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

Interações entre floresta, chuva e solo em áreas com lençol freático superficial na Amazônia Central

Juliana Schietti de Almeida

Manaus, Amazonas
Outubro, 2013

Juliana Schietti de Almeida

Interações entre floresta, chuva e solo em áreas com lençol freático superficial na Amazônia Central

Orientador: Dr. William E. Magnusson

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

Manaus, Amazonas
Outubro, 2013

Banca examinadora

Avaliador	Instituição de origem	Parecer
Christopher Baraloto	Institut National de la Rechercce Agronomique - INRA	Aprovada
Maria Teresa Fernandez Piedade	Instituto Nacional de Pesquisas da Amazônia - INPA	Aprovada
Niro Higuchi	Instituto Nacional de Pesquisas da Amazônia - INPA	Aprovada
Philip M. Fearnside	Instituto Nacional de Pesquisas da Amazônia - INPA	Aprovada
José Júlio de Toledo	Universidade Estadual de Roraima - UERR	Aprovada

S332 Schietti de Almeida, Juliana
Interações entre floresta, chuva e solo em áreas com lençol freático superficial na Amazônia Central / Juliana Schietti de Almeida. --- Manaus : [s.n.], 2014.
x, 147 f. : il. color.

Tese (Doutorado) --- INPA, Manaus, 2014.
Orientador : William E. Magnusson.
Área de concentração : Ecologia.

1. Estrutura da floresta. 2. Gradientes ambientais. 3. Água no solo I. Título.

CDD 634.9

Sinopse

Este estudo foi realizado em duas áreas na Amazônia Central, a Reserva Ducke ao norte de Manaus e o interflúvio Purus-Madeira, ao sul do Rio Amazonas. Ambas áreas apresentam lençol freático superficial mas propriedades físico-químicas do solo distintas e o regime de precipitação varia entre as áreas. Investigou-se a importância da profundidade do lençol freático para as variações de composição de espécies de plantas de diferentes formas de vida. A estrutura da floresta, foi caracterizadas pela densidade de caules, massa média das árvores e altura do dossel. Foi avaliada a relação desses componentes estruturais com fatores ambientais que interagem entre si, como a textura do solo, fertilidade, profundidade do lençol freático e chuva. Além disso, foi investigada a contribuição dos fatores estruturais (densidade de caules e massa média individual) e de gradientes ambientais para as variações nos estoques de biomassa da floresta.

Palavras-chave: Diversidade florística, estrutura da floresta, biomassa, floresta tropical, gradientes ambientais, água no solo.

Agradecimentos

Agradeço meu orientador Bill Magnusson por ter sido sempre presente e participativo. Obrigada por dedicar seu tempo e por revisar meus textos em tempo recorde!

Meu agradecimento especial aos que também me orientaram em algum período de desenvolvimento da tese: Flávia R.C. Costa, colaboradora no trabalho e amiga, acompanhou de perto todas as fases da tese; Jochen Schöngart que abriu as portas de seu laboratório, me deu todo apoio necessário e me apresentou o mundo da dendroecologia; e Javier Tomasella que esteve desde o início na elaboração e implementação da parte hidrológica do Projeto, sua participação foi muito importante para o desenvolvimento desse estudo interdisciplinar.

Agradeço Scott Saleska por ter proporcionado a oportunidade trabalhar com LiDAR e por me receber em seu laboratório na Universidade do Arizona, durante o doutorado sanduíche. Ao Scott Stark pela grande ajuda me ensinando diversos passos de programação em R e por ter disponibilizado seus códigos para análises dos dados de LiDAR. Agradeço também ao Bruce Nelson que gentilmente me cedeu um espaço em seu escritório, onde trabalhei nos primeiros meses da tese.

Tantas pessoas participaram do trabalho de campo que seria difícil listar todos os nomes sem deixar alguém de fora. Agradeço imensamente a todos os assistentes que se dispuseram a medir árvores, carregar sensores, coletar solo, instalar poços, monitorar o lençol freático e principalmente a trabalhar em equipe. Algumas pessoas estiveram mais presentes e a esses tenho uma gratidão especial: Naza little (Nazaré Araújo), Kelly Sarmento, Paola Bleicker, alunos egressos do IFAM, Jonas Cícero de Oliveira, Marcelo do Amaral Jacaúna, Thainá Khights, Fabio Soares, Celinho baixista, o pessoal do Castanho e arredores: Dorival, Zé Roberto, Joãozinho, Davison, Manoel, Davi, Diniz e Luciano Pajú. Agradeço também a Carmosina por ajudar no treinamento da primeira equipe de medição de vegetação e a Cida Freitas e a toda equipe de infra-estrutura do PPBio que batalhou para dar suporte a este e a muitos outros trabalhos ao longo da BR-319.

Agradeço às pessoas incrivelmente solidárias que vivem ao longo da BR-319 e que nos acolheram inúmeras vezes em suas casas ou que nos ajudaram a desatolar carros e reconstruir pontes para que pudéssemos seguir viagem: Dona Maria e Seu João, Dona Tereza e Seu Zé da Coroa, Dona Mocinha, Dona Irene e muito outros.

Agradeço a contribuição inestimável de Andresa Viana, que desembaraça todos os problemas burocráticos e financeiros para o bom andamento do trabalho e não perde o bom humor. Obrigada amiguinha!

Thaise Emilio foi a parceira de empreitada! Aprendemos muito nesses anos de trabalho juntas. Difícil resumir tantas experiências conjuntas de como cavar um, ou 100, poços, tirar espinho de palmeira, fugir do ataque das cabas, cuidar da equipe na hora do aperto, trabalhar em colaboração com inúmeras pessoas e manter a tranquilidade. Zeca Purri também merece um agradecimento especial; sua contribuição foi fundamental. Agradeço também ao Demétrius Martins e Bruno Cintra pelo aprendizado de trabalho em colaboração.

Aos "parentes" da familia vegetal: Pri Souza, Carol Levis, Flávia Santana, Cadu Barbosa, Nando Figueiredo, Cintia Freitas, Fê Coelho e Karina Melgaço e às meninas do laboratório de Dendroecologia: Sejana Arteaga e Eliane Pernambuco. Aos bolsistas Rafael Stern e Angélica Nunes, que contribuíram muito para o andamento do trabalho. Obrigada também ao Celso, técnico do Max-Planck, pelo apoio com o material para as coletas de amostras de madeira.

Aos amigos pelo bons momentos que fizerem esses quatro anos serem mais divertidos: Mano Borges, Bogão, Tito, Amunda Mortati, Thiago André, Catá Jakovac, Dé Junqueira, Zeca Purri, Flávia Pezinho, Saci, Zé Luis Camargo, Carlos André, Veronika Leitold, Mimi Kurtin e Kenia Weidmann. E um agradecimento especial a minha amiga querida, também fornecedora de peconhas, acessórios e orientações para coletas botânicas nas horas de desespero, Ana Andrade. Muito bom saber que posso contar contigo, espero sempre poder retribuir sua amizade e carinho.

Minha família sempre me deu apoio incondicional no trabalho e na vida. Nem tenho como agradecê-los meus queridos pai Marcio, mãe Dódoia, irmão Tiago, tias Gláucia e Celinha e avós que já se foram. Também agradeço Suely Beggiato, Luiz Baccaro, Isa e Gabi pelo acolhimento.

Por último (e mais importante), agradeço meu marido Fabricio Baccaro, companheiro tão querido que faz minha vida mais alegre e tranquila. Obrigada pelo apoio e por nossas conversas sobre ciência que contribuíram imensamente para esse trabalho (e para outros que ainda virão)!

Resumo

A relação entre distribuição de espécies, estrutura da floresta e gradientes ambientais é um tema central em ecologia. No entanto, as relações de funcionamento da floresta considerando a grande variabilidade ambiental na Amazônia ainda são pouco conhecidas, especialmente em áreas onde o lençol freático é superficial. Nesta tese, investiguei o papel de gradientes de chuva, profundidade do lençol freático e características físicas do solo nas variações da composição florística, estrutura da floresta e estoques de biomassa na Amazônia Central. Avaliei se um novo indicador de profundidade de lençol freático obtido de sensoriamento remoto pode ser usado como preditor de variações na composição florística de diferentes formas de vida (capítulo 1), como componentes estruturais da floresta (densidade de indivíduos e massa média individual) e estoques de biomassa são influenciados por gradientes de precipitação e características do solo (capítulo 2), e se gradientes ambientais ligados ao suprimento de água no solo são fatores limitantes para a altura do dossel (capítulo 3). O primeiro estudo foi realizado na Reserva Ducke ao norte de Manaus, onde o relevo é dissecado e as áreas próximas dos cursos d'água tem lençol freático raso e são arenosas. Os estudos relatados nos capítulos 2 e 3 foram desenvolvidos ao longo do interflúvio Purus-Madeira, onde o relevo é relativamente plano, o lençol freático é raso, mesmo distante dos cursos d'água, e o solo é predominantemente siltoso. A composição de espécies de plantas teve uma forte relação com o índice de profundidade do lençol freático na floresta de terra-firme ao norte de Manaus, sugerindo que o acesso ao lençol freático tem um papel importante para o estabelecimento de espécies. As florestas em áreas com lençol freático raso apresentaram maior variação na composição de espécies. Esse padrão pode estar associado ao maior dinamismo da vegetação nessas áreas, onde o volume de solo aerado para o desenvolvimento de raízes é limitado, a ancoragem é baixa devido ao solo arenoso e os indivíduos estão mais suscetíveis a morte por desenraizamento. As áreas onde há maior variação na composição de espécies podem se estender por centenas de metros de distância do curso d'água e não são protegidas pelos critérios atuais da legislação ambiental brasileira, que leva em conta distâncias horizontais da drenagem (30 m para o caso do porte dos cursos d'água estudados). Os níveis de flutuação do lençol freático estão correlacionados com as características físicas do solo, como profundidade efetiva para o desenvolvimento de raízes, e condições anóxicas. Solos mais rasos e impeditivos sustentam florestas com indivíduos de menor massa e em maior adensamento, o que suporta a hipótese de que solos mais restritivos estão associados a florestas mais dinâmicas. Solos rasos, siltosos e com lençol freático superficial também estiveram associados a florestas com dossel mais baixo, sugerindo que o excesso de água e o espaço reduzido para o desenvolvimento de raízes são limitantes para o crescimento da floresta. O efeito positivo de estações secas mais prolongadas sobre a massa média dos indivíduos também indica limitações ao acúmulo de biomassa relacionadas ao excesso de água em áreas de lençol freático superficial. Os resultados dos três estudos sugerem que florestas sobre lençol freático raso e solos com características físicas impeditivas têm estrutura mais raquítica e provavelmente são mais dinâmicas e com maior variação na composição de espécies. A limitação de crescimento por excesso de água no solo parece ser um mecanismo subestimado para entender a estrutura e funcionamento das florestas sobre lençol freático superficial na Amazônia Central, e isso implica que as expectativas atuais de repostas da floresta à mudanças climáticas devem ser revistas.

On the interactions between forests, rainfall and soil in shallow water-table areas in Central Amazonia

Abstract

A central issue in ecology is the relationship between environmental gradients, species composition and forest structure. However, there is large environmental variability in Amazonia and these relationships have been little studied, especially in areas where the water table is shallow. I investigated the role of rainfall, water-table depth and soil physical properties on the variation in floristic composition, forest structure and biomass stocks in Central Amazonia. I evaluated if a new proxy for water table depth derived from remote sensing can be used as a predictor of floristic composition in different life forms (chapter 1), how forest structure components (stem density and the average individual mass) and biomass stocks are affected by rainfall gradients and soil properties (chapter 2), and if environmental gradients linked to soil water supply are limiting factors to canopy height (chapter 3). The first study was conducted in Reserva Ducke, north of Manaus, where the relief is dissected and the areas close to the streams have shallow water tables and sandy soils. The studies presented in chapters 2 and 3 were conducted in the Purus-Madeira interfluve, where the relief is relatively flat, the soil is predominately silty, and the water table is shallow even far from streams. Plant-species composition was strongly related to the proxy for water-table depth in the terra-firme forest north of Manaus, suggesting that water-table access differentially affects species establishment. Forests over shallow water tables had larger variation in species composition. This pattern may be associated with more dynamic forests in areas where the aerated soil volume for root development is limited by the shallow water table, anchorage is low due to sandy soils and individuals are more susceptible to death by uprooting. The areas where with most variation in species composition extend to hundreds of meters from the streams. Brazilian environmental law does not fully protect these areas of shallow water table because it considers only short horizontal distances from streams (30 m for small streams). Water table fluctuations are correlated with soil physical properties, such as the effective depth to which roots develop, and anoxic conditions. Shallower and more impeditive soils sustained forests with lower mean individual mass and higher stem density, supporting the hypothesis of a more dynamic forest over more restrictive soils. Shallow silty

soils and superficial water table were also associated with lower canopy heights, suggesting that water excess and reduced space for root development limit forest growth. The positive effect of longer dry seasons on mean individual mass also indicates limitations to biomass accumulation related to water excess in areas of shallow water table. The results of the three studies suggest that forests over shallow water table and impeditive soils to root development are more rachitic in structure, and probably are more dynamic, with larger variation in species composition. Growth limitation by water excess seems to be an underappreciated mechanism affecting the structure and functioning of forests over shallow water table in central Amazonia, implying that current expectations of forest responses to droughts should be reconsidered.

Sumário

BANCA EXAMINADORA III

AGRADECIMENTOS V

RESUMO VII

ABSTRACT IX

LISTA DE TABELAS 14

LISTA DE FIGURAS 17

INTRODUÇÃO GERAL 21

OBJETIVO GERAL 24

- OBJETIVOS ESPECÍFICOS 24

CAPÍTULO 1 25

VERTICAL DISTANCE FROM DRAINAGE DRIVES FLORISTIC COMPOSITION CHANGES IN AN AMAZONIAN RAINFOREST 26

- ABSTRACT 27
- INTRODUCTION 28
- MATERIALS AND METHODS 30
  - *Study area* 30
  - *Floristic datasets* 31
  - *Height above the nearest drainage - HAND* 32
  - *Horizontal distance from nearest drainage – HDND* 33
  - *Height above sea level – HASL* 34
  - *Data analyses* 34
- RESULTS 36
  - *Patterns of floristic composition changes* 36
  - *Predictors of floristic-composition changes: HAND versus HASL and HDND* 36
- DISCUSSION 37
  - *Changes in floristic composition along the HAND gradient* 37
  - *Plant life forms* 39
  - *HAND versus HASL and HDND* 40
  - *Implications for conservation strategies and climate change* 41
- CONCLUSIONS 42
- ACKNOWLEDGMENTS 43
- NOTES ON CONTRIBUTORS 43

References 44
Supplementary online material – Plant Ecology & Diversity 59

CAPÍTULO 2 61

LINKING FOREST STRUCTURE AND STAND BIOMASS ALONG NATURAL DISTURBANCE GRADIENTS IN CENTRAL AMAZONIA 62

Summary 63
Introduction 64
Methods 66
Study area 66
Environmental gradients 67
Data analyses 68
Results 69
Forest-structure components and stand biomass 70
Environmental-gradient effects 70
Discussion 71
Relationships between stand-biomass distribution and forest-structure components 72
Seasonality and natural disturbances 72
Acknowledgements 75
References 76
Supporting Information 90

CAPÍTULO 3 97

ENVIRONMENTAL LIMITS TO CANOPY HEIGHT IN CENTRAL AMAZONIA 98

Summary 99
Introduction 100
Methods 101
Study area 101
Canopy height and diameter measurements 102
Species composition 103
Disturbance and environmental gradients 103
Data analysis 104
Results 105
Canopy height along the Purus-Madeira interfluve 105
Canopy height along environmental gradients 105
Discussion 106

Canopy height in forests of the Purus-Madeira interfluve ... *106*
Environmental limits to canopy height ... *107*
Intraspecific variation in tree height ... *109*
Implications of shallow water table for the functioning of the amazon forest ... *109*
REFERENCES ... 111
SUPPLEMENTARY INFORMATION ... 123

SÍNTESE ... 124

REFERÊNCIAS BIBLIOGRÁFICAS ... 127

APÊNDICE 1. PARECER DA AULA DE QUALIFICAÇÃO ... 143

APÊNDICE 2. ATA DE DEFESA PÚBLICA ... 144

Lista de Tabelas

Capitulo 1- Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest

Table 1. Numbers of species and sampling design for the six life forms sampled in the permanent plots of the Reserva Ducke, Manaus, Brazil. *D*, diameter measured at 130 cm from the rooting point. H, height from the ground. 53

Table 2. Percent of variance captured by quantitative and qualitative Non-Metric Multidimensional Scaling (NMDS) ordination in one axis for six life forms individually and all six combined (All life forms), based on data from 72 permanent forest plots, Reserva Ducke, Manaus, Barzil. Probabilities (*P*), r^2_{adj} (r^2) and parameters of the exponential decay model (equation 1) between life form/all life forms species composition, given by the NMDS axis, and the three predictors: height above the nearest drainage (HAND), horizontal distance from nearest drainage (HDND) and Shuttle Radar Topography Mission – height above sea level (SRTM-HASL). Delta Akaike Information Criterion (ΔAIC) values for a subset of 18 plots are presented for comparisons among models of plant composition for the six life forms. ΔAIC was calculated in relation to tree species composition versus HAND model, which had the most support. 54

Table S1. Candidate models for prediction of composition changes in five plant life history types and all species combined (Flora). Three predictors: height above the nearest drainage (HAND), horizontal distance from drainage (HDND) and height above sea level (HASL) were tested in simple and multiple linear regressions. All variables were log10 transformed to improve normality. Minimal adequate model was selected based on Akaike Information Criterion (AIC). Models with Δ AIC < 2 (in bold) support no differences between models. HDND was calculated using flow direction paths between plots and drainage and HASL was derived from Shuttle Radar Topography Mission SRTM) data. 59

Capítulo 2 - Linking forest structure and stand biomass along natural disturbance gradients in central Amazonia

Table 1. Forest structure properties and environmental gradients along the Purus-Madeira interfluve, in central-south Amazonia. 82

Table 2. Results of the linear mixed-effect models (LMM) for the density of stems, average individual mass and stand biomass of individuals with dbh ≥ 1 cm in function of dry season length, available phosphorus (available P) and soil physical restrictions represented by index 1, (fixed effects). Sites were considered as random effect in all models. The Akaike information criterion values (AIC) and the marginal (R^2_{marg}) and conditional (R^2_{cond}) coefficients of determination (R^2) are presented. Marginal R^2 shows the models adjusted only considering fixed effects and conditional R^2 correspond to the full model, including the random effect. The relative contribution of predictors is given by the standardized coefficients of the LMMs. Probability for each predictor is shown in parentheses. Standardized coefficients in bold have $p < 0.05$. 83

Table S1. Scaling exponent (*a*), allometric constant (*b*), number of measured trees (n trees) and the coefficient of determination (r^2) for the Height-Diameter (H-D) allometric models adjusted for each of the 11 sites along the Purus-Madeira interfluve in central Amazonia. H-D models were adjusted using power functions, $H = b * D^a$. 90

Table S2. Components of the soil physical restriction index from (Quesada *et al.* 2010). The summation of all components gives the index 1. 91

Table S3. Comparison of two candidate models for explaining variations in stand biomass ($Biomass_{st}$), one including available phosphorus (P_a) and the other including total phosphorus (P_{tot}) pool. Both models included site as a random factor. The model with available phosphorus had the best fit based on Akaike Information Criteria, AIC, values (best fitting-model has the lowest AIC value). Delta AIC gives the difference in relation to the AIC value of the best fitting-model and values higher than 2 have low support (Burnham & Anderson 2004). 92

Table S4. Results of the linear mixed-effect models (LMM) for the density of stems, average individual mass and stand biomass of individuals with dbh ≥ 10 cm in function of dry season length, available phosphorus (available P) and soil physical restrictions represented by index 1, (fixed effects). Sites were considered as random effect in all models. The Akaike information criterion values (AIC) and the marginal (R^2_{marg}) and conditional (R^2_{cond}) coefficients of determination (R^2) are presented. Marginal R^2 shows the models adjusted only considering fixed effects and conditional R^2 correspond to the full model, including the random effect. The relative contribution of predictors is given by the standardized coefficients of the LMMs. Probability for each predictor is shown in parentheses. Standardized coefficients in bold have $p < 0.05$. 93

Capítulo 3 - Environmental limits to canopy height in Central Amazonia

Table 1. Mean values and the range of variation (minimum – maximum) of canopy-height metrics derived from ground LiDAR and environmental gradients evaluated as drivers of canopy height in the Purus-Madeira interfluve, in Central Amazonia. Median value is presented for soil depth score. 114

Table 02. Results of linear mixed-effect models (LMM) relating mean canopy height and maximum canopy height to species composition changes (summarized by a NMDS ordination) as a function of water-table level, canopy tree-species composition, canopy-tree mean diameter, soil-depth score, silt fraction and annual precipitation (fixed effects). Site was considered as a random effect in all models. Marginal R^2 (R^2_{marg}) shows the models adjusted only considering fixed effects, and conditional R^2 (R^2_{cond}) corresponds to the full model, including the random effect (site effect). The relative contribution of predictors is given by the standardized coefficients of the LMMs. Probability of independent contributions for each predictor is shown in parentheses. 115

Table S1. Results of linear mixed-effect models (LMM) relating mean canopy height and maximum canopy height, derived from portable ground LiDAR, to the frequency of storms per year, canopy trees species composition (given by NMDS axis) and canopy trees mean diameter (fixed effects). Site was considered as a random effect in all models. The marginal (R^2_{marg}) and conditional (R^2_{cond}) coefficients of determination (R^2) are presented. Marginal R^2 shows the models adjusted only considering fixed effects and conditional R^2 corresponds to the full model, including the random effect (site effect). The relative contribution of predictors is given by the standardized coefficients of the LMMs. Probability of independent contributions for each predictor is shown in parentheses... 123

Lista de Figuras

Capitulo 1- Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest

Figure 1. The Reserva Ducke, Manaus, Brazil grid system with 72 uniformly-distributed permanent plots and HAND (height above the nearest drainage) data in the background. Centre lines of plots follow terrain contours. 56

Figure 2. Relationships between quantitative composition changes of six life forms and all species combined and HAND (height above the nearest drainage), Reserva Ducke, Manaus, Brazil. Dashed lines show the thresholds of vertical distance from drainage below which 90% of the changes in species composition take place: (a) Lianas, r2adj = 0.82 and threshold of 15m; (b) trees, r2adj = 0.72 and threshold of 18 m; (c) palms, r2adj = 0.67 and threshold of 13 m; (d) ferns, r2adj = 0.58 and threshold of 11 m; (e) shrubs, r2adj = 0.49 and threshold of 8 m; (f) herbs, r2adj = 0.26 and threshold of 18 m and (g) all life forms, r2adj = 0.84 and threshold of 13 m. Changes in species composition were reduced to one dimension, using Non-Metric Multidimensional Scaling (NMDS). 57

Figure 3. A schematic view of where the major part of floristic composition changes takes place along the vertical distances from nearest drainage (HAND) gradient. Horizontal dashed lines show HAND thresholds for 90% of composition changes in shrubs (8 m), all life forms combined (13 m) and trees (18 m). Water table fluctuation zone is shown in grey. Horizontal distance from drainage (HDND) that corresponds to 18 m HAND threshold in the Reserva Ducke, Manaus, Brazil extends 350 m and is highlighted by the black arrow in the schema. 58

Capítulo 2 - Linking forest structure and stand biomass along natural disturbance gradients in central Amazonia

Figure 1. Map of the study area showing the 600 km transect along the interfluve between the Purus and Madeira Rivers in central Amazonia. Eleven research sites (1 - 11) are located along the transect. Each site has 5 1ha plots where trees were measured. Boxplots show the variation in stand biomass, density of stems and average individual mass along the transect. Stand biomass and density of stems show higher values in the central region of

the interfluve and lower values in the north and southwestern extremes. The mean individual mass shows an opposite pattern. 84

Figure 2. Relationships between (left) mean individual mass and density of stems ($r^2 = 0.75$, scaling factor, $b = -0.67$); and (right) stand biomass and the density of stems ($r^2 = 0.42$, scaling factor, $b = 0.33$) for individuals with dbh $\geq$ 1 cm in 55-1ha plots in central Amazonia. Variables were log-transformed and both relationships were statistically significant ($p < 0.001$). The individual mass relationship agrees with self-thinning theory, while the relationship between total stand biomass and density does not—self-thinning predicts a negative relationship. 85

Figure 3. Cumulative proportions of stand biomass in 2cm size classes over all 55 1-ha plots along the Purus-Madeira interfluve, in central Amazonia (upper). The lower graphs show data for three plots, exemplifying the extremes (19 – 53 cm) and mean diameter value (19 cm) at 50% stand biomass accumulation (dashed lines). Red bars show the biomass per 2 cm DBH interval and the black points show the cumulative biomass curve. 86

Figure 4. Left - Density histograms showing that more than 60% percent of the plots in the Purus-Madeira interfluve hold less than 5% of the stand biomass in large trees (dbh $\geq$ 70 cm). Right - Approximately 75% of the plots contained half of the stand biomass in trees with diameter below 27 cm. Red dashed lines show the mean values for the x-axis........... 87

Figure 5. Partial relations from multiple regressions investigating the effects of dry-season length, frequency of storms, soil-available phosphorus and soil physical restrictions on the (upper) density of stems ($R^2_{marginal} = 0.70$), (center) individual mass ($R^2_{marginal} = 0.52$) and (bottom) stand biomass ($R^2_{marginal} = 0.57$) in forests along the Purus-Madeira interfluve, in central Amazonia. Fitted lines indicate fixed effects probabilities < 0.05 in the linear mixed-model analyses excluding outliers (open circles, see the main text for more details). 88

Figure 6. Path analysis showing the magnitude of direct effects (top), given by standardized coefficients of linear mixed-models, of environmental gradients on forest-structure components. The indirect effects of environmental gradients on stand biomass via forest structure components (bottom) show the multiplicand of the standardized coefficients along each path and the sum of these indirect effects (net indirect effects). Note that dry-season length and frequency of storms have strong and opposite effects on stand biomass via density of stems and mean individual mass. For dry-season length, the opposite effects were counterbalanced and no significant effect of seasonality was seen on stand

biomass. Arrow width indicates the relative strength of the effects and the dashed line show no effect ($p \geq 0.05$). Asterisks indicate significance levels (*** $p \leq 0.001$,** $p < 0.005$ and * $p < 0.05$). 89

Figure S1. Relationships between (left) mean individual mass and density of stems ($r^2 = 0.39$, scaling factor, $a = -0.68$); and (right) stand biomass and the density of stems ($r^2 = 0.12$, $a = 0.32$) for individuals with dbh ≥ 10 cm in 55-1ha plots along the Purus-Madeira interfluve in central Amazonia. Variables were log-transformed and both relationships were statistically significant ($p < 0.05$). 96

Capítulo 3 - Environmental limits to canopy height in Central Amazonia

Figure 1. Map of the study area showing the 600 km transect along the interfluve between the Purus and Madeira Rivers in central Amazonia. Eleven research sites (1 - 11) are located along the transect. 116

Figure 2. Canopy height surface (green line) derived from portable ground LiDAR in four selected transects (of the 55) surveyed along the Purus-Madeira interfluve, in Central Amazonia. Black continuous lines show values of mean canopy height and dashed lines show the values of maximum canopy height calculated as the higher 99% quantile values. 117

Figure 3. Relathionships between stand-level height metrics from portable ground LiDAR and from individual tree (dbh >= 30 cm) measurements. (a) Mean canopy height calculated from tree individual heights ($\mathrm{MCH}_{\mathrm{tree}}$) predicts 77% of the variance in the same metric derived from portable ground LiDAR, $\mathrm{MCH}_{\mathrm{gLidar}}$, ($MCH_{gLidar} = -5.46 + 1.2\ MCH_{tree}$, $p < 0.001$). (b) Maximum canopy height (MaxCH), estimated from the high 99% quantile, from tree individual heights predicts 71% of the variance in the same metric derived from portable LiDAR ($MaxCH_{gLidar} = 0.76 + 8.34\ MCH_{tree}$, $p < 0.001$). 118

Figure 4. Spatial variation in mean and maximum canopy height in the 11 sites along the Purus-Madeira interfluve, south of the Amazonas River in central Amazonia. Forests in the northeastern part of the transect have lower canopy than in the southwestern, except for the last site (11) which is located on an alluvial terrace. 119

Figure 5. Partial plots from two multiple regression models showing direct drivers of mean and maximum canopy height. Upper panel - Partial regressions between mean canopy height, lowest water-table level, species composition (one-dimensional solution to non-metric multidimensional scaling analysis) and the mean diameter of trees with dbh ≥ 30

cm (R2 marginal = 0.71). Lower panel - Partial plots from a a multiple regression relating maximum canopy height to mean water-table level, soil depth score (higher scores denotes shallower soils) and the mean diameter of trees with dbh ≥ 30 cm (R2 marginal = 0.61). Fitted lines indicate fixed-effect probabilities < 0.05 in the linear mixed-model analyses (see Table 2). 120

Figure 6. Path analysis showing the magnitude of direct and indirect effects, given by standardized coefficients from linear mixed-effect models (with probabilities < 0.005), of environmental gradients, species composition and the average diameter (dbh ≥ 30 cm) in relation to the stand mean canopy height. Arrow widths show the magnitude of the effects.. 121

Figure 7. Path analysis showing the magnitude of direct and indirect effects, given by standardized coefficients from linear mixed-effect models (with probabilities < 0.005), of environmental gradients and mean tree diameter (dbh ≥ 30 cm) to stand maximum canopy height... 122

Introdução Geral

Um tema central em ecologia é a relação entre fatores ambientais e variações na estrutura e composição de espécies da floresta. Diversos estudos em florestas tropicais investigaram às diferenças em diversidade florística e características estruturais das florestas em função da sazonalidade de chuvas, fertilidade e tipos de solo (Gentry 1988; Phillips *et al.* 1994; Vormisto *et al.* 2000; ter Steege *et al.* 2003; Malhi *et al.* 2006; Castilho *et al.* 2006; Peña-Claros *et al.* 2012). No entanto, pouco se sabe sobre essas relações em florestas de terra-firme em que o lençol freático é raso (Jirka *et al.* 2007; Ferry *et al.* 2010).

O lençol freático raso parece ser uma característica comum em escala global (Fan, Li, & Miguez-Macho 2013) e também na Amazônia, onde estima-se que cerca de 36% da bacia tem lençol freático com profundidade < 5m e cerca de 60% tem o lençol com profundidade < 10m (Fan & Miguez-Macho 2010). O lençol freático pouco profundo pode sustentar o funcionamento das florestas durante a estação seca pelo acesso direto das raízes à zona saturada ou à franja capilar (Miguez-Macho & Fan 2012), que é a água que sobe da zona saturada pelos poros do solo por capilaridade. Se por um lado o lençol freático superficial pode contribuir para manutenção da evapotranspiração e crescimento das plantas durante a estação seca, é provável que, nos períodos em que o nível do lençol é mais superficial, existam condições desfavoráveis na zona de raízes devido a depleção de oxigênio no solo. O lençol superficial portanto, pode ter efeitos negativos, como a limitação de processos fisiológicos ativos e restrição do desenvolvimento de raízes (Nicoll & Ray 1996), comprometendo a tomada de nutrientes, crescimento e ancoragem.

As características físicas do solo, como densidade e textura, também exercem um papel importante no desenvolvimento das raízes, tanto pelo impedimento em caso de solos densos (Taylor & Brar 1991) como pelo "estímulo" de busca de água em solos de textura grossa que têm baixa capacidade de retenção (Jackson, Sperry, & Dawson 2000). Solos com caraterísticas físicas mais restritivas ao desenvolvimento de raízes podem estar associados a florestas mais dinâmicas e de menor porte, sendo um provável iniciador de distúrbios endógenos na vegetação (Quesada *et al.* 2012a). Além disso, em casos de distúrbios naturais exógenos, como tempestades de vento, solos com características restritivas ao desenvolvimento de raízes podem deixar as árvores mais suscetíveis a derrubada e desenraizamento. A importância dessas variáveis para o entendimento de diversos aspectos da floresta, como composição de espécies, dinâmica demográfica e acúmulo de biomassa, motivaram os estudos desenvolvidos nesta tese.

Uma das restrições para o desenvolvimento de estudos considerando a flutuação do lençol freático ou outras medidas de água no solo são os custos (financeiros e de tempo) para monitorar as variações sazonais sobre uma escala espacial relevante aos processos ecológicos. No capítulo 1 da tese, investiguei um novo indicador (*proxy*) de profundidade do lençol freático (a distância vertical do terreno em relação a drenagem mais próxima) derivado de dados de sensoriamento remoto, como preditor das variações de composição florística em 6 formas de vida: árvores, lianas, palmeiras, arbustos, ervas e samambaias. Esse estudo foi realizado na Reserva Ducke, um sítio de pesquisa ecológica de longa duração que cobre uma área de 64 km^2 e possui um banco de dados que permitiu a compilação dos levantamentos de espécies de plantas em cerca de 70 parcelas permanentes distribuídas sobre um gradiente topográfico com variação na profundidade do lençol freático.

A Reserva Ducke é uma área de floresta ombrófila densa de terra-firme localizada ao norte de Manaus. O relevo nessa região é bem dissecado pela rede de drenagem (com cursos d'água perenes) e apresenta platôs, áreas mais altas de solos argilosos e bem drenados, e baixios, áreas próximas dos cursos d'água com solos arenosos que ficam encharcadas pelo transbordamento do lençol freático durante a época chuvosa (Chauvel, Lucas, & Boulet 1987). A região ao norte de Manaus têm importantes sítios de pesquisa e é uma das áreas mais bem estudadas da Amazônia. No entanto, os padrões de funcionamento da floresta e relações hidrológicas encontrados nesta região podem não se aplicar a outras partes da bacia (Malhi *et al.* 1998; Saleska *et al.* 2003; Huete *et al.* 2006). Existe uma grande variabilidade no clima e tipos solos na Amazônia (Sombroek 2000, 2001) e as diversas combinações edafo-climáticas podem resultar em padrões diferentes de estrutura e funcionamento da floresta.

Nos capítulos 2 e 3 da tese, investiguei como a estrutura e estoques de biomassa da floresta variam em relação a gradientes de condições hídricas, solo e distúrbios naturais no interflúvio Purus-Madeira, uma região pouco estudada e de características ambientais bem distintas da região ao norte de Manaus. A região entre os rios Purus e Madeira, na calha sul do Rio Amazonas, tem solos predominantemente siltosos, mal drenados e com relevo plano (Sombroek 2000). Há uma considerável variação no regime de precipitação ao longo dessa área, muitos cursos d'água não são perenes, o lençol freático é raso (Fan & Miguez-Macho 2010), e diversas áreas permanecem encharcadas durante o período chuvoso, mesmo estando afastadas dos corpos d'água.

No capítulo 2, investiguei como dois componentes estruturais da floresta (a densidade de indivíduos e a massa média individual) e os estoques de biomassa acima do solo comportam-se ao longo de gradientes de sazonalidade de chuvas, frequência de tempestades, fósforo disponível no solo e restrições físicas do solo. A densidade de indivíduos e a massa média individual são os componentes que determinam o estoque de biomassa de uma floresta. Existe controvérsia na literatura a respeito das relações entre estoques de biomassa e gradientes ambientais, como por exemplo, de características físicas e químicas do solo (Paoli, Curran, & Slik 2008; Baraloto *et al.* 2011). No entanto, não é conhecido se as diferentes conclusões resultam de variação espacial nas relações com biomassa, ou se é porque os gradientes ambientais podem ter efeitos distintos nos diferentes componentes da biomassa. Portanto, para entender as relações entre estoques de biomassa e gradientes ambientais, avaliei como esses gradientes atuam na biomassa de forma indireta, via densidade de indivíduos e massa média individual.

No capítulo 3, avaliei métricas de um componente de estrutura vertical da floresta, a altura do dossel. Diversos estudos investigaram limitações biofísicas para entender a altura máxima das árvores (Yoder *et al.* 1994; Ryan & Yoder 1997; Niklas 2007), mas pouca atenção foi dada ao entendimento das limitações de altura causadas por propriedades hidráulicas do solo e suprimento de água (Jackson *et al.* 2000). Neste capítulo investiguei se as características físicas do solo, a profundidade do lençol freático e o regime de precipitação limitam a altura das florestas ao longo do interflúvio Purus-Madeira. Para estimar altura do dossel usei um sensor LiDAR (light detection and ranging) portátil que permite levantamentos rápidos da altura das árvores (Parker, Harding, & Berger 2004).

