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

ESTRUTURA FUNCIONAL DAS COMUNIDADES ARBÓREAS DE FLORESTAS ALAGÁVEIS NA AMAZÔNIA CENTRAL

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Manaus, Amazonas
Março, 2019

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ESTRUTURA FUNCIONAL DAS COMUNIDADES ARBÓREAS DE FLORESTAS ALAGÁVEIS NA AMAZÔNIA CENTRAL

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

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

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Sinopse

Nesta tese investigamos como os filtros ambientais alagamento sazonal e propriedades do solo determinam a estrutura funcional de florestas alagáveis amazônicas. Foram usados dados de comunidades para comparar a composição funcional entre florestas de várzea e igapó, e entender as respostas funcionais da vegetação em relação a gradientes hídricos e edáficos, dados de pares congenéricos para entender a influência do habitat na divergência de atributos em espécies filogeneticamente próximas, e dados de espécies para entender a relação da densidade da madeira entre diferentes partes da planta.

Palavras-chave: 1. Atributos funcionais. 2. Gradientes ambientais. 3. Solos. 4. Alagamento sazonal. 5. Florestas tropicais.

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“LOKAH SAMASTAH
SUKHINO BHAVANTHU”

que todos os seres
sejam felizes
e livres

RESUMO

Entender a estrutura das comunidades vegetais é essencial para fazer predições ecológicas frente às mudanças ambientais. Como as florestas alagáveis tropicais são um alvo crescente dos impactos antrópicos, elas necessitam de mais estudos para fundamentar estratégias eficazes para sua conservação. Nesta tese investigamos a estrutura funcional de comunidades arbóreas de florestas alagáveis de várzea e igapó de águas pretas da Amazônia Central, em relação ao alagamento sazonal e as propriedades do solo. As propriedades do solo foram bons preditores da variação dos atributos funcionais, diferenciando as estratégias ecológicas entre as comunidades de várzea e igapó. As comunidades de várzea se caracterizaram por possuírem valores de atributos relacionados ao melhor uso e captação dos recursos e um crescimento rápido, enquanto que as comunidades do igapó se caracterizaram por possuírem valores de atributos para melhor conservação dos recursos, desenvolvimento de tecidos mais resistentes e, consequentemente, crescimento mais lento. Surpreendentemente, o nível e a duração do alagamento tiveram pouca influência na variação dos atributos, mesmo entre as comunidades com o mesmo tipo de solo. Nós também encontramos que a diferenciação dos atributos funcionais entre várzea e igapó ocorre mesmo entre espécies filogeneticamente próximas, com o mesmo padrão de diferenciação entre as estratégias aquisição versus conservação de recursos, indicando a ocorrência do processo de especialização do habitat. Nossos resultados também mostraram que o atributo densidade da madeira difere entre o caule e o ramo, tanto nas várzeas quanto nos igapós, em comparação com a terra firme. Isto sugere a existência de estratégias ecológicas relacionadas à características abióticas específicas atuando sobre a comunidade arbórea dos ecossistemas alagáveis. Podemos concluir com nossos resultados, que as propriedades do solo em escala local são fatores determinantes na estruturação funcional das comunidades de árvores das florestas alagáveis, e são responsáveis pela diferenciação na composição de espécies e nas estratégias ecológicas entre estas comunidades, contribuindo para o aumento da diversidade de espécies em florestas alagáveis na Amazônia. Nós recomendamos que as estratégias para conservação das florestas alagáveis devam ser elaboradas para cada tipo de floresta, considerando suas diferenças funcionais.

