

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA
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**ESTRUTURA, COMPOSIÇÃO E DIVERSIDADE EM FLORESTAS
ALAGÁVEIS DE VÁRZEA DE MARÉ E DE IGAPÓ E SUAS RELAÇÕES
COM VARIÁVEIS EDÁFICAS E O PERÍODO DE INUNDAÇÃO NO AMAPÁ,
AMAZÔNIA ORIENTAL, BRASIL**

MARCELO DE JESUS VEIGA CARIM

Manaus, Amazonas

Junho, 2016

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COM VARIÁVEIS EDÁFICAS E O PERÍODO DE INUNDAÇÃO NO AMAPÁ,
AMAZÔNIA ORIENTAL, BRASIL**

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Estrutura, composição e diversidade em florestas alagáveis de várzea de maré e de igapó e suas relações com variáveis edáficas e o período de inundação no Amapá, Amazônia oriental, Brasil. / Marcelo de Jesus Veiga Carim. --- Manaus: [s.n.], 2016. 95 f.: il., color.

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Sinopse:

Avaliou-se os padrões ecológicos e fitossociológicos em floresta de várzea e igapó sob diferente regime de inundação e suas relações com variáveis ambientais, especialmente solo.

Palavras-chave: hidropérido, diversidade, biomassa, similaridade

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Estrutura, composição e diversidade em florestas alagáveis de várzea de maré e de igapó e suas relações com variáveis edáficas e o período de inundação no Amapá, Amazônia oriental, Brasil

Resumo. O objetivo deste estudo foi avaliar os padrões ecológicos e fitossociológicos em florestas alagáveis de várzea e igapó sob diferentes regimes de inundações e suas relações com variáveis ambientais, especialmente solo no Estado do Amapá, Amazônia oriental, Brasil. Foram registrados todos os indivíduos arbóreos, vivos, com diâmetro à altura do peito (DAP) ≥ 10 cm. Inventariou-se 26 parcelas de 100 x 100 m (1 ha cada), distribuídas em 13 hectares em cada tipologia florestal. As análises de gradientes, realizadas por meio de análise de componentes principais e análise de correspondência canônica foram suficientes para explicar a associação das parcelas e a distribuição das espécies. Optou-se por avaliar a biomassa acima do solo através do modelo alométrico já testado em florestas úmidas em que considera as variáveis de densidade da madeira (p), altura (H) e a área basal (AB). Registrou-se 10.575 árvores pertencentes 343 espécies, 172 gêneros e 49 famílias, com densidade média de 406.73 ± 61.27 árvores ha^{-1} e 27.2 ± 11.13 $m^2 ha^{-1}$ de área basal nos 26 hectares amostrados. Fabaceae, Arecaceae, Malvaceae, Meliaceae e Rubiaceae, foram mais importantes na várzea, juntas responderam por 74.76 do índice de valor de importância familiar (IVIF%). Para o igapó destacaram-se Fabaceae, Lecythidaceae, Euphorbiaceae, Malvaceae e Arecaceae, juntas responderam por 57.05 do índice de valor de importância (IVIF%). Houve diferença significativa entre os dois tipos de floresta em termos de número médio de indivíduos, espécies, diversidade e altura. No entanto, não diferiram significativamente para média de equabilidade, diâmetro, dominância e área basal. No igapó, acidez, alumínio, regime de inundação, potássio e areia influenciaram a distribuição das espécies, em ordem decrescente de significância. Na várzea, a associação das espécies com as variáveis ambientais mostraram associação com a capacidade de troca catiônica, saturação de bases, regime de inundação, potássio e, antagonicamente a silte, cálcio, fósforo e pH. A biomassa estimada para os dois ecossistemas, apresentaram praticamente a mesma média ($198,56$ Mg/ha^{-1}). No igapó a amplitude maior foi de $326,83$ $Mg ha^{-1}$ e na várzea foi $272,12$ $Mg ha^{-1}$. O regime de inundação teve média de $61 \pm 25,69$ dias/ano e $21 \pm 1,33$ dias/ano, respectivamente, no igapó e na várzea. Na várzea a parcela com menor biomassa foi positivamente relacionada com o período de inundação. No igapó foi negativamente relacionada com pH e fração de silte. No geral, a biomassa apresentou pouca relação com as variáveis edáficas nos dois ambientes. Conclui-se que por mais que as variáveis hidroedáficas caracterizam as diferenças no gradiente ambiental, estas apresentaram pouco reflexo na distribuição das espécies e, estas, respondem basicamente ao período de inundação e a acidez do solo.

Palavras-chaves: Amazônia oriental, fitossociologia, diversidade, biomassa, várzea de maré, igapó

Structure, composition and diversity in tidal-várzea and igapó flooded forests and their relationships with edaphic variables and inundation duration in eastern Amazonia, Amapá, Brazil.

Abstract. The objective of this study was to evaluate ecological and phytosociological patterns in flooded forests of várzea and igapó under different inundation regimes and their relationships with environmental variables, especially soil, in eastern Amazonia, Amapá, Brazil. All live trees with diameter at breast height (DBH) ≥ 10 cm were documented. A total of 26 100 x 100 m 1-ha plots were inventoried, distributed in 13 hectares within each forest typology. Gradient analysis, using both principal components analysis and canonical correspondence analysis, were sufficient to explain associations of plots and the distribution of species. Above ground biomass was evaluated using an allometric model already tested in humid forests, which considers wood density (ρ), height (H), and basal area (BA). In the 26 hectares sampled a total of 10,575 trees pertaining to 343 species, 172 genera and 49 families were registered, with mean wood density of 406.73 ± 61.27 trees ha^{-1} and mean basal area of 27.2 ± 11.13 $\text{m}^2 \text{ha}^{-1}$. Fabaceae, Arecaceae, Malvaceae, Meliaceae and Rubiaceae were the most important in várzea, together accounting for 74.76% of the family importance value index (FIVI%). In igapó, Fabaceae, Lecythidaceae, Euphorbiaceae, Malvaceae and Arecaceae stand out, accounting for 57.05% of the family importance value index (FIVI%). There were significant differences among forest types in regards to the mean number of individuals, species, diversity and height. However, they did not significantly differ in mean equitability, diameter, dominance and basal area. In igapó, acidity, aluminum, inundation regime, potassium and sand influence the distribution of species, in decreasing order of significance. In várzea, the associations of species with environmental variables showed association with cation exchange capacity, base saturation, inundation regime, potassium and antagonistically with silt, calcium, phosphorous and pH. Estimated biomass for each ecosystem showed practically the same mean (198.56 Mg/ha^{-1}). In igapó the largest amplitude was 326.83 Mg ha^{-1} and for várzea, 272.12 Mg ha^{-1} . The inundation regime had a mean of 61 ± 25.69 days/year and 21 ± 1.33 days/year in igapó and várzea respectively. In várzea, the plot with least biomass was positively related with the duration of inundation. In igapó, was negatively related with pH and the silt fraction. In general, biomass showed little relation with edaphic variables in both environments. In conclusion, while hydro-edaphic variables characterize differences in the environmental gradient, these are poorly reflected in the distribution of species, which basically respond to duration of inundation and soil acidity.

Key words: eastern Amazonia, phytosociology, diversity, biomass, tidal-várzea, igapó

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1. INTRODUÇÃO GERAL

Florestas inundadas representam cerca de 20% do bioma amazônico (Junk *et al.*, 2010). Os tipos mais representativos de florestas inundaáveis na Amazônia são as florestas de várzea e floresta de igapó. Historicamente, os conceitos em relação às áreas inundáveis sempre foram empregados de forma muito obscura (Prance, 1980). A denominação do termo “igapó” se dava como sendo áreas de pântanos ou florestas úmidas e “várzea” como sujeita a inundações periódicas (Richards, 1952; Pires, 1961; Prance, 1980).

Bem próximo a esse conceito, Ducke e Black (1953; 1954) e Aubréville (1961) definiram o termo “várzea” para toda floresta periodicamente inundável e “igapó” para floresta sobre solo que nunca fica seco. Sioli (1951), Geissner (1968) e Moreira (1970), propuseram que as várzeas seriam florestas inundáveis por água branca e igapó florestas inundáveis por água preta. Takeuchi (1962), no entanto, incluiu o solo em sua análise, onde verificou que as florestas de igapó crescem sobre solos de baixa fertilidade, caracterizando assim cada ambiente, com sua florística distinta.

Observa-se uma evolução contínua sobre as definições que envolvem todo o conjunto de áreas úmidas e suas características. As áreas úmidas são diferenciadas de acordo com as suas propriedades físico-químicas e qualidade da água (Sioli, 1956). Prance (1980) estabeleceu que o tipo de água dos rios da Amazônia é um importante fator na composição da vegetação inundável. A primeira classificação de áreas úmidas da Amazônia, baseada no conceito de pulso de inundações (Junk *et al.*, 1989), foi proposta por Junk e Piedade (2005), posteriormente foi fundamentada e ampliada por Junk *et al.* (2011). Este conceito, baseado nas definições atuais, considerando as condições hidrológicas e vegetação, culmina com a classificação de áreas úmidas brasileiras (Junk *et al.*, 2011; Junk *et al.*, 2014).

As variações no tipo de solo, regime de inundações, topografia, clima e disponibilidade de nutrientes são consideradas como os fatores que influenciam na composição, riqueza e estrutura da vegetação de florestas inundáveis, e repercutem na dominância, limitando ou favorecendo determinadas espécies e famílias botânicas (Ferreira e Almeida, 2005; Haugaasen e Peres, 2006; Assis e Wittmann, 2011).

Florestas de igapó com cerca de 180.000 km² compreendem ambientes de baixa fertilidade e produtividade, inundadas por rios de águas negras ou claras, cuja vegetação se desenvolve sobre solos com baixa disponibilidade de nutrientes. Florestas de várzea ocorrem ao longo dos canais que drenam os Andes e o sopé andino, estes rios são carregados com

sedimentos férteis, ricos em nutrientes e cobrem aproximadamente 300.000 km² da bacia amazônica (Melack e Hess, 2010; Junk *et al.* 2011). Refletem um sistema onde o ciclo de enchente e de vazante dos rios exerce forte influência sobre a composição e a dinâmica da vegetação proporcionando um quadro único para a compreensão das estruturas e funções ecológicas em sistemas periodicamente alagados (Junk *et al.*, 1989).

Durante a fase de inundação ocorrem mudanças fisiológicas nas plantas, envolvendo a redução na respiração das raízes e na captação de nutrientes, o que afeta diretamente o ritmo de crescimento das plantas, ocorre também a perda ou troca de folhas em muitas espécies, redução da fotossíntese e formação de anéis de crescimento (Worbes, 1997; Wittmann e Parolin, 1999; Schöngart *et al.*, 2004). Como consequência, os organismos desenvolvem inúmeras estratégias morfofisiológicas para adaptarem-se às condições extremas (Parolin *et al.*, 2010).

Muitos estudos retratam o efeito do regime de inundação e das propriedades físico-químicas do solo na distribuição das espécies arbóreas em florestas alagadas na bacia Amazônica, particularmente na sua região ocidental e central (Piedade *et al.*, 2005; Ferreira e Almeida, 2005; Ter Steege *et al.*, 2006; Wittmann *et al.*, 2006; Haugaasen e Peres, 2006; Assis e Wittmann, 2011; Ferreira e Parolin, 2011; Assis *et al.*, 2014; Targhetta *et al.*, 2015), bem como a contribuição dos sedimentos transportados para fertilidade da várzea (Filizola e Guyot, 2009; Junk *et al.*, 2011), em contrapartida à pobreza nutricional dos rios de igapó (Sioli, 1956; Keel e Prance, 1979; Quesada *et al.*, 2011). Assim, as inundações podem aparecer como fator de regulação das propriedades químicas e texturais de solo, como também da densidade de espécies (Budke, 2007). Estudos revelam que as florestas de várzeas amazônicas são as florestas alagáveis com maior riqueza de espécies do mundo (Wittmann *et al.*, 2006).

Para a Amazônia oriental, a maioria dos trabalhos retrata o ambiente de floresta de várzea e igapó no âmbito de sua estrutura e diversidade (Almeida *et al.*, 2004; Gama *et al.*, 2005; Santos e Jardim, 2006; Salomão *et al.*, 2007; Queiroz e Machado, 2008; Carim *et al.*, 2008; Almeida e Jardim, 2011; Ferreira *et al.*, 2013; Carim *et al.*, 2014). No entanto, não há nenhum trabalho que retrate a distribuição de espécies arbóreas associadas a fatores hidroedáficos nesta parte da Amazônia.



Figura 1. Floresta de águas brancas (várzea), bacia do rio Mazagão, Amazônia oriental.



Figura 2. Floresta de águas claras (igapó), bacia do rio Jari, Amazônia oriental.

Além da composição florística e diversidade, a biomassa é um parâmetro importante na caracterização da vegetação, por ser dependente das condições ambientais. Estas condições são influenciadas por fatores climáticos, hidrológicos, pedológicos, relevo e também pelos nutrientes (Chave *et al.*, 2004). Na floresta de várzea o acúmulo de biomassa e fixação de carbono é cerca de duas vezes maior que no igapó, devido ao acelerado incremento radial anual na várzea (Worbes, 1997; Malhi *et al.*, 2006; Schöngart *et al.*, 2005).

O acúmulo de biomassa é diferente de local para local e de indivíduo para indivíduo, e esta variação é reflexo dos diversos fatores ambientais aos quais a planta está suscetível, além dos fatores inerentes à própria planta (Soares *et al.*, 2011). Alguns estudos em florestas tropicais observaram uma correlação entre biomassa e os gradientes de textura, fertilidade do solo e topografia do terreno (Laurance *et al.*, 1999; Cummings *et al.*, 2002; Castilho *et al.*, 2006). As estimativas de biomassa em florestas tropicais são geralmente realizadas utilizando-se modelos alométricos (Higuchi *et al.*, 1998; Chambers *et al.*, 2001; Clark *et al.*, 2001; Baker *et al.*, 2004;

Chave *et al.*, 2005; Malhi *et al.*, 2006), através de variáveis independentes como DAP, altura e densidade da madeira (Silveira *et al.*, 2008).

A obtenção de desses dados pode ser obtida por meio dos métodos diretos (destrutivo) ou pelo método indireto (não destrutivo), mais rápido, não corta, não pesa e nem seca nenhum indivíduo, pode amostrar uma área maior e maior número de indivíduos, pois, utiliza variáveis mais facilmente obtidas no campo, como o diâmetro e altura (Higuchi *et al.*, 1998; Santos *et al.*, 2004) e densidade da madeira. Modelos alométricos que consideram ao mesmo tempo altura, diâmetro (área basal) e densidade da madeira são mais precisos (Chave *et al.*, 2005). As estimativas de biomassa acima do solo através do método indireto fornecem dados essenciais que permitem a extrapolação de estoques de biomassa e carbono para os ecossistemas avaliados (Somogyi *et al.*, 2006).

Muitos estudos têm se preocupado em gerar modelos alométricos consistentes para estimativas de biomassa lenhosa acima do solo, principalmente em florestas de terra-firme na Amazônia (Chambers *et al.*, 2001; Chave *et al.*, 2005; Cummings *et al.*, 2002; Baker *et al.*, 2004; Higuchi *et al.*, 1998). Para florestas alagáveis ainda não existem modelos alométricos específicos, seja igapó ou várzea. Considerando a grande extensão de áreas inundáveis de igapó e várzea no Estado do Amapá, até o momento não se registrou estudos na região sobre a biomassa acima do solo contida nestes dois ecossistemas.

Em geral, este estudo visa contribuir com dados florísticos, estrutural, biomassa e hidroedáficos em duas bacias inundáveis na Amazônia oriental, Estado do Amapá. Essas informações básicas contribuirão para compreender os mecanismos que determinam a distribuição, estrutura e a composição de espécies das comunidades de plantas arbóreas. Para o Estado do Amapá, o estudo visa preencher uma importante lacuna, dado que estudos sobre ecossistemas alagáveis no Estado são limitados.

As informações geradas dizem respeito a um conjunto de questões e hipóteses direcionadas para o entendimento da estrutura, composição e distribuição de espécies arbóreas em florestas alagáveis sob o efeito de diferentes variáveis ambientais, para a compreensão de sua estruturação, bem como o funcionamento de seus diversos componentes ecológicos para, a partir daí, avaliar as diferenças e similaridades entre os dois ecossistemas.

A hipótese que norteia este trabalho é que a floresta de várzea sob regime de inundação diária, terá menor riqueza e diversidade de espécies em relação a floresta de igapó sob regime sazonal, independente das condições nutricionais do solo.

Esta tese está organizada em capítulos, representando artigos independentes, que foram submetidos à publicação em revistas de circulação internacional. A estrutura conta com uma introdução geral e conclusão final, compreendendo todo arcabouço de informações que nortearam este trabalho.

O capítulo I descreve as diferenças e similaridades entre floresta de várzea e igapó na Amazônia oriental, considerando aspectos como diversidade, similaridade, estrutura e composição dentro e entre estas florestas.

O capítulo II analisa as relações entre fatores edáficos e o período de inundação na distribuição de espécies arbóreas nas duas florestas. Neste capítulo, procurou-se entender se os preditores ambientais determinam a distribuição das espécies ao longo do gradiente hidroedáfico sob regime polimodal (maré) e monomodal.

O capítulo III compara os padrões periódicos de inundação de florestas sob regime de marés e sazonalmente alagadas e suas relações com o estoque de biomassa vegetal acima do solo, considerando a influência das características físico-químicas do solo.

2. OBJETIVOS

2.1 Objetivo Geral

Avaliar padrões ecológicos e fitossociológicos em floresta de várzea de maré e igapó sob diferentes regimes de inundação e suas relações com variáveis ambientais, especialmente solo.

2.2 Objetivos Específicos

1. Caracterizar e comparar as áreas de estudo com relação a estrutura, composição, riqueza e diversidade florística do componente arbóreo;
2. Analisar a influência do período de inundação e fatores físico-químicos do solo na distribuição de espécies arbóreas;
3. Caracterizar e comparar a biomassa viva acima do solo do componente arbóreo nas áreas a serem estudadas.

Capítulo 1

Carim, M. J. V., Wittmann, F., Piedade, M. T. F., Ter Steege, H., Torres, A. M., Costa Neto, S. V. & Tostes, L. C. L. Composition, diversity and structure of tidal-várzea and igapó floodplain forests in eastern Amazonia, Brazil. Submetido *Plant Ecology*

Composition, Diversity and Structure of tidal-várzea and igapó floodplain forests in eastern Amazonia, Brazil

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Abstract The objective of this study was to evaluate the composition, diversity and structure of tidal-várzea and igapó forests in eastern Amazonia, Amapá, Brazil. All live tree individuals with diameter at breast height (dbh) ≥ 10 cm were registered. A total of 130 plots measuring 10x100 m were inventoried, distributed among 13 hectares in each of the two forest typologies. A total of 10,575 trees were reported, belonging to 343 species, 172 genera and 49 families. For all 26 hectares sampled, mean tree density was 406 ± 61.27 trees ha^{-1} and mean basal area was 27.2 ± 11.13 $\text{m}^2 \text{ha}^{-1}$. Fabaceae, Arecaceae, Malvaceae, Meliaceae and Rubiaceae were the most important families in tidal-várzea, together accounting for 74.76 of the family importance value index (FIVI%). In igapó, the most important families were , Lecythidaceae, Euphorbiaceae, Malvaceae and Arecaceae, which together accounted for 57.05 of the family important value index (FIVI%). Smaller diameter trees measuring between 10 and 30 cm dbh dominated the landscape, accounting for 75.52% of all individuals sampled. In general, 80% (8,285) individuals were under 24 m in height, while only 1.32% of trees (140) reached heights above 34m. There was evidence for statistically significant mean differences among tidal-várzea and igapó in regards to the number of individuals, species, diversity and tree height. However no mean differences were detected for equitability, dbh, dominance and basal area. Compositional patterns showed low similarity between the evaluated areas, indicating the existence of phtyogeographic pattern based on species distribution.

