to plants comes from rainfall (and consequently from groundwater), but edaphic characteristics play a major role in microsite moisture availability (Comita & Engelbrecht 2009).

Soil properties have long been known to influence many ecological processes, and are related to above ground tree biomass (Castilho et al. 2006, Laurance et al. 1999) and plant species composition and distribution (Costa et al. 2009, Kinupp & Magnusson 2005, Bohlman et al. 2008, Laurance et al. 2010). To a smaller extent soil properties also are related to adult tree mortality (Toledo et al. 2012). Adult trees have fully developed root systems, and therefore are expected to be able to access deep water, while seedlings root system covers less area and usually do not provide access to deeper water (Gerhardt 1996). Thus the capacity to resist droughts changes according to the ontogenetic stage of the plant, and given the higher susceptibility of seedlings to water shortage, is at the initial development stages that droughts can most influence a species distributional pattern (Engelbrecht et al. 2005, 2007).

There is a vast literature on seedling response to droughts, focusing on few species (Engelbrecht et al. 2005, 2006, Slot & Poorter 2007, Tyree et al. 2003) or at the community level (Bunker & Carson 2005, Comita & Engelbrecht 2009), with most studies being performed in greenhouses, or in field manipulations along gradients of rainfall or light. Despite the success of these studies in describing seedling mortality as a function of water availability, it is difficult to understand the effects of water deficit across different topo-edaphic environments given that comparing studies performed at different locations might result in biogeographic issues (Phillips et al. 2010). To our knowledge no study on seedling mortality has been performed on a scale large enough to encompass environmental variation that allows evaluation of seedling community mortality caused by the interaction of rainfall shortages with a gradient in soil texture.

In the present study we included a substantial gradient in soil texture, which allowed us to draw comparisons of seedling mortality between extremes of this gradient. Considering the influence of water availability on seedling establishment success, we aimed to understand (1) how drought effects on seedling establishment differ across sites with different soil texture at a Central Amazon tropical forest, and (2) how this variability responds to the seasonal variation of rainfall. Hodnett, Vendrame, Filho, et al. (1997) found that sites at lower altitudes in central Amazonia had the water table near the surface even during the dry season, and predicted that vegetation on those sites would suffer less water stress. However low altitude sites at our study site have sandy soils, and therefore a low potential to retain water. In this context, we hypothesized that, (1) tree seedling mortality and recruitment varies according to rainfall and is different along different soil textures, (2) tree mortality is higher in sandier sites located in lower altitudes.

METHODS

STUDY SITE – This study was conducted at Reserva Florestal Adolpho Ducke (hereafter referred to as Ducke), a terra firme tropical forest that covers an area of 100 km^2 at the northern limit of the city of Manaus (02^{o}55’s, 59^{o}59’w, Figure 1) in the Brazilian state of Amazonas. The vegetation in the area is mainly dense terra firme forest, with some patches of white sand forest. Canopy trees reach 35-40 m height (Ribeiro et al. 1999), the understory receives low light levels and is characterized by a high abundance of acaulescent palms (Guillaumet & Kahn 1982). The soil texture gradient goes from clayey latosols in the plateaus (with up to 90% clay content) to sandier soils downhill from the ridges, until they are almost pure sand soil in the valleys. Soil texture related information was accessed from previously collected data available at http://ppbio.inpa.gov.br/Eng/inventarios/ducke/pterrestre/.

The mean annual temperature is 26°C, the humidity ranges from 84–91% and there are two distinct seasons: a dry season from June to November, with minimum rainfall at July (mean of 93 mm) and a rainy season from December to May, with maximum rainfall at February (mean of 299 mm) (Marques Filho et al. 2009). At Ducke, the period of 2009 to 2011 had very erratic weather; the rainy seasons of 2009-10 and 2010-11 had rainfall of 1730 and 2300 mm, respectively, while the dry seasons of 2009, 2010 and 2011 had rainfall of 263, 526 and 528 mm, respectively.

We conducted our study in 30 permanent plots that were set up as part of the Brazilian Long-Term Ecological Research Program (PELD) and the Brazilian Program for Biodiversity Research (PPBIO). The plots are systematically distributed within a trail grid system covering 25 km^2, 1 km distant from each other, and are 250 m long with the width of each plot varying according to the taxa or the life stage to be studied (Magnusson et al. 2005). Since the plots follow the altitudinal contours, the altitude is maintained constant throughout the plot length, which is important at Ducke where topography variation (39 -109 meter a.s.l) is highly correlated with soil texture (Costa et al. 2005). Knowing that at Ducke soil texture strongly influences plant community composition (Costa et al. 2009, 2005, Kinupp & Magnusson 2005, Drucker et al. 2008), and following Schietti et al. (in press), who indicated the environmental limits causing plant composition changes along this gradient, we divided the soils into two classes: "sandy" plots where the soil contained less than 15% clay and "clayey" plots where clay content was greater than 15%.

SEEDLING RECRUITMENT MONITORING AND RAINFALL DATA – Seedling recruitment and mortality was monitored at 15 1 m^2 sub-plots placed along each of the 30 250 m plots (a total of 450 sub-plots), in which all seedlings up to 50 cm height were tagged and mapped. Every month seedling mortality and recruitment were monitored, with new seedlings being tagged and mapped as well. Seedling recruitment and mortality monitoring started in August 2009 and ended in December 2010 and June 2011, respectively. Data on rainfall was collected at the meteorology station at Ducke (CDAM/INPA), with maximum distance to a plot of approximately 8 km.

DATA ANALYSIS – All the analysis was undertaken in the community scale, for the identification status of most of the seedlings did not allowed us to evaluate species responses in an individual fashion. Differences in seedling mortality and recruitment across seasons and environments were determined with Student's t-test. Because the point was to observe the temporal changes in seedling mortality, we used the raw data, which included the temporal trends that were removed from subsequent analyses. For the seasonal analysis, we considered the rainy season as going from December to May, and the dry season from June to September.

To assess the periodic component of seedling mortality and recruitment in each environment, the initial step was to identify if there were significant trends in the time series using two mixed models with the Restricted Maximum Likelihood (REML) method to compare and choose the best fit. Since the subsequent analyses demanded stationary time series, trend was removed when present, and the detrended time series were used as response variables. To determine the correlation between each response time series (seedling recruitment and mortality) and the explanatory time series (rainfall) we ran cross-correlation functions (CCF), in order to identify the past values of rainfall (hereafter “rainfall lags”) that were more correlated to the present values of the response variables. After identifying the rainfall lags with higher correlation with mortality and recruitment, we used these lags as explanatory variables in multiple lagged-regression models to evaluate how far back in the rainfall record was it possible to observe influences on seedling mortality and recruitment.

Given that seedling mortality is expected to vary not only as a function of the previous rainfall, but also with the previous seedling recruitment, we built a path analysis to determine the direct and indirect (through seedling recruitment) effects of rainfall on seedling mortality. The path model included only the rainfall lags with stronger correlation with either seedling recruitment or mortality in the CCFs.

All analyses were performed in R version 2.15.1 (R Development Core Team 2010). Mixed models were implemented with the lmer function of the lme4 package (Bates & Maechler 2011), detrending was performed using the function detrend of the RSEIS package (Lees 2011) and cross-correlation functions were performed in nlme package (Pinheiro et al. 2011).

RESULTS

Seedling mortality varied greatly among 2009/2010/2011 following the weather differences across those years. More seedlings died in the rainy season of December 2009 to May 2010 (mean=135.42 dead seedlings) than in the same period of 2010/11 (mean=80.14, t=1.83, p=0.01) when all seedlings were analyzed together. That pattern was the same when analyzing seedlings according to soil texture (Fig. 2). Mortality for all seedlings in the dry season of 2010 was unexpectedly higher (mean=333.00) than in the dry season of 2009 (mean=214.00, t=4.27, p=0.01), but that pattern did not appear when analyzed separately by soil type. When searching for trends in mortality in 2009, 2010 and 2011, the mixed model identified a significant trend of decreasing mortality for seedlings on sandy soils across the period (p=0.003). The trend for clayey plots was not significant (p=0.11).

The cross-correlation analysis indicated that the mortality of seedlings was negatively correlated with the rainfall of the immediately previous month from which seedling death was observed (t_{-1}), being significant for seedlings from clayey and sandy soils, and also for all seedlings pooled together (Fig.3). There was a weaker negative correlation of mortality with the rainfall lag -2 (t_{-2}), and even though it was not significant, it still indicates a tendency of rainfall lags further back in time influencing mortality. The rainfall in the same month in which seedling death was observed (t_0) was significantly negatively correlated with mortality only in sandy plots. The greater rainfall lags (t_{-4}, t_{-5} and t_{-6}) had high positive correlation with seedling mortality. Despite the negative effects that rainfall excess might have on seedling establishment success, such strong positive influence is contrary to what was expected, given that the events are too far apart. Therefore, we tested only the mortality of seedlings less than four months old, which could not be the result of high rainfall 4 to 6 months before. The same result arose, indicating that the positive correlation has no biological basis, and is a simply product of the way the analysis proceeds, finding any match between cycles.

Recruitment of seedlings was significantly and positively correlated with rainfall for all seedlings together and at clayey/sandy soils for rainfall lags -1 and -2 (t_{-1} and t_{-2}) (Fig.4). Rainfall lag zero (t_0) was not significantly correlated with clay seedling's recruitment, and rainfall at t_{-3} was not significant for recruitment for all seedlings and those in clay plots but not for those in sandy soils.

The lagged regression models (Table 1) indicated that rainfall had a greater influence in sandy soils, for which the same rainfall lags explained 55 and 85% of the variance in sandy soil mortality and recruitment, respectively, compared to 35 and 45% for seedlings in clayey soils. In addition, seedlings in sandy soils were affected by the lack of rain more promptly than those in clayey soils. The rainfall registered for the same month as the death event (lag t_0) was significantly correlated with the death of seedlings only in sandy soil (Fig.3). Also, only the rainfall at t_0 significantly affected seedling mortality in the sand, according to the multiple lagged-regression (Table 1).

Multiple lagged-regression of recruitment as a function of rainfall lags also indicated that rainfall has a greater effect on the regeneration process in the sandy plots than clayey plots. In the sandy plots lags t_0, t_{-1} and t_{-2} explained approximately 85% of the recruitment variation, while the same lags explained 45% of recruitment variation in clay plots. The main effect of rainfall on mortality is direct for either seedlings pooled together or separated according to soil texture (Fig.5). None of the regressions involving seedling recruitment were significant (Table 1).

DISCUSSION

MORTALITY ACROSS SEASONS – Intense annual variation in precipitation is the natural seasonal pattern in the Central Amazon, but the recent years have seen a tendency towards climatic extremes (Antonio, Satyamurty, & Mendes, 2012). The period during which we monitored seedling establishment and mortality comprised two climatic extremes, with a drought period in 2009, with a total of 263 mm in the dry period (against 526 mm in the same period of 2010), that ended with a late and weak rainy season with low rainfall of 1731 mm (compared to 2301 mm in the rainy season of 2010).

Seedling community mortality did not decline when the rainy season started, as we would expect. That may be due to the fact that drought events may not only directly induce seedling mortality, but also indirectly predispose seedlings to die by increasing the magnitude of attacks of predators, pathogens or competitors (Engelbrecht et al. 2005, Gerhardt 1996). Not only the extreme drought of 2009 caused the death of many seedlings, but also stressed the surviving seedlings. This situation was aggravated by the weak subsequent rainy season. In addition, the weakened seedlings may have suffered with the increase of pathogens and the physical damage caused by overland flow of water that comes with wet season (Daws et al. 2005).

Plants respond to drought in different ways, and the optimal strategy is closely linked to the extention and intensity of the drought period. There are seedlings that do not close their stomata to avoid water loss (anisohydric plants), which allows photosynthesis to continue, but may lead it to hydraulic failure if the drought persists for longer periods (mcdowell et al. 2008). Some seedlings avoid losing water by closing the stomata (isohydric plants), but with that strategy photosynthesis is drastically reduced, and the persistence of the plant would depend upon its carbon reserves. Leaf shedding may also reduce photosynthesis and therefore contribute to carbon starvation (Tyree et al. 1993). Any of these strategies may work well during water shortage periods, but as the dry season of 2009 was very strong and long, seedlings that survived into the next rainy season may have depleted their reserves and become more susceptible to other stresses.

MORTALITY ACROSS ENVIRONMENTS – Unlike adult trees, that respond to drought events for extended periods after drought occurrence (Phillips et al. 2010), we found as a general pattern that the time elapsed between a below average rainfall and an increase in seedling death was relatively short, within a month at most. That means that even short drought events have the potential to change recruitment outcomes by increasing seedling mortality.

Our data indicate a clear interaction between rainfall and soil type on seedling mortality. Not only are seedlings in sandier soils more affected by drought, but also the response to that stress is faster in this environment, since only in sandier plots was mortality negatively related to the rainfall in the same month in which the seedlings died. Engelbrecht et al. (2002) were not able to observe immediate effect of drought on seedling mortality at Barro Colorado, a result that is probably due to the clayey soils of the study site, in which there is no environment comparable with the sandy valleys at Ducke.

The higher and faster mortality in the valleys might be a response to the water content in the soil, which is much more variable in sandy soils. The water table in the sandy valleys of our study site can be very superficial (up to 0.6 m deep) during high rainfall periods, but quickly dries down in the absence of rain, attaining more than 1.8 m depth as a lower extreme (Hodnett et al. 1997). There is a delay of months between the beginning of the dry season and the retreat of the water table. Hence, the increase in mortality in the same month that rainy season ceases suggests that the water table level plays a secondary role in the water supply of seedlings, which tend to rely mainly on superficial water provided by rainfall. This community pattern agrees with the observation that *Quercus* seedlings might rely on different water sources than conspecific adult (Cavender-Bares & Bazzaz 2000). Thus, the limited root system of seedlings, combined with the poor capacity of sandy soils in retaining water from rainfall and/or to uptake water from lower soil layers through capillarity may be responsible for the higher mortality in this environment. Clayey soils have a higher water retention capacity, so not only does the water from the rainy season remain available at the surface for a longer period into the dry season, but also the water from the scarcer and shorter rainfalls does not percolate as fast as in sandy areas.

The higher mortality related to soil texture might be more relevant in the initial stages of development of a tree, when the root system is not fully developed, reaching neither great area nor depths. Williamson et al. (2000) found no differences in adult tree mortality across sites with different clay content when studying the effects of an El Niño drought in Amazonia, which indicates that adult individuals have access to deeper water sources. At Ducke, adult mortality has a weak but significant relationship to edaphic features, which mainly explain death by snapping or uprooting, and is usually consequence of storms rather than drought (Toledo et al., 2012), which also points to lower stress due lack of water in adult individuals.

With higher drought-related mortality, the thinning process tends to be much stronger in sandy sites, which may lead to different species composition among different environments. Schietti et al. (2012) found that tree species composition at Ducke varies more among sandy valley sites than does among clayey plateau sites, a sign of heavier environmental filtering strength at those sites. Laurance et al. (2010) found more tree diversity (species richness and Fisher's α) at clayey soil sites, indicating that sandier soil sites may accommodate a narrower range of species due to its higher environmental stress.

The main impact of premature drought-related seedling mortality may be that valleys suffer impacts even in weak dry seasons or during "dry spells" in rainy seasons, as was found by Engelbrecht et al. (2006) for pioneer species. There is an ongoing tendency of intensification of rainy extremes in the Manaus area (Santos et al. 2012), which might increase the frequency of temporary flooding events in the valleys, and consequently seedling mortality due to higher pathogen activity and/or water flow damage (Daws et al. 2005). The changes in the rainfall system of Amazonian forests are undeniable (Marengo et al. 2012), and the current reduction in the interval between extreme drought events (Tomasella et al. 2011) may have a profound influence on seedling establishment, plant distribution and ultimately in community composition.

ACKNOWLEDGMENTS

We thank Renato Almeida de Azevedo, Camila Saraiva dos Anjos, Francisca Denise da Costa and several field assistants for the help in the field; Cristian Dambros for implementing R-scripts and for graphic design; The Climate and Hydric Resources

Sector of INPA (CDAM/INPA) for providing the rainfall data. This study was funded with a phd fellowship from the Brazilian National Research Council (CNPq) to CEAB during field work. Financial support was granted by CNPq/Universal (473447/2008-5) to FRCC and CNPq/CT-Amazônia (575637/2008-0) to Bruce Walker Nelson. Logistical support was provided by Instituto Nacional de Pesquisas da Amazônia (INPA) and Brazilian Program for Biodiversity Research (PPBio). Data repositories are maintained by PPBio, Brazilian Long-Term Ecological Research Program (PELD) and the National Institute of Science and Technology for Amazonian Biodiversity (INCT – CENBAM).

LITERATURE CITED

BATES, D., M. MAECHLER, AND B. BOLKER, 2011. LME4: Linear mixed-effects models using S4 classes. R Package version 0.999375-42. Http://cran.r-project.org/package=lme4

BOHLMAN, S.A., W.F. LAURANCE, S.G. LAURANCE, H.E.M. NASCIMENTO, P.M. FEARNSIDE, AND A. ANDRADE, 2008. Importance of soils, topography and geographic distance in structuring central Amazonian tree communities. Journal of Vegetation Science 19: 863–874.

BUNKER, D.E., AND W.P. CARSON, 2005. Drought stress and tropical forest woody seedlings: effect on community structure and composition. Journal of Ecology 93: 794–806.

CASTILHO, C.V., W.E. MAGNUSSON, R.N.O. DE ARAÚJO, R.C.C. LUIZÃO, F.J. LUIZÃO, A.P. LIMA, AND N. HIGUCHI, 2006. Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography. Forest Ecology and Management 234: 85–96.

CAVENDER-BARES, J., AND F. A. BAZZAZ, 2000. Changes in drought response strategies with ontogeny in Quercus rubra: implications for scaling from seedlings to mature trees. Oecologia 124: 8–18.

COMITA, L.S., AND B.M.J. ENGELBRECHT, 2009. Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. Ecology 90: 2755–2765.

COSTA, F., J. GUILLAUMET, AND A. LIMA, 2009. Gradients within gradients: The mesoscale distribution patterns of palms in a central Amazonian forest. Journal of Vegetation 20: 69–78.

COSTA, F.R.C., W.E. MAGNUSSON, AND R.C. LUIZÃO, 2005. Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. Journal of Ecology 93: 863–878.

DAWS, M.I., T.R.H. PEARSON, D.F.R.P. BURSLEM, C.E. MULLINS, AND J.W. DALLING, 2005. Effects of topographic position, leaf litter and seed size on seedling demography in a semi-deciduous tropical forest in Panamá. Plant Ecology 179: 93–105.

DRUCKER, D.P., F.R.C. COSTA, AND W.E. MAGNUSSON, 2008. How wide is the riparian zone of small streams in tropical forests? A test with terrestrial herbs. Journal of Tropical Ecology 24: 65–74.

ENGELBRECHT, B.M.J., L.S. COMITA, R. CONDIT, T.A. KURSAR, M.T. TYREE, B.L. TURNER, AND S.P. HUBBELL, 2007. Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447: 80–82.

ENGELBRECHT, B.M.J., J.W. DALLING, T.R.H. PEARSON, R.L. WOLF, D. A GÁLVEZ, T. KOEHLER, M.T. TYREE, AND T. A KURSAR, 2006. Short dry spells in the wet season increase mortality of tropical pioneer seedlings. Oecologia 148: 258–69.

ENGELBRECHT, B.M.J., T.A. KURSAR, AND M.T. TYREE, 2005. Drought effects on seedling survival in a tropical moist forest. Trees 19: 312–321.

ENGELBRECHT, B.M.J., S.J. WRIGHT, AND D. DE STEVEN, 2002. Survival and ecophysiology of tree seedlings during El Niño drought in a tropical moist forest in Panama. Journal of Tropical Ecology 18: 569–579.

GENTRY, A.H., 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden 75: 1–34.

GERHARDT, K., 1996. Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. Forest Ecology and Management 82: 33–48.

GUILLAUMET, J.-L., AND F. KAHN, 1982. Structure et dynamisme de la forêt. Acta Amazonica, Suplemento 12: 61–77.

HODNETT, M.G., I. VENDRAME, A.D.O. MARQUES FILHO, M.D. OYAMA, AND J. TOMASELLA, 1997. Soil water storage and groundwater behaviour in a catenary sequence beneath forest in central Amazonia: I. Comparisons between plateau, slope and valley floor. Hydrology and Earth System Sciences 1: 279–290.

KINUPP, V.F., AND W.E. MAGNUSSON, 2005. Spatial patterns in the understorey shrub genus Psychotria in central Amazonia: effects of distance and topography. Journal of Tropical Ecology 21: 363–374.

LAURANCE, S.G., W.F. LAURANCE, A. ANDRADE, P.M. FEARNSIDE, K.E. HARMS, A. VICENTINI, AND R.C.C. LUIZÃO, 2010. Influence of soils and topography on Amazonian tree diversity: a landscape-scale study. Journal of Vegetation Science 21: 96–106. Available at: http://doi.wiley.com/10.1111/j.1654-1103.2009.01122.x [Accessed September 30, 2010].

LAURANCE, W.F., P.M. FEARNSIDE, S.G. LAURANCE, P. DELAMONICA, T.E. LOVEJOY, J.M. RANKIN-DE MERONA, J.Q. CHAMBERS, AND C. GASCON, 1999. Relationship between soils and Amazon forest biomass: a landscape-scale study. Forest Ecology and Management 118: 127–138.

LEES, J.M., 2011. RSEIS: seismic time series analysis tools. R package version 2.7-1. Http://cran.r-project.org/package=RSEIS

LLORET, F., J. PEÑUELAS, P. PRIETO, L. LLORENS, AND M. ESTIARTE, 2009. Plant community changes induced by experimental climate change: Seedling and adult species composition. Perspectives in Plant Ecology, Evolution and Systematics 11: 53–63.

MAGNUSSON, W.E., A.P. LIMA, R. LUIZÃO, F. LUIZÃO, F.R.C. COSTA, C.V. CASTILHO, AND V.F. KINUPP, 2005. RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. Biota Neotropica 5: 19–24.

MARENGO, J. A., B. LIEBMANN, A. M. GRIMM, V. MISRA, P.L. SILVA DIAS, I.F. A. CAVALCANTI, L.M.V. CARVALHO, E.H. BERBERY, T. AMBRIZZI, C.S. VERA, A. C. SAULO, J. NOGUES-PAEGLE, E. ZIPSER, A. SETH, AND L.M. ALVES, 2012. Recent developments on the South American monsoon system. International Journal of Climatology 32: 1–21.

MARQUES FILHO, A.D.O., S.J.F. FERREIRA, S.Á.F. MIRANDA, A.D. OLIVEIRA, M. FILHO, S. JOSÉ, F. FERREIRA, S. ÁTILA, AND F. MIRANDA, 2009. Surface runoff model in the Reserva Florestal Adolpho Ducke experimental watershed. Acta Amazonica 39: 907–922.

MCDOWELL, N., W.T. POCKMAN, C.D. ALLEN, D.D. BRESHEARS, N. COBB, T. KOLB, J. PLAUT, J. SPERRY, A. WEST, D.G. WILLIAMS, AND E. A YEPEZ, 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? The New phytologist 178: 719–39.

PHILLIPS, O.L. ET AL., 2010. Drought-mortality relationships for tropical forests. The New phytologist 187: 631–46.

PINHEIRO, J., D. BATES, S. DEBROY, D. SARKAR AND THE R DEVELOPMENT CORE TEAM, 2011. NLME: Linear and nonlinear effects models. R package version 3.1-98.

PITMAN, N.C.A., J. TERBORGH, M. SILMAN, P. NÚÑEZ, D.A. NEILL, C.E. CERÓN, W.A. PALACIOS, AND M. AULESTIA, 2002. A comparison of tree species diversity in two upper amazonian forests. Ecology 83: 3210–3224.

R DEVELOPMENT CORE TEAM, 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, URL http://www.R-project.org/

RIBEIRO, J.E.L., M.J. HOPKINS, A. VICENTINI, C.A. SOTHERS, M. COSTA, J.M. BRITO, M.A.D. SOUZA, L.H.P. MARTINS, P.A.C. ASSUNÇÃO, E.C. PEREIRA, C.F. SILVA, M.R. MESQUITA, AND L.C. PROCÓPIO, 1999. Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônica Central, Manaus: INPA-DFID.

SANTOS, C.A. DOS, P. SATYAMURTY, AND E.M. DOS SANTOS, 2012. Trends of extreme climatic indices for Manaus - AM region. Acta Amazonica 42: 329–336.

SCHIETTI, J., T. EMILIO, C.D. RENNÓ, D.P. DRUCKER, F. COSTA, A. NOGUEIRA, F. FIGUEIREDO, C.V. CASTILHO, V. KINUPP, J-L. GUILLAUMET, A.R.M. GARCIA, A.P. LIMA, AND W.E. MAGNUSSON, 2013. Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. Plant Ecology & Diversity, in press.

SLOT, M., AND L. POORTER, 2007. Diversity of Tropical Tree Seedling Responses to Drought. Biotropica 39: 683–690.

TOLEDO, J.J. DE, W.E. MAGNUSSON, C.V. CASTILHO, AND H.E.M. NASCIMENTO, 2012. Tree mode of death in Central Amazonia: Effects of soil and topography on tree mortality associated with storm disturbances. Forest Ecology and Management 263: 253–261.