Objetivo geral

Esclarecer o papel de gradientes de chuva, profundidade do lençol freático e características físicas do solo nas variações da composição florística, estrutura da floresta e estoques de biomassa na Amazônia Central.

Objetivos específicos

1. Determinar se um novo indicador de profundidade de lençol freático obtido de sensoriamento remoto pode ser usado como preditor de variações na composição florística de diferentes formas de vida;

2. Determinar como componentes estruturais da floresta (densidade de indivíduos e massa média individual) e estoques de biomassa são influenciados por gradientes de precipitação e características do solo;

3. Determinar se gradientes ambientais ligados ao suprimento de água no solo são fatores limitantes para altura do dossel.

Capítulo 1

—

Schietti, J., Emilio, T., Rennó, C. D., Drucker, D.P., Costa, F.R.C., Nogueira, A., Baccaro, F.B., Figueiredo, F., Castilho, C.V., Kinupp, V., Guillaumet, J.L., Garcia, A.R.M., Lima, A.P., Magnusson, W.E. 2013. Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. *Plant Ecology & Diversity*. DOI: 10.1080/17550874.2013.783642

Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest

Juliana Schietti[a]*, Thaise Emilio[a], Camilo D. Rennó[b], Debora P. Drucker[c], Flávia R.C. Costa[d], Anselmo Nogueira[e], Fabricio B. Baccaro[a], Fernando Figueiredo[d], Carolina V. Castilho[f], Valdely Kinupp[g], Jean-Louis Guillaumet[h], Ana Raquel M. Garcia[a], Albertina P. Lima[d] and William E. Magnusson[d]

[a]*Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia – INPA, Manaus, Brazil*; [b]*Divisão de Processamento de Imagens/OBT, Instituto Nacional de Pesquisas Espaciais – INPE, São José dos Campos, Brazil*; [c]*EMBRAPA - Monitoramento por Satélite, Campinas, Sao Paulo, Brazil*; [d] *Coordenação de Pesquisa em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia – INPA, Manaus, Brazil*; [e] *Departamento de Botânica, Instituto de Biociência, Universidade de São Paulo, São Paulo, Brazil*; [f] *EMBRAPA - Centro de Pesquisa Agroflorestal de Roraima, Boa Vista, Roraima, Brazil*; [g] *Herbário EAFM, Instituto Federal de Educação, Ciência e Tecnologia do Amazonas, (IFAM-CMZL), Manaus, Brazil*; [h] *Laboratoire de Phanérogamie - Muséum National d'Histoire Naturelle, Paris, France.*

* Corresponding author. Email: jujuschietti@gmail.com

Abstract

Background: Plant composition changes with topography and edaphic gradients that correlate with soil-water and nutrient availability. Data on soil water for the Amazon Basin are scarce, limiting the possibility of distinguishing between soil and soil-water influences on plant composition.

Aim: We tested a new proxy for water table depth, the terrain height above nearest drainage (HAND), as a predictor of composition in trees, lianas, palms, shrubs, and herbs and compared HAND to conventional measures of height above sea level (HASL) and horizontal distances from nearest drainage (HDND).

Methods: Plant-species composition in 72 plots distributed across 64 km^2 of lowland evergreen 'terra firme' forest was summarised using Non-Metric Multidimensional Scaling (NMDS). NMDS scores were regressed against estimates of HAND, HASL and HDND.

Results: Plant composition was highly correlated with the vertical distance from water table, capturing up to 82% of variation. All life forms showed highest turnover rates in the zone with seasonally water-saturated soils, which can extend 350 m from stream margins.

Conclusions: Floristic composition is closely related to water table depth, and HAND appears to be the most robust available topographical metric of soil-water gradients. Brazilian conservation laws protecting 30 m-wide riparian buffers are likely to be too narrow to encompass the full zone of highest floristic turnover and may be ineffective in safeguarding riparian plant diversity.

Keywords: beta diversity; HAND; distance from stream; plant species composition; soil hydrology; SRTM; terra firme forest; topography; tropical rain forest; water table.

Introduction

Soil water controls many aspects of forest ecosystem dynamics, including forest structure (Jirka *et al.* 2007), vegetation-atmosphere interactions (Rodriguez-Iturbe 2000), tree growth and mortality (Phillips *et al.* 2009), and species distribution and composition (Pyke et al. 2001; Gibbons and Newbery 2002; Groom 2004; Engelbrecht et al. 2007; Jirka et al. 2007; Balvanera et al. 2011). However, few studies have investigated the direct relationship between the variability of soil water and plant species distribution (Engelbrecht *et al.* 2007; Comita & Engelbrecht 2009), so little is known about how assemblage composition changes along hydrological gradients.

Direct measures of soil water are scarce and unevenly distributed across the Amazon Basin, restricting opportunities to directly relate changes in plant composition to soil-water gradients. It is costly and time consuming to monitor soil-water variables, such as soil moisture or water table fluctuations, at relevant spatial scales in the field and remote-sensing data that can be used to infer soil moisture have many restrictions in forested areas (Salas *et al.* 2002; Smith 2002). This seems to be the main reason that researchers often use topographical variables, such as slope and differences in height above sea level (HASL), to predict plant-composition changes instead of using soil-water variables, even when drainage or soil-water availability is likely to be one of the most important variables that affect species distributions (Tuomisto and Poulsen 2000; Costa et al. 2005; Costa et al. 2009). Therefore, the use of proxies for soil-water availability is a promising strategy to investigate species distribution and soil-water relationships in Amazonian forests (see Balvanera et al. 2011, Kanagaraj et al. 2011).

Topographic position frequently controls soil-water gradients and soil properties (Daws et al. 2002; Brown et al. 2004), with water availability being lower in uplands and higher in valleys, where the water table is vertically closer to the surface. Also, areas horizontally far from streams tend to be more well-drained than areas horizontally close to streams (Campling et al. 2002; Kravchenko et al. 2002). Both vertical and horizontal distances from streams are useful proxies for plant-available water because soil draining potential is a function of vertical rise and horizontal flow (Marshall et al. 1996). It has been shown that plant composition changes along gradients of horizontal distance from a stream (Naiman et al. 1997; Sabo et al. 2005; Drucker et al. 2008; Costa et al. 2009), and horizontal distances are currently used to define strips along stream margins for riparian-forest protection in Brazil. Horizontal and vertical distances are correlated in micro watershed because the terrain becomes higher with distance from the stream. Nevertheless, horizontal distances from stream may not represent a change in soil-water conditions in large flat areas connected to the drainage (Rennó *et al.* 2008). Such waterlogged areas may extend far from streams but they remain vertically close to water table. Therefore vertical distance from stream should be a better predictor of the hydrological condition experienced by plants, especially in predominantly flat topography. Silvertown et al. (1999) had shown that plant species segregated in water table gradients even in the absence of obvious topographic variation and argued that many types of plant communities may be structured by soil hydrology gradients. However, until now the potential of vertical distance from water table in driving plant composition differences has been overlooked in tropical forests since we found only one study addressing plant-composition changes related to water table depth in tropical forests (Jirka *et al.* 2007).

Species distribution may be shaped by the topography-driven water gradient (Balvanera et al. 2011), based on distinct water requirements (Engelbrecht *et al.* 2007). Therefore, it is reasonable to expect that plant functional groups with distinctive morphologies, such as trees, lianas, palms, shrubs and herbs, will also respond differently to the gradient of topography-driven water availability. For many reasons, rooting depth may be a key factor that affects plant growth and survival (Groom 2004). Rooting depth is sensitive to water shortage or excess. Deep-rooting plants, such as trees (Nepstad *et al.* 1994) and lianas (Restom & Nepstad 2004; Schnitzer 2005) in higher topography, have more access to groundwater throughout the year than shallow rooted plants such as herbs. If maximum rooting depth plays an important role in plant water access, the distribution of shallow rooted plants is probably more strongly affected by topography-driven water gradients, such as vertical distances from water table, than deep-rooted plants.

The test of spatially explicit proxies derived from remote sensing to predict plant composition changes is of great importance for extrapolations and production of regional diversity maps (Schulman *et al.* 2007; Albernaz *et al.* 2012). Maps of diversity are necessary for conservation planning and for estimates of diversity losses due to forest degradation and environmental changes. Detailed topographic data have become available since 2000 from the Shuttle Radar Topography Mission (SRTM). Even though it represents vegetation-canopy topography, rather than terrain topography, the SRTM digital elevation model (DEM) has high vertical resolution (1 m) and free near-global coverage. As terrain topography usually varies much more than canopy topography, the SRTM DEM highlights geomorphological features and is useful as a surrogate for terrain topography and for hydrological modelling (Valeriano *et al.* 2006). Therefore, SRTM-HASL has been used as a predictive variable for plant species distribution (Prates-Clark et al. 2008; Raes et al. 2009) and for above-ground live biomass (Saatchi *et al.* 2007) in tropical forests. An algorithm to calculate the height above the nearest drainage (HAND), a proxy for vertical distance from the water table, based on SRTM-DEM was developed by Rennó et al. (2008). The height above the drainage was shown to be correlated with the water table level and hydrological conditions of the terrain (Rennó *et al.* 2008; Nobre *et al.* 2011), and therefore might be a better predictor of plant-species distribution than traditional measures, such as HASL and horizontal distances from drainage (HDND).

Predictors of species distributions are important to understand present distributions and likely distributions under climate change. Therefore, we tested the hypothesis that HAND is a better predictor of species composition than terrain topography or horizontal distance from streams for species in six plant life forms: trees, lianas, palms, shrubs, non-fern herbs and ferns. To test if life forms responded differently to vertical distance from water gradient, we compared the strength of the life-form relationships with HAND in a lowland evergreen terra firme forest in the Central Amazonia. We hypothesised that species composition in shallow-rooted life forms should be better related to HAND than in deep-rooted life forms.

Materials and methods

Study area

The study was conducted in the Reserva Ducke, or Ducke Forest Reserve of the Instituto Nacional de Pesquisas da Amazônia (INPA) in central Amazonia, located 26 km north-west of Manaus (2° 55' 47.80" S; 59° 58' 30.34" W). The Reserve covers 10,000 ha (10 km × 10 km) of lowland evergreen terra-firme tropical rain forest, with a 30-37 m high closed canopy and emergent trees reaching 40-45 m (Ribeiro *et al.* 1999). Soils are derived from tertiary marine sediments from the Alter do Chão formation. The local relief is dissected by the hydrographic system, resulting in a landscape formed by plateaux and valleys, where the clay fraction decreases as elevation decreases (Chauvel et al. 1987). The dominant soil type is clayey yellow latosol typic Haplorthox or Acrorthoxon the plateaux where the water table is deep, transitioning to less clayey red-yellow (Orthoxic Tropohumult or Palehumult) soils on slopes. Soils are sandy on the valley bottoms with hydromorphic podsols (Tropohumods–Troporthods) (Chauvel et al. 1987) where the water table is close to surface and the soils are almost permanently waterlogged during the rainy season. Reserva Ducke is generally considered to contain relatively uniform dense forest and is not subject to flooding by large rivers.

The mean annual temperature at Reserva Ducke between 1965 and 1980 was 26 ºC and the annual rainfall ca. 2400 mm with monthly maximum in March (~330 mm) and minimum in August with < 100 mm (Marques-Filho *et al.* 1981). The dry season occurs between July and September, but on average only two months have rainfall lower than 100 mm (Marques-Filho *et al.* 1981). The drainage system in Reserva Ducke is formed by streams of first to third order (Figure 1), ranging from less than a metre to ca. 10 m wide. The valley bottoms (flat areas along the streams, known locally as '*baixios*') vary in size up to about 150 m from stream margins (D. Drucker, unpublished data), and often contain swampy pools due to the proximity of the water table to the surface in these areas.

Reserva Ducke has a grid of regularly spaced east-west and north-south trails covering 64 km^2. Trails allow access to 72 permanent plots regularly distributed across the landscape that were installed in 2000 (Costa & Magnusson 2010). The plots are separated from each other by a minimum distance of 1 km (Figure 1). In each plot, a 250 m long centre line follows the contour to minimise variation in depth to water table and soil variables within the plots. The width of the plot varies according to the taxa of interest (Magnusson *et al.* 2005; Costa & Magnusson 2010).

Floristic datasets

Reserva Ducke has been the site of numerous studies of plant assemblages in association with soil/topographical gradients (Costa et al. 2005; Kinupp and Magnusson 2005; Costa 2006; Drucker et al. 2008; Costa et al. 2009; Nogueira et al. 2011) and an extensive floristic dataset exists for the area. We compiled six datasets of plants with different life forms frequently used in ecological studies: (1) trees, (2) lianas, (3) palms, (4) shrubs, (5) non-fern herbs and (6) ferns, and a combined dataset of (7) all species in the six groups sampled in Reserva Ducke. These datasets include 741 plant species sampled over 72 plots (all life forms were sampled together in a sub-sample of 22 plots). All plants were recorded along the entire length of the 250 m long plot centre line in each plot. The width of the plot varied according to the relative abundance of groups, ranging from 1 m for ferns to 40 m for trees over 30 cm DBH (see Table 1). Details on the sampling protocols are available in the metadata associated with the data for each life form at http://ppbio.inpa.gov.br/repositorio/dados.

Height above the nearest drainage - HAND

HAND values were shown to be correlated with water table level categories within the same geological formation with dissected clayey-plateau and sandy-valley landscapes (Chauvel et al. 1987), about 60 km from Reserva Ducke (Rennó *et al.* 2008). Conceptually, HAND represents the relative water gravitational potential (or vertical relative draining potential), although no direct correlation of HAND values and soil-water potential or soil moisture has yet been made. The water gravitational potential is a component of the soil water potential, which reflects difficulty for plants to extract soil water or to avoid excess water. High HAND values mean large gravitational potential (high vertical draining potential) and low HAND values mean low gravitational potential (low vertical draining potential) and proximity to the water table, where lack of drainage leads to waterlogging (Nobre *et al.* 2011).

The HAND algorithm developed by Rennó et al. (2008) calculates the vertical distance between points on the terrain and their nearest drainage, based on a digital elevation model (SRTM in this study). The nearest drainage for each terrain point is the stream to which the water from that point is drained. Therefore, the nearest drainage is not defined based on Euclidean distances but using flow-direction paths, which follow the topography (from one point to its steepest downslope neighbour) and has topological continuity. The most important step in the calculation of HAND values is the definition of the drainage network density because this is the base for the calculations of terrain vertical distances from drainage. This step needs field calibration for the establishment of the stream origins (the head-waters), which are defined by the minimum-contributing-area threshold. The lower this minimum-contributing-area threshold the higher the drainage network density (more streams are taken into account). If this threshold is too low, the algorithm can create false small streams and low HAND values will be attributed to terrains close to these false streams. Conversely, if the minimum-contributing-area threshold is too high, small streams will not be included in the drainage network and HAND values will be higher than the real vertical distance from the terrain and its nearest drainage. Different minimum-contributing-area thresholds can be used to represent differences in the drainage density from dry season to wet season for seasonal streams.

We calculated HAND values for Reserva Ducke based on SRTM-DEM (90 m spatial resolution) using a 30 pixel minimum contribution area (= 0.41 km^2) and validated several small streams and headwaters along the trail system in the field.

Using GIS, we extracted (with bilinear interpolation) HAND values for 25 locations along the permanent-plot centre lines (Figure 1). Values of HAND obtained for each location where averaged per plot. The mean HAND values for the 72 plots ranged from 1 to 53 m (mean = 22 m).

Horizontal distance from nearest drainage – HDND

Horizontal distances from nearest drainage (HDND) are usually related to soil drainage classes (Campling et al. 2002; Kravchenko et al. 2002). Areas horizontally close to streams are also more likely to waterlog and to receive sediment deposits from streams. We calculated HDND from plots to nearest drainage using two types of distances: Euclidian distance (HDND-Euclidean) and water-flow direction distance (HDND-flowdir). The HDND-Euclidean is the usual horizontal distance calculated with GIS tools in which the smallest distances are calculated between plots and nearest drainages, without regard to hydrological connection between plots and drainage. The HDND-flowdir is calculated using flow paths between plots and drainages, so the plots are always hydrologically connected to drainage. HDND-Euclidean and HDND-flowdir are highly correlated in Reserva Ducke ($r = 0.95$) and HAND is correlated with HDND-Euclidean ($r = 0.80$) and with HDND-flowdir ($r = 0.86$), based on data for the 72 plots of this study.

Using GIS, we extracted (with bilinear interpolation) HDND values for 25 locations along the permanent-plot centre lines. Values of HDND obtained for each location where averaged per plot. The HDND-Euclidean values for the 72 plots ranged from 27 to 601 m (average = 234 m) and HDND-flowdir values ranged from 27 to 756 m (average = 250 m).

Height above sea level – HASL

Height above sea level was obtained from radar data (SRTM-HASL) and from direct ground measurements (ground-HASL). Ground-HASL and SRTM-HASL were highly correlated ($r = 0.94$), and HAND was correlated with SRTM-HASL ($r = 0.89$) based on data for the 72 plots. SRTM-HASL was compared with HAND and HDND as a predictor of floristic composition changes. Ground-HASL was used only to estimate the accuracy of the SRTM-HASL measurements.

SRTM-HASL data for Reserva Ducke was obtained from http://www2.jpl.nasa.gov/srtm/, with a horizontal resolution of 3 arc-second (90 m near the equator) and a vertical resolution of 1 m. The C Band of the Radar has a strong interaction with the vegetation canopy, so the SRTM data represents mostly the canopy surface in densely forested areas (Valeriano *et al.* 2006). We used the same procedure described for HAND and HDND to extract SRTM-HASL data for 25 locations along the central line of each plot. Values were average per plot and the SRTM-HASL ranged from 53 to 114 m. The average for all plots in Reserva Ducke was 82 m.

Ground-HASL for the centre lines in the 72 plots was accurately measured by a professional topographer (A. T. Cardoso e Silva) using a theodolite and the Brazilian High Precision Altimetric Network (http://www.ibge.gov.br). As the 250 m centre line of the plots follows the terrain contour, the elevation above the sea level is the same at all points along the centre line of the plots. Ground-HASL values are available from http://ppbio.inpa.gov.br/knb/style/skins/ppbio/. The values of ground-HASL ranged from 39 to 110 m in the 72 plots. The average ground-HASL was 76 m.

Data analyses

Plant species composition matrices of each life form were reduced to one dimension using Non-Metric Multidimensional Scaling (NMDS). Ordinations were based on relative abundance (quantitative composition) and on presence-absence of species (qualitative composition). Ordinations of presence-absence data used the Sørensen dissimilarity index and quantitative ordinations were based on data standardised by total abundance per plot and used the Bray-Curtis dissimilarity index. The adjusted r^2 of the dissimilarity matrices of original data regressed against the dissimilarity along the one-dimensional ordination was used to evaluate the adequacy of the ordinations for each life form (McCune & Grace 2002). Most variation in ordinations based on plant-species relative abundance and presence/absence was captured by one dimension in the NMDS. The percent of variance captured by one dimension-NMDS ranged from 57% for shrubs to 92% for palms (Table 2).

To investigate if plant quantitative- and qualitative-composition changes were related to HAND, we tested this predictor for the six life forms and for all species using an exponential-decay function with three parameters (Species Composition = $y_0 + a \exp^{-b^* \text{predictor}}$, equation 1). We tested other non-linear functions (inverse polynomial of first and second order, quadratic and exponential decay with two parameters) but the exponential decay function with three parameters captured relationships as well or better than the other functions in all cases. Therefore, we only report the results of the exponential decay with three parameters. The delta Akaike information criterion (Δ AIC) was calculated to compare differences in model strength among life forms. Δ AIC > 2 indicates stronger support for a given model than other models in the comparison (Burnham & Anderson 2004). As the AIC values are sensitive to the number of sampling units (Burnham & Anderson 2004), we used only the plots where all life forms were sampled for model-fit comparisons among life forms.

In order to locate positions along the HAND gradient where the rates of change in plant-species composition slowed along the exponential-decay gradient, we calculated HAND values corresponding to the part of the curve at which a change of 90% in species composition occurred. The same threshold (90%) was used for all plant groups to standardise the comparisons among groups. We identified this HAND threshold for the six life forms and for all species combined.

To compare the predictive power, related to plant composition changes, of HAND with that of HDND and SRTM-HASL, we tested these three predictors together in multiple linear regressions where we selected the minimum adequate model (Calcagno & de Mazancourt 2010). The automated model selection, implemented by the package glmulti (Calcagno and de Mazancourt 2010) finds the best model among all possible models based on their AIC ranking. The variables were log-transformed prior to analysis to meet the assumptions of linear regression models. All analyses were carried out in the R-environment, version 2.15.1 (R Core Team 2011).

Results

Patterns of floristic composition changes

Changes in plant-species composition were closely related to the height above the nearest drainage. HAND alone explained between 26% and 82% of variance in the ordination using quantitative species composition and all life forms had the same pattern of change in species composition along the HAND gradient. Higher rates of change in species composition occurred close to the drainage, with a decrease to almost no change as the vertical distance from the nearest drainage increased (Figure 2). However, the strength of this relationship differed among life forms (Δ AIC > 2 for all groups, Table 2). Major changes in plant species composition (90% of the changes) occurred within vertical distances from drainage of 8-18 m (corresponding horizontal distances of about 60 to 350 m), indicating that a strong change in composition takes place in the transition between the valley bottoms and higher elevations (Figure 3). This threshold of plant-species composition change varied among life forms, from a HAND value of 8 m in shrubs to 18 m above the nearest drainage in trees and herbs (Figure 2).

Qualitative-composition changes were consistent with the results of quantitative changes, with similar relative rates of change along the HAND gradient. However, the explanatory power of HAND for lianas, palms and all life forms combined was lower for qualitative-composition compared to quantitative-composition changes (Table 2). The strengths of relationships with HAND were similar between palms and shrubs (Δ AIC < 2) but differed among other plant groups. The distance above the nearest drainage below which 90% of the changes in plant composition occurred for qualitative data was 8 m for shrubs, 10 m for lianas, 11 m for palms, 13 m for ferns, 14 m for trees and 18 m for herbs.

Predictors of floristic-composition changes: HAND versus HASL and HDND

Changes in species composition of the plant life-form types examined and all species combined were more closely related to HAND than to HASL and HDND. HAND was the best single predictor of floristic composition and the addition of HASL and HDND to models did not increase model support (Δ AIC < 2, Table S1). There was no support (Δ AIC < 2 in all cases) for differences between Euclidean distance and flow-direction paths for predicting floristic-composition changes (Δ AIC < 2), so we report only results for HDND-flowdir (Table 2).

We used SRTM-HASL as the altitudinal predictor in the model selection procedures because SRTM data are spatially explicit, similarly to HAND and HDND, allowing extrapolations, while ground-HASL data are available for few locations in Amazonia, restricting extrapolation to other areas. The comparison between SRTM-HASL and ground-HASL however, showed different supports for models of floristic composition. When only HASL predictors were considered, SRTM-HASL had more support for predictions of tree, palm and shrub species composition changes than ground-HASL (Δ AIC > 2 in all cases). The other plant life forms (lianas, herbs and ferns) were better predicted by ground-HASL than SRTM-HASL (Δ AIC > 2 in all cases).

Discussion

Changes in floristic composition along the HAND gradient

In this study, plant-composition changes at the mesoscale were closely related to vertical distance from the nearest drainage (HAND), with an exponential decay of changes in species composition as HAND increased. About 90% of the changes in species composition took place below a HAND threshold of 8 to 18 m, depending of plant life form (13 m for all life forms combined), suggesting that soil hydrology, probably in combination with other edaphic features, plays an important role in determining plant-assemblage composition.

That 90% of changes in species composition occur up to 8 to 18 m above the drainage, depending on life form, indicates that most changes in composition take place in areas affected by seasonal water table fluctuations. The upper limit of the water table in a well-studied micro-catchment close to the Reserva Ducke has been estimated as 16 m above the drainage (Tomasella *et al.* 2008). This zone of water table fluctuation encompasses the valley bottom and the lower parts of slopes, and the water table level in the valley ranges from water at the ground surface (waterlogged) to less than 1 m below the surface at the end of dry season in average years (Hodnett et al. 1997; Drucker et al. 2008). This suggests that the seasonal water table fluctuations leading to frequent waterlogging in valleys may promote a distinct plant-species composition in these areas, possibly related to higher stem mortality and recruitment (see Phillips et al. 1994). In the Reserva Ducke, the mortality of small trees ($4 \geq$ dbh < 30 cm) in the valleys and on the slopes was 40% higher (between 2003-2008) than on plateaux and uprooting was an important mode of death (Toledo *et al.* 2012). Uprooting may be caused by low anchorage due to limited production and establishment of roots in waterlogged anoxic conditions in valleys, by poor anchorage in the sandy soils of valley bottoms, and by the higher phosphorus availability in valleys and lower-slope soils that may reduce the investment in roots (see Toledo et al. 2012). The high stem mortality may create greater recruitment opportunities than on the plateaux, and that, combined with diverse seed rain (Harms 1997), could lead to higher species turnover through space and time in riparian areas. Conversely, the lower soil-water availability on the plateaux, especially in the dry season (Hodnett *et al.* 1997), associated with lower mortality (Toledo *et al.* 2012), could be selecting for establishment of a more drought-tolerant assemblage composition on the upper slopes and higher lands (Newbery et al 1996; Gibbons and Newbery 2002). This could explain the lesser differences in plant species composition found in areas with higher vertical distances to the drainage.

Other processes that may affect the pattern of compositional changes along a HAND gradient are differential tolerance to anoxic conditions (Joly & Crawfordf 1982; Junk 1997; Scarano *et al.* 1997; Svenning 2001; Parolin 2002), differential root : shoot biomass ratios (Joslin, Wolfe, & Hanson 2000) and dispersal patterns and limitations (Dalling et al. 1998; Ozinga et al. 2005; Parmentier and Hardy 2009). Most of these processes affect seed germination, individual establishment, survivorship and recruitment, and may contribute to the higher rates of change in species composition with distance from stream in areas vertically close to the drainage.

Other factors, such as soil physical and chemical properties, are correlated with HAND in the Reserva Ducke and should also be considered as possible determinants of patterns of changes in composition. Soil texture affects water retention (Hodnett & Tomasella 2002) in soil surface layers and in some circumstances this could counter balance the effects of higher vertical distances. Clay content is highly correlated with HAND in the Reserva Ducke ($r = 0.88$) and clay content can affect soil water availability for plants (Hodnett & Tomasella 2002). Nutrient availability is linked to soil physical properties and water availability (Baldwin & Mitchell 2000) and should also interact with the HAND gradient. Further studies in sites with distinct correlations between topography and soil characteristics, e.g. Iquitos region (Western Amazonia) where clayey and nutrient rich soils are at higher elevations and sandy, nutrient poor soils are at lower elevations (Vormisto *et al.* 2000), are necessary to disentangling the effects of soil nutrients, soil physical properties and HAND on plant-composition changes.

Plant life forms

The strength of the relationship between plant composition and HAND varied among life forms. The six life forms differed in mean maximum plant size, resource use and reproductive patterns, but soil-water gradients should play an important role in establishment and maintenance for all plants. Tropical rainforest herbs, ferns, shrubs and palms have shallow root systems (Becker and Castillo 1990; Ramos et al. 2009) and our expectation was that compositional changes in these plant groups would be more closely related to the HAND gradient due to their limited access to ground water. However, contrary to this expectation, deep-rooted plants, such as lianas and trees, had more variation explained by HAND than ferns, shrubs and herbs. A possible reason is that the life forms, with shallow roots and smaller sizes, may depend more than the other life-history types on the small-scale and seasonal variation in soil water in the surface layers (see Marthews et al. 2008), rather than on access to deep water. Drucker et al. (2008) documented fine-scale changes in herb species composition along a gradient of horizontal distance from streams in the Reserva Ducke and ferns life cycle are highly dependent on free-water (Page 2002). The weaker relationships with HAND for herbs, shrubs and ferns may be due to the fact that HAND is a proxy with stationary measurements of vertical distances to the water table, and with relatively coarse spatial resolution in this study (90 m x 90 m pixels).

Given the differences in rooting depth of the life forms, changes in turnover rates would be expected to occur at higher HAND thresholds for deep rooting plants and at lower HAND thresholds for shallow rooted-plants. Deep-rooted plants, however, may have access to water even at higher vertical distances from the water table, and therefore not show changes in composition until well away from streams. To provide further understanding of the role of root depth for the turnover rates, we regressed the HAND thresholds for the major changes of the six life forms against their respective maximum rooting depth. We compiled data on rooting depth in tropical forests for the six plants groups from published papers and unpublished information. Root depth can reach up to 18 m for trees (Nepstad *et al.* 1994), 0.6

m for palms (Ramos *et al.* 2009), 0.7 m for shrubs (Becker & Castillo 1990), 0.7 m on herbs and 0.3 m for ferns (F.R.C. Costa, unpublished data). No published data was found for root depth of adult lianas, but Restom and Nepstad (2004) reported 10 m for vine seedlings. Therefore, we used the same depth for lianas as for trees. Based on these data, there was no relation between HAND thresholds for major changes in composition and maximum rooting depth ($r^2 = 0.27$; $P = 0.29$; n = 6), indicating that this trait might not be linked to the differences among life forms. There is a large variation in rooting depths within life forms and their ontogeny (Canadell *et al.* 1996; Jackson *et al.* 1996), but the lack of available information on species rooting depth presently restricts detailed analysis.

Despite the large variation in rooting deep among plant life forms, Jackson et al. (1996) and Galbraith (in press) have shown that the majority of the roots in tropical forests are within the first 2 m of the soil surface, and that root biomass decrease exponentially with depth. Therefore, the deep roots of trees and lianas may not contribute greatly to water balance. There is surprisingly little literature on this subject and further detailed studies are needed to investigate the relationship between rooting depth, species turnover along edaphic gradients, and access to the water table.

HAND versus HASL and HDND

Earlier studies have shown that tree (Valencia *et al.* 2004), palm (Costa *et al.* 2009), shrub (Kinupp & Magnusson 2005) and herb, including fern (Costa et al. 2005) assemblage compositions are correlated with HASL in Amazonian forests. In this study, we showed that ordinations of all species, considering the life forms listed above and lianas together, also can be predicted by HASL and HDND. However, we found that, on its own, HAND was a better predictor of plant-composition changes at the mesoscale than HASL or HDND, even in the Reserva Ducke, where HASL is correlated with soil physical properties, nutrients and water availability (Chauvel et al. 1987; Hodnett et al. 1997). The main difference between HAND and HASL is that HAND values are relative to the local drainage (not to sea level), so it is a quantitative descriptor of the vertical distance from the saturated zone or the water table (Rennó *et al.* 2008; Nobre *et al.* 2011). For plants, access to ground water will be lower in areas with high HAND values, independent of HASL. Hydrologically similar terrains, such as valleys (or riparian areas), can be located at different HASL, but their HAND values will be near zero because they are vertically close to the saturated zone. As HAND measures distance to the local drainage, it should be a robust proxy for comparisons between areas located at different HASL.

HDND, together with HAND, is an important variable for determining soil draining because long horizontal distances from streams have higher draining potential and areas close to streams are usually poorly drained (Bell et al. 1994; Campling et al. 2002; Kravchenko et al. 2002). The finding that HAND was a better predictor of floristic composition than HDND indicates that changes in horizontal distance from drainage should be less important for plants than vertical distances from water table. It also indicates that HDND might be inappropriate to represent flat areas near streams (i.e. large bottom valleys), because these are waterlogged and poorly drained areas that sometimes can have relative high values of HDND. In the Reserva Ducke, there was a positive correlation between horizontal and vertical distances from drainage, even in large valley bottoms, but the shape and direction of this relation may vary across sites with distinct parent material and hydro-geological histories (e.g. in case of terrain depressions far from streams). The consistency of HAND being a better predictor than HDND of floristic composition should be tested on different geomorphologies, given the geological complexity of the Amazon Basin.

Implications for conservation strategies and climate change

The finding that the areas of higher species turnover and distinct floristic composition are also the areas directly affected by the water table fluctuation has implications for conservation planning and prediction of climate-change effects. In Brazil, environmental legislation protects the riparian zones that vary in width (horizontal distance from the stream margins) according to the stream size. Streams up to 10 m wide, such as those found in the Reserva Ducke, have protected zones that are 30 m wide on each margin. Our results indicate that zones of 30 m width along streams margins are insufficient for conservation of riparian areas because they do not include the areas of highest assemblage turnover (see Figure 3). In the Reserva Ducke, vertical distances from drainage of 8 to 18 m, where the composition changes slow down, correspond to horizontal distances of about 60 to 250 m (but one plot 15 m above the drainage was horizontally 350 m distant from a stream). Vertical distance from drainage, rather than only the horizontal distance, should be considered in the defining riparian habitats for conservation of riparian ecosystems. The critical vertical distance from drainage for conservation purposes could be defined by the upper limits of the water table fluctuation zone and this should vary across Amazonian landscapes due to variations in precipitation, topography and soil properties.

Although the long-term climate variability in Amazonia is complex, with opposite trends in precipitation or no clear patterns over different regions of the basin (Marengo 2004), large-scale numerical models project significant Amazonian drying and shift in vegetation types in the twenty-first century (Cox et al. 2000, 2008, Oyama 2003 but see Malhi et al. 2009). Evidence for a transition to a disturbance-dominated regime in some parts of the Amazon Basin was found recently (Davidson *et al.* 2012), and tree-ring chronology indicates increasing severity of El Niño events in the last two centuries (Schöngart *et al.* 2004). If climate becomes dryer, with more severe droughts, the soil-water storage and water table will decrease. A decrease in the water table level would narrow the areas of highest floristic turnover into smaller horizontal distances from streams. Further, this would cause shifts in species composition in riparian areas, because of differences in drought tolerance (Engelbrecht *et al.* 2007). Plants confined to plateaux areas could migrate downhill to track water table level changes. However, plants already confined to environments near drainages may not have many options to migrate to similar environments, because there are locally no similar environments and most species in tropical forests are not adapted for long-distance dispersal (Clark *et al.* 2005; Colwell *et al.* 2008; Terborgh *et al.* 2011). These species could become endangered by lack of suitable habitat.

Conclusions

This study has shown that changes in floristic composition are closely related to HAND in central Amazonia, suggesting an important role of soil hydrology for species composition and turnover in terra firme forests. The highest floristic turnover was found to occur in areas influenced by seasonal water table fluctuations and this finding has important implications for forest conservation. Brazilian environmental legislation protects riparian forests in strips of 30 m wide from small stream margins. Our results indicate that these 30 m strips are far too narrow to protect the areas of high species turnover close to the water table. In the Reserva Ducke, we found that these areas can reach 250 m from the streams. We recommend that vertical distances from the drainage (and seasonal water table fluctuation) rather than only horizontal distances should be used in the delimitation of riparian habitats for conservation of plant diversity and ecosystem functioning.

The strong relationships found between plant composition and HAND opens a promising opportunity to investigate plant species distribution and assemblage composition changes over larger scales, since HAND is based on SRTM data, available for the entire Amazon Basin.

Acknowledgments

Data used in this paper were obtained from data repositories maintained by the Brazilian Programme for Biodiversity Research (PPBio) and the National Institute for Amazonian Biodiversity (INCT-CENBAM). The field infrastructure was installed by the Programa Norte de Pós-Graduação (PNOPG-CAPES) and maintained by Brazilian PELD (LTER) Program financed by CNPq. J.S. and T.E. were supported during this study by a CNPq fellowship. Part of this manuscript was developed during the workshops of PPBio/PPGECO-INPA at Reserva Ducke and RAINFOR (Gordon and Betty Moore Foundation)-UFAC workshop in Rio Branco, Brazil, 2011. We thank Laszlo Nagy, Toby Marthews and one anonymous reviewer for the positive insights and suggestions on the manuscript structure.

Notes on contributors

Juliana Schietti is a Ph.D. student interested in understanding how variation in forest structure and functioning are related to hydrological processes.

Thaise Emilio is a Ph.D. student. She has been working with plant species and vegetation distribution across Amazonia. She is especially interested in palms and how environmental conditions drive their distribution and abundance.

Camilo D. Rennó is researcher working mostly on hydrology, image processing and geotechnologies.

Debora P. Drucker is an analyst in technology transfer and is interested in information management advancements to enable synthesis studies in ecology and biodiversity and foster dissemination of scientific knowledge.

Flávia R. C. Costa is a researcher, working mostly on the ecological determinants of plant species and assemblage distributions, and the impacts of human use on these.