Key words: Amazonia, phytosociology, diversity, dominance

Introduction

Igapó and várzea forests are considered distinct floodplain habitats. The former covers an area of approximately 180,000 km² and is characterized by its low soil fertility and low productivity (Melack and Hess 2010). The latter covers approximately 300,000 km², distributed along channel margins that drain the Andes and Andean foothills. Rivers of várzea floodplains thus carry large suspended loads of nutrient-rich sediments (Melack and Hess 2010).

Many Amazonian wetland forests are affected by periodic inundation, resulting in cycles of terrestrial and aquatic phases. These flood pulses strongly influence vegetation composition and dynamics, thus providing a unique opportunity to further our understanding of ecological structure and function within periodically flooded systems (Junk et al., 1989). As a consequence of the often extreme environmental conditions, wetland organisms have developed a number of morpho-physiological coping strategies (Parolin et al. 2010).

Relatively few studies compare várzea and igapó (Worbes 1997; Haugaasen and Peres 2006; Almeida and Jardim 2011; Salomão et al. 2007; Ferreira and Parolin 2011; Ferreira et al. 2013). Comparative studies in central and western Amazonia support the idea that várzea is more species rich (Haugaasen and Peres 2006; Wittmann et al. 2006). Indeed, várzea is considered the most species rich wetland tree community in the world, with well-over 1000 tree species (Wittmann et al. 2010).

The objective of this study is to compare the forest structure, composition and diversity of tidal-várzea and igapó in two watersheds of eastern Amazonia. The following hypotheses were tested i) the diversity and phytosociological patterns differ significantly between tidal-várzea and igapó forests, and ii) the diversity and phytosociological patterns do not differ significantly between the flooded forests of this study in relation to other flooded periodically Amazon.

Materials and methods

Study Area

We studied two alluvial forests in different watersheds of eastern Amazonia, located in southern Amapá, northern Brazil. The first watershed represents tidal-várzea, and is drained by the Mazagão river, located within the municipality of Mazagão between 00° 14' 06" and 00° 15' 54" latitude and 51° 20' 06" e 51° 23' 42" longitude. The second watershed represents igapó, and is drained by the Jari river, located in the municipality of Laranjal do Jari between 00° 30' 00" e 01° 06' 00" latitude and 52° 18' 00" e 52° 38' 00" longitude (Fig. 1). In both watersheds

the climate is tropical with a mean annual temperature of 27.5 °C and mean rainfall of 2,158 mm (Vásquez and Rabelo 1999).

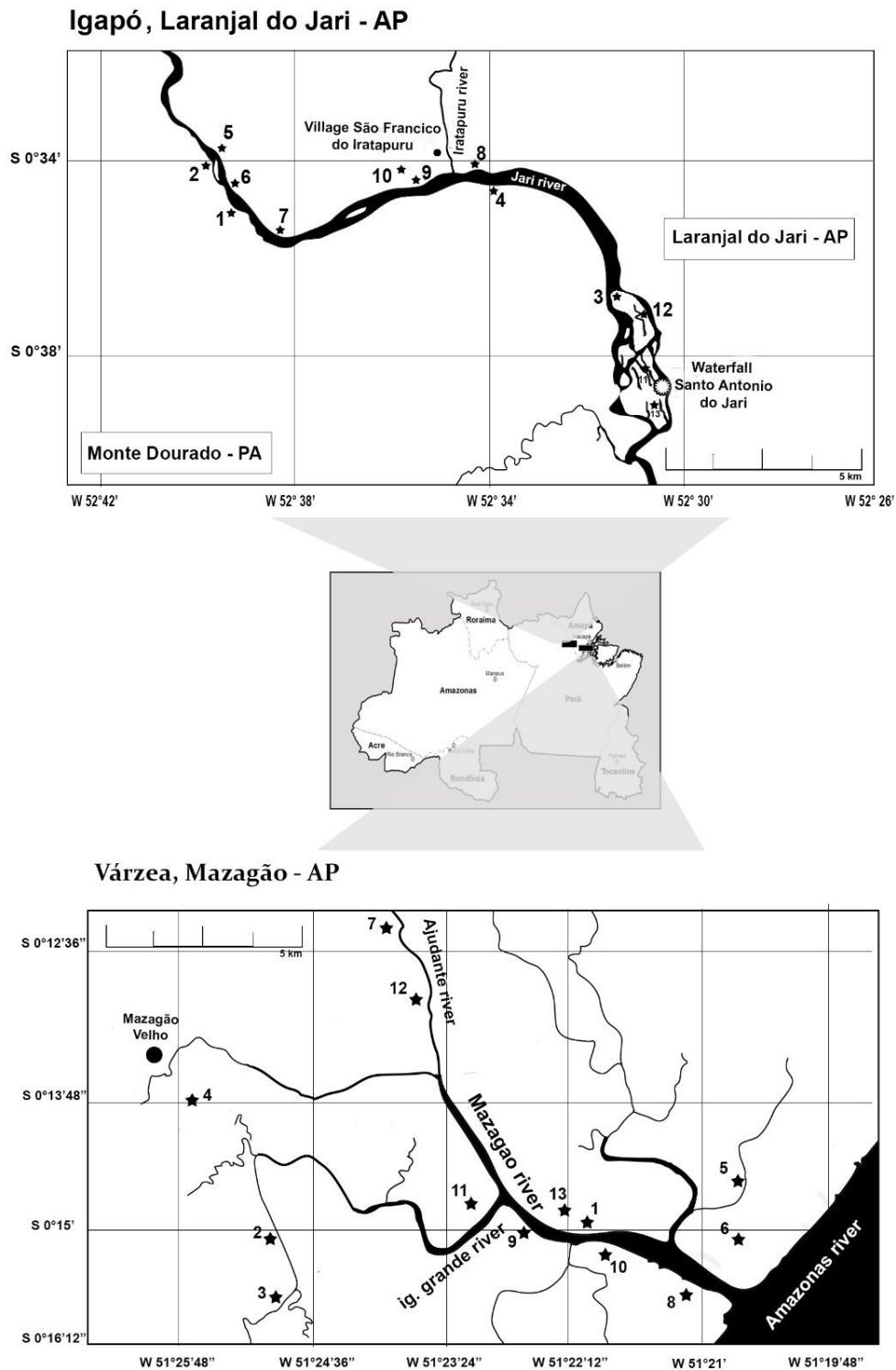


Figure 1 Locations of the plots distributed among two watershed representing igapó and várzea forests in eastern Amazonia, Brazil.

The studied igapó forest lies predominantly within the Guiana Shield, a geological formation of pre-Cambrian, crystalline bedrock underlying northern Amazonia. Soils in this geological region are predominantly sandy to clayey latosols (Vásquez and Rabelo 1999). Water supply to the local watershed is derived from local rainfall, without contribution from tidal flow. The studied tidal-várzea occurs within an estuarine complex, deriving its water supply from Andean runoff, innumerable tributaries, and local rainfall on the watershed. In addition, two daily tidal flows of predominantly freshwater affect the estuarine várzea, thus giving rise to the name tidal-várzea. Soils are generally haplic gleysols with very clayey to silty texture (Queiroz and Machado 2008).

Floristic Inventory and Data Collection

Vegetation was sampled in 26 1-hectare plots (100 m x 100 m), divided into 13 hectares for each habitat (várzea and igapó). Each plot was comprised of 10, 1,000 m² (10 x 100 m) subplots. Only live individuals with trunk diameters at breast height (dbh) \geq 10 cm were considered. In cases where individuals had multiple branches \geq 10 cm dbh, each branch was reported. All plots were georeferenced with a GPS. All individuals were tagged with aluminum plaques and identified in the field with the aid of parataxonomists. APG III (2009) was adopted for taxonomic classification. Voucher specimens of individuals that could not be identified in the field were collected for subsequent comparison at the Herbário Amapaense (HAMAB – IEPA). After determination to the lowest possible taxonomic rank, the vouchers were incorporated into the herbarium: numbers 18185 to 18201.

Data Analysis

To elucidate compositional differences between tidal-várzea and igapó, for each community we ranked species and families from most to least important, given as the summation of each taxa's relative abundance, relative frequency, and relative basal area. Importance values for each taxon are reported as a percentage of the total. Trends in compositional pattern were also assessed through a cluster analysis of plots using an average linkage method (UPGMA). The dissimilarity matrix used for clustering was based on pair-wise comparisons of plot composition using the Bray-Curtis similarity metric for abundance data.

To quantify vegetation structure of várzea and igapó habitat, for each plot we calculated stem density, mean basal area, and mean tree height. Also, to assess differences in diversity among habitats plot-level diversity was estimated as Fisher's α coefficient and species richness (Fisher et al. 1943). Additionally, species accumulation curves were compared for várzea and

igapó. Mean differences in plot-level structure and diversity measurements among the two habitats were assessed using t-tests (Zar 2010).

To understand how structure and diversity metrics might vary within tidal-várzea and igapó, we also assessed mean differences among upstream, intermediate, and downstream sites within each habitat. To do so, we used an analysis of variance and Tukey's test for multiple comparisons. To check whether the assumptions of normally distributed data were fulfilled for use of parametric analyses, we used the Shapiro-Wilk test. We used PAST v.2.04 software for all analyses (Hammer et al. 2001).

Results

Vegetation composition, structure and diversity

In total, we recorded 10,575 trees (dbh \geq 10 cm) distributed among 343 species, 172 genera and 49 families (Fig. 2). For várzea, we recorded 5,461 trees distributed among 98 species, 80 genera and 29 families. For igapó, we recorded 5,114 trees distributed among 285 species, 150 genera and 45 families.

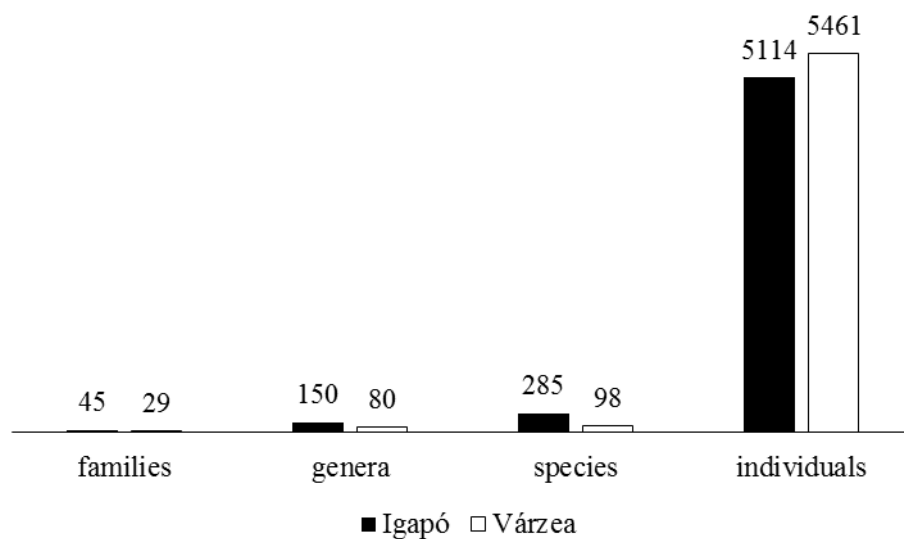


Figure 2. Total number of sampled individuals, species, genera and families in the studied várzea and igapó forests located in eastern Amazonia, Brazil.

In várzea, the most important families were Fabaceae, Arecaceae, Malvaceae, Meliaceae and Rubiaceae, which together accounted for 74.76% of the family importance value index (FIVI). In igapó the most important families were Fabaceae, Lecythidaceae, Euphorbiaceae, Malvaceae and Arecaceae, together accounting for 57.05% of the family importance value index (FIVI). A total of 25 families (~51%) are common to both várzea and

igapó, but Fabaceae stands out as the most important family in both habitats (Table 1). Several rare families contributed only 1 individual to várzea and igapó each, including Amarilidaceae, Araliaceae, Bixaceae, Convolvulaceae, Hypericaceae, Olacaceae, Salicaceae and Violaceae.

Table 1. The important families in descending order of importance in sampled tidal-várzea and igapó located in eastern Amazonia, Brazil. For each family, the number of individuals (N), the number of species (S), the basal area (BA), and the Family Importance Value Index (FIVI %) is reported

Family	Igapó				Family	Várzea			
	N	S	BA	FIVI		N	S	BA	FIVI
Fabaceae	1510	67	90.24	27.97	Fabaceae	2093	28	152.3	39.18
Lecythidaceae	675	15	18.42	10.14	Arecaceae	1427	6	45.83	17.83
Euphorbiaceae	229	9	34.51	6.69	Malvaceae	476	9	22.16	7.56
Malvaceae	292	14	21.00	6.16	Meliaceae	316	4	20.68	6.24
Arecaceae	401	7	16.64	6.09	Rubiaceae	148	1	20.86	3.95
Meliaceae	202	6	13.90	4.11	Chrysobalanaceae	156	3	12.33	3.66
Chrysobalanaceae	182	11	14.30	3.90	Sapotaceae	130	6	13.59	3.55
Burseraceae	203	11	7.45	3.76	Myristicaceae	145	1	8.91	3.20
Anacardiaceae	152	4	15.26	3.62	Euphorbiaceae	81	3	11.75	2.49
Moraceae	121	10	12.46	3.30	Anacardiaceae	69	1	10.48	2.00
Lauraceae	167	12	7.98	3.05	Lauraceae	73	5	3.49	1.71
Combretaceae	78	3	11.09	2.31	Moraceae	36	3	5.18	1.56
Sapotaceae	89	15	6.67	2.14	Lecythidaceae	48	3	1.77	1.05
Apocynaceae	111	7	4.45	1.99	Clusiaceae	43	3	1.71	0.98
Myrtaceae	96	13	2.68	1.89	Rutaceae	46	2	1.29	0.93
Subtotal (n =15)	4.508	204	277.05	87.12	Subtotal (n =15)	5.287	78	332.41	95.89
Other Families	606	81	36.84	12.88	Other Families	174	20	57.59	4.11
Total	5114	285	313.89	100	Total	5461	98	390	100

Among species, approximately 13% (44) occurred in both várzea and igapó. Of these the most important were *Pentaclethra macroloba* (Willd.) Kuntze, *Hevea brasiliensis* (Willd. ex A.Juss.) Müll.Arg., *Spondias mombim* L., *Virola surinamensis* (Rol. ex Rottb.) Warb. and *Mora paraenses* (Ducke) Ducke (Table 2). The five most important species in igapó and tidal-várzea accounted for 35.23% and 35.7% of the cumulative importance for each habitat, respectively. The 15 most important species in igapó accounted for approximately 50% of total importance, while in várzea the 15 most important species accounted for 60%. Species represented by a single individual accounted for about 20% (n=56) of species in igapó and 17% (n = 16) in tidal-várzea.

Table 2 The important species in descending order of importance in sampled tidal-várzea and igapó located in eastern Amazonia, Brazil. For each species, the basal area (BA – m²), the number of individuals (N), sampling unit (U) and the Importance Value Index (IVI %) is reported.

Igapó					Várzea				
Species	BA	N	U	IVI	Species	BA	N	U	IVI
<i>Pentaclethra maculosa</i> (Fabaceae)	40.88	840	13	11.49	<i>Mora paraensis</i> (Fabaceae)	97.06	837	13	14.25
<i>Hevea brasiliensis</i> (Euphorbiaceae)	32.03	199	11	7.05	<i>Astrocaryum murumuru</i> (Arecaceae)	18.64	911	13	8.01
<i>Attalea maripa</i> (Arecaceae)	13.39	226	11	4.34	<i>Pentaclethra maculosa</i> (Fabaceae)	21.92	483	13	5.65
<i>Gustavia augusta</i> (Lecythidaceae)	5.51	336	12	4.16	<i>Carapa guianensis</i> (Meliaceae)	18.67	259	12	3.9
<i>Carapa guianensis</i> (Meliaceae)	12.71	156	9	8.19	<i>Matisia paraensis</i> (Malvaceae)	14.45	300	13	3.89
<i>Spondias mombin</i> (Anacardiaceae)	12.83	130	12	3.55	<i>Calycophyllum spruceanum</i> (Rubiaceae)	25.45	148	11	3.6
<i>Parinari excelsa</i> (Chrysobalanaceae)	10.62	108	9	3.32	<i>Swartzia cardiosperma</i> (Fabaceae)	13.67	231	12	3.31
<i>Terminalia dichotoma</i> (Combretaceae)	9.89	71	11	2.75	<i>Virola surinamensis</i> (Myristicaceae)	13.48	145	13	2.9
<i>Eschweilera atropetiolata</i> (Lecythidaceae)	5.79	113	13	2.27	<i>Manicaria saccifera</i> (Arecaceae)	9.55	159	12	2.59
<i>Virola surinamensis</i> (Myristicaceae)	6.93	56	10	2.03	<i>Licania heteromorpha</i> (Chrysobalanaceae)	9.36	85	13	2.19
<i>Quararibea guianensis</i> (Malvaceae)	2.48	113	11	1.65	<i>Spondias mombin</i> (Anacardiaceae)	10.48	69	12	2.08
<i>Cordia tetrandra</i> (Boraginaceae)	4.41	61	10	1.27	<i>Hevea brasiliensis</i> (Euphorbiaceae)	8.35	63	13	1.93
<i>Vatairea guianensis</i> (Fabaceae)	5.00	60	8	1.25	<i>Mauritia flexuosa</i> (Arecaceae)	10.49	91	6	1.84
<i>Eschweilera coriacea</i> (Lecythidaceae)	2.07	76	13	1.24	<i>Attalea excelsa</i> (Arecaceae)	7.85	80	10	1.8
<i>Ceiba pentandra</i> (Malvaceae)	8.91	6	6	1.23	<i>Campsiandra laurifolia</i> (Fabaceae)	5.40	90	10	1.65
Subtotal (n =15)	173.45	2551	-	55.79	Subtotal (n =15)	284.82	3951	-	59.59
Other Species	140.44	2.563	-	44.21	Other Species	104.18	1510	-	40.41
Total	313.89	5114	-	100	Total	390	5461	-	100

Diameter distributions in both tidal-várzea and igapó showed an inverse J curve (Fig. 3). The smallest diameter class (between 10 and 30 cm) included the most individuals, accounting for 74.75% and 76.34% of individuals in tidal-várzea and igapó respectively. Only 80 trees (0.76%) had trunks greater than 90 cm dbh, with 56 (1.03%) belonging to tidal-várzea and 24 (0.47%) to igapó.