TOMASELLA, J., L.S. BORMA, J.A. MARENGO, D.A. RODRIGUEZ, L.A. CUARTAS, C. A. NOBRE, AND M.C.R. PRADO, 2011. The droughts of 1996-1997 and 2004-2005 in Amazonia: hydrological response in the river main-stem. Hydrological Processes 25: 1228–1242.

TYREE, M., B. ENGELBRECHT, G. VARGAS, AND T.A. KURSAR, 2003. Desiccation tolerance of five tropical seedlings in Panama. Relationship to a field assessment of drought performance. Plant Physiology 132: 1439–1447.

TYREE, M.T., H. COCHARD, P. CRUIZIAT, B. SINCLAIR, AND T. AMEGLIO, 1993. Drought-induced leaf shedding in walnut: evidence for vulnerability segmentation. Plant, Cell and Environment 16: 879–882.

WILLIAMSON, G.B., W.F. LAURANCE, A.A. OLIVEIRA, P. DELAMONICA, C. GASCON, T.E. LOVEJOY, AND L. POHL, 2000. Amazonian Tree Mortality during the 1997 El Nino Drought. Conservation Biology 14: 1538–1542.

List of figures

FIGURE 1: Ducke Reserve, located in the north region of Manaus, Amazonas State, Brazil. At the right is the trail grid (lines) that gives access to the 30 plots used on this study (white dots) placed on a map of the altitudinal variation, and darker color indicates higher places.

FIGURE 2: Absolute seedling mortality in different seasons (rainy season from December to May, and dry season from July to October); black bars represent all seedlings pooled together, gray bars are seedlings in clay plots, white bars are seedlings in sand plots and the shading is rainfall (mm/month).

FIGURE 3. Cross-correlation values at different lags of seedling mortality and rain (mm); all dead seedlings pooled together (black bars), seedling mortality at clay soil plots (gray bar) and seedling mortality at sand soil plots (white bar). The dashed lines indicate the CI interval based on sample covariances, and values equal or greater than that are considered significant.

FIGURE 4. Cross-correlation values at different past lags of seedling recruitment and rain (mm). Showed all recruited seedlings pooled together (black bars), seedling recruitment at clay soil plots (gray bar) and seedling recruitment at sand soil plots (white bar). The dashed lines indicate the CI interval based on sample covariances, and values equal or greater than that are considered significant.

FIGURE 5. Path analysis of rainfall effect on seedling mortality both direct and as an indirect factor passing through seedling recruitment, with all seedlings pooled together (a), seedlings in clay soils (b) and seedlings in sandy soils (c). Strength of relationship is

represented by the thickness of the arrows. Asteriks near relationship values indicate significance (*=p<0.05 and **=p<0.01).

Fig. 1

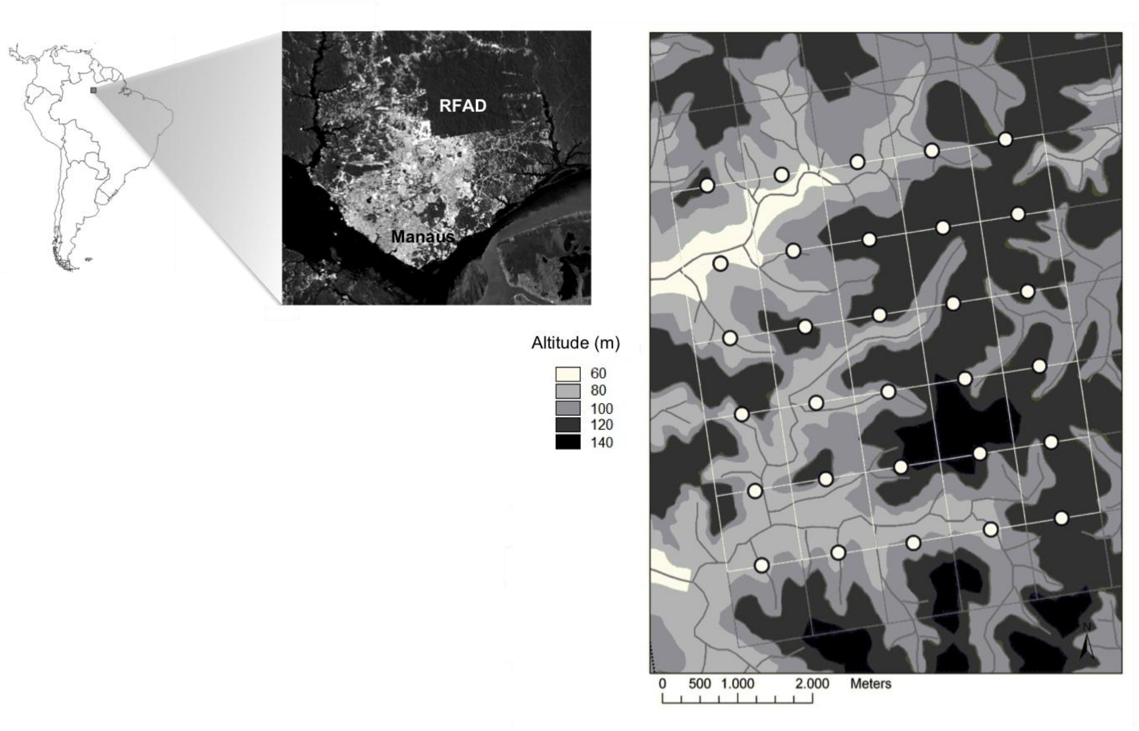
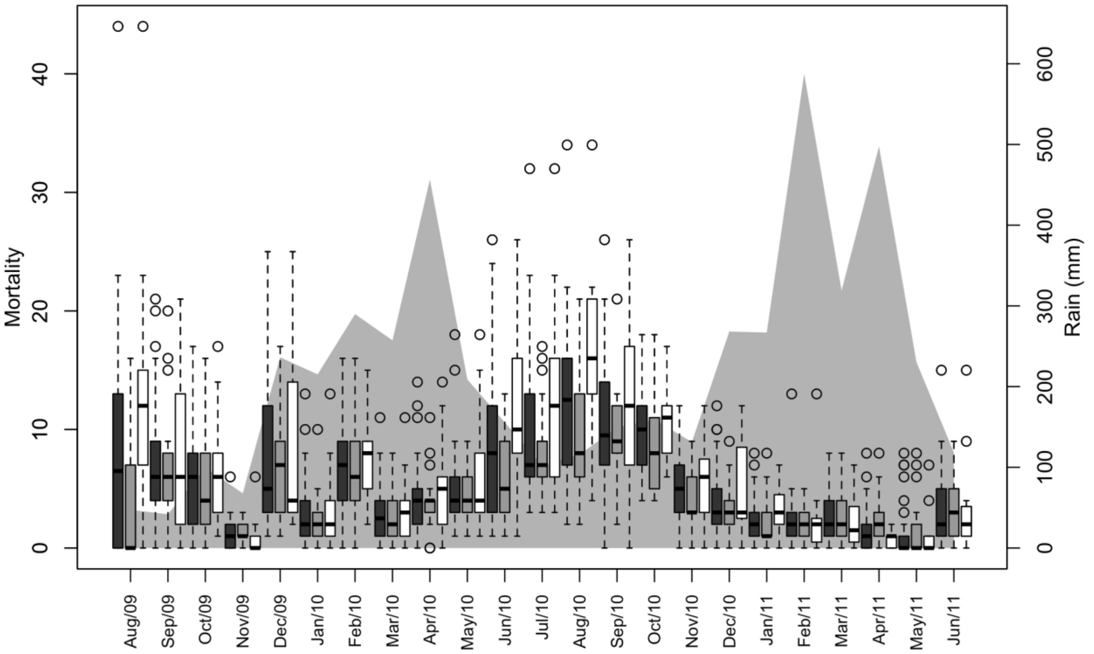

RFAD
Manaus
Altitude (m)
60
80
100
120
140
0
500
1.000
2.000
Meters
N

Fig. 2


Mortality
0
10
20
30
40
Rain (mm)
0
100
200
300
400
500
600
Aug/09
Sep/09
Oct/09
Nov/09
Dec/09
Jan/10
Feb/10
Mar/10
Apr/10
May/10
Jun/10
Jul/10
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May/11
Jun/11

Fig. 3

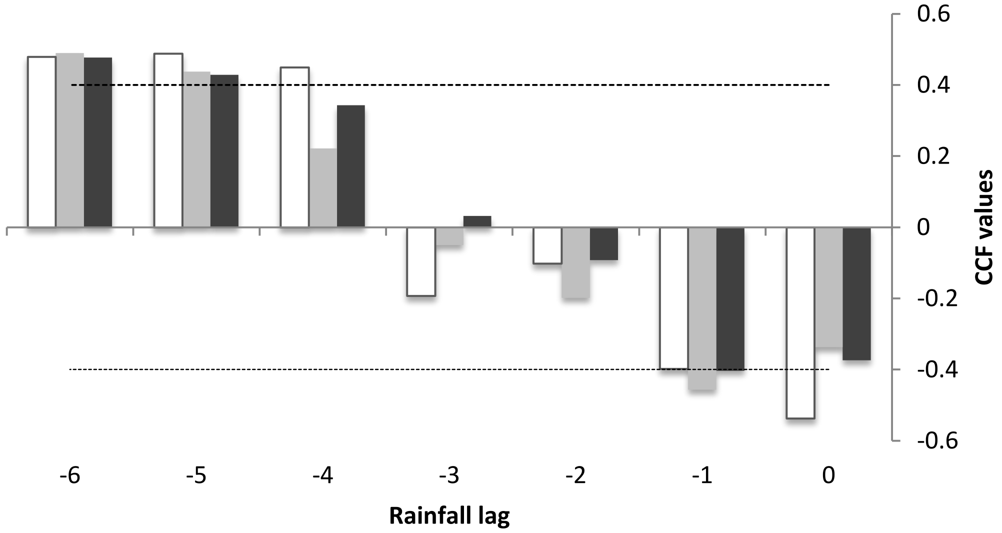

Fig. 4

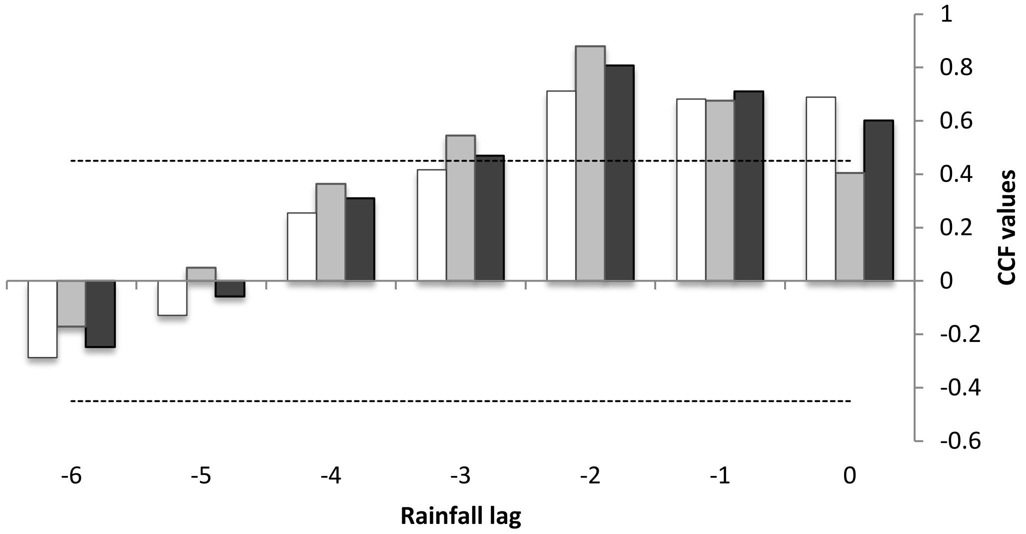

Fig. 5

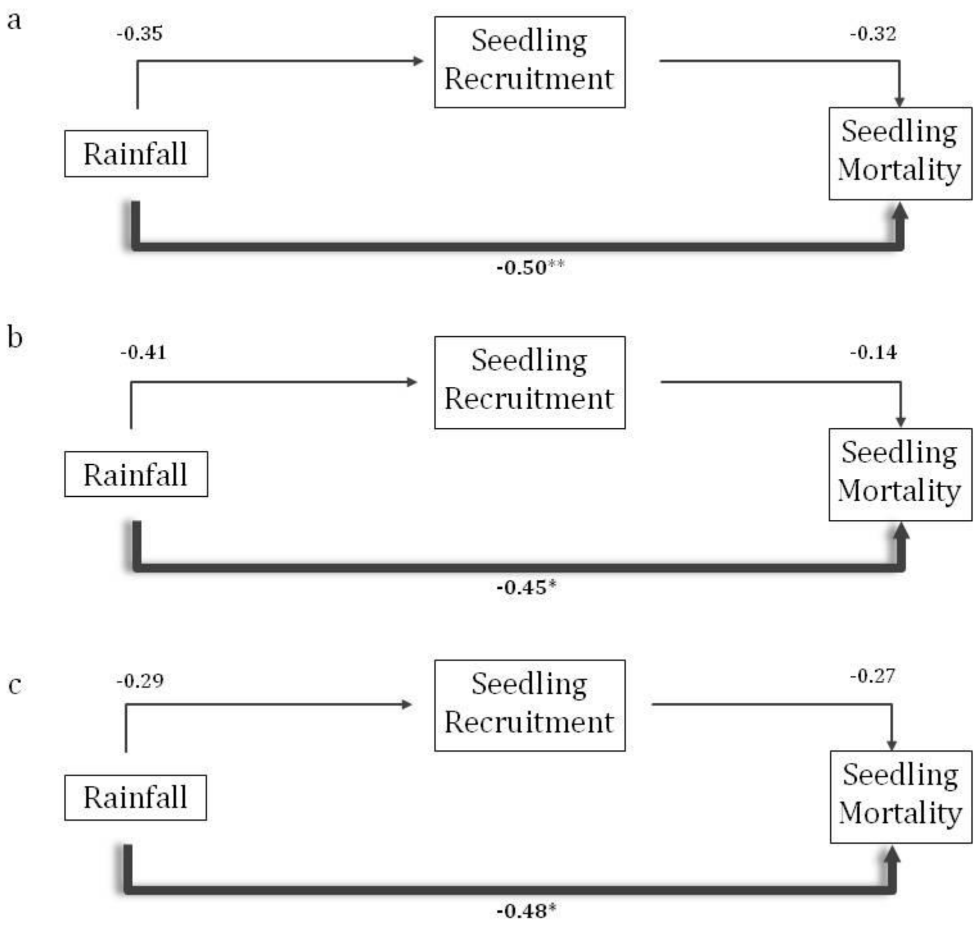
a
-0.35
Seedling Recruitment
-0.32
Rainfall
Seedling Mortality
-0.50**
b
-0.41
Seedling Recruitment
-0.14
Rainfall
Seedling Mortality
-0.45*
c
-0.29
Seedling Recruitment
-0.27
Rainfall
Seedling Mortality
-0.48*

TABLE 1. Multiple regressions of seedling mortality and recruitment on past lags of rainfall values (mm). The regression coefficient for each lag and coefficient of determination (r^2) and F of each model are shown. Significance levels: *5 %, ** 1 % and *** 0.1 %.

	Class	Model	Lag t_{-0}	Lag t_{-1}	Lag t_{-2}	Lag t_{-3}	R^2	F
Mortality	Total	Alldeath~Rlag0 + Rlag-1 + Rlag-2	-6.58	-11.14*	-0.84		0.31*	4.10
	Clay soil	Claydeath~Rlag0 + Rlag-1 + Rlag-2 + Rlag-3	-4.31	-4.61*	0.84	-1.69	0.34*	3.57
	Sand soil	Sanddeath~Rlag0 + Rlag-1 + Rlag-2 + Rlag-3	-7.53*	-5.58	1.53	-3.94	0.50**	6.04
Recruitment	Total	Clayrecruit~Rlag0 + Rlag-1 + Rlag-2 + Rlag-3	73.83**	2.72	-52.97*	-22.85	0.74**	10.42
	Clay soil	Clayrecruit~Rlag0 + Rlag-1 + Rlag-2	27.66*	-2.55	-26.33	-	0.45*	4.85
	Sand soil	Clayrecruit~Rlag0 + Rlag-1 + Rlag-2	56.59***	-4.45	-37.12***	-	0.85***	27.97

Capítulo 2

Barbosa, C.E.A., Costa, F.R.C., Castilho, C.V., Freitas, C.G. Distribution of trees and palms across a soil clay gradient vary through ontogeny. Manuscript in preparation for Biotropica.

LRH: Barbosa, Costa, Castilho and Freitas

RRH: Habitat limitation and ontogenetic stages

Distribution of trees and palms across a soil clay gradient vary through ontogeny

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Received: ________________ Revision accepted: __________________

ABSTRACT (269 words)

Plant distributions may be limited to portions of environmental gradients, which might indicate physiological constraints, competitive exclusion, or both, and topo-edaphic gradient is acknowledged as important forces structuring tropical communities. However, as plant requirements change across ontogenetic stages, the structuring effects might differ according to plant life stage. Our objective was to determine if the distribution of trees and palms across a soil texture gradient differed according to the ontogenetic stages. To accomplish that we compared the distribution of adults and seedlings across the soil texture gradient for 22 tree and palm species in a central Amazon forest. The environment limitation point for each ontogenetic stage of each species were calculated by comparing the standard deviation of the environmental gradient values of the plots in which we found individuals of a species with a null distribution of standard deviation values, calculated by randomly sampling the environmental gradient within the whole sample. We found significant differences in environmental limitation across ontogenetic stages. For eight species adults had distribution more limited than seedlings, indicating a tendency for habitat contraction as plants grew older. Two species had distribution limited only during seedling stage, which might indicate temporal and/or spatial fruiting asynchrony across the soil gradient. Only one species had its distribution limited by the environment in both life stages, but seedlings were limited to a broader portion of the clay soil gradient. As plants respond differently to environmental conditions throughout development stages, not accounting for the environment filters on earlier stages of development might compromise the ability to predict plant distribution and ultimately community composition in the present context of environmental changes.

Key words: central Amazon, habitat association, seedlings, soil texture.

PLANT DISTRIBUTIONS ARE KNOWN TO BE ASSOCIATED WITH EDAPHIC AND TOPOGRAPHIC features, such as soil texture and fertility (Costa et al. 2005, Bohlman et al. 2008, Laurance et al. 2010, Givnish 1999, Kinupp & Magnusson 2005). However most of the distribution patterns are described considering only the end of community development process, being based on the relation of adult individuals with different environment variables, therefore habitat associations that were established before, at earlier life stages, have historically received less attention (Webb & Peart 2000).

Species requirements change as plants grow older (Schupp 1994), so evaluating only the association with habitat of adult individuals can mask niches that are suitable for seedling emergence outside the adult range. Therefore seedlings and adults of the same species might be distinctly limited to different portions of the same environmental gradient, even though some degree of distribution overlapping would be expected. Edaphic features are among the most studied environmental variables related to plant habitat associations, being directly linked with many of the environmental features that are known to affect the success of site occupancy by seedlings, such as predation (Fine et al. 2004) and water availability (Comita & Engelbrecht 2009).

Even though topo-edaphic gradients are known to influence plant distribution, much of the effort to describe plant association to soil characteristics were made in sites where those gradients are not long enough (e.g., few soil types) to well represent the environmental heterogeneity of the Amazon forest (Phillips et al. 2003). The present study was undertaken at a central Amazon forest that encompasses great topographic and edaphic variability, ranging from low valleys with essentially sandy soils to plateaus with soils with more than 90% clay in its composition. By studying the distribution of seedlings and adults of 22 tree and palm species along this gradient, and considering the changes in plant needs along life stages, we expect that the distribution of the species across an environmental gradient will be different according to the ontogenetic phase. Therefore the aim of this study was to answer the following question: Do the distribution of the analyzed species vary according to their ontogenetic stage across a gradient of soil characteristics?

METHODS

STUDY SITE – The study was conducted at Reserva Florestal Adolpho Ducke (hereafter referred as Ducke), a terra firme tropical forest that covers an area of 100 km^2 at the northern limit of the city of Manaus (02^{o}55’s, 59^{o}59’w, Figure 1) in the Brazilian state of Amazonas. The vegetation in the area is mainly dense terra firme forest, with some patches of white sand forest. Canopy trees reach 35-40 m height (Ribeiro et al. 1999), the understory receives low light levels and is characterized by a high abundance of acaulescent palms (Guillaumet & Kahn 1982). The mean annual temperature is 26 °C, the humidity ranges from 84–91% and there are two distinct seasons: a dry season from June to November, with minimum rainfall at July (mean of 93 mm) and a rainy season from December to May, with maximum rainfall at February (mean of 299 mm) (Marques Filho et al. 2009). There is a wide variation in soil composition across the plots, with clay content ranging from 1.62% at the sandiest plot, and increasing clay content moving uphill to the ridges, reaching a maximum of 87% clay in the plateaus. Soil texture data were assessed from previously collected data available at http://ppbio.inpa.gov.br/Eng/inventarios/ducke/pterrestre/. At Ducke the soil texture is determined simply by the proportion of clay and sand, with little influence of silt on the composition (Bravard & Righi 1989). Thus we decided to use the clay content as soil texture indicator.

We conducted our study in 30 permanent plots that were set up as part of the Brazilian Long-Term Ecological Research Program and the Brazilian Program for Biodiversity Research. The plots are systematically distributed within a trail grid system, 1 km distant from each other, and are 250 m long with the width of each plot varying according to the taxa or the life stage to be studied (Magnusson et al. 2005). Since the plots follow the altitudinal contours, the altitude is maintained constant throughout the plot length, which is important at Ducke where topography variation (39 -109 meter a.s.l) is highly correlated with clay content (Costa et al. 2005).

TREE AND SEEDLINGS' DATA – To compare the distribution of adult individuals and conspecific seedlings across the soil texture gradient, we selected 22 species (16 tree and 6 palm species – Table 1) from a census database of all trees within the 30 plots. The species chosen are relatively common within Duckes' flora as adults, with the exception of the rare species *Buchenavia grandis* (Ribeiro et al. 1999), and are well represented within the seedling community as well. The species choice was also influenced by the identificability of the individuals in the seedling stage. The adult trees database was collected by Carolina Volkmer Castilho (unpublished data), who used a sub-sampling of the plots according to the tree size. Trees with DBH ≥ 1cm were mapped, tagged and identified in 0.1 ha (250 x 4 m), while trees with DBH ≥ 10 cm were sampled in 0.5 ha (250 x 20 m) and trees with DBH ≥ 30 cm were sampled in the whole plot area (250 x 40 m, 1 ha). *Geonoma aspiidifolia* has a relatively small trunk diameter as an adult, which would exclude most individuals from the sampling according to this protocol. Therefore all *G. aspiidifolia* higher than 1 m (considered adults, accordingly to Henderson (1995) and Lorenzi, Noblick, Kahn, & Pereira (2010)) were sampled across the whole plot (250 x 4 m). The recruitment of seedlings was monitored monthly from August 2009 to December 2010 over 450 m^2 (15 $1m^2$ sub-plots placed along each of the 30 250 m plots). All seedlings up to 50 cm tall were tagged, mapped and identified to species level, and new seedlings were tagged and mapped in each monitoring.

DATA ANALYSIS – To test the limitation of species to portions of the soil texture gradient we used the habitat specificity index developed by Kinupp & Magnusson (2005). The statistic of environment limitation is the range of distribution of a species across the soil texture gradient, estimated by calculating the standard deviation of clay content in the soil of the sites in which the species occurred. We than randomly sampled clay content values of the same number of sites occupied by a given species across all the 30 sites in the study area, allowing us to calculate a null distribution of standard deviation values. That procedure was repeated 999 times and the proportion of standard deviation values expected by chance that were lower than or equal to the observed standard deviation were used to test if a species is no more specialized than expected by chance. This analysis uses solely values of presence/absence of species, though the figures display the abundances of species in each plot. This analysis may be inefficient in some cases, as for species with bimodal distribution of specificity (e.g., environment preference for both the extremes of the gradient). In this situation, the standard deviation range could indicate no environment specificity, despite the non-random distribution along the gradient. Nevertheless, none of the species analyzed had this pattern of limited distribution at both ends of the soil texture gradient.

For the species that were limited to any portion of the soil texture gradient, we calculated the gradient value from which the species is no longer found. That was done using a regression tree, which divided the gradient values into two groups: the soil clay concentration values in which a species is absent, and the values in which a species occur. The regression trees were performed using the rpart R-package, version 3.1-54 (Therneau & Atkinson 2012).

RESULTS

Within the 22 species we counted a total of 2449 adult individuals and 748 seedlings. As a general pattern, environmental filtering has different effects according to life stage, and we found adults to be more environmentally limited than seedlings in eight species (36.4 %). Twelve species (54.5 %) did not show any environmental limitation, whether in adult or seedling stage, being distributed throughout the whole soil texture gradient. Two species (9.1%) had an opposite limitation pattern, with seedlings, rather than adults, being limited to a portion of the soil texture gradient.