Anselmo Nogueira is a post-doctoral researcher interested in understanding factors related to the plant distribution, specially of lianas, and also the evolution and ecology of animal-plant interactions.

Fernando O. G. Figueiredo is an M.Sc. researcher interested in understand the distribution of tropical herbs along edaphic and climate gradients.

Fabricio B. Baccaro is a Ph.D. student, is interested in ecology and evolution of parasite-host interactions.

Carolina V. Castilho is a biologist interested in long-term ecological studies, and uses permanent plots to evaluate changes in biomass, structure, and tree-species composition in tropical forests.

Valdely Kinupp is a professor interested in wild food plants, ethnobotany, economic botany, agroecology and plant taxonomy.

Jean-Louis Guillaumet works on tropical phytogeography.

Ana Raquel M. Garcia is a biologist who has studied the distribution and abundance of shrubs in the Reserva Ducke.

Albertina P. Lima works on different aspect of Amazonian biodiversity.

William E. Magnusson coordinates the Programme for Biodiversity Research (PPBio) in western Amazonia.

References

Albernaz AL, Pressey RL, Costa LRF, Moreira MP, Ramos JF, Assunção PA, Franciscon CH. 2012. Tree species compositional change and conservation implications in the white-water flooded forests of the Brazilian Amazon. Journal of Biogeography 39:869–883.

Baldwin DS, Mitchell AM. 2000. The effects of drying and re-flooding on the sediment and soil nutrient dynamics of soil lowland river-floodplain systems: a synthesis. Regulated Rivers: Research and Managment 467:457–467.

Balvanera P, Quijas S, Pérez-Jiménez. 2011. Distribution Patterns of Tropical Dry Forest Trees Along a Mesoscale Water Availability Gradient. Biotropica 43:414–422.

Becker P, Castillo A. 1990. Root architecture of shrubs and saplings in the understory of a tropical moist forest in lowland Panama. Biotropica 22:242–249.

Bell JC, Cunningham RL, Havens MW. 1994. Soil Drainage Class Probability Mapping Using a Soil-Landscape Model. Soil Science Society of America Journal 58:464–470.

Brown DJ, Clayton MK, McSweeney K. 2004. Potential terrain controls on soil color, texture contrast and grain-size deposition for the original catena landscape in Uganda. Geoderma 122:51–72.

Burnham KP, Anderson DR. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods & Research 33:261–304.

Calcagno V, De Mazancourt C. 2010. glmulti : An R package for easy automated model selection with (generalized) linear models. Journal of Statistical Software 34:1–29.

Campling P, Gobin A, Feyen J. 2002. Logistic Modeling to Spatially Predict the Probability of Soil Drainage Classes. Soil Science Society of America Journal 66:1390–1401.

Canadell J, Jackson RB, Ehleringer JR, Mooney HA, Sala OE, Schulze ED. 1996. Maximum Rooting Depth of Vegetation Types at the Global Scale. Oecologia 108:583–595.

Chauvel A, Lucas Y, Boulet R. 1987. On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. Experimentia 43:234–241.

Clark C, Poulsen J, Bolker B, Connor E, Parker V. 2005. Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. Ecology 86:2684–2694.

Colwell RK, Brehm G, Cardelús CL, Gilman AC, Longino JT. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322:258.

Comita LS, Engelbrecht BMJ. 2009. Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. Ecology 90:2755–2765.

Costa FRC, Guillaumet J-L, Lima A, Pereira O. 2009. Gradients within gradients: the mesoscale distribution patterns of palms in a central Amazonian forest. Journal of Vegetation Science 20:69–78.

Costa FRC, Magnusson WE, Luizao RC. 2005. Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. Journal of Ecology 93:863–878.

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.

Costa FRC. 2006. Mesoscale Gradients of Herb Richness and Abundance in Central Amazonia. Biotropica 38:711–717.

Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408:184–7.

Cox PM, Harris PP, Huntingford C, Betts RA, Collins M, Jones CD, Jupp TE, Marengo JA, Nobre CA. 2008. Increasing risk of Amazonian drought due to decreasing aerosol pollution. Nature 453:212–5.

Dalling J, Hubbell SP, Silvera K. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. Journal of Ecology 86:674–689.

Davidson EA, De Araújo AC, Artaxo P, Balch JK, Brown IF, C. Bustamante MM, Coe MT, DeFries RS, Keller M, Longo M, et al. 2012. The Amazon basin in transition. Nature 481:321–328.

Daws MI, Mullins CE, Burslem DFRP, Paton SR, Dalling JW. 2002. Topographic position affects the water regime in a semideciduous tropical forest in Panama. Plant and Soil 238:79–90.

Drucker DP, Costa FRC, Magnusson WE. 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 BMJ, Comita LS, Condit R, Kursar T a, Tyree MT, Turner BL, Hubbell SP. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447:80–2.

Gibbons JM, Newbery DM. 2002. Drought avoidance and the effect of local topography on trees in the understorey of Bornean lowland rain forest. Plant Ecology 164:1–18.

Groom PK. 2004. Rooting depth and plant water relations explain species distribution patterns within a sandplain landscape. Functional Plant Biology 31:423–428.

Harms KE. 1997. Habitat-Specialization and Seed-Dispersal Limitation in a Neotropical Forest. Princeton University.

Hodnett MG, Tomasella J. 2002. Marked differences between van Genuchten soil water-retention parameters for temperate and tropical soils: a new water-retention pedo-transfer functions developed for tropical soils. Geoderma 108:155–180.

Hodnett MG, Vendrame I, Marques Filho DO, Oyama M, Tomasella J. 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 1:265–277.

Jackson RB, Canadell J, Ehleringer HA, Mooney HA, Schulze ED, Sala OE. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108:389–411.

Jirka S, McDonald AJ, Johnson MS, Feldpausch TR, Couto EG, Riha SJ. 2007. Relationships between soil hydrology and forest structure and composition in the southern Brazilian Amazon. Journal of Vegetation Science 18:183–194.

Joly CA, Crawfordf RMM. 1982. Variation in Tolerance and Metabolic Responses to Flooding in some Tropical Trees. Journal of Experimental Botany 33:799–809.

Joslin JD, Wolfe MH, Hanson PJ. 2000. Effects of altered water regimes on forest root systems. New Phytologist 147:117–129.

Junk WJ. 1997. The Central Amazon Floodplain: Ecology of a Pulsing System. Springer.

Kanagaraj R, Wiegand T, Comita LS, Huth A. 2011. Tropical tree species assemblages in topographical habitats change in time and with life stage. Journal of Ecology 99:1441–1452.

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.

Kravchenko AN, Bollero GA, Omonode RA, Bullock DG. 2002. Quantitative Mapping of Soil Drainage Classes Using Topographical Data and Soil Electrical Conductivity. Soil Science Society of America Journal 66:235–243.

Magnusson WE, Lima AP, Luizão R, Luizão F, Costa FRC, Castilho CV, Kinupp V. 2005. RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. Biota Neotropica 5:19–24.

Malhi Y, Aragão L, Galbraith D, Huntingford C, Fisher R, Zelazowski P, Sitch S, Mcsweeney C, Meir P. 2009. Exploring the likelihood and mechanism of a climate-change-induced dieback of the. Proceedings of the National Academy of Science 49:20610–20615.

Marengo JA. 2004. Interdecadal variability and trends of rainfall across the Amazon basin. Theoretical and Applied Climatology 78:79–96.

Marques-Filho A de O, Ribeiro M de NG, Santos HM, Santos JM. 1981. Estudos climatologicos da Reserva Florestal Ducke - Manaus-AM. IV. Precipitacao. Acta Amazonica 11:759–768.

Marshall TJ, Holmes JW, Rose C. 1996. Soil Physics. 3rd ed. Cambridge: Cambridge University Press.

Marthews TTR, Burslem DFRPD, Paton SRR, Yangüez F, Mullins CEE. 2008. Soil drying in a tropical forest : Three distinct environments controlled by gap size. Ecological Modelling 216:369–384.

McCune B, Grace AJB. 2002. Analysis of Ecological Communities. MjM Software Design.

Naiman RJ, Henri D, Décamps H. 1997. The ecology of interfaces: riparian zones. Annual review of Ecology and Systematics 28:621–658.

Nepstad DC, Carvalho CR, Davidson EA, Jipp PH, Lefebvre PA, Negreiros GH, Silva ED, Stone TA, Trumbore SE, Vieira S. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonia forests and pastures. Nature 372:666–669.

Newbery DM, Campbell EJF, Proctor J, Still MJ. 1996. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia. Species composition and patterns in the understorey. 122:193–220.

Nobre AD, Cuartas LA, Hodnett M, Rennó CD, Rodrigues G, Silveira A, Waterloo M, Saleska S. 2011. Height Above the Nearest Drainage – a hydrologically relevant new terrain model. Journal of Hydrology 404:13–29.

Nogueira A, Costa FRC, Castilho CV. 2011. Liana abundance patterns: the role of ecological filters during development. Biotropica 43:442–449.

Oyama MD. 2003. A new climate-vegetation equilibrium state for Tropical South America. Geophysical Research Letters 30:10–13.

Ozinga W, Schaminée J, Bekker R, Bonn S, Poschold P, Tackenberg O, Bakker J, Van Groenendael JM. 2005. Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. Oikos 108:555–561.

Page CN. 2002. Ecological strategies in fern evolution: a neopteridological overview. Review of Palaeobotany and Palynology 119:1–33.

Parmentier I, Hardy OJ. 2009. The impact of ecological differentiation and dispersal limitation on species turnover and phylogenetic structure of inselberg’s plant communities. Ecography 32:613–622.

Parolin P. 2002. Submergence tolerance vs. escape from submergence: two strategies of seedling establishment in Amazonian floodplains. Environmental and Experimental Botany 48:177–186.

Phillips OL, Aragão LEOC, Lewis SL, Fisher JB, Lloyd J, López-González G, Malhi Y, Monteagudo A, Peacock J, Quesada CA, et al. 2009. Drought sensitivity of the Amazon rainforest. Science 323:1344–1347.

Phillips OL, Hall P, Gentry AH, Sawyer SA, Vásquez R. 1994. Dynamics and species richness of tropical rain forests. Proceedings of the National Academy of Science 91:2805–2809.

Prates-Clark CDC, Saatchi SS, Agosti D. 2008. Predicting geographical distribution models of high-value timber trees in the Amazon Basin using remotely sensed data. Ecological Modelling 211:309–323.

Pyke CR, Condit R, Aguilar S, Lao S. 2001. Floristic composition across a climatic gradient in a neotropical lowland forest. Journal of Vegetation Science 12:553–566.

R 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/.

Raes N, Roos MC, Slik JWF, Van Loon EE, Steege H Ter. 2009. Botanical richness and endemicity patterns of Borneo derived from species distribution models. Ecography 32:180–192.

Ramos A, Folegatti MV, Bovi MLA, Diotto AV. 2009. Distribuição espacial do sistema radicular da pupunheira em função de lâminas de irrigação. Irriga 14:431–440.

Rennó CD, Nobre AD, Cuartas LA, Soares JV, Hodnett MG, Tomasella J, Waterloo MJ. 2008. HAND, a new terrain descriptor using SRTM-DEM: Mapping terra-firme rainforest environments in Amazonia. Remote Sensing of Environment 112:3469–3481.

Restom TG, Nepstad DC. 2004. Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia. Forest Ecology and Management 190:109–118.

Ribeiro JELS, Hopkins MJG, Vicentini A, Sothers CA, Costa MAS, Brito JM, Souza MAD, Martins LH, Lohmann LG, Assunção PA, et al. 1999. Flora da Reserva Ducke. Guia de identificação das plantas vasculares de uma floresta de terra firme na Amazônia Central. Manaus: INPA - DFID.

Rodriguez-Iturbe I. 2000. Ecohydrology: A hydrologic perspective of climate-soil-vegetation dynamics. Water Resources Research 36:3–9.

Saatchi SS, Houghton RA, Dos Santos Alvalá RC, Soares J V., Yu Y. 2007. Distribution of aboveground live biomass in the Amazon basin.

Sabo JL, Sponseller MD, Gade K, Harms T, Heffernan J, Jani A, Katz G, Soykan C, Watts J, Welter J. 2005. Riparian zones increase regional species richness by harboring different, not more, species. Ecology 86:56–62.

Salas W a., Ducey MJ, Rignot E, Skole D. 2002. Assessment of JERS-1 SAR for monitoring secondary vegetation in Amazonia: I. Spatial and temporal variability in backscatter across a chrono-sequence of secondary vegetation stands in Rondonia. International Journal of Remote Sensing 23:1357–1379.

Scarano FR, Ribeiro KT, De Moraes LFD, De Lima HC. 1997. Plant establishment on flooded and unflooded patches of a freshwater swamp forest in southeastern Brazil. Journal of Tropical Ecology 14:793–803.

Schnitzer SA. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. The American Naturalist 166:262–76.

Schulman L, Ruokolainen K, Junikka L, Sääksjärvi IE, Salo M, Juvonen S-K, Salo J, Higgins M. 2007. Amazonian biodiversity and protected areas: do they meet? Biodiversity and Conservation 16:3011–3051.

Schöngart J, Junk WJ, Piedade MTF, Ayres JM, Huttermann A, Worbes M, Schongart J. 2004. Teleconnection between tree growth in the Amazonian floodplains and the El Nino-Southern Oscillation effect. Global Change Biology 10:683–692.

Silvertown J, Dodd M, Gowing D, Mountford J. 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. Nature 400:61–63.

Smith LC. 2002. Emerging applications of interferometric synthetic aperture radar (InSAR) in geomorphology and hydrology. Annals of the Association of American Geographers 92:385–398.

Svenning J-C. 2001. On the role of microenvironmental heterogeneity in ecology and diversification of neotropical rain-forest palms (Arecaceae). The Botanical Review 67:1–53.

Terborgh J, Loayza PA, Dexter K, Cornejo F, Carrasco C. 2011. Decomposing dispersal limitation: limits on fecundity or seed distribution? Journal of Ecology 99:935–944.

Toledo JJ, Magnusson WE, Castilho C V, Nascimento HEM. 2012. Forest Ecology and Management 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, Hodnett MG, Cuartas LA, Nobre AD, Waterloo MJ, Oliveira SM. 2008. The water balance of an Amazonian micro-catchment: the effect of interannual variability of rainfall on hydrological behaviour. Hydrological Processes 22:2133–2147.

Tuomisto H, Poulsen AD. 2000. Pteridophyte diversity and species composition in four Amazonian rain forests. Journal of Vegetation Science 11:383–396.

Valencia R, Foster RB, Villa G, Svenning J, Hernández C, Romoleroux K, Losos E, Magård E, Balslev H. 2004. Tree species distributions and local habitat variation in the Amazon : large forest plot in eastern Ecuador. Journal of Ecology 92:214–229.

Valeriano M, Kuplich T, Storino M, Amaral B, Mendesjr J, Lima D. 2006. Modeling small watersheds in Brazilian Amazonia with shuttle radar topographic mission-90m data. Computers & Geosciences 32:1169–1181.

Vormisto J, Phillips OL, Ruokolainen K, Tuomisto H, Vásques R. 2000. A comparison of fine-scale distribution patterns of four plant groups in an Amazonian rainforest. Ecography 23:349–359.

Table 1. Numbers of species and sampling design for the six life forms sampled in the permanent plots of the Reserva Ducke, Manaus, Brazil. *D*, diameter measured at 130 cm from the rooting point. H, height from the ground.

Life form	**Taxon included**	**Number of species**	**Number of plots**	**Plot area**	**Inclusion limit**
Trees			72	0.5-1 ha	> 10-30 cm DBH
	Burseraceae	40			
	Chrysobalanaceae	46			
	Euphorbiaceae	31			
	Fabaceae	139			
	Lauraceae	100			
	Lecythidaceae	42			
	Moraceae	32			
	Myristicaceae	21			
	Sapotaceae	69			
Lianas	Bignoniaceae	42	32	0.25-1 ha	> 1-5 cm *D*
Palms	Arecaceae	44	72	0.1 ha	> 100 cm H
Shrubs	Rubiaceae (*Psychotria)*	23	57	0.1 ha	No limit
	Piperaceae *(Piper)*	26	57	0.1 ha	> 50 cm H
Herbs			56	0.05 ha	> 5 cm H
	Poales	22			
	Zingiberales	27			
	Other	12			
Ferns			54	0.025 ha	> 5 cm H
	Pteridophyta	21			
	Lycophyta	4			
All species	All above	741	22	All above	All above

Table 2. Percent of variance captured by quantitative and qualitative Non-Metric Multidimensional Scaling (NMDS) ordination in one axis for six life forms individually and all six combined (All life forms), based on data from 72 permanent forest plots, Reserva Ducke, Manaus, Barzil. Probabilities (*P*), r^2_{adj} (r^2) and parameters of the exponential decay model (equation 1) between life form/all life forms species composition, given by the NMDS axis, and the three predictors: height above the nearest drainage (HAND), horizontal distance from nearest drainage (HDND) and Shuttle Radar Topography Mission – height above sea level (SRTM-HASL). Delta Akaike Information Criterion (ΔAIC) values for a subset of 18 plots are presented for comparisons among models of plant composition for the six life forms. ΔAIC was calculated in relation to tree species composition versus HAND model, which had the most support.

Life form Variance explained NMDS -1 dimension (Quantitative/qualitative)	**Predictor**	**Quantitative Composition Changes**					**Qualitative Composition Changes**					
		y_0	**a**	**b**	**r^2**	**ΔAIC**	**y_0**	**a**	**b**	**r^2**	**ΔAIC**	***P***
Tree	**HAND**	**-0.31**	**1.54**	**0.13**	**0.72**	0.00	**-0.21**	**1.31**	**0.17**	**0.74**	0.00	**< 0.001**
(80% / 80%)	HDND	-0.32	1.41	0.01	0.48		-0.21	1.29	0.01	0.48		< 0.001
	SRTM-HASL	-0.47	15.35	0.05	0.57		-0.41	8.72	0.04	0.56		< 0.001
Liana	**HAND**	**-0.68**	**2.75**	**0.16**	**0.82**	16.06	**-0.48**	**2.49**	**0.23**	**0.72**	22.81	**< 0.001**
(60% / 79%)	HDND	-0.75	3.30	0.01	0.77		-0.48	3.12	0.02	0.64		< 0.001
	SRTM-HASL	-0.85	78.88	0.06	0.77		-0.49	347.67	0.10	0.61		< 0.001
Palm	**HAND**	**-0.38**	**2.40**	**0.18**	**0.67**	13.98	**-0.16**	**1.16**	**0.21**	**0.41**	9.88	**< 0.001**
(92% / 87%)	HDND	-0.31	2.96	0.02	0.42		-0.13	1.36	0.02	0.22		< 0.001

	SRTM-HASL	-0.52	36.00	0.06	0.44		-0.21	18.20	0.06	0.23		< 0.001
Shrubs	**HAND**	**-0.23**	**2.30**	**0.28**	**0.49**	24.83	**-0.19**	**2.10**	**0.31**	**0.63**	9.81	**< 0.001**
(57% / 72%)	HDND	-0.23	3.13	0.03	0.35		-0.18	3.30	0.03	0.43		< 0.001
	SRTM-HASL	-0.35	33.10	0.06	0.26		-0.39	17.50	0.05	0.42		< 0.001
Herbs	**HAND**	**-0.23**	**1.13**	**0.13**	**0.26**	8.97	**-0.23**	**1.13**	**0.13**	**0.26**	16.61	**< 0.001**
(64% / 65%)	HDND	-0.20	1.45	0.17	0.20		-0.20	1.43	0.68	0.21		< 0.001
	SRTM-HASL	-0.25	46.71	0.07	0.16		-0.25	49.64	0.07	0.17		< 0.004
Ferns	**HAND**	**-0.49**	**3.63**	**0.20**	**0.58**	44.73	**-0.27**	**1.75**	**0.17**	**0.56**	33.51	**< 0.001**
(75% / 86%)	HDND	0.45	4.67	0.02	0.43		-0.24	1.91	0.02	0.37		< 0.002
	SRTM-HASL	-0.67	80.54	0.06	0.32		0.32	-0.40	24.86	0.32		< 0.001
All life forms	**HAND**	**-0.38**	**1.73**	**0.17**	**0.84**	-	**-0.20**	**1.19**	**0.25**	**0.68**	-	**< 0.001**
(83% / 84%)	HDND	-0.39	2.00	0.01	0.76		-0.19	1.63	0.02	0.62		< 0.001
	SRTM-HASL	-0.48	123.92	0.08	0.72		-0.24	78.44	0.08	0.42		< 0.002

Figures

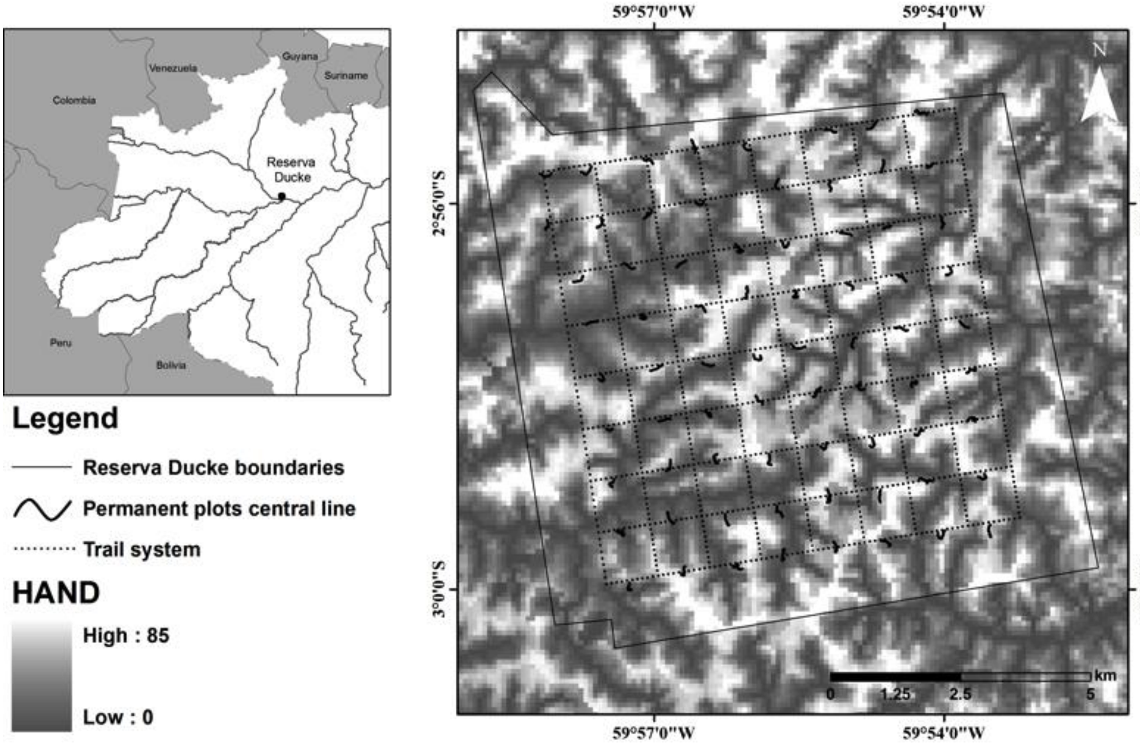


Figure 1. The Reserva Ducke, Manaus, Brazil grid system with 72 uniformly-distributed permanent plots and HAND (height above the nearest drainage) data in the background. Centre lines of plots follow terrain contours.

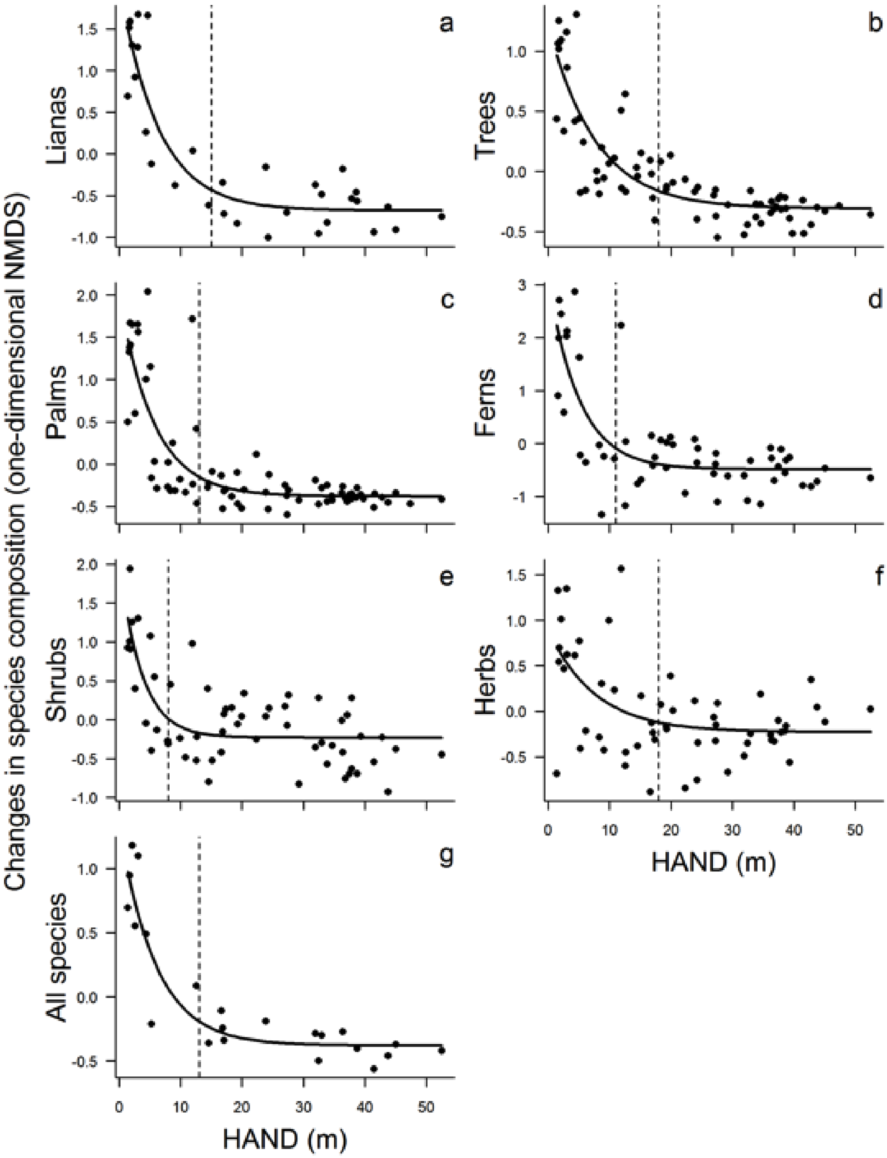


Figure 2. Relationships between quantitative composition changes of six life forms and all species combined and HAND (height above the nearest drainage), Reserva Ducke, Manaus, Brazil. Dashed lines show the thresholds of vertical distance from drainage below which 90% of the changes in species composition take place: (a) Lianas, r2adj = 0.82 and threshold of 15m; (b) trees, r2adj = 0.72 and threshold of 18 m; (c) palms, r2adj = 0.67 and threshold of 13 m; (d) ferns, r2adj = 0.58 and threshold of 11 m; (e) shrubs, r2adj = 0.49 and threshold of 8 m; (f) herbs, r2adj = 0.26 and threshold of 18 m and (g) all life forms, r2adj = 0.84 and threshold of 13 m. Changes in species composition were reduced to one dimension, using Non-Metric Multidimensional Scaling (NMDS).

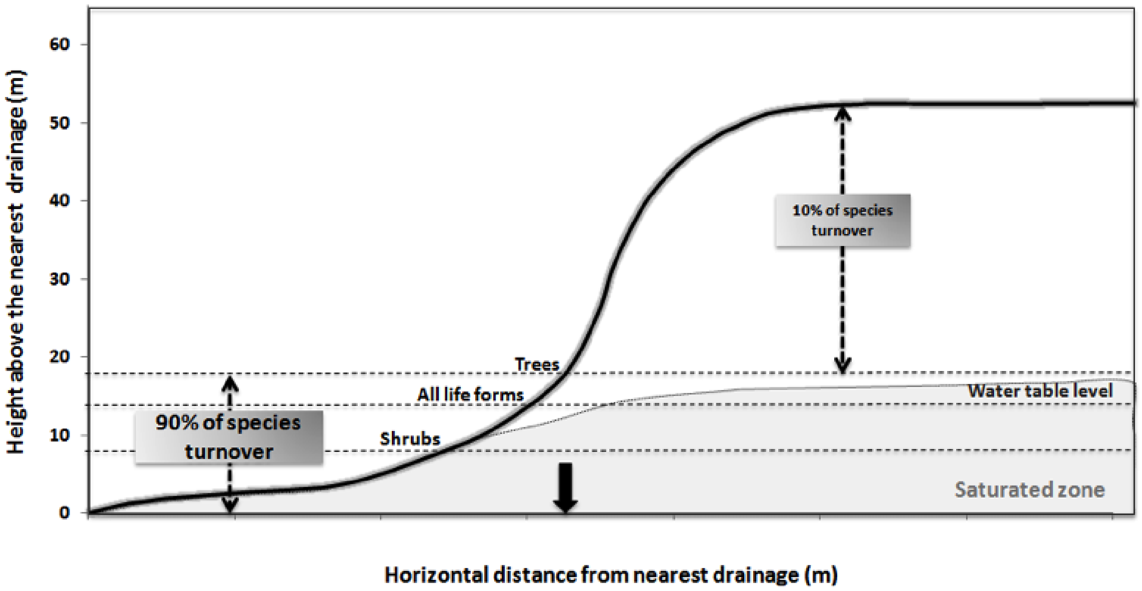


Figure 3. A schematic view of where the major part of floristic composition changes takes place along the vertical distances from nearest drainage (HAND) gradient. Horizontal dashed lines show HAND thresholds for 90% of composition changes in shrubs (8 m), all life forms combined (13 m) and trees (18 m). Water table fluctuation zone is shown in grey. Horizontal distance from drainage (HDND) that corresponds to 18 m HAND threshold in the Reserva Ducke, Manaus, Brazil extends 350 m and is highlighted by the black arrow in the schema.

Supplementary online material – Plant Ecology & Diversity

Table S1. Candidate models for prediction of composition changes in five plant life history types and all species combined (Flora). Three predictors: height above the nearest drainage (HAND), horizontal distance from drainage (HDND) and height above sea level (HASL) were tested in simple and multiple linear regressions. All variables were log10 transformed to improve normality. Minimal adequate model was selected based on Akaike Information Criterion (AIC). Models with Δ AIC < 2 (in bold) support no differences between models. HDND was calculated using flow direction paths between plots and drainage and HASL was derived from Shuttle Radar Topography Mission SRTM) data.

Plant History Type	**Model**	**Δ AIC**
Trees	**Species composition = 1 + HAND + HDND**	**0**
	Species composition = 1 + HAND	**0.31**
	Species composition = 1 + HAND + HDND + HASL	**1.78**
	Species composition = 1 + HAND + HASL	2.15
	Species composition = 1 + HDND + HASL	25.98
	Species composition = 1 + HASL	30.17
	Species composition = 1 + HDND	39.72
Lianas	**Species composition = 1 + HAND**	**0**
	Species composition = 1 + HAND + HASL	**1.42**
	Species composition = 1 + HDND + HASL	**1.72**
	Species composition = 1 + HAND + HDND	**1.74**
	Species composition = 1 + HAND + HDND + HASL	2.82
	Species composition = 1 + HDND	5.02
	Species composition = 1 + HASL	6.78
Palms	**Species composition = 1 + HAND + HDND**	**0**
	Species composition = 1 + HAND	**0.98**
	Species composition = 1 + HAND + HDND + HASL	**1.22**
	Species composition = 1 + HAND + HASL	2.11
	Species composition = 1 + HDND + HASL	20.69
	Species composition = 1 + HASL	22.38
	Species composition = 1 + HDND	24.37
Shrubs	**Species composition = 1 + HAND + HASL**	0
	Species composition = 1 + HAND	0.82
	Species composition = 1 + HAND + HDND + HASL	1.87
	Species composition = 1 + HAND + HDND	2.61
	Species composition = 1 + HDND	11.52
	Species composition = 1 + HDND + HASL	13.13
	Species composition = 1 + HASL	18.45

Herbs	**Species composition = 1 + HAND**	**0**
	Species composition = 1 + HAND + HASL	**1.59**
	Species composition = 1 + HAND + HDND	**1.91**
	Species composition = 1 + HAND + HDND + HASL	3.52
	Species composition = 1 + HDND	5.25
	Species composition = 1 + HDND + HASL	6.46
	Species composition = 1 + HASL	7.00
Ferns	**Species composition = 1 + HAND**	**0**
	Species composition = 1 + HAND + HASL	**0.27**
	Species composition = 1 + HAND + HDND	**2.00**
	Species composition = 1 + HAND + HDND + HASL	2.26
	Species composition = 1 + HDND	9.41
	Species composition = 1 + HDND + HASL	10.79
	Species composition = 1 + HASL	17.08
Flora	**Species composition = 1 + HAND**	**0**
	Species composition = 1 + HAND + HASL	**1.73**
	Species composition = 1 + HAND + HDND	**1.96**
	Species composition = 1 + HAND + HDND + HASL	3.72
	Species composition = 1 + HDND + HASL	7.34
	Species composition = 1 + HDND	7.98
	Species composition = 1 + HASL	14.46

Capítulo 2

Schietti, J., Martins, D.L., Emilio, T., Souza, P., Levis, C., Pinto, J.L.P.V., Moulatlet, G., Stark, S.C., Baccaro, F.B., Sarmento, K., de Araújo, R.N.O., Costa, F.R.C., Schöngart, J., Quesada, C.A., Saleska, S.R., Tomasella, J., Magnusson, W. Linking forest structure and stand biomass along natural disturbance gradients in central Amazonia. Manuscrito em preparação para *Journal of Ecology*.

Linking forest structure and stand biomass along natural disturbance gradients in central Amazonia

Juliana Schietti*[1], Demétrius Martins[2], Thaise Emilio[1], Priscila Souza[2], Carolina Levis[2], José Luis Purri da Veiga Pinto[3], Gabriel Moulatlet[2], Scott C. Stark[4], Fabricio B. Baccaro[5], Kelly Sarmento[2], R. Nazaré O. de Araújo[6], Flávia R. C. Costa[2], Jochen Schöngart[1,7], Carlos A. Quesada[8], Scott R. Saleska[4], Javier Tomasella[9], William E. Magnusson[2,6]

[1] Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia (INPA). Av. Ephigênio Sales 2239, 69011-970, Manaus, AM, Brazil.

[2] Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA). Av. Ephigênio Sales 2239, CEP 69011-970, Manaus, Amazonas, Brazil

[3] Programa de Capacitação Institucional (PCI/Geoma), Instituto Nacional de Pesquisas da Amazônia (INPA). Av. Ephigênio Sales 2239, CEP 69011-970, Manaus, Amazonas, Brazil.

[4] Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, 85721, USA

[5] Departamento de Biologia, Universidade Federal do Amazonas – UFAM

[6] Centro de Estudos Integrados da Biodiversidade Amazônica – INCT CENBAM

[7] Max Planck Institute for Chemistry, Biogeochemistry Department, Mainz, Germany

[8] Coordenação de Dinâmica Ambiental, Instituto Nacional de Pesquisas da Amazônia (INPA). Av. Ephigênio Sales 2239, CEP 69011-970, Manaus, Amazonas, Brazil

[9] Centro Nacional de Monitoramento e Alertas de Desastres Naturais (Cemaden/MCTI). Rodovia Presidente Dutra, Km 40, CEP: 12630-000, Cachoeira Paulista, SP, Brazil

* author for correspondence: jujuschietti@gmail.com

Running headline: *Structure and biomass in the Amazon forest*

Summary

1. A negative relationship between stand biomass and the density of stems is expected to develop during the self-thinning process in resource-limited forests; this leads to a large proportion of the total biomass occurring in large trees. Nevertheless, frequent disturbance regimes can reduce self-thinning and the accumulation of large trees.

2. We investigated size-density relationships and the contribution of large trees (dbh ≥ 70cm) to stand biomass in 55 1-ha plots along a 600 km transect in central Amazonia. The effects of seasonality and disturbance gradients on forest-structure components (density of stems and mean individual mass) and stand biomass were examined.

3. Stand biomass increased in forests with higher density of stems. Forests in areas with longer dry seasons had a lower density of stems; however, individual mass (and wood density) was higher in these regions. These components of biomass seem to counterbalance each other and no effect of seasonality was detected on stand biomass.