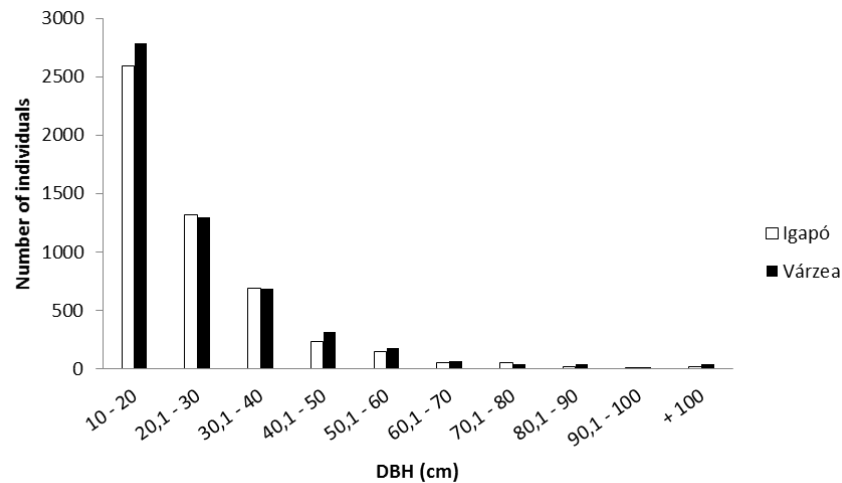


Figure 3. Diameter distribution of trees in tidal-várzea and igapó in eastern Amazonia, Brazil.

In igapó the three most important families accounted for 45% (143.17 m²) of the total basal area, including Fabaceae, Lecythidaceae and Euphorbiaceae. The species accounting for the largest proportion of igapó basal area included *Pentaclethra macroloba* (40.88 m²), *Hevea brasiliensis* (32.03 m²) and *Attalea maripa* (13.39 m²). In várzea, the three most important families, Fabaceae, Arecaceae and Malvaceae, accounted for approximately 60% (230.37 m²) of the total basal area. The species accounting for the largest proportion of tidal-várzea basal area included *Mora paraenses*, *Pentaclethra macroloba* and *Astrocaryum murumuru*. The relatively high basal areas of these species were due largely to their high abundance.

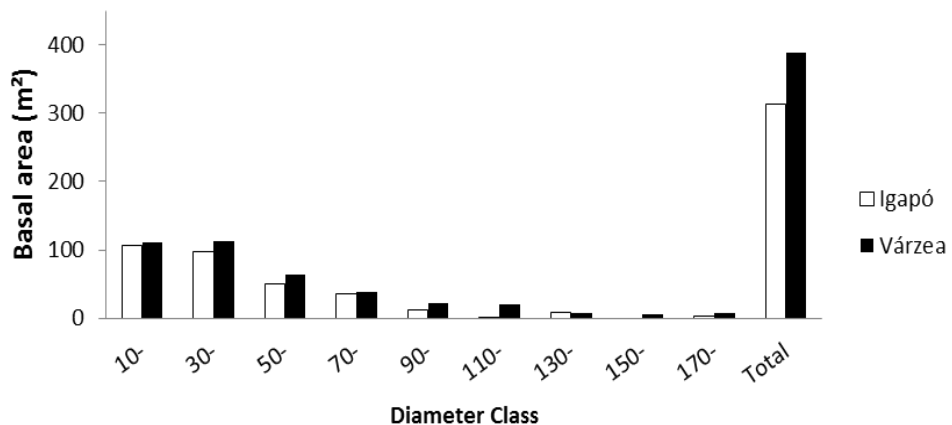


Figure 4. Basal area of stems of different diameter classes in tidal-várzea and igapó in eastern Amazonia, Brazil.

The height distribution curves of individuals showed different patterns for tidal-várzea and igapó (Fig. 5). In várzea, the number of individuals monotonically decreased with

increasing height class. The largest proportion of individuals (53.74%) was under 14 m, while 36.11 % were between 14 and 24 m, and 8.61% were between 24 and 34 m in height. A total of 84 trees (1.54%) had heights over 34 m, representing canopy emergents in tidal-várzea. These tidal-várzea emergents included species such as *Mora paraenses* (Ducke), *Manilkara huberi* (Ducke) A. Chev., *Calycophyllum spruceanum* (Benth.) K. Schum., *Olmedia caloneura* Huber. and *Ceiba pentandra* (L.) Gaertn., with heights between 35 and 43 m.

In contrast, igapó showed a monomodal height class distribution, with the largest fraction of individuals (49.51%) in the second height class between 14 and 24 m tall. The lower height class accounted for 35.82% of individuals, while larger height classes accounted for 13.57% and 1.09% (56 emergent trees) of individuals. Emergents in igapó include *Ceiba pentandra* (L.) Gaertn., *Hevea brasiliensis* and *Goupia glabra* Aubl. In general, individuals <24 m tall accounted for 80% of all individuals in both tidal-várzea and igapó.

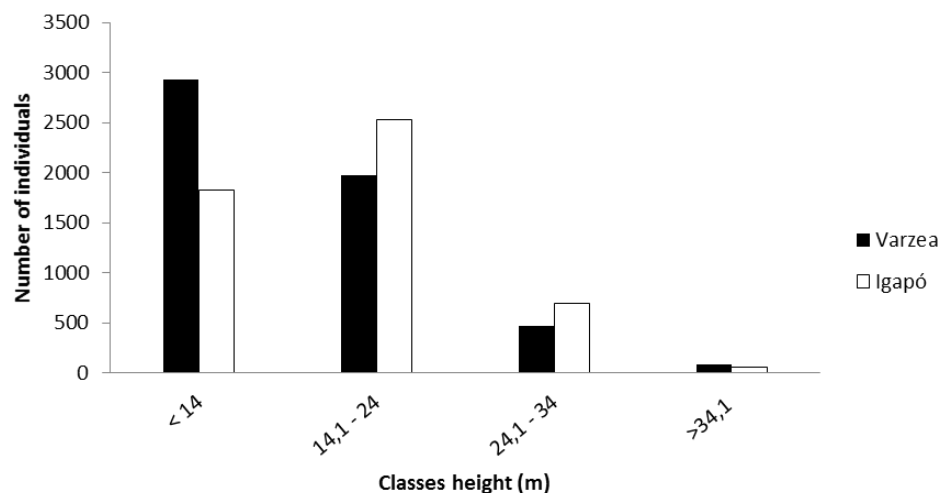


Figure 5. Height distribution of individuals in tidal-várzea and igapó in eastern Amazonia, Brazil.

For most structural variables assessed, there was more variation within tidal-várzea and igapó habitats than between them. Mean tree density for all 26 ha was estimated to be 406.73 ± 61.27 trees ha^{-1} . Tidal-várzea had 27 more trees ha^{-1} than igapó, on average, but this difference was not statistically significant ($p < 0.01$) (Table 3). Mean basal area for all plots was 27.2 ± 11.13 $\text{m}^2 \text{ha}^{-1}$. Although tidal-várzea had a mean basal area 5.57 $\text{m}^2 \text{ha}^{-1}$ higher relative to igapó, there was no evidence for consistent differences among habitats ($p > 0.05$). For mean tree height, igapó trees were, on average, 2.26 m taller than those of tidal-várzea ($p < 0.05$).

Fisher's α ranged from 8.46 to 16.53 (mean = 11.10 ± 2.1) for tidal-várzea and from 9.78 to 28.32 (mean = 18.54 ± 5.2) for igapó, indicating higher mean alpha diversity for igapó ($p < 0.001$) (Table 3).

Table 3. Means and standard errors for tree density (individuals ha⁻¹), species (S), diversity (Alfa fisher), equitability (J), mean diameter (mD), mean height (mHT), mean basal area (mBA) of plots in tidal-várzea and igapó. The sample size in each habitat is 13 plots.

Variables	Várzea	Igapó	t-test	
			T	P
N	420.08±60.47 a	390.34±50.47 b	3.28	**
S	40.23±5.01 a	63.23±13.35 b	2.41	**
α Fisher	11.10±2.1 a	18.54±5.2 b	2.14	***
J	0.75±0.06 a	0.79±0.06 a	1.38	Ns
mD	25.34±9.01 a	23.93±4.03 a	1.60	Ns
mHT	14.8±2.19 a	17.06±2.74 b	1.51	*
mBA	29.92±14.24 a	24.15±6.09 a	1.81	Ns

Rarefaction curves also showed that igapó is almost three times more species rich than várzea over the sampled area (Fig 6). In tidal-várzea the expected rate of new species was low, even as soon as the second plot. In contrast, in igapó new species were accumulated throughout. There was no evidence for differences in equitability (J) between tidal-várzea and igapó ($p > 0.05$).

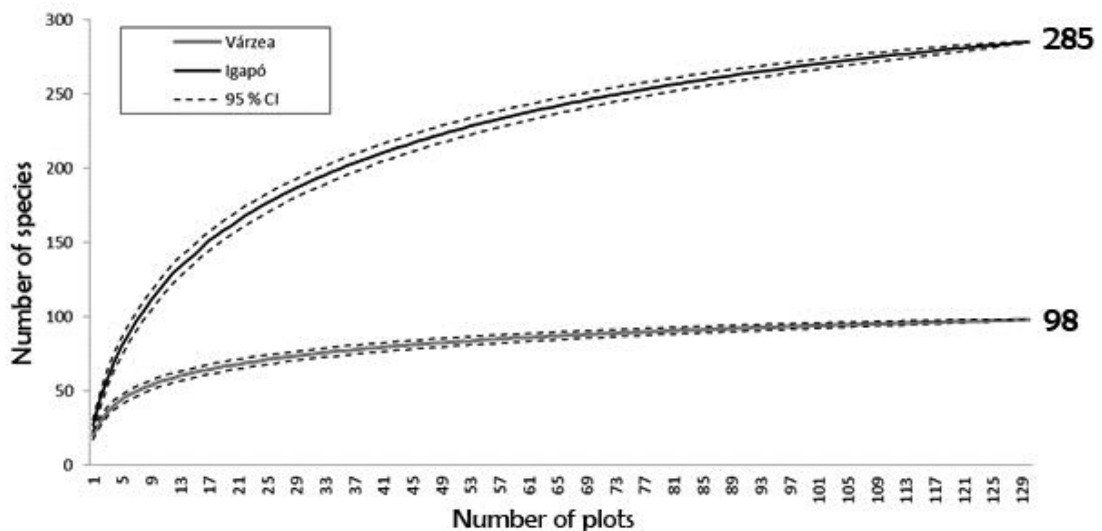


Figure 6. Expected species accumulation curves by plot, based on random samples of the data, for tidal-várzea and igapó in eastern Amazonia, Brazil.

In igapó comparison of upstream, intermediate and downstream sites showed significant differences in regards to mean trunk diameter ($p < 0.05$), mean tree height ($p < 0.05$), basal area ($p < 0.01$), and the number of individuals ($p < 0.001$). However there was no evidence for differences in Fisher's alpha or plot species richness ($p > 0.05$). For the variables assessed,

excepting tree density, upstream sites showed the highest values, while downstream sites the lowest.

In tidal-várzea there was no evidence of mean differences in Fisher's alpha, plot richness and structural variables among upstream, intermediate, and downstream site classes. However, downstream sites had, on average, between 9 and 15% less tree stems than upstream site classes ($p < 0.001$) and showed higher values for mean trunk diameter, height and basal area (Table 4).

Table 4. Plot-wise mean and standard error for tree density (individuals ha^{-1}), species richness (S), diversity (alfa de fischer), equitability (J), mean trunk diameter (mD), mean tree height (mHT), and mean basal area (mBA), for tidal-várzea and igapó. Values are based on sample sizes ranging from 3 to 7, as indicated by the number of plots in each class (see plot id row).

Variable	Igapó			ANOVA	Várzea			ANOVA
	Up-stream	Inter-mediate	Down-stream	P	Up-stream	Inter-mediate	Down-stream	P
N	370.5±50.7a	410.5±48.5b	429±45.9b	***	370.5±41a	430.43±37b	430.3±70.3b	***
S	57.8±12.1a	57.7±a	52±3.5a	ns	40.6±4.5a	37.7±0.57a	41.1±6.7a	ns
Fisher	20.31±5.3a	18.3±8.6a	16.8±3.5a	ns	11.65±1.8a	9.7±0.18a	11.31±2.9a	ns
mD	24.2±4.6a	25.8±3.9a	22.3±2.8b	**	24.9±1.9a	23.35±2.3a	26.39±12.a	ns
mBA	24.6±1a	27.9±1a	22±0.7b	**	25±0.63a	25.5±0.63a	34.1±4.35a	ns
mHT	17.7±3a	18.56±2.4a	16±1.9b	*	15.73±1.5a	13.6±1.73a	14.9±2.4a	Ns
Plot id	1,2,5,6,7	3,11,12,13	4,8,9,10		4,7,12	2,3,11,	1,5,6,8,9,10,13	

The dendrogram clusters revealed that the major division in regards to vegetation composition corresponded to the different habitats: tidal-várzea and igapó (Fig 7). Moreover, the dendrogram aided in indentifying differences in compositional pattern within tidal-várzea and igapó. Specifically, in igapó dendrogram clusters accorded well with upstream, intermediate, and downstream groups, indicating compositional change along the river course.

Upstream sites in igapó had more variable composition than both intermediate and downstream groups. In contrast, plot-wise comparisons in tidal-várzea all had similarities above 0.5, indicating less compositional variation among plots relative to igapó. Likewise, upstream, intermediate, and downstream sites did not form clusters as in igapó.

Worth mention is that despite strong compositional differences, several species were widely distributed among most plots regardless of plot position along the river course or among dendrogram clusters. The most important of these include, for example, *Pentaclethra*

macroloba, *Gustavia augusta*, *Mora paraensis*, *Astrocaryum murumuru*, *Matisia paraenses*, *Carapa guianensis* and *Swartzia cardiosperma*.

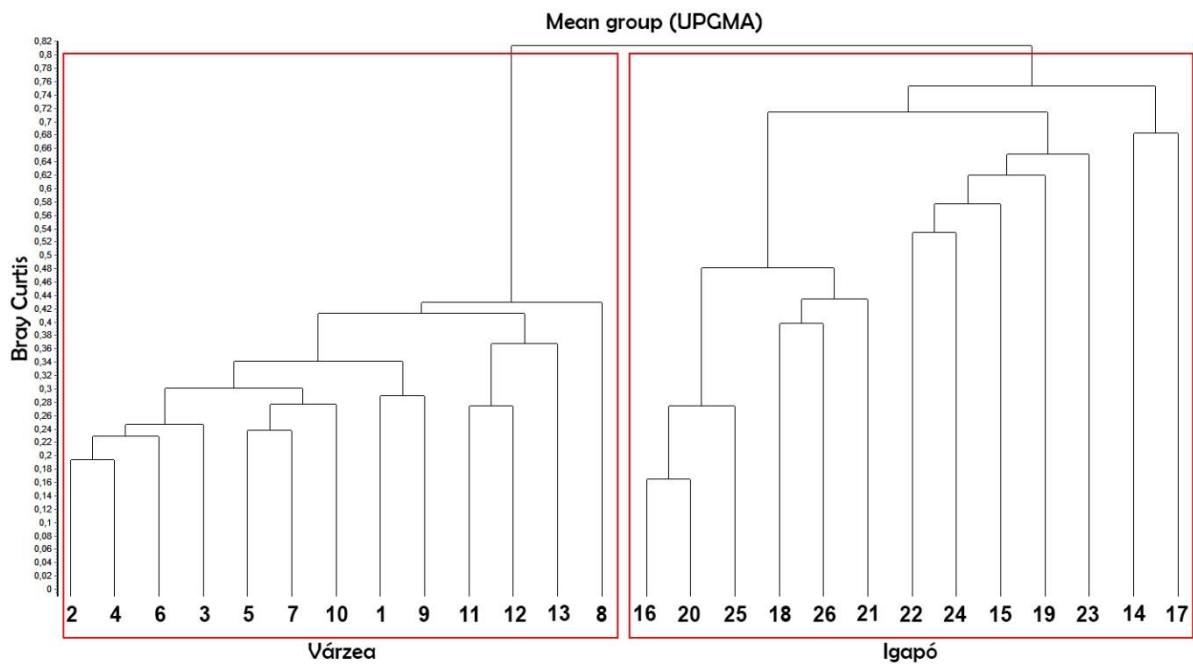


Figure 7. Results of an UPGMA cluster analysis based on the Bray-Curtis dissimilarity matrix of all 26 plots studied in tidal-várzea and igapó in eastern Amazonia, Brazil.

Discussion

The five most important families in each habitat accounted for about 82% and 60% of trees in tidal-várzea and igapó, respectively. They also accounted for the largest proportion of species richness, including 50% and 35% of species reported for tidal-várzea and igapó, respectively. Our study thus confirms the idea that few families and species dominate tropical forests (Lima Filho et al. 2001; Wittmann et al. 2002; 2004; Parolin et al. 2010; Wittmann and Parolin 2005; Ferreira et al. 2010; Parolin et al. 2010). In the floodplain conditions studied here patterns of dominance are even more severe, likely contributing to the hyperdominant status reported for some families and species (ter Steege et al. 2013).

Among the most important families occurring in both tidal-várzea and igapó communities are Fabaceae, Arecaceae, Lecythidaceae and Rubiaceae. Dominance by Fabaceae was due to its high species richness, abundance, and mean basal area. The family's most important representatives included *Pentaclethra macroloba* in igapó and *Mora paraenses* in tidal-várzea. These species have been reported in other floristic studies of eastern Amazonian tidal-várzea (Almeida et al. 2004) and igapó (Ferreira et al. 2013), indicating a wider pattern of

dominance beyond the samples of this study. The ranking of other families in regards to importance varies between tidal-várzea and igapó.

We found that tidal-várzea and igapó are similar in regards to several of the measured structural variables. For example, in the sense that over 75% of individuals had dbh between 10 and 30 cm, the diameter class distribution observed in both habitats is similar, and similar to those found in other studies of várzea and igapó (Lima filho et al. 2001; Cattaneo et al. 2002; Rabelo et al. 2002; Wittmann et al. 2002; Wittmann et al. 2004; Almeida et al. 2004; Wittmann and Parolin 2005; Santos and Jardim 2006; Haugaasen and Peres 2006; Carim et al. 2008; Amaral et al. 2009; Ferreira et al. 2010; Almeida and Jardim 2011; Wittman et al. 2013).

The inverted J-shaped distribution curve for dbh is characteristic for tropical forests (Silva Júnior 2004; Haugaasen and Peres 2006; Carim et al. 2008; 2015) and is understood to indicate a positive balance between recruitment and mortality. We did not find evidence that the studied forests differed in terms of basal area and mean trunk diameter. Mean tree height was greater in igapó than in tidal-várzea, however in both habitats the majority of individuals were less than 24 m tall. In tidal-várzea the largest proportion of individuals were binned into the shortest height class, an understandable finding considering the limiting conditions of environmental instability, where specialized morpho-anatomical attributes are required for establishment (Wittmann et al. 2002; 2004; Wittmann and Parolin 2005; Parolin et al. 2010).

Tidal-várzea and igapó showed similar physiognomic structure, distinguished only by a slight increase of mean height of trees of igapó. Many studies point to ecological tradeoffs for species occurring in habitats with contrasting soil nutrient resources -- one manifestation of these tradeoffs is the size of individuals, with smaller individuals expected in sites with lower nutritional resources (Coomes and Grubb 1996; Fine et al. 2006; Targhetta et al. 2015). Contrary to these studies, we show that, despite large differences in soil fertility, the tidal-várzea and igapó investigated here have similar physiognomic structure and are comprised of trees of similar size.

Carim et al. (2015) analyzed 14 hectares of terra firme forest adjacent of the igapó forest of this study, reporting similar findings in regards to composition, diversity, and structure. For example, *Pentaclethra macroloba* occurs in the 15 most important species in both the igapó of this study and the Carim et al. (2015) terra firme study. In 2008 the same author, with collaborators, studied 5 hectares of tidal-várzea in a different location of the Amazonian estuary, finding practically the same results for vegetation structure, composition and diversity as the tidal-várzea considered in the current study. Gama et al. (2005) compared the distribution

of species in várzea and terra firme in the State of Para, reporting that 85.6% of species were exclusive to terra firme, 5.2% were exclusive to várzea, and 9.2% occurred in both terra firme and várzea. These general findings have been corroborated by a number of authors (Almeida et al. 2004; Santos et al. 2006; Queiroz and Machado 2008; Carim et al. 2014).