FUNCTIONAL STRUCTURE OF TREE COMMUNITIES OF FLOODPLAIN FORESTS IN CENTRAL AMAZONIA

ABSTRACT

Understanding the structure of plant communities is essential to make ecological predictions about environmental changes. As tropical floodplains are a growing target for anthropogenic impacts, they require further studies to support effective conservation strategies. In this thesis, we investigated the functional structure of tree communities of *várzea* and *igapó* floodplain forests in Central Amazonia, in relation to seasonal flooding and soil properties. Soil properties were good predictors of functional traits variation, differentiating ecological strategies between várzea and igapó communities. Várzea communities were characterized by trait values related to a better use and acquisition of resources and a fast growth, while igapó communities were characterized by trait values related to a better conservation of resources, development of persistent tissues and, consequently, slow growth. Surprisingly, flooding level and duration influenced little traits variation, even within communities with the same soil type. We also found that traits differentiation between várzea and igapó occurred even between species phylogenetically related with the same pattern of differentiation among the strategies of acquisition versus conservation of resources, indicating the process of habitat specialization. Our results also showed that the attribute wood density differs between the stem and the branch, both in the várzea and igapós, compared to the terra firme. This suggests the existence of ecological strategies related to specific abiotic conditions acting on the arboreal community of floodplain ecosystems. Based on our results, we conclude that soil properties in local scale are determinant factors for functional structure in tree communities of floodplain forests, and are responsible for the differentiation in species composition and ecological strategies between these communities, contributing to the increase in species diversity in Amazonian floodplain forests. We recommend that the development of ecological strategies for floodplain forests conservation should be prepared for each forest type, considerating their different functions.

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INTRODUÇÃO GERAL

As florestas tropicais, como a Amazônia, são ambientes altamente biodiversos que vivenciam uma alta pressão antrópica, que cresce tanto em escala quanto em intensidade (ASSESSMENT, 2005; MALHI et al., 2008; NOBRE et al., 2016). A alteração na cobertura vegetal, somada a outros fatores, tais como a poluição e o aquecimento global, têm grandes consequências para os organismos e para os ecossistemas (ASSESSMENT, 2005; FOLEY et al., 2005). Uma das principais consequências das mudanças ambientais é a perda de espécies, principalmente pelas alterações ou perda dos habitats naturais (PIMM; RAVEN, 2000). Uma vez que a biodiversidade é considerada uma das forças principais que influencia a dinâmica dos ecossistemas, a perda de espécies pode ser um ponto crucial na manutenção do equilíbrio dos ambientes naturais (HOOPER et al., 2012). Nesse sentido, entender como as espécies respondem às características abióticas do ambiente e como isso determina a formação das comunidades biológicas é a base para predizer quais serão as respostas das espécies e das comunidades frente a mudanças ambientais e, assim, desenvolver planos para a conservação dos ecossistemas. Para lidar com este cenário, é necessário o desenvolvimento de conhecimento científico acerca da dinâmica das comunidades biológicas, e de sua interação com o meio abiótico.

Na Amazônia, as florestas alagáveis (glossário) cobrem grande parte da bacia amazônica (JUNK et al., 2011; MELACK; HESS, 2010). As florestas alagáveis sujeitas a um pulso de inundação monomodal e previsível, permanacem alagadas durante meses ao longo do ano, gerando uma complexa rede de relações entre o ambiente aquático e a vegetação terrestre adjacente. Apesar de sua grande extensão e importância, ainda existem lacunas acerca de como a vegetação arbórea destas florestas irá responder frente à mudanças ambientais, tais como eventos extremos de secas e cheias, ocasionados pela alteração no ciclo hidrológico em resposta ao avanço do desmatamento e das mudanças climáticas (MARENGO; ESPINOZA, 2016).