4. Contrary to expectation large trees contained a low percentage of stand biomass—on average 5%--while half of the stand biomass was represented by small trees with diameters < 27 cm. This likely indicates that persistent or strong disturbance plays a critical role in forest structure and biomass in the south-central Amazon. Frequent storms and soil physical constraints were identified as sources of disturbance in the region. Forests with higher frequency of exogenous disturbances showed higher stand biomass due to the increase in stem packing.

Synthesis: The effects of environmental gradients on specific structural components of stand biomass differ such that strong positive effects on one component can mitigate or reverse strong negative effects on other component. Future work on the determinants of stand biomass should investigate the contributions of individual components to biomass and must reevaluate the disturbance paradigm—disturbance may lead to high densities of intermediate sized individuals, enhancing stand biomass.

Key-words: aboveground biomass, community ecology, large trees, self-thinning, stem density, storms, tropical lowland forest.

Introduction

Biomass stocks and forest structure vary widely across forest ecosystems. Since stand biomass is mainly a product of the average plant size and the density of stems, these forest-structure components largely determine stand biomass. Forest structure, and therefore stand biomass, responds to gradients of environmental conditions and disturbance regimes (Urquiza-Haas, Dolman, & Peres 2007; Slik *et al.* 2010). Despite the recognized importance of these gradients, a general principle linked to resource limitation that was initially observed in monospecific stands seems to determine the occupation of space and biomass accumulation. Over time or across different communities, the average individual size increases with the decrease in density of stems (Westoby 1984). As plants grow there is less space for individuals, resulting in a self-thinning process. The self-thinning rule (Yoda *et al.* 1963) describes the density-dependent plant mortality due to competition in crowded even-aged stems. Mortality in self-thinning stands is a function of biomass accumulation that results from individuals occupying more area and volume as they grow (Westoby 1984).

Self-thinning has been demonstrated in many planted and natural stands and also in assemblages composed of mixed species and ages (White 1981; Westoby 1984; Niklas, Midgley, & Enquist 2003a; Luyssaert *et al.* 2008). The self-thinning relationship also can be expressed as the inverse relationship between stand biomass and maximum density of individuals (Weller 1987; Petraitis 1995). A general allometric scaling model for crowded tree-dominated assemblages (Niklas *et al.* 2003a) predicts that the average plant biomass (B_i) scales as the -4/3 exponent of stem density ($B_i = N_{stems}^{-4/3}$) and the total stand biomass (TB) scales as the -1/3 exponent of stem density ($TB = N_{stems}^{-1/3}$). These negative relationships with stem density imply that greater biomass stocks should be found in forests with fewer stems and larger individuals (Midgley 2001), and that the major part of the stand biomass should be found in the larger individuals in the stand.

Evidence suggests that large trees—specifically, those defined as diameter at breast height (dbh) > 70 cm—comprise the largest component of biomass in forests. Nearly half of the stand biomass can be attributed to large individuals in mixed-conifer forests in North America (Lutz et al 2012) and in tropical forests in Asia (Paoli et al 2007) and Africa (Slik *et al.* 2013). In Neotropical forests, a large but variable (14 to 45%) proportion of stand biomass is attributed to trees with dbh > 70cm (Brown *et al.* 1995; Brown, Schroeder, & Birdsey 1997; Clark & Clark 1996; Chave, Riéra, & Dubois 2001; Chave *et al.* 2003; Slik *et al.* 2013).

One explanation for the variable contribution of large trees to stand biomass across forests may be disturbance regimes. Frequent disturbances may prevent self-thinning and the development of large-statured high biomass stands. By causing density-independent mortality disturbance may alter the densities of individuals relative to expectations of thinning theory and prevent individuals from reaching larger diameters (Niklas, Midgley, & Rand 2003b). If the disturbance regime is more important than resource limitation, the relationship between stand biomass and number of stems will strongly deviate from the self-thinning rule and trees will not fully fill canopy space. In this case, stand biomass will increase with the density of stems and increasing space filling in the canopy, in contrast to the negative relationship predicted by the self-thinning rule. Furthermore, if disturbance preferentially impact larger trees as in the case of prolonged droughts (Phillips *et al.* 2010), stand biomass may be concentrated in small to midsize stems because large individuals should be rare.

In the Amazon basin, there is an east-west gradient of forest dynamics and structure that has been attributed to soil conditions initiating endogenous disturbance (Phillips *et al.* 2004; Quesada *et al.* 2012a) and storms causing large exogenous disturbances, such as blow-downs (Espírito-Santo *et al.* 2010). Higher turnover rates (Phillips *et al.* 2004) and lower stand-biomass stocks were found in the more fertile and less structured soils in western Amazonia (Quesada *et al.* 2012a), contrasting to the less dynamic and higher biomass forests in poorer well-structured soils in eastern Amazonia. If these hypotheses are correct, forest-structure components related to biomass (density of stems and average individual size) should vary in relation to the frequency of storms, soil physical restrictions and fertility gradients. Patterns postulated to be related to disturbances are superimposed on patterns associated with seasonality (dry-season length) that should result in a gradient of decrease in biomass where the climate is more seasonal (Malhi *et al.* 2006).

We investigated the relationships between stand structural variables, stand biomass, seasonality and environmental gradients of endogenous and exogenous disturbance in 55 permanent plots along a 600 km transect, from near Manaus in central Amazonia to Humaitá on the south-western frontier of the Amazon forest. This transect along the Madeira-Purus interfluve is topographically relatively homogeneous, but covers gradients in seasonality, frequency of storms, and soil physical structure and fertility. Although most of the hypotheses related to biomass accumulation make similar predictions about the spatial distribution of biomass, dissecting overall biomass into its components (density of stems and mean individual mass) and within size classes allowed us to gain insights into the most likely mechanisms causing geographical patterns.

Methods

Study area

The study was conducted in 55 1ha plots along a 600 km transect in the Purus-Madeira interfluve, south of the Amazon River in central Amazonia (Fig. 1). The plots were distributed in 11 research sites along the BR-319, a road that has been largely abandoned for regular traffic since the 1970s. In each site, 5 plots were regularly distributed along a 5 km trail and the plots were 1 km apart. Plots were established at least 1 km from the road to avoid secondary forests. The Purus-Madeira interfluvial region has a relatively recent geological origin with unstable sediments from Late Pleistocene or Early Eocene with predominantly flat topography (Sombroek 2000); elevation above sea level varies from 27 to 80 meters along the transect (Shuttle Radar Topography data). This region is part of the Amazon basin “Loamy plains” (Sombroek 2000), a landform covering around 11% of the Amazon basin, including the low interfluvial areas of Rio Negro-Amazonas and Juruá-Purus-Madeira.

Soils are mainly Gleysols and Plinthosols with poor water drainage and the predominant texture is silt to fine sand (Sombroek 2000). The water table is shallow, within 7m of the surface throughout the year in most of the area (J. Schietti & T. Emilio unpublished data). The mean annual precipitation varied from 2000 to 2400 mm, with a number of consecutive months with less than a 100 mm of rainfall (a threshold generally considered an indicator of the dry season) ranging from 1 month to the north of the transect to 4 month per year in the south (Sombroek 2001). Large areas are waterlogged during the rainy season, and many of the small streams dry out during the dry season. The vegetation is classified as lowland dense rainforests in the north and lowland open rainforests dominated by palms in the south (BRASIL 1974).

Vegetation data

Diameter at breast height of 30,239 stems including trees and palms was measured in the 55 plots. The plots had a 250 m central transect that follows the terrain elevation to minimize variation in soil characteristics and water-table depth in the plots. We followed a hierarchical system to measure the trees and palms along the 250 m plot central line (Magnusson *et al.* 2005). All stems with dbh $\geq$ 30 cm were measured in approximately 1 ha (250 x 40 m), stems with dbh $\geq$ 10 cm were measured in a subplot of approximately 0.5 ha (250 x 20 m) and stems with dbh $\geq$ 1 cm were measured in subplot of approximately 0.025 ha (250 x 1 m).

Biomass of individual trees was calculated based on diameter (D), height (H) and wood density (ρ_w). We used equation (1) for moist-forest stands from Chave *et al.* (2005) with parameters adjusted for by Feldpausch *et al.* (2012).

$$\text{Biomass} = \exp(-2.9205 + 0.9894 \times \ln(D^2 \rho_w H)) \qquad (1)$$

Tree height was estimated using D-H allometric equations adjusted for each of the 11 research sites along the transect. The diameter and height of 1544 trees (on average 129 trees per site) were measured in different diameter classes (D. Martins, unpublished data). Heights were estimated by a single observer using a Vertex hypsometer (Vertex Laser VL400 Ultrasonic-Laser Hypsometer III, Haglöf of Sweden). We used a power model to fit the H-D allometric equations (Table S1, Supporting Information).

Wood density was obtained from the global wood density database (Zanne *et al.* 2009; Chave *et al.* 2009) for 12 plots where plant identification was available. In the other 43 plots, we took a core sample from the trunk of 20 canopy trees randomly selected along the plot with dbh $\geq$ 30 cm to determine the wood density by the dry weight per fresh volume. The mean value per plot was used for the biomass calculations of the individuals that were not sampled.

The density of stems and stand biomass were extrapolated to the area of 1ha per plot. The average individual mass was calculated by dividing the stand biomass per plot by the density of stems.

Environmental gradients

Seasonality was calculated based on daily precipitation data interpolated from a network of rain gauges in the region for the period from 1973 to 2011 (CPTEC/INPE). Dry-season length was indexed by the mean number of months per year with precipitation < 100 mm for the 38-year period.

The frequency of storms was indexed by the number of days with precipitation ≥ 20 mm in 1999, which is strongly correlated with the occurrence of blow-downs in the Brazilian Amazon (Espírito-Santo *et al.* 2010). Daily precipitation was integrated from NOAA (National Oceanic and Atmospheric Administration) satellites images with 4 km resolution and 10.7 mm band from NOAA satellites 8 (see Espírito-Santo *et al.* 2010 for methods details).

As a proxy of soil fertility, we assessed the total and available phosphorus (extracted with Mehlich-1) in topsoil samples (EMBRAPA 2011). Phosphorus was identified as the most important nutrient for biomass production in Amazonian forests (Quesada *et al.* 2012a). Soil phosphorus was analyzed in a compound sample derived from 6 subsamples from the first 30 cm depth of soil collected along the central line in each of the 55 plots.

Soil physical restrictions were scored based on effective soil depth, a qualitative structural index, anoxic conditions and topography following Quesada *et al.* (2010). The scores for soil physical limitations are semi-quantitative. Summing the scores of all soil-constraint categories we calculated the index 1 of soil physical limitations, which can vary from 0 to 16 (Quesada *et al.* 2010). Higher scores denote more limited soil conditions for plants. The soil physical classification was made based on soil effective depth (presence of roots), soil structure (bulk density) and anoxic conditions (depth of soil saturation), (see Table S2, Supporting Information); all determined in 2m deep pits dug in each research site and in soil-profile samples from all plots (D. Martins unpublished data; J. Schietti & T. Emilio, unpublished data).

Data analyses

To evaluate the extent of self-thinning relationships in the Purus-Madeira interfluvial region we investigated the direction of the relationships between the average individual mass per plot or stand biomass with the density of stems by simple linear regression. All variables were $\log_{10}$ transformed. We also investigated the importance of size classes to stand-biomass accumulation by determining (i) the diametric classes at which half of the stand biomass, starting from the smallest individuals, was accumulated at the plot scale and (ii) what was the percentage of the stand biomass accumulated in large trees (dbh ≥ 70 cm). For the first analysis, we first calculated biomass in 2 cm diameter bins before finding the half-stand-biomass value.

To investigate the variations in forest-structure components and stand biomass along environmental gradients we used linear mixed-effect models (LMM) of the density of stems, mean individual mass and stand biomass against dry-season length, frequency of storms, soil fertility and soil physical restrictions (fixed effects). The density of stems and the average individual mass were log 10-transformed. Site was included in the model as a random effect to account for the nested design (plots within sites) (Zuur *et al.* 2009). One variable of soil phosphorus was selected by the comparison of two candidate models for stand biomass prediction including as fixed factors the length of dry season, frequency of storms, soil physical restrictions given by the index 1 and one of the two pools of phosphorus (total and available). The best model was selected using Akaike Information Criterion (AIC) following Burnham & Anderson (2004), Table S2 in Supporting Information.

We used the standardized coefficients (beta coefficients) in a path analyses of the lowest AIC linear mixed-effect models to quantify the indirect effects of environment gradients on stand biomass via density of stems and individual mass (by multiplying beta coefficients along the paths). The magnitude of the contributions of the density of stems and the individual mass to stand biomass were given by the beta coefficients of a multiple linear regression with all variables log10-transformed. The net indirect effect of each environmental gradient on stand biomass was calculated by summing effects via density of stems and mean individual mass.

Analyses were undertaken for minimum diameters of 1 and 10 cm. Results for all individuals above 1 cm dbh are presented in the manuscript. Results for 10 cm diameter analyses are given in Table S3, Fig. S1 and Fig. S2 in the Supporting Information. All analyses were undertaken in R 3.0.0. (R Core Team 2013). LMM analyses were conducted with the package lme4 (Bates, Maechler, & Bolker 2013). Significance levels for LMM parameters were calculated using the package languageR (Baayen 2011) and the marginal and conditional LMM R^2 were calculated using the package MuMIn (Bartoń 2013).

Results

Stand biomass in the Purus-Madeira interfluve ranged from 140 to 324 $Mg.ha^{-1}$ (mean = 245 $Mg.ha^{-1}$). The number of individuals per ha varied from 2,192 to 11,475 considering all individuals with dbh ≥ 1 cm, and from 450 to 1,088 considering individuals with dbh ≥ 10 cm

(Table 1). Stand biomass was higher in the central area of the interfluve and lower in the north-eastern and south-western extremes. A similar spatial pattern was found for the density of stems and an opposite trend for the average individual mass, with higher average individual mass in forests at the extremes of the transect and lower average individual mass in the central area of the transect (Fig.1)

Forest-structure components and stand biomass

There was a negative relationship between mean individual mass and the density of stems; supporting self-thinning expectations for resource-limited forests. However, higher stand biomass was found in forests with more densely packed stems (Fig. 2), suggesting additional mechanisms, such as exogenous disturbances, might play a role in stand-biomass accumulation in the region. Large individuals (dbh ≥ 70 cm) were rare in the forests along the Purus-Madeira interfluve; on average there were 1.8 trees per ha (ranging from 0 - 11 trees.ha^{-1}) with dbh > 70 cm, and they accounted for only 5.36% of stand biomass (Fig. 4). Between 50 and 60% of stand biomass was stored in small to midsize classes. On average, half of the stand biomass was accumulated in individuals with diameters up to 27 cm. This dbh threshold of 50% biomass accumulation ranged from 19 to 53 cm in individual plots (Fig. 3), but in 70% of the plots more than 50% of the biomass was accumulated in individuals with diameters up to 27 cm (Fig. 4). The diameter at which half of stand biomass was accumulated was positively correlated with the mean individual mass ($r = 0.62$; $p < 0.001$) and with maximum diameter in the plot ($r = 0.80$; $p < 0.001$).

Stand biomass was higher in forests with more stems and with higher mean individual mass per tree. However, the magnitude of contribution of the density of stems to stand biomass was higher than the contribution of the mean individual mass (beta coefficients were 1.98 and 1.53, respectively), Fig. 6.

Environmental-gradient effects

Forests with longer dry seasons had lower densities of stems, higher mean individual mass and no significant trend in stand biomass (Table 02). The frequency of storms positively affected the density of stems and stand biomass, and lower mean individual mass was found in sites with higher frequencies of storms. Soils with more available P had lower density of stems and lower stand biomass, but no trend was found in the mean individual mass. Soils with more physical restrictions had lower mean individual mass and higher density of stems. No trend was found for stand biomass and soil physical restriction indices (Fig 5). Three plots were very different from the others in the combination between stand structure and biomass and the environmental characteristics. Two of these plots were along stream margins and one had notable abundance of a monocot called "sororoca" (*Phenakosperma guyanensis*). The leverage of these putative outlier plots appeared to mask relationships with stand biomass and create a spurious relationship with mean individual mass. Thus we excluded these plots from the linear mixed-model analyses, however, they are presented in the partial regression graphs on Fig. 5.

Path analysis indicated indirect effects of seasonality, frequency of storms and soil characteristics on stand biomass via forest-structure components (Fig 6). Dry-season length had strong and opposite effects on stand biomass by both decreasing the density of stems (standardized coefficient, b_{sd} = -0.91) and increasing the mean individual mass (b_{sd} = 0.78). These effects counterbalanced each other and resulted in a low negative net effect (b_{sd} = -0.13) of the dry-season gradient on stand biomass. The frequency of storms had a positive indirect effect on stand biomass, by increasing the density of stems (b_{sd} = 0.93). This positive effect via density of stems was stronger than the negative effect of decreasing mean individual mass (b_{sd} = -0.60). Therefore, there was a positive net effect of the frequency of storms on stand biomass (b_{sd} = 0.34) due mainly to the increase in stem packing. Soil phosphorus availability limited stand biomass negatively affecting only the density of stems (b_{sd} = -0.42). No indirect effect via mean individual mass was found. Soil physical restrictions had an extremely low net effect on stand biomass (b_{sd} = -0.07) because of the opposite effects of increasing the density of stems and decreasing the mean individual mass.

Discussion

The relationship between stand biomass and density of stems was positive in the forests along the Purus-Madeira interfluve in central Amazonia. Large trees are rare in these forests, they contribute relatively little to stand biomass and most of the stand biomass is in small- to mid-size diameter classes. These results indicate that disturbance regimes may play a major role in regional variation in aboveground biomass and total carbon stocks. Another prediction of self-thinning theory did hold up, however: mean individual mass scaled with stem density according to an inverse power law (though with a -2/3 scaling exponent). Thus, the resource limitation and density-dependent mortality dynamics associated with self thinning also appear to affect biomass and forest structure. Future work should seek to reconcile these patterns with additional research into the mechanisms of size structured dynamics and regional variation in forest biomass.

Relationships between stand-biomass distribution and forest-structure components

Static size distributions may reflect disturbance regimes (Brown *et al.* 1997; Williams, Hill, & Ryan 2013) and give insights into phenomena driving forest structure (Niklas *et al.* 2003b). In most plots in the Purus-Madeira interfluve, half of the stand biomass occurs in trees below 27 cm dbh while only around 5% occurs in large trees (>70 cm dbh). A low proportion of biomass in large trees is considered a structural indicator of past disturbance and a present recovery stage in tropical forests (Brown & Lugo 1992; Brown *et al.* 1997). These findings suggest that forests along Purus-Madeira interfluve may be experiencing regimes of frequent disturbances, since these can prevent trees reaching large diameters or cause higher mortality in large trees (Niklas *et al.* 2003b; Coomes *et al.* 2003). However, future work will need to consider additional factors that may control maximum tree size.

Gap formation by mortality of large trees increases light and space availability and initiates a stage of understory recovery in which competitive thinning is reduced due to the decrease in stem density (Brokaw 1985; Clark 1992). Later in the regeneration process, the density of stems increases and density-dependent mortality becomes more important. If disturbances are frequent, the positive relationship between stand biomass and density of individuals found in the forests of the Purus-Madeira interfluve could be a result of recovering states from past perturbations in the canopy. There appears to be a balance between biomass accumulation driven by density-dependent and disturbance-initiated mortality in which resource limitation does not offset biomass accumulation from recovery states in these forests.

Seasonality and natural disturbances

Dry-season length is considered a constraint for biomass accumulation (Chave *et al.* 2004; Malhi *et al.* 2006). We found strong indirect and opposite effects of dry-season length on stand biomass via stand structural components. Forests in sites with longer dry seasons along the Purus-Madeira interfluve had lower densities of stems but higher mean individual mass. Previous studies have also shown higher density of stems in more aseasonal forests (ter Steege *et al.* 2003; Phillips *et al.* 2004; Slik *et al.* 2010). This can be linked to higher germination and recruitment of new individuals in wet-season conditions (Lieberman & Li 1992), with possibly more nutrient availability associated with the soil-water regime (Baldwin & Mitchell 2000). The opposite trend in mean individual mass with dry-season length may be essentially a self-thinning result of the variation in the density of stems, or an indication that wet-season conditions could be unfavorable for individual biomass accumulation in this region. The poor soil-water drainage (Sombroek 2000) and the shallow water table in the Purus-Madeira interfluve (Fan & Miguez-Macho 2010) is also associated with lower light availability due to higher cloud coverage during rainy season. These factors could limit tree growth during the wet season (Paoli *et al.* 2008; Ferry *et al.* 2010; Slik *et al.* 2010). Despite the relatively strong effects of dry-season length on stand structural components, no significant direct effect of seasonality was found on stand biomass. It is likely that opposite effects of stem density and mean individual biomass counterbalanced each other, resulting in an insignificant overall effect of dry-season length on stand biomass.

The frequency of storms had a positive effect on stand biomass along the Purus-Madeira interfluve. Forests with more frequent storms displayed greater stem density and had lower mean individual mass. The higher density of stems is expected in more recently disturbed forests, as a response to gap formation in the canopy and increased resource availability (Brokaw 1985; Denslow 1995). Wind disturbances, such as blowdowns, are associated with the occurrence of heavy storms (Nelson *et al.* 1994; Espírito-Santo *et al.* 2010) and they can open large gaps in the forest, spread over kilometers. The size distribution of these gaps follows a power-law function (Nelson et al 1994; Fisher et al 2008) with many small gaps with less than 0.1 ha (Negrón-Juárez *et al.* 2011) to a few large gaps that can cover more than 3000 ha (Nelson *et al.* 1994). Small and frequent gaps can produce a mosaic of mixed stages forests in the landscape (Fisher *et al.* 2008; Chambers *et al.* 2013). The mortality of stems due to windfalls is around 20% and mid-sized trees seem to be more susceptible to mortality (D. M. Marra, unpublished data). The lower mean mass of individuals in forests experiencing more frequent storms is likely to be a result of the higher mortality rates associated with wind disturbances preventing trees reaching larger sizes.

More fertile soils in the western Amazon usually maintain lower stand biomass than forests in east of the basin on less-fertile soils. This large scale pattern has been associated with higher versus lower turnover rates (Phillips *et al.* 2004), with more fertile soils being also more physically restrictive (Quesada *et al.* 2010) and supporting fast-growing species that invest less in mass structure and have lower wood density and lower maximum heights (van Schaik & Mirmanto 1985; Baker, Phillips, & Malhi 2004; Quesada *et al.* 2012a). In the Purus-Madeira interfluve, soils with more available phosphorus had lower stand biomass in accordance with the pattern of more phosphorus-rich soils having lower stand biomass, but no tendency was found in the mean mass of individuals. Stand biomass was lower due to the decreasing number of stems per area in soils with more available phosphorus. We would expect higher stem packing in more fertile soils if this results from more disturbance initiated by soil conditions. More disturbance would increase space and light availability for new recruits. The influence of phosphorus on stand biomass is controversial (Paoli *et al.* 2008; Baraloto *et al.* 2011b) and the mechanisms explaining lower density of stems and stand biomass in more phosphorus-rich soils needs further investigations.

Our results showed that the mean individual mass decreases with soil restrictions and the density of stems had a tendency to increase in more restrictive soil physical conditions. Although no effect on stand biomass was detected, the trends in forest-structure components are what are expected for forests with small-sized trees due to the positive feedback caused by soil-initiated disturbances (Quesada *et al.* 2012a). The mortality caused by exogenous disturbances, such as windstorms, appears to be magnified by restrictive soil physical conditions, with trees becoming more susceptible to uprooting in shallow soils that give low anchorage. This mechanism may be particularly important in the forests along the Purus-Madeira interfluve due to the high frequency of storms (Espírito-Santo *et al.* 2010) and the relatively restrictive structure of the soils in the region (Martins et al., in press).

Accumulation of stand biomass results from a multitude of effects operating at many different scales. However, the effects of these on stand biomass in an area must act through density of stems and/or mean mass of individual trees. We have shown that the effects of environmental gradients on these components are variable and that even strong positive effects on one component may be canceled out by strong negative effects on the other. It is also not known how these relationships may respond to future perturbations, such as climate change or human exploitation of the forest. Future studies of the determinants of plot-level biomass in tropical forests should investigate the individual components of biomass, and perhaps even and perhaps even additional decomposition to contributions of height, diameter and wood density. To improve our understanding and predictions of stand biomass distribution it is necessary to investigate the effects of environmental gradients on all components of biomass.

Acknowledgements

We thank the many field assistants that helped on the forest inventories and environmental data collection; the residents along the BR-319 highway that always gave us support during field campaigns and pickups stuck; and Angélica C.G. Nunes for entering field data. The National Council for Scientific and Technological Development (CNPq) and the Program of doctorate sandwich PDSE/CAPES awarded stipends to JS during the development of this work. This work was supported by PRONEX - FAPEAM (1600/2006), Hidroveg Universal CNPq (473308/2009-6), FAPESP/FAPEM (465/2010), PPBio Manaus (CNPq 558318/2009-6), Projeto Cenários FINEP/CNPq (52.0103/2009-2) and INCT CENBAM. We thank Fernando Espírito-Santo for making the data of frequency of storms available for this study.

References

Baayen, R.H. (2011) languageR: Data sets and functions with “Analyzing Linguistic Data: A practical introduction to statistics”.. R package version 1.4.

Baker, T., Phillips, O. & Malhi, Y. (2004) Variation in wood density determines spatial patterns inAmazonian forest biomass. Global Change …, 545–562.

Baldwin, D.S. & Mitchell, A.M. (2000) The effects of drying and re-flooding on the sediment and soil nutrient dynamics of soil lowland river-floodplain systems: a synthesis. Regulated Rivers: Research and Managment, 467, 457–467.

Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Hérault, B., Dávila, N., Mesones, I., Rios, M., Valderrama, E. & Fine, P.V. a. (2011) Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. Global Change Biology, 17, 2677–2688.

Bartoń, K. (2013) MuMIn: Multi-model inference. R package version 1.9.5.

Bates, D., Maechler, M. & Bolker, B. (2013) lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-2.

BRASIL. (1974) Projeto RADAM Folha SB20 Purus. Rio de Janeiro.

Brokaw, N. (1985) Gap-Phase Regeneration in a Tropical Forest. Ecology, 66, 682–687.

Brown, S. & Lugo, A. (1992) Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. Interciencia, 17, 8–18.

Brown, I.F., Martinelli, L.A., Thomas, W.W., Moreira, M.Z., Ferreira, C.A.C. & Victoria, R.A. (1995) Uncertainty in the biomass of Amazonian forests- An example from Rondonia, Brazil. Forest Ecology and Management, 75, 175–189.

Brown, S., Schroeder, P. & Birdsey, R. (1997) Aboveground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. Forest Ecology and Management, 96, 37–47.

Burnham, K.P. & Anderson, D.R. (2004) Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods & Research, 33, 261–304.

Chambers, J.Q., Negrón-Juárez, R.I., Marra, D.M., Di Vittorio, A., Tews, J., Roberts, D., Ribeiro, G.H.P.M., Trumbore, S.E. & Higuchi, N. (2013) The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. Proceedings of the National Academy of Sciences of the United States of America, 110, 3949–3954.

Chave, J., Andalo, C., Brown, S., Cairns, M. a, Chambers, J.Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B.W., Ogawa, H., Puig, H., Riéra, B. & Yamakura, T. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia, 145, 87–99.

Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S. & Perez, R. (2004) Error propagation and scaling for tropical forest biomass estimates. Philosophical transactions of the Royal Society of London. Series B, Biological sciences, 359, 409–20.

Chave, J., Condit, R., Lao, S., Caspersen, J.P., Foster, R.B. & Hubbell, S.P. (2003) Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. Journal of Ecology, 91, 240–252.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. Ecology letters, 12, 351–66.

Chave, J., Riéra, B. & Dubois, M.-A. (2001) Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. Journal of Tropical Ecology, 17, 79–96.

Clark, J.S. (1992) Density-independent mortality, density compensation, gap formation, and self-thinning in plant populations. Theoretical Population Biology, 42, 172–198.

Clark, D.B. & Clark, D.A. (1996) Abundance , growth and mortality of very large trees in neotropical lowland rain forest. , 80, 235–244.

Coomes, D. a., Duncan, R.P., Allen, R.B. & Truscott, J. (2003) Disturbances prevent stem size-density distributions in natural forests from following scaling relationships. Ecology Letters, 6, 980–989.

Denslow, J.S. (1995) Disturbance and Diversity in Tropical Rain Forests : The Density Effect. Ecological applications, 5, 962–968.

EMBRAPA. (2011) Manual de Métodos de Análise de Solo, 2nd ed. Rio de Janeiro.

Espírito-Santo, F.D.B., Keller, M., Braswell, B., Nelson, B.W., Frolking, S. & Vicente, G. (2010) Storm intensity and old-growth forest disturbances in the Amazon region. Geophysical Research Letters, 37, 1–6.

Fan, Y. & Miguez-Macho, G. (2010) Potential groundwater contribution to Amazon evapotranspiration. Hydrology and Earth System Sciences, 14, 2039–2056.

Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brienen, R.J.W., Gloor, E., Monteagudo Mendoza, a., et al. (2012a) Tree height integrated into pan-tropical forest biomass estimates. Biogeosciences Discussions, 9, 3381–3403.

Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brienen, R.J.W., Gloor, M., Monteagudo Mendoza, A., et al. (2012b) Tree height integrated into pantropical forest biomass estimates. Biogeosciences, 9, 3381–3403.

Ferry, B., Morneau, F., Bontemps, J.-D., Blanc, L. & Freycon, V. (2010) Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. Journal of Ecology, 98, 106–116.

Fisher, J.I., Hurtt, G.C., Thomas, R.Q. & Chambers, J.Q. (2008) Clustered disturbances lead to bias in large-scale estimates based on forest sample plots. Ecology letters, 11, 554–63.

Lieberman, D. & Li, M. (1992) Seedling recruitment patterns in a tropical dry forest in Ghana. Journal of Vegetation Science, 3, 375–382.

Luyssaert, S., Schulze, E.-D., Börner, A., Knohl, A., Hessenmöller, D., Law, B.E., Ciais, P. & Grace, J. (2008) Old-growth forests as global carbon sinks. Nature, 455, 213–5.

Magnusson, W.E., Lima, A.P., Luizão, R., Luizão, F., Costa, F.R.C., Castilho, C.V. & Kinupp, V. (2005) RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. Biota Neotropica, 5, 19–24.

Malhi, Y., Wood, D., Baker, T.R., Wright, J., Phillips, O.L., Cochrane, T., Meir, P., Chave, J., Almeida, S., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D. a., Vargas, P.N., Pitman, N.C. a., Quesada, C.A., Salomao, R., Silva, J.N.M., Lezama, A.T., Terborgh, J., Martinez, R.V. & Vinceti, B. (2006) The regional variation of aboveground live biomass in old-growth Amazonian forests. Global Change Biology, 12, 1107–1138.

Midgley, J.J. (2001) Do mixed-species mixed-size indigenous forests also follow the self-thinning line? , 16, 661–662.

Negrón-Juárez, R.I., Chambers, J.Q., Marra, D.M., Ribeiro, G.H.P.M., Rifai, S.W., Higuchi, N. & Roberts, D. (2011) Detection of subpixel treefall gaps with Landsat imagery in Central Amazon forests. Remote Sensing of Environment, 115, 3322–3328.

Nelson, B., Kapos, V., Adams, J., Oliveira, W.J. & Braun, O.P.. (1994) Forest disturbance by large blowdowns in the Brazilian Amazon. Ecology, 75, 853–858.

Niklas, K.J., Midgley, J.J. & Enquist, B.J. (2003a) A general model for mass–growth-density relations across tree-dominated communities. Evolutionary Ecology Research, 5, 459–468.

Niklas, K.J., Midgley, J.J. & Rand, R.H. (2003b) Tree size frequency distributions, plant density, age and community disturbance. Ecology Letters, 6, 405–411.

Paoli, G.D., Curran, L.M. & Slik, J.W.F. (2008) Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo. Oecologia, 155, 287–99.

Petraitis, P.S. (1995) Use of Average vs. Total Biomass in Self-Thinning Relationships. Ecology, 76, 656–658.

Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, W.F., Lewis, S.L., Lloyd, J., Malhi, Y., Monteagudo, a, Neill, D. a, Vargas, P.N., Silva, J.N.M., Terborgh, J., Martínez, R.V., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J. a, Czimczik, C.I., Di Fiore, a, Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E.M., Olivier, J., Palacios, W., Patiño, S., Pitman, N.C. a, Quesada, C. a, Saldias, M., Lezama, a T. & Vinceti, B. (2004) Pattern and process in Amazon tree turnover, 1976-2001. Philosophical transactions of the Royal Society of London. Series B, Biological sciences, 359, 381–407.

Phillips, O.L., van der Heijden, G., Lewis, S.L., López-González, G., Aragão, L.E.O.C., Lloyd, J., et al. (2010) Drought-mortality relationships for tropical forests. The New phytologist, 187, 631–46.

Quesada, C. a., Lloyd, J., Schwarz, M., Patiño, S., Baker, T.R., Czimczik, C., Fyllas, N.M., Martinelli, L., Nardoto, G.B., Schmerler, J., Santos, a. J.B., Hodnett, M.G., Herrera, R., Luizão, F.J., Arneth, a., Lloyd, G., Dezzeo, N., Hilke, I., Kuhlmann, I., Raessler, M., Brand, W. a., Geilmann, H., Moraes Filho, J.O., Carvalho, F.P., Araujo Filho, R.N., Chaves, J.E., Cruz Junior, O.F., Pimentel, T.P. & Paiva, R. (2010) Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. Biogeosciences, 7, 1515–1541.

Quesada, C.A., Phillips, O.L., Schwarz, M., Czimczik, C.I., Baker, T.R., Patiño, S., Fyllas, N.M., Hodnett, M.G., Herrera, R., Almeida, S., Alvarez Dávila, E., Arneth, a., Arroyo, L., Chao, K.J., Dezzeo, N., Erwin, T., di Fiore, A., Higuchi, N., Honorio Coronado, E., Jimenez, E.M., Killeen, T., Lezama, a. T., Lloyd, G., López-González, G., Luizão, F.J., Malhi, Y., Monteagudo, A., Neill, D. a., Núñez Vargas, P., Paiva, R., Peacock, J., Peñuela, M.C., Peña Cruz, A., Pitman, N., Priante Filho, N., Prieto, a., Ramírez, H., Rudas, A., Salomão, R., Santos, A.J.B., Schmerler, J., Silva, N., Silveira, M., Vásquez, R., Vieira, I., Terborgh, J. & Lloyd, J. (2012) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. Biogeosciences, 9, 2203–2246.

R Core Team. (2013) R: A language and environment for statistical computing.

Van Schaik, C.P. & Mirmanto, E. (1985) Spatial variation in the structure and litterfall of a Sumatran rain forest. Biotropica, 17, 196–205.

Slik, J.W.F., Aiba, S.-I., Brearley, F.Q., Cannon, C.H., Forshed, O., Kitayama, K., Nagamasu, H., Nilus, R., Payne, J., Paoli, G., Poulsen, A.D., Raes, N., Sheil, D., Sidiyasa, K., Suzuki, E. & van Valkenburg, J.L.C.H. (2010) Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. Global Ecology and Biogeography, 19, 50–60.

Slik, J.W.F., Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., et al. (2013) Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. Global Ecology and Biogeography, n/a–n/a.

Sombroek, W. (2000) Amazon landforms and soils in relation to biologcal diversity. Acta Amazonica, 30, 81–100.

Sombroek, W. (2001) Spatial and Temporal Patterns of Amazon Rainfall Consequences for the Planning of Agricultural Occupation and. , 30.

Ter Steege, H., Pitman, N., Sabatier, D., Castellanos, H., Van Der Hout, P., Daly, D.C., Silveira, M., Phillips, O., Vasquez, R., Van Andel, T., Duivenvoorden, J., Oliveira, A.A., Ek, R., Lilwah, R., Thomas, R., Van Essen, J., Baider, C., Maas, P., Mori, S., Terborgh, J., Vargas, P.N., Mogollón, H. & Morawetz, W. (2003) A spatial model of tree α-diversity and tree density for the Amazon. Biodiversity & Conservation, 12, 2255–2277.

Urquiza-Haas, T., Dolman, P.M. & Peres, C.A. (2007) Regional scale variation in forest structure and biomass in the Yucatan Peninsula, Mexico: Effects of forest disturbance. Forest Ecology and Management, 247, 80–90.

Weller, D.E. (1987) Self-Thinning Exponent Correlated with Allometric Measures of Plant Geometry. Ecology, 68, 813–821.