Many studies point to differences between várzea and igapó in the Amazon region. Some authors report greater richness and diversity in igapó (Worbes 1997; Ferreira et al. 2010). On the other hand, the majority of comparative studies find that várzea is richer, especially in central and western Amazonia (Haugaasen and Peres 2006; Wittmann et al. 2006). Indeed, várzea is widely considered the richest floodplain flora in the world, contributing more than 1000 tree species (Wittmann et al. 2010). Here, we found a large difference in regards to species richness among habitats, with igapó approximately three times richer than tidal-várzea. This finding thus stands in stark contrast with most comparative studies (e.g., Black et al. 1950; Campbell et al. 1986; Ferreira 1997; Ferreira and Prance 1998; Prance 1979; ter Steege et al. 2000; Wittmann and Junk 2003; Ferreira et al. 2010).

While the two systems we studied are completely divergent in regards to species richness and diversity, we verify strong similarity in physiognomic structure. Comparison to other studies indicates minimal variation in composition, diversity, and structure within tidal-várzea and within igapó ecosystems in the eastern Amazon. Composition, however, is likely to change at larger biogeographic scales including the central and western Amazon (Wittmann and Junk 2003). In sum, this study does not support the hypothesis that várzea is more species rich and diverse than igapó.

Conclusion

In conclusion, this study is a preliminary attempt to compare várzea and igapó in eastern Amazonia. The comparison is based on a large, quantitative dataset that substantially increases our understanding of these environments, contributing essential data needed to make recommendations for the classification and management of Amazonian wetlands, which is led by the Group for Monitoring and Sustainable Use of Amazonian Wetlands (MAUA/INPA).

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Capítulo 2

Carim, M.J.V, Wittmann, F., Piedade, M. T. F., Ter Steege, H., Tostes, A. M. & Tostes, L. C. L. T. A
The influence of hydro-edaphic factors in the distribution of tree species in white-water tidal
floodplains and clear water floodplains in eastern Amazonia, Brazil. Submetido a *Plant
ecology*

The influence of hydro-edaphic factors in the distribution of tree species in white-water tidal floodplains and clear water floodplains in eastern Amazonia, Brazil

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Abstract The objective of the present work was to analyze correlations of tree species distribution with environmental factors in inundated tidal várzea and igapó forests of eastern Amazonia, Amapá, Brazil. Soil texture, soil chemistry, hydroperiod, and species composition were systematically assessed in 26 ha⁻¹ plots divided equally between várzea and igapó forest types. All living trees with diameter at breast height (dbh) \geq 10 cm were registered. In total, it was documented 10,575 trees distributed among 343 species, 172 genera and 49 families. The PCA was used on measured hydroedaphic variables to identify major environmental differences among groups of sites. The CCA was employed as a way to assess the associations of measured environmental variables and species distributions. In igapó, acidity, aluminum concentration, flood duration, potassium and sand content influenced species distribution in decreasing order of significance. At the várzea, CEC, SB, silte, Ca, days-inundated, pH K, and P content affected species distribution in decreasing order of significance. Micronutrients did not show any effect on species distribution on both environments. One may conclude that in the várzea forest the species distribution respond strongly to a major number of environmental factors. On the other hand, the igapó tree species distribution is affected mainly by the acidity variability and aluminum toxicity.

Keywords floristic, inundation regime, soil variables, distribution

Introduction

In the Amazon, inundated forests cover an area totaling 600,000 km² (Melack and Hess 2010). These forests are affected by periodic inundation resulting in transitional terrestrial and aquatic phases over the course of an annual cycle (Junk et al. 1989). As such, inundated forests reflect a laterally pulsating system that exerts strong influences on floodplain vegetation composition and dynamics, offering a unique window to further understand how environmental heterogeneity structures diverse tropical communities (Junk et al. 1989). In response to the often extreme conditions of flood and drought common in inundated forests, plants have purportedly evolved a variety of morphophysiological coping (Parolin et al. 2010).

The most representative types of inundated forests in the Amazon are associated with white water rivers (várzea) and black or clear water rivers (igapó) (Prance 1979). Sioli (1956) proposed a river classification system in the Amazon based on physio-chemical parameters of river water, water origin, and the geology of the respective watershed. Largely consistent with Sioli (1956) original classification, Junk et al. (2011) suggested a hierarchical framework of wetland classification based on climate, hydrology, water chemistry, sedimentology and botanical criteria. Igapó forests cover approximately 180,000 km² of relatively low-fertility and low-productivity environments. Várzea forests occur along channels draining the Andes and the Andean foothills. These rivers carry fertile sediments that are rich in nutrients and cover approximately 300,000 km² within the Amazon basin (Melack and Hess 2010).

Variation in soil type, flood duration, climate and nutrient availability are considered to be important factors that influence composition, richness and vegetation structure in Amazonian wetlands (Ferreira and Almeida 2005; Haugaasen and Peres 2006; Assis and Wittmann 2011; Ter Steege et al. 2013; Targhetta et al. 2015).

Many studies highlight the effect of inundation regime and soil physio-chemistry on the distribution of tree species in flooded forests of the Amazon basin (Piedade et al. 2005; Ferreira and Almeida 2005; Ter Steege et al. 2006; Wittmann et al. 2006; Haugaasen and Peres 2006; Assis and Wittmann 2011; Ferreira and Parolin 2011; Ter Steege et al. 2013; Assis et al. 2014; Targhetta et al. 2015), the role of transported sediments in explaining the relative high fertility of várzea, and the lack of these fertile sediments in nutrient-impoverished igapó, have also been highlighted (Sioli 1956; Keel and Prance 1979; Filizola and Guyot 2009; Junk et al. 2011; Quesada et al. 2011). In this sense, inundation appears to be a factor that regulates soil chemistry and texture (Budke 2007).

In eastern Amazonia the majority of work on várzea and igapó inundated forests has focused on questions of vegetation structure and diversity (Almeida et al. 2004; Gama et al. 2005; Santos and Jardim 2006; Salomão et al. 2007; Queiroz and Machado 2008; Carim et al. 2008; Almeida and Jardim 2011; Ferreira et al. 2013; Carim et al. 2014). However, not a single work describes how tree species distributions are associated with hydro-edaphic factors in this part of the Amazon.

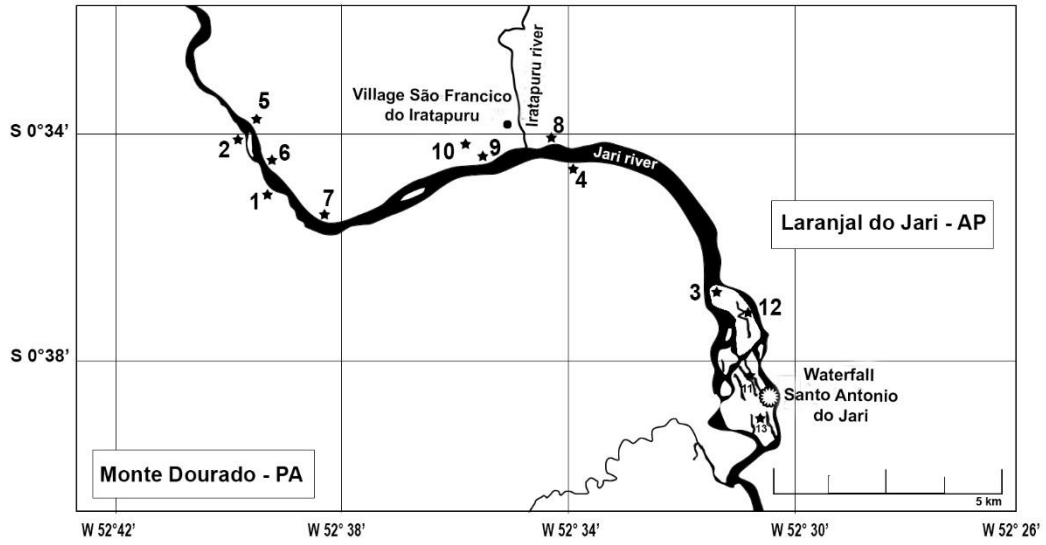
The objective of the present research was to investigate the influence of inundation regime and soil variables on the distribution of tree species in várzea and igapó in the eastern Amazon. The following hypothesis was formulated so as to better understand the studied forests: i) species distribution is affected principally by inundation regime and not by soil fertility or texture.

Materials and methods

Study area

This study took place in areas of alluvial forest pertaining to two watersheds of eastern Amazonia located in southern Amapá, northern Brazil. The first watershed is drained by the Mazagão river and located within the municipality of Mazagão between 00° 14' 06" and 00° 15' 54" latitude and 51° 20' 06" e 51° 23' 42" longitude. The second watershed is drained by the Jari river and located in the municipality of Laranjal do Jari between 00° 30' 00" e 01° 06' 00" latitude and 52° 18' 00" e 52° 38' 00" longitude (Fig. 1). In both regions the climate is tropical with a mean annual temperature of 27.5°C and a mean annual precipitation of 2,158.8 mm (Rabelo et al. 2006).

Igapó, Laranjal do Jari - AP



Várzea, Mazagão - AP

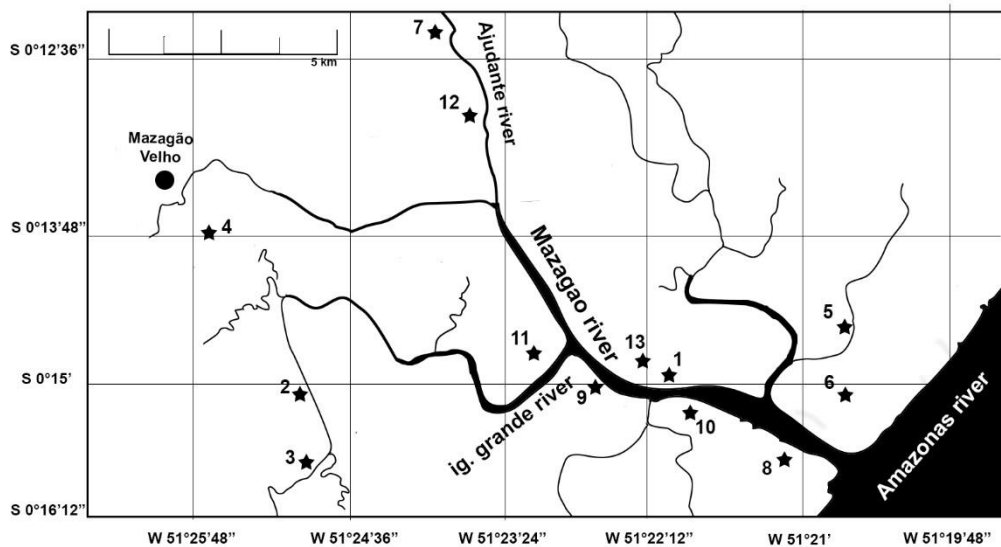


Figure 1. Map of locations of várzea and igapó inundated forest sites in the two studied watersheds of eastern Amazonia, Brazil.

Igapó forests are located near the northern border of the Amazon basin on the Guiana Shield. This geological formation is characterized by pre-Cambrian crystalline bedrock and sandy to clayey latosols (Rabelo et al. 2006). The studied várzea forests occur within an estuarine complex and is supplied by waters originating from the Andes as well as local precipitation drained by many small tributaries. Two cycles of daily tidal floods of predominantly fresh water are associated with this estuarine complex, giving rise to tidal várzea forests. Soils in this complex are classified as haplic gleysols with very clayey to silty texture (Queiroz and Machado 2008).

Floristic Inventory and Data Collection

A total of 26 1-ha (100 x 100 m) floristic inventories were completed, divided equally between várzea and igapó (13 ha in each ecosystem). Each inventory was divided into 10 subplots of 1,000 m² (10 x 100 m). In each subplot individuals with a diameter at breast height (DBH) \geq 10 cm were reported. Individuals with trunks branching below 1.3 m were also reported and assigned the minimum dbh. All inventoried hectare sites were georeferenced with the aid of a GPS. Identified to species in the field with the aid of parataxonomists. Botanical samples of individuals that could not be identified in the field were collected for later taxonomic confirmation at the Herbarium Amapaense (HAMAB - IEPA). APG III (2009) was adopted for taxonomic classification. A total of 17 species were incorporated into Herbarium (HAMAB - IEPA) with collection registry numbers ranging from 18185 to 18201.

Environmental Variables

To obtain information on the mean inundation of plots, the mean annual inundation level for each individual was calculated based on the height of the water marks recorded by the high water levels during 2012. With data made available from the National Water Agency (ANA) and the Hydrological Information System (*HidroWeb*), daily water level recordings for the Amazon river (Maracá station- AP, código: 00051004), and Jari river (San Francisco station – AP, código: 00052000) were obtained for the periods 1976 to 2004, and 1970 to 2007, respectively. The mean inundation for each plot was calculated as the mean inundation experienced by all individuals in each plot (Wittmann et al. 2002).

Soil Sampling

Three substrate samples corresponding to the top 20 cm of soil were collected from two extreme ends and the center point (0 - 50 - 100 m) of each hectare plot. The three soil samples

from each plot were homogenized, resulting in one soil sample per hectare plot. An analysis of micronutrient concentration was carried out at Embrapa/Eastern Amazonia. Macronutrients were analyzed at Embrapa/AP, and soil texture (percent sand, silt and clay) was quantified at the Aquatic Research Nucleus - CPAQ/IEPA-AP. For the soil texture analysis, the sand fraction was sifted while the silt and clay fractions were separated by means of the pipette method, in accord with procedures suggested by Embrapa (1997). Additionally, potential acidity ($H^+ + Al^{3+}$), pH in water and in KCL 1 mol L^{-1} , organic material (OM), exchangeable base cations (Ca, Mg, K), aluminum (Al^{3+}) and available phosphorous (P) were determined in accord with Camargo et al. (1986). Based on these analyses the following indices were calculated: sum of bases (SB), cation exchange capacity (CEC), base saturation (V%) and Aluminum saturation (m%).

Data Analysis

With the goal of identifying and evaluating significant differences within each environment and between environments, soil physiochemical variables and inundation levels were subjected to Tukey's multiple comparison test for normally distributed data at the 5% significance level. A matrix comprised of 21 hydro-edaphic variables (only continuous variables), for subsequent data exploration by ordination methods. Principal Components Analysis was used to visualize the distribution of plots according to environmental predictors. Variables that were redundant or that contributed little to the total variation were eliminated (Gotelli 2001). The variables that were proportions were transformed by the expression $\log_{10}(n + 1)$ in order to compensate for deviations caused by a few elevated values.

To identify patterns of species distribution that were potentially associated with environmental variation we used canonical correspondences analysis (CCA) (Ter Braak 1987). The technique helps explore relationships between a species abundance matrix and a matrix of environmental variables (Oliveira Filho et al. 1997; Botrel et al. 2002). Only species with a minimum number of 15 sampled individuals were included in the final species matrix (SM) (Ter Braak 1995). The association of environmental variables with the SM was assessed using a step-wise procedure based on Monte Carlo permutation tests for significance (10,000 iterations, $\alpha = 0.05$) (Manly, 1991). Variables without statistically significant associations were removed.

After a preliminary run of the CCA, variables that were weakly correlated with the SM, or highly redundant with other environmental variables were removed. The final CCA was

assessed with the variables that were most representative and most strongly correlated with the ordination axes for each environment. All statistical analyses were performed in the PAST program (Hammer and Harper 2009).

Results

Floristics

A total of 10,575 trees with dbh ≥ 10 cm were reported, distributed among 343 species, 172 genera and 49 families. Mean tree density was 406.73 ± 61.27 stems ha^{-1} averaged across the 26 hectares sampled. Considering várzea forests alone, we sampled 5,461 tree stems with a mean density of 420.08 ± 60.82 trees ha^{-1} . Sampled individuals were distributed among 98 species, 80 genera, and 29 families. For igapó we sampled a total of 5,114 tree stems with an average density of 393.38 ± 37.42 stems ha^{-1} . These trees were distributed among 285 species, 150 genera and 45 families.

Environmental Variables

For the great majority of measured environmental variables, excepting potential acidity ($\text{H}+\text{Al}^{3+}$) and Zn, we found strong differences between várzea igapó forest types. Soils were more acidic in igapó. Várzea was associated with higher concentrations of most chemical elements except Al, $\text{H}+\text{Al}^{3+}$ and Fe. The silt fraction was more pronounced in várzea while the sand fraction was more pronounced in igapó. Significant difference in the clay fraction was not found among the two environments. A comparison of flood duration among the two habitats indicated that várzea forests were inundated for a shorter period of time. The estimated mean days-inundated across all várzea sites was 20.65 ± 7.36 days, compared to 59 ± 25.75 days in igapó. The range of estimated days-inundated in várzea was 25, ranging from 8 days in the least flooded sites to 33 days in the most flooded sites. In igapó sites, the estimated range of days-inundated was 80, with the least flooded sites inundated 23 days and the most flooded sites inundated for 103 days. The two forest types showed a significant difference for this variable (Table 1).

Table 1. Mean (\pm standard deviation) and results of analysis of variance tests for measured hydro-edaphic variables in sampled várzea and igapó forests of eastern Amazonia.

variables	Várzea	Igapó	Teste t	
	N = 130	N = 130	F	P
Inundation	20.65 \pm 7.36 a	59.0 \pm 25.75 b	1.93	***
pH em H ₂ O	5.73 \pm 0.13 a	4.37 \pm 0.64 c	1.7	***
OM (dag/kg)	35.18 \pm 8.96 a	20.09 \pm 7.8 c	1.92	***
P (mg/dm ³)	12.26 \pm 5.9 a	9.75 \pm 3.77 c	1.41	***
K (mg/dm ³)	0.18 \pm 0.03 a	0.11 \pm 0.04 c	1.48	***
Ca (cmolc/dm ³)	11.75 \pm 1.91 a	0.052 \pm 0.16 c	1.30	***
Ca+Mg (cmolc/dm ³)	16.03 \pm 2.2 a	1.71 \pm 0.66 c	1.33	***
Al (cmolc/dm ³)	0.14 \pm 0.05 a	1.24 \pm 0.7 b	1.8	***
H+Al	4.14 \pm 0.81 a	5.9 \pm 2.69 c	1.4	**
SB	16.25 \pm 2.17 a	0.67 \pm 0.65 c	1.8	***
CEC	20.36 \pm 2.65 a	6.2 \pm 2.58 c	1.2	**
V%	82.92 \pm 2.69 a	12.77 \pm 7.47 c	8522	***
m(%)	1.08 \pm 0.27 a	60.63 \pm 19.69 c	1.9	***
Mg (Cmolc dm ⁻³)	4.1 \pm 0.94 a	0.13 \pm 0.25 c	1.29	***
Fe (mg dm ⁻³)	551.08 \pm 169.73 a	826.54 \pm 196.81 c	1.87	***
Cu (mg dm ⁻³)	3.7 \pm 0.5 a	1.99 \pm 0.66 c	374.1	***
Mn (mg dm ⁻³)	370.96 \pm 125.44 a	66.9 \pm 36.2 b	446.2	***
Zn (mg dm ⁻³)	6.11 \pm 1.51 a	5.26 \pm 2.45 b	79.91	*
Sand (%)	46.69 \pm 7.76 a	80.14 \pm 10.55 b	388.9	***
Silt (%)	55.55 \pm 9.75 a	16.78 \pm 9.64 b	578.7	***
Clay (%)	3.21 \pm 0.54	2.96 \pm 2.28	1.394	ns

Values followed by the same letter do not significantly differ based on the Tukey-Kramer test ($p < 0.05$). * = significant ($p < 0.05$); ** = significant ($p < 0.01$); *** = significant ($p < 0.001$); ns = not significant.