Os principais efeitos do alagamento sazonal para as florestas são a falta de oxigênio disponível no nível de raiz das plantas, e a imposição de limitações para o seu estabelecimento, crescimento e reprodução durante a fase alagada (PAROLIN et al., 2004). Para lidar com estas condições, as árvores que habitam estes ecossistemas possuem um conjunto de características (atributos) e estratégias ecológicas. Por exemplo, a respiração anaeróbica, a produção de raízes adventícias e lenticelas hipertrofiadas e o desenvolvimento de aerênquima, auxiliam na obtenção de oxigênio (LOBO; JOLY, 1998; PAROLIN, 2012). As folhas das árvores geralmente apresentam características consideradas xeromórficas, que são importantes para lidar com o estresse hídrico durante a fase terrestre, como a presença de parede celular e cutícula espessa (PAROLIN et al., 2004). As espécies também sincronizam a produção de folhas e sementes com o alagamento. A deciduosidade das folhas durante a cheia permite a redução do gasto energético, por meio de um estado de dormência ou de um crescimento mais lento durante a fase alagada (PAROLIN et al., 2002; SCHÖNGART et al., 2002). Já os frutos amadurecem durante a cheia, e as sementes são liberadas e germinam quando o nível da água desce e as condições se tornam favoráveis, neste caso, as sementes apresentam viabilidade mais longa, podendo permanecer submersas ou flutuando na água até a fase seca (LOPEZ, 2001; PAROLIN et al., 2004). Outras espécies germinam na água, reduzindo, assim, o tempo de crescimento durante a fase terrestre (FERREIRA et al., 2010). Além da dispersão pela água, as sementes também são dispersas pelo vento e por várias espécies de peixes (WEISS; ZUANON; PIEDADE, 2016).

Os principais tipos de florestas alagáveis são denominados de várzea e igapó, e estão relacionados às características hidrológicas e químicas das águas dos rios que as inundam (SIOLI, 1984). As diferenças nas características das águas dos rios interferem na quantidade de nutrientes disponíveis no solo e, consequentemente, na composição de espécies e na estrutura da vegetação, diferenciando estes dois tipos de floresta (JUNK et al., 2011; PRANCE, 1979). As florestas de várzea são aquelas inundadas por águas brancas (barrentas), como o rio Solimões, que carregam sedimentos dos períodos Terciário e Quaternário, de origem Andina e Pré-Andina (JUNK et al., 2011; SIOLI, 1984). Estes sedimentos são ricos em minerais argilosos que possuem alta capacidade de troca iônica, o que torna os solos férteis, quando comparados aos solos dos igapós (KARIN FURCH, 1997). A média de inundação na várzea é de 7,5 metros de profundidade, o que corresponde a aproximadamente 230 dias de alagamento por ano. Outra característica importante da paisagem de várzea é o alto dinamismo e migração dos canais do rio, que leva à erosão e sedimentação das áreas, resultando em uma dinâmica sucessional rápida. Esse dinamismo da várzea leva à formação de pequenos mosaicos de paisagem em escala reduzida, resultando em habitats variados com diferente elevação e substratos, que podem ser distinguidos pela diferença na composição florística e estrutura da vegetação (JUNK et al., 2011; WITTMANN; JUNK; PIEDADE, 2004). Isto somado à alta fertilidade do solo contribui para uma alta diversidade de espécies. As florestas de várzea são as florestas alagáveis mais ricas em espécies de árvores do mundo (WITTMANN et al., 2006); muitas das espécies são compartilhadas com as espécies de florestas de terra-firme, mas há um alto endemismo de espécies que são adaptadas ao alagamento periódico (WITTMANN et al., 2013).

As florestas de igapó são aquelas inundadas por rios de águas pretas ou claras (neste estudo, consideramos apenas igapós de águas pretas), como o rio Negro, que carregam sedimentos do período Terciário, com origem no Escudo da Guiana e do Escudo Central Brasileiro (SIOLI, 1984). Estas águas são pobres em sedimentos em suspensão, que carregam uma menor quantidade de nutrientes e uma maior concentração de ácidos húlmicos e fúlvicos, e os solos das planícies alagáveis associadas são caracterizados por baixa fertilidade e elevada acidez (JUNK et al., 2015; KARIN FURCH, 1997). Em comparação com a várzea, as planícies de inundação dos igapós são mais estáveis, pois possuem menor quantidade de sedimentos em suspensão, leitos arenosos e menor velocidade de corrente (JUNK et al., 2015). A inundação no igapó pode chegar a 9,0-9,5 metros, o que corresponde a 280-290 dias de alagamento por ano. No geral, os igapós são menos ricos em espécies arbóreas comparados às várzeas, e compartilham mais espécies com as campinaranas e savanas amazônicas (JUNK et al., 2011, 2015).