Westoby, M. (1984) The self-thinning rule. Advances in ecological research, 14, 167–225.

White, J. (1981) The allometric interpretation of the self-thinning rule. Journal of Theoretical Biology, 89, 475–500.

Williams, M., Hill, T.C. & Ryan, C.M. (2013) Using biomass distributions to determine probability and intensity of tropical forest disturbance. Plant Ecology & Diversity, 6, 87–99.

Yoda, K., Kira, T., Ogawa, H. & Hozumi, K. (1963) Self-thinning in overcrowded pure stands under cultivated and natural conditions. Journal of the Institute of Polytechnics, Osaka City University, Series D, 14, 107–129.

Zanne, A., Lopez-Gonzalez, G., Coomes, D., Ilic, J., Jansen, S., Lewis, S., Miller, R., Swenson, N., Wiemann, M. & Chave, J. (2009) Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository.

Zuur, A., Ieno, E.N., Walker, N., Savellev, A.A. & Smith, G.M. (2009) Mixed Effects Models and Extensions in Ecology with R. Springer, New York.

Table 1. Forest structure properties and environmental gradients along the Purus-Madeira interfluve, in central-south Amazonia.

Stand properties	**Mean (Minimum - maximum)**	
	dbh >= 1cm	**dbh >= 10 cm**
Stand biomass (Mg.ha^{-1})	245.09 (140.44 - 324.32)	219.71 (128.30 - 299.71)
Basal area (m^{2}.ha^{-1})	30.72 (19.90 - 38.90)	24.92 (15.89 - 30.51)
Stem density (individuals.ha^{-1})	6705.67 (2,192 - 11,475)	731.85 (450 - 1,088)
Average individual biomass (Mg)	0.040 (0.02 - 0.078)	0.310 (0.18 - 0.56)
Percent of stand biomass in small size classes (1 <= dbh < 10 cm)	10.40 (3.10 - 15.51)	-
Number of trees per ha with dbh >= 70	1.8 (0 - 11)	-
Percent of biomass in trees with dbh >= 70 cm	5.36 (0 - 27)	-
Maximum diameter (cm)	82.98 (48.4 - 184.9)	-
Environmental gradients		
Annual precipitation (mm)	2263 (2124 - 2458)	
Dry season length (months.year^{-1})	2.95 (2 - 4)	
Frequency of storms (days.year^{-1})	51.38 (35 - 60)	
Soil available phosphorus (mg.Kg^{-1})	2.24 (0.65 - 6.38)	
Soil total phosphorus (mg.Kg^{-1})	136.09 (97.40 - 197.39)	
Soil depth score	2 (0 - 4)	
Soil structure score	2.95 (1 - 4)	
Topography score	0.18 (0 - 1)	
Soil saturation score	2.12 (0 - 4)	
Soil index 1	7.23 (2- 11)	

Table 2. Results of the linear mixed-effect models (LMM) for the density of stems, average individual mass and stand biomass of individuals with dbh ≥ 1 cm in function of dry season length, available phosphorus (available P) and soil physical restrictions represented by index 1, (fixed effects). Sites were considered as random effect in all models. The Akaike information criterion values (AIC) and the marginal (R^2_{marg}) and conditional (R^2_{cond}) coefficients of determination (R^2) are presented. Marginal R^2 shows the models adjusted only considering fixed effects and conditional R^2 correspond to the full model, including the random effect. The relative contribution of predictors is given by the standardized coefficients of the LMMs. Probability for each predictor is shown in parentheses. Standardized coefficients in bold have $p < 0.05$.

Dependent variables	AIC	R2		Relative contribution of predictors			
		R^2_{marg}	R^2_{cond}	Dry season length	Frequency of storms	Available P	Soil restrictions
Density of stems	-69.54	0.69	0.83	**-0.46** (0.000)	**0.47** (0.002)	**-0.21** (0.020)	**0.17** (0.038)
Individual mass	-70.79	0.51	0.71	**0.51** (0.002)	**-0.39** (0.030)	0.11 (0.445)	**-0.27** (0.026)
Stand biomass	-103.4	0.57	0.57	-0.14 (0.218)	**0.30** (0.048)	**-0.50** (0.003)	0.05 (0.824)

Figures

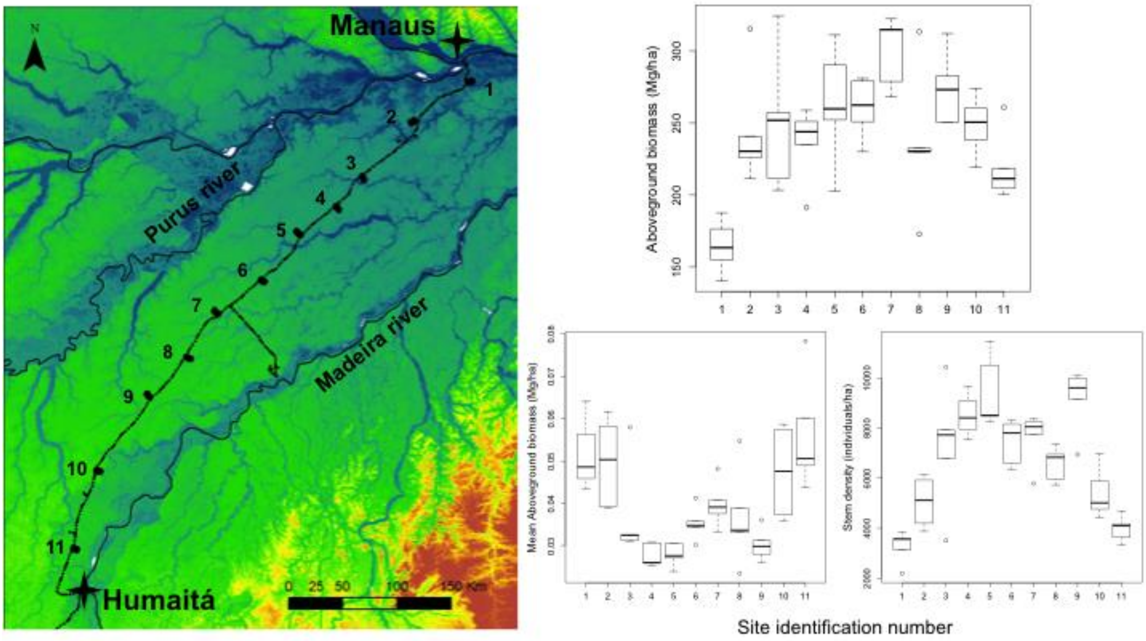


Figure 1. Map of the study area showing the 600 km transect along the interfluve between the Purus and Madeira Rivers in central Amazonia. Eleven research sites (1 - 11) are located along the transect. Each site has 5 1ha plots where trees were measured. Boxplots show the variation in stand biomass, density of stems and average individual mass along the transect. Stand biomass and density of stems show higher values in the central region of the interfluve and lower values in the north and southwestern extremes. The mean individual mass shows an opposite pattern.

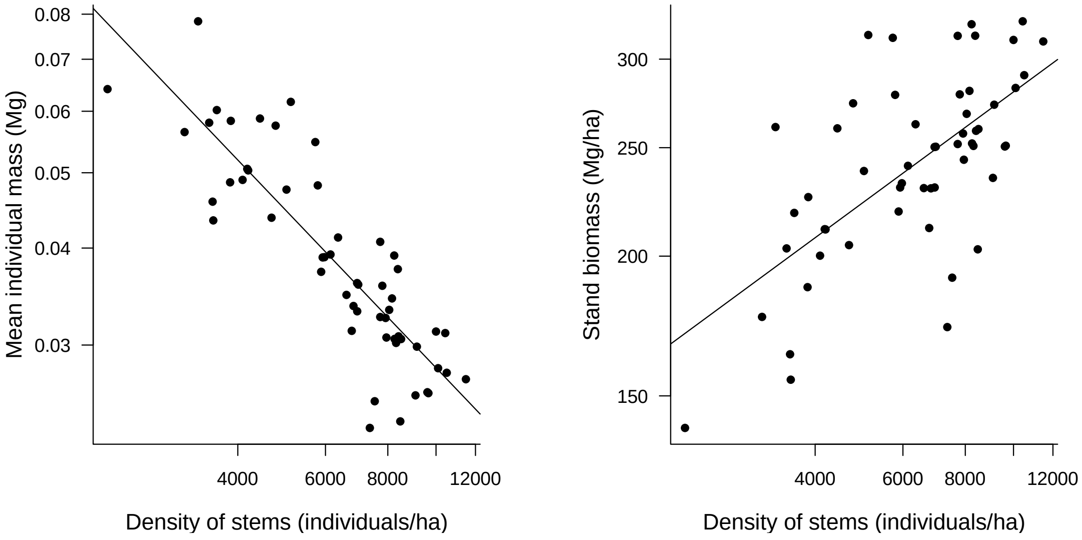


Figure 2. Relationships between (left) mean individual mass and density of stems ($r^2 = 0.75$, scaling factor, $b = -0.67$); and (right) stand biomass and the density of stems ($r^2 = 0.42$, scaling factor, $b = 0.33$) for individuals with dbh ≥ 1 cm in 55-1ha plots in central Amazonia. Variables were log-transformed and both relationships were statistically significant ($p < 0.001$). The individual mass relationship agrees with self-thinning theory, while the relationship between total stand biomass and density does not—self-thinning predicts a negative relationship.

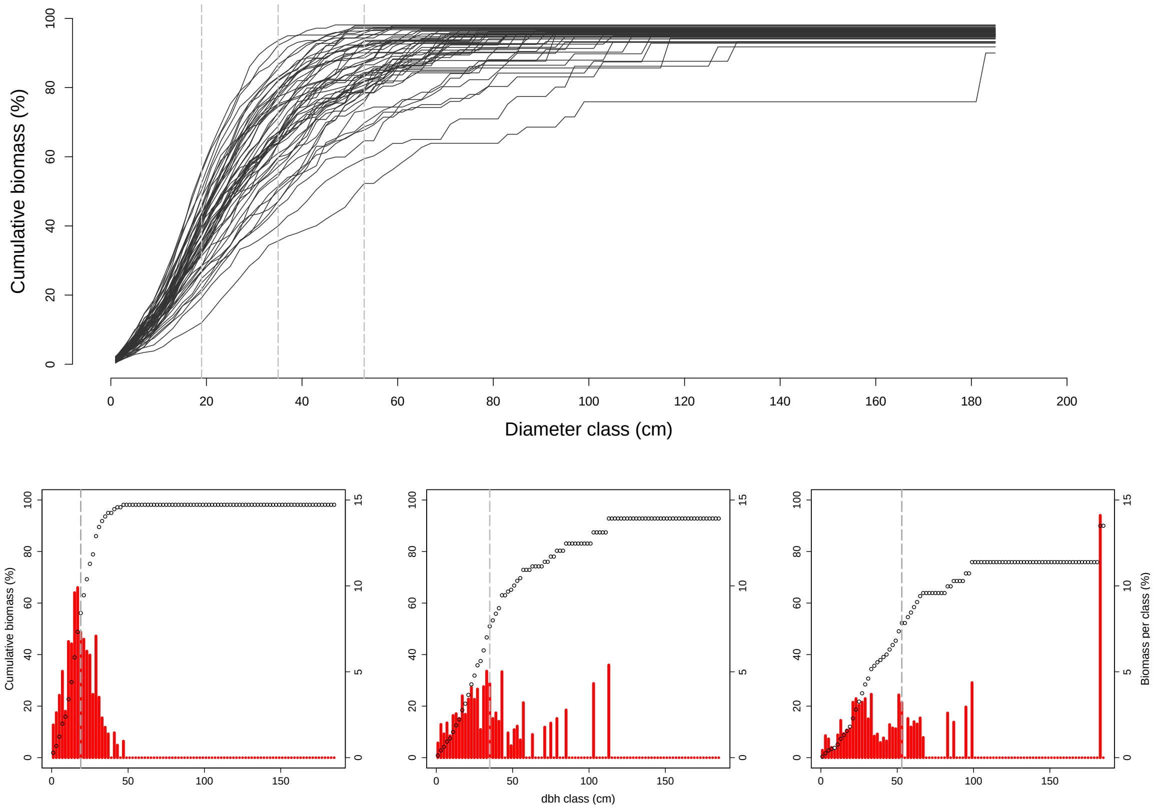


Figure 3. Cumulative proportions of stand biomass in 2cm size classes over all 55 1-ha plots along the Purus-Madeira interfluve, in central Amazonia (upper). The lower graphs show data for three plots, exemplifying the extremes (19 – 53 cm) and mean diameter value (19 cm) at 50% stand biomass accumulation (dashed lines). Red bars show the biomass per 2 cm DBH interval and the black points show the cumulative biomass curve.

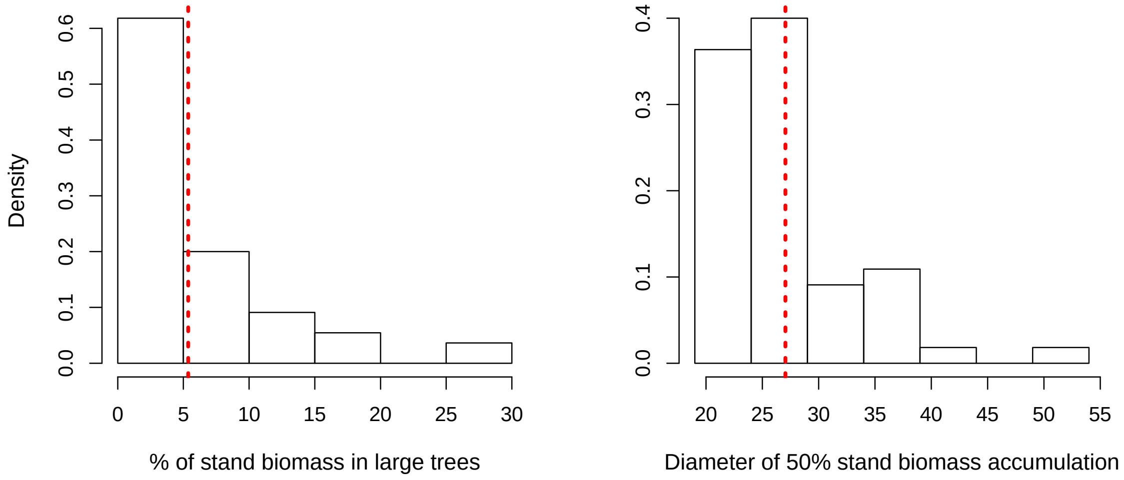


Figure 4. Left - Density histograms showing that more than 60% percent of the plots in the Purus-Madeira interfluve hold less than 5% of the stand biomass in large trees (dbh ≥ 70 cm). Right - Approximately 75% of the plots contained half of the stand biomass in trees with diameter below 27 cm. Red dashed lines show the mean values for the x-axis.

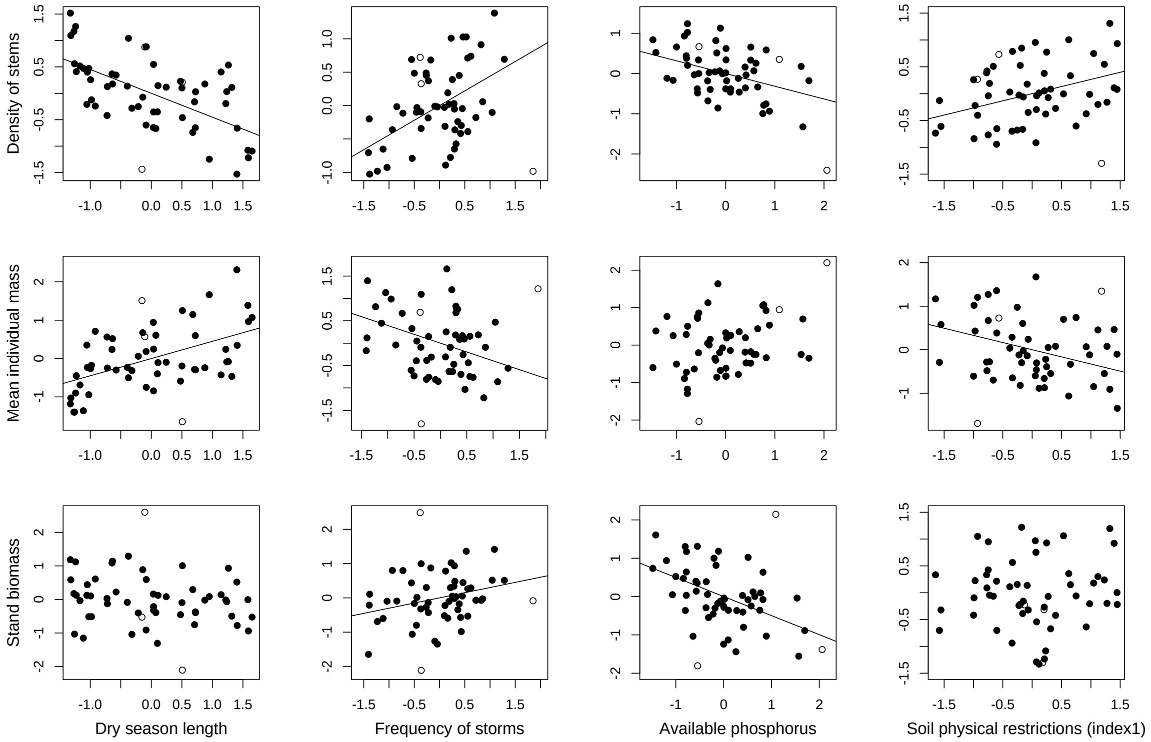
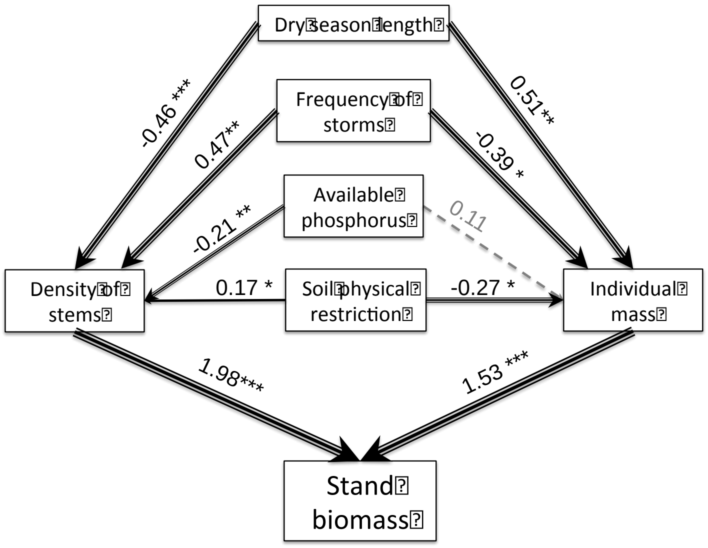


Figure 5. Partial relations from multiple regressions investigating the effects of dry-season length, frequency of storms, soil-available phosphorus and soil physical restrictions on the (upper) density of stems ($R^2_{marginal} = 0.70$), (center) individual mass ($R^2_{marginal} = 0.52$) and (bottom) stand biomass ($R^2_{marginal} = 0.57$) in forests along the Purus-Madeira interfluve, in central Amazonia. Fitted lines indicate fixed effects probabilities < 0.05 in the linear mixed-model analyses excluding outliers (open circles, see the main text for more details).



Indirect effects via density of stems and individual mass

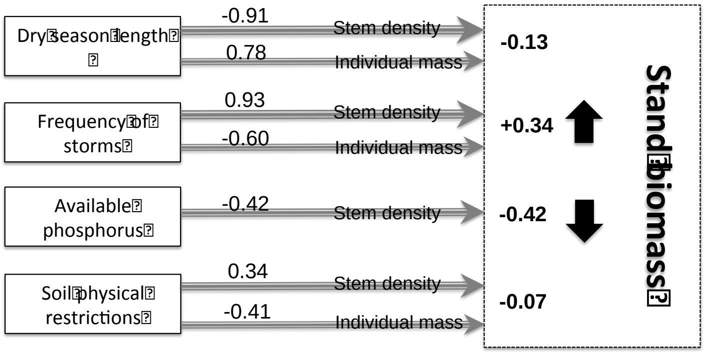


Figure 6. Path analysis showing the magnitude of direct effects (top), given by standardized coefficients of linear mixed-models, of environmental gradients on forest-structure components. The indirect effects of environmental gradients on stand biomass via forest structure components (bottom) show the multiplicand of the standardized coefficients along each path and the sum of these indirect effects (net indirect effects). Note that dry-season length and frequency of storms have strong and opposite effects on stand biomass via density of stems and mean individual mass. For dry-season length, the opposite effects were counterbalanced and no significant effect of seasonality was seen on stand biomass. Arrow width indicates the relative strength of the effects and the dashed line show no effect ($p \geq 0.05$). Asterisks indicate significance levels (*** $p \leq 0.001$,** $p < 0.005$ and * $p < 0.05$).

Supporting Information

Table S1. Scaling exponent (*a*), allometric constant (*b*), number of measured trees (n trees) and the coefficient of determination (r^2) for the Height-Diameter (H-D) allometric models adjusted for each of the 11 sites along the Purus-Madeira interfluve in central Amazonia. H-D models were adjusted using power functions, $H = b * D^a$.

Site	*b*	*a*	n trees	r^2
1	3.24	0.52	60	0.84
2	4.85	0.42	161	0.74
3	5.17	0.38	168	0.67
4	4.76	0.40	160	0.66
5	4.03	0.46	110	0.71
6	4.88	0.41	163	0.72
7	5.58	0.39	102	0.74
8	5.12	0.40	164	0.83
9	4.51	0.43	156	0.75
10	6.23	0.36	58	0.69
11	4.13	0.46	117	0.84

Table S2. Components of the soil physical restriction index from (Quesada *et al.* 2010). The summation of all components gives the index 1.

Soil physical restrictions rating categories	**Score**
Effective soil depth (soil depth, hardpans)	
Shallow soils (less than 20 cm)	4
Less shallow (20 to 50 cm)	3
Hardpan or rock that allows vertical root growth; other soils between 50 and 100 cm deep.	2
Hardpan, rocks or C horizon ≥ 100 cm deep	1
Deep soils ≥ 150 cm	0
Soil structure	
Very dense, very hard, very compact, without aggregation, root restrictive	4
Dense, compact, little aggregation, lower root restriction	3
Hard, medium to high density and/or with weak or block like structure	2
Loose sand, slightly dense; well aggregated in sub angular blocks, discontinuous pans	1
Good aggregation, friable, low density	0
Topography	
Very steep > 45º	4
Steep 20º to 44º	3
Gentle undulating 8º to 19º	2
Gentle sloping 1º to 8º	1
Flat 0º	0
Anoxic conditions	
Constantly flooded; patches of stagnated water	4
Seasonally flooded; soils with high clay content and very low porosity and/or dominated by plinthite	3
Deep saturated zone (maximum high of saturation 50 cm deep); redox features	2
Deep saturated zone (maximum high of saturation > 100 cm deep); deep redox features	1
Unsaturated conditions	0

Table S3. Comparison of two candidate models for explaining variations in stand biomass ($Biomass_{st}$), one including available phosphorus (P_a) and the other including total phosphorus (P_{tot}) pool. Both models included site as a random factor. The model with available phosphorus had the best fit based on Akaike Information Criteria, AIC, values (best fitting-model has the lowest AIC value). Delta AIC gives the difference in relation to the AIC value of the best fitting-model and values higher than 2 have low support (Burnham & Anderson 2004).

Model	**AIC value**	**Delta AIC**
$Biomass_{st} = a + b1 * DSL + b2 * freq. storms + b3 * P_a + b4 * index\ 1 + site$	-76.95	0
$Biomass_{st} = a + b1 * DSL + b2 * freq. storms + b3 * P_{tot} + b4 * index\ 1 + site$	-69.87	7.09

Table S4. Results of the linear mixed-effect models (LMM) for the density of stems, average individual mass and stand biomass of individuals with dbh ≥ 10 cm in function of dry season length, available phosphorus (available P) and soil physical restrictions represented by index 1, (fixed effects). Sites were considered as random effect in all models. The Akaike information criterion values (AIC) and the marginal (R^2_{marg}) and conditional (R^2_{cond}) coefficients of determination (R^2) are presented. Marginal R^2 shows the models adjusted only considering fixed effects and conditional R^2 correspond to the full model, including the random effect. The relative contribution of predictors is given by the standardized coefficients of the LMMs. Probability for each predictor is shown in parentheses. Standardized coefficients in bold have $p < 0.05$.

Dependent variables	AIC	R2		Relative contribution of predictors			
		R^2_{marg}	R^2_{cond}	Dry season length	Frequency of storms	Available P	Soil restrictions
Density of stems	-90.16	0.39	0.64	**-0.45** (0.011)	0.33 (0.124)	-0.04 (0.350)	**0.38** (0.004)
Individual mass	-69.56	0.30	0.54	**0.35** (0.042)	0.01 (0.956)	-0.18 (0.281)	**-0.42** (0.008)
Stand biomass	-98.60	0.54	0.54	-0.07 (0.534)	**0.31** (0.046)	**-0.49** (0.004)	0.02 (0.965)

Table S5. Plot level values of stem density, individual average basal area and biomass and total stand biomass for all stems above 1 cm diameter and for stems above 10 cm diameter.

Site	Plot identification	Stem density (individuals/ha^{-1})	Average basal area (m^{2})	Basal area (m2.ha^{-1})	Average biomass (Mg)	Total biomass (Mg.ha^{-1})
M01	M01_TN_0500	3861 - 661	0.01 - 0.03	25.32 - 20.61	0.05 - 0.25	187.62 - 166.94
M01	M01_TN_1500	3562 - 482	0.01 - 0.04	22.92 - 18.26	0.05 - 0.3	163.44 - 143.4
M01	M01_TN_2500	2192 - 472	0.01 - 0.04	19.9 - 16.81	0.06 - 0.27	140.44 - 128.3
M01	M01_TN_3500	3129 - 569	0.01 - 0.04	25.44 - 21.54	0.06 - 0.28	176.49 - 160.08
M01	M01_TN_4500	3573 - 493	0.01 - 0.03	20.85 - 15.89	0.04 - 0.27	155.07 - 133.4
M02	M02_TN_0500	4197 - 717	0.01 - 0.03	28.13 - 24.28	0.05 - 0.27	211.3 - 195.88
M02	M02_TN_1500	5923 - 683	0.01 - 0.04	30.98 - 24.75	0.04 - 0.3	230.36 - 203.56
M02	M02_TN_2500	3874 - 714	0.01 - 0.03	26.39 - 22.94	0.06 - 0.29	225.86 - 209.34
M02	M02_TN_3500	6139 - 699	0 - 0.03	27.94 - 23.46	0.04 - 0.32	240.86 - 221.4
M02	M02_TN_4500	5112 - 632	0.01 - 0.05	33.12 - 28.66	0.06 - 0.47	315.29 - 294.42
M03	M03_TN_4500	7920 - 840	0 - 0.03	31.97 - 24.59	0.03 - 0.26	257.44 - 222.54
M03	M03_TS_0500	7726 - 686	0 - 0.03	28.65 - 23.07	0.03 - 0.33	251.89 - 226.56
M03	M03_TS_1500	10434 - 834	0 - 0.04	36.71 - 29.72	0.03 - 0.35	324.32 - 292.65
M03	M03_TS_2500	3505 - 545	0.01 - 0.03	22.05 - 17.13	0.06 - 0.32	203.22 - 176.11
M03	M03_TS_3500	6773 - 693	0 - 0.03	27.4 - 21.87	0.03 - 0.27	211.92 - 187.51
M04	M04_TN_(-)0500	7533 - 893	0 - 0.03	28.6 - 22.52	0.03 - 0.19	191.33 - 166.75
M04	M04_TN_0500	9091 - 971	0 - 0.03	33.37 - 26.66	0.03 - 0.21	234.96 - 208.06
M04	M04_TN_1500	7950 - 1030	0 - 0.02	32.4 - 25.73	0.03 - 0.21	243.91 - 213.1
M04	M04_TN_2500	8408 - 1088	0 - 0.02	35.1 - 27.02	0.03 - 0.2	258.86 - 220.71
M04	M04_TN_3500	9651 - 931	0 - 0.03	33.84 - 25.3	0.03 - 0.23	251.06 - 212.12
M05	M05_TN_(-)0500	8478 - 678	0 - 0.03	27.95 - 22	0.02 - 0.27	202.84 - 179.75
M05	M05_TN_0500	8257 - 977	0 - 0.03	37.19 - 30.18	0.03 - 0.23	252.21 - 224.68
M05	M05_TN_1500	8507 - 827	0 - 0.03	34.9 - 27.04	0.03 - 0.27	259.8 - 226.52
M05	M05_TN_2500	10506 - 986	0 - 0.03	37.28 - 28.72	0.03 - 0.25	290.25 - 250.81
M05	M05_TN_3500	11475 - 995	0 - 0.03	38.9 - 30.51	0.03 - 0.28	311.12 - 274.1
M06	M06_TN_(-)0500	6359 - 839	0.01 - 0.04	34.82 - 29.7	0.04 - 0.29	262.4 - 241.47
M06	M06_TN_0500	8160 - 640	0 - 0.04	34.53 - 27.56	0.03 - 0.4	281.04 - 253.48
M06	M06_TN_1500	6609 - 529	0 - 0.05	29.71 - 24.81	0.03 - 0.4	230.05 - 212.3
M06	M06_TN_2500	7801 - 761	0 - 0.04	35.86 - 28.05	0.04 - 0.32	279.02 - 245.45
M06	M06_TN_3500	8312 - 752	0 - 0.04	35.22 - 28.33	0.03 - 0.3	250.91 - 224.14
M07	M07_TS_0500	5788 - 708	0.01 - 0.04	30.93 - 24.84	0.05 - 0.35	278.76 - 248
M07	M07_TS_1500	7726 - 766	0 - 0.04	34.35 - 27.91	0.04 - 0.37	314.75 - 283.3
M07	M07_TS_2500	8240 - 720	0 - 0.04	34.24 - 26.93	0.04 - 0.4	322.31 - 285.29
M07	M07_TS_3500	8052 - 852	0 - 0.03	33.66 - 27.39	0.03 - 0.28	268.08 - 240.05
M07	M07_TS_4500	8379 - 859	0 - 0.03	35.83 - 28.26	0.04 - 0.32	314.85 - 277.4
M08	M08_TS_0500	5725 - 605	0.01 - 0.05	33.46 - 29.83	0.05 - 0.5	313.43 - 299.71
M08	M08_TS_1500	7365 - 725	0 - 0.03	27.17 - 21.2	0.02 - 0.21	172.83 - 150.83
M08	M08_TS_2500	6948 - 708	0 - 0.04	31.58 - 24.89	0.03 - 0.29	230.34 - 203.56
M08	M08_TS_3500	5970 - 610	0 - 0.04	29.45 - 23.19	0.04 - 0.34	232.38 - 205.22

M08	M08_TS_4500	6828 - 868	0 - 0.03	33.51 - 28.29	0.03 - 0.24	229.96 - 210.3
M09	M09_TS_0500	6945 - 905	0 - 0.03	32.53 - 27	0.04 - 0.25	250.36 - 226.48
M09	M09_TS_1500	9149 - 869	0 - 0.03	31.61 - 26.15	0.03 - 0.29	273.15 - 248.41
M09	M09_TS_2500	9609 - 769	0 - 0.03	30.88 - 24.1	0.03 - 0.29	250.61 - 220.74
M09	M09_TS_3500	9997 - 757	0 - 0.03	32.77 - 26.27	0.03 - 0.37	312.11 - 279.06
M09	M09_TS_4500	10096 - 776	0 - 0.03	31.36 - 23.37	0.03 - 0.31	282.75 - 241.06
M10	M10_TS_0500	6980 - 620	0 - 0.04	32.3 - 25.52	0.04 - 0.36	250.53 - 222.94
M10	M10_TS_1500	4766 - 606	0.01 - 0.05	32.53 - 27.78	0.06 - 0.42	273.96 - 254.1
M10	M10_TS_2500	5882 - 522	0 - 0.04	27.8 - 22.85	0.04 - 0.38	219.25 - 200.35
M10	M10_TS_3500	4432 - 512	0.01 - 0.05	28.44 - 24.55	0.06 - 0.48	260.18 - 243.78
M10	M10_TS_4500	5011 - 571	0.01 - 0.04	30.63 - 24.85	0.05 - 0.38	238.34 - 214.49
M11	M11_TN_0500	4676 - 716	0.01 - 0.03	28.02 - 22.39	0.04 - 0.25	204.61 - 180.42
M11	M11_TN_1500	3330 - 450	0.01 - 0.06	29.82 - 27.53	0.08 - 0.56	260.84 - 252.74
M11	M11_TN_2500	4180 - 620	0.01 - 0.04	26.77 - 22.87	0.05 - 0.31	211.39 - 194.37
M11	M11_TN_3500	3631 - 751	0.01 - 0.03	27.83 - 24.18	0.06 - 0.27	218.62 - 202.82
M11	M11_TN_4500	4090 - 770	0.01 - 0.03	24.65 - 20.97	0.05 - 0.24	200.22 - 182.89

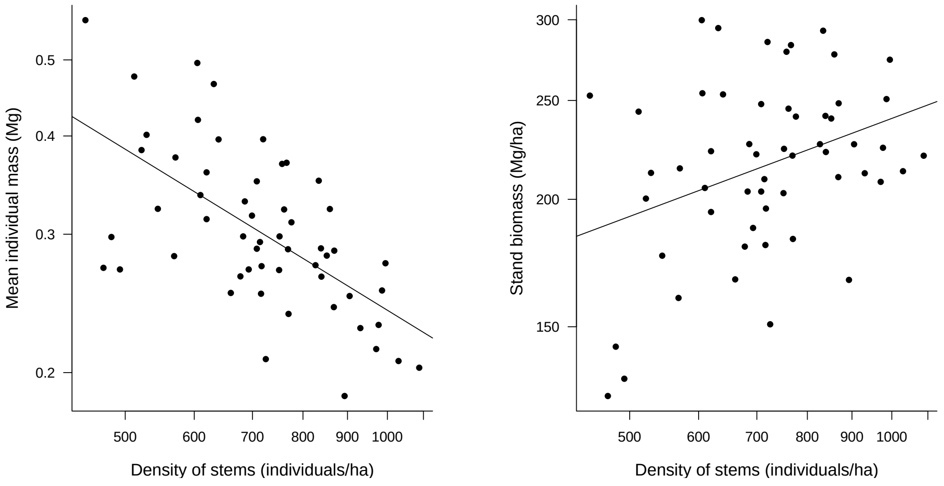


Figure S1. Relationships between (left) mean individual mass and density of stems ($r^2 = 0.39$, scaling factor, $a = -0.68$); and (right) stand biomass and the density of stems ($r^2 = 0.12$, $a = 0.32$) for individuals with dbh ≥ 10 cm in 55-1ha plots along the Purus-Madeira interfluve in central Amazonia. Variables were log-transformed and both relationships were statistically significant ($p < 0.05$).

Capítulo 3

Schietti, J., Stark, S.C., Souza, P., Martins, D.L., Emilio, T., Levis, C., Pinto, J.L.P.V., Silva, D.C., Costa, F.R.C., Schöngart, J., Tomasella, J., Saleska, S.R., Magnusson, W. Environmental limits to canopy height in Central Amazonia. Manuscrito em preparação para *Functional Ecology*.

Environmental limits to canopy height in Central Amazonia

Juliana Schietti*[1], Scott C. Stark[2], Priscila Souza[3], Demétrius Martins[3], Thaise Emilio[1], Carolina Levis[3], José Luis Purri da Veiga Pinto[4], Dorival Cruz da Silva[5], Flávia R. C. Costa[3], Jochen Schöngart[1,6], Javier Tomasella[7], Scott R. Saleska[2], William E. Magnusson[3, 5]

[1] Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia (INPA). Av. Ephigênio Sales 2239, 69011-970, Manaus, AM, Brazil.

[2] Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, 85721, USA

[3] Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA). Av. Ephigênio Sales 2239, CEP 69011-970, Manaus, Amazonas, Brazil

[4] Programa de Capacitação Institucional (PCI/Geoma), Instituto Nacional de Pesquisas da Amazônia (INPA). Av. Ephigênio Sales 2239, CEP 69011-970, Manaus, Amazonas, Brazil.