We examined how environmental variables covaried in each environment and the extent to which environmental variables covaried in a (dis)similar fashion in different environments using PCA. To do this, we compared the separate PCAs of measured environmental variables of each forest type. In both analyses, the first two axes accounted for the great majority of measured environmental variation among sites.

The two primary axes explained 84.56% and 76.59% of the total environmental variation in igapó and várzea, respectively. In igapó the first and second axes accounted for 59.76%, and 24 respectively. In várzea, the first and second axes accounted for 55.53% and 21.06% of the total variation of measured environmental variables among sites. In both typologies, three groups of sites could be identified in the PCA according to their environment (Table 2). In each forest type the three clusters identified by the PCA were geographically situated along a river continuum, indicating spatial autocorrelation in measured hydro-edaphic variables along an upstream-downstream gradient. As such, for each forest type, plots were

grouped according the distance from the river mouth; including downstream, intermediate, and upstream sites.

In igapó, sites classified as upstream were associated with relatively high sand content, high acidity, and greater days-inundated. Intermediate sites were associated with higher micronutrient concentrations and high CEC, while sites classified as downstream, proximate to the mouth of the Jari river, were associated with relatively high silt content. In várzea, sites classified as upstream were associated with relatively high concentrations of P, Zn, Mn, and organic material. The intermediate cluster of sites was associated with higher silt content and pH. In the justante cluster, sites were associated with high concentrations of Ca, K, and SB, higher CEC, more inundation-days, and higher sand content (Table 2).

Table 2. Principal components analysis (PCA) showing the distribution of sites along the two primary ordination axes according to their hydroedaphic variables. Results are shown for both igapó and várzea forests of eastern Amazonia.

IGAPÓ						
River Position	Site ID	Hectares	Variable	Axis 1	Axis 2	P
Upstream	1,2,5,6,7	5	Inundation	-0.2995	0.5233	>0.001
			Sand	-0.7338	0.6342	>0.001
			K	-0.4507	0.4898	>0.001
			pH	-0.5598	-0.1382	>0.001
Intermediate	4,8,9,10	4	CEC	0.7987	0.3808	>0.001
			Al	0.659	0.0726	>0.001
			Fe	0.875	0.3686	>0.001
			Zn	0.3417	0.8844	>0.001
			Mn	0.4829	0.7988	>0.001
			Cu	0.7409	0.3478	>0.001
Downstream	3,11,12,13	4	Silt	0.8197	-0.5128	>0.001
VÁRZEA						
River Position	Site ID	Hectares	Variable	Axis 1	Axis 2	P
Upstream	4,7,12	3	OM	-0.5526	0.8196	>0.001
			P	-0.9304	0.441	>0.001
			Zn	-0.8103	0.5703	>0.001
			Mn	-0.7105	0.6865	>0.001
Intermediate	2,3,11	3	Silt	-0.5191	-0.7219	>0.001
			pH	-0.5089	-0.2468	>0.001
Downstream	1,5,6,8,9,10,13	6	Inundation	0.8071	0.3064	>0.001
			K	0.4966	0.8328	>0.001
			Ca	0.9807	-0.1161	>0.001
			SB	0.9748	0.1688	>0.001
			CEC	0.9492	0.2281	>0.001
			Sand	0.4696	0.7589	>0.001

Species Ordination

The results of the CCA indicate that the two first ordination axes defined by the measured environmental variables jointly explained 64.1% e 84.6% of the total variation in the distribution of species in igapó and várzea forests, respectively. As such, the results were sufficient to describe the relationships among species and environmental variables. The Monte Carlo test (based on 999 permutations), demonstrated that the two canonical axes were highly significant ($p < 0.001$) in each of two typologies.

The correlation of each environmental variable to the canonical axes can provide insight into factors that might control community structure. In general, the longer the environmental vector, the stronger the relationship of that variable with the community. Additionally, the position of a species relative to an environmental vector can be used to interpret the relationship between species and measured environmental variables (Table 3).

Table 3. Weighted correlations of measured environmental variables with the first two CCA ordination axes for igapó forest.

Variables	Axis 1	Axis 2
Acidity (pH)	0.73378	-0.04209
Aluminum	-0.3957	0.683841
Inundation	0.373456	0.581524
Potassium (K)	0.538412	-0.198665
Sand	0.33738	0.08975

In the CCA, species in igapó were most strongly influenced by variation in pH, K, and sand content, environmental variables that were all highly correlated with the first canonical axis. Although axis 1 illustrates the strongest pattern in species distribution, many species also responded to environmental factors highly correlated with axis 2, days-inundated and aluminum concentration. Differences in species distributions along these axes likely reflects niche differences in regards to measured environmental variables. That said, many species clustered near the center of the CCA diagram, indicating that perhaps great the majority of species are not strongly responsive to measured environmental variation, at least within the scope of our subsample (Fig. 2).

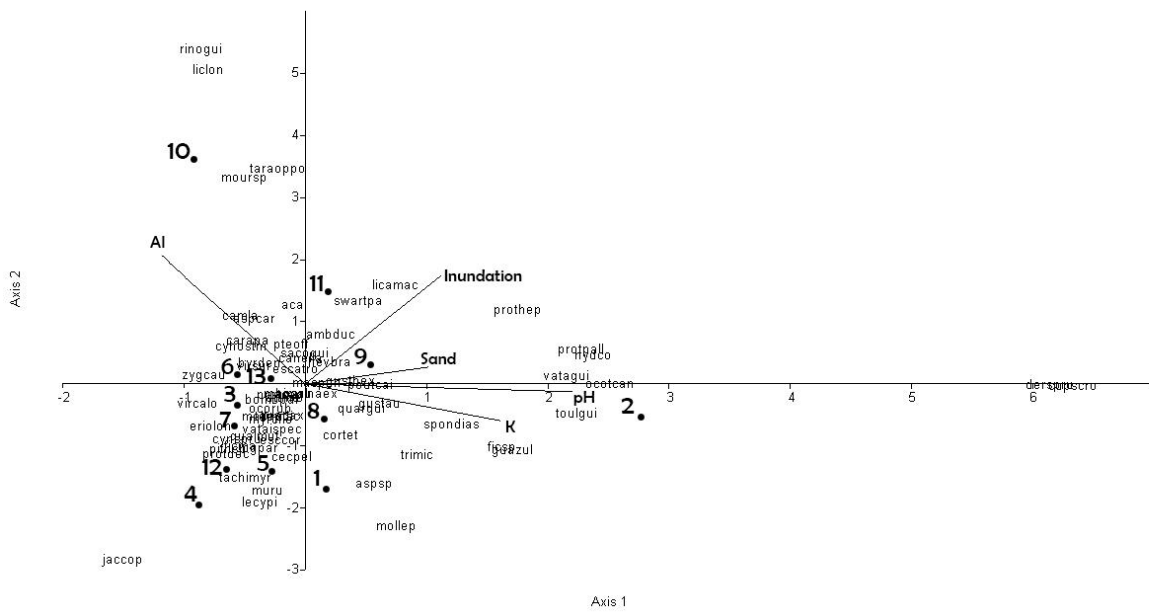


Figure 2. Canonical correspondence analysis diagram of species and sites in igapó forests in eastern Amazonia, Brazil.

In várzea forest, all measured environmental variables demonstrated a strong correlation with the first canonical ordination axis. In any case, the separation of sample units according to the environmental variables as indicated by the PCA did not show a clear separation along the canonical ordination gradient. Species distributions were most strongly associated with a number covarying environmental variables that were highly correlated with axis 1: negative with CEC, SB, days-inundated, K and positively with silt, Ca, P and pH (Fig. 3).

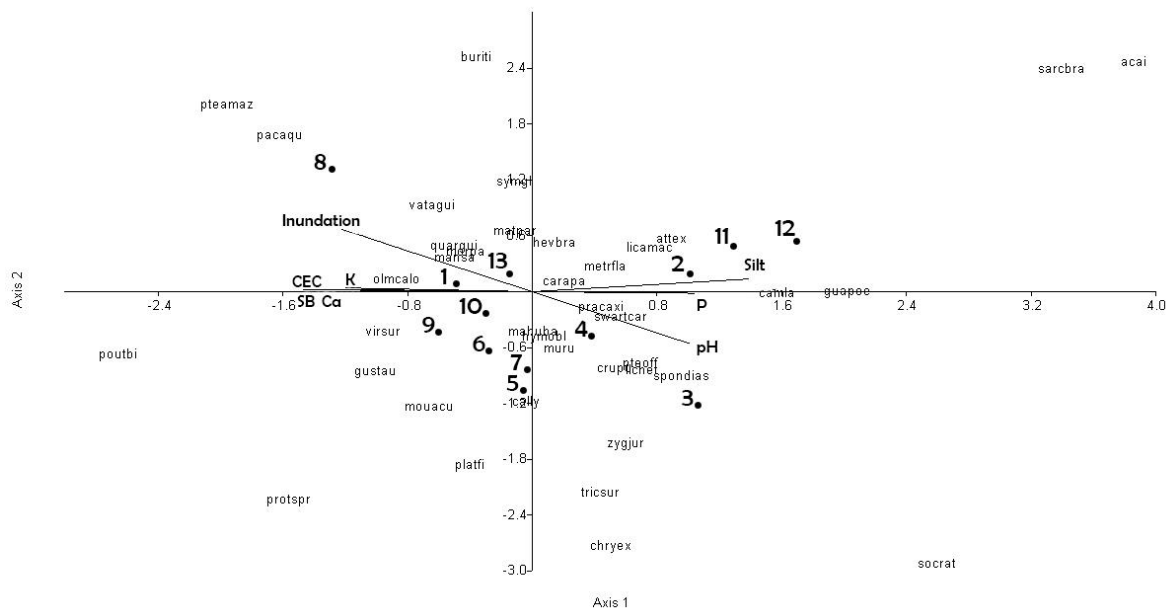


Figure 3. Canonical correspondence analysis diagram of species and sites in várzea forests in eastern Amazonia, Brazil.

However, the differences in species distributions along this gradient appear to reflect shifts in species abundances, rather than species substitution. In this sense, despite apparent niche differences among species as portrayed by the CCA, one might still consider that most of the species examined here are habitat generalists, at least along the subset of the gradient examined (Tabela 4).

Table 4. Weighted correlations of measured environmental variables with the first two CCA ordination axes for várzea forest

Variables	Axis 1	Axis 2
CEC	-0.731063	0.050872
SB	-0.712678	0.054463
Silt	0.697130	0.065524
Ca	0.669455	0.134975
Inundation	-0.611023	0.342850
K	-0.594632	0.015483
P	0.519454	0.006071
Acidity (pH)	0.506528	-0.31976

Discussion

Environmental Variation

The majority of studies in igapó and várzea forests in eastern Amazonia report on the diversity, composition and structure of these forest typologies (Almeida et al. 2004; Santos and Jardim 2006; Carim et al. 2008; Amaral et al. 2009; Ferreira et al. 2010; Almeida and Jardim 2011; Batista et al. 2011; Ferreira et al. 2013). Few studies report on the influence of the inundation regime and soil physio-chemical factors in the distribution of tree species in this region (Haugaasen and Peres 2006; Ferreira and Parolin 2011).

Using principal components analysis we sought to identify general patterns of environmental variation within and among forest types, with specific emphasis on soil properties and inundation duration. The present study highlights significant differences among forest types for all measured environmental variables. In particular, várzea is, on average, more fertile than igapó, and there appears to be little variation in soil fertility within várzea.

The clear separation of plots according to environmental variables indicates differences in the composition of these factors along the environmental gradient. Three groups of sites were identified in each of the two environments, influenced by different variables acting in concert or acting individually.

In general igapó is sandier and várzea is siltier. However we were surprised to find a significant percentage of silt content in a group of igapó plots located downstream the Jari river,

near the river's junction with the Amazon river. This suggests the possibility that alluvial sediment deposits originating from white water rivers may have penetrated blackwater rivers in the past, perhaps caused by extreme inundation events (Haugaasen and Peres 2006; Irion et al. 2010).

At an intermediate position along the Jari river axis (igapó), one group of sites was strongly associated with high micronutrient concentrations (Fe, Zn, Mn and Cu) as well high CEC and Al. Notably, high concentrations of Fe, Mn, and Al demonstrated elevated levels of toxicity in the environment (Assis et al., 2014). Upstream, we observed higher sand concentrations, acidity (pH), days-inundated and potassium. In any case, generally low soil pH and high Al concentration might indicate intense weathering (Quesada et al. 2011).

A number of sites that were geographically located near the junction of the Mazagão and Amazon rivers formed a distinct cluster in the PCA of environmental. The differences in the concentration of Ca, SB, CEC and sand in downstream sites might generally be explained by complex river flow patterns driven by interacting daily tidal ebbs and flows originating from the ocean to the east, with annual flood pulses of rivers driven by seasonal rainfall patterns in distant reaches of eastern Amazon basin.

Specifically, elevated levels of sand might be associated with the sediment transport by tidal currents, coming from the Amazon River, with the enough strength to invade the Mazagão River, causing a deposition of the sandy sediments at the latter river mouth region. As the tide rises at the Mazagão River, it loses energy and consequently, there is a formation of silty soils. Sites located upstream Mazagão River were associated with high levels of organic material, high P availability, and high concentrations of micronutrients. These patterns may be associated with decreasing tidal influence in more upstream (Quesada et al. 2011).

Species distribution along the environmental gradient

The CCA was used as a tool to interpret potential relationships between species distributions and measured environmental variables. In both environments the analyses revealed that the majority of species, although did not show specific pattern associated to the environmental differences pointed by the PCA, presented high correlation among abundance of species and selected variables in the CCA.

At the igapó forest, acidity (pH), Al, days-inundated, K and sand in decreasing order of importance, were the variables that presented the highest correlation with the two CCA axis. However, the results indicated a high edaphic heterogeneity along the environmental gradient,

with chemical variations and texture from downstream to upstream at the Jari River. Related to the texture, it was observed the domination of sandy soils upstream, associated positively to days-inundated, K, pH e Al.

Frequently, igapó forest soils are associated to high acidity and nutritional poorness, as described by Haugaasen and Peres (2006) and Quesada et al. (2011). Surprisingly, the species-variables relation when associated to environmental gradient differences along the downstream and upstream axis did not demonstrate relevant effects in the species distribution. This could explain the concentration of them in the center of CCA diagram. It was found that 28 of 66 species in the igapó forest (42.42%) did not present affinity with any selected variable.

Whatsoever, low pH values associated to flooding tend to diminish the availability of other nutrients, which yields an environment with limiting conditions. This behavior suggests that the availability of many nutrients to the plants indirectly is influenced by pH. In a limited resources environment, the species distribution must undergo the specific nutrient influences that favors the liberation of other nutrients (John et al. 2006).

For várzea forest, several soil attributes covaried with inundation regime as indicated by the position of environmental vectors in the CCA. Mainly, sites presenting less days-inundated tended to have more silt content, higher pH, and greater P concentration. Species response to this environmental gradient was strong. While species-environment associations found here might be interpreted as differential species response to a heterogenous environment (i.e., habitat filtering) alternative mechanisms may also explain the patterns, such as dispersal limitation and priority effects (Assis et al. 2014). It was identified that 21 of the 39 species (51.3%) in the várzea forest did not show compatibility with any of selected variables.

In the várzea forest it was also observed a strong spatial segregation of the sample sites along Mazagão River, with groups formation starting from the mouth towards the upstream river course. A major group was observed in the mouth at the junction to the Amazon River, with seven sites. In the Mazagão upriver direction, the sites formation at the midway and upstream were not well defined, as presented by the PCA.

Related to the observed environmental gradient, significant correlations between inundation, CEC, SB and K, which greatly influenced the grouping of sample units downstream. Silt, Ca, P and pH show important association to sample sites at the mid-course of Mazagão River. Nonetheless, it seems clear, as said before, that the influence of the Amazon River over Mazagão River appears to be preponderant for the environment structuration. Although the nutrient effect and the substrate sound to be determinant for the species

distribution (Haugaasen and Peres 2006; Budke et al. 2007; Filizola and Guyot 2009; Ferreira et al. 2013), this is not evident in the present work. The tendency of low specific habitats could explain the distribution of many species at the Amazonian várzeas (Wittmann et al. 2013).

The present study demonstrates that few species occurred distantly from the center of the ordination diagram on both environments, indicating that the majority of species have a large tolerance with regards to some utilized environmental variables. As a consequence, species present a general distribution pattern. In accord with Rodrigues et al. (2007), species have gradually different tolerance intervals to environmental variables. At some optimal point along resource gradients or habitat conditions a species reaches maximum abundance level, from which abundance declines towards more extreme conditions.

However, in order to characterized species in regards to their preferred habitats, it is necessary that the tendencies demonstrated by species in one study also be observed in other study areas (Dalanesi et al. 2004; Rocha et al. 2005). The majority of species identified in the present work are generalists, occurring along the entire inundation and soil gradient we studied. For example, *Pentaclethra macroloba* (Willd.) Kuntze, *Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg., *Spondias mombin* L. and *Virola surinamensis* (Rol. ex Rottb.) Warb. are distributed among nearly all sites in both environments.

Few species seem to present an high degree of habitat specificity in regards to hydroedaphic conditions. Adventitious roots, aerenchyma and lenticels are adaptations presented by the majority of tree species that are tolerant to inundation. The presence of specific traits that increase species tolerance to flooded conditions may explain the wide distribution of some species along the flood gradient we studied (Parolin et al. 2010; Junk et al. 2010).

However, the period of flooding is substantially different throughout the Amazon basin, with variations from west to east of up to 240 days/year. This variability in flood duration could possibly control the distribution of species along the gradient of inundated forests in the Amazon (Wittmann et al. 2006, 2013). Notwithstanding, the flooding days interval in this study vary from 25 to 80 days for the várzea and igapó forest, respectively. In this sense, the duration of inundation days is small compared to other places in the Amazon (Wittmann et al. 2006, 2013; Targhetta et al. 2015). Thus, it must affect the species distribution in a different way if compared to regional scale.

While in our study the distribution of species did not conform to environmental variation in either of the two environments, the great majority of studies suggest that hydroedaphic variability is an important source of habitat heterogeneity, and thus beta diversity, at landscape

scales (Wittmann et al. 2006; Filizola and Guyot 2009; Junk et al. 2011). At last, one could suggest that in the várzea forest studied, the species distribution responds strongly to a larger number of environmental variables. As for the igapó forest, the distribution of the species are more related to the soil acidity and aluminum toxicity.

Our study suggests that small-scale environmental heterogeneity within and between different wetland forest types has large repercussions in regards to species local distribution pattern and community composition (Wittmann et al. 2006; Albernaz et al. 2011). Thus, we attribute the differences in species distribution and composition observed in this study principally to species responses to a heterogeneous environment, as opposed to alternative mechanisms that can produce similar spatial pattern, such as dispersal limitation.

Conclusions

This work results demonstrated a wide variation between várzea and igapó forests, especially in regards to differences in inundation regime and nutritional status. It indicates that the trees species distribution are influenced by different variables in the várzea and igapó forests; however, a considerable non-explained variation exists.