As florestas alagáveis apresentam, portanto, dois principais filtros ambientais que influenciam as comunidades vegetais: o alagamento sazonal e as características edáficas. Os filtros ambientais são um dos principais processos envolvidos no desenvolvimento das assembleias de comunidades vegetais, pois selecionam as espécies e indivíduos que possuem características (atributos funcionais; ver glossário) que permitem sua sobrevivência, crescimento e reprodução em condições abióticas específicas (KEDDY, 1992). Características ambientais como nutrientes do solo, topografia, disponibilidade de água, incidência de luz, entre outros, são reconhecidos como determinantes para a ocorrência, distribuição e coexistência de muitas espécies de plantas (SILVERTOWN, 2004), e atuam nos diferentes estágios de vida dos vegetais, desde os processos de germinação das sementes, estabelecimento e desenvolvimento dos indivíduos jovens, até a persistência e a reprodução durante a fase adulta.

Somado aos filtros ambientais abióticos, as interações bióticas também possuem um papel fundamental no desenvolvimento das assembleias de comunidades vegetais. Quando os recursos se tornam limitantes, a competição entre os indivíduos e espécies aumenta. Outros fatores como a presença de patógenos e/ou herbívoros também aumentam os processos competitivos em uma comunidade (GRIME, 1974; TILMAN, 1990). Além de capacidade de captação de recursos em determinadas características ambientais, a presença de estratégias complementares em relação às outras espécies também colabora para o sucesso das espécies. A hipótese do ‘Limite de Similaridade’ (MACARTHUR; LEVINS, 1967) prediz que diferenças nas características e estratégias de captação de recursos e defesa podem auxiliar na captura de recursos ainda não utilizados e diminuir os impactos ocasionados por herbívoros e patógenos.

Ambos os processos, filtro ambiental e limite de similaridade, contribuem para o desenvolvimento das comunidades vegetais ao longo de gradientes ambientais. Quando o filtro ambiental é o processo predominante na determinação do sucesso das espécies, espera-se que poucos atributos funcionais similares e que melhor respondem ao filtro ambiental sejam dominantes na comunidade. Por outro lado, se o limite de similaridade é o processo determinante no sucesso das espécies, espera-se que atributos funcionais complementares (divergência de atributos) sejam dominantes, permitindo a coexistência das espécies (GRIME, 2006).

As barreiras geográficas e os limites de dispersão sempre foram descritos como processos chave na formação das comunidades vegetais, pois são os primeiros fatores que determinam o *pool* de espécies regional. Muitos autores têm demonstrado, entretanto, que as características do ambiente possuem papel fundamental para a manutenção da alta diversidade de espécies presente em florestas tropicais (CONDIT et al., 2012). Devido à alta heterogeneidade ambiental das florestas tropicais, mudanças abióticas em escala local levam a um processo de especialização das espécies em função de atributos que favorecem cada microhabitat, o que aumenta a coexistência das espécies e, consequentemente, aumenta a diversidade (FINE, 2004; SVENNING, 1999; VALENCIA et al., 2004). Este processo tem sido importante para entender a estruturação de comunidades vegetais biodiversas como a Amazônia, e ressalta a importância da atuação dos filtros ambientais nos atributos funcionais das espécies e comunidades vegetais.

Os atributos funcionais são elementos chave para entender a relação das espécies com o meio abiótico, tanto pela resposta das espécies a determinadas condições ambientais, como pela sua influência no funcionamento do ecossistema (DÍAZ; CABIDO, 2001). A abordagem funcional é uma ferramenta que permite ampliar o conhecimento do nível de espécie para o nível de comunidade, podendo contribuir para o desenvolvimento de predições ecológicas (MCGILL et al., 2006).