[5] Centro de Estudos Integrados da Biodiversidade Amazônica – INCT CENBAM

[6] Max Planck Institute for Chemistry, Biogeochemistry Department, Mainz, Germany

[7] Centro Nacional de Monitoramento e Alertas de Desastres Naturais (Cemaden/MCTI). Rodovia Presidente Dutra, Km 40, CEP: 12630-000, Cachoeira Paulista, SP, Brazil

* author for correspondence: jujuschietti@gmail.com

Summary

1. The heights of taller trees determine forest-canopy height, which affects many aspects of forest functioning. Based on studies of individual tree dimensions, maximum height is biophysically limited under optimal growth conditions. However, environmental conditions such as water supply and disturbance regimes seem to prevent trees achieving their potential heights in many forests, resulting in environmental limitation of canopy height at the stand level.

3. We investigated water table depth, soil depth, soil texture, annual precipitation and frequency of storms as possible environmental drivers of mean and maximum canopy height in 51 plots in lowland rainforest along a 600 km transect in central Amazonia. Variation in canopy height due to between-site variation in canopy-species composition and average diameter were also investigated.

4. Mean and maximum canopy height were estimated using a portable ground LiDAR device, which confers rapid and standardized canopy-height assessment. The direct and indirect (via species composition and average diameter) influences of environmental gradients on canopy height were examined using linear mixed-effect models and path analysis.

5. Shallow water table, annual precipitation, silt content and shallow soils were the main factors limiting canopy height, suggesting that water excess, poor water drainage and low anchorage are important constraints for growth in height in these forests. Species composition explained part of the among-site variation in mean canopy height, but was unrelated to maximum canopy height.

6. Direct relationships between canopy height and environmental gradients (not explained by changes in species composition) indicate that intraspecific among-site variation in tree stature may cause much of the variation in canopy height. Future studies should focus on linking species plasticity to canopy height-variation along environmental gradients.

Introduction

Height confers advantages to taller forest trees, such as higher light availability, more exposure to pollinators and greater potential dispersal distances. However, biophysical constraints limit the maximum height trees can achieve. The maximum height at which trees can support their own weight without breaking may be reached when height scales to the 2/3 power of diameter (McMahon 1973). Besides mechanical limitation, maximum height may also be limited in many cases by the higher resistance to water flow from roots to the canopy in taller trees. Taller trees should close their stomata earlier in the day to prevent cavitation. Therefore, as trees get older and taller, productivity decreases and less carbon is allocated for wood growth (Yoder *et al.* 1994; Ryan & Yoder 1997).

These hypotheses of biophysical limitations to tree height have been debated in the literature (Friend 1993; Ryan & Yoder 1997; Becker, Meinzer, & Wullschleger 2000; Niklas & Spatz 2004; Ryan, Phillips, & Bond 2006; Niklas 2007), but less attention has been paid to the role of environmental gradients as factors limiting height. Tree growth in height seems to be frequently limited by environmental conditions and disturbance regimes since maximum heights found in many forest canopies are not close to the buckling limit (Mcmahon 1973; King *et al.* 2009). Moreover, increased hydraulic limitation, as a function of path length, seems not to be a universal mechanism of height limitation (Becker *et al.* 2000; Ryan *et al.* 2006), since similar leaf water potentials can be found in trees of different heights within the same species (Koch *et al.* 2004). Increased resistance to water transport from roots to canopy leaves, ultimately resulting in stomata closure, is certainly an important mechanism of growth limitation. However, this mechanism may be more affected by water supply (Koch *et al.* 2004), soil texture and water retention capacity (Jackson *et al.* 2000; Hacke *et al.* 2000) than by path length.

Disturbance regimes, such as windstorms, when frequent, may prevent trees reaching their potential heights, producing forests with shorter canopies. Frequent disturbances increase mortality rates and change the tree size distribution, decreasing the density of large trees (Brown *et al.* 1997; Niklas *et al.* 2003b; Coomes *et al.* 2003). Forests with higher canopies are observed in low disturbance regimes, such as the sequoia or lowland wind-protected dipterocarp forests, where trees are able to reach heights closer to their potential maximum (Koch *et al.* 2004; King *et al.* 2009). Soil depth can make trees more or less susceptible to uprooting during windstorms. Shallow soils imply limited root space and generally lower anchorage for trees. Therefore, it is reasonable to expect forests with higher canopies in areas with deeper soils and lower frequency of disturbances.

Species can achieve distinctive maximum heights and their plasticity to cope with environmental conditions is a result of their evolutionary histories. At the stand level, canopy height will be determined by the height of the tallest trees in the local area. Hence, among-site differences in canopy height may be determined either by changes in canopy species composition or plasticity to local environmental conditions. If environmental conditions play a major role in limiting canopy height it is expected that canopy-height variation will be more directly related to environmental gradients than to changes in species composition.

p

Methods

Study area

The study was conducted in 51 plots along a 600 km transect in the Purus-Madeira interfluve, south of the Amazon River in central Amazonia (Fig. 1). The plots were distributed in 11 research sites along the BR-319, a road that has been largely abandoned for regular traffic since the 1980s (Fearnside & de Alencastro Graça 2006). In each site, 5 plots were regularly distributed along a 5 km trail at 1 km intervals. Plots were established at least 1 km from the road to avoid secondary forests. The Purus-Madeira interfluve has a relatively recent geological origin resulting in unstable sediments from the Late Pleistocene or Early Eocene with predominantly flat topography (Sombroek 2000). Elevation above sea level varies from 27 to 80 meters along the transect (Shuttle Radar Topography data). This region is part of the Amazon basin “Loamy plains” (Sombroek 2000), a landform covering around 11% of the Amazon basin, including the low interfluvial areas of Rio Negro-Amazonas and Juruá-Purus-Madeira.

Soils are mainly Gleysols and Plinthosols with poor water drainage and the predominant texture is silt to fine sand. The mean annual precipitation varied from 2000 to 2400 mm between 1960 and 1990, with the number of consecutive months with less than a 100 mm of rainfall (a threshold generally considered an indicator of the dry season) ranging from 1 month in the north of the transect to 4 months per year in the south (Sombroek, 2001). Large areas are waterlogged during the rainy season, and many of the small streams dry out during the dry season. The vegetation is classified as lowland dense rainforests in the north and lowland open rainforests dominated by palms in the south (BRASIL 1974).

Canopy height and diameter measurements

Canopy height was estimated along the central line of the 51 plots in the Purus-Madeira interfluve using a portable ground LiDAR (light detection and ranging), Riegl LD90-3100VHS-FLP system (Horn, Austria). Ground LiDAR generates a vertical one-dimensional canopy profile along the transect (Parker & Russ 2004). From the canopy surface profile of each plot we calculated two canopy-height metrics, the mean canopy height, defined as the mean surface value, and the maximum canopy height, defined as the higher 99% quantile values (Fig. 2).

The same canopy-height metrics were calculated from individual tree measurements. Thirty-three trees with diameter at breast height (dbh) ≥ 30 cm were selected in 27 plots (2-3 plots per site). Ten trees in each diametric class of 30-40 cm, 40-50cm, 50-60cm and > 60cm were selected by chance in each plot. More trees were selected in smaller classes when not enough trees were found in the two largest classes. These trees had the total height estimated by a single observer using a Vertex hypsometer (Vertex Laser VL400 Ultrasonic-Laser Hypsometer III, Haglöf of Sweden) (D. Martins, unpublished data).

Mean canopy height and maximum canopy height derived from ground LiDAR can be predicted by the same metrics calculated from individual-tree measurements within the plot area. Mean canopy height of the trees measured with the hypsometer explained 77% of the variance in mean height estimated by ground LiDAR, and maximum canopy height of the trees measured with the hypsometer explained 71% of the variance in maximum height estimated by ground LiDAR (Fig. 3).

Variation in canopy height may be largely determined by stand mean diameter, based on the well-known height-diameter allometric relationship (Niklas 1994). Taller canopies may be a result of the area having larger trees. To account for the relationship between height and diameter in canopy-height variation, we included the average diameter of trees (dbh ≥ 30 cm) per plot as a co-variable in the following analyses. This allows us to ask whether trees are taller than expected for their overall size. Trees with diameter ≥ 30 cm at 1.30 m (or at higher location in cases of buttress or other deformations) were measured in all 51 of the 1 ha plots. According to field classification of canopy-strata position in these forests, 99% of trees with dbh $\geq$ 30 cm had their canopies totally or partially exposed to direct solar radiation (J. Schietti, unpublished data). Therefore, trees with dbh $\geq$ 30 cm were considered to be canopy trees in this study.

Species composition

In a subset of 21 plots where floristic identification of trees was available (P. Souza, unpublished data), we investigated if variation in mean and maximum canopy height were associated with species composition of trees with dbh $\geq$ 30 cm. If canopy height varied with species composition we also investigated which environmental gradients were affecting canopy height via species composition. Trees with dbh $\geq$ 30 cm were identified to species in plots with dimensions of 40 x 250 m (~ 1 ha), 20m to each side of the central line where the ground LiDAR survey was undertaken.

The tree-species composition matrix was summarized in one dimension using non-metric multidimensional scaling (NMDS). Species ordination was based on relative abundance (standardized by total abundance per plot) and on presence and absence of species. The Bray-Curtis dissimilarity index was used in both ordinations. To evaluate the adequacy of the species ordinations, we used the adjusted r^2 of the dissimilarity matrices of original data regressed against the dissimilarity along the one-dimensional ordination (McCune & Grace 2002). The percentage of variance captured by one-dimensional NMDS was 41%, for species relative abundance, and 34% for species presence-absence.

Disturbance and environmental gradients

As a measure of the exogenous-disturbance regime in the region, we used the frequency of storms in 1999 (Espírito-Santo *et al.* 2010). The geographical distribution of blowdowns has been shown to be correlated with the frequency of storms, indexed by the number of days with precipitation $\geq$ 20 mm, in the Brazilian Amazon in two different periods (Nelson *et al.* 1994; Espírito-Santo *et al.* 2010). To estimate the frequency of days with heavy rainfall ($\geq$ 20 mm), daily precipitation in 1999 was integrated from NOAA (National Oceanic and Atmospheric Administration) satellite images with 4 km resolution and the 10.7 mm band from NOAA satellite 8 (see Espírito-Santo *et al.* 2010 for methods details).

Water table depth was manually monitored at frequencies varying from monthly to three times per year (at highest and lowest levels) in 7m-deep wells in all plots from Aug-2010 to Mar-2013. The mean water table depth, and the highest and lowest levels were computed for all 51 plots over the monitored period.

Soil texture was analysed in a compound sample derived from 6 subsamples from the first 30 cm depth of soil collected along the central line in each of the 51 plots. Fractions (%) of silt, sand and clay were determined and, because soils are predominantly silty in the region (Sombroek 2000), the fraction of silt was used as proxy for soil-water retention.

Soils were scored for physical limitations for plants in all plots following Quesada *et al.* (2010). Soil effective depth (presence of roots) was evaluated and scored from 0 to 5. Higher scores denote more limited soil conditions for plants. Score 0 indicates deep soils (≥ 150 cm); score 1 indicates hardpan, rocks or C horizon ≥ 100 cm; score 2 indicates hardpan or rock that allows vertical root growth or other soils between 50 and 100 cm deep; score 3 indicates relatively shallow soils (20 to 50 cm) and score 4 indicates shallow soils (less than 20 cm deep). Soil-depth limitation scores were based on 2m deep pits dug in each research site and in soil-profile samples from all plots (D. Martins, unpublished data; J. Schietti & T. Emilio, unpublished data).

Data analysis

The direct and indirect effects (via species composition) of environmental gradients and exogenous disturbance on canopy height were evaluated using linear mixed-effect models (Zuur *et al.* 2009) and path analyses (McCune & Grace 2002). Site was included in the models as a random effect to account for the nested design (plots within sites) (Zuur *et al.* 2009).

We first evaluated if environmental gradients were associated with species-composition changes and the average diameter of trees with dbh ≥ 30 cm. Gradients that were not related to species composition and the average diameter were evaluated as variables directly affecting canopy height, together with species composition and mean diameter.

We used the standardized coefficients, or beta coefficients (b_{coef}), of the linear mixed-effect models to quantify direct and indirect effects on canopy height metrics. We used path analysis to evaluate the indirect effects of environment gradients on canopy height via species composition (by multiplying beta coefficients along the paths) and the net indirect effects by summing paths (McCune & Grace 2002).

Results

Canopy height along the Purus-Madeira interfluve

Mean canopy height in the Purus-Madeira interfluve varied between 17 and 27 m (average = 22 m) and maximum heights were between 25 and 44 m (average = 32m) (Table 1). Forest in the northeast of the transect generally had lower mean canopy height than forest in the southern portion of the study region (Fig. 4).

Canopy height along environmental gradients

The water table was within 7m of the surface in most (82 %) of the plots. Mean water table depth in the plots was around 3m, the average annual depth varying from 5m to 1m depth (Table 1). The soil-depth score varied between 0 and 4, but 73% of the plots scored between 2 and 3, indicating soil depths for root growth from 20 to 100 cm in most of the plots. Silt fraction varied between 13 to 72%. On average, soil texture in the plots was 52% silt, 28% sand and 19% clay. The frequency of storms, given by the number of days with heavy rain (≥ 20 mm) in 1999, ranged from 35 to 60 days.

The frequency of storms was higher is areas where the soil was deeper (r = 0.50), with larger sand fractions (r = 0.39) and with a lower water table level (r = 0.42). Therefore, the influence of the frequency of storms on canopy height metrics was evaluated in different models that included this variable instead of the water table level.

Different models explained variation in mean and maximum canopy height along the forests in the Purus-Madeira interfluve (Table 2). Mean canopy height was directly influenced by the canopy-species composition, canopy mean diameter and by the mean water table level (Fig. 5 and 6), while maximum canopy height varied only in relation to environmental gradients and the mean diameter of canopy trees. There was no detectable influence of canopy-species composition on maximum canopy height (Fig. 5 and 7).

Mean canopy height was lower in areas with higher minimum water table level and with larger soil silt fractions. The mean water table level had a direct and negative effect (b_{coef} = - 0.40) on canopy height while the silt fraction had an indirect effect, via species composition and mean diameter of canopy trees. Path analysis indicated that silt fraction had a weak negative effect on canopy height via species composition (b_{coef}= -0.09, given by the multiplication of paths in Fig. 6), and a stronger negative effect via mean diameter of canopy trees (b_{coef}= -0.24). Summing these indirect effects, silt fraction had a negative net effect on mean canopy height (b_{coef}= -0.30). In contrast, mean annual precipitation had opposite effects on mean canopy height, via canopy trees species composition (b= 0.25) and via mean diameter (b = -0.17). Because these effects cancelled each other out the net effect of annual precipitation on mean canopy height was low (b_{coef}= -0.08).

Maximum canopy height was lower in areas with higher mean water table level and shallower soils. Also, silt fraction and higher mean annual precipitation had negative indirect effects on maximum canopy height by limiting the mean diameter of canopy trees (Fig. 7).

Frequency of storms had a positive direct effect on both mean and maximum canopy height (Table S1 in Supporting Information).

Discussion

Canopy height in forests of the Purus-Madeira interfluve

A previous study has shown that trees in forests around Manaus are taller for any given diameter than trees in forests of Brazilian south and southwest Amazonia (Nogueira *et al.* 2008). However, no study had so far estimated the height of the forests between these two regions. We showed that canopy height along Purus-Madeira transect does not simply decrease from the Manaus region to the south-western Brazilian Amazon. In fact, we found shorter forests in the north-eastern part of the transect, closer to Manaus, and taller forests in the south-western part of the transect (except for the last site that is located on an alluvial terrace). Intra-regional variation in canopy height emphasizes the importance of understanding environmental drivers of canopy height.

Environmental limits to canopy height

Shallow water table level was an important factor limiting canopy height in the forests along the Purus-Madeira interfluve. A shallow water table may maintain water supply for plants during the dry season (Miguez-Macho & Fan 2012). However, high water-table levels may cause oxygen depletion in the root zone and limit tree growth. Sixty-seven percent of the plots had water table levels within the first meter of soil at some part of the year, and 45% within the first 50cm, where most part of the roots are usually found in tropical evergreen forests (Canadell *et al.* 1996). Oxygen depletion in the root zone causes mineral nutrition problems, such as decreased potassium content in the leaves and in the whole plant (Sojka 1992; Sojka, Oosterhuis, & Scott 2005), because potassium uptake and maintenance are active processes (Kozlowski 1984). Potassium is fundamental for the maintenance of guard-cell turgor and stomatal openness for leaf-gas exchanges with the atmosphere (Sojka 1992; Sojka *et al.* 2005). Stomatal closure or decrease in stomatal aperture initially caused by oxygen depletion in the root zone decreases photosynthetic activity and limits shoot growth in many plants (Kozlowski 1984, 1997; Sojka *et al.* 2005). If excess-water conditions persist, many species not able to maintain physiological activity, close their stomata, enter physiological dormancy, and limit stem growth until favourable soil-water conditions return (Worbes 1995; Schöngart *et al.* 2002).

Soils with higher silt content were associated with forests where trees in the canopy strata had smaller mean diameters, resulting in lower mean and maximum canopy heights. Hydraulic and physical properties linked to silty texture might explain the negative effect of this soil fraction on canopy height. Soils with higher silt content have greater water-retention capacity compared to coarser-texture soils and, in the case of Purus-Madeira silty-loam soils, they also present poor water drainage (Sombroek 2000). The capillary fringe rising from the water table level can extend the zone of oxygen depletion closer to the ground surface where most part of the roots grow. The capillary fringe is the zone above the water table where the air-entry pressure is less than that required to penetrate the water table (Berkowitz, Silliman, & Dunn 2004). This layer in which water fills up soil pores through capillarity can extend to 1.5 m above water table level in silty loam soils (Dingman 2002) and it can favor superficial soil saturation in shallow water-table conditions (within 1m deep) (Fan & Miguez-Macho 2010). A third characteristic, not related to water excess, is that soils with higher silt content might be also more resistant to root penetration, impairing root development and nutrient absorption. All these characteristics associated with higher silt-content soils (low water drainage, high water holding capacity, relatively thick capillary fringe accompanied by shallow water table and resistance to root penetration), indicate unfavourable conditions for stem growth.

Forests in areas with higher mean annual precipitation had canopy trees with smaller mean diameters resulting in a negative effect of precipitation on canopy height. Contrary to our findings, previous studies in Southeast Asia showed that forest stature accompanied the precipitation gradient in the region, with lower stature forests in drier and more seasonal climates (Kira 1974). Kira (1974) showed that trees with the same diameter were taller in forests with higher annual precipitation. Feldpausch *et al.* (2011) also found changes in height-diameter allometry along precipitation gradients in a pan tropical evaluation, with stouter trees in places with longer dry seasons. Our results indicate that variation in mean and maximum canopy height along the precipitation gradient is accompanied by variations in the diameter of canopy trees resulting in higher or lower canopy heights. The negative effect of mean annual precipitation on the average diameter of trees indicates again that stem growth might be limited by water excess in these forests.

Besides the negative effect of mean annual precipitation on canopy-height metrics via average diameter, the net effect of precipitation (given by the sum of paths in the path analysis) had a very low contribution to variation in mean canopy height. Mean annual precipitation had a positive effect on mean canopy height via species composition, indicating a filter for taller canopy species where annual precipitation is higher. These opposite indirect effects, via diameter and species composition, had similar magnitude and cancelled out each other resulting in a weak effect of annual precipitation on mean canopy height. The opposite effects of annual precipitation did not occur for maximum canopy height. Silt fraction also had an indirect effect on mean canopy height via species composition, but it was in the same direction as the effect via average diameter, both limiting mean canopy height. These results indicate that soils with higher silt fractions are associated with lower-stature species.

Higher frequency of wind disturbances associated with heavy rains (Nelson *et al.* 1994; Espírito-Santo *et al.* 2010) was expected to prevent trees reaching taller statures and result in lower canopy heights. However, contrary to our expectation, the frequency of storms (heavy rains) had a positive effect on canopy height. Soils were deeper, had higher sand content, and the mean water-table level tended to be deeper in areas where storms were more frequent. A possible explanation is that heavy rains, usually associated with the dry season (Nelson *et al.* 1994), could be a water source in areas of higher soil-water drainage due to higher sand fraction and lower water table level. The lowest water table level in 42% of plots was below 6m. The indications that water excess in the wet season is the main limiting factor of canopy height in these forests may be compounded by lower water table levels associated with coarser surface-soil textures during the dry season, which may also limit canopy height. Deeper soils also allow better root development and anchorage, and this could lead to trees being less susceptible to uprooting during storm events, a hypothesis supported by the fact that maximum canopy height in forests along the Purus-Madeira interfluve increased with soil depth.

Intraspecific variation in tree height

The direct effect of water table level on canopy height, unrelated to species composition or average diameter of canopy trees, indicates that intraspecific variation in tree height along this gradient may explain much of the among-site variation in both mean and maximum canopy height. Variation in maximum canopy height seems to reflect intraspecific variation in tree stature along a soil-depth gradient rather than differences in species composition. Future studies should investigate height variation within species broadly spread along water table and soil-depth gradients for a more mechanistic understanding of environmental limits to tree height.

Implications of shallow water table for the functioning of the amazon forest

Shallow water table is a more common feature than previously thought on the global scale (Fan *et al.* 2013) and also in the Amazon basin (Fan & Miguez-Macho 2010). Shallow water-table depth, < 5 m or < 10m is estimated for 36% and 60%, respectively, of the Amazon basin, based on a compilation of literature, data on wells in government archives and hydrological modelling (Fan & Miguez-Macho 2010). Our observations of shallow water table along approximately 600km of predominantly terra-firme forests in Central Amazonia corroborate the scenario in which water table should play an important role maintaining forest functioning during the dry season (Miguez- Macho & Fan 2012). However, our results also indicate that shallow water tables associated with fine-particle soils may limit tree growth and ultimately canopy height. Forests over shallow water tables should be viewed in a new perspective for a better understanding of its seasonal functioning both in relation to responses to drought and in relation to waterlogging.

References

Becker, P., Meinzer, F.C. & Wullschleger, S.D. (2000) Hydraulic limitation of tree height : a critique. Functional Ecology, 14, 4–11.

Berkowitz, B., Silliman, S.E. & Dunn, A.M. (2004) Impact of the Capillary Fringe on Local Flow , Chemical Migration , and Microbiology. Vadose Zone Journal, 3, 534–548.

BRASIL. (1974) Projeto RADAM Folha SB20 Purus. Rio de Janeiro.

Brown, S., Schroeder, P. & Birdsey, R. (1997) Aboveground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. Forest Ecology and Management, 96, 37–47.

Canadell, J., Jackson, R.B., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.D. (1996) Maximum Rooting Depth of Vegetation Types at the Global Scale. Oecologia, 108, 583–595.

Coomes, D. a., Duncan, R.P., Allen, R.B. & Truscott, J. (2003) Disturbances prevent stem size-density distributions in natural forests from following scaling relationships. Ecology Letters, 6, 980–989.

Dingman, S.L. (2002) Physical Hydrology, 2nd ed. Prentice Hall, Upper Saddle River, N J.

Espírito-Santo, F.D.B., Keller, M., Braswell, B., Nelson, B.W., Frolking, S. & Vicente, G. (2010) Storm intensity and old-growth forest disturbances in the Amazon region. Geophysical Research Letters, 37, 1–6.

Fan, Y., Li, H. & Miguez-Macho, G. (2013) Global patterns of groundwater table depth. Science (New York, N.Y.), 339, 940–3.

Fan, Y. & Miguez-Macho, G. (2010) Potential groundwater contribution to Amazon evapotranspiration. Hydrology and Earth System Sciences, 14, 2039–2056.

Fearnside, P.M. & de Alencastro Graça, P.M.L. (2006) BR-319: Brazil’s Manaus-Porto Velho highway and the potential impact of linking the arc of deforestation to central amazonia. Environmental management, 38, 705–16.

Feldpausch, T.R., Banin, L., Phillips, O.L., Baker, T.R., Lewis, S.L., Quesada, C.A., et al. (2011) Height-diameter allometry of tropical forest trees. Biogeosciences, 8, 1081–1106.

Friend, A. (1993) The prediction and physiological significance of tree height. Vegetation Dynamics & Global Change (ed A.M. Solomon), pp. 101–115. Springer Science.

Hacke, U.G., Sperry, J.S., Ewers, B.E., Ellsworth, D.S., Schäfer, K.V.R. & Oren, R. (2000) Influence of soil porosity on water use in Pinus taeda. Oecologia, 124, 495–505.

Jackson, R.B., Sperry, J.S. & Dawson, T.E. (2000) Root water uptake and transport : using physiological predictions. , 5.

King, D. a., Davies, S.J., Tan, S. & Nur Supardi, M.N. (2009) Trees approach gravitational limits to height in tall lowland forests of Malaysia. Functional Ecology, 23, 284–291.

Kira, T. (1974) Community architecture and . organic matter dynamics in tropical lowland rain forests of Southeast Asia with special reference to Pasoh Forest , West Malaysia.

Koch, G.W., Sillett, S.C., Jennings, G.M. & Davis, S.D. (2004) The limits to tree height. Nature, 428, 851–4.

Kozlowski, T.T. (1984) Plant Responses to Flooding of Soil. Bioscience, 34, 162–167.

Kozlowski, T.T. (1997) Responses of woody plants to flooding and salinity. Tree Physiology, 17, 490–490.

McCune, B. & Grace, A.J.B. (2002) Analysis of Ecological Communities. MjM Software Design.

McMahon, T. (1973) Size and Shape in Biology. Science, 173, 1201–1204.

Mcmahon, T. (1973) Size and Shape in Biology Thomas. Science, 179, 1201–1204.

Miguez-Macho, G. & Fan, Y. (2012) The role of groundwater in the Amazon water cycle: 1. Influence on seasonal streamflow, flooding and wetlands. Journal of Geophysical Research, 117, D15113.

Miguez ‐ Macho, G. & Fan, Y. (2012) The role of groundwater in the Amazon water cycle: 2. Influence on seasonal soil moisture and evapotranspiration. Journal of Geophysical Research, 117.

Nelson, B., Kapos, V., Adams, J., Oliveira, W.J. & Braun, O.P.. (1994) Forest disturbance by large blowdowns in the Brazilian Amazon. Ecology, 75, 853–858.

Niklas, K.J. (1994) Plant Allometry: The Scaling of for and Process. The University of Chicago Press, Chicago, IL.

Niklas, K.J. (2007) Maximum plant height and the biophysical factors that limit it. Tree physiology, 27, 433–40.

Niklas, K.J., Midgley, J.J. & Rand, R.H. (2003) Tree size frequency distributions, plant density, age and community disturbance. Ecology Letters, 6, 405–411.

Niklas, K.J. & Spatz, H.-C. (2004) Growth and hydraulic (not mechanical) constraints govern the scaling of tree height and mass. Proceedings of the National Academy of Science, 101, 15661–15663.

Nogueira, E.M., Nelson, B.W., Fearnside, P.M., França, M.B. & Oliveira, Á.C. (2008) Tree height in Brazil's "arc of deforestation": shorter trees in south and southwest Amazonia imply lower biomass. Forest Ecology and Management, 255, 2963–2972.

Parker, G.G. & Russ, M.E. (2004) The canopy surface and stand development: assessing forest canopy structure and complexity with near-surface altimetry. Forest Ecology and Management, 189, 307–315.

Quesada, C. a., Lloyd, J., Schwarz, M., Patiño, S., Baker, T.R., Czimczik, C., Fyllas, N.M., Martinelli, L., Nardoto, G.B., Schmerler, J., Santos, a. J.B., Hodnett, M.G., Herrera, R., Luizão, F.J., Arneth, a., Lloyd, G., Dezzeo, N., Hilke, I., Kuhlmann, I., Raessler, M., Brand, W. a., Geilmann, H., Moraes Filho, J.O., Carvalho, F.P., Araujo Filho, R.N., Chaves, J.E., Cruz Junior, O.F., Pimentel, T.P. & Paiva, R. (2010) Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. Biogeosciences, 7, 1515–1541.

Ryan, M.G., Phillips, N. & Bond, B.J. (2006) The hydraulic limitation hypothesis revisited. Plant, Cell and Environment, 29, 367–381.

Ryan, M. & Yoder, B. (1997) Hydraulic Limits to Tree Height and Tree Growth. Bioscience, 47, 235–242.

Schöngart, J., Piedade, M.T.F., Ludwigshausen, S., Horna, V. & Worbes, M. (2002) Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. Journal of Tropical Ecology, 18, 581–597.

Sojka, R.E. (1992) Stomatal closure in oxygen-stressed plants. Soil Science, 154, 269–280.

Sojka, R.E., Oosterhuis, D.M. & Scott, H.D. (2005) Root Oxygen Deprivation and the and Gas Exchange.

Sombroek, W. (2000) Amazon landforms and soils in relation to biologcal diversity. Acta Amazonica, 30, 81–100.

Worbes, M. (1995) How to measure growth dynamics in tropical trees. IAWA, 16, 337–351.

Yoder, B., Ryan, M.G., Waring, R.H., Schoettle, A.W. & Kaufmann, M.R. (1994) Evidence of reduced photosynthesis rates in old trees.pdf. Forest Science, 40, 513–527.

Zuur, A., Ieno, E.N., Walker, N., Savellev, A.A. & Smith, G.M. (2009) Mixed Effects Models and Extensions in Ecology with R. Springer, New York.

Table 1. Mean values and the range of variation (minimum – maximum) of canopy-height metrics derived from ground LiDAR and environmental gradients evaluated as drivers of canopy height in the Purus-Madeira interfluve, in Central Amazonia. Median value is presented for soil depth score.

Variables	**Mean/Median (min - max)**
Mean canopy height (m)	22.12 (16.86 - 27.73)
Maximum canopy height (m)	31.82 (25 - 44.16)
Mean diameter (cm)	40.15 (34.6 - 47.39)
Mean water-table level (m)	-2.91 (< -7 - 0.43)
Lowest water-table level (m)	-5.17 (< -7 - -1.46)
Highest water-table level (m)	-1.05 (< -7 - 2.34)
Soil depth score	2 (0 - 4)
Silt fraction (%)	52.28 (13.25 - 74.25)
Sand fraction (%)	28.81 (7.14 - 58.33)
Clay fraction (%)	18.9 (7.08 - 38)
Frequency of storms (days/year)	51.73 (35 - 60)
Annual precipitation (mm)	2291 (2111 - 2489)

Table 02. Results of linear mixed-effect models (LMM) relating mean canopy height and maximum canopy height to species composition changes (summarized by a NMDS ordination) as a function of water-table level, canopy tree-species composition, canopy-tree mean diameter, soil-depth score, silt fraction and annual precipitation (fixed effects). Site was considered as a random effect in all models. Marginal R^2 (R^2_{marg}) shows the models adjusted only considering fixed effects, and conditional R^2 (R^2_{cond}) corresponds to the full model, including the random effect (site effect). The relative contribution of predictors is given by the standardized coefficients of the LMMs. Probability of independent contributions for each predictor is shown in parentheses.

Dependent variables	AIC	$R2_{marg}$	$R2_{cond}$	Relative contribution of predictors (beta coefficients)					
				Water table	Species composition	Mean diameter	Soil depth	Silt fraction	Annual precipitation
Mean canopy height	39.71	0.71	0.91	-0.40 (0.009)	-0.43 (0.001)	0.54 (< 0.001)	--	--	--
Maximum canopy height	118.5	0.61	0.72	-0.23 (0.009)	--	0.63 (< 0.001)	-0.28 (0.009)	--	--
Mean diameter	143.4	0.30	0.55	--	--	--	--	-0.45 (0.001)	-0.32 (0.001)
Species composition	48.81	0.36	0.88	--	--	--	--	0.20 (0.018)	-0.58 (0.002)

Figures

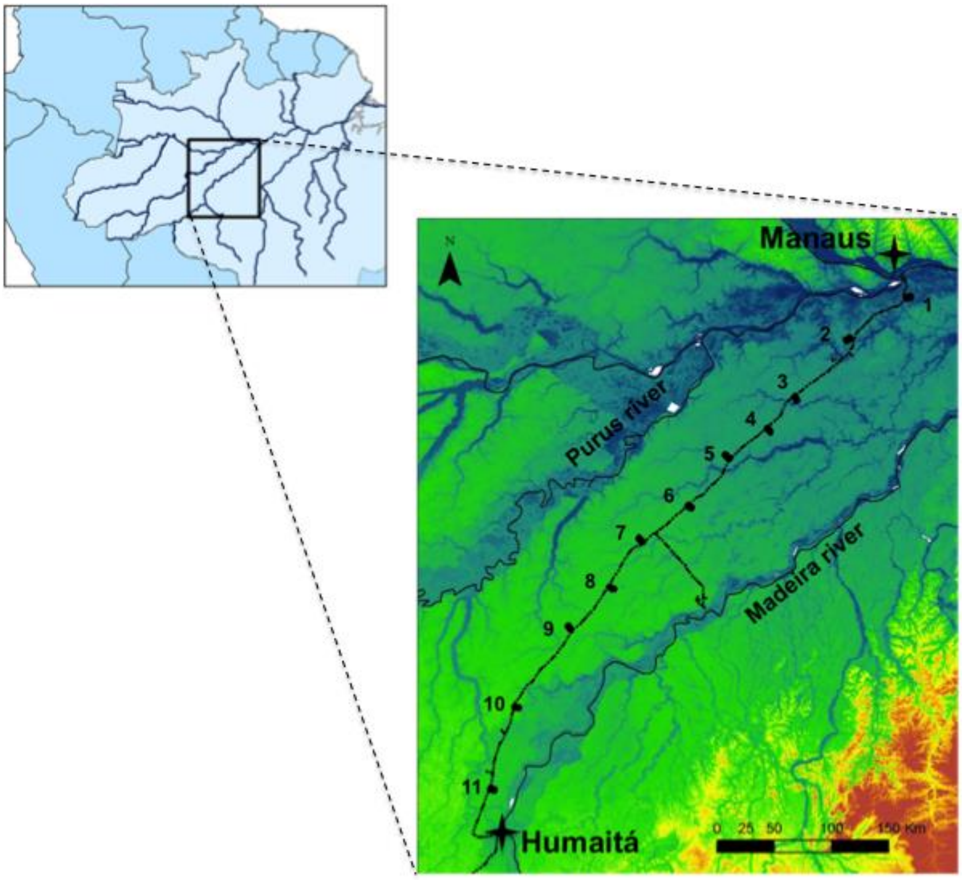


Figure 1. Map of the study area showing the 600 km transect along the interfluve between the Purus and Madeira Rivers in central Amazonia. Eleven research sites (1 - 11) are located along the transect.

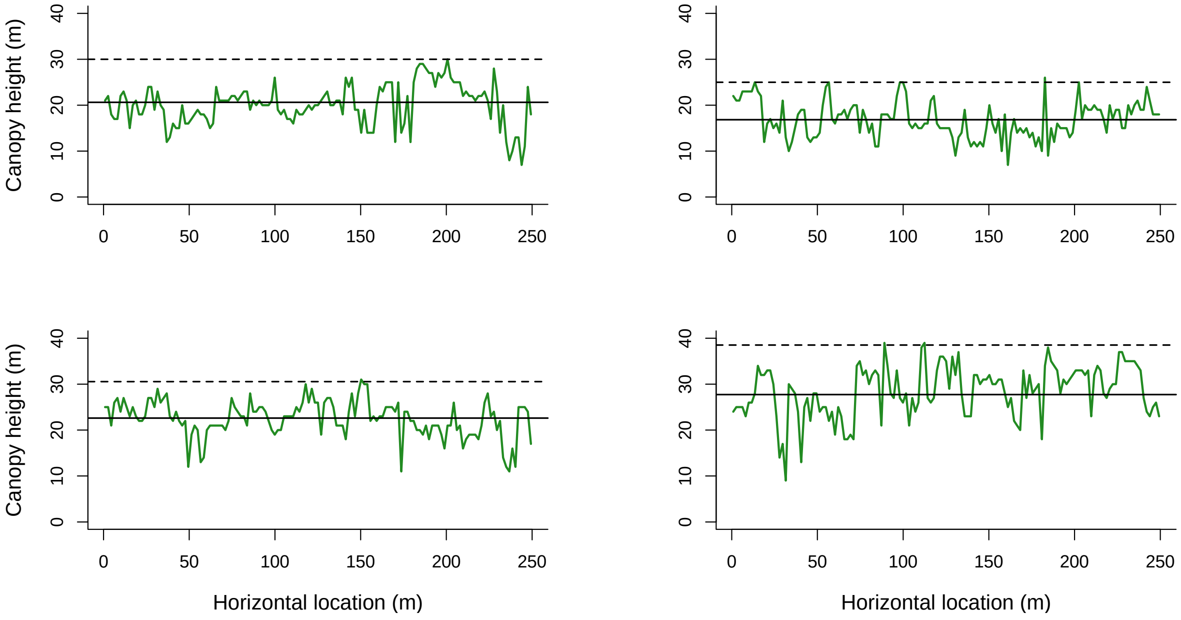


Figure 2. Canopy height surface (green line) derived from portable ground LiDAR in four selected transects (of the 55) surveyed along the Purus-Madeira interfluve, in Central Amazonia. Black continuous lines show values of mean canopy height and dashed lines show the values of maximum canopy height calculated as the higher 99% quantile values.