Clarisia racemosa adults were more associated to the clayey half of the gradient, being well distributed in sites with more than 67 % (p=0.048) of clay content, while seedlings did not have any tendency of be associated to any portion of the gradient (Fig. 2a). Adults of *Protium hebetatum* were distributed along a broader range of the soil texture gradient (Fig. 2b), but also mostly on clayey plots and did not occur only at the sandier extreme (sites with less than 4 % of clay, p=0.034), as were *Protium apiculatum* (p=0.001; Fig. 2c), *Geonoma aspiidifolia* (p=0.002; Fig. 3a), and *Oenocarpus bacaba* (p=0.001; Fig. 3b) adults. Seedlings of *P. hebetatum*, *P. apiculatum*, *G. aspiidifolia* and *O. Bacaba* did not tend to be limited to any portion of the gradient.

Oenocarpus bataua was the only species for which both ontogenetic stages evaluated were limited to portions of the soil gradient (Fig. 4), with adults occurring in soils with no more than 13% (p<0.001) of clay content. Its seedlings occurred along a broader range of soil textures, being limited to soils with up to 60% of clay content (p=0.012).

Some species did not occur only in the clayey extreme of the gradient, as *Conceveiba guianensis* adults (Fig. 5a), found in sites with clay contents of no more than 86% (p=0.021). *Protium subserratum* adults were found at all but the clayey extreme of the gradient (upper limit of 82% of clay content, p=0.019; Fig. 5b). Both *C. Guianensis* and *P. Subserratum* seedlings were not environmentally limited.

Simarouba amara adults had a broad distribution along all types of soils, but its seedlings occurred mostly at soils with less than 38% of clay content (p<0.001; Fig. 6a). The same pattern was found for *Oenocarpus minor*, with adults well distributed, and seedlings limited by soils with less than 4% of clay content (p=0.012; Fig. 6b).

DISCUSSION

Given the fact that seeds are usually dispersed to sites near the parent trees, the position of seedlings is expected to be associated with the position of conspecific adults. Nevertheless, the individual seed dispersal capacity of the species may tilt this expectation, and seedling distributions might occupy a broader range of habitats than later ontogenetic stages (Webb & Peart 2000). In the present study we found species in which adults were more associated to portions of the soil clay gradient, and conspecific seedlings that occupied both a broader or narrower portion of the same gradient. That reflects the importance of soil texture on determining suitability of a site and driving plant distribution (Laurance et al. 2010, Bohlman et al. 2008, Comita et al. 2007).

Of the nine species in which any environmental association was observed in adult individuals, five showed preference for clayey soils. Based on its distributional patterns, adults of *Geonoma aspiidifolia*, *Oenocarpus bacaba*, *Protium hebetatum*, and *Protium apiculatum* can be considered “clay generalists”, as they occur in plots with 4 % of clay composition or more, avoiding only the sandier extreme of the soil texture gradient. Clay in soil composition guarantees the presence of cations needed for plant development, since these cations are easily washed away with the rainwater in sandy soils (Fearnside & Leal Filho 2001), which may indicate sandy soils sites are more restrictive environments. In addition, the variability of the water table depth in sandy soils, which reaches very superficial levels during the rainy season, might preclude the occupation of those sites by the clay generalists. That's because the ability of seedlings and trees to survive through long periods in a situation of root anoxia (caused by the superficial water table in sandy soils) might be determinant for the success of a site occupancy (Lopez & Kursar, 1999).

On the other extreme are the adults of *Conceveiba guianensis* and *Protium subserratum*, which were only absent at the clayey end of the gradient. These species might be sensitive to greater difficulties in obtaining water held in clayey soil, which tightly holds the water into the soil pores in the soil matrix (Fearnside & Leal Filho 2001).

Most of the species that were associated with a portion of the clay soil gradient were so in the adult stage (the exception was Oenocarpus bataua, discussed below), with seedlings having a broader distribution along that gradient. Webb & Peart (2000) theorized that this situation arises from seedlings having greater success in the sites in which adults are associated, but being able to recruit at different sites in which they arrive through dispersal. That way the degree of seedling association to a habitat would be partially explained by the dispersal ability of the species.

Oenocarpus bataua was the only species with habitat association in both life stages, going from sites with up to 60 % of clay content as seedlings to sites with a maximum of 13 % of clay soil content when adults. Contraction of species distribution from seed to adulthood is a result of increasing mortality as plants develop outside the "preferred" habitat (Comita et al. 2007). A similar distribution pattern was described by Freitas (2012) for *O. Bataua* juveniles, and adults in the reproductive stage as well. Brum (2011) found a similar habitat association pattern for young seedlings and juveniles. In addition, *O. Bataua* was the only species associated to the sandier extreme of the soil texture gradient. The mechanisms behind *O. Bataua* preferences for sandy waterlogged sites are yet to be revealed, as the distribution patterns are very different across the Amazon basin, going from a restriction to clayey, well drained soils in Eastern Amazon, to restriction to sandy soils in Central Amazon (Montufar & Pintaud 2006). In a controlled experiment, Brum (2011) found no clear relation of seed germination and seedling survival of *O. Bataua* with soil texture or waterlogging, which indicates that the adult distribution might not be defined in the very early life stages. Maybe the relation of this palm distribution to soil texture and hydrology has been a misleading conclusion, taking away the focus from other potential environment features that might be involved. Light availability is known to be a structuring agent on plant distribution (reviewed in Svenning 2001), and might be regulating *O. Bataua* distribution. As light in the understory tends to decrease as we move down to sandier soils given the reduction of lateral light incidence (Ediriweera et al. 2008, Fladeland et al. 2003), we might be observing a shift in the light requirements and/or plant competitive capacity as seedlings develop to adulthood.

Seedlings with stronger habitat association than adults is not what one would expect, as adults should only exist where a seedling can establish, but that was the pattern found for *Simarouba amara* and *Oenocarpus minor*. Considering some reproductive biological aspects of those species, our result might indicate difficulties in detecting seedlings of these species. Fruit production of these species varies spatially across the soil texture gradient and temporally through the fruiting seasons. Freitas (2012) found at Ducke that despite producing fruits across the whole soil texture gradient, *O. Minor* produces fewer fruits in steeper areas, and, as a consequence, the abundance of seedlings in those areas tends to be lower. In addition, there is evidence that despite an even distribution along the whole soil texture gradient, there are some palm species that have variation in the number of fructification scars on individuals of equivalent sizes (Thaíse Emilio, personal comm.). That is indicative of the age at reproduction, and the number of reproductive cycles variation across different environments within the same population. As a consequence, one would expect variation in seedling densities. *Simarouba amara* has irregular fructification cycles, with great variation in the number of individuals fruiting each year, and even skipping production occasionally (Pinto, Ribeiro, Alencar, & Barbosa, 2005). We might also be observing a situation predicted by Webb & Peart (2000), in which few seedlings are relatively successful in sub-optimal sites while the majority of seedlings that were dispersed near the maternal adult suffer with greater density-dependent mortality, leading to an apparent mismatch between seedling and adult distributions. Finally, since we have no data on reproductive events for all adult trees considered for this study, individuals that we are considering to be of reproductive age might not yet be.

One of the main purposes of understanding the mechanisms underneath plant distributions is to improve the ability to predict plant species composition, allowing more efficient conservation planning in the current context or in future scenarios. However, we showed that plant species might respond differently to environmental conditions throughout developmental stages, and might have different requirements and/or tolerance capacity at earlier stages, resulting in seedlings being present at different ranges from adults. As the current predictions of environmental changes are confirmed, it is feasible to expect the distribution range of plants to be altered, and regardless of the tendency for expansion or contraction of the occupied area, not accounting for the impacts on earlier stages of development might compromise the ability to predict plant distribution and ultimately community composition.

ACKNOWLEDGMENTS

We thank Juliana Menger, Camila Saraiva dos Anjos, Francisca Denise da Costa and several field assistants for the help in the field. This study was funded with a phd fellowship from the Brazilian National Research Council (CNPq) to CEAB during field work. Financial support was granted by CNPq/Universal (473447/2008-5) to FRCC and CNPq/CT-Amazônia (575637/2008-0) to Bruce Walker Nelson. Logistical support was provided by Instituto Nacional de Pesquisas da Amazônia (INPA) and Brazilian Biodiversity Research Program (PPBio). Data repositories are maintained by ppbio, Brazilian Long-Term Ecological Research Program (PELD) and the National Institute of Science and Technology for Amazonian Biodiversity (INCT – CENBAM).

LITERATURE CITED

BOHLMAN, S.A., W.F. LAURANCE, S.G. LAURANCE, H.E.M. NASCIMENTO, P.M. FEARNSIDE, AND A. ANDRADE, 2008. Importance of soils, topography and geographic distance in structuring central Amazonian tree communities. Journal of Vegetation Science 19: 863–874.

BRAVARD, S., AND D. RIGHI, 1989. Geochemical differences in an Oxisol-Spodosol toposequence of Amazonia, Brazil. Geoderma 44: 29–42.

BRUM, H.D., 2011. Distribuição espacial de três espécies de palmeiras do gênero Oenocarpus ao longo de um gradiente edafo-topográfico na Amazônia Central. UNICAMP.

COMITA, L.S., AND B.M.J. ENGELBRECHT, 2009. Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. Ecology 90: p.2755–65.

COMITA, L.S., R. CONDIT, AND S.P. HUBBELL, 2007. Developmental changes in habitat associations of tropical trees. Journal of Ecology 95: 482–492.

COSTA, F.R.C., W.E. MAGNUSSON, AND R.C. LUIZÃO, 2005. Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. Journal of Ecology 93: 863–878.

EDIRIWEERA, S., B.M.P. SINGHAKUMARA, AND M.S. ASHTON, 2008. Variation in canopy structure, light and soil nutrition across elevation of a Sri Lankan tropical rain forest. Forest Ecology and Management 256: p.1339–1349.

FEARNSIDE, P.M., AND N. LEAL FILHO, 2001. Soil and development in Amazonia: lessons from the Biological Dynamics of Forest Fragments Project. In R. O. Bierregaard, C. Gascon, T. E. Lovejoy, and R. C. G. Mesquita (Eds.) Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest. P. 478, New Haven, Connecticut: Yale University Press.

FINE, P.V.A., I. MESONES, AND P.D. COLEY, 2004. Herbivores promote habitat specialization by trees in Amazonian forests. Science (New York, N.Y.) 305: 663–5.

FLADELAND, M.M., M.S. ASHTON, AND X. LEE, 2003. Landscape variations in understory PAR for a mixed deciduous forest in New England, USA. Agricultural and Forest Meteorology 118: p.137–141.

FREITAS, C.G. DE, 2012. Reprodução, distribuição e padrões de co-ocorrência em uma comunidade de palmeiras na Amazônia central: Uma abordagem teórica e experimental. Instituto Nacional de Pesquisas da Amazônia - INPA.

GIVNISH, T., 1999. On the causes of gradients in tropical tree diversity. Journal of Ecology 87: 193–210.

GUILLAUMET, J.-L., AND F. KAHN, 1982. Structure et dynamisme de la forêt. Acta Amazonica, Suplemento 12: 61–77.

HENDERSON, A., 1995. The Palms of the Amazon, New York, NY: Oxford University.

KINUPP, V.F., AND W.E. MAGNUSSON, 2005. Spatial patterns in the understorey shrub genus Psychotria in central Amazonia: effects of distance and topography. Journal of Tropical Ecology 21: 363–374.

LAURANCE, S.G., W.F. LAURANCE, A. ANDRADE, P.M. FEARNSIDE, K.E. HARMS, A. VICENTINI, AND R.C.C. LUIZÃO, 2010. Influence of soils and topography on Amazonian tree diversity: a landscape-scale study. Journal of Vegetation Science 21: 96–106.

LOPEZ, O.R., AND T. A. KURSAR, 1999. Flood tolerance of four tropical tree species. Tree Physiology 19: 925–932.

LORENZI, H., L. NOBLICK, F. KAHN, AND E. PEREIRA, 2010. Flora Brasileira Lorenzi. (Arecaceae), Nova Odessa, São Paulo, Brazil: Instituto Plantarum.

MAGNUSSON, W.E., A.P. LIMA, R. LUIZÃO, F. LUIZÃO, F.R.C. COSTA, C.V. CASTILHO, AND V.F. KINUPP, 2005. RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. Biota Neotropica 5: 19–24.

MARQUES FILHO, A.D.O., S.J.F. FERREIRA, S.Á.F. MIRANDA, A.D. OLIVEIRA, M. FILHO, S. JOSÉ, F. FERREIRA, S. ÁTILA, AND F. MIRANDA, 2009. Surface runoff model in the

Reserva Florestal Adolpho Ducke experimental watershed. Acta Amazonica 39: 907–922.

MONTUFAR, R., AND J.-C. PINTAUD, 2006. Variation in species composition, abundance and microhabitat preferences among western Amazonian terra firme palm communities. Botanical Journal of the Linnean Society 151: 127–140.

PHILLIPS, O.L., P.N. VARGAS, A.L. MONTEAGUDO, A.P. CRUZ, M.-E.C. ZANS, W.G. SANCHEZ, M. YLI-HALLA, AND S. ROSE, 2003. Habitat association among Amazonian tree species: a landscape-scale approach. Journal of Ecology 91: 757–775.

PINTO, A.M., R.J. RIBEIRO, J. DA C. ALENCAR, AND A.P. BARBOSA, 2005. Phenology of Simarouba amara Aubl. In the Adolpho Ducke Forest Reserve. Acta Amazonica 35: p.347 – 352.

RIBEIRO, J.E.L., M.J. HOPKINS, A. VICENTINI, C.A. SOTHERS, M. COSTA, J.M. BRITO, M.A.D. SOUZA, L.H.P. MARTINS, P.A.C. ASSUNÇÃO, E.C. PEREIRA, C.F. SILVA, M.R. MESQUITA, AND L.C. PROCÓPIO, 1999. Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônica Central, Manaus: INPA-DFID.

SVENNING, J.-C., 2001. On the Role of Microenvironmental Heterogeneity in the Ecology and Diversification of Neotropical Rain-Forest Palms (Arecaceae). The Botanical Review 67: p.1–53.

THERNEAU, T.M., AND B. ATKINSON, 2012. Package “rpart.” P.1–30.

WEBB, C.O., AND D.R. PEART, 2000. Habitat associations of trees and seedlings in a Bornean rain forest. Journal of Ecology 88: p.464–478.

Figure legends

FIGURE 1: Ducke Reserve, located at the north region of Manaus, Amazonas State, Brazil. At the right is the trail grid (lines) that gives access to the 30 plots used on this study (white dots) placed on a map of the altitudinal variation, and darker color indicates higher places.

FIGURE 2: Density of seedlings and adults in 30 sites distributed along a soil clay content gradient. Adults of the tree species (A) *Clarisia racemosa*, (B) *Protium hebetatum* and (C) *Protium apiculatum* have a tendency of being associated to the clayey part of the soil texture gradient.

FIGURE 3: Density of seedlings and adults in 30 sites distributed along a soil clay content gradient. Species are (A) *Geonoma aspiidifolia* and (B) *Oenocarpus bacaba*.

FIGURE 4: Density of *Oenocarpus bataua* in 30 sites distributed along a soil clay content gradient, with adults being more associated to sandier sites than seedlings.

FIGURE 5: Density of seedlings and adults in 30 sites distributed along a soil clay content gradient. Adults of the tree species (A) *Conceveiba guianensis* and (B) *Protium subserratum* do not occur only in the clayey end of the gradient.

FIGURE 6: Density of seedlings and adults in 30 sites distributed along a soil clay content gradient. Seedlings of the species (A) *Simarouba amara* and (B) *Oenocarpus minor* were associated, while adults occur through the whole gradient.

Fig. 1

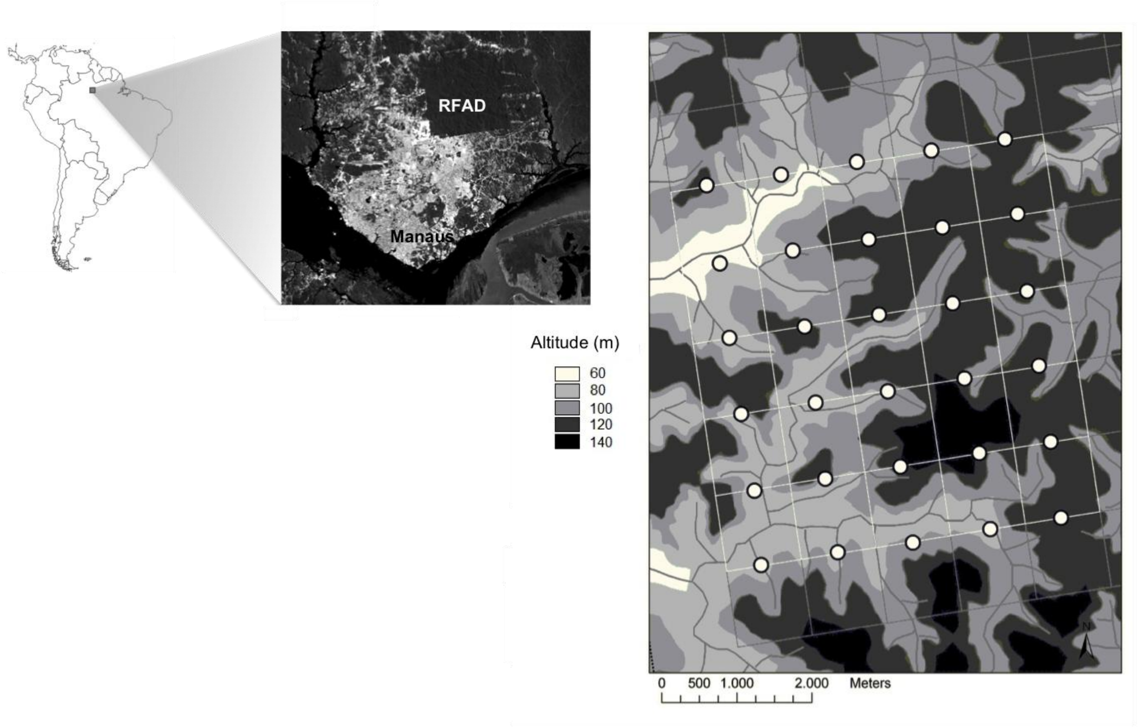
RFAD
Manaus
Altitude (m)
60
80
100
120
140
0
500
1.000
2.000
Meters
N

Fig. 2

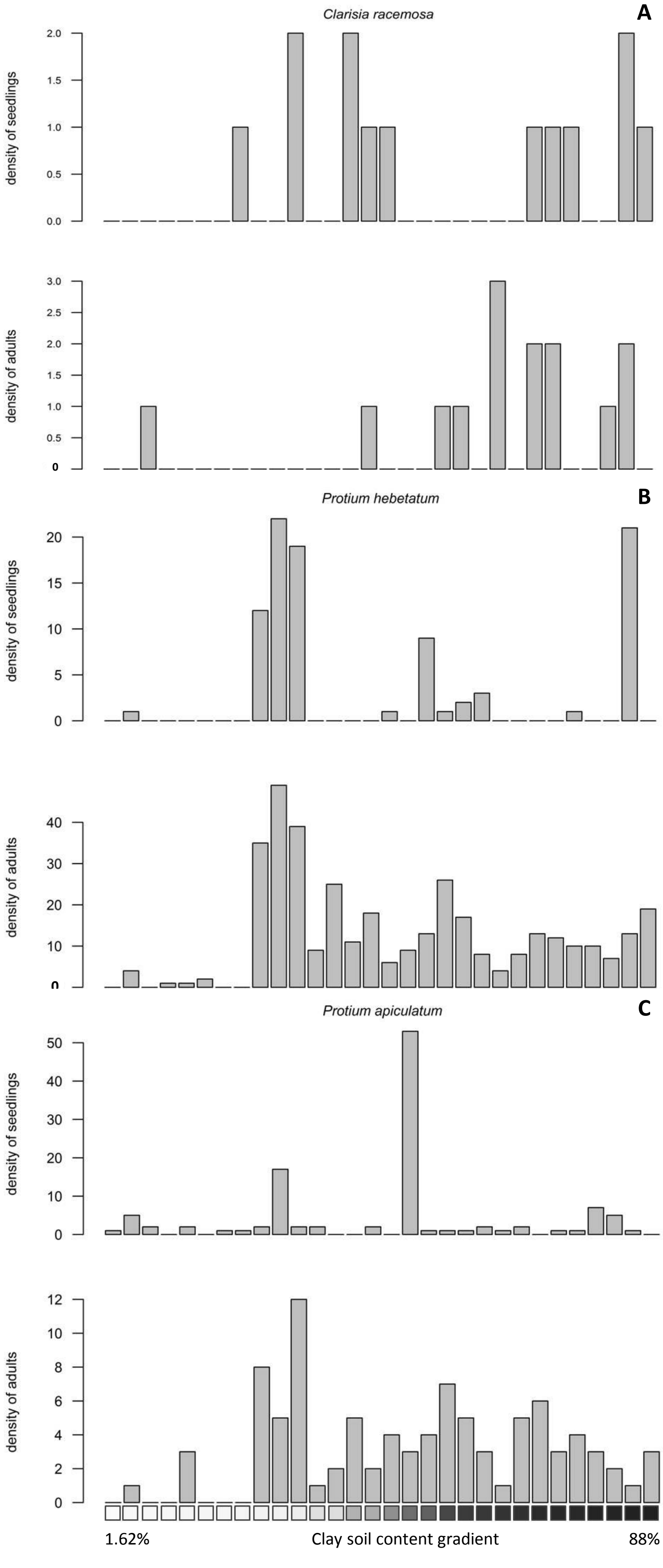
Clarisia racemosa
A
density of seedlings
2.0
1.5
1.0
0.5
0.0
density of adults
3.0
2.5
2.0
1.5
1.0
0.5
0
Protium hebetatum
B
density of seedlings
20
15
10
5
0
density of adults
40
30
20
10
0
Protium apiculatum
C
density of seedlings
50
40
30
20
10
0
density of adults
12
10
8
6
4
2
0
1.62%
Clay soil content gradient
88%

Fig. 3

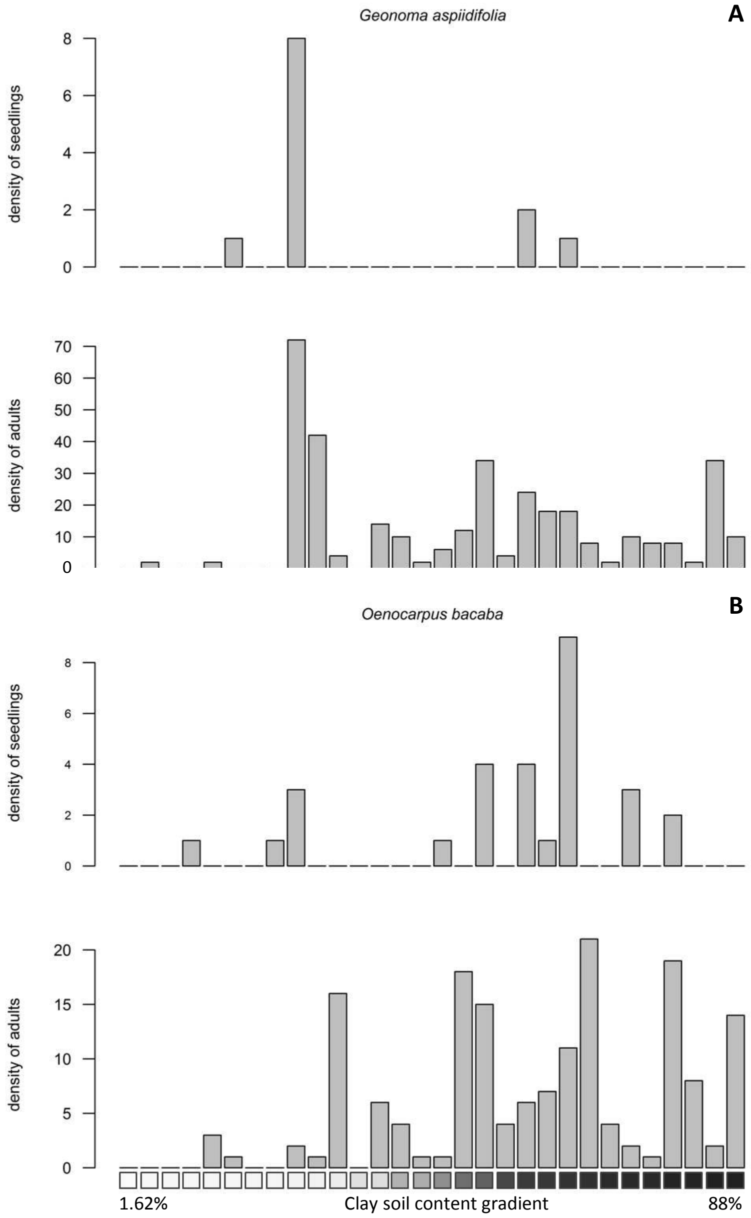
Geonoma aspiidifolia
A
density of seedlings
0
2
4
6
8
density of adults
0
10
20
30
40
50
60
70
Oenocarpus bacaba
B
density of seedlings
0
2
4
6
8
density of adults
0
5
10
15
20
1.62%
Clay soil content gradient
88%