Species distributions are expected to result from a combination of abiotic (e.g., environmental filtering) and biotic (e.g., competition) factors, and the interaction of these processes in an environmentally heterogeneous landscape. In this sense, any conclusions regarding species distributions in terms of environmental variables can only approximate a generalization once the same pattern has been repeatedly observed in a variety of areas. In this fashion, the principal findings of the present study serve as a basis in the search of answers that can help explain, for example, whether or not species distribution patterns follow some specific pattern in each region of the Amazon, and what causes determine these differences.

The results presented in this study comprise a first attempt to compare várzea and igapó forests in eastern Amazonia. The results are based on a large, quantitative dataset, substantially increasing our understanding of these environments and contributing essential data needed to make recommendations for the classification and management of Amazonian wetlands.

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Capítulo 3

Carim, M.J.V, Wittmann, F., Piedade, M. T. F., Guimarães, J. R. S, Takyama, L. R., Tostes, L. C. L. Above ground woody biomass estimated along the flood gradient of várzea and igapó forests in the eastern Amazon, State of Amapá, Brazil. Submetido a *Wetlands Ecology and Management*

Above ground woody biomass estimate along the flood gradient of várzea and igapó forests in the eastern Amazon, State of Amapá, Brazil

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Abstract This study aimed to estimate the woody biomass above ground along the flooding gradient of two hydrographic basin at the Amapá State. They were allocated 26 plots of one hectare (100 x 100m), 13 plots in each environment (várzea and igapó forests). It was considered all living individuals with DBH \geq 10 cm. To assess the biomass it was used the allometric model already tested in rainforests, where it considers the variables: wood density (ρ), height (H) and basal area (BA). The biomass estimated for both ecosystems presented the same average (198.56 Mg.ha⁻¹). In the igapó forest the amplitude was 326.83 Mg.ha⁻¹ and in the várzea was 272.12 Mg.ha⁻¹. The flood regime averaged 61 ± 25.69 days/year and 21 ± 1.33 days/year in the igapó and várzea forest, respectively. The biomass was positively related to soil gradient (sand percentage) in igapó and silt on the várzea. The flood and edaphic soil variables had little influence in both environments biomass. Few species in both environments showed greater accumulation of biomass. Generally, the same species occurs in the two environments increasing the biomass in both ecosystems, with little influence of soil variables.

Keywords rainforest, hydroperiod, biomass, structure, Amapá.

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Introduction

The tropical rainforests are characterized by their biodiversity and high biological productivity rate with great accumulation of biomass and carbon (Santos et al. 2004) and have been identified as alternatives for reduction of greenhouse effect gases. Due to the debate on the role of forests on global climate change, the evaluation of forest biomass became important in this context, increasing the demand for research to quantify the potential of forest ecosystems to sequester carbon from the atmosphere and biomass stock (Higuchi et al. 1998; Ketterings et al. 2001; Melo and Durigan 2006; Silveira et al. 2008).

The stock of the woody biomass indicates the quality of environmental conditions such as climate, hydrology, soil structure, vegetation and nutrient availability (Chave et al. 2004). The stock of biomass is different from location to location and from individual to individual and this variation is a result of several environmental factors to which the plant is susceptible, in addition to factors inherent in the plant itself (Soares et al. 2011). Some studies of rainforests in central Amazonia report a correlation between biomass and gradients of texture and fertility of soils, and land topography (Laurance et al. 1999; Cummings et al. 2002; Castilho et al. 2006).

The estimates of biomass and carbon sequestration in tropical forests are usually performed using allometric models (Higuchi et al. 1998; Chambers et al. 2001; Clark et al. 2001; Baker et al. 2004; Chave et al. 2005; Malhi et al. 2006), by means of independent variables such as dbh, height and density of the wood (Silveira et al. 2008). Obtained through direct methods (destructive) or the indirect method (non-destructive), the latter becomes faster, because does not cut, nor weigh, nor dry any individual; it can sample a larger area and more individuals, as it work with field variables, such as the diameter and height (Higuchi et al. 1998; Santos et al. 2004). Allometric models that consider both height, diameter (basal area) and wood density are more accurate (Chave et al. 2005). The aboveground biomass estimates, through the indirect method provide essential data that allows extrapolation of biomass and carbon stocks for the evaluated ecosystems (Somogyi et al. 2006).

Many studies have been done to generate consistent allometric models for woody aboveground biomass estimates, mainly in dry land forests in Amazonia (Higuchi et al. 1998; Chambers et al. 2001; Cummings et al. 2002; Baker et al. 2004; Chave et al. 2005). For flooded forests no specific allometric models exists, such as for igapó and várzea. In this work, it was chosen an allometric model that closest represent the environment studied (Chave et al. 2005).

Considering the large extension of igapó and várzea forests in the state of Amapá, there are not registered studies in the region on the aboveground biomass contained in these two

environments. Thus, the aim of this work is to estimate the woody biomass aboveground along the flood gradient of igapó and várzea forests of two watersheds in the Amapá State using allometric equations for non-destructive method and answer the following questions: The periodic of flooding under tidal regime and seasonally flooded interfere with the supply of plant biomass stock of these environments? The physicochemical characteristics of the soil can interfere with the plant biomass of these environments?

Material and methods

Study area

The study was conducted in areas of alluvial forest belonging to two river basins in the eastern Amazon, in the Amapá State, Brazil. The first is located in the basin of the Amazon River in the municipality of Mazagão. The second is in the Jari River watershed, whose main course is originated in the Guyana shield, in the Laranjal of Jari municipality (Fig. 1).

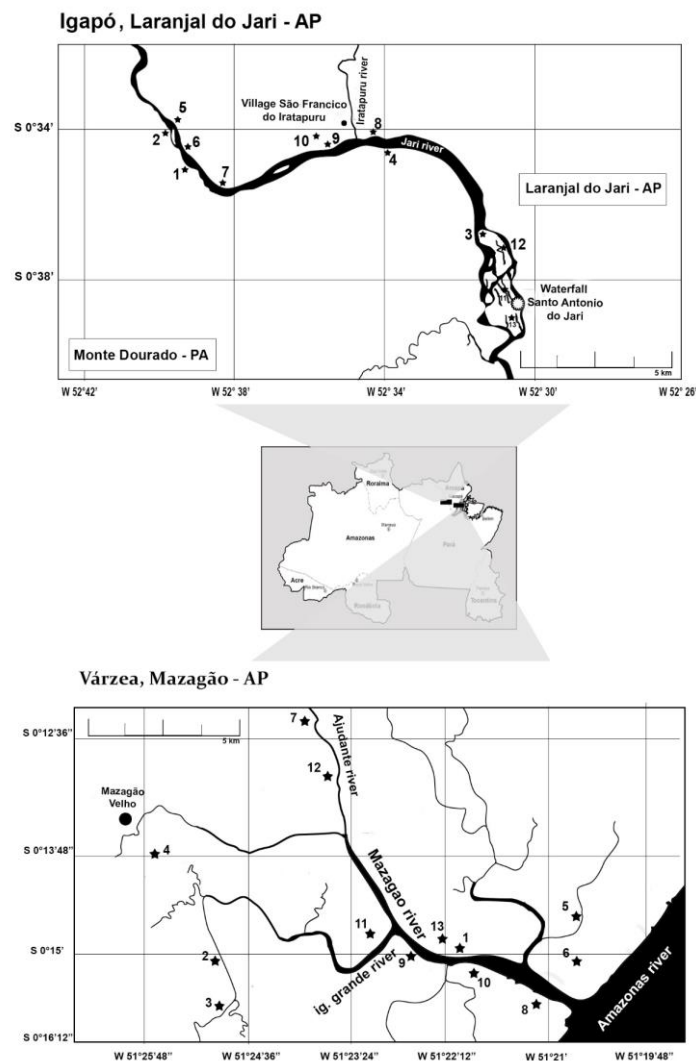


Fig. 1 Location of the two study areas in the eastern Amazon, Amapá State, Brazil.

The two areas are under the Ami climate domain type (hot and humid) , high relative humidity (over 80 %), high annual rainfall (2,000 mm to 2,500 mm); with a small dry season of 3 to 4 months and a rainy period from December to June; minimum temperature of 23° C and a maximum of 33° C (Vásques and Rabelo 1999). The soil of the study area is classified as Eutrophic Humic-Glei low to moderate, clayey texture (Queiroz and Machado 2008).

Floristic inventory

Vegetation was sampled in 26 1-hectare plots (100 m x 100 m), divided into 13 hectares for each habitat (várzea and igapó). Each plot was comprised of 10, 1,000 m² (10 x 100 m) subplots. It was considered all individuals with diameter at breast height (DBH) \geq 10 cm were measured with the help of a diameter tape, and their height of the subjects was estimated with the aid of a graduated stick of six meters long. All plots were geo-referenced using GPS.

The species were identified in the field with the help of parataxonomists; unidentified copies had their botanical materials collected for further taxonomic confirmation at the Amapaense Herbarium (HAMAB), located at the Institute of Scientific and Technological Research of Amapá State - IEPA. the system APG III (2009) was used to classify the plants. The name of the listed species was updated using the database Tropic Missouri Botanical Garden (<http://www.tropicos.org/>).

Data collection – flood elevation

To obtain the average flood level for the plots, the averaged annual flooding for each sampled individual was measured by recording the flood heights printed on the trees for the last flood of year 2012. Based on data provided by the National Water Agency (ANA) through the Hydrological Information System (*Hidroweb*) daily levels of the Amazon River (Maracá Station - AP, code: 00051004) for the period 1976-2004 and the Jari River (San Francisco Station - AP , code: 00052000) for the 1970-2007 time frame were obtained.

Subtracting the inundation level from the maximum flood height reached by the river in 2012, it was obtained the minimum level from which the individual was flooded. This value was used as a reference for calculating the average flood of individuals for the period of each historical series for the two watersheds. Based on these data, it was calculated the number of days that each individual was flooded every year and from there the average flood time (in days.yr⁻¹) for the entire period cited. The average flood for each plot corresponds to the average of the floods of individuals in the plot (Wittmann et al. 2002).

Data collection – soils

To compose the data matrix of the study, information was collected from the environment of each plot, related to soil variables and duration of flooding. Three surface soil samples were collected (0-20 cm) obtained at the edges and middle of each hectare. The three soil samples from each plot were homogenized, resulting in one soil sample per plot. Analyses of micronutrients were held at the EMBRAPA/Western Amazon Soil Laboratory; macronutrients were analyzed at the EMBRAPA/AP Soil Laboratory and the grain size (percentage of sand, silt and clay) at the Laboratory of Sediment and Water Geochemistry - CPAQ/IEPA-AP.

In particle size analysis, the sand fraction was sieved while silt and clay were separated by the method of the pipette, according to the procedures suggested by EMBRAPA (1997). The soil variables determined according to Camargo et al. (1986) were: pH in water and KCl 1 mol.L⁻¹, the potential acidity (H + Al³⁺), organic matter, calcium bases (Ca), magnesium (Mg), potassium (K) and Aluminum (Al³⁺) contents and assimilable phosphorus (P). From these, the following parameters were calculated: sum of bases (SB), cation exchange capacity (CEC), base saturation (V %) and Al saturation (mass %).

Data analysis

For estimating woody aboveground biomass (AGB), it was considered the allometric model defined by Cannel (1984), as follows: $AGB = F \times p \times H \times BA$, tested on rainforests (Chave et al. 2005; Wittmann et al. 2008; Targhetta et al. 2015). The basal area (BA) was calculated for all individuals from the equation: $BA = \pi DAP^2/4$ (Chave et al. 2005). It was also used a correction factor ($F = 0.6$), which takes into account loss of biomass due to branches in the crown and assumes that the branches do not change with increasing size of the individual (Cannell 1984; Chave et al. 2005; Wittmann et al. 2008).

For the calculation of palm trees biomass, it was employed the allometric model developed by Frangi and Lugo (1985), which only takes into consideration the height (H) as a key variable that explains the change in biomass of these species. The values of the two models were joined together to obtain the average biomass values of each area.

The specific densities of the sampled species were obtained based on the literature, prioritizing work in rainforests; for the species for which data are not available in the literature, it was used the average of the specific densities found for the same gender (Chave et al. 2005;

2006). For those species or genera whose data were not found, the approach was to average the densities of each plot separately, applied to individuals of the same plot (Baker et al. 2004).

Statistical calculations were processed using the PAST software (Hammer et al. 2001). The t-test (Student) was applied to compare the biomass between the two environments. For soil gradient analysis the Principal Components Analysis (PCA correlation) was employed to reduce the dimensionality of the soil variables and describe the most significant variables for igapó and várzea forests. To determine the relationship between biomass and soil gradient, it was used a simple correlation with biomass as the dependent variable and the first axis of the PCA as an independent variable.

Results

Forest structure and aboveground biomass

In total, it was registered 5,114 specimens, with an average of 393 individuals per hectare, distributed into 285 species, 150 genera and 45 families in the igapó forest. In the várzea, there were 5,461 individuals represented by 98 species, 80 genera and 29 families with an average of 420 individuals per hectare.

For aboveground biomass of tree species plus palm trees, the variation was 84.10 to 326.83 Mg.ha⁻¹, with an average of 198.56 ± 78.28 Mg.ha⁻¹ in igapó forest. The range of biomass for the várzea forest was 83.81 to 272.12 Mg.ha⁻¹, with a mean of 198.06 ± 53.33 Mg.ha⁻¹. Biomass between the two ecosystems did not differ statistically (Student t-test, $p > 0.05$).

The igapó had an average diameter estimated of 23.90 ± 14.73 cm and mean height of 17.03 ± 6.34 m. *Ceiba pentandra* L. Gaertn. recorded the largest diameter (173.80 cm) and a higher height (43 m). In the várzea environment the average diameter was 24.37 ± 14.26 cm and mean height of 14.68 ± 7.07 m where *Hura crepitans* L., presented the largest diameter (186.53 cm) and substantial height in this environment, along with *Mora paraensis* Ducke, *Ceiba pentandra*, *Virola guianensis* Aubl. and *Tachigali myrmecophila* Ducke, all with 40 m.

The sum of basal area between igapó plots ranged from 15.60 to 35.55 m², averaging 24.35 ± 6.44 m².ha⁻¹; in the várzea, the variation was from 21.53 to 32.48 m².ha⁻¹, averaging 29.92 ± 3.41 m².ha⁻¹. The subjects were grouped into diameter classes at intervals of 10 cm, where the higher percentage of biomass was presented in the intermediate dbh class (20.1 to 30 and 30.1 to 40 cm, with low density of individuals with regard to first-class but with high concentrations of basal area (39.98 %) in igapó and (31.77 %) in várzea forests. Despite the

lower classes have higher abundance of individuals, such as igapó (50%) and várzea (51%), these yielded smaller fraction of biomass (Fig. 2 and 3).

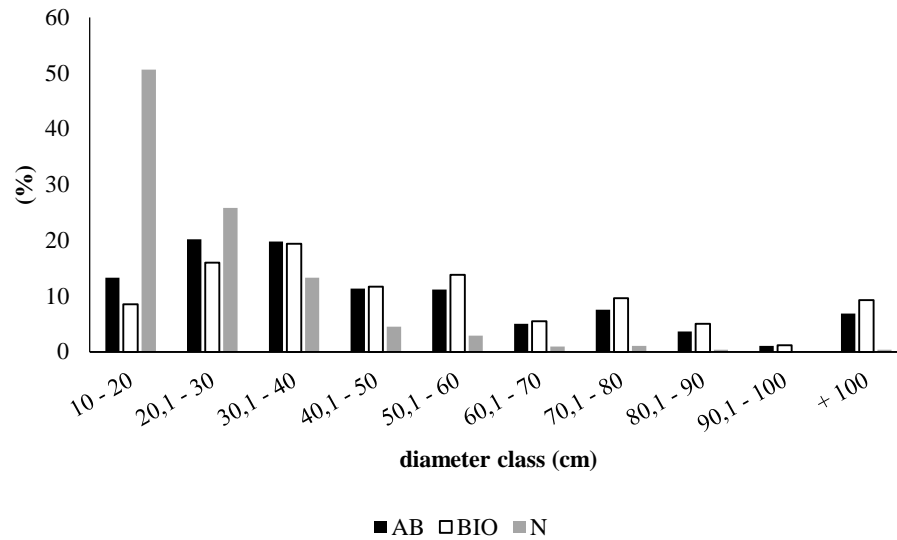


Fig. 2 Number of individuals (N), basal area (AB) and biomass (BIO) of the igapó forest.

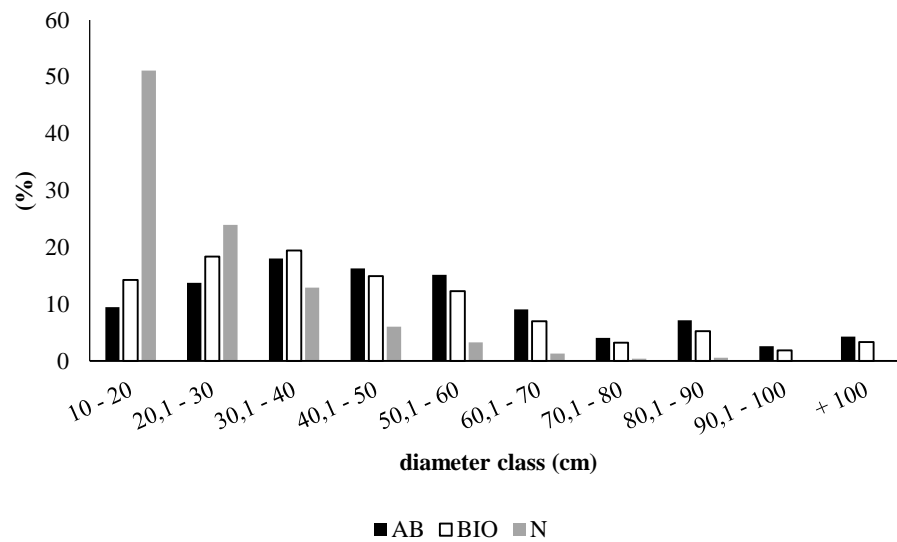


Fig. 3 Number of individuals (N), basal area (AB) and biomass (BIO) of the várzea forest.

Effects of flooding regime

The flood time was understood as a variation of climatic environment. There was no correlation between the flood of time comparing the two environments. The flood time responded differently within each environment, at the várzea forest associations showed slight negative correlations for density and plant height.

In the igapó forest, the mean height of the water column was 0.81 ± 0.35 cm, with maximum measurements reaching 170 cm, where the flood time ranged from 32 to 94 days/year (average of 61 ± 25.69 days/year), as the relief variation considering all the flood plain. For the várzea forest, the height of the column of water registered by the individuals was 0.45 ± 0.13 cm, with maximum values up to 1.00 m, and the flood duration within 4 to 60 days/year (mean of 21 ± 1.33 days / year).

In the várzea, the plot 1 located on the right bank of the Mazagão river and distant about 3 km from the mouth (confluence with the Amazon River), showed higher biomass ($272.12 \text{ Mg}\cdot\text{ha}^{-1}$), followed by the plot 13 ($267.85 \text{ Mg}\cdot\text{ha}^{-1}$); this second, located 300 meters from the first parcel. At the other end, the plot 8 presented lower biomass ($83.82 \text{ Mg}\cdot\text{ha}^{-1}$), and is located closer to the mouth, at about 800. This plot had strong positive relationship on the axis 1 with flood, Ca, SB and CEC.