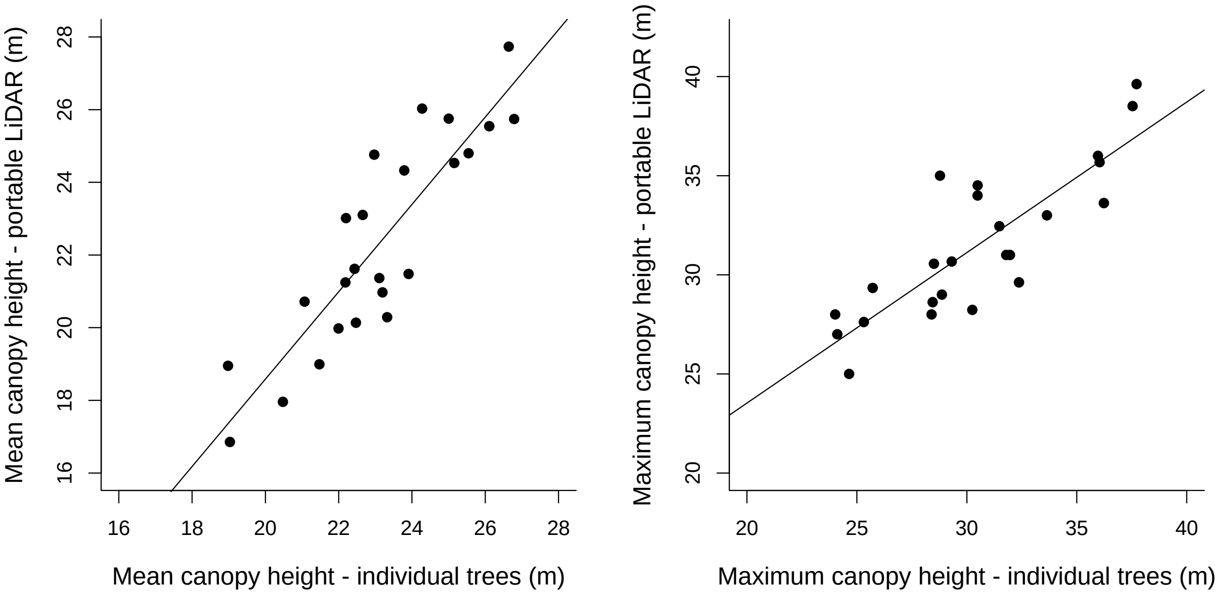


Figure 3. Relathionships between stand-level height metrics from portable ground LiDAR and from individual tree (dbh >= 30 cm) measurements. (a) Mean canopy height calculated from tree individual heights (MCH_{tree}) predicts 77% of the variance in the same metric derived from portable ground LiDAR, MCH_{gLidar}, ($MCH_{gLidar} = -5.46 + 1.2\ MCH_{tree}$, $p < 0.001$). (b) Maximum canopy height (MaxCH), estimated from the high 99% quantile, from tree individual heights predicts 71% of the variance in the same metric derived from portable LiDAR ($MaxCH_{gLidar} = 0.76 + 8.34\ MCH_{tree}$, $p < 0.001$).

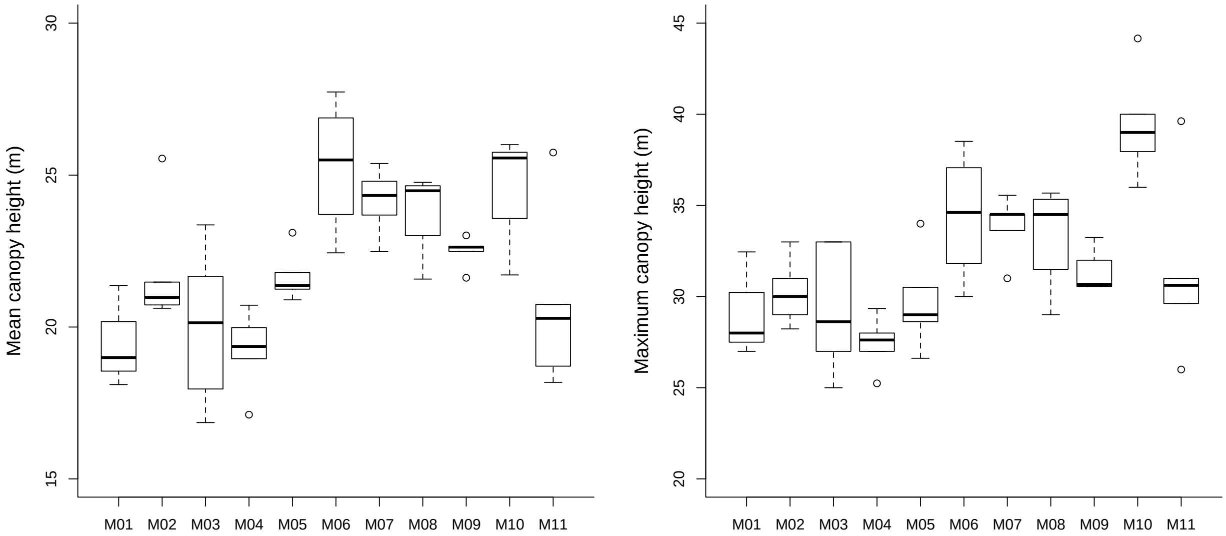


Figure 4. Spatial variation in mean and maximum canopy height in the 11 sites along the Purus-Madeira interfluve, south of the Amazonas River in central Amazonia. Forests in the northeastern part of the transect have lower canopy than in the southwestern, except for the last site (11) which is located on an alluvial terrace.

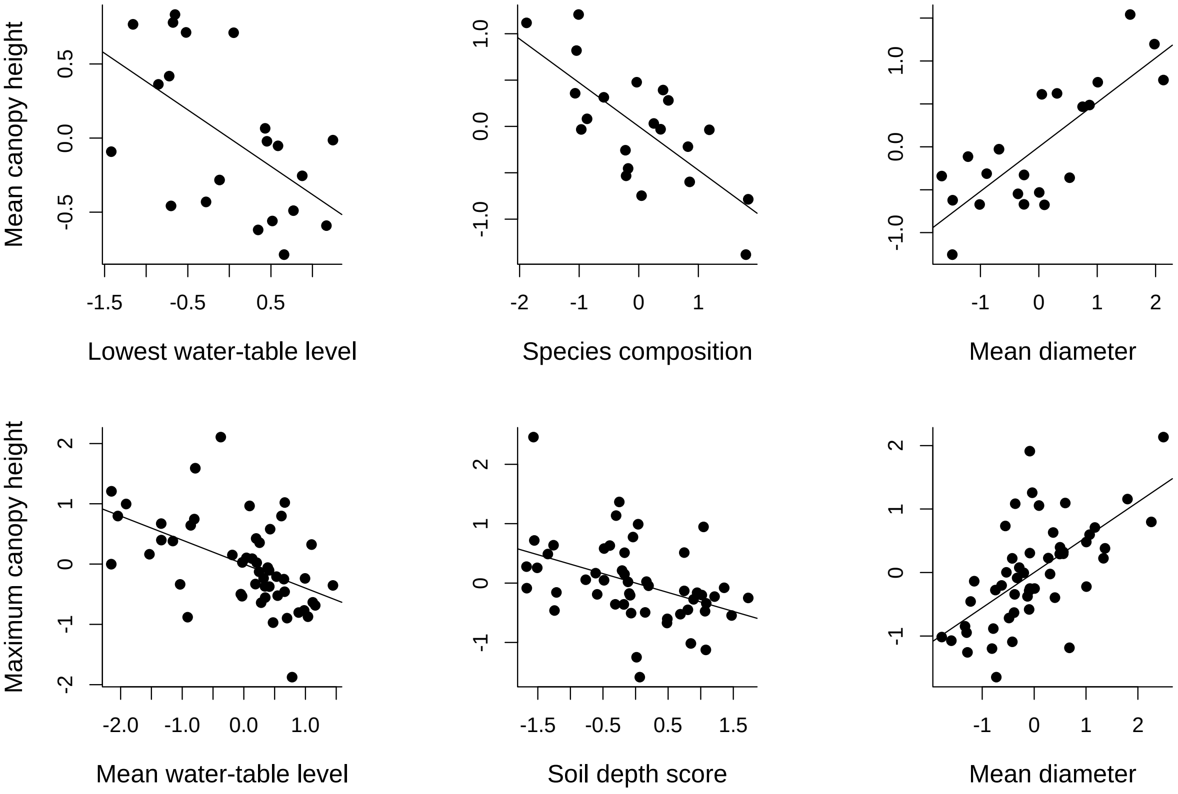


Figure 5. Partial plots from two multiple regression models showing direct drivers of mean and maximum canopy height. Upper panel - Partial regressions between mean canopy height, lowest water-table level, species composition (one-dimensional solution to non-metric multidimensional scaling analysis) and the mean diameter of trees with dbh ≥ 30 cm (R2 marginal = 0.71). Lower panel - Partial plots from a a multiple regression relating maximum canopy height to mean water-table level, soil depth score (higher scores denotes shallower soils) and the mean diameter of trees with dbh ≥ 30 cm (R2 marginal = 0.61). Fitted lines indicate fixed-effect probabilities < 0.05 in the linear mixed-model analyses (see Table 2).

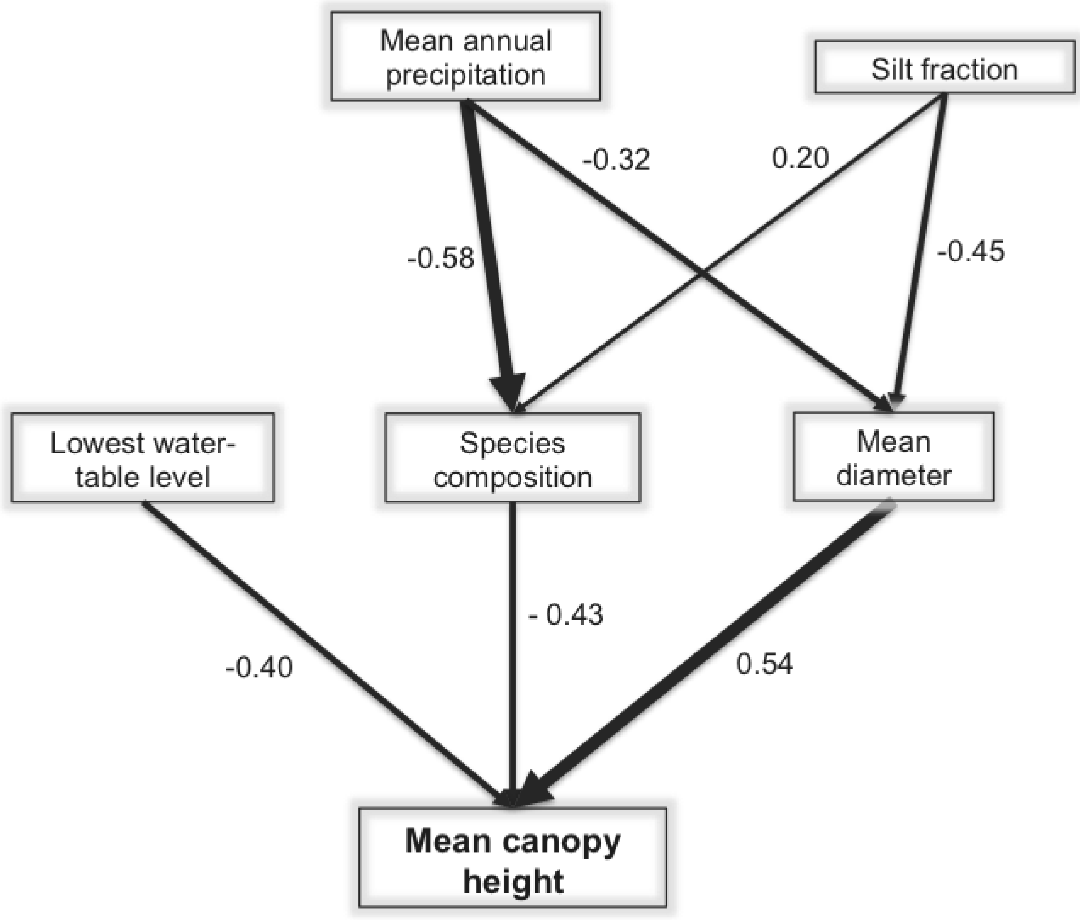


Figure 6. Path analysis showing the magnitude of direct and indirect effects, given by standardized coefficients from linear mixed-effect models (with probabilities < 0.005), of environmental gradients, species composition and the average diameter (dbh ≥ 30 cm) in relation to the stand mean canopy height. Arrow widths show the magnitude of the effects.

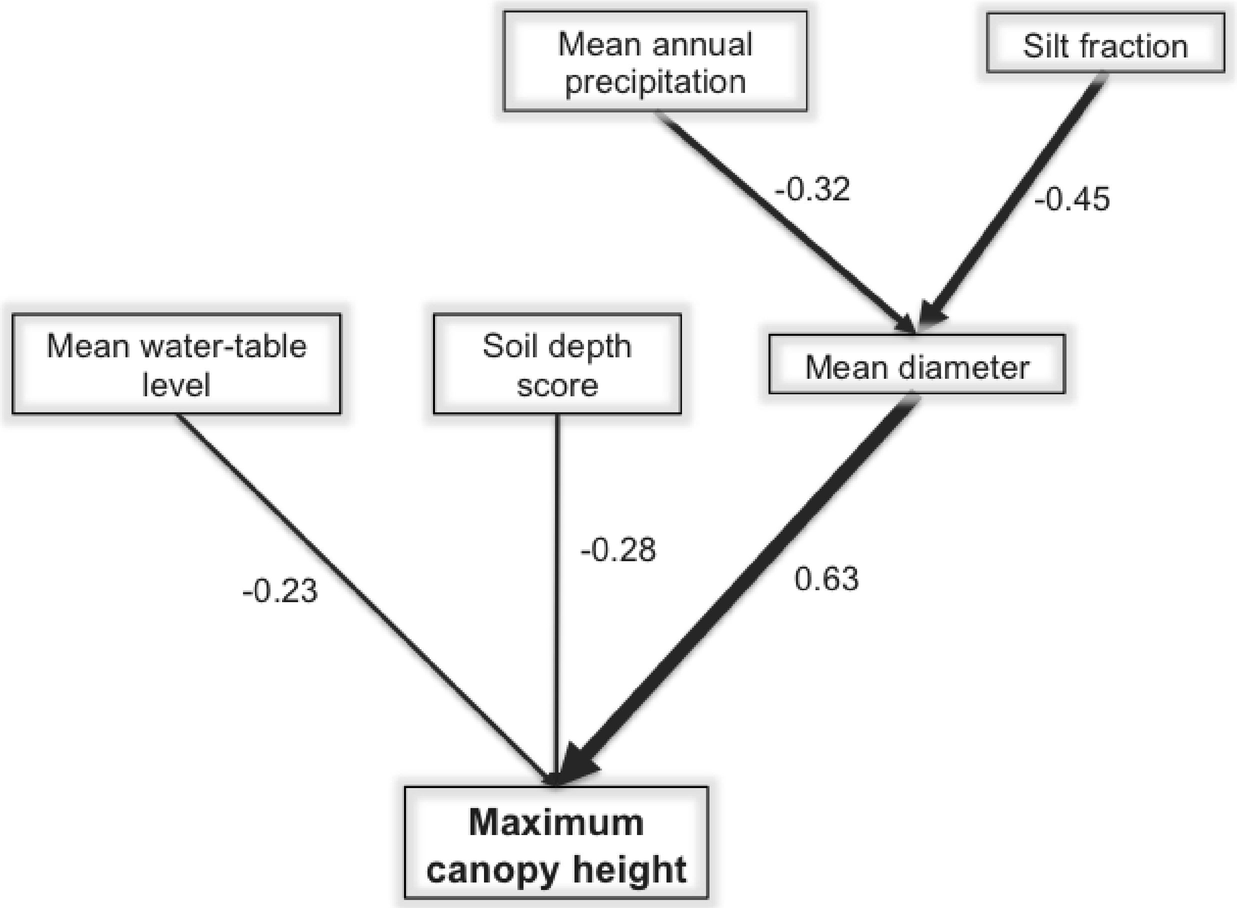


Figure 7. Path analysis showing the magnitude of direct and indirect effects, given by standardized coefficients from linear mixed-effect models (with probabilities < 0.005), of environmental gradients and mean tree diameter (dbh ≥ 30 cm) to stand maximum canopy height.

Supplementary Information

Table S1. Results of linear mixed-effect models (LMM) relating mean canopy height and maximum canopy height, derived from portable ground LiDAR, to the frequency of storms per year, canopy trees species composition (given by NMDS axis) and canopy trees mean diameter (fixed effects). Site was considered as a random effect in all models. The marginal (R^2_{marg}) and conditional (R^2_{cond}) coefficients of determination (R^2) are presented. Marginal R^2 shows the models adjusted only considering fixed effects and conditional R^2 corresponds to the full model, including the random effect (site effect). The relative contribution of predictors is given by the standardized coefficients of the LMMs. Probability of independent contributions for each predictor is shown in parentheses.

Dependent variables	AIC	$R2_{marg}$	$R2_{cond}$	Relative contribution of predictors (beta coefficients)		
				Frequency of storms	Species composition	Mean diameter
Mean canopy height	45.28	0.69	0.81	-0.30 (0.023)	-0.28 (0.041)	0.55 (< 0.001)
Maximum canopy height	116	0.51	0.74	-0.32 (0.014)	--	0.73 (< 0.001)

SÍNTESE

Os resultados dos três capítulos desta tese permitem um avanço no entendimento de como as propriedades físicas do solo e profundidade do lençol freático afetam a estrutura, estoques de biomassa e composição de espécies de plantas em florestas da Amazônia Central. O lençol freático raso está presente tanto nas áreas de baixios e parte baixa das encostas nas florestas com relevo dissecado ao norte de Manaus, como em vastas extensões de áreas relativamente planas ao sul do rio Amazonas, no interflúvio Purus-Madeira. O lençol freático próximo da superfície associado às propriedades físicas do solo determinam condições de suprimento de água e aeração para as raízes que podem afetar o estabelecimento, crescimento e acúmulo de biomassa em plantas.

A variação na composição de espécies de plantas de diferentes formas de vida na região ao norte de Manaus está fortemente relacionada com a distância vertical da drenagem mais próxima, sugerindo que o acesso ao lençol freático tem um papel importante no estabelecimento de espécies nessas florestas de terra-firme. Os resultados do capítulo 1 mostraram que as florestas que estão na zona de flutuação do lençol freático (até 18 m acima da drenagem nessa região, Tomasella *et al.* 2008) são as florestas onde ocorre a maior parte (cerca de 90%) das variações em composição florística. As áreas altas em relação à drenagem têm baixa complementaridade de espécies em relação as áreas verticalmente próximas à drenagem. Um dos possíveis mecanismos para explicar a maior substituição (*turnover*) de espécies no espaço em áreas onde o lençol freático é raso, é que as florestas nessas áreas são mais dinâmicas. As limitações associadas ao lençol freático raso e aos solos arenosos presentes nessas áreas, como menor volume aerado de solo para desenvolvimento de raízes e baixa ancoragem, provavelmente causam maior mortalidade de árvores (Toledo *et al.* 2012) devido à queda por desenraizamento (Toledo, Magnusson, & Castilho 2013). Essas áreas de lençol freático raso podem ter maior chance de recrutamento de novas espécies, tanto pelo dinamismo da vegetação como pelo acesso à água durante a estação (K. Melgaço, dados não publicados), do que áreas com lençol freático mais profundo, que podem sofrer estresse hídrico durante a estação seca (Hodnett *et al.* 1997) e onde a demografia da vegetação é menos dinâmica.

A relação entre composição florística e distância vertical da drenagem tem uma forte implicação para conservação de florestas ripárias. As áreas verticalmente próximas da drenagem, onde há maior variação na composição de espécies, podem se estender por centenas de metros de distância do curso d'água (até 350 m na Reserva Ducke). A legislação florestal brasileira protege as florestas ripárias em faixas de somente 30m de largura ao longo de cursos d'água (para canais de até 10 metros de largura) e portanto, não protege as áreas úmidas de alta complementaridade de espécies de plantas.

Características físicas do solo, como profundidade efetiva (onde há desenvolvimento de raízes) e condições anóxicas estão correlacionadas com os níveis de flutuação do lençol freático. Essas características, contabilizadas no índice de restrições físicas do solo de Quesada *et al.* (2010), indicam que solos mais impeditivos estão associados a florestas com maior densidade de indivíduos e menor massa média individual. Esses resultados (capítulo 2) suportam a hipótese de que as restrições físicas do solo promovem uma floresta mais dinâmica (Quesada *et al.* 2012a), com maior densidade de indivíduos de menor porte, apesar de não ter sido detectada variação nos estoques de biomassa em função do gradiente de restrição física do solo.

Solos com maior conteúdo de fósforo disponível estiveram associados a florestas com menor biomassa, corroborando estudos anteriores que encontram menores estoques de biomassa associados a solos mais férteis (Baker *et al.* 2004; Malhi *et al.* 2006; Quesada *et al.* 2012a). Um dos mecanismos que explicaria florestas com menor estoque de biomassa em solo mais férteis também está relacionado as características físicas do solo. Solos com estrutura física impeditiva ao desenvolvimento de raízes em geral são também mais férteis, devido a dependência de processos pedológicos comuns no desenvolvimento dos solos (Quesada *et al.* 2012b). Por isso, florestas mais dinâmicas associadas a solos com características físicas mais restritivas também estariam associadas a solos mais férteis (Phillips *et al.* 2004), o que suportaria espécies de crescimento mais rápido, com menor densidade da madeira e menor porte, pois o tempo de residência nessas florestas é menor (Quesada *et al.* 2012b). No entanto, no interflúvio Purus-Madeira há um efeito negativo da disponibilidade de fósforo no solo sobre a densidade de caules, sugerindo um mecanismo diferente do proposto por Quesada et al 2012, em que se esperaria encontrar maior densidade de caules de menor porte em florestas mais dinâmicas devido a maior mortalidade e recrutamento.

Áreas com lençol freático mais raso parecem também estar associadas a florestas com dossel médio mais baixo e com menos emergentes, caracterizando menor altura máxima do dossel, como mostrado no capítulo 3. As variações de altura média do dossel são em parte determinadas por diferenças na composição de espécies presentes no dossel (árvores com dap ≥ 30cm). A variação na composição de espécies de árvores de dossel não teve relação com a profundidade do lençol freático. No entanto, outro estudo considerando todas as classes diamétricas acima de 10 cm nas mesmas áreas (P. Souza, dados não publicados) encontrou uma relação similar a encontrada na Reserva Ducke (capítulo 1). A relação direta entre profundidade do lençol freático e altura média e máxima do dossel, sem efeitos indiretos via composição de espécies, implica em variação intraespecífica de altura das árvores em função do gradiente de profundidade do lençol freático. Essa hipótese deve ser investigada em estudos futuros e pode trazer um avanço no entendimento dos mecanismos determinando variações na altura das florestas.

Os resultados dos três capítulos indicam que a presença de lençol freático superficial, associada a características físicas do solo impeditivas ao desenvolvimento de raízes, mantém florestas de estrutura mais raquítica, com maior densidade de indivíduos de menor porte, árvores grandes raras e portanto, dossel mais baixo. Além disso, as florestas com lençol freático raso e solo arenoso podem apresentar maior variabilidade na composição de espécies do que florestas com lençol freático profundo, provavelmente devido ao maior dinamismo da vegetação nas áreas de lençol superficial e solo de textura grossa que confere baixa ancoragem.

Os efeitos negativos do lençol freático raso sobre a estrutura e biomassa das florestas do interflúvio Purus-Madeira indicam que o excesso de água exerce uma importante limitação sobre o crescimento de árvores nessa região. Portanto, os modelos de funcionamento da floresta em resposta a eventos de seca ou chuva em excesso devem ser revistos, levando-se em conta não somente o regime de chuvas mas também a profundidade do lençol e as características físicas locais do solo que, em conjunto, determinam o suprimento sazonal de água da floresta.

REFERÊNCIAS BIBLIOGRÁFICAS

Albernaz, A.L., Pressey, R.L., Costa, L.R.F., Moreira, M.P., Ramos, J.F., Assunção, P.A. & Franciscon, C.H. (2012) Tree species compositional change and conservation implications in the white-water flooded forests of the Brazilian Amazon. *Journal of Biogeography*, **39**, 869–883.

Baayen, R.H. (2011) languageR: Data sets and functions with "Analyzing Linguistic Data: A practical introduction to statistics".. R package version 1.4.

Baker, T., Phillips, O. & Malhi, Y. (2004) Variation in wood density determines spatial patterns inAmazonian forest biomass. *Global Change …*, 545–562.

Baldwin, D.S. & Mitchell, A.M. (2000) The effects of drying and re-flooding on the sediment and soil nutrient dynamics of soil lowland river-floodplain systems: a synthesis. *Regulated Rivers: Research and Managment*, **467**, 457–467.

Balvanera, P., Quijas, S. & Pérez-Jiménez. (2011) Distribution Patterns of Tropical Dry Forest Trees Along a Mesoscale Water Availability Gradient. *Biotropica*, **43**, 414–422.

Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Hérault, B., Dávila, N., Mesones, I., Rios, M., Valderrama, E. & Fine, P.V. a. (2011a) Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Global Change Biology*, **17**, 2677–2688.

Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Hérault, B., Dávila, N., Mesones, I., Rios, M., Valderrama, E. & Fine, P.V. a. (2011b) Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Global Change Biology*, **17**, 2677–2688.

Bartoń, K. (2013) MuMIn: Multi-model inference. R package version 1.9.5.

Bates, D., Maechler, M. & Bolker, B. (2013) lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-2.

Becker, P. & Castillo, A. (1990) Root architecture of shrubs and saplings in the understory of a tropical moist forest in lowland Panama. *Biotropica*, **22**, 242–249.

Becker, P., Meinzer, F.C. & Wullschleger, S.D. (2000) Hydraulic limitation of tree height : a critique. *Functional Ecology*, **14**, 4–11.

Bell, J.C., Cunningham, R.L. & Havens, M.W. (1994) Soil Drainage Class Probability Mapping Using a Soil-Landscape Model. *Soil Science Society of America Journal*, **58**, 464–470.

Berkowitz, B., Silliman, S.E. & Dunn, A.M. (2004) Impact of the Capillary Fringe on Local Flow , Chemical Migration , and Microbiology. *Vadose Zone Journal*, **3**, 534–548.

BRASIL. (1974) *Projeto RADAM Folha SB20 Purus.* Rio de Janeiro.

Brokaw, N. (1985) Gap-Phase Regeneration in a Tropical Forest. *Ecology*, **66**, 682–687.

Brown, D.J., Clayton, M.K. & McSweeney, K. (2004) Potential terrain controls on soil color, texture contrast and grain-size deposition for the original catena landscape in Uganda. *Geoderma*, **122**, 51–72.

Brown, S. & Lugo, A. (1992) Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. *Interciencia*, **17**, 8–18.

Brown, I.F., Martinelli, L.A., Thomas, W.W., Moreira, M.Z., Ferreira, C.A.C. & Victoria, R.A. (1995) Uncertainty in the biomass of Amazonian forests- An example from Rondonia, Brazil. *Forest Ecology and Management*, **75**, 175–189.

Brown, S., Schroeder, P. & Birdsey, R. (1997) Aboveground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. *Forest Ecology and Management*, **96**, 37–47.

Burnham, K.P. & Anderson, D.R. (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research*, **33**, 261–304.

Calcagno, V. & de Mazancourt, C. (2010) glmulti : An R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software*, **34**, 1–29.

Campling, P., Gobin, A. & Feyen, J. (2002) Logistic Modeling to Spatially Predict the Probability of Soil Drainage Classes. *Soil Science Society of America Journal*, **66**, 1390–1401.

Canadell, J., Jackson, R.B., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.D. (1996) Maximum Rooting Depth of Vegetation Types at the Global Scale. *Oecologia*, **108**, 583–595.

Castilho, C. V., Magnusson, W.E., de Araújo, R.N.O., Luizão, R.C.C., Luizão, F.J., Lima, A.P., Higuchi, N. & de Castilho, C. V. (2006) Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography. *Forest Ecology and Management*, **234**, 85–96.

Chambers, J.Q., Negrón-Juárez, R.I., Marra, D.M., Di Vittorio, A., Tews, J., Roberts, D., Ribeiro, G.H.P.M., Trumbore, S.E. & Higuchi, N. (2013) The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 3949–3954.

Chauvel, A., Lucas, Y. & Boulet, R. (1987) On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. *Experimentia*, **43**, 234–241.

Chave, J., Andalo, C., Brown, S., Cairns, M. a, Chambers, J.Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B.W., Ogawa, H., Puig, H., Riéra, B. & Yamakura, T. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, **145**, 87–99.

Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S. & Perez, R. (2004) Error propagation and scaling for tropical forest biomass estimates. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **359**, 409–20.

Chave, J., Condit, R., Lao, S., Caspersen, J.P., Foster, R.B. & Hubbell, S.P. (2003) Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. *Journal of Ecology*, **91**, 240–252.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology letters*, **12**, 351–66.

Chave, J., Riéra, B. & Dubois, M.-A. (2001) Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. *Journal of Tropical Ecology*, **17**, 79–96.

Clark, J.S. (1992) Density-independent mortality, density compensation, gap formation, and self-thinning in plant populations. *Theoretical Population Biology*, **42**, 172–198.

Clark, D.B. & Clark, D.A. (1996) Abundance , growth and mortality of very large trees in neotropical lowland rain forest. , **80**, 235–244.

Clark, C., Poulsen, J., Bolker, B., Connor, E. & Parker, V. (2005) Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology*, **86**, 2684–2694.

Colwell, R.K., Brehm, G., Cardelús, C.L., Gilman, A.C. & Longino, J.T. (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, **322**, 258.

Comita, L.S. & Engelbrecht, B.M.J. (2009) Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. *Ecology*, **90**, 2755–2765.

Coomes, D. a., Duncan, R.P., Allen, R.B. & Truscott, J. (2003) Disturbances prevent stem size-density distributions in natural forests from following scaling relationships. *Ecology Letters*, **6**, 980–989.

Costa, F.R.C. (2006) Mesoscale Gradients of Herb Richness and Abundance in Central Amazonia. *Biotropica*, **38**, 711–717.

Costa, F.R.C., Guillaumet, J.-L., Lima, A. & Pereira, O. (2009) Gradients within gradients: the mesoscale distribution patterns of palms in a central Amazonian forest. *Journal of Vegetation Science*, **20**, 69–78.

Costa, F.R.C. & Magnusson, W.E. (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.

Costa, F.R.C., Magnusson, W.E. & Luizao, R.C. (2005) Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. *Journal of Ecology*, **93**, 863–878.

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A. & Totterdell, I.J. (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, **408**, 184–7.

Cox, P.M., Harris, P.P., Huntingford, C., Betts, R.A., Collins, M., Jones, C.D., Jupp, T.E., Marengo, J.A. & Nobre, C.A. (2008) Increasing risk of Amazonian drought due to decreasing aerosol pollution. *Nature*, **453**, 212–5.

Dalling, J., Hubbell, S.P. & Silvera, K. (1998) Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Ecology*, **86**, 674–689.

Davidson, E.A., de Araújo, A.C., Artaxo, P., Balch, J.K., Brown, I.F., C. Bustamante, M.M., Coe, M.T., DeFries, R.S., Keller, M., Longo, M., Munger, J.W., Schroeder, W., Soares-Filho, B.S., Souza, C.M., Wofsy, S.C. & C Bustamante, M.M. (2012) The Amazon basin in transition. *Nature*, **481**, 321–328.

Daws, M.I., Mullins, C.E., Burslem, D.F.R.P., Paton, S.R. & Dalling, J.W. (2002) Topographic position affects the water regime in a semideciduous tropical forest in Panama. *Plant and Soil*, **238**, 79–90.

Denslow, J.S. (1995) Disturbance and Diversity in Tropical Rain Forests : The Density Effect. *Ecological applications*, **5**, 962–968.

Dingman, S.L. (2002) *Physical Hydrology*, 2nd ed. Prentice Hall, Upper Saddle River, N J.

Drucker, D.P., Costa, F.R.C. & Magnusson, W.E. (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.

EMBRAPA. (2011) *Manual de Métodos de Análise de Solo*, 2nd ed. Rio de Janeiro.

Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T. a, Tyree, M.T., Turner, B.L. & Hubbell, S.P. (2007) Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, **447**, 80–2.

Espírito-Santo, F.D.B., Keller, M., Braswell, B., Nelson, B.W., Frolking, S. & Vicente, G. (2010) Storm intensity and old-growth forest disturbances in the Amazon region. *Geophysical Research Letters*, **37**, 1–6.

Fan, Y., Li, H. & Miguez-Macho, G. (2013) Global patterns of groundwater table depth. *Science (New York, N.Y.)*, **339**, 940–3.

Fan, Y. & Miguez-Macho, G. (2010) Potential groundwater contribution to Amazon evapotranspiration. *Hydrology and Earth System Sciences*, **14**, 2039–2056.

Fearnside, P.M. & de Alencastro Graça, P.M.L. (2006) BR-319: Brazil's Manaus-Porto Velho highway and the potential impact of linking the arc of deforestation to central amazonia. *Environmental management*, **38**, 705–16.

Feldpausch, T.R., Banin, L., Phillips, O.L., Baker, T.R., Lewis, S.L., Quesada, C.A., *et al.* (2011) Height-diameter allometry of tropical forest trees. *Biogeosciences*, **8**, 1081–1106.

Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brienen, R.J.W., Gloor, E., Monteagudo Mendoza, a., *et al.* (2012a) Tree height integrated into pan-tropical forest biomass estimates. *Biogeosciences Discussions*, **9**, 3381–3403.

Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brienen, R.J.W., Gloor, M., Monteagudo Mendoza, A., *et al.* (2012b) Tree height integrated into pantropical forest biomass estimates. *Biogeosciences*, **9**, 3381–3403.

Ferry, B., Morneau, F., Bontemps, J.-D., Blanc, L. & Freycon, V. (2010) Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *Journal of Ecology*, **98**, 106–116.

Fisher, J.I., Hurtt, G.C., Thomas, R.Q. & Chambers, J.Q. (2008) Clustered disturbances lead to bias in large-scale estimates based on forest sample plots. *Ecology letters*, **11**, 554–63.

Friend, A. (1993) The prediction and physiological significance of tree height. *Vegetation Dynamics & Global Change* (ed A.M. Solomon), pp. 101–115. Springer Science.

Gibbons, J.M. & Newbery, D.M. (2002) Drought avoidance and the effect of local topography on trees in the understorey of Bornean lowland rain forest. *Plant Ecology*, **164**, 1–18.

Groom, P.K. (2004) Rooting depth and plant water relations explain species distribution patterns within a sandplain landscape. *Functional Plant Biology*, **31**, 423–428.

Hacke, U.G., Sperry, J.S., Ewers, B.E., Ellsworth, D.S., Schäfer, K.V.R. & Oren, R. (2000) Influence of soil porosity on water use in Pinus taeda. *Oecologia*, **124**, 495–505.

Harms, K.E. (1997) *Habitat-Specialization and Seed-Dispersal Limitation in a Neotropical Forest*. Princeton University.

Hodnett, M.G. & Tomasella, J. (2002) Marked differences between van Genuchten soil water-retention parameters for temperate and tropical soils: a new water-retention pedo-transfer functions developed for tropical soils. *Geoderma*, **108**, 155–180.

Hodnett, M.G., Vendrame, I., Marques Filho, D.O., Oyama, M. & Tomasella, J. (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**, 265–277.

Huete, A.R., Didan, K., Shimabukuro, Y.E., Ratana, P., Saleska, S.R., Hutyra, L.R., Yang, W., Nemani, R.R. & Myneni, R. (2006) Amazon rainforests green-up with sunlight in dry season. *Geophysical Research Letters*, **33**, 2–5.