Fig. 4

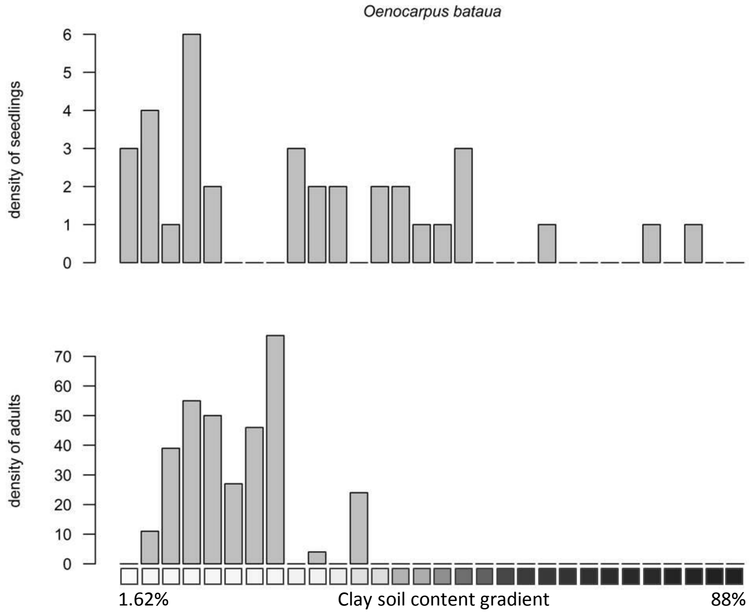
Oenocarpus bataua
density of seedlings
0
1
2
3
4
5
6
density of adults
0
10
20
30
40
50
60
70
1.62%
Clay soil content gradient
88%

Fig. 5

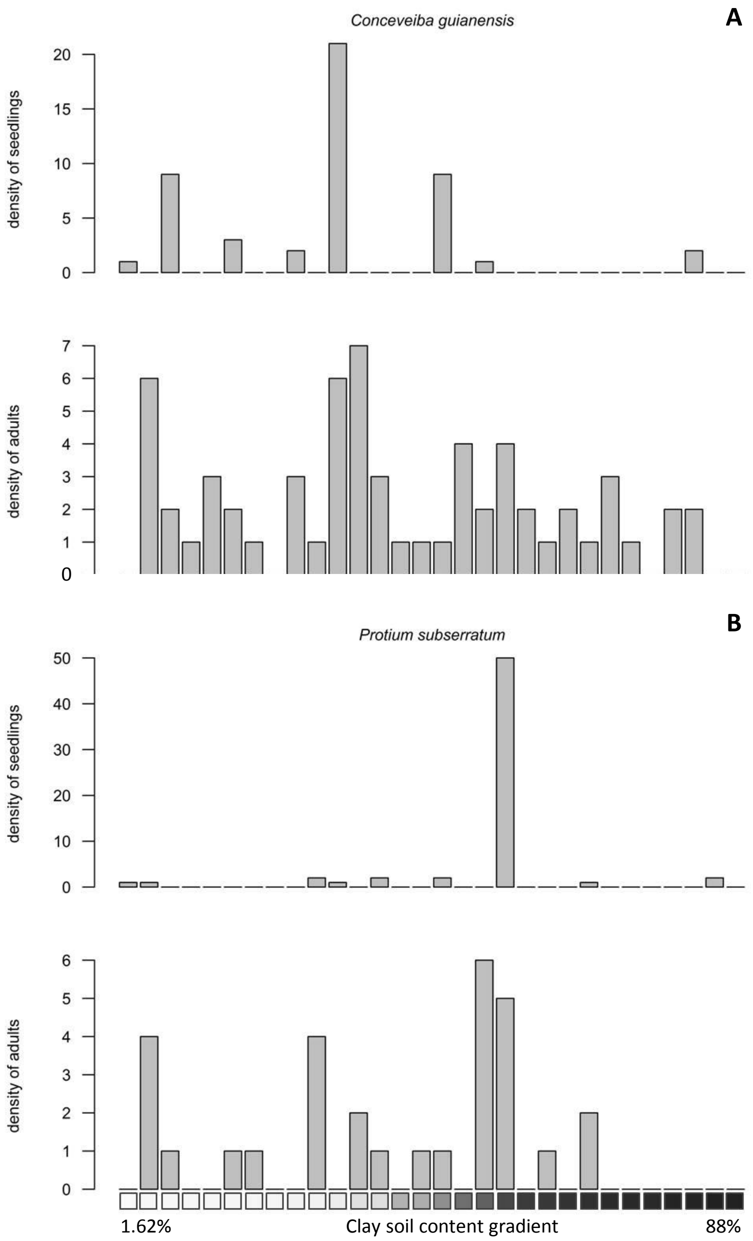
Conceveiba guianensis
A
density of seedlings
0
5
10
15
20
density of adults
0
1
2
3
4
5
6
7
Protium subserratum
B
density of seedlings
0
10
20
30
40
50
density of adults
0
1
2
3
4
5
6
1.62%
Clay soil content gradient
88%

Fig. 6

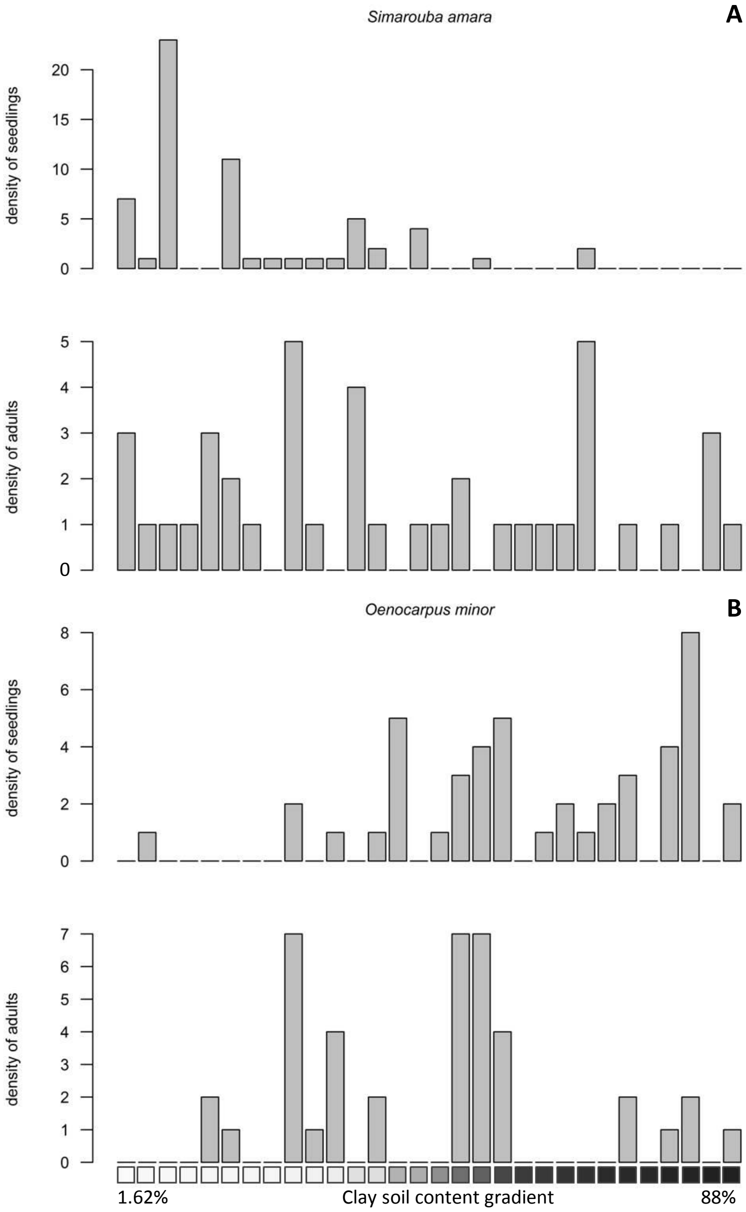
Simarouba amara
A
density of seedlings
0
5
10
15
20
density of adults
0
1
2
3
4
5
Oenocarpus minor
B
density of seedlings
0
2
4
6
8
density of adults
0
1
2
3
4
5
6
7
1.62%
Clay soil content gradient
88%

TABLE 1. Species tested for habitat association at Ducke Reserve. The habitat specificity index applied is based on the standard deviation of clay content in the soil of the sites in which the species occurred, compared to a null distribution of the standard deviation values. It was calculated for adults (a) and seedlings (s). Significance levels: *5 %, ** 1 % and *** 0.1 %. The gradient limit (percentage of clay in soil composition) is presented for species that showed habitat association.

Species	Family		Original standard deviation	Gradient limit
Brosimum rubescens Taub.	Moraceae	A	36.34	-
		S	36.35	-
Buchenavia grandis Ducke	Combretaceae		34.30	-
			46.54	-
Clarisia racemosa Ruiz & Pav.	Moraceae		**29.46***	67.43
			34.51	-
Conceveiba guianensis Aubl.	Euphorbiaceae		**34.96***	86.54
			33.10	-
Diplotropis triloba Gleason	Fabaceae		41.44	-
			36.05	-
Endopleura uchi (Huber) Cuartrec.	Humiricaceae		**29.86***	74.89
			33.79	-
Eschweilera coriacea (DC.) S.A. Mori	Lecythidaceae		36.26	-
			40.92	-
Euterpe precatoria Mart.	Arecaceae		36.71	-
			38.65	-
Geonoma aspiidifolia Spruce	Arecaceae		**33.65*****	4.27
			42.92	-
Hevea guianensis Aubl.	Euphorbiaceae		36.68	-
			39.51	-
Inga gracilifolia Ducke	Fabaceae		34.61	-
			33.96	-
Iriartella setigera (Mart.) H. Wendl.	Arecaceae		34.89	-
			35.70	-
Mabea subsessilis Pax & K. Hoffm.	Euphorbiaceae		33.82	-
			2.38	-
Micropholis guyanensis (A. DC.) Pierre	Sapotaceae		36.08	-
			36.66	-
Oenocarpus bacaba Mart.	Arecaceae		**33.57*****	4.27
			35.63	-
Oenocarpus bataua Mart.	Arecaceae		**2.84*****	12.43
			31.72**	59.62
Oenocarpus minor Mart.	Arecaceae		37.54	-
			32.49**	4.27
Protium apiculatum Swart	Burseraceae		**34.03*****	4.27
			37.21	-
Protium gallosum D. C. Daly	Burseraceae		30.06^{+}	-
			41.61	-

TABLE 1.Species tested for habitat association at Ducke Reserve. The habitat specificity index applied is based on the standard deviation of clay content in the soil of the sites in which the species occurred, compared to a null distribution of the standard deviation values. It was calculated for adults (a) and seedlings (s). Significance levels: *5 %, ** 1 % and *** 0.1 %. The gradient limit (percentage of clay in soil composition) is presented for species that showed habitat association.

Species	Family	Original standard deviation	Gradient limit
Protium hebetatum D. C. Daly	Burseraceae	**35.26***	4.27
		35.89	-
Protium subserratum (Engl.) Engl.	Burseraceae	**31.68***	82.30
		36.39	-
Simarouba amara Aubl.	Simaroubaceae	36.64	-
		24.84***	37.41
Sorocea guilleminiana Gaudich.	Moraceae	34.57	-
		28.27	-

Capítulo 3

Barbosa, C.E.A., Misiewicz, T.M., Fine, P.V.A. Fine, Costa, F.R.C. Plant ontogeny, spatial distance, and soil type influence patterns of relatedness on a common Amazonian tree. Manuscript accepted on plos ONE.

Plant Ontogeny, Spatial Distance, and Soil Type Influence Patterns of Relatedness on a Common Amazonian Tree

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Key-words: plant recruitment, tropical forest, density dependence, seedling mortality, environmental filter, soil texture, clay, sand, SGS.

Abstract

The formation of spatial genetic structure (SGS) may originate from different patterns of seed deposition in the landscape, and is mostly determined by seed dispersal limitation. However after dispersal mechanisms acting throughout plant development stages, such as environment filtration and herbivores or pathogens attacks has the potential to either disrupt or intensify the SGS pattern found. We investigated how the genotype of *Protium subserratum* (Burseraceae), a common tree species in the Ducke Reserve, Brazil, is distributed across the landscape. We used seven microsatellite markers to assess the spatial genetic structure among plants at different life stages and at different environments. Based on patterns of relatedness among plants of different sizes, we inferred in which ontogenetic stage occurred most of the changes in SGS, and compared their effects across soil types. Relatedness among seedlings decreased when distance between seedlings increased, especially for the youngest seedlings. However juveniles and adults did not follow this trend, as relatedness values were higher among neighboring individuals in this size class. Contrasting relatedness patterns between seedlings and larger individuals suggests a trade-off between the negative effects of being near closely-related adults (e.g. herbivore and pathogen attack) and the advantage of being in a site favorable to establishment. We also found that soil texture strongly influenced density-dependence patterns, as young seedlings in clay soils were more related to each other than were seedlings in bottomland sandy soils, suggesting that the mechanisms that creates and maintain SGS within a population may interact with environmental heterogeneity.

Introduction

Patterns of positive spatial genetic structure (SGS) derive from dispersal limitation which results in closely-related seeds of a given plant species being deposited close to one another [1,2], with genotypes spatially distributed in a non-random fashion [3]. However, once a seed arrives at a site, both abiotic and biotic factors affect plant recruitment, which ultimately determines the distribution of individuals in the landscape [4], and thus SGS patterns become rearranged over time. Microhabitat characteristics can be particularly important in the adjustment of SGS as seedling development proceeds, because factors that promote seedling success or mortality such as pathogens, predation, competition and resource availability can differ drastically at very small scales [5–7].

In addition to each species' dispersal capabilities, the temporal asynchrony of seed production and fecundity variation among adults in a population also influence population-level patterns of SGS. If for each reproductive event in a population a different set of individuals produced seeds within a year, greater positive SGS would be found within individuals of that year's offspring, and relatedness of seedlings among different plant size classes would be reduced. Also, adults with higher fecundity, which disproportionally contribute to the seed shadow composition [8], should produce larger numbers of seedlings, leading to two possible outcomes. One is the increase in the chance that more individuals of the descendents of these "superfecund" adults would reach adulthood. In this scenario adults would be more related to each other than would be expected by chance. Furthermore, greater production of seeds would enhance the probability of more distant seed dispersal, which could disrupt SGS within less fecund offspring, by the input of seeds with different genotypes. On the other hand, if most mother trees in a population produce seeds every year, this would mean that most seeds in any given location should be closely-related. In this case, the pattern of positive SGS might prevail despite the additional input of seeds with different genotypes dispersed from adults with asynchronous reproduction.

Patterns of SGS that emerge in the seed shadow of the maternal tree may also be influenced by density or distance-dependent mortality. The establishment success of propagules is inversely related to the distance from their maternal parent, which is explained by the higher probability of attack by specialist herbivores and pathogens that are associated with maternal trees [9,10]. This mechanism is the core of the Janzen and Connell hypothesis, which predicts that density and/or distance-responsive natural pathogens and herbivores cause a disproportionate amount of mortality near adult trees [9–11]. This hypothesis could be extended to the intraspecific level, especially in cases when variation in resistance to specialist herbivores or pathogens is present in a plant population, and considering that seedlings and mother trees are more likely to share phenotypes involved with resistance to enemies [12,13]. In this way, the natural enemies associated with the mother tree that attack neighboring seedlings could be targeting genotypes more similar to the adult, which would result in disruption of the SGS patterns predicted by seed dispersal limitation. Thus the positive patterns of SGS in individuals from the youngest seedling stages would be predicted to disappear in older development stages. Furthermore, the degree of SGS disappearance should thus be regulated by the strength of the density/distance-related mortality.

Although the proximity to conspecific adults might lead to increased density or distance-related seedling mortality, for a shade-tolerant tree species the site where a reproductive conspecific adult has successfully established is most likely to offer “optimal” abiotic conditions for seedling establishment [14,15]. In this scenario, there would be a tendency of seedlings to recruit to adulthood around their maternal tree, with positive spatial genetic structure being detectable throughout all development stages of the species, especially in stages older than the youngest seedlings.

Moreover, the periodicity of fruit production, the amount of fruit produced and/or dispersed, density and distance-dependent mortality and even the suitability of a site for seedling recruitment should interact with environmental heterogeneity. Resource availability influences both the amount of fruit produced [16,17] and the periodicity of the reproduction events of a tree population [8]. Additionally, seedling establishment may be affected by highly variable abiotic (water, nutrients and light availability [18]) or biotic factors, including litter depth [19], competition [5] and natural enemies [20,21]), that might result in “optimal” sites being more common at particular habitats across an environmental gradient. Finally, plant mortality due to herbivore attacks may differ according to soil characteristics [22]. Given the variation of seedling establishment with environmental factors, SGS patterns might vary within the same population that occurs across an environmental gradient in different habitat types.

The processes involved in the formation of SGS patterns described above are not all mutually exclusive and might occur simultaneously and/or have stronger effects at different age classes, Here, we attempt to observe how the relatedness patterns among individuals of a common Amazonian tree species change with ontogenetic stage: from very young seedlings to adults. Second, we investigate the effect of habitat characteristics (represented here by soil texture) in driving SGS patterns.

Methods

Study species and study site

Protium subserratum (Engl.) Engl. (Burseraceae) is a widespread species in northern Amazonia, extending into Guyana, French Guyana, the Brazilian Amazon, Ecuador, Peru, Colombia and Venezuela. This dioecious tree species occurs across a range of soil types including clay, sandy clay and white-sand [23] and its red fruits are thought to be dispersed by birds and monkeys [24]. We studied a population of *P. Subserratum* along an edaphic/topographic gradient within the Reserva Florestal Adolpho Ducke (hereafter referred as Ducke), where the species is found on a soil gradient that transitions from sandy soil in low elevation areas (39 m a.s.l.) To more nutrient rich clay soil at higher elevation areas (109 m a.s.l.).

Ducke is a terra firme tropical forest that covers an area of 100 km^2 at the northern limit of the city of Manaus (02^o55's, 59^o59'w, Fig. 1) in the Brazilian state of Amazonas. It is a closed canopy forest, with trees reaching 35-40 m height [25] and includes a high abundance of understorey palms [26]. Ducke is under the jurisdiction of the Brazilian National Institute for Amazon Research (INPA), which issued permits for the sampling involved in the present study. In addition the studied species is not an endangered or protected species.

Study Design

We conducted our study in 30 of the 72 permanent plots that were set up as part of the Brazilian Long-Term Ecological Research Program and the Research Program in Biodiversity [27]. The plots are systematically distributed within a trail grid system, 1km distant from each other, and are 250 meters long with the width of each transect varying according to the taxa or the life stage to be studied [28]. Tree size classes define the plot width, which is 4 m for DBH $\geq$ 1cm, 20 m for DBH $\geq$ 10 cm and 40 m for DBH $\geq$ 30 cm. Within these limits all trees are mapped and tagged. The plots follow the altitudinal contours, which results in a constant altitude throughout the plot length, important at Ducke, where topography is highly correlated with clay content [29].

Data collection

In each of the 30 plots the sampling took place along the 250 meters transect, in four lines (2 m wide) that were parallel to the central line (Fig.1). We counted and marked the geographic location of all *P. Subserratum* seedlings and saplings along these lines with a handheld GPS unit and estimated the height of each individual. Leaflets were collected and dried in silica-gel for genetic analysis. Juveniles and adults that were outside the collection lines but were within the plots and mapped from previous studies were also sampled. To expand the sample of each adult's seed shadow extra seedlings were sampled around adults in a cross-shaped sampling design in concentric circles around the trunk (Fig.1).

Sampled individuals were categorized in four size classes: seedlings up to 20 cm in height (first-year seedlings), seedlings 21 to 40 cm in height (young seedlings), seedlings from 41 and 100 cm in height (saplings) and all juvenile and adult trees taller than 200cm (juveniles and adults) (Table 1). Only four individuals in the 100-200 cm size class were counted in all of the plots and as a result this size class was excluded from our study. Because all subsequent analyses rely on the comparison of pairs of individuals, only plots that had at least two individuals in any size class were included (14 of the 30 plots).

Information on soil texture for each plot was gathered from previously collected data that is available at http://ppbio.inpa.gov.br/knb/metacat/fecosta.4.5/ppbio. At Ducke soil texture strongly influences plant community composition [30]. Schietti et al. [31] have shown that despite the fact that soil texture changes in a continuous fashion, plant composition changes abruptly when soils shift from very sandy (less than 15% of clay in its composition) to higher in clay content. Accordingly, we divided the soils into two classes: "sandy" plots when they contain less than 15% clay and “clay” plots when clay content was greater than 15%.

Genetic Data

Microsatellite genotyping and genetic diversity

Genomic DNA was extracted from 360 individuals (Table 1) using a dneasy Plant Mini Kit (Qiagen, Santa Clarita, California, USA) and all samples were genotyped using seven microsatellite markers specifically developed for P. Subserratum (Prot28, Prot29, Prot67, Prot70, Prot71, Prot78, Prot83 - [32]). Polymerase chain reactions (PCR) were performed in a total reaction volume of 12.30μl containing 1μl genomic DNA, 6.30μl 2X gotaq Green Master Mix (Promega, Madison, Wisconsin, USA), 0.4 μm of un-tagged primer, 0.2 μm of tag-modified primer and 0.2 μm of M13R primer fluorescently labeled with 6-FAM or Hex [33] and dnase free water. Amplifications were initialized with a denaturation step of 2 min and 30 s at 95^{o}c, followed by four touch-down cycles, repeated five times each, denaturation at 95^{o}c for 20 s, annealing temperatures of 55, 53, 50, 49^{o}c, respectively for each touch-down step, for 20 s, followed by a ramp of 2^{o}c/s to 45^{o}c, extension temperature at 72^{o}c for 30 s, and a final cycle of 95^{o}c for 20 s, 45^{o}c for 20 s, 72^{o}c for 30 s, repeated 15 times with a final extension at 72^{o}c for 10 minutes. The allele sizes of the resulting fluorescent labeled fragments were determined using the size standard LIZ-500 on an ABI 3730 DNA Analyzer (Applied Biosystems, Foster City, California, USA). Peaks were scored using Peak Scanner version 1.0 (Applied Biosystems).

Number of alleles (A), observed (H_o) and expected heterozygosity (H_e) were calculated in genalex version 6.1 [34]. Departure from Hardy-Weinberg equilibrium and linkage disequilibrium were calculated using Genepop 4.0.10 [35] and probability of null alleles was calculated with Cervus 3.0 [36].

Spatial distribution of genetic variation across the landscape

The distribution pattern of genetic variation across the landscape was assessed using Spatial Genetic Analysis (SGS) to examine genetic relatedness as a function of the spatial separation among individuals. This multivariate approach was used to test the autocorrelation (r) between geographic distance (expressed in meters between each pair) and genetic distance (a Euclidean distance measure) matrices [37] at the plot scale (250m). The coefficient r ranges from -1 to 1 and gives a measure of genetic similarity between individuals within each distance class (positive values refer to degree of relatedness and negative values mean individuals are less related than expected at random). It is similar to Moran's – $I^{(h)}$ coefficient, except that r accounts for the number of times an individual is paired with other individuals in the same distance class, while Moran's I considers an individual pairing at any distance class in a binary way (paired/not paired). In order to determine if null alleles could be influencing the r-value calculations, additional estimates of relatedness were calculated using ML-Relate [38], which accommodates the presence of null alleles, to determine the effect of null alleles relative to our initial relatedness estimates.

The null hypothesis of random distribution of genotypes was created by randomly permuting the genotypes among the sampling locations. After repeating the permutation 999 times it was possible to calculate r-values and then create an empirical null distribution for each distance class, allowing the construction of a confidence interval (95% CI). Significant autocorrelation was inferred each time an observed r-value occurred outside the confidence interval. The error bars calculated for each r-value also give information on the significance of the autocorrelation, in which significant autocorrelation at each distance class was inferred only when the error bar did not cross the x-axis. In order to determine if the observed autocorrelation values represent credible evidence of fine scale genetic structure and to test all the distance classes, p-values were calculated using the methods of Smouse et al. [39]. The p-values were then used to calculate a probability metric ω [40] following Smouse et al. [39], which allowed us to evaluate the hypothesis of no autocorrelation at any distance.

To evaluate the extent of the seed shadow overlap on SGS in each life stage and its effects on relatedness patterns among plants at different life stages, we performed a “between-generation” analysis [41], in which the relatedness is calculated for pairs of individuals formed by a seedling (first-year seedling, young seedling or sapling) and an adult, yielding the degree of relatedness of the seedlings with their closest adults. A “within-generation” analysis was also undertaken to measure the relatedness among seedlings of each size class and all individuals pooled together. A similar within and between generation relatedness is expected when the seed shadow overlap is low, because very young seedlings have greater probability of being most closely related to their closest adult. Higher relatedness within seedlings would indicate that they share parents outside the sampling area, and that those adults contribute substantially to the plot seed rain composition. The relatedness index used was Nason’s kinship coefficient Fij [42], calculated on spagedi 1.3 [43]. The coefficient of relatedness (r) used is the double of the value of Fij assuming neither individual is inbred [44].