Atributos funcionais de plantas são características mensuradas ao nível do indivíduo, e que indicam o uso e a aquisição de recursos pelas plantas. Este balanço planta-recurso determina tanto o sucesso adaptativo das espécies em determinado ambiente, como também a sua contribuição para os processos ecossistêmicos, como os fluxos de matéria e energia (MCGILL et al., 2006; REICH et al., 2003). Os atributos funcionais que determinam o sucesso das espécies em condições abióticas específicas são denominados de *atributos resposta*. Já os atributos que determinam como as espécies contribuem para os processos ecossistêmicos são denominados de *atributos efeito* (VIOLLE et al., 2007).

Os atributos resposta refletem como os organismos respondem à determinadas condições ambientais e, por esta razão, são centrais para a compreensão da performance das plantas em relação a filtros ambientais (DIAZ et al., 1997). A composição funcional de uma comunidade, dada pelos atributos dominantes, indica o padrão geral dessa comunidade, pois reflete as principais respostas dos indivíduos aos filtros ambientais. A composição funcional também é importante para a manutenção dos processos ecossistêmicos, pois pode indicar quais os principais atributos que estão relacionados à maioria dos fluxos de energia dentro do ecossistema (Teoria da Razão de Massa; GRIME, 1998). Já a diversidade de atributos e a variação nos valores do atributos podem indicar a variabilidade de estratégias ecológicas de uma comunidade. Uma maior diversidade significa um maior número de respostas possíveis dos indivíduos frente às mudanças ambientais e maior eficiência no uso dos recursos (Teoria da complementariedade de nicho; TILMAN, 1999), e pode indicar o potencial de adaptação e resiliência das comunidades frente às mudanças ambientais (SAKSCHEWSKI et al., 2016; VAN DER SANDE et al., 2017).

As plantas investem de forma diferente em seus tecidos dependendo das condições do ambiente que habitam. A combinação de diferentes atributos das espécies refeletem suas estratégias ecológicas, tanto para a captação de recursos como para a defesa contra herbivoria e doenças. A troca entre estratégias (*trade-off*) em relação a gradientes de recursos (aquisição de recursos versus conservação de recursos) é reconhecida em escala global, para diferentes regiões, tipos de vegetação e espécies (DÍAZ et al., 2004; REICH, 2014; WRIGHT et al., 2004). O *trade-off* aquisição-conservação de recursos aponta para o extremo de um contínuo de estratégia das plantas, partindo de um extremo onde as espécies investem em tecidos com baixo custo de produção, eficiente aquisição de recursos e crescimento rápido, para um extremo onde as espécies investem em tecidos persistentes, com eficiente conservação de recursos e crescimento lento (CHAVE et al., 2009; WRIGHT et al., 2004). Ao longo deste contínuo há um gradiente de variação dos atributos, e a posição das espécies é indicada pelos seus atributos funcionais. Por exemplo, o '*world leaf* *economic spectrum'* (WRIGHT et al., 2004) descreve um contínuo de estratégia que varia de um extremo de espécies com produção de folhas de baixo custo, com altas taxas fotossintéticas e que maximizam o uso e captura de recursos, para outro extremo de espécies cujas folhas têm um alto custo de produção, toleram stress, são mais resistentes à danos físicos, e investem na conservação de recursos. Além dos atributos foliares, este *trade-off* também foi descrito para outras partes das plantas, como raízes e troncos (FRESCHET et al., 2010; REICH, 2014).

A composição funcional e a diversidade funcional de uma comunidade indicam os padrões gerais das espécies em relação às características ambientais e suas principais estratégias ecológicas, ao nível de toda da planta, e podem auxiliar na compreensão das respostas das espécies em relação às mudanças ambientais. Esta visão geral dos padrões ecológicos pode ser uma ferramenta chave para a elaboração de predições ecológicas mais robustas em relação a futuros cenários ambientais. Nesta tese, nós buscamos entender qual o papel de filtros ambientais