The igapó forest environment registered higher amplitude of biomass compared to the várzea forest. The plots showed higher biomass in the plot 7 ($326.83 \text{ Mg}\cdot\text{ha}^{-1}$) and the plot 12 ($314.71 \text{ Mg}\cdot\text{ha}^{-1}$), distant approximately 14 km from each other, and different average flood period of 70 and 57 days/year were recorded, respectively. At the other extreme, the lowest volume of biomass occurred in plot 2 ($84.11 \text{ Mg}\cdot\text{ha}^{-1}$), with a mean of 53 days/years flooded and strong negative relationship with the axis 1 with pH and silt content (Table 1).

Table 1 Period of flood (days) and aboveground woody biomass for each plot inventoried on each ecosystem and their respective mean and standard deviation.

Plot	Várzea		Igapó	
	Flood (Days)	Biomass ($\text{Mg}\cdot\text{ha}^{-1}$)	Flood (Days)	Biomass ($\text{Mg}\cdot\text{ha}^{-1}$)
1	20	272.1227	34	157.62
2	20	183.6489	53	84.107
3	23	130.1038	38	272.6999
4	20	192.0225	33	146.5542
5	22	212.8982	37	159.7956
6	21	187.8018	32	297.7037
7	21	162.0498	70	326.8355

8	21	83.81629	94	138.6855
9	23	189.04935	91	187.1326
10	20	253.2377	77	179.8588
11	23	228.6905	93	188.6971
12	22	211.4719	57	314.7054
13	18	267.852	94	126.9136
Maximum	23	272.1227	94	326.8355
Minimum	18	83.8162	32	84.107
Mean + Standard Deviation	21.06±1.32	198.56±78.29	61.72±25.66	198.06±53.34

Edaphic variables and simple correlation

Throughout the PCA, it was evaluated the strength of the interactions of the physical environment with the vegetation structure; this analysis was done for each environment separately. From all initial variables, only ten and fifteen of them showed significant associations with elements of vegetation structure in the várzea and igapó, respectively. The soils were more acidic in the igapó and poorer in nutrients related to the várzea. In the igapó it was found a higher fraction of sand and in the várzea forest the soil presented more silt content.

The resultant effect of the interaction of the variables with the environment by the principal component analysis showed the strength of the key variables in grouping the plots, defining the separation into three distinct groups in each type of forest. For igapó the environmental variables that most influenced the grouping of plots 1, 2, 5, 6, and 7 were strongly associated with sand fraction (average values of 80%), acidity (pH) and the flood regime. The plots 4,8,9 and 10 located near the entrance to the Iratapuru River showed strong correlation with micronutrients (Fe, Zn, Mn and Cu) and cation exchange capacity (CEC), but far downstream approximately 8 km from this group, plots 3, 11, 12, and 13 presented good correlation with silt.

In the várzea forest, plots 4, 7 and 12 were strongly influenced by phosphorus (P), zinc (Zn) and organic matter (OM); the 2,3 and 11 plots showed a good correlation with silt and acidity (pH). Near the junction of the Amazon with the Mazagão Rivers, were formed a group with the highest number of plots (1, 5, 6, 8, 9, 10 and 13), which presented strong correlation with calcium (Ca), base saturation (SB), cation exchange capacity (CEC), potassium (K), flood regime and sand. To better evaluate the effects of soil on the biomass variables, it was used simple Pearson correlation (p) where the soil gradients most significant in the structure of the vegetation were related to biomass (Table 2).

Table 2 Correlation among the edaphic variables and the axis generated by the PCAs for igapó and Várzea.

Edaphic Variables	Igapó	Várzea
Flood	-0.0978	-0.08652
P	-	0.11683
OM	0.00512	-0.5526
K	-0.2507	0.37866
Al	0.25562	-
H+Al	0.33022	-0.13825
CEC	0.29826	-0.25617
Mg	-7.2155	-
Sand	-0.05823	0.4696
Silt	-0.2914	0.07013
Fe	0.16878	0.33236
Zn	0.00743	-0.8103
Mn	-0.06721	-

Discussion

Biomass amounts presented in two areas did not show statistical differences, the two types of vegetation environments had the same average biomass values ($198.56 \text{ Mg}\cdot\text{ha}^{-1}$). However, within each environment, the biomass presented great variability between plots. The flooded forests (várzea and igapó) have up less biomass when compared to the upland of forests, ranging $150\text{-}300 \text{ Mg}\cdot\text{ha}^{-1}$ (Malhi et al. 2006; Saatch et al. 2007; Targhetta et al. 2015). Comparing to the two ecosystems, the studies done in the Amazon rainforest indicates that the várzea possesses above-ground biomass averages higher than the igapó forest.

Studies in the Amazon region were performed regards the quantification of biomass in floodplain forests (Cummings et al. 2002; Malhi et al. 2006; Haugaasen and Peres 2006; Saachi et al. 2007; Wittmann et al. 2008; Schöngart and Wittmann 2010; Targhetta et al. 2015), but for várzea and igapó forests environment there are few reported work, and thus, it makes difficulty to compare the two ecosystems.

In várzea forest in the eastern Amazon, Almeida et al. (2004) estimated the values of 171 to $215 \text{ Mg}\cdot\text{ha}^{-1}$. Malhi et al. (2006) in western Amazonian várzea forests, obtained values around 195 to $357 \text{ Mg}\cdot\text{ha}^{-1}$. Targhetta et al. (2015), recorded variation of 88 to $196 \text{ Mg}\cdot\text{ha}^{-1}$, with an average of $141 \text{ Mg}\cdot\text{ha}^{-1}$, for igapó forest using the same allometric model used in the present study. In the State of Amapá, these studies are still scarce, there were not recorded work on biomass in flooded environments, most studies are restricted only to evaluate its structure

and diversity, in all cases in várzea forest (Rabelo et al. 2002; Almeida et al. 2004; Queiroz and Machado 2008; Carim et al. 2008; Batista et al. 2013).

In this study the várzea presented more soil nutrients in relation to the igapó forest, similar fact presented by other studies in the Amazon (Irion et al. 1997; Junk 1997; Parolin 2000). Through the principal component analysis, the resulting effect of the interaction of variables with the environment showed the formation of three separate plot groups in each environment. Two plots were recorded with less accumulation of biomass: parcel 8 in the várzea ($83.81 \text{ Mg}\cdot\text{ha}^{-1}$) and plots 2 in the igapó environment ($84.10 \text{ Mg}\cdot\text{ha}^{-1}$). In the várzea, this plot presented good positive relationship on the axis 1 with flooding, CA, SB and CEC. In the igapó with an average of 53 days/years flooding period, strong negative relationship on the axis 1 with pH and silt were detected. Sand and silt fractions significantly influenced the structure and abundance in várzea with sand content providing a good correlation with the diameter of individuals.

Few edaphic elements correlate to the biomass in both environments. Some work in the Amazon, studying biomass and edaphic factors reported little or no relationship between the two set of variables (Clark and Clark 2000; Chave et al. 2001; Targhetta et al. 2015). The flood regime always has a strong correlation with biomass. In this study the flood period was significant when correlated with biomass for the two environments, followed by sand fractions in igapó and silt content on the várzea. The texture is considered one of the most important soil characteristics, because it directly influences the relationship between organic matter, ions and draining soil (Silver et al. 2000; Fearnside and Leal Filho 2001).

Any effect of the soil on the occurrence of emerging species may have a large influence on the estimate of biomass, because some big individuals may be responsible for a large share of biomass (Brown and Lugo 1992; Clark and Clark 1996; Castilho et al. 2006). Independent of the plant type, vegetation structure and biomass in Amazonian forests are interpreted as dependent and are often influenced by two factors, namely: flooding, that cause less biomass, in seasonally flooded soils or highly flooded (Wittmann et al. 2004; Baraloto et al. 2010) and nutrient availability in the soil (Laurance et al. 1999; Paoli et al. 2008; Quesada et al. 2011).

Among the species recorded, 44 were common to both environments, where they contributed significantly to the stock of forest biomass. In the igapó those species accounted for 50.7% of the total abundance and 51.7% of forest biomass; in the várzea it was even greater: 69.6% of the total abundance and 74.4% of all forest biomass. These emerging individuals may be responsible for a large share of biomass stock, as was the case of the species *Pentaclethra*

macroloba (Willd.) Kuntze (12.23%), *Hevea brasiliensis* L. (11.01%), *Parinari sublime* Sabine (5.68%), *Carapa guianensis* Aubl. (5.42%), and *Terminalia dichotoma* G. Mey. (4.32%). Together they sum 38.66% of all registered biomass and 26.87 % of the total individuals in the igapó forest. In the várzea, only the species *Mora paraensis*, represented 34.29% of all of the biomass in this environment. *Astrocaryum murumuru* Mart. had more individuals (14%) but comprised only 2.5 % of the total biomass.

The contribution of one species in terms of abundance differs substantially from their contribution to ecosystem functions in general (Fauset et al. 2015). Only one species, in the case of *Mora paraensis*, was the second most abundant with 837 individuals and contributed 30% of the total biomass in the várzea forest. In the igapó only two species: *Pentaclethra macroloba* and *Hevea brasiliensis* contributed with 22% of total biomass. Species with low abundance have large fraction of biomass, this is due to characteristics of the species with large dbh and wood density that can contribute to biomass volume with so few individuals (Fauset et al. 2015).

Trees with dbh above 40 cm influenced significantly to the accumulation of biomass in a given environment, which provide more than 60% of the biomass (Chave et al. 2001; Lindner 2010). This study have shown that these trees have contributed to high biomass in the classes of intermediate diameters (20.1 to 30.1 cm, and 30 to 40 cm) where, despite the density of individuals, presented a large basal area in the two environments, and consequently higher fraction of biomass.

Large trees may be directly influencing for the similar average biomass present in the two environments and the increase biomass of certain portions in the igapó forest. When removing individuals over 70 cm DBH for analysis, the várzea environment is then characterized by high average biomass $162.06 \text{ Mg}\cdot\text{ha}^{-1}$ and high amplitude ($254.51 \text{ Mg}\cdot\text{ha}^{-1}$); by the same procedure, the igapó forest biomass average falls to $154.00 \text{ Mg}\cdot\text{ha}^{-1}$ and amplitude of $229.00 \text{ Mg}\cdot\text{ha}^{-1}$. The impact of these individuals in relation to biomass also comes from the fact that they can store large amounts of biomass with low abundance (Paoli et al. 2008). Any impact on these trees either by global change or other disorders that affect the abundance and persistence of these great individuals, is therefore, likely to have a major effect on forest biomass (Paoli et al. 2008).

The species that stood out, are widely distributed in the várzea environment in the estuary under tidal regime (Amaral et al. 2004; Queiroz and Machado 2008; Carim et al. 2008). They are commonly found in both environments, and have a greater tolerance to environmental

variations, occupy a variety of habitats and produce large populations, showing that they occur in a general way in these environments (Wittmann et al. 2006). They are tolerant to seasonal floods, but not restricted to highly flooded environments (Wittmann et al. 2006). Because of its shape to adapt to these environments, they start to exert strong influence on the biomass of each environment.

The present study shows that species adapt differently to availability of nutrients in the soil and ground conditions. Although some individuals from flooded forests are more tolerant to flooding, supporting greater inundation time (Wittmann et al. 2002), the flood can still be considered a limiting factor for the populations of várzea plants. The investigated species; if located in areas that experience a smaller influence of flooding, may have not developed effective adaptation mechanisms (Wittmann et al. 2002; 2008). Small variations in topography can also cause a rapid change in the duration of flooding and changing in environmental conditions over short distances (Worbes 1997).

Some studies show that the flood regime have a strong impact on the development of individual trees, with low diameter increment rates during the rainy season, as demonstrated for várzea and igapó forests in the Amazon (Schöngart et al. 2002). In addition to the limited growth, another consequence of flooding is the zoning of different species that are distributed along the flood gradient according to their competitive ability and adaptability to the environment (Wittmann et al. 2006).

Conclusions

The results of this study showed that the stock of biomass of both ecosystems were not significantly different, had low values compared to upland forests and values very close to studies in floodplain forests. Also, higher variation of biomass within igapó than within varzea was found. The two environments presented lower biomass than other sites of flooded forest in the Amazon region, which have had recorded the highest stock of biomass among várzea forests. Emergent species showed great influence on biomass of these environments than canopy or lower strata species.

Internal environmental variables had direct relation to the plots and the zonation of some dominant species. The flood time was strongly correlated with the biomass in both environments, especially the várzea. Sand in igapó and silt content in the várzea forest were the soil variables that also influenced in the correlation with the biomass.

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CONCLUSÃO GERAL

Este estudo avalia a estrutura, composição, diversidade e biomassa em florestas alagáveis de várzea de maré (água branca) e de igapó (água clara) e suas relações com variáveis edáficas e o período de inundação na Amazônia Oriental. O trabalho foi realizado em área de várzea de maré na bacia do rio Mazagão e em área de igapó na bacia do rio Jari, estado do Amapá.

O estudo ratifica a proposição de diversos autores sobre a dominância de poucas famílias e espécies em florestas tropicais. Fabaceae, Arecaceae, Lecythidaceae e Rubiaceae estão entre as cinco mais importantes nas comunidades estudadas. A floresta alagável de várzea de maré apresentou padrão estrutural e ecológico semelhante às demais florestas de várzea na Amazônia oriental, divergindo na composição das mesmas tipologias no resto da Amazônia. A floresta alagável de igapó apresentou elevada diversidade e riqueza de espécies, chegando a apresentar aproximadamente três vezes mais espécies que a várzea.

As características estruturais entre as duas florestas alagáveis mostraram-se semelhantes. A distribuição das classes diamétricas observada para os dois ecossistemas é similar à encontrada por outros estudos em florestas alagáveis de várzea e de igapó, com mais de 75% dos indivíduos apresentando DAP entre 10 e 30 cm.

Na floresta de várzea de maré registrou-se maior número de indivíduos na primeira classe de altura, perfeitamente compreensível para as condições de florestas inequidâneas onde a taxa de recrutamento é bem elevada. Apesar do ambiente de várzea ser de instabilidade, onde mecanismos morfoanatômicos são indispensáveis para o estabelecimento dos indivíduos, a diferença em altura dos indivíduos entre as duas florestas estudadas não foram significativos, a maioria dos indivíduos concentrou-se até 24 metros de altura para os dois ambientes, com a floresta de igapó mostrando indivíduos um pouco mais alto que a floresta de várzea.

Na área florestada de várzea de maré, a distribuição espacial dos solos transportados está intimamente associada à hidrodinâmica (pulso de inundação polimodal) que é determinante na distribuição das variáveis físico-químicas. Observou-se a jusante do rio Mazagão, próximo do rio Amazonas, a porção mais fortemente influenciada pelo regime de inundação por maré e elevados valores de cálcio, soma de bases, CTC, K e areia. Na porção intermediária da bacia, notou-se uma área hidrodinamicamente mais estável, permitindo a sedimentação de partículas menores, com a conseqüente formação de solos siltosos, apresentando acidez moderada. E a

montante do rio Mazagão, formou-se um gradiente influenciado por elevadas concentrações de matéria orgânica favorecendo um fornecimento de P e micronutrientes.

Na área florestada de igapó, o pH baixo do solo e a alta concentração de Al indicam intensa intemperização do material de origem. A jusante do rio Jari identificou-se significativo percentual de silte, indicando a deposição de sedimentos aluviais nas áreas de planalto por fenômenos extremos de inundação por rios de água branca. Na porção intermediária da bacia do rio Jari, predominantemente de águas claras, formou-se um grupo de parcelas fortemente associado a altos valores de micronutrientes (Fe, Zn, Mn e Cu) juntamente com a CTC e Al. A montante, verificou-se o agrupamento de parcelas fortemente influenciadas pela areia, acidez (pH), regime de inundação (monomodal) e potássio.

Nas florestas alagáveis de várzea e igapó, poucas espécies apresentaram grande estoque de biomassa. De modo geral, as mesmas espécies ocorrem nos dois ambientes elevando a biomassa nos dois ecossistemas, com as variáveis edáficas de solo pouco influenciando na biomassa.

Por fim, este trabalho apresenta contribuições para um melhor conhecimento e classificação de áreas úmidas na Amazônia oriental, assim como informações para estabelecimento de políticas públicas.

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APENDICE A. Lista das espécies arbóreas registradas nos 26 hectares inventariados nas duas bacias hidrográficas de águas claras (igapó), no Município de Laranjal do Jari e águas brancas (várzea), no município de Mazagão. As espécies estão ordenadas com suas respectivas famílias e locais de ocorrência no estudo.

Família / Espécie	Ocorrência
Amaryllidaceae	
<i>Amaryllis belladonna</i> L.	várzea
Anacardiaceae	
<i>Anacardium giganteum</i> W. Hancock ex Engl.	igapó
<i>Astronium lecointei</i> Ducke	igapó
<i>Spondias mombin</i> L.	igapó/várzea
<i>Tapirira guianensis</i> Aubl.	igapó
Annonaceae	
<i>Annona montana</i> Macfad.	igapó
<i>Duguetia</i> sp.	igapó
<i>Duguetia spixiana</i> Mart.	várzea
<i>Ephedranthus amazonicus</i> R.E. Fr.	igapó
<i>Guatteria poeppigiana</i> Mart.	igapó/várzea
<i>Unonopsis guatterioides</i> (A. DC.) R.E. Fr.	igapó
<i>Xylopia aromatica</i> (Lam.) Mart.	igapó
<i>Xylopia benthamii</i> R.E. Fr.	igapó
<i>Xylopia</i> sp.	igapó
Apocynaceae	
<i>Ambelania duckei</i> Markgr.	igapó
<i>Aspidosperma carapanauba</i> Pichon	igapó
<i>Aspidosperma nitidum</i> Benth. ex Müll. Arg.	igapó
<i>Aspidosperma</i> sp.	igapó
<i>Himatanthus sucuuba</i> (Spruce ex Müll. Arg.) Woodson	igapó
<i>Malouetia lata</i> Markgr.	igapó
<i>Malouetia</i> sp.	igapó
Araliaceae	
<i>Schefflera morototoni</i> (Aubl.) Maguire, Steyer. & Frodin	várzea
Arecaceae	
<i>Astrocaryum jauari</i> Mart.	igapó
<i>Astrocaryum murumuru</i> Mart.	igapó/várzea
<i>Attalea excelsa</i> Mart. ex Spreng.	várzea
<i>Attalea maripa</i> (Aubl.) Mart.	igapó

<i>Euterpe oleracea</i> Mart.	igapó/várzea
<i>Manicaria saccifera</i> Gaertn.	várzea
<i>Mauritia flexuosa</i> L. f.	várzea
<i>Oenocarpus bacaba</i> Mart.	igapó
<i>Socratea exorrhiza</i> (Mart.) H. Wendl.	várzea
<i>Syagrus cocoides</i> Mart.	igapó
<i>Syagrus vagans</i> (Bondar) A.D. Hawkes	igapó
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Bignoniaceae	
<i>Jacaranda copaia</i> (Aubl.) D. Don	igapó
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Bixaceae	
<i>Cochlospermum orinocense</i> (Kunth) Steud.	igapó
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Boraginaceae	
<i>Cordia bicolor</i> A. DC.	igapó
<i>Cordia exaltata</i> Lam.	igapó
<i>Cordia scabrida</i> Mart.	igapó
<i>Cordia scabrifolia</i> A. DC.	igapó
<i>Cordia sellowiana</i> Cham.	igapó
<i>Cordia tetrandra</i> Aubl.	igapó
<hr/>	
Burseraceae	
<i>Protium apiculatum</i> Swart	igapó
<i>Protium decandrum</i> (Aubl.) Marchand	igapó
<i>Protium heptaphyllum</i> (Aubl.) Marchand	igapó
<i>Protium krukoffii</i> Swart	igapó
<i>Protium pallidum</i> Cuatrec.	igapó
<i>Protium panamense</i> (Rose) I.M. Johnst.	igapó
<i>Protium sagotianum</i> Marchand	igapó
<i>Protium spruceanum</i> (Benth.) Engl.	igapó/várzea
<i>Protium trifoliolatum</i> Engl.	igapó
<i>Tetragastris panamensis</i> (Engl.) Kuntze	igapó
<hr/>	
Calophyllaceae	
<i>Calophyllum brasiliense</i> Cambess.	igapó/várzea
<i>Caraipa guianensis</i> Aubl.	igapó
<i>Caraipa richardiana</i> Cambess.	igapó
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Caryocaraceae	
<i>Caryocar microcarpum</i> Ducke	igapó
<i>Caryocar villosum</i> (Aubl.) Pers.	igapó
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Chrysobalanaceae	
<i>Couepia guianensis</i> Aubl.	igapó
<i>Licania apetala</i> (E. Mey.) Fritsch	igapó