In order to explore the effect of developmental stage and environmental features on the spatial organization of individuals, autocorrelation tests were performed independently with all samples pooled and also according to plant size class and soil type. In the analyses comparing spatial patterns between soil types, all seedlings up to 40 cm were pooled to increase sample sizes, so at least one pair of individuals was compared in each distance class; fewer than two individuals in some distance classes precluded analysis of soil-related patterns for larger plants. To evaluate if the differences among the fine-scale genetic structure patterns of the size and soil types were significant, we used a non-parametric heterogeneity test. This encompasses the autocorrelation coefficient values calculated for each lag of each group and the pooled correlogram as the null hypothesis reference frame. This test accounts for differences in sample size by applying a weighted average bias correction [39]. All correlograms and related tests were undertaken in genalex v.6.1 [34]. To minimize the effects of incomplete genotypes the interpolation option was applied in the creation of the genetic distance matrices.

Results

Genetic Diversity

The number of alleles per locus ranged from four (Prot71 and Prot78) to 12 (Prot29), with a mean value of 7.71 alleles per locus. Mean expected heterozygosity (H_e) was 0.66 and observed heterozygosity (H_o) was 0.60 (Table 2). Of the seven microsatellites, only one (Prot 71) departed from Hardy-Weinberg expectations. Null alleles were detected in loci Prot67 (P = 0.071), Prot70 (P = 0.068) and Prot 78 (P = 0.068) however, correcting for the presence of null alleles and recalculating the r-values using ML-Relate resulted in no significant change, corroborating our initial r-values. Accordingly, our initial r-values were used in all further analyses.

Spatial genetic structure and plant size

The relatedness of 40cm seedlings was greater than expected by chance throughout most of the plot, for either 50 m (Fig. 2) or 10 m (Fig. 3) distance interval classes, showing that the results are robust to the choice of distance interval. All four plant size classes had individuals more related with each other than expected by chance in the first distance class (0-50m – Table 3). The relatedness among individuals decreases either within each plant size class as spatial distance increases (for all plant size classes) and among different plant size classes, as plants grow taller (r-values of first-year seedlings > young seedlings > saplings – Fig. 2). Juveniles and adults showed high relatedness among individuals in the first 100 meters (Fig. 2), although only results from the first distance class (0-50m) can be considered robust, due the small number of pairs compared especially at the 51-100m and 201-250 m distance classes. The multiclass test criteria (ω) performed separately for each plant size class allows an evaluation of the credibility of autocorrelations, and all four size classes had significant SGS pattern at least in one distance class (Table 3).

According to the heterogeneity test of relatedness patterns (r-values), the three first size classes were statistically similar (Table 4). Only the first-year and young seedlings differed in the second distance class, reflecting a significant drop in the r-values of the latter (Fig. 2). First-year seedlings, young seedlings and saplings had relatedness patterns different from the juveniles/adult tree class (p=0.09, p=0.03 and p=0.03, respectively).

There was a strong positive autocorrelation when all sample sizes were pooled across all individuals and plots sampled at Ducke (Fig. 3). This pattern appears to be driven by the high positive autocorrelation among first-year and young seedlings at the plot scale, as the relatedness among juveniles and adults does not present a consistent pattern across the length of the plot.

The between-generation SGS, which focused on pairs of individuals that included one adult and one seedling, showed that adults exhibited weak genetic relatedness with nearby seedlings, while within-generation relatedness was generally higher (Fig. 4). This pattern was strongest for the first-year seedlings, which were more genetically similar to other seedlings of the same size class than with nearby adults, especially in the first three distance classes

(Fig. 4A). Low relatedness between first-year seedlings and adults indicates that seedlings were dispersed from adults outside the sampling area. Differences in relatedness within and between generations for the young seedling size class decreases as age class increases (Fig. 4B), while the saplings show a shift at the fourth distance class, when individuals from this size class became less related to each other than they were to adults in the plot (Fig. 4C).

Spatial genetic structure and soil type

The SGS among first-year and young seedlings was significantly different from random when all samples from all plots were pooled, regardless of their position along the environmental gradient. Since soil texture is a good proxy for topographic position and correlates with plant species composition at our study site [29,30], we ran two separate SGS analyses based on plot soil texture. The results have shown that soil type influences SGS patterns, as we found positive autocorrelation in the clay plots throughout all distance intervals. By contrast, seedlings from sandy soils were significantly positively autocorrelated only in the first three distance classes (up to 150m) after which individuals were no more related with each other than would be expected by chance, since r-values falls within the CI area (Fig. 5).

We found significant differences between SGS for plants inhabiting different soil types (Fisher's ω = 18.962, P = 0.034 – Table 6). This result was due to the low relatedness coefficient (r-values lower than expected under the null distribution) of seedlings sampled at the fourth distance class (Fig. 5).

Discussion

Patterns across plant ontogeny

Spatial genetic structure is often consequence of limited seed dispersal [45], when seeds and seedlings present higher relatedness with the nearby adults. *Protium subserratum*, despite having dispersers with high mobility potential, has the majority of its fruits deposited beneath the tree crown with extremely high seedling abundances (C.E. Barbosa, pers. observ.). However, in examining the SGS patterns of this tree, we found that younger seedlings presented higher genetic similarity with their neighboring seedlings than with the closest adults. This pattern could result from pulses of seeds coming from distant, unsampled adults further away from the study sites. In addition, the frequency of fruiting cycles might vary among the adults of the same population [8,17], which could change the SGS observed in a given cohort. Fecundity variation is another factor that may influence SGS, because adults with greater seed production should be over-represented in the seed shadow composition, yielding more seedlings related with each other.

We also found that relatedness decreased between first-year seedlings and saplings. This reduction in relatedness could result from disproportionate mortality near conspecific adults due to density and/or distance-responsive enemies. From a initially highly genetically autocorrelated seed shadow, thinning of closely related individuals occurs as the seedlings grow taller, as shown by the decreasing autocorrelation values from one size class to the next. One mechanism that would cause this pattern is if anti-herbivore defenses were variable within populations and closely related plants express identical anti-herbivore defenses [12,13]. Specialist natural enemies may use these defenses as cues, and genetically distant individual seedlings may escape notice when in a group of conspecifics. Strong evidence of higher mortality within closely related seedlings was described recently in Choo et al. [46], in which the proportion of seedlings dispersed near the maternal parent decreased by threefold throughout the development stages evaluated, while the proportion of non-related seedlings remained similar. Alternatively, fungal pathogens may have strong negative effects on young seedlings near parent trees [6], but both herbivore and pathogen negative effects may subside as seedlings mature.

The differences we found in relatedness between first-year and young seedlings agrees with other studies that evaluated SGS throughout different life stages [47,48]. Zhou & Chen [2] detected SGS dissipation as seeds and seedlings developed to the sapling and adult stages, but they could not determine the stage at which density dependence began because they did not measure young seedlings. Hamrick et al. [49] also found SGS at seedling and sapling stages and Hardesty et al. [50] identified differences on SGS patterns when comparing size classes of a tropical tree species, but unlike our study did not detect SGS among individuals at the adult stage.

Seeds from distant parents dispersed from outside the studied area, might accumulate over multiple fruiting years, causing the decrease of relatedness as seedlings age. In this scenario we would expect the youngest seedlings to be closely-related to local adults, but that genetic-relatedness would be reduced as seedlings grew older [41]. However the between-generation analysis (Fig. 4) does not support this hypothesis as the observed youngest seedlings were less related with the adults than within themselves. In fact relatedness was more and more similar to adults as the cohorts aged, which might help to explain the high relationship values among juvenile and adult tree individuals in the first distance classes. The adults and juveniles were more related to each other than would be expected by chance, which is contrary to the tendency for relatedness to decrease, which we found for earlier stages of development. The adults of the first distance class had the highest relatedness value (n=17, r=0.34, more than twice the first-year seedlings' r-value). However, the r-values among juveniles and trees, as well as the ones for the greater distance classes of the saplings, should be carefully interpreted as they derived from a small number of comparisons. Nevertheless, the pattern of greater relatedness within adults and juveniles trees is strengthened by the fact that the within-generation relatedness values that we observed were much higher than the between-generation relatedness for the first size class, and these values showed a clear tendency to decrease as seedlings aged, until the sapling stage where the plants' relatedness values are more similar to the adults.

Our finding of the reduction in relatedness within seedlings as plants grow older, yet exhibiting higher relatedness values with adults, could be explained by a life-stage conflict, as predicted by Schupp [51], in which the trade-off between the positive and negative aspects of being nearby a reproductive adult should vary according to the ontogenetic stage. Thus, being close to an adult might be much more detrimental to young seedlings than for saplings and adults, as the higher probability of herbivore and/or pathogens attack greatly surpasses the advantage of being in the same site of a reproductive adult (i.e., an "optimal" site for establishment) in an early life stage. Additionally, contrary to the prediction of Janzen's graphical model of high seedling mortality at specific distances from adults [9,11] and supporting studies such as Alvarez-Loayza & Terborgh [20] that observed extremely high seedling mortality, some *P. subserratum* seedlings do escape mortality in close proximity to adults. The clustering of genetically closely related juveniles and adults might result from uneven seed distribution, with seeds from the same maternal tree being dispersed to the same place [52,53], resulting in clumping of related individuals. Besides these possibilities, we would also expect that most seedlings would derive from nearby individuals of *P. subserratum*, considering the deposition of large numbers of seeds near the maternal adult year after year compared to the minor contribution of seeds dispersing from adults at greater distances. In that context, the probability that the seedlings that do escape from predation will be related to the nearest adults is higher. Our results stand in contrast to studies that found individuals related to each other, but away from the maternal individual [54–56]. Finally, closely related adults may themselves relate to the reproductive success of a few previous adults from past generations, and may thus be a consequence of episodic reproduction or founder effects.

Steinitz et al. [57] found contrasting results in a temperate forest in a study of older pine saplings and adult trees. They reported that density dependent mortality strengthened with age, working as a spacing mechanism all the way to adulthood. The authors argue that a possible explanation for this pattern would be the increase in competition with conspecific adult trees. Our results are more in accordance with those found by Latouche-Hallé et al. [58] for a tropical tree species at French Guiana, where genetic relatedness was higher in adults that were close together, which they credited to overlapping generations in adult cohorts being more dissimilar at greater distances.

Patterns across soil types

Even within the same population of *P. subserratum*, and along a relatively short environmental gradient, relatedness patterns appear to be significantly different between soil types. In slopes and ridges, where the clay plots were located, the relatedness values among individuals 150 m distant from each other were higher than in the lower areas (the sandy plots of the valleys), in which relatedness between individuals was no different than what would be expected by chance. This pattern may be explained by two interconnected factors: soil type and topography.

Soils in central Amazonia are notoriously poor and sandy soils are significantly less fertile than clay soils. Differences in seed output caused by soil nutrient properties could change the size of seed shadows, thus affecting SGS patterns. But since tree diameter is a good predictor of fecundity potential [59,60], and at Ducke the size of *P. subserratum* trees is similar across the soil texture gradient (r^2=-0.03, p=0.72, unpublished data), it is reasonable to expect similar seed output throughout the soil texture gradient. Variation in the number of reproductive adults may also influence SGS as a result of overlapping seed shadows [49], but the abundance of *P. subserratum* adults is also similar along the soil texture gradient, therefore the chances of overlapping seed shadows should be constant throughout the gradient.

Subtle environmental gradients not only may affect an individual's growth [61], but they can also influence the chemical defenses against predation [13] and ultimately act as a selective agent on genotypes. Despite the evidence of stronger herbivore pressure in forest on clay soil sites [22], the impact of leaf attack in poor soils is higher, because the replacement of the leaf tissue lost to herbivores should be much more difficult in a low nutrient environment [22]. Stronger herbivore impacts on mortality in sandy habitats could lead to higher density/distance related mortality and ultimately result in the lower genetic autocorrelation among seedlings in sandy soils.

Nevertheless, density/distance dependent mortality might be overwhelmed by abiotic factors that regulate establishment success. We found higher mortality of *P. subserratum* seedlings in clay plots (45%) than in sandy plots (16%) in a parallel study conducted during a two year period (C. E. Barbosa, unpublished data), which is the opposite of what would be expected because clay plots exhibited stronger patterns of spatial genetic structure than did sandy plots. The increased mortality might be related to drought during the dry season, which tends to have stronger effects in clay soil areas that are located away from streams. However drought-related mortality probably happens regardless of the proximity to conspecific adults and should not influence the spatial genetic structure patterns found here.

Additionally, valleys may receive a more genetically diverse seed influx from higher places, due a topographic effect of seeds being carried down by gravity as well as by rainwater from the steeper areas. Even in the absence of rain, seeds from trees in higher areas have a higher probability of being dispersed to the valleys by birds, gravity or wind than seeds from valley trees have of being moved to higher sites. This could lead to a greater genetic diversity in valleys, and hence to a lower genetic relatedness among seedlings.

Edaphic gradients and topography have a large influence in driving plant species composition in the Amazon [30,62] and density/distance-dependent mortality could be one of the mechanisms involved. The evidence we found for contrasting JC effects between sandy and clay soils at Ducke may be part of a more general mechanism influencing community-level patterns in different soil types and could contribute to the high turnover of plant community composition in the Central Amazonian lowlands [31].

Conclusions

We observed spatial genetic structure patterns in all evaluated stages of *P. subserratum*, with a tendency for relatedness to decrease across the early stages of development. However, this tendency was not found in the adults, which presented high SGS. That may be an indication that particular genotypes are better adapted to a very local scale, resulting in more genetically spatially-autocorrelated adults, as they would be more likely to share traits for the same abiotic and biotic environments. The different SGS patterns that we found between clayey and sandy soils may represent another layer of trait selection acting on a higher spatial scale.

The presence of SGS across environments in seedlings of a species so broadly distributed across the whole Amazon forest could be an indication that *P. subserratum* may be more locally adapted to soil type than previously assumed, and shows the impact that habitat heterogeneity can have on genotype distribution. Future studies should investigate if the SGS differences among environments are sustained across subsequent plant development stages including among adults in different soil types. Environmental heterogeneity across the landscape are known to be driver of speciation [63] with the action of ecological selection on genotypes. Fine et al. [64], when analyzing extremely poor soils (white sands) in contrast with more fertile clay soils, found that the soil type interacts with herbivore pressure leading to habitat specialization. We speculate that our findings here might represent an intermediate stage in that process, as the downslope sandy soils at Central Amazon are not as poor as white sand soils, therefore should be a less extreme gradient. Nevertheless the differences between habitats were sufficient to establish diverse patterns of genetic structure among environments.

Acknowledgements

We thank Cíntia Gomes de Freitas, Renato Almeida Azevedo, Camila Saraiva dos Anjos, Elessandra Gomes and several field assistants for assistance in the field. Felipe Zapata and Krista Beckley provided helpful support in the laboratory. Carolina V. Castilho provided data on the location and size of juvenile and adult trees. Ângela M. Ribeiro provided valuable comments that greatly improved the manuscript.

References

1. Hardy OJ, Maggia L, Bandou E, Breyne P, Caron H, et al. (2006) Fine-scale genetic structure and gene dispersal inferences in 10 neotropical tree species. Molecular Ecology 15: 559–571. Doi:10.1111/j.1365-294X.2005.02785.x.

2. Zhou H-P, Chen J (2010) Spatial genetic structure in an understorey dioecious fig species: the roles of seed rain, seed and pollen-mediated gene flow, and local selection. Journal of Ecology 98: 1168–1177. Doi:10.1111/j.1365-2745.2010.01683.x.

3. Vekemans X, Hardy OJ (2004) New insights from fine-scale spatial genetic structure analyses in plant populations. Molecular Ecology 13: 921–935. Doi:10.1046/j.1365-294X.2004.02076.x.

4. Muller-Landau H, Wright S (2002) Assessing recruitment limitation: concepts, methods and case-studies from a tropical forest. In: Levey DJ, Silva WR, Galetti M,

editors. Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. São Pedro, Brazil. Pp. 35–53.

5. Wright SJ (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130: 1–14. Doi:10.1007/s004420100809.

6. Mangan SA, Schnitzer SA, Herre EA, Mack KML, Valencia MC, et al. (2010) Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. Nature 466: 752–755. Doi:10.1038/nature09273.

7. Comita LS, Muller-landau HC, Aguilar S, Hubbell SP (2010) Asymmetric Density Dependence Shapes Species Abundances in a Tropical Tree Community. Science 329: 330–332. Doi:10.1126/science.1190772.

8. De Steven D, Wright SJ (2002) Consequences of Variable Reproduction for Seedling Recruitment in Three Neotropical Tree Species. Ecology 83: 2315–2327. Doi:10.1890/0012-9658(2002)083[2315:COVRFS]2.0.CO;2.

9. Janzen DH (1970) Herbivores and the Number of Tree Species in Tropical Forests. The American Naturalist 104: 501–528.

10. Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: Boer PJ den, Gradwell GR, editors. Dynamics of populations. Pudoc, Wageningen, Netherlands: Centre of Agricultural Publishing and Documentation. Pp. 298–312.

11. Clark DA, Clark DB (1984) Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. The American Naturalist 124: 769–788.

12. Langenheim JH, Stubblebine WH (1983) Variation in leaf resin composition between parent tree and progeny in Hymenaea: implications for herbivory in the humid tropics. Biochemistry Systematics and Ecology 11: 97–106.

13. Brenes-Arguedas T, Coley PD (2005) Phenotypic variation and spatial structure of secondary chemistry in a natural population of a tropical tree species. OIKOS 108: 410–420.

14. Poorter L (2007) Are species adapted to their regeneration niche, adult niche, or both? The American Naturalist 169: 433–442. Doi:10.1086/512045.

15. Schupp EW (1995) Seed-Seedling Conflicts, Habitat Choice, and Patterns of Plant Recruitment. American Journal of Botany 82: 399–409.

16. Crawley MJ (1990) The population dynamics of plants. Philosophical transactions of the Royal Society of London Series B, Biological Sciences 330: 125–140.

17. Herrera CM, Jordano P, Guitián J, Traveset A (1998) Annual Variability in Seed Production by Woody Plants and the Masting Concept: Reassessment of Principles and and Relationship to Pollination and Seed Dispersal. The American Naturalist 152: 576–594.

18. Leishman MR, Wright IJ, Moles AT, Westoby M (2000) The Evolutionary Ecology of Seed Size. In: Fenner M, editor. Seeds: The ecology of regeneration in plant communities. CAB International. Pp. 31–58.

19. Molofsky J, Augspurger CK (1992) The Effect of Leaf Litter on Early Seedling Establishment in a Tropical Forest. Ecology 73: 68 – 77.

20. Alvarez-Loayza P, Terborgh J (2011) Fates of seedling carpets in an Amazonian floodplain forest: intra-cohort competition or attack by enemies? Journal of Ecology 99: 1045–1054. Doi:10.1111/j.1365-2745.2011.01835.x.

21. Muller-Landau HC, Dalling JW, Harms KE (2004) Seed dispersal and density-dependent seed and seedling survival in Trichilia and Miconia. In: Losos E, Leigh EG, editors. Tropical Forest Diversity and Dynamism. Pp. 340–362.

22. Fine PVA, Miller ZJ, Mesones I, Irazuzta S, Appel HM, et al. (2006) The growth-defense trade-off and habitat specialization by plants in Amazonian forests. Ecology 87: 150–162.

23. Daly DC, Fine PVA (2011) A New Amazonian Section of Protium (Burseraceae) including both Edaphic Specialist and Generalist Taxa. Studies in Neotropical Burseraceae XVI. Systematic Botany 36: 939–949. Doi:10.1600/036364411X604958.

24. Fine PVA, Zapata F, Daly DC, Mesones I, Misiewicz TM, et al. (2013) The importance of environmental heterogeneity and spatial distance in generating phylogeographic structure in edaphic specialist and generalist tree species of Protium (Burseraceae) across the Amazon Basin. Journal of Biogeography: In press. Doi:10.1111/j.1365-2699.2011.02645.x.

25. Ribeiro JEL, Hopkins MJ, Vicentini A, Sothers CA, Costa M, et al. (1999) Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônica Central. Manaus: INPA-DFID.

26. Guillaumet J-L, Kahn F (1982) Structure et dynamisme de la forêt. Acta Amazonica, Suplemento 12: 61–77.

27. Costa FRC, Magnusson WE (2010) The Need for Large-Scale, Integrated Studies of Biodiversity - the Experience of the Program for Biodiversity Research in Brazilian Amazonia. Natureza & Conservação 08: 3–12. Doi:10.4322/natcon.00801001.

28. Magnusson WE, Lima AP, Luizão R, Luizão F, Costa FRC, et al. (2005) RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. Biota Neotropica 5: 19–24. Doi:10.1590/S1676-06032005000300002.

29. Costa FRC, Magnusson WE, Luizão RC (2005) Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. Journal of Ecology 93: 863–878. Doi:10.1111/j.1365-2745.2005.01020.x.

30. Costa F, Guillaumet J, Lima A (2009) Gradients within gradients: The mesoscale distribution patterns of palms in a central Amazonian forest. Journal of Vegetation Science 20: 69–78. Doi:10.3170/2008-8-18478.

31. Schietti J, Emilio T, Rennó CD, Drucker DP, Costa F, Nogueira A, Figueiredo F, Castilho CV, Kinupp V, Guillaumet JL, Garcia ARM, Lima AP, And Magnusson WE (2013) Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. Plant Ecology & Diversity, in press. Doi: 10.1080/17550874.2013.783642

32. Misiewicz TM, Barbosa CEA, Fine PVA (2012) Microsatellite primers for an Amazonian lowland tropical tree, Protium subserratum (Burseraceae). American Journal of Botany 99: e465–7. Doi:10.3732/ajb.1200229.

33. Schuelke M (2000) An economic method for the fluorescent labeling of PCR fragments: A poor man’s approach to genotyping for research and high-throughput diagnostics. Nature 18: 233–234.

34. Peakall R, Smouse PE (2006) Genalex 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6: 288–295. Doi:10.1111/j.1471-8286.2005.01155.x.

35. Raymond M, Rousset F (1995) GENEPOP (Version 1.2): Population Genetics Software for Exact Tests and Ecumenicism. Journal of Heredity 86: 248–249.

36. Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Molecular Ecology 16: 1099–1106. Doi:10.1111/j.1365-294X.2007.03089.x.

37. Smouse PE, Peakall R (1999) Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. Heredity 82: 561–573.

38. Kalinowski ST, Wagner AP, Taper ML (2006) ML-RELATE: a computer program for maximum likelihood estimation of relatedness and relationship. Molecular Ecology Notes 6: 576–579. Doi:10.1111/j.1471-8286.2006.01256.x.

39. Smouse PE, Peakall R, Gonzales E (2008) A heterogeneity test for fine-scale genetic structure. Molecular Ecology 17: 3389–3400. Doi:10.1111/j.1365-294X.2008.03839.x.

40. Fisher RA (1958) Statistical methods for research workers. 13th ed. New York: Hafner.

41. Hampe A, El Masri L, Petit RJ (2010) Origin of spatial genetic structure in an expanding oak population. Molecular Ecology 19: 459–471. Doi:10.1111/j.1365-294X.2009.04492.x.

42. Loiselle BA, Sork VL, Nason J, Graham C (1995) Spatial genetic structure of a tropical understory shrub, Psychotria officinalis (Rubiaceae). American Journal of Botany 82: 1420–1425.

43. Hardy OJ, Vekemans X (2002) spagedi : a versatile computer program to analyse spatial genetic structure at the individual or population leves. Molecular Ecology Notes 2: 618–620. Doi:10.1046/j.1471-8278 .2002.00305.x.

44. Blouin MS (2003) DNA-based methods for pedigree reconstruction and kinship analysis in natural populations. Trends in Ecology & Evolution 18: 503–511. Doi:10.1016/S0169-5347(03)00225-8.

45. Epperson BK (2000) Spatial genetic structure and non-equilibrium demographics within plant populations. Plant Species Biology 15: 269–279. Doi:10.1046/j.1442-1984.2000.00046.x.

46. Choo J, Juenger TE, Simpson BB (2012) Consequences of frugivore-mediated seed dispersal for the spatial and genetic structures of a neotropical palm. Molecular Ecology 21: 1019–1031. Doi:10.1111/j.1365-294X.2011.05425.x.

47. Jones FA, Hubbell SP (2006) Demographic spatial genetic structure of the Neotropical tree, Jacaranda copaia. Molecular Ecology 15: 3205–3217. Doi:10.1111/j.1365-294X.2006.03023.x.

48. Troupin D, Nathan R, Vendramin GG (2006) Analysis of spatial genetic structure in an expanding Pinus halepensis population reveals development of fine-scale genetic clustering over time. Molecular Ecology 15: 3617–3630. Doi:10.1111/j.1365-294X.2006.03047.x.

49. Hamrick J, Murawski DA, Nason JD (1993) The influence of seed dispersal mechanisms on the genetic structure of tropical tree populations. Vegetatio 107/108: 281–297. Doi:10.1007/BF00052230.

50. Hardesty BD, Dick CW, Kremer A, Hubbell S, Bermingham E (2005) Spatial genetic structure of Simarouba amara Aubl. (Simaroubaceae), a dioecious, animal-dispersed Neotropical tree, on Barro Colorado Island, Panama. Heredity 95: 290–297. Doi:10.1038/sj.hdy.6800714.

51. Schupp EW (2007) The suitability of a site for seed dispersal is context-dependent. In: Dennis A, Schupp E, Green R, Westcott D, editors. Seed dispersal: theory and its application in a changing world. Wallingford UK: CABI. Pp. 445–462.

52. Hamrick JL, Trapnell DW (2011) Using population genetic analyses to understand seed dispersal patterns. Acta Oecologica 37: 641–649. Doi:10.1016/j.actao.2011.05.008.