Jackson, R.B., Canadell, J., Ehleringer, H.A., Mooney, H.A., Schulze, E.D. & Sala, O.E. (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia*, **108**, 389–411.

Jackson, R.B., Sperry, J.S. & Dawson, T.E. (2000) Root water uptake and transport : using physiological predictions. , **5**.

Jirka, S., McDonald, A.J., Johnson, M.S., Feldpausch, T.R., Couto, E.G. & Riha, S.J. (2007) Relationships between soil hydrology and forest structure and composition in the southern Brazilian Amazon. *Journal of Vegetation Science*, **18**, 183–194.

Joly, C.A. & Crawfordf, R.M.M. (1982) Variation in Tolerance and Metabolic Responses to Flooding in some Tropical Trees. *Journal of Experimental Botany*, **33**, 799–809.

Joslin, J.D., Wolfe, M.H. & Hanson, P.J. (2000) Effects of altered water regimes on forest root systems. *New Phytologist*, **147**, 117–129.

Junk, W.J. (1997) *The Central Amazon Floodplain: Ecology of a Pulsing System*. Springer.

Kanagaraj, R., Wiegand, T., Comita, L.S. & Huth, A. (2011) Tropical tree species assemblages in topographical habitats change in time and with life stage. *Journal of Ecology*, **99**, 1441–1452.

King, D. a., Davies, S.J., Tan, S. & Nur Supardi, M.N. (2009) Trees approach gravitational limits to height in tall lowland forests of Malaysia. *Functional Ecology*, **23**, 284–291.

Kinupp, V.F. & Magnusson, W.E. (2005) Spatial patterns in the understorey shrub genus Psychotria in central Amazonia: effects of distance and topography. *Journal of Tropical Ecology*, **21**, 363–374.

Kira, T. (1974) Community architecture and . organic matter dynamics in tropical lowland rain forests of Southeast Asia with special reference to Pasoh Forest , West Malaysia.

Koch, G.W., Sillett, S.C., Jennings, G.M. & Davis, S.D. (2004) The limits to tree height. *Nature*, **428**, 851–4.

Kozlowski, T.T. (1984) Plant Responses to Flooding of Soil. *Bioscience*, **34**, 162–167.

Kozlowski, T.T. (1997) Responses of woody plants to flooding and salinity. *Tree Physiology*, **17**, 490–490.

Kravchenko, A.N., Bollero, G.A., Omonode, R.A. & Bullock, D.G. (2002) Quantitative Mapping of Soil Drainage Classes Using Topographical Data and Soil Electrical Conductivity. *Soil Science Society of America Journal*, **66**, 235–243.

Lieberman, D. & Li, M. (1992) Seedling recruitment patterns in a tropical dry forest in Ghana. *Journal of Vegetation Science*, **3**, 375–382.

Luyssaert, S., Schulze, E.-D., Börner, A., Knohl, A., Hessenmöller, D., Law, B.E., Ciais, P. & Grace, J. (2008) Old-growth forests as global carbon sinks. *Nature*, **455**, 213–5.

Magnusson, W.E., Lima, A.P., Luizão, R., Luizão, F., Costa, F.R.C., Castilho, C.V. & Kinupp, V. (2005) RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. *Biota Neotropica*, **5**, 19–24.

Malhi, Y., Aragão, L., Galbraith, D., Huntingford, C., Fisher, R., Zelazowski, P., Sitch, S., Mcsweeney, C. & Meir, P. (2009) Exploring the likelihood and mechanism of a climate-change-induced dieback of the. *Proceedings of the National Academy of Science*, **49**, 20610–20615.

Malhi, Y., Nobre, A., Grace, J., Kruijt, B., Pereira, M.G.P., Culf, A. & Scott, S. (1998) Carbon dioxide transfer over a Central Amazonian rain forest. *Journal of Geophysical Research*, **103**, 31593–31612.

Malhi, Y., Wood, D., Baker, T.R., Wright, J., Phillips, O.L., Cochrane, T., Meir, P., Chave, J., Almeida, S., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D. a., Vargas, P.N., Pitman, N.C. a., Quesada, C.A., Salomao, R., Silva, J.N.M., Lezama, A.T., Terborgh, J., Martinez, R.V. & Vinceti, B. (2006) The regional variation of aboveground live biomass in old-growth Amazonian forests. *Global Change Biology*, **12**, 1107–1138.

Marengo, J.A. (2004) Interdecadal variability and trends of rainfall across the Amazon basin. *Theoretical and Applied Climatology*, **78**, 79–96.

Marques-Filho, A. de O., Ribeiro, M. de N.G., Santos, H.M. & Santos, J.M. (1981) Estudos climatologicos da Reserva Florestal Ducke - Manaus-AM. IV. Precipitacao. *Acta Amazonica*, **11**, 759–768.

Marshall, T.J., Holmes, J.W. & Rose, C.. (1996) *Soil Physics*, 3rd ed. Cambridge University Press, Cambridge.

Marthews, T.T.R., Burslem, D.F.R.P.D., Paton, S.R.R., Yangüez, F. & Mullins, C.E.E. (2008) Soil drying in a tropical forest : Three distinct environments controlled by gap size. *Ecological Modelling*, **216**, 369–384.

McCune, B. & Grace, A.J.B. (2002) *Analysis of Ecological Communities*. MjM Software Design.

McMahon, T. (1973) Size and Shape in Biology. *Science*, **173**, 1201–1204.

Mcmahon, T. (1973) Size and Shape in Biology Thomas. *Science*, **179**, 1201–1204.

Midgley, J.J. (2001) Do mixed-species mixed-size indigenous forests also follow the self-thinning line? , **16**, 661–662.

Miguez-Macho, G. & Fan, Y. (2012) The role of groundwater in the Amazon water cycle: 1. Influence on seasonal streamflow, flooding and wetlands. *Journal of Geophysical Research*, **117**, D15113.

Miguez-Macho, G. & Fan, Y. (2012) The role of groundwater in the Amazon water cycle: 2. Influence on seasonal soil moisture and evapotranspiration. *Journal of Geophysical Research*, **117**.

Naiman, R.J., Henri, D. & Décamps, H. (1997) The ecology of interfaces: riparian zones. *Annual review of Ecology and Systematics*, **28**, 621–658.

Negrón-Juárez, R.I., Chambers, J.Q., Marra, D.M., Ribeiro, G.H.P.M., Rifai, S.W., Higuchi, N. & Roberts, D. (2011) Detection of subpixel treefall gaps with Landsat imagery in Central Amazon forests. *Remote Sensing of Environment*, **115**, 3322–3328.

Nelson, B., Kapos, V., Adams, J., Oliveira, W.J. & Braun, O.P.. (1994) Forest disturbance by large blowdowns in the Brazilian Amazon. *Ecology*, **75**, 853–858.

Nepstad, D.C., Carvalho, C.R., Davidson, E.A., Jipp, P.H., Lefebvre, P.A., Negreiros, G.H., Silva, E.D., Stone, T.A., Trumbore, S.E. & Vieira, S. (1994) The role of deep roots in the hydrological and carbon cycles of Amazonia forests and pastures. *Nature*, **372**, 666–669.

Newbery, D.M., Campbell, E.J.F., Proctor, J. & Still, M.J. (1996) Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia. Species composition and patterns in the understorey. , **122**, 193–220.

Nicoll, B.C. & Ray, D. (1996) Adaptive growth of tree root systems in response to wind action and site conditions. *Tree physiology*, **16**, 891–898.

Niklas, K.J. (1994) *Plant Allometry: The Scaling of for and Process*. The University of Chicago Press, Chicago, IL.

Niklas, K.J. (2007) Maximum plant height and the biophysical factors that limit it. *Tree physiology*, **27**, 433–40.

Niklas, K.J., Midgley, J.J. & Enquist, B.J. (2003a) A general model for mass–growth-density relations across tree-dominated communities. *Evolutionary Ecology Research*, **5**, 459–468.

Niklas, K.J., Midgley, J.J. & Rand, R.H. (2003b) Tree size frequency distributions, plant density, age and community disturbance. *Ecology Letters*, **6**, 405–411.

Niklas, K.J. & Spatz, H.-C. (2004) Growth and hydraulic (not mechanical) constraints govern the scaling of tree height and mass. *Proceedings of the National Academy of Science*, **101**, 15661–15663.

Nobre, A.D., Cuartas, L.A., Hodnett, M., Rennó, C.D., Rodrigues, G., Silveira, A., Waterloo, M. & Saleska, S. (2011) Height Above the Nearest Drainage – a hydrologically relevant new terrain model. *Journal of Hydrology*, **404**, 13–29.

Nogueira, A., Costa, F.R.C. & Castilho, C.V. (2011) Liana abundance patterns: the role of ecological filters during development. *Biotropica*, **43**, 442–449.

Nogueira, E.M., Nelson, B.W., Fearnside, P.M., França, M.B. & Oliveira, Á.C. (2008) Tree height in Brazil's "arc of deforestation": shorter trees in south and southwest Amazonia imply lower biomass. *Forest Ecology and Management*, **255**, 2963–2972.

Oyama, M.D. (2003) A new climate-vegetation equilibrium state for Tropical South America. *Geophysical Research Letters*, **30**, 10–13.

Ozinga, W., Schaminée, J., Bekker, R., Bonn, S., Poschold, P., Tackenberg, O., Bakker, J. & van Groenendael, J.M. (2005) Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. *Oikos*, **108**, 555–561.

Page, C.N. (2002) Ecological strategies in fern evolution: a neopteridological overview. *Review of Palaeobotany and Palynology*, **119**, 1–33.

Paoli, G.D., Curran, L.M. & Slik, J.W.F. (2008) Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo. *Oecologia*, **155**, 287–99.

Parker, G.G., Harding, D.J. & Berger, M.L. (2004) A portable LIDAR system for rapid determination of forest canopy structure. *Journal of Applied Ecology*, **41**, 755–767.

Parker, G.G. & Russ, M.E. (2004) The canopy surface and stand development: assessing forest canopy structure and complexity with near-surface altimetry. *Forest Ecology and Management*, **189**, 307–315.

Parmentier, I. & Hardy, O.J. (2009) The impact of ecological differentiation and dispersal limitation on species turnover and phylogenetic structure of inselberg's plant communities. *Ecography*, **32**, 613–622.

Parolin, P. (2002) Submergence tolerance vs. escape from submergence: two strategies of seedling establishment in Amazonian floodplains. *Environmental and Experimental Botany*, **48**, 177–186.

Peña-Claros, M., Poorter, L., Alarcón, A., Blate, G., Choque, U., Fredericksen, T.S., Justiniano, M.J., Leaño, C., Licona, J.C., Pariona, W., Putz, F.E., Quevedo, L. & Toledo, M. (2012) Soil effects on forest structure and diversity in a moist and a dry tropical forest. *Biotropica*, **44**, 276–283.

Petraitis, P.S. (1995) Use of Average vs. Total Biomass in Self-Thinning Relationships. *Ecology*, **76**, 656–658.

Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., López-González, G., *et al.* (2009) Drought sensitivity of the Amazon rainforest. *Science*, **323**, 1344–1347.

Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, W.F., Lewis, S.L., Lloyd, J., Malhi, Y., Monteagudo, a, Neill, D. a, Vargas, P.N., Silva, J.N.M., Terborgh, J., Martínez, R.V., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J. a, Czimczik, C.I., Di Fiore, a, Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E.M., Olivier, J., Palacios, W., Patiño, S., Pitman, N.C. a, Quesada, C. a, Saldias, M., Lezama, a T. & Vinceti, B. (2004) Pattern and process in Amazon tree turnover, 1976-2001. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **359**, 381–407.

Phillips, O.L., Hall, P., Gentry, A.H., Sawyer, S.A. & Vásquez, R. (1994) Dynamics and species richness of tropical rain forests. *Proceedings of the National Academy of Science*, **91**, 2805–2809.

Phillips, O.L., van der Heijden, G., Lewis, S.L., López-González, G., Aragão, L.E.O.C., Lloyd, J., *et al.* (2010) Drought-mortality relationships for tropical forests. *The New phytologist*, **187**, 631–46.

Prates-Clark, C.D.C., Saatchi, S.S. & Agosti, D. (2008) Predicting geographical distribution models of high-value timber trees in the Amazon Basin using remotely sensed data. *Ecological Modelling*, **211**, 309–323.

Pyke, C.R., Condit, R., Aguilar, S. & Lao, S. (2001) Floristic composition across a climatic gradient in a neotropical lowland forest. *Journal of Vegetation Science*, **12**, 553–566.

Quesada, C. a., Lloyd, J., Schwarz, M., Patiño, S., Baker, T.R., Czimczik, C., Fyllas, N.M., Martinelli, L., Nardoto, G.B., Schmerler, J., Santos, a. J.B., Hodnett, M.G., Herrera, R., Luizão, F.J., Arneth, a., Lloyd, G., Dezzeo, N., Hilke, I., Kuhlmann, I., Raessler, M., Brand, W. a., Geilmann, H., Moraes Filho, J.O., Carvalho, F.P., Araujo Filho, R.N., Chaves, J.E., Cruz Junior, O.F., Pimentel, T.P. & Paiva, R. (2010) Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences*, **7**, 1515–1541.

Quesada, C.A., Phillips, O.L., Schwarz, M., Czimczik, C.I., Baker, T.R., Patiño, S., Fyllas, N.M., Hodnett, M.G., Herrera, R., Almeida, S., Alvarez Dávila, E., Arneth, a., Arroyo, L., Chao, K.J., Dezzeo, N., Erwin, T., di Fiore, A., Higuchi, N., Honorio Coronado, E., Jimenez, E.M., Killeen, T., Lezama, a. T., Lloyd, G., López-González, G., Luizão, F.J., Malhi, Y., Monteagudo, A., Neill, D. a., Núñez Vargas, P., Paiva, R., Peacock, J., Peñuela, M.C., Peña Cruz, A., Pitman, N., Priante Filho, N., Prieto, a., Ramírez, H., Rudas, A., Salomão, R., Santos, A.J.B., Schmerler, J., Silva, N., Silveira, M., Vásquez, R., Vieira, I., Terborgh,

J. & Lloyd, J. (2012a) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences*, **9**, 2203–2246.

Quesada, C. a., Phillips, O.L., Schwarz, M., Czimczik, C.I., Baker, T.R., Patiño, S., Fyllas, N.M., Hodnett, M.G., Herrera, R., Almeida, S., Alvarez Dávila, E., Arneth, a., Arroyo, L., Chao, K.J., Dezzeo, N., Erwin, T., di Fiore, a., Higuchi, N., Honorio Coronado, E., Jimenez, E.M., Killeen, T., Lezama, a. T., Lloyd, G., López-González, G., Luizão, F.J., Malhi, Y., Monteagudo, a., Neill, D. a., Núñez Vargas, P., Paiva, R., Peacock, J., Peñuela, M.C., Peña Cruz, a., Pitman, N., Priante Filho, N., Prieto, a., Ramírez, H., Rudas, a., Salomão, R., Santos, a. J.B., Schmerler, J., Silva, N., Silveira, M., Vásquez, R., Vieira, I., Terborgh, J. & Lloyd, J. (2012b) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences*, **9**, 2203–2246.

R 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/.

R Core Team. (2013) R: A language and environment for statistical computing.

Raes, N., Roos, M.C., Slik, J.W.F., Van Loon, E.E. & Steege, H. Ter. (2009) Botanical richness and endemicity patterns of Borneo derived from species distribution models. *Ecography*, **32**, 180–192.

Ramos, A., Folegatti, M.V., Bovi, M.L.A. & Diotto, A.V. (2009) Distribuição espacial do sistema radicular da pupunheira em função de lâminas de irrigação. *Irriga*, **14**, 431–440.

Rennó, C.D., Nobre, A.D., Cuartas, L.A., Soares, J.V., Hodnett, M.G., Tomasella, J. & Waterloo, M.J. (2008) HAND, a new terrain descriptor using SRTM-DEM: Mapping terra-firme rainforest environments in Amazonia. *Remote Sensing of Environment*, **112**, 3469–3481.

Restom, T.G. & Nepstad, D.C. (2004) Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia. *Forest Ecology and Management*, **190**, 109–118.

Ribeiro, J.E.L.S., Hopkins, M.J.G., Vicentini, A., Sothers, C.A., Costa, M.A.S., Brito, J.M., Souza, M.A.D., Martins, L.H., Lohmann, L.G., Assunção, P.A., Pereira, E.C., Silva, C.F., Mesquita, M.R. & Procópio, L.C. (1999) *Flora Da Reserva Ducke. Guia de Identificação Das Plantas Vasculares de Uma Floresta de Terra Firme Na Amazônia Central.* INPA - DFID, Manaus.

Rodriguez-Iturbe, I. (2000) Ecohydrology: A hydrologic perspective of climate-soil-vegetation dynamics. *Water Resources Research*, **36**, 3–9.

Ryan, M.G., Phillips, N. & Bond, B.J. (2006) The hydraulic limitation hypothesis revisited. *Plant, Cell and Environment*, **29**, 367–381.

Ryan, M. & Yoder, B. (1997) Hydraulic Limits to Tree Height and Tree Growth. *Bioscience*, **47**, 235–242.

Saatchi, S.S., Houghton, R.A., Dos Santos Alvalá, R.C., Soares, J. V. & Yu, Y. (2007) *Distribution of Aboveground Live Biomass in the Amazon Basin*.

Sabo, J.L., Sponseller, M.D., Gade, K., Harms, T., Heffernan, J., Jani, A., Katz, G., Soykan, C., Watts, J. & Welter, J. (2005) Riparian zones increase regional species richness by harboring different, not more, species. *Ecology*, **86**, 56–62.

Salas, W. a., Ducey, M.J., Rignot, E. & Skole, D. (2002) Assessment of JERS-1 SAR for monitoring secondary vegetation in Amazonia: I. Spatial and temporal variability in backscatter across a chrono-sequence of secondary vegetation stands in Rondonia. *International Journal of Remote Sensing*, **23**, 1357–1379.

Saleska, S.R., Miller, S.D., Matross, D.M., Goulden, M.L., Wofsy, S.C., da Rocha, H.R., de Camargo, P.B., Crill, P., Daube, B.C., de Freitas, H.C., Hutyra, L., Keller, M., Kirchhoff, V., Menton, M., Munger, J.W., Pyle, E.H., Rice, A.H. & Silva, H. (2003) Carbon in Amazon forests: unexpected seasonal fluxes and disturbance-induced losses. *Science (New York, N.Y.)*, **302**, 1554–7.

Scarano, F.R., Ribeiro, K.T., de Moraes, L.F.D. & de Lima, H.C. (1997) Plant establishment on flooded and unflooded patches of a freshwater swamp forest in southeastern Brazil. *Journal of Tropical Ecology*, **14**, 793–803.

Van Schaik, C.P. & Mirmanto, E. (1985) Spatial variation in the structure and litterfall of a Sumatran rain forest. *Biotropica*, **17**, 196–205.

Schnitzer, S.A. (2005) A mechanistic explanation for global patterns of liana abundance and distribution. *The American Naturalist*, **166**, 262–76.

Schöngart, J., Junk, W.J., Piedade, M.T.F., Ayres, J.M., Huttermann, A., Worbes, M. & Schongart, J. (2004) Teleconnection between tree growth in the Amazonian floodplains and the El Nino-Southern Oscillation effect. *Global Change Biology*, **10**, 683–692.

Schöngart, J., Piedade, M.T.F., Ludwigshausen, S., Horna, V. & Worbes, M. (2002) Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. *Journal of Tropical Ecology*, **18**, 581–597.

Schulman, L., Ruokolainen, K., Junikka, L., Sääksjärvi, I.E., Salo, M., Juvonen, S.-K., Salo, J. & Higgins, M. (2007) Amazonian biodiversity and protected areas: do they meet? *Biodiversity and Conservation*, **16**, 3011–3051.

Silvertown, J., Dodd, M., Gowing, D. & Mountford, J. (1999) Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature*, **400**, 61–63.

Slik, J.W.F., Aiba, S.-I., Brearley, F.Q., Cannon, C.H., Forshed, O., Kitayama, K., Nagamasu, H., Nilus, R., Payne, J., Paoli, G., Poulsen, A.D., Raes, N., Sheil, D., Sidiyasa, K., Suzuki, E. & van Valkenburg, J.L.C.H. (2010) Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. *Global Ecology and Biogeography*, **19**, 50–60.

Slik, J.W.F., Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., *et al.* (2013) Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography*, n/a–n/a.

Smith, L.C. (2002) Emerging applications of interferometric synthetic aperture radar (InSAR) in geomorphology and hydrology. *Annals of the Association of American Geographers*, **92**, 385–398.

Sojka, R.E. (1992) Stomatal closure in oxygen-stressed plants. *Soil Science*, **154**, 269–280.

Sojka, R.E., Oosterhuis, D.M. & Scott, H.D. (2005) Root Oxygen Deprivation and the and Gas Exchange.

Sombroek, W. (2000) Amazon landforms and soils in relation to biologcal diversity. *Acta Amazonica*, **30**, 81–100.

Sombroek, W. (2001) Spatial and Temporal Patterns of Amazon Rainfall Consequences for the Planning of Agricultural Occupation and. , **30**.

Ter Steege, H., Pitman, N., Sabatier, D., Castellanos, H., Van Der Hout, P., Daly, D.C., Silveira, M., Phillips, O., Vasquez, R., Van Andel, T., Duivenvoorden, J., Oliveira, A.A., Ek, R., Lilwah, R., Thomas, R., Van Essen, J., Baider, C., Maas, P., Mori, S., Terborgh, J., Vargas, P.N., Mogollón, H. & Morawetz, W. (2003) A spatial model of tree α-diversity and tree density for the Amazon. *Biodiversity & Conservation*, **12**, 2255–2277.

Svenning, J.-C. (2001) On the role of microenvironmental heterogeneity in ecology and diversification of neotropical rain-forest palms (Arecaceae). *The Botanical Review*, **67**, 1–53.

Taylor, H.M. & Brar, G.S. (1991) Effect of soil compaction on root development. *Soil & Tillage Research*, **19**, 111–119.

Terborgh, J., Loayza, P.A., Dexter, K., Cornejo, F. & Carrasco, C. (2011) Decomposing dispersal limitation: limits on fecundity or seed distribution? *Journal of Ecology*, **99**, 935–944.

Toledo, J.J., Magnusson, W.E. & Castilho, C. V. (2013) Competition, exogenous disturbances and senescence shape tree size distribution in tropical forest: evidence from tree mode of death in Central Amazonia (ed K Woods). *Journal of Vegetation Science*, **24**, 651–663.

Toledo, J.J., Magnusson, W.E., Castilho, C. V & Nascimento, H.E.M. (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., Hodnett, M.G., Cuartas, L.A., Nobre, A.D., Waterloo, M.J. & Oliveira, S.M. (2008) The water balance of an Amazonian micro-catchment: the effect of interannual variability of rainfall on hydrological behaviour. *Hydrological Processes*, **22**, 2133–2147.

Tuomisto, H. & Poulsen, A.D. (2000) Pteridophyte diversity and species composition in four Amazonian rain forests. *Journal of Vegetation Science*, **11**, 383–396.

Urquiza-Haas, T., Dolman, P.M. & Peres, C.A. (2007) Regional scale variation in forest structure and biomass in the Yucatan Peninsula, Mexico: Effects of forest disturbance. *Forest Ecology and Management*, **247**, 80–90.

Valencia, R., Foster, R.B., Villa, G., Svenning, J., Hernández, C., Romoleroux, K., Losos, E., Magård, E. & Balslev, H. (2004) Tree species distributions and local habitat variation in the Amazon : large forest plot in eastern Ecuador. *Journal of Ecology*, **92**, 214–229.

Valeriano, M., Kuplich, T., Storino, M., Amaral, B., Mendesjr, J. & Lima, D. (2006) Modeling small watersheds in Brazilian Amazonia with shuttle radar topographic mission-90m data. *Computers & Geosciences*, **32**, 1169–1181.

Vormisto, J., Phillips, O.L., Ruokolainen, K., Tuomisto, H. & Vásques, R. (2000) A comparison of fine-scale distribution patterns of four plant groups in an Amazonian rainforest. *Ecography*, **23**, 349–359.

Weller, D.E. (1987) Self-Thinning Exponent Correlated with Allometric Measures of Plant Geometry. *Ecology*, **68**, 813–821.

Westoby, M. (1984) The self-thinning rule. *Advances in ecological research*, **14**, 167–225.

White, J. (1981) The allometric interpretation of the self-thinning rule. *Journal of Theoretical Biology*, **89**, 475–500.

Williams, M., Hill, T.C. & Ryan, C.M. (2013) Using biomass distributions to determine probability and intensity of tropical forest disturbance. *Plant Ecology & Diversity*, **6**, 87–99.

Worbes, M. (1995) How to measure growth dynamics in tropical trees. *IAWA*, **16**, 337–351.

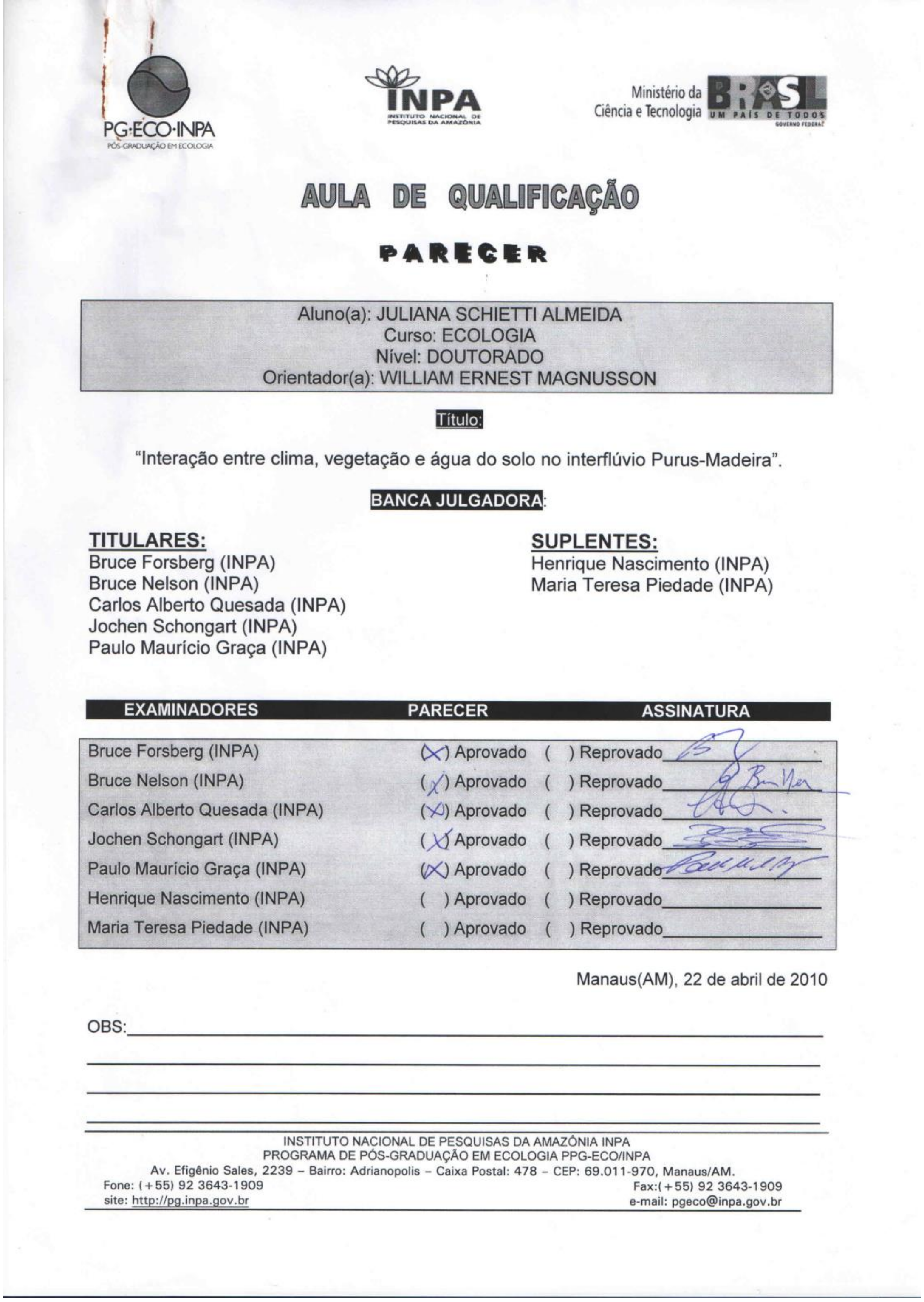
Yoda, K., Kira, T., Ogawa, H. & Hozumi, K. (1963) Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of the Institute of Polytechnics, Osaka City University, Series D*, **14**, 107–129.

Yoder, B., Ryan, M.G., Waring, R.H., Schoettle, A.W. & Kaufmann, M.R. (1994) Evidence of reduced photosynthesis rates in old trees.pdf. *Forest Science*, **40**, 513–527.

Zanne, A., Lopez-Gonzalez, G., Coomes, D., Ilic, J., Jansen, S., Lewis, S., Miller, R., Swenson, N., Wiemann, M. & Chave, J. (2009) Data from: Towards a worldwide wood economics spectrum. *Dryad Digital Repository*.

Zuur, A., Ieno, E.N., Walker, N., Savellev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

Apêndice 1. Parecer da Aula de qualificação



PG·ECO·INPA
PÓS-GRADUAÇÃO EM ECOLOGIA

INPA
INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

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

AULA DE QUALIFICAÇÃO

PARECER

Aluno(a): JULIANA SCHIETTI ALMEIDA
Curso: ECOLOGIA
Nível: DOUTORADO
Orientador(a): WILLIAM ERNEST MAGNUSSON

Título:

"Interação entre clima, vegetação e água do solo no interflúvio Purus-Madeira".

BANCA JULGADORA:

TITULARES:
Bruce Forsberg (INPA)
Bruce Nelson (INPA)
Carlos Alberto Quesada (INPA)
Jochen Schongart (INPA)
Paulo Maurício Graça (INPA)

SUPLENTES:
Henrique Nascimento (INPA)
Maria Teresa Piedade (INPA)

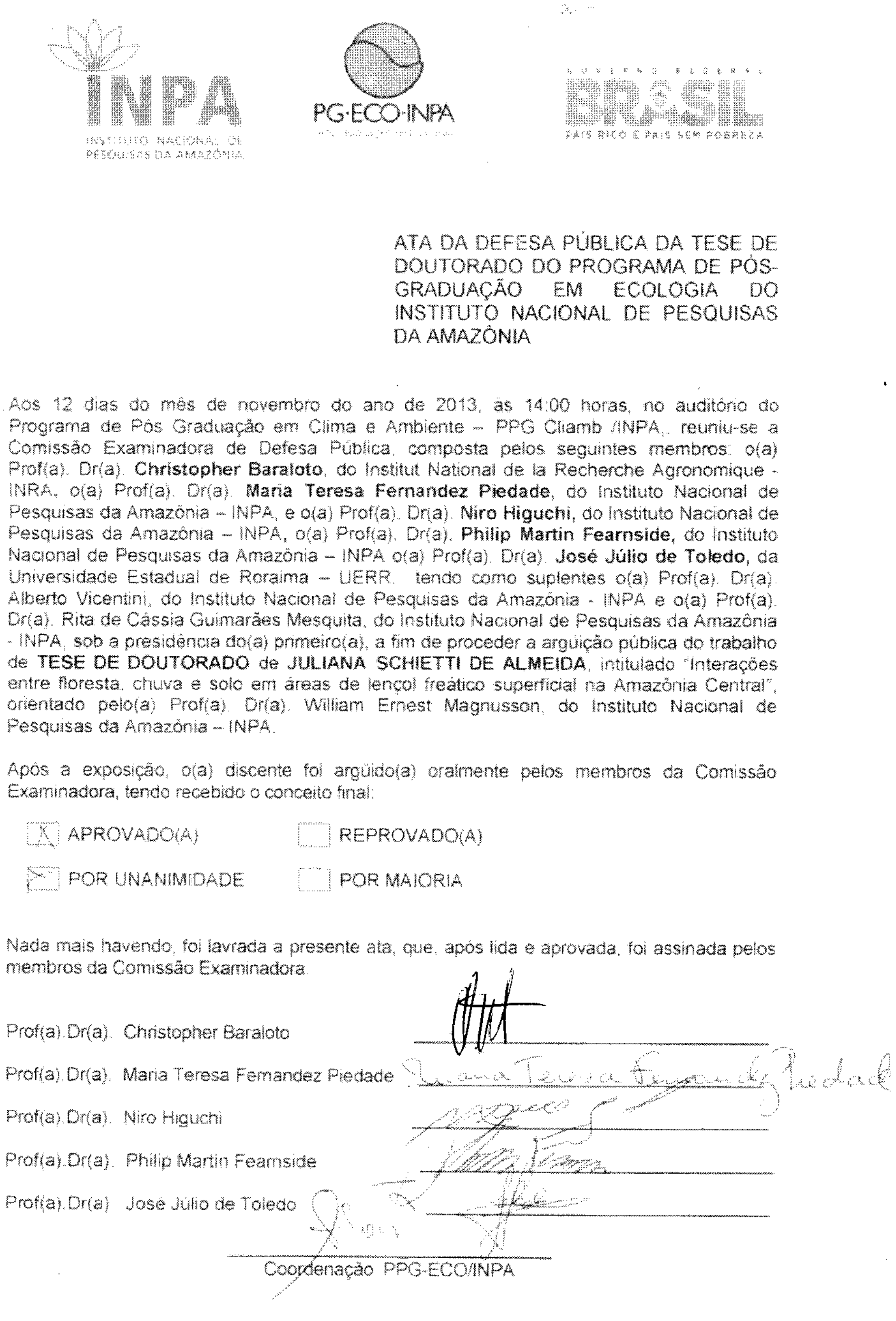
EXAMINADORES	PARECER	ASSINATURA
Bruce Forsberg (INPA)	(X) Aprovado ( ) Reprovado	
Bruce Nelson (INPA)	(X) Aprovado ( ) Reprovado	
Carlos Alberto Quesada (INPA)	(X) Aprovado ( ) Reprovado	
Jochen Schongart (INPA)	(X) Aprovado ( ) Reprovado	
Paulo Maurício Graça (INPA)	(X) Aprovado ( ) Reprovado	
Henrique Nascimento (INPA)	( ) Aprovado ( ) Reprovado	
Maria Teresa Piedade (INPA)	( ) Aprovado ( ) Reprovado	

Manaus(AM), 22 de abril de 2010

OBS:____

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA INPA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA PPG-ECO/INPA
Av. Efigênio Sales, 2239 – Bairro: Adrianopolis – Caixa Postal: 478 – CEP: 69.011-970, Manaus/AM.
Fone: (+55) 92 3643-1909 Fax:(+55) 92 3643-1909
site: http://pg.inpa.gov.br e-mail: pgeco@inpa.gov.br

Apêndice 2. Ata de defesa pública



INPA
INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

PG·ECO·INPA

GOVERNO FEDERAL
BRASIL
PAÍS RICO É PAÍS SEM POBREZA

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

Aos 12 dias do mês de novembro do ano de 2013, 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). **Christopher Baraloto**, do Institut National de la Recherche Agronomique - INRA, o(a) Prof(a). Dr(a). **Maria Teresa Fernandez Piedade**, do Instituto Nacional de Pesquisas da Amazônia – INPA, e o(a) Prof(a). Dr(a). **Niro Higuchi**, do Instituto Nacional de Pesquisas da Amazônia – INPA, o(a) Prof(a). Dr(a). **Philip Martin Fearnside**, do Instituto Nacional de Pesquisas da Amazônia – INPA o(a) Prof(a). Dr(a). **José Júlio de Toledo**, da Universidade Estadual de Roraima – UERR. tendo como suplentes o(a) Prof(a). Dr(a). Alberto Vicentini, do Instituto Nacional de Pesquisas da Amazônia - INPA e o(a) Prof(a). Dr(a). Rita de Cássia Guimarães Mesquita, 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 **JULIANA SCHIETTI DE ALMEIDA**, intitulado "Interações entre floresta, chuva e solo em áreas de lençol freático superficial na Amazônia Central", orientado pelo(a) Prof(a). Dr(a). William Ernest Magnusson, 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). Christopher Baraloto

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

Prof(a).Dr(a). Niro Higuchi

Prof(a).Dr(a). Philip Martin Fearnside

Prof(a).Dr(a). José Júlio de Toledo

Coordenação PPG-ECO/INPA