<i>Licania egleri</i> Prance	igapó
<i>Licania heteromorpha</i> Benth.	igapó/várzea
<i>Licania longistyla</i> (Hook. f.) Fritsch	igapó
<i>Licania macrophylla</i> Benth.	igapó/várzea
<i>Licania membranacea</i> Sagot ex Laness.	igapó
<i>Licania octandra</i> (Hoffmanns. ex Roem. & Schult.) Kuntze	igapó
<i>Licania sclerophylla</i> (Hook. f.) Fritsch	igapó
<i>Licania</i> sp.	igapó
<i>Parinari excelsa</i> Sabine	igapó/várzea
<hr/>	
Clusiaceae	
<i>Platonia insignis</i> Mart.	várzea
<i>Rhedia brasiliensis</i> (Mart.) Planch. & Triana	igapó
<i>Rhedia macrophylla</i> (Mart.) Planch. & Triana	igapó/várzea
<i>Symphonia globulifera</i> L. f.	várzea
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Combretaceae	
<i>Buchenavia grandis</i> Ducke	igapó
<i>Buchenavia parvifolia</i> Ducke	igapó
<i>Combretum Cacoucia</i> Exell	várzea
<i>Terminalia dichotoma</i> G. Mey.	igapó
<i>Terminalia guyanensis</i> Eichler	várzea
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Convolvulaceae	
<i>Maripa guianensis</i> Sagot ex Gleason	igapó
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Dichapetalaceae	
<i>Tapura singularis</i> Ducke	igapó
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Ebenaceae	
<i>Diospyros artanthifolia</i> Mart. ex Miq.	igapó
<i>Diospyros guianensis</i> (Aubl.) Gürke	igapó
<i>Diospyros kaki</i> Thunb.	igapó
<hr/>	
Elaeocarpaceae	
<i>Sloanea eichleri</i> K. Schum.	igapó
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Euphorbiaceae	
<i>Actinostemon</i> sp.	igapó
<i>Conceveiba guianensis</i> Aubl.	igapó
<i>Croton</i> sp.	igapó
<i>Hevea brasiliensis</i> (Willd. ex A. Juss.) Müll. Arg.	igapó/várzea
<i>Hevea guianensis</i> Aubl.	igapó
<i>Hura crepitans</i> L.	igapó/várzea
<i>Sapium aucuparium</i> Jacq.	igapó
<i>Sapium lanceolatum</i> (Müll. Arg.) Huber	várzea

Sapium pedicellatum Huber

igapó

Fabaceae

<i>Abarema jupunba</i> (Willd.) Britton & Killip	igapó
<i>Acosmium nitens</i> (Vogel) Yakovlev	igapó
<i>Alexa grandiflora</i> Ducke	igapó
<i>Andira stipulacea</i> Benth.	igapó
<i>Campsiandra laurifolia</i> Benth.	igapó/várzea
<i>Cassia</i> sp.	igapó
<i>Crudia oblonga</i> Benth.	igapó
<i>Crudia pubescens</i> Spruce ex Benth.	várzea
<i>Cynometra hostmanii</i> Tul.	igapó
<i>Cynometra hostmanniana</i> Tul.	igapó
<i>Cynometra marginata</i> Benth.	várzea
<i>Cynometra</i> sp.	igapó
<i>Cynometra spruceana</i> Benth.	igapó/várzea
<i>Derris spruceana</i> (Benth.) Ducke	igapó
<i>Dialium guianense</i> (Aubl.) Sandwith	igapó
<i>Diploptropis martiusii</i> Benth.	igapó
<i>Dipteryx odorata</i> (Aubl.) Willd.	várzea
<i>Dussia discolor</i> (Benth.) Amshoff	igapó
<i>Enterolobium schomburgkii</i> (Benth.) Benth.	igapó
<i>Eperua bijuga</i> Mart. ex Benth.	igapó
<i>Eperua falcata</i> Aubl.	igapó
<i>Hydrochorea corymbosa</i> (Rich.) Barneby & J.W. Grimes	igapó
<i>Hydrochorea</i> sp.	igapó
<i>Hymenaea courbaril</i> L.	várzea
<i>Hymenaea oblongifolia</i> Huber	várzea
<i>Hymenolobium petraeum</i> Ducke	Igapó
<i>Inga alba</i> (Sw.) Willd.	Igapó
<i>Inga barbata</i> Benth.	igapó/várzea
<i>Inga brachystachys</i> Ducke	Igapó
<i>Inga cayennensis</i> Sagot ex Benth.	Igapó
<i>Inga cinnamomea</i> Spruce ex Benth.	igapó/várzea
<i>Inga dumosa</i> Benth.	várzea
<i>Inga edulis</i> Mart.	igapó/várzea
<i>Inga ferruginea</i> Guill. & Perr.	Igapó
<i>Inga grandiflora</i> Ducke	Igapó
<i>Inga marginata</i> Willd.	Igapó
<i>Inga paraensis</i> Ducke	Igapó
<i>Inga rubiginosa</i> (Rich.) DC.	Igapó
<i>Inga</i> sp.	Igapó
<i>Inga</i> sp1.	várzea
<i>Inga splendens</i> Willd.	Igapó
<i>Inga stipularis</i> DC.	Igapó
<i>Inga velutina</i> Willd.	várzea

<i>Macrolobium acaciifolium</i> (Benth.) Benth.	Igapó
<i>Macrolobium bifolium</i> (Aubl.) Pers.	Igapó
<i>Macrolobium latifolium</i> Vogel	Igapó
<i>Macrolobium pendulum</i> Willd. ex Vogel	Igapó
<i>Martiodendron</i> sp.	Igapó
<i>Mora paraensis</i> (Ducke) Ducke	igapó/várzea
<i>Ormosia coutinhoi</i> Ducke	várzea
<i>Ormosia flava</i> (Ducke) Rudd	Igapó
<i>Ormosia grossa</i> Rudd	Igapó
<i>Parkia discolor</i> Spruce ex Benth.	várzea
<i>Parkia pendula</i> (Willd.) Benth. ex Walp.	Igapó
<i>Parkia ulei</i> (Harms) Kuhlm.	Igapó
<i>Pentaclethra macroloba</i> (Willd.) Kuntze	igapó/várzea
<i>Pithecellobium inaequale</i> (Humb. & Bonpl. ex Willd.) Benth.	várzea
<i>Pithecellobium latifolium</i> (L.) Benth.	Igapó
<i>Pithecellobium</i> sp.	Igapó
<i>Platymiscium filipes</i> Benth.	várzea
<i>Pterocarpus amazonicus</i> Huber	várzea
<i>Pterocarpus amazonum</i> (Mart. ex Benth.) Amshoff	Igapó
<i>Pterocarpus officinalis</i> Jacq.	igapó/várzea
<i>Sclerolobium paniculatum</i> Vogel	Igapó
<i>Stryphnodendron pulcherrimum</i> (Willd.) Hochr.	Igapó
<i>Swartzia acuminata</i> Willd. ex Vogel	várzea
<i>Swartzia arborescens</i> (Aubl.) Pittier	Igapó
<i>Swartzia brachyrachis</i> Harms	Igapó
<i>Swartzia cardiosperma</i> Spruce ex Benth.	várzea
<i>Swartzia laurifolia</i> Benth.	Igapó
<i>Swartzia panacoco</i> (Aubl.) R.S. Cowan	Igapó
<i>Swartzia polyphylla</i> DC.	Igapó
<i>Swartzia racemosa</i> Benth.	Igapó
<i>Sweetia fruticosa</i> Spreng.	várzea
<i>Tachigali myrmecophila</i> (Ducke) Ducke	igapó/várzea
<i>Tachigali paniculata</i> Aubl.	Igapó
<i>Taralea oppositifolia</i> Aubl.	Igapó
<i>Vatairea guianensis</i> Aubl.	igapó/várzea
<i>Vataireopsis speciosa</i> Ducke	igapó/várzea
<i>Zollernia paraensis</i> Huber	Igapó
<i>Zygia cauliflora</i> (Willd.) Killip	Igapó
<i>Zygia juruana</i> (Harms) L. Rico	várzea
<i>Zygia latifolia</i> (L.) Fawc. & Rendle	Igapó

Goupiaceae

<i>Goupia glabra</i> Aubl.	Igapó
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Hernandiaceae

<i>Hernandia guianensis</i> Aubl.	várzea
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Humiriaceae

Sacoglottis guianensis Benth. igapó/várzea

Hypericaceae

Vismia cayennensis (Jacq.) Pers. Igapó

Lauraceae

Aniba guianensis Aubl. várzea
Aniba puchury-minor (Mart.) Mez várzea
Endlicheria sp. Igapó
Licaria cannella (Meisn.) Kosterm. igapó/várzea
Licaria mahuba (A. Samp.) Kosterm. várzea
Mezilaurus itauba (Meisn.) Taub. ex Mez Igapó
Ocotea canaliculata (Rich.) Mez Igapó
Ocotea caudata (Nees) Mez Igapó
Ocotea fragrantissima Ducke Igapó
Ocotea glomerata (Nees) Mez Igapó
Ocotea guianensis Aubl. Igapó
Ocotea paniculata Nees Igapó
Ocotea rubra Mez Igapó
Ocotea sp. igapó/várzea

Lecythidaceae

Lecythis jarana (Huber ex Ducke) A.C. Sm. Igapó
Lecythis pisonis Cambess. Igapó
Allantoma lineata (Mart. & O. Berg) Miers várzea
Bertholletia excelsa Bonpl. Igapó
Couratari guianensis Aubl. Igapó
Couratari pulchra Sandwith Igapó
Eschweilera amazonica R. Knuth Igapó
Eschweilera atropetiolata S.A. Mori Igapó
Eschweilera coriacea (DC.) S.A. Mori Igapó
Eschweilera pedicellata (Rich.) S.A. Mori Igapó
Gustavia augusta L. igapó/várzea
Gustavia hexapetala (Aubl.) Sm. igapó/várzea
Lecythis idatimon Aubl. Igapó
Lecythis lurida (Miers) S.A. Mori Igapó
Lecythis sp. Igapó

Malpighiaceae

Byrsonima densa (Poir.) DC. Igapó
Byrsonima sp. Igapó

Malvaceae

Apeiba burchellii Sprague várzea

<i>Apeiba tibourbou</i> Aubl.	Igapó
<i>Bombax munguba</i> Mart.	várzea
<i>Bombax paraensis</i> Ducke	Igapó
<i>Ceiba pentandra</i> (L.) Gaertn.	igapó/várzea
<i>Eriotheca longipedicellata</i> (Ducke) A. Robyns	Igapó
<i>Guazuma ulmifolia</i> Lam.	Igapó
<i>Luehea speciosa</i> Willd.	Igapó
<i>Lueheopsis duckeana</i> Burret	Igapó
<i>Matisia ochrocalyx</i> K. Schum.	várzea
<i>Matisia paraensis</i> Huber	várzea
<i>Mollia lepidoptera</i> Mart.	Igapó
<i>Mollia lepidota</i> Spruce ex Benth.	Igapó
<i>Mollia</i> sp.	Igapó
<i>Pachira aquatica</i> Aubl.	várzea
<i>Quararibea guianensis</i> Aubl.	igapó/várzea
<i>Sterculia pruriens</i> (Aubl.) K. Schum.	Igapó
<i>Sterculia speciosa</i> K. Schum.	igapó/várzea
<i>Theobroma cacao</i> L.	várzea
<i>Theobroma subincanum</i> Mart.	Igapó
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Melastomataceae	
<i>Miconia ceramicarpa</i> (DC.) Cogn.	várzea
<i>Miconia</i> sp.	Igapó
<i>Mouriri acutiflora</i> Naudin	igapó/várzea
<i>Mouriri apiranga</i> Spruce ex Triana	Igapó
<i>Mouriri brachyanthera</i> Ducke	Igapó
<i>Mouriri princeps</i> Naudin	várzea
<i>Mouriri</i> sp.	Igapó
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Meliaceae	
<i>Carapa guianensis</i> Aubl.	igapó/várzea
<i>Cedrela odorata</i> L.	várzea
<i>Guarea guidonia</i> (L.) Sleumer	Igapó
<i>Guarea septentrionalis</i> C.DC	Igapó
<i>Guarea</i> sp.	Igapó
<i>Trichilia micrantha</i> Benth.	Igapó
<i>Trichilia paraensis</i> C. DC.	várzea
<i>Trichilia quadrijuga</i> Kunth.	Igapó
<i>Trichilia surinamensis</i> (Miq.) C. DC.	várzea
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Moraceae	
<i>Brosimum guianense</i> (Aubl.) Huber	Igapó
<i>Brosimum lactescens</i> (S. Moore) C.C. Berg	Igapó
<i>Clarisia racemosa</i> Ruiz & Pav.	Igapó
<i>Ficus maxima</i> Mill.	igapó/várzea
<i>Ficus nymphaeifolia</i> Mill.	Igapó

<i>Ficus pertusa</i> L. f.	igapó/várzea
<i>Ficus</i> sp.	Igapó
<i>Maquira calophylla</i> (Poepp. & Endl.) C.C. Berg	Igapó
<i>Maquira coriacea</i> (H. Karst.) C.C. Berg	Igapó
<i>Maquira guianensis</i> Aubl.	Igapó
<i>Olmedia caloneura</i> Huber	várzea
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Myristicaceae	
<i>Virola calophylla</i> (Spruce) Warb.	Igapó
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Myrtaceae	
<i>Calyptranthes speciosa</i> Sagot.	várzea
<i>Campomanesia grandiflora</i> (Aubl.) Sagot.	Igapó
<i>Campomanesia</i> sp.	Igapó
<i>Eugenia brachypoda</i> DC.	Igapó
<i>Eugenia brownsbergii</i> Amshoff	várzea
<i>Eugenia egensis</i> DC.	Igapó
<i>Eugenia flavescens</i> DC.	Igapó
<i>Eugenia omissa</i> McVaugh	Igapó
<i>Eugenia patrisii</i> Vahl	Igapó
<i>Eugenia rufidula</i> Lundell	Igapó
<i>Eugenia</i> sp.	Igapó
<i>Eugenia tapacumensis</i> O. Berg	Igapó
<i>Myrcia fallax</i> (Rich.) DC.	Igapó
<i>Myrcia paivae</i> O. Berg	Igapó
<i>Myrciaria floribunda</i> (H. West ex Willd.) O. Berg	igapó/várzea
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Nyctaginaceae	
<i>Guapira oppositifolia</i> (Vell.) Reitz	Igapó
<i>Guapira venosa</i> (Choisy) Lundell	Igapó
<i>Pisonia tomentosa</i> Casar.	Igapó
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Olacaceae	
<i>Chanochiton kappleri</i> (Sagot ex Engl.) Ducke	Igapó
<i>Dulacia candida</i> (Poepp.) Kuntze	Igapó
<i>Heisteria acuminata</i> (Bonpl.) Engl.	Igapó
<i>Minquartia guianensis</i> Aubl.	igapó/várzea
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Peraceae	
<i>Pogonophora schomburgkiana</i> Miers ex Benth.	Igapó
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Polygonaceae	
<i>Coccoloba</i> sp.	Igapó
<i>Triplaris surinamensis</i> Cham.	Igapó
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Quinaceae	

<i>Quiina amazonica</i> A.C. Sm.	Igapó
Rubiaceae	
<i>Calycophyllum spruceanum</i> (Benth.) Hook. f. ex K. Schum.	igapó/várzea
<i>Amaioua guianensis</i> Aubl.	Igapó
<i>Capirona huberiana</i> Ducke	Igapó
<i>Genipa americana</i> L.	Igapó
<i>Genipa spruceana</i> Steyererm.	Igapó
Rutaceae	
<i>Metrodorea flavida</i> K. Krause	igapó/várzea
<i>Zanthoxylum rhoifolium</i> Lam.	igapó/várzea
<i>Zanthoxylum riedelianum</i> Engl.	Igapó
<i>Zanthoxylum sp.</i>	Igapó
Salicaceae	
<i>Banara guianensis</i> Aubl.	igapó/várzea
<i>Casearia pitumba</i> Sleumer	Igapó
<i>Laetia procera</i> (Poepp.) Eichler	Igapó
Sapindaceae	
<i>Allophylus sp.</i>	Igapó
<i>Cupania paniculata</i> Cambess	Igapó
<i>Cupania scrobiculata</i> Rich.	Igapó
<i>Pseudima frutescens</i> (Aubl.) Radlk.	Igapó
<i>Talisia retusa</i> R.S. Cowan	Igapó
<i>Talisia veraluciana</i> Guarim	Igapó
<i>Toulicia guianensis</i> Aubl.	Igapó
Sapotaceae	
<i>Toulicia guianensis</i> Aubl.	Igapó
<i>Chrysophyllum excelsum</i> Huber	várzea
<i>Chrysophyllum sp.</i>	Igapó
<i>Chrysophyllum sparsiflorum</i> Klotzsch ex Miq.	Igapó
<i>Ecclinusa guianensis</i> Eyma	Igapó
<i>Manilkara huberi</i> (Ducke) A. Chev.	igapó/várzea
<i>Micropholis guyanensis</i> (A. DC.) Pierre	Igapó
<i>Neoxythece sp.</i>	Igapó
<i>Pouteria biloculares</i> (Winkler) Baehni.	várzea
<i>Pouteria caimito</i> (Ruiz & Pav.) Radlk.	Igapó
<i>Pouteria filipes</i> Eyma	Igapó
<i>Pouteria guianensis</i> Aubl.	Igapó
<i>Pouteria jariensis</i> Pires & T.D. Penn.	Igapó
<i>Pouteria oppositifolia</i> (Ducke) Baehni	Igapó
<i>Pouteria pachycarpa</i> Pires	várzea
<i>Pouteria sagotiana</i> (Baill.) Eyma	várzea

<i>Pouteria torta</i> (Mart.) Radlk.	Igapó
<i>Sarcaulus brasiliensis</i> (A. DC.) Eyma	igapó/várzea
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Simaroubaceae	
<i>Simarouba amara</i> Aubl.	Igapó
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Urticaceae	
<i>Cecropia latiloba</i> Miq.	Igapó
<i>Cecropia obtusa</i> Trécul	Igapó
<i>Cecropia palmata</i> Willd.	igapó/várzea
<i>Cecropia peltata</i> L.	Igapó
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Violaceae	
<i>Rinorea guianensis</i> Aubl.	igapó/várzea
<i>Rinorea passoura</i> Kuntze	Igapó
<i>Rinorea racemosa</i> (Mart.) Kuntze	Igapó
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Vochysiaceae	
<i>Qualea multiflora</i> Mart.	Igapó
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