53. Karubian J, Sork VL, Roorda T, Durães R, Smith TB (2010) Destination-based seed dispersal homogenizes genetic structure of a tropical palm. Molecular Ecology 19: 1745–1753. Doi:10.1111/j.1365-294X.2010.04600.x.

54. Gonzales E, Hamrick JL, Smouse PE, Trapnell DW, Peakall R (2010) The Impact of Landscape Disturbance on Spatial Genetic Structure in the Guanacaste Tree, Enterolobium cyclocarpum (Fabaceae). Journal of Heredity 101: 133–143. Doi:10.1093/jhered/esp101.

55. Sezen UU, Chazdon RL, Holsinger KE (2009) Proximity is not a proxy for parentage in an animal-dispersed Neotropical canopy palm. Proceedings of the Royal Society B 276: 2037–2044. Doi:10.1098/rspb.2008.1793.

56. Born C, Hardy OJ, Chevallier M-H, Ossari S, Attéké C, et al. (2008) Small-scale spatial genetic structure in the Central African rainforest tree species Aucoumea klaineana: a stepwise approach to infer the impact of limited gene dispersal, population history and habitat fragmentation. Molecular Ecology 17: 2041–2050. Doi:10.1111/j.1365-294X.2007.03685.x.

57. Steinitz O, Troupin D, Vendramin GG, Nathan R (2011) Genetic evidence for a Janzen–Connell recruitment pattern in reproductive offspring of Pinus halepensis trees. Molecular Ecology 20: 4152–4164. Doi:10.1111/j.1365-294X.2011.05203.x.

58. Latouche-Hallé C, Ramboer A, Bandou E, Caron H, Kremer A (2003) Nuclear and chloroplast genetic structure indicate fine-scale spatial dynamics in a neotropical tree population. Heredity 91: 181–190. Doi:10.1038/sj.hdy.6800296.

59. Thomas SC (1996) Reproductive allometry in Malaysian rain forest trees: Biomechanics versus optimal allocation. Evolutionary Ecology 10: 517–530. Doi:10.1007/BF01237882.

60. Schurr FM, Steinitz O, Nathan R (2008) Plant fecundity and seed dispersal in spatially heterogeneous environments: models, mechanisms and estimation. Journal of Ecology 96: 628–641. Doi:10.1111/j.1365-2745.2007.0.

61. Smith DS, Schweitzer JA, Turk P, Bailey JK, Hart SC, et al. (2011) Soil-mediated local adaptation alters seedling survival and performance. Plant and Soil 352: 243–251. Doi:10.1007/s11104-011-0992-7.

62. Kinupp VF, Magnusson WE (2005) Spatial patterns in the understorey shrub genus Psychotria in central Amazonia: effects of distance and topography. Journal of Tropical Ecology 21: 363–374. Doi:10.1017/S0266467405002440.

63. Rundle HD, Nosil P (2005) Ecological speciation. Ecology Letters 8: 336–352. Doi:10.1111/j.1461-0248.2004.00715.x.

64. Fine PVA, Mesones I, Coley PD (2004) Herbivores promote habitat specialization by trees in Amazonian forests. Science (New York, NY) 305: 663–665. Doi:10.1126/science.1098982.

Data accessibility

Sampling locations, soil type, tree sizes and microsatellite genotypes for all individuals are available at the data repository of the Brazilian Biodiversity Research Program (PPBio) at http://peld.inpa.gov.br/knb/metacat/prisouza.29.13/peld.

Figure Legends

Figure 1. Site location and sampling design. Study site location in the Central Amazon, north of Manaus, Brazil. The trail grid is shown in the right figure and the plots that contained sufficient individuals for SGS analyses are represented by black dots. Topographical variation is shown in a grey-scale, from low (white) to high areas (black). In the lower left of the figure the sampling scheme is depicted, including 5 sampling lines of 2 m width and 250 m length. The extra sampling area conducted around each adult (black dot), is represented by points around it (open circles), excluding areas previously sampled in the lines (gray circles).

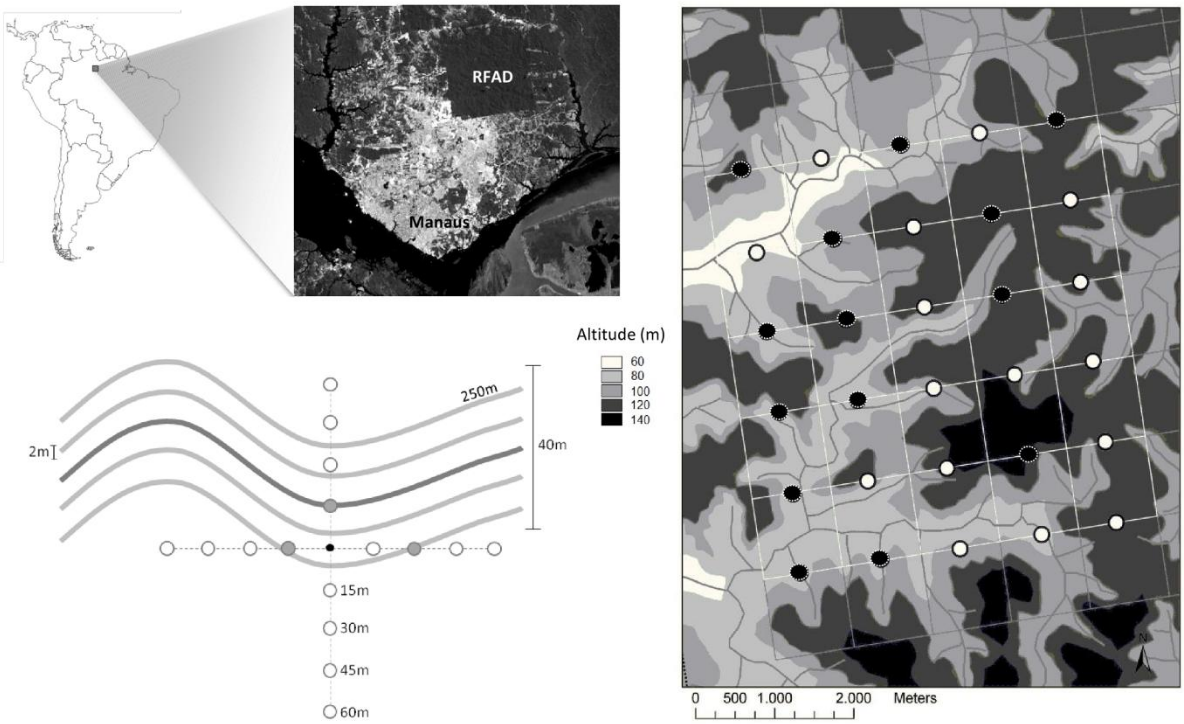
Figure 2. Spatial genetic structure at different life stages of *Protium subserratum*. Correlogram presenting SGS for *P. subserratum* seedlings of different height classes sampled at 14 plots at Ducke: (A) are seedlings up to 20 cm tall; (B) are seedlings from 21 to 40 cm tall, (C) are seedlings from 41 to 100 cm tall and (D) are juveniles and adults taller than 200 cm. The points indicate r-values with the error bars and the dashed lines are the upper and lower 95% CI limits around the mean value (r=0) of the null distribution of a random distribution of alleles in space. The number of pairs compared at each distance class is reported in table 3.

Figure 3. Spatial genetic structure calculated for (A) plants smaller than 40 cm, (B) plants taller than 40 cm and (C) all individuals pooled together. Correlogram of SGS for *P. subserratum* plants sampled at Ducke. The points indicate r-values with the error bars and the dashed lines are the upper and lower 95% CI limits around the mean value (r=0) of the null distribution of a random distribution of alleles in space. Distance classes represent 10 m intervals, from 10 to 250m.

Figure 4. Inter-generational genetic structure analysis: seedling/seedling similarity vs. Seedling/adult similarity. Kinship values (F_{ij}) of adult-seedling pairs (continuous lines) and seedling-seedling pairs (dotted lines) for each plant size class along five distance classes. (A) for first-year seedlings, (B) for young seedlings, (C) for saplings and (D) for all size classes pooled together.

Figure 5. Spatial genetic structure of *Protium subserratum* seedlings at different soil types. Correlograms of SGS for 40 cm height *P. subserratum* seedlings at plots with different soil texture at Ducke: (A) are seedlings in clayey soils and (B) are seedlings in sandy soils. The points indicate r-values with error bars and the dashed lines represent 95% CI limits around the mean value (r=0) of the null distribution of a random distribution of alleles in space. The number of comparisons for each distance class is reported in table 5.

Fig. 1


RFAD
Manaus
Altitude (m)
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80
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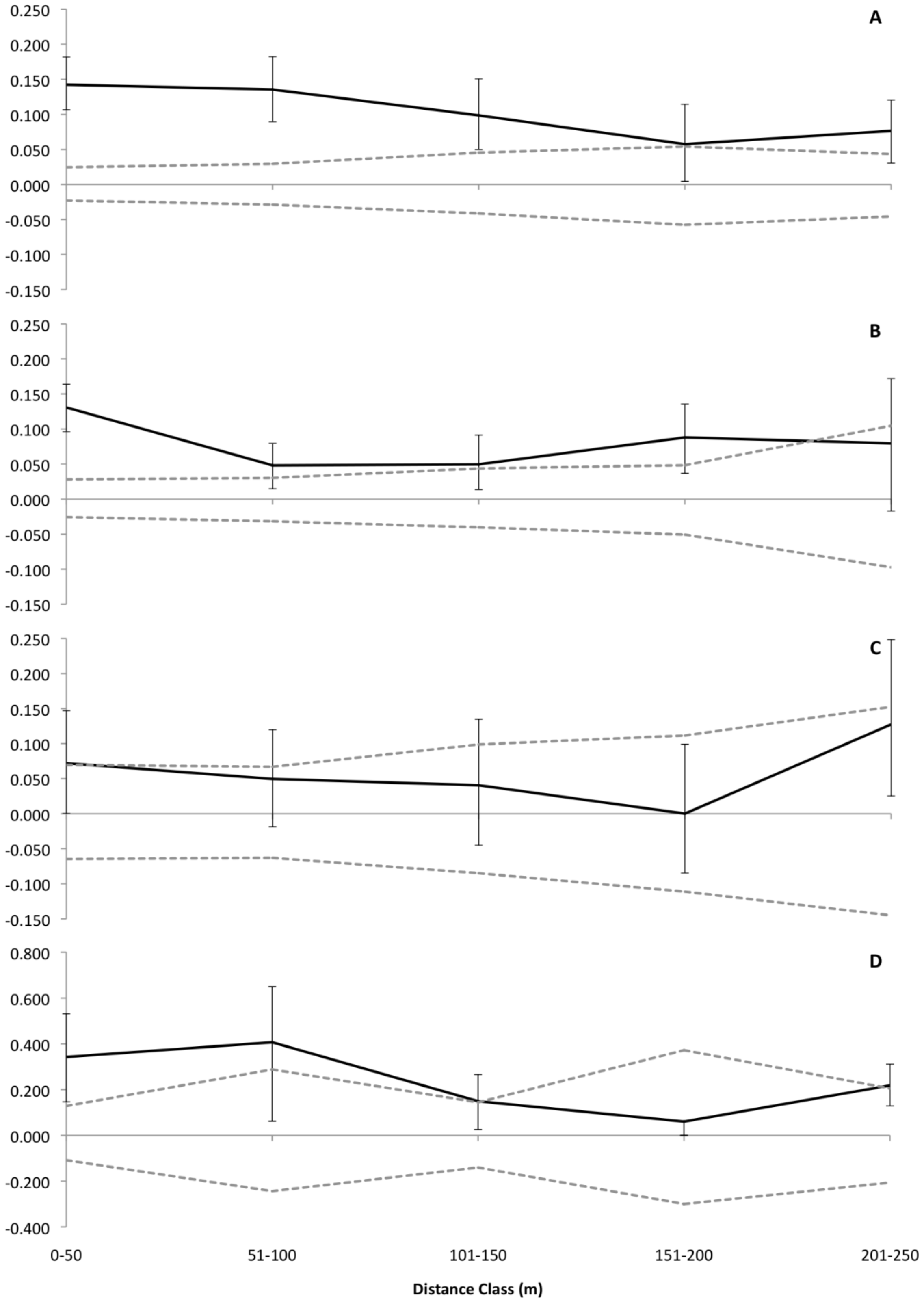
Fig. 2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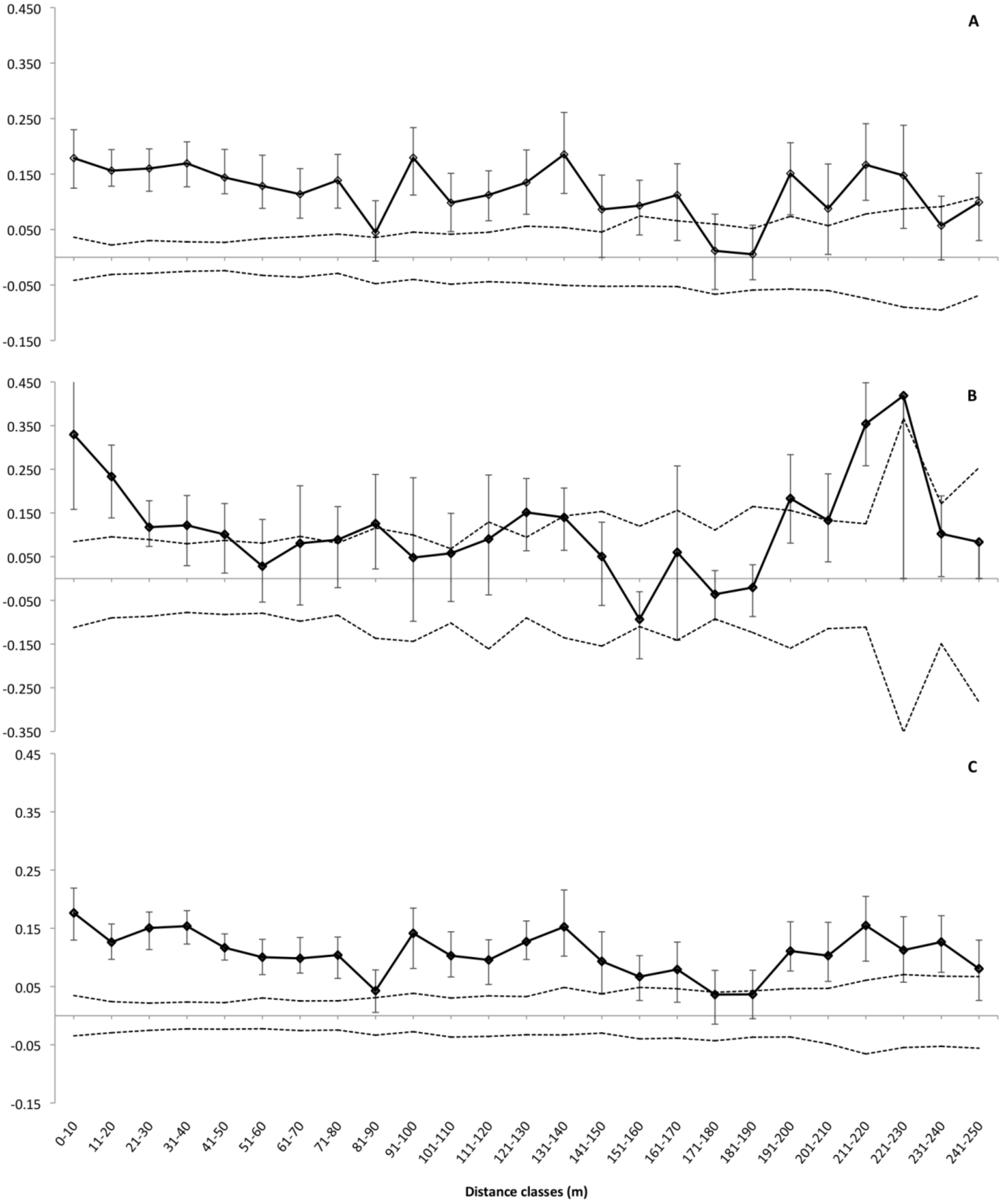
0.000
-0.050
-0.100
-0.150
0.800
0.600
0.400
0.200
0.000
-0.200
-0.400
0-50
51-100
101-150
151-200
201-250
Distance Class (m)

Fig. 3


A
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-0.050
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0.15
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-0.05
-0.15
0-10
11-20
21-30
31-40
41-50
51-60
61-70
71-80
81-90
91-100
101-110
111-120
121-130
131-140
141-150
151-160
161-170
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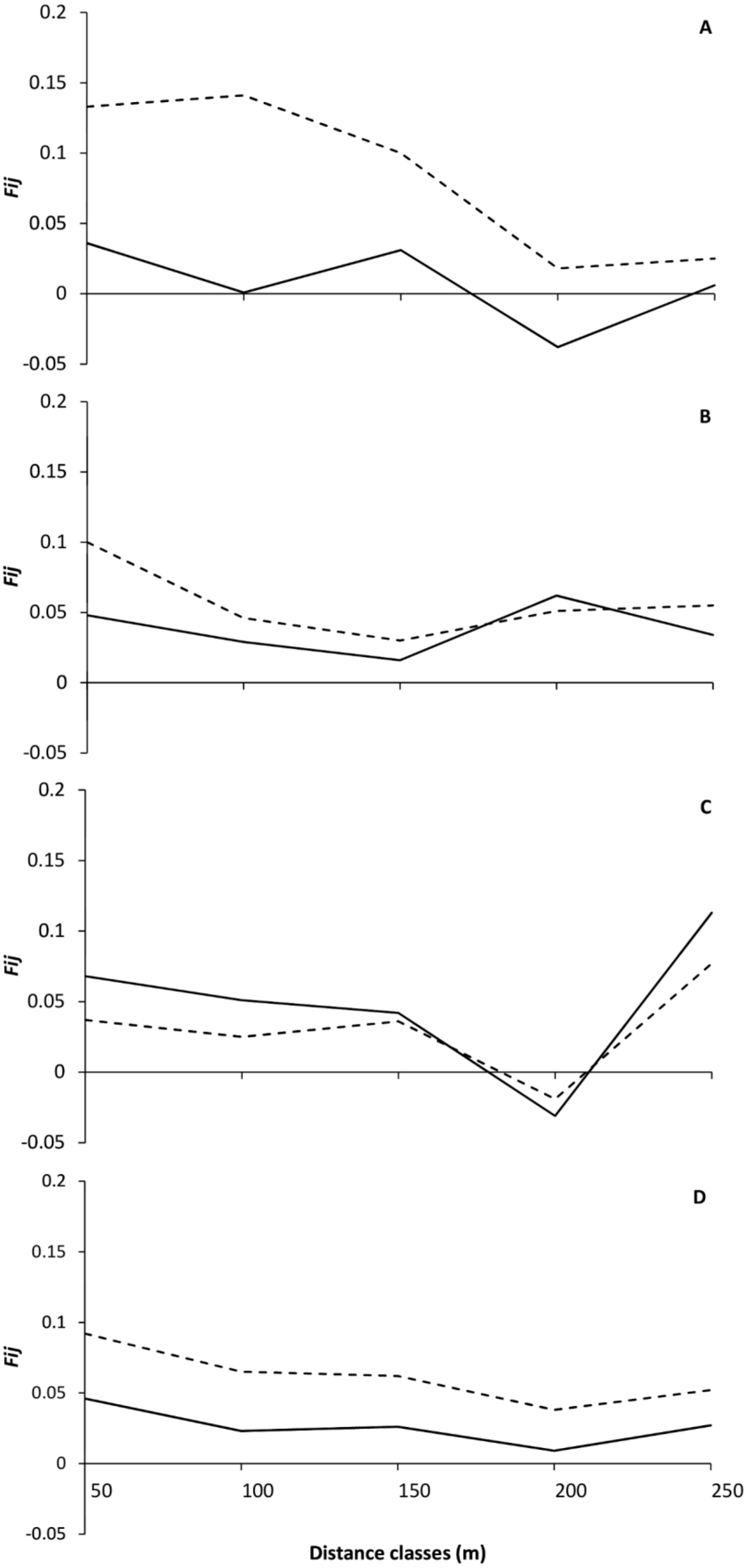
191-200
201-210
211-220
221-230
231-240
241-250
Distance classes (m)

734 **Fig. 4**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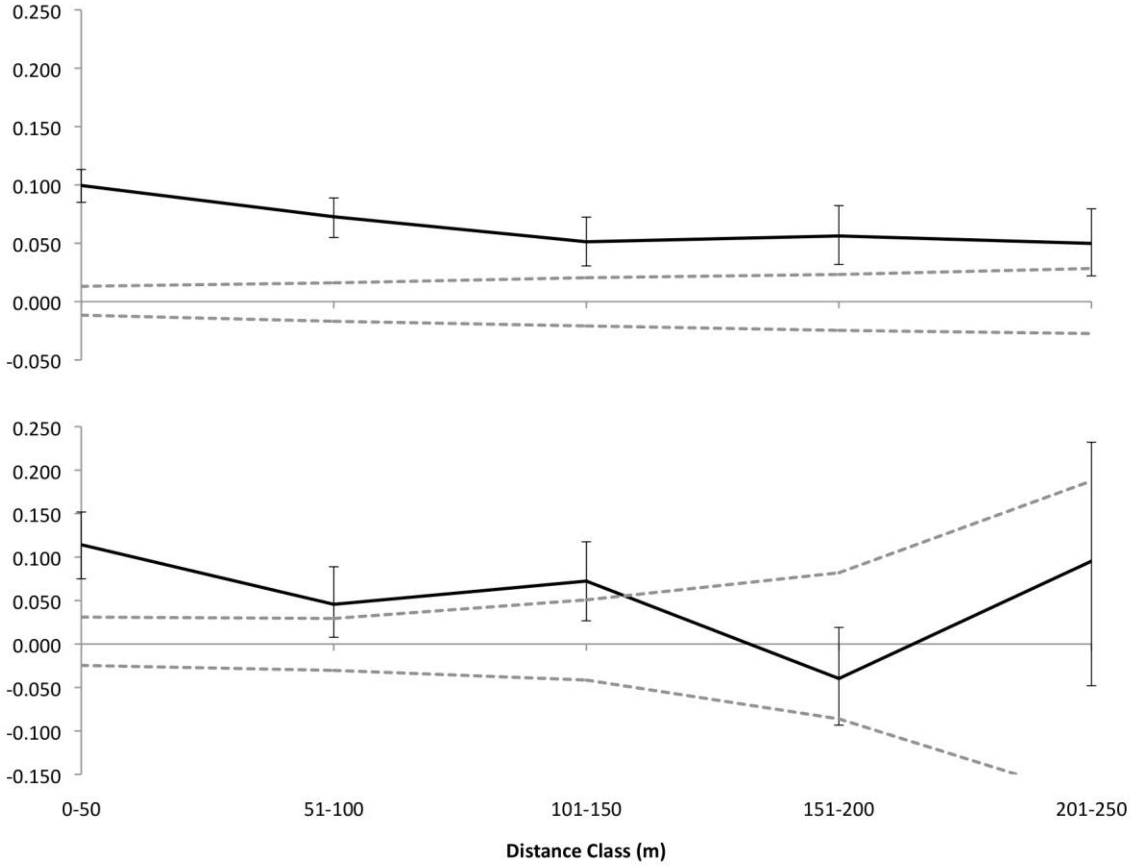
100
150
200
250
Distance classes (m)

735

Fig. 5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-0.050
-0.100
-0.150
0-50
51-100
101-150
151-200
201-250
Distance Class (m)

Table 1. Number of individuals from the four different size classes at each plot, soil category (sandy for less than 15% of clay in soil composition, and clay for more than 15% of clay) and the total number of seedlings included in the genetic analysis for each size class.

Plot	Soil type	Clay %	First-year seedlings	Young seedlings	Saplings	Juveniles & Adults	**Total**
Lo8_1500	Sandy	2.68	11	14	3	3	**31**
Lo8_0500	Sandy	2.74	16	8	4	1	**29**
Lo4_1500	Sandy	3.79	6	5	1	1	**13**
Lo3_2500	Sandy	4.99	10	11	3	3	**27**
Lo6_1500	Sandy	11.81	1	1	3	1	**6**
Lo7_0500	Sandy	13.04	7	5	7	1	**20**
Lo6_0500	Clay	32.24	5	11	3	1	**20**
Lo5_2500	Clay	42.57	12	11	6	1	**30**
Lo3_0500	Clay	62.40	9	14	10	5	**38**
Lo7_3500	Clay	72.46	22	10	5	5	**42**
Lo4_3500	Clay	77.33	25	12	2	4	**43**
Lo3_4500	Clay	78.28	5	6	4	1	**16**
Lo5_1500	Clay	81.31	7	12	3	4	**26**
Lo5_3500	Clay	83.30	6	10	3	0	**19**
Total			**142**	**130**	**57**	**31**	**360**

Table 2. Summary of genetic diversity. Sample size (n), average allele number per locus (Na), effective allele number (Ne), number of private alleles and frequencies in parenthesis (Pa), observed heterozygosity (H_o), expected heterozygosity (H_e) and fixation index (F). Standard error values are within parenthesis.

Groupings	N	Na	Ne	Pa	H_o	H_e	F
First-year sdls.	142	6.4(0.99)	3.3(0.43)	3(0.004)	0.6(0.04)	0.7(0.04)	0.1(0.04)
Young sdls.	130	6.7(0.84)	3.3(0.42)	3(0.011)	0.6(0.04)	0.7(0.04)	0.1(0.02)
Sapling sdls.	57	6.4(0.90)	3.1(0.43)	1(0.01)	0.6(0.04)	0.6(0.04)	0.0(0.05)
Adult/juvenile	30	5.3(0.75)	2.8(0.26)	1(0.017)	0.6(0.07)	0.6(0.04)	0.0(0.07)
Clay	166	6.7(0.89)	3.2(0.47)	7(0.010)	0.6(0.04)	0.6(0.04)	0.0(0.01)
Sand	74	6.1(0.67)	3.2(0.36)	3(0.028)	0.5(0.04)	0.7(0.04)	0.2(0.06)

Table 3. Tests for the significance of autocorrelation at each distance class, presenting number of pairs tested (n), autocorrelation r-values (r) and the multiclass test criteria (ω) shown for: i) first-year seedlings (<20cm); ii) young seedlings (21-40cm); iii) saplings (41-100cm); and iv) juveniles and trees (>200cm). Significance represented by * <0.05, ** <0.01; *** <0.001.

		Size class			
Distance Class (m)		First-year seedlings	Young seedlings	Saplings	Juveniles and trees
0-50	N	383	241	41	17
	R	0.14^{***}	0.13^{***}	0.07^{*}	0.34^{***}
51-100		257	194	39	3
		0.13^{***}	0.05^{***}	0.05	0.40^{**}
101-150		119	101	20	11
		0.10^{***}	0.05^{*}	0.04	0.15^{*}
151-200		69	77	14	2
		0.06^{*}	0.09^{***}	0.00	0.06
201-250		108	17	8	6
		0.08^{**}	0.08	0.13^{*}	0.29^{*}
Multiclass comparison	N	142	130	57	31
	Ω	61.10^{***}	53.11^{***}	23.70^{**}	41.42^{***}

Table 4. Comparisons of autocorrelation patterns of fine-scale genetic structure between size classes of *P. subserratum* at Ducke, Manaus, Brazil. Statistics and associated probabilities for the differences in SGS between plant size classes, for each distance class (t^2) and for the whole correlogram (ω). Significance represented by $^{+}$<0.1, * <0.05, ** <0.01; *** <0.001.

	T^2					
	Distance classes (m)					Ω-test
Size class pairs	0-50	51-100	101-150	151-200	201-250	
First-year vs. Young	0.17	7.83^{**}	2.05	0.62	0.00	18.61^{*}
First-year vs. Sapling	1.47	2.41	0.84	0.76	0.34	12.37
First-year vs. Adult/juvenile	4.80^{*}	2.56	0.37	0.00	2.17	16.19^{+}
Young vs. Sapling	1.01	0.00	0.02	1.83	0.23	6.79
Young vs. Adult/juvenile	5.44^{*}	4.27^{*}	1.42	0.03	1.71	19.87^{*}
Sapling vs. Adult/juvenile	7.02^{**}	4.15^{*}	1.22	0.12	0.57	20.48^{*}

Table 5. Tests for the significance of autocorrelation at each distance class for first-year and young seedlings at clay and sandy soils, presenting number of pairs tested (n), autocorrelation r-values (r). Multiclass test criteria (ω) for testing the hypothesis of “no autocorrelation” at any distance class. Significance represented by * <0.05, ** <0.01; *** <0.001.

Distance class (m)		Soil type	
		Clay	Sand
0-50	N	1080	369
	R	0.10^{***}	0.11^{***}
51-100		632	329
		0.07^{***}	0.05^{**}
101-150		400	149
		0.05^{***}	0.07^{**}
151-200		308	53
		0.06^{***}	-0.04
201-250		206	10
		0.05^{***}	0.09
Multiclass comparison	N	196	96
	Ω	69.08^{***}	43.85^{***}

Table 6. Comparisons of autocorrelation patterns of fine-scale genetic structure between soil types of *P. subserratum* at Ducke. Statistics and associated probabilities for the differences in SGS between seedlings up to 40cm height located at sandy and clayey soils, for each lag (t^2) and for the whole correlogram (ω). Significance represented by * <0.05, ** <0.01; *** <0.001.

Distance class (m)	Sand vs. Clay plots
0-50	T^2=0.63
51-100	T^2=1.73
101-150	T^2=0.80
151-200	T^2=7.82**
201-250	T^2=0.37
Multiclass Comparison	Ω =18.962*

Síntese

Resultados indicam que os períodos de seca são bastante negativos para o sucesso no estabelecimento de plântulas, podendo alterar a distribuição das mesmas. Plântulas respondem à falta de chuva em velocidade e intensidade diferentes de acordo com o tipo de solo onde se encontram. Em solos argilosos os efeitos do início da estação seca resultam em mortalidade de plântulas com cerca de mês de atraso. Já em plântulas que estão em solos arenosos a mortalidade aumenta imediatamente após o início da seca. Anos com seca extrema podem resultar em alta mortalidade em todo o gradiente de textura do solo, além de predispor as plântulas que sobrevivem ao período de seca a mortalidade posterior, podendo causar uma alta mortalidade caso o período chuvoso subsequente não seja pleno.

Encontramos ainda que em plantas jovens de Protium subserratum que são espacialmente próximas umas às outras tendem a se tornar menos geneticamente similares entre si a medida que a distancia entre eles aumenta, e este efeito aumenta conforme as plântulas ficam mais velhas. No entanto arvoretas e adultos apresentaram padrão inverso, com indivíduos exibindo maiores valores de similaridade genética com seus vizinhos mais próximos. Isso pode ser resultado de um balanço compensatório entre a desvantagem de estar próximo a um adulto da mesma espécie, e assim poder sofrer com ataques de patógenos e herbívoros atraídos pela alta densidade de indivíduos (e essa desvantagem é maior para plântulas do que para arvoretas e adultos), e as vantagens de se estar em um sítio ótimo para o estabelecimento até a fase adulta. Além disso encontramos que o tipo de solo modula a força dos efeitos de denso-dependencia, sendo mais fortes em plântulas estabelecidas em solos arenosos.

Observamos que algumas espécies de árvores e palmeiras são associadas a porções do gradiente de textura do solo, e em geral essa associação se dá no estágio adulto. De maneira geral as plântulas, ao contrário dos adultos, possuem distribuição irrestrita por todo o gradiente ambiental, indicando que os requerimentos dessas espécies mudam conforme os estágios ontogenéticos evoluem, levando a uma contração em sua distribuição quando na fase adulta.

Referências bibliográficas

ALVAREZ-LOAYZA, P.; TERBORGH, J. Fates of seedling carpets in an Amazonian floodplain forest: intra-cohort competition or attack by enemies? **Journal of Ecology**, v. 99, n. 4, p. 1045-1054, 30 jul 2011.

AUGSPURGER, C. K.; KELLY, C. K. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. **Oecologia**, v. 61, n. 2, p. 211-217, fev 1984.

BOHLMAN, S. A.; LAURANCE, W. F.; LAURANCE, S. G. Et al. Importance of soils, topography and geographic distance in structuring central Amazonian tree communities. **Journal of Vegetation Science**, v. 19, n. 6, p. 863-874, 29 dez 2008.

BRAVARD, S.; RIGHI, D. Geochemical differences in an Oxisol-Spodosol toposequence of Amazonia, Brazil. **Geoderma**, v. 44, p. 29-42, 1989.

BRENES-ARGUEDAS, T.; COLEY, P. D. Phenotypic variation and spatial structure of secondary chemistry in a natural population of a tropical tree species. **OIKOS**, v. 108, p. 410-420, 2005.

BRUM, H. D. **Distribuição espacial de tres espécies de palmeiras do gênero Oenocarpus ao longo de um gradiente edafo-topográfico na Amazônia Central**. [S.l.]: UNICAMP, 2011.

BUNKER, D. E.; CARSON, W. P. Drought stress and tropical forest woody seedlings: effect on community structure and composition. **Journal of Ecology**, v. 93, n. 4, p. 794-806, 15 jun 2005.

CASTILHO, C. V.; MAGNUSSON, W. E.; ARAÚJO, R. N. O. DE; et al. Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography. **Forest Ecology and Management**, v. 234, n. 1-3, p. 85-96, out 2006.

CAVENDER-BARES, J.; BAZZAZ, F. A. Changes in drought response strategies with ontogeny in Quercus rubra: implications for scaling from seedlings to mature trees. **Oecologia**, v. 124, n. 1, p. 8-18, 21 jul 2000.

CLARK, D. A.; CLARK, D. B. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. **The American Naturalist**, v. 124, n. 6, p. 769-788, 1984.

COMITA, L. S.; CONDIT, R.; HUBBELL, S. P. Developmental changes in habitat associations of tropical trees. **Journal of Ecology**, v. 95, n. 3, p. 482-492, maio 2007.

COMITA, L. S.; ENGELBRECHT, BETTINA M J. Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. **Ecology**, v. 90, n. 10, p. 2755-65, out 2009.

COMITA, L. S.; MULLER-LANDAU, H. C.; AGUILAR, S.; HUBBELL, S. P. Asymmetric Density Dependence Shapes Species Abundances in a Tropical Tree Community. **Science**, v. 329, n. 5989, p. 330-332, jun 2010.

CONNELL, J. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: BOER, P. J. DEN; GRADWELL, G. R. (Eds.). **Dynamics of populations**. Pudoc, Wageningen, Netherlands: Centre of Agricultural Publishing and Documentation, 1971. P. 298-312.

COSTA, F.; GUILLAUMET, J.; LIMA, A. Gradients within gradients: The mesoscale distribution patterns of palms in a central Amazonian forest. **Journal of Vegetation**, v. 20, p. 69-78, 2009.

COSTA, FLAVIA R. C.; MAGNUSSON, W. E.; LUIZÃO, R. C. Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. **Journal of Ecology**, v. 93, n. 5, p. 863-878, out 2005.

DALY, D. C.; FINE, P. V. A. A New Amazonian Section of Protium (Burseraceae) including both Edaphic Specialist and Generalist Taxa. Studies in Neotropical Burseraceae XVI. **Systematic Botany**, v. 36, n. 4, p. 939-949, 14 nov 2011.

DAWS, M. I.; PEARSON, T. R. H.; BURSLEM, D. F. R. P.; MULLINS, C. E.; DALLING, J. W. Effects of topographic position, leaf litter and seed size on seedling demography in a semi-deciduous tropical forest in Panamá. **Plant Ecology**, v. 179, n. 1, p. 93-105, jul 2005.

DRUCKER, DEBORA PIGNATARI; COSTA, FLÁVIA REGINA CAPELLOTTO; MAGNUSSON, W. E. How wide is the riparian zone of small streams in tropical forests? A test with terrestrial herbs. **Journal of Tropical Ecology**, v. 24, n. 01, p. 65-74, jan 2008.

ENGELBRECHT, BETTINA M J; COMITA, L. S.; CONDIT, R. Et al. Drought sensitivity shapes species distribution patterns in tropical forests. **Nature**, v. 447, n. 7140, p. 80-2, maio 2007.

ENGELBRECHT, BETTINA M J; DALLING, J. W.; PEARSON, T. R. H. Et al. Short dry spells in the wet season increase mortality of tropical pioneer seedlings. **Oecologia**, v. 148, n. 2, p. 258-69, jun 2006.

ENGELBRECHT, BETTINA M J; KURSAR, T. A.; TYREE, MELVIN T. Drought effects on seedling survival in a tropical moist forest. **Trees**, v. 19, p. 312-321, 4 mar 2005.

ENGELBRECHT, BETTINA M. J.; WRIGHT, S. JOSEPH; STEVEN, D. DE. Survival and ecophysiology of tree seedlings during El Niño drought in a tropical moist forest in Panama. **Journal of Tropical Ecology**, v. 18, n. 04, p. 569-579, 10 jul 2002.

FEARNSIDE, PHILLIP M.; LEAL FILHO, N. Soil and development in Amazonia: lessons from the Biological Dynamics of Forest Fragments Project. In: BIERREGAARD, R. O.; GASCON, C.; LOVEJOY, T. E.; MESQUITA, R. C. G. (Eds.). **Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest**. New Haven, Connecticut: Yale University Press, 2001. P. 478.

FINE, P. V. A.; MESONES, I.; COLEY, P. D. Herbivores promote habitat specialization by trees in Amazonian forests. **Science (New York, N.Y.)**, v. 305, n. 5684, p. 663-5, 30 jul 2004.

FINE, P. V. A.; MILLER, Z. J.; MESONES, I. Et al. The growth-defense trade-off and habitat specialization by plants in Amazonian forests. **Ecology**, v. 87, n. 7, p. 150–162, 2006.

FINE, P. V. A.; ZAPATA, F.; DALY, D. C. Et al. The importance of environmental heterogeneity and spatial distance in generating phylogeographic structure in edaphic specialist and generalist tree species of Protium (Burseraceae) across the Amazon Basin. **Journal of Biogeography**, p. Doi: 10.1111/j.1365-2699.2011.02645.x, 9 jan 2012.

FISHER, R. A. **Statistical methods for research workers**. 13. Ed. New York: Hafner, 1958. P. 356

FREITAS, C. G. DE. **Reprodução, distribuição e padrões de co-ocorrência em uma comunidade de palmeiras na Amazônia central: Uma abordagem teórica e experimental**. [S.l.]: Instituto Nacional de Pesquisas da Amazônia - INPA, 2012.

GENTRY, A. H. Changes in plant community diversity and floristic composition on environmental and geographical gradients. **Annals of the Missouri Botanical Garden**, v. 75, n. 1, p. 1-34, 1988.

GERHARDT, K. Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. **Forest Ecology and Management**, v. 82, n. 95, p. 33-48, abr 1996.

GIVNISH, T. On the causes of gradients in tropical tree diversity. **Journal of Ecology**, v. 87, p. 193-210, 1999.

GONZALES, E.; HAMRICK, J. L.; SMOUSE, P. E.; TRAPNELL, D. W.; PEAKALL, R. The Impact of Landscape Disturbance on Spatial Genetic Structure in the Guanacaste Tree, Enterolobium cyclocarpum (Fabaceae). **Journal of Heredity**, v. 101, n. 2, p. 133–143, 2010.

GUILLAUMET, J.-L.; KAHN, FRANCIS. Structure et dynamisme de la forêt. **Acta Amazonica, Suplemento**, v. 12, n. 3, p. 61-77, 1982.

HAMMOND, D.; BROWN, V. Disturbance, phenology and life-history characteristics: factors influencing distance/density-dependent attack on tropical seeds and seedlings. **Dynamics of tropical communities**. [S.l: s.n.], 1998. P. 51 - 78.

HAMRICK, J.; MURAWSKI, D. A.; NASON, J. D. The influence of seed dispersal mechanisms on the genetic structure of tropical tree populations. **Vegetatio**, v. 107/108, p. 281-297, 1993.

HARMS, K. E.; WRIGHT, S JOSEPH; CALDERÓN, O.; HERNÁNDEZ, A.; HERRE, E. A. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. **Nature**, v. 404, n. 6777, p. 493-5, mar 2000.

HENDERSON, A. **The Palms of the Amazon**. New York, NY: Oxford University, 1995. P. 361

HODNETT, M. G.; VENDRAME, I.; MARQUES FILHO, A. D. O.; OYAMA, M. D.; TOMASELLA, J. Soil water storage and groundwater behaviour in a catenary sequence beneath forest in central Amazonia: I. Comparisons between plateau, slope and valley floor. **Hydrology and Earth System Sciences**, v. 1, n. 2, p. 279-290, 1997.

HYATT, L. A.; ROSENBERG, M. S.; HOWARD, T. G. Et al. The distance dependence prediction of the Janzen-Connell hypothesis: a meta-analysis. **Oikos**, v. 103, n. 3, p. 590-602, dez 2003.

JANZEN, D. H. Herbivores and the Number of Tree Species in Tropical Forests. **The American Naturalist**, v. 104, n. 940, p. 501-528, 1970.

KALINOWSKI, S. T.; TAPER, M. L.; MARSHALL, T. C. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. **Molecular ecology**, v. 16, n. 5, p. 1099-106, mar 2007.

KALINOWSKI, S. T.; WAGNER, A. P.; TAPER, M. L. ML-RELATE: a computer program for maximum likelihood estimation of relatedness and relationship. **Molecular Ecology Notes**, v. 6, n. 2, p. 576-579, jun 2006.

KINUPP, V. F.; MAGNUSSON, W. E. Spatial patterns in the understorey shrub genus Psychotria in central Amazonia: effects of distance and topography. **Journal of Tropical Ecology**, v. 21, n. 4, p. 363-374, 27 jun 2005.

LANGENHEIM, J. H.; STUBBLEBINE, W. H. Variation in leaf resin composition between parent tree and progeny in Hymenaea: implications for herbivory in the humid tropics. **Biochemistry Systematics and Ecology**, v. 11, n. 2, p. 97-106, 1983.

LATOUCHE-HALLÉ, C.; RAMBOER, A.; BANDOU, E.; CARON, H.; KREMER, A. Nuclear and chloroplast genetic structure indicate fine-scale spatial dynamics in a neotropical tree population. **Heredity**, v. 91, n. 2, p. 181-90, ago 2003.

LAURANCE, S. G.; LAURANCE, W. F.; ANDRADE, A. Et al. Influence of soils and topography on Amazonian tree diversity: a landscape-scale study. **Journal of Vegetation Science**, v. 21, n. 1, p. 96-106, fev 2010.

LAURANCE, W. F.; FEARNSIDE, PHILIP M; LAURANCE, S. G. Et al. Relationship between soils and Amazon forest biomass: a landscape-scale study. **Forest Ecology and Management**, v. 118, n. 1-3, p. 127-138, jun 1999.

LEISHMAN, M. R.; WRIGHT, I. J.; MOLES, A. T.; WESTOBY, M. The Evolutionary Ecology of Seed Size. In: FENNER, M. (Ed.). **Seeds: The ecology of regeneration in plant communities**. Second ed. [S.l.]: CAB International, 2000. P. 31-58.

LLORET, F.; PEÑUELAS, J.; PRIETO, P.; LLORENS, L.; ESTIARTE, M. Plant community changes induced by experimental climate change: Seedling and adult species composition. **Perspectives in Plant Ecology, Evolution and Systematics**, v. 11, n. 1, p. 53-63, fev 2009.

LOPEZ, O. R.; KURSAR, T. A. Flood tolerance of four tropical tree species. **Tree Physiology**, v. 19, n. 14, p. 925-932, dez 1999.

LORENZI, H.; NOBLICK, L.; KAHN, F.; PEREIRA, E. **Flora Brasileira Lorenzi. (Arecaceae)**. Nova Odessa, São Paulo, Brazil: Instituto Plantarum, 2010.

MAGNUSSON, W. E.; LIMA, A. P.; LUIZÃO, R. Et al. RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. **Biota Neotropica**, v. 5, n. 2, p. 19-24, 2005.

MANGAN, S. A; SCHNITZER, S. A; HERRE, E. A; et al. Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. **Nature**, v. 466, n. 7307, p. 752-5, 5 ago 2010.

MARENGO, J. A.; LIEBMANN, B.; GRIMM, A. M. Et al. Recent developments on the South American monsoon system. **International Journal of Climatology**, v. 32, n. 1, p. 1-21, 9 jan 2012.

MARQUES FILHO, A. D. O.; FERREIRA, S. J. F.; MIRANDA, S. Á. F. Et al. Surface runoff model in the Reserva Florestal Adolpho Ducke experimental watershed. **Acta Amazonica**, v. 39, n. 4, p. 907-922, 2009.

MCDOWELL, N.; POCKMAN, W. T.; ALLEN, C. D. Et al. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? **The New phytologist**, v. 178, n. 4, p. 719-39, jan 2008.

MISIEWICZ, T. M.; BARBOSA, C. E. A.; FINE, P. V. A. Microsatellite primers for an Amazonian lowland tropical tree, Protium subserratum (Burseraceae). P. In review, [S.d.].

MOLOFSKY, J.; AUGSPURGER, C. K. The Effect of Leaf Litter on Early Seedling Establishment in a Tropical Forest. **Ecology**, v. 73, n. 1, p. 68 - 77, 1992.

MONTUFAR, R.; PINTAUD, J.-C. Variation in species composition, abundance and microhabitat preferences among western Amazonian terra firme palm communities. **Botanical Journal of the Linnean Society**, v. 151, n. 1, p. 127-140, maio 2006.

MULLER-LANDAU, H.; WRIGHT, S. Assessing recruitment limitation: concepts, methods and case-studies from a tropical forest. In: LEVEY, D. J.; SILVA, W. R.; GALETTI, M. (Eds.). **Seed Dispersal and Frugivory: Ecology, Evolution and Conservation**. São Pedro, Brazil: [s.n.], 2002. P. 35-53.

PACKER, A.; CLAY, K. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. **Nature**, v. 404, p. 278-281, 2000.

PEAKALL, ROD; SMOUSE, P. E. Genalex 6: genetic analysis in Excel. Population genetic software for teaching and research. **Molecular Ecology Notes**, v. 6, n. 1, p. 288-295, mar 2006.

PHILLIPS, O. L.; HEIJDEN, G. VAN DER; LEWIS, S. L. Et al. Drought-mortality relationships for tropical forests. **The New phytologist**, v. 187, n. 3, p. 631-46, ago 2010.

PHILLIPS, O. L.; VARGAS, P. N.; MONTEAGUDO, A. L. Et al. Habitat association among Amazonian tree species: a landscape-scale approach. **Journal of Ecology**, v. 91, n. 5, p. 757-775, out 2003.

PINTO, A. M.; RIBEIRO, R. J.; ALENCAR, J. DA C.; BARBOSA, A. P. Phenology of Simarouba amara Aubl. In the Adolpho Ducke Forest Reserve. **Acta Amazonica**, v. 35, n. 3, p. 347 - 352, 2005.

PITMAN, N. C. A.; TERBORGH, J.; SILMAN, M. Et al. A comparison of tree species diversity in two upper amazonian forests. **Ecology**, v. 83, n. 11, p. 3210-3224, 2002.

POORTER, L. Are species adapted to their regeneration niche, adult niche, or both? **The American naturalist**, v. 169, n. 4, p. 433-42, abr 2007.

RAYMOND, M.; ROUSSET, F. GENEPOP (Version 1.2): Population Genetics Software for Exact Tests and Ecumenicism. **J. Hered.**, v. 86, n. 3, p. 248-249, 1 maio 1995.

RIBEIRO, J. E. L.; HOPKINS, M. J.; VICENTINI, A. Et al. **Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônica Central**. Manaus: INPA-DFID, 1999. P. 816

SANTOS, C. A. DOS; SATYAMURTY, P.; SANTOS, E. M. DOS. Trends of extreme climatic indices for Manaus - AM region. **Acta Amazonica**, v. 42, n. 3, p. 329-336, 2012.

SCHIETTI, J.; EMILIO, T.; RENNÓ, C. D.; DRUCKER, DEBORA P; FLÁVIA, R. C. et al. Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. **Plant Ecology & Diversity**, in press, 2013.

SCHUELKE, M. An economic method for the fluorescent labeling of PCR fragments: A poor man's approach to genotyping for research and high-throughput diagnostics. **Nature**, v. 18, n. February, p. 233-234, 2000.

SCHUPP, E. W. The suitability of a site for seed dispersal is context-dependent. In: DENNIS, A.; SCHUPP, E.; GREEN, R.; WESTCOTT, D. (Eds.). **Seed dispersal: theory and its application in a changing world**. Wallingford UK: CABI, 2007. P. 445-462.

SCHURR, F. M.; STEINITZ, OFER; NATHAN, RAN. Plant fecundity and seed dispersal in spatially heterogeneous environments: models, mechanisms and estimation. **Journal of Ecology**, v. 96, p. 628-641, 2008.

SLOT, M.; POORTER, L. Diversity of Tropical Tree Seedling Responses to Drought. **Biotropica**, v. 39, n. 6, p. 683-690, nov 2007.

SMITH, D. S.; SCHWEITZER, J. A.; TURK, P. Et al. Soil-mediated local adaptation alters seedling survival and performance. **Plant and Soil**, v. 352, n. 1-2, p. 243-251, 20 set 2011.

SMOUSE, P. E.; PEAKALL, ROD. Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. **Heredity**, v. 82, p. 561-573, 1999.

SMOUSE, P. E.; PEAKALL, ROD; GONZALES, EVA. A heterogeneity test for fine-scale genetic structure. **Molecular Ecology**, v. 17, n. 14, p. 3389-3400, jul 2008.

STEINITZ, O.; TROUPIN, D.; VENDRAMIN, G. G.; NATHAN, R. Genetic evidence for a Janzen–Connell recruitment pattern in reproductive offspring of Pinus halepensis trees. **Molecular Ecology**, v. 20, n. 19, p. 4152-4164, out 2011.

SVENNING, J.-C. On the Role of Microenvironmental Heterogeneity in the Ecology and Diversification of Neotropical Rain-Forest Palms (Arecaceae). **The Botanical Review**, v. 67, n. 1, p. 1-53, 2001.

THOMAS, S. C. Reproductive allometry in Malaysian rain forest trees: Biomechanics versus optimal allocation. **Evolutionary Ecology**, v. 10, n. 5, p. 517-530, 1 set 1996.

TOLEDO, J. J. DE; MAGNUSSON, W. E.; CASTILHO, C. V.; NASCIMENTO, HENRIQUE E.M. Tree mode of death in Central Amazonia: Effects of soil and topography on tree mortality associated with storm disturbances. **Forest Ecology and Management**, v. 263, p. 253-261, jan 2012.

TOMASELLA, JAVIER; BORMA, L. S.; MARENGO, J. A. Et al. The droughts of 1996-1997 and 2004-2005 in Amazonia: hydrological response in the river main-stem. **Hydrological Processes**, v. 25, n. 8, p. 1228-1242, 15 abr 2011.

TYREE, M.; ENGELBRECHT, B.; VARGAS, G.; KURSAR, T. A. Desiccation tolerance of five tropical seedlings in Panama. Relationship to a field assessment of drought performance. **Plant Physiology**, v. 132, p. 1439-1447, 1 jul 2003.

TYREE, M. T.; COCHARD, H.; CRUIZIAT, P.; SINCLAIR, B.; AMEGLIO, T. Drought-induced leaf shedding in walnut: evidence for vulnerability segmentation. **Plant, Cell and Environment**, v. 16, n. 7, p. 879-882, set 1993.

WEBB, C. O.; PEART, D. R. Habitat associations of trees and seedlings in a Bornean rain forest. **Journal of Ecology**, v. 88, p. 464-478, 2000.

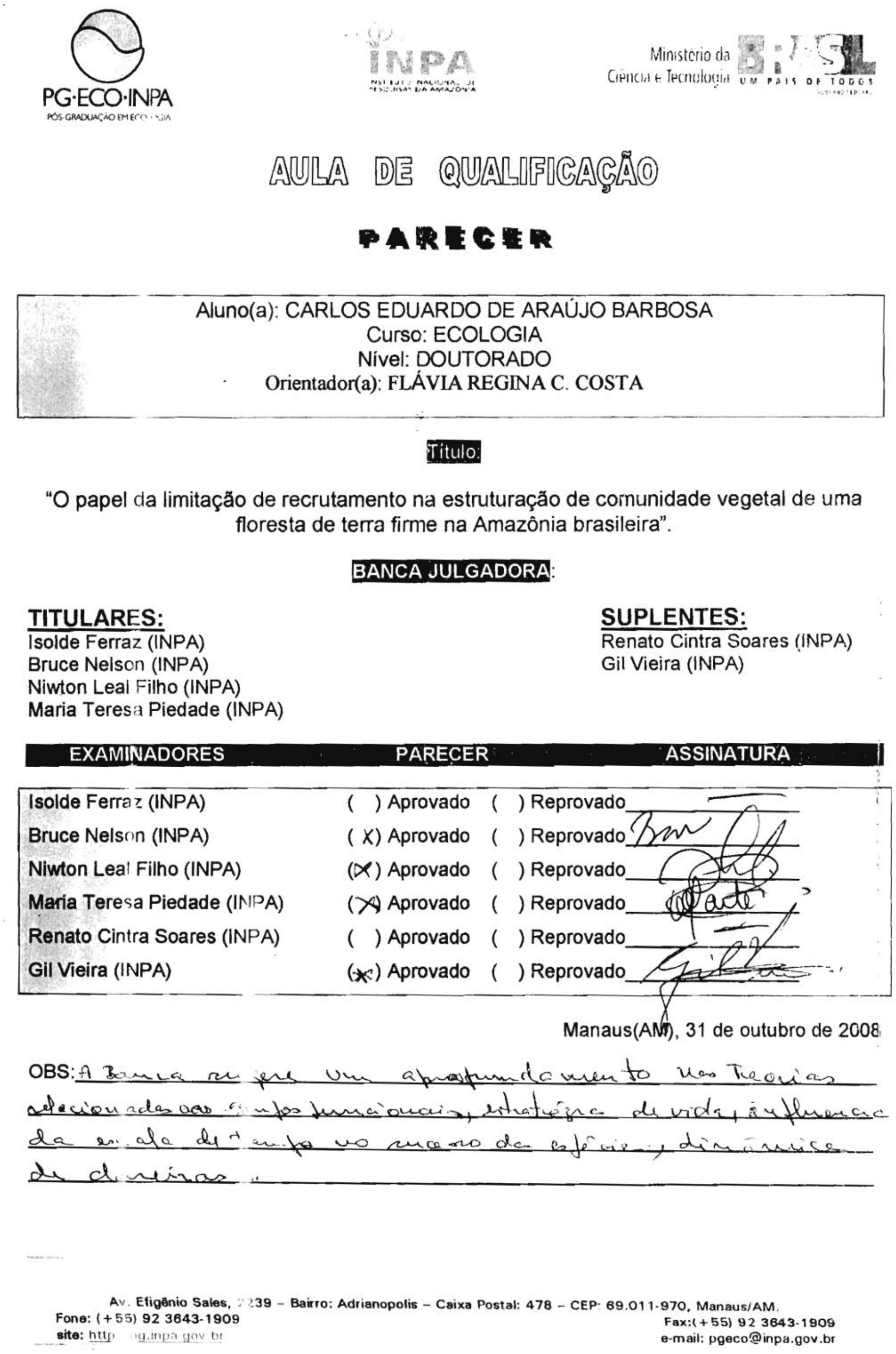
WILLIAMSON, G. B.; LAURANCE, W. F.; OLIVEIRA, A. A. Et al. Amazonian Tree Mortality during the 1997 El Nino Drought. **Conservation Biology**, v. 14, n. 5, p. 1538-1542, 18 out 2000.

WILLS, C.; HARMS, K. E.; CONDIT, R. Et al. Nonrandom processes maintain diversity in tropical forests. **Science**, v. 311, n. 5760, p. 527-31, 27 jan 2006.

WRIGHT, STUART JOSEPH. Plant diversity in tropical forests: a review of mechanisms of species coexistence. **Oecologia**, v. 130, p. 1-14, 2002.

ZHOU, H.-P.; CHEN, J. Spatial genetic structure in an understorey dioecious fig species: the roles of seed rain, seed and pollen-mediated gene flow, and local selection. **Journal of Ecology**, v. 98, n. 5, p. 1168-1177, 14 jun 2010.

Apêndice 1 – Ata da aula de qualificação



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Ministério da Ciência e Tecnologia
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AULA DE QUALIFICAÇÃO

PARECER

Aluno(a): CARLOS EDUARDO DE ARAÚJO BARBOSA
Curso: ECOLOGIA
Nível: DOUTORADO
Orientador(a): FLÁVIA REGINA C. COSTA

Título:

"O papel da limitação de recrutamento na estruturação de comunidade vegetal de uma floresta de terra firme na Amazônia brasileira".

BANCA JULGADORA:

TITULARES:	SUPLENTES:
Isolde Ferraz (INPA)	Renato Cintra Soares (INPA)
Bruce Nelson (INPA)	Gil Vieira (INPA)
Niwton Leal Filho (INPA)	
Maria Teresa Piedade (INPA)	

EXAMINADORES	PARECER		ASSINATURA
Isolde Ferraz (INPA)	( ) Aprovado	( ) Reprovado	
Bruce Nelson (INPA)	(X) Aprovado	( ) Reprovado	
Niwton Leal Filho (INPA)	(X) Aprovado	( ) Reprovado	
Maria Teresa Piedade (INPA)	(X) Aprovado	( ) Reprovado	
Renato Cintra Soares (INPA)	( ) Aprovado	( ) Reprovado	
Gil Vieira (INPA)	(X) Aprovado	( ) Reprovado	

Manaus(AM), 31 de outubro de 2008

OBS: A Banca sugere um aprofundamento nas Teorias relacionadas aos grupos funcionais, estratégia de vida, à influência da escala de tempo no sucesso das espécies, dinâmica de clareiras.

Av. Efigênio Sales, 2239 – Bairro: Adrianopolis – Caixa Postal: 478 – CEP: 69.011-970, Manaus/AM.
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AULA DE QUALIFICAÇÃO

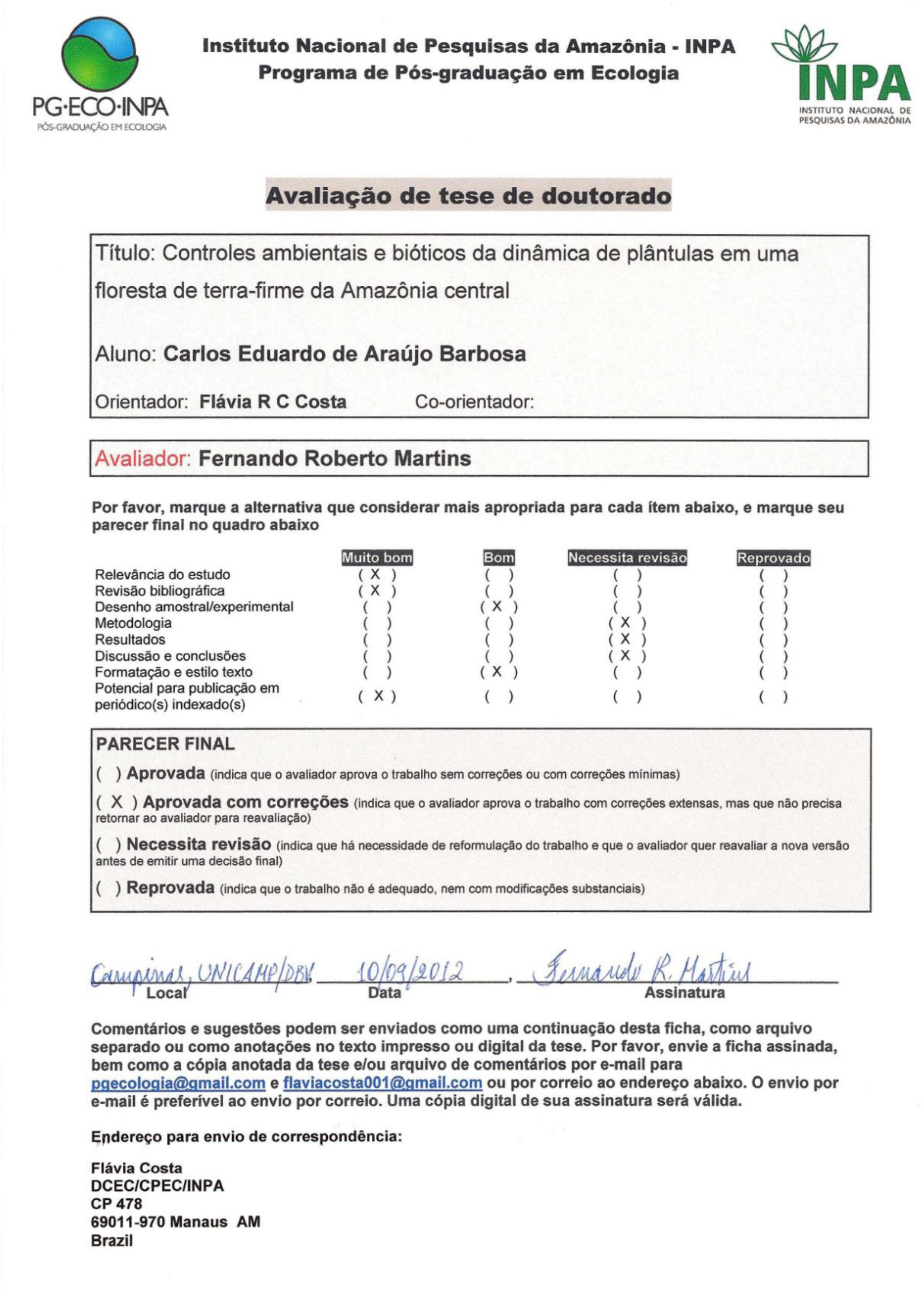
Aluno(a): CARLOS EDUARDO DE ARAÚJO BARBOSA
Curso: _ECOLOGIA__ Nível: ( ) Mestrado (X) Doutorado
Dia: _31_/_10_/_2008_
Hora: _14:30:00_ hs
Local: SALA DE AULA DO PROGRAMA DE PÓS-GRADUAÇÃO EM ENTOMOLOGIA
Orientador(a): FLÁVIA REGINA C. COSTA

LISTA DE PRESENÇA

Nº	NOME DO ALUNO	CURSO	ASSINATURA
01	Annelise R. Figueiredo	Entomo	
02	Virginia Campos Diniz Bernardes	BADPI	Virginia Campos
03	Edson Varga Lopes	Doc. - UEM	
04	Marcelo [illegible]	WCS	
05	Rafael [illegible]	TCEN	
06	Joana D'Arc de Paula	Ecologia	
07	MELISSA TEIXEIRA ROSAS	ECOLOGIA	Melissa Rosas
08	PATRÍCIA MARIA SO A DE ABREU.	ECOLOGIA	Abreu
09	BRUNO GARCIA LUIZE	ECOLOGIA	
10	FÁBIA GIORGIA ANJOS DE ANDRADE	ECOLOGIA	Fábia G Andrade
11	Maurice S. Tomio n Nelson	Ecologia	
12	Carlos Eduardo Nader	Ecologia	Carlos Nader
13	ÍTALO MARTINS DA COSTA MOUTINHO	CPEC	
14	Guilherme Gerhardt Mazzochini	Ecologia	
15	Bernardo Monteiro Flores	Ecologia	Bernardo
16	Harold Martin Wright	Ecologia	
17	Anderson Saldanha Bueno	Ecologia	Anderson
18	IGOR LUIS KAEFER	ECOLOGIA	Igor Luis Kaefer
19	Thelma Mendes Pontes	Ecologia	Pontes
20	Aleksander Had Ribeiro	CFT	
21	Cristian de Sales Dambros	Entomologia	
22	Cintia Gomes de Freitas	CPEC	Cintia G. Freitas
23	RAFAEL GONÇALVES DE OLIVEIRA	CFT	Rafael Gonçalves Oliveira
24	VICTOR LANDEIRO	ECOLOGIA	Victor L. Landeiro
25	STELA VALENTI RAUPP	CPEC	Stela Raupp

FAVOR DEVOLVER ESTA LISTA À SECRETARIA DE PÓS-GRADUAÇÃO

Apêndice 2 – Pareceres dos avaliadores do trabalho escrito



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Avaliação de tese de doutorado

Título: Controles ambientais e bióticos da dinâmica de plântulas em uma floresta de terra-firme da Amazônia central

Aluno: **Carlos Eduardo de Araújo Barbosa**

Orientador: **Flávia R C Costa** Co-orientador:

Avaliador: **Fernando Roberto Martins**

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

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

(X) **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)

Campinas, UNICAMP/DBV 10/09/2012, Fernando R. Martins
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Referee evaluation sheet for PhD thesis

Title: Environmental and biotic drivers of seedling dynamics in a terra firme forest in a Central Amazon forest

Candidate: **Carlos Eduardo de Araújo Barbosa**

Supervisor: **Flávia R C Costa** Co-supervisor:

Examiner: **Kyle Harms (**Louisiana State University)

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

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Kyle E. Harms

______LSU_______________, ___Sept. 17, 2012_______, ____
Place Date Signature

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Mailing address:

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

Referee evaluation sheet for PhD thesis

Title: Environmental and biotic drivers of seedling dynamics in a terra firme forest in a Central Amazon forest

Candidate: **Carlos Eduardo de Araújo Barbosa**

Supervisor: **Flávia R C Costa** Co-supervisor:

Examiner: **Margaret Metz**

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)	( )	( )	( )	( )

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Margaret Metz

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

Referee evaluation sheet for PhD thesis

Title: Environmental and biotic drivers of seedling dynamics in a terra firme forest in a Central Amazon forest

Candidate: **Carlos Eduardo de Araújo Barbosa**

Supervisor: **Flávia R C Costa** Co-supervisor:

Examiner: **Robin Chazdon**

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)	( )	( )	( )	( )
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FINAL EVALUATION

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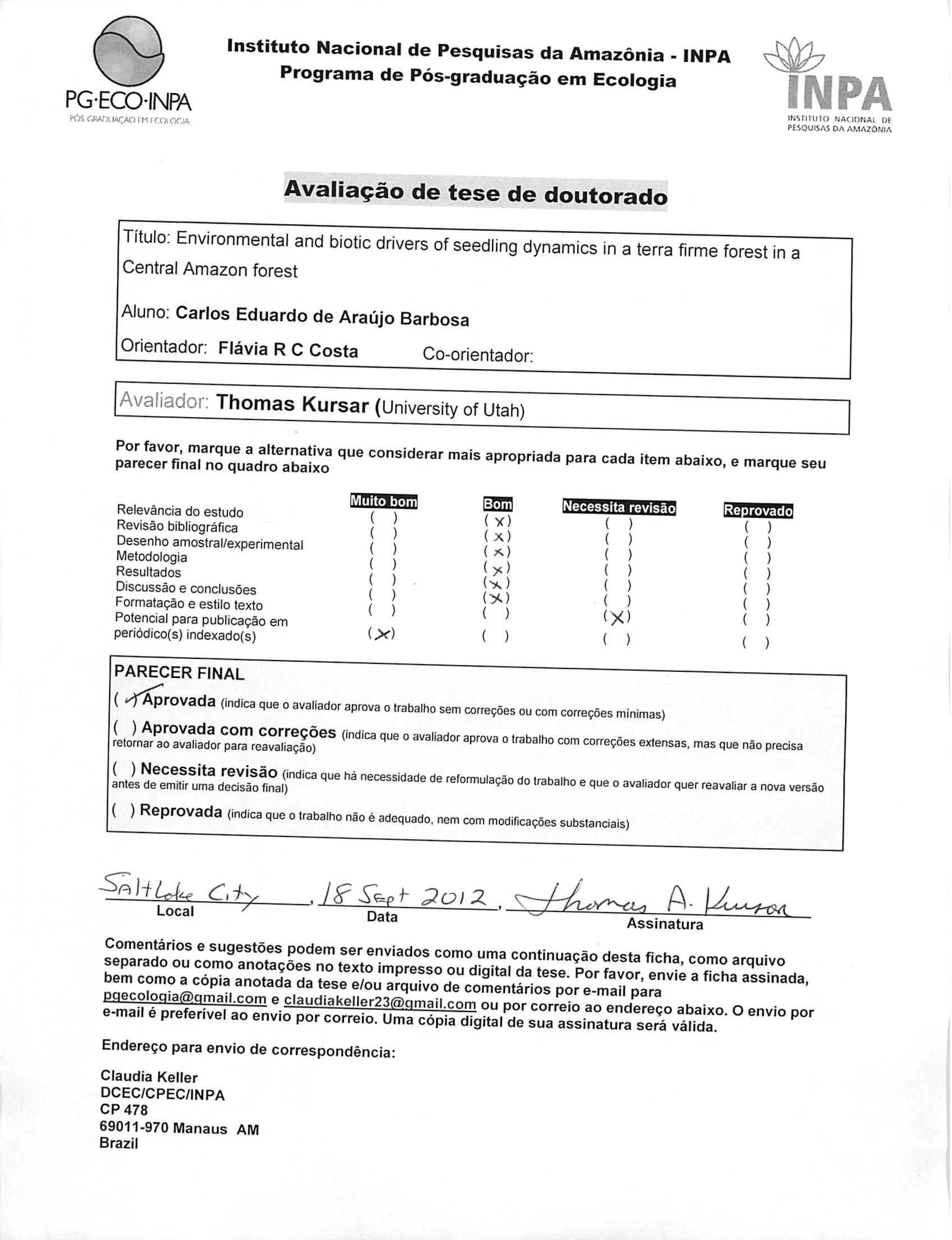

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Avaliação de tese de doutorado

Título: Environmental and biotic drivers of seedling dynamics in a terra firme forest in a Central Amazon forest

Aluno: **Carlos Eduardo de Araújo Barbosa**

Orientador: **Flávia R C Costa** Co-orientador:

Avaliador: **Thomas Kursar (**University of Utah)

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**
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Potencial para publicação em periódico(s) indexado(s)	(X)	( )	( )	( )

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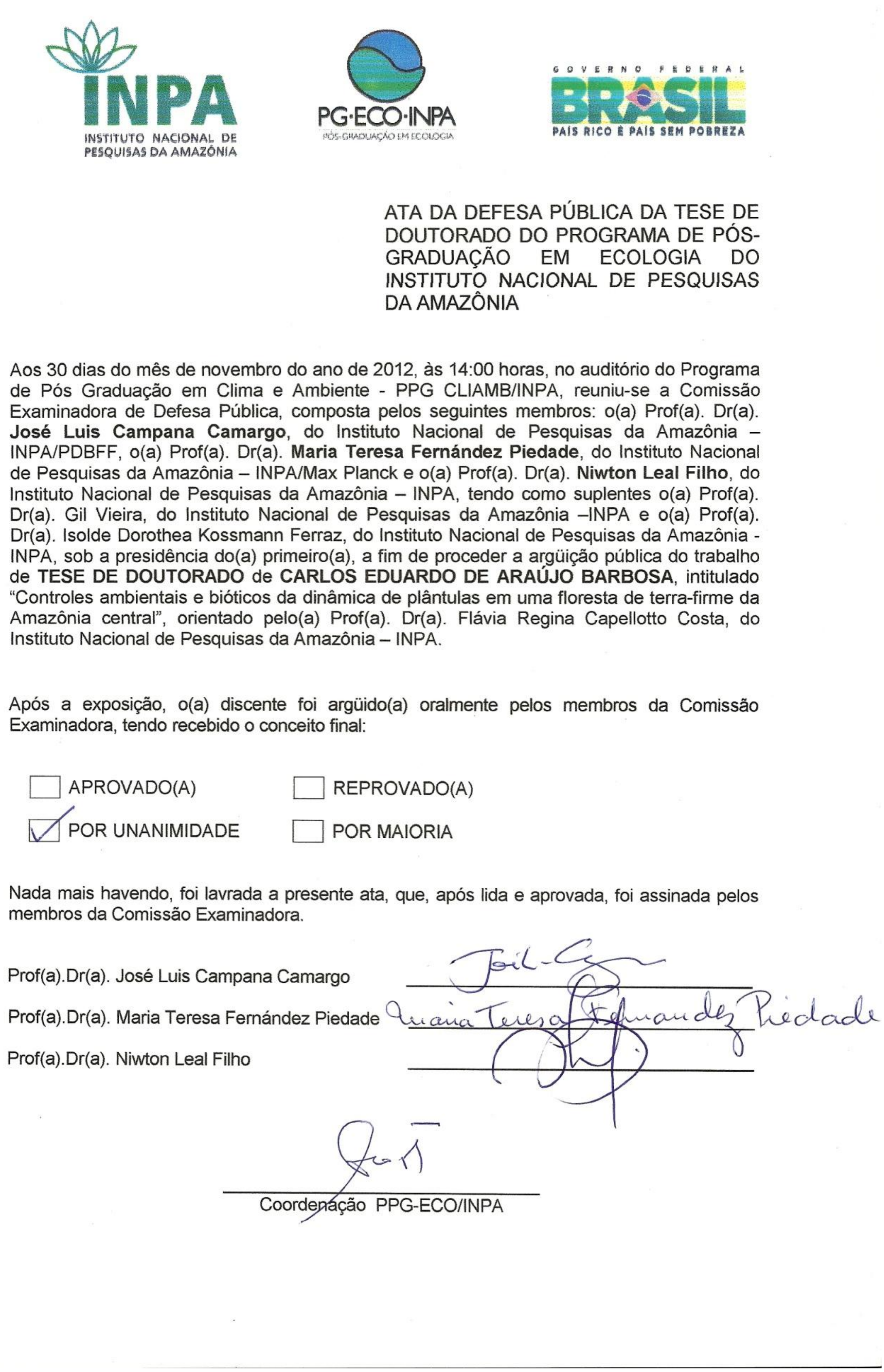
Apêndice 3 – Parecer dos avaliadores da defesa pública



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

Aos 30 dias do mês de novembro do ano de 2012, às 14:00 horas, no auditório do Programa de Pós Graduação em Clima e Ambiente - PPG CLIAMB/INPA, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **José Luis Campana Camargo**, do Instituto Nacional de Pesquisas da Amazônia – INPA/PDBFF, o(a) Prof(a). Dr(a). **Maria Teresa Fernández Piedade**, do Instituto Nacional de Pesquisas da Amazônia – INPA/Max Planck e o(a) Prof(a). Dr(a). **Niwton Leal Filho**, do Instituto Nacional de Pesquisas da Amazônia – INPA, tendo como suplentes o(a) Prof(a). Dr(a). Gil Vieira, do Instituto Nacional de Pesquisas da Amazônia –INPA e o(a) Prof(a). Dr(a). Isolde Dorothea Kossmann Ferraz, do Instituto Nacional de Pesquisas da Amazônia - INPA, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública do trabalho de **TESE DE DOUTORADO** de **CARLOS EDUARDO DE ARAÚJO BARBOSA**, intitulado "Controles ambientais e bióticos da dinâmica de plântulas em uma floresta de terra-firme da Amazônia central", orientado pelo(a) Prof(a). Dr(a). Flávia Regina Capellotto Costa, do Instituto Nacional de Pesquisas da Amazônia – INPA.

Após a exposição, o(a) discente foi argüido(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). José Luis Campana Camargo ____________________

Prof(a).Dr(a). Maria Teresa Fernández Piedade Maria Teresa Fernandez Piedade

Prof(a).Dr(a). Niwton Leal Filho ____________________

____
Coordenação PPG-ECO/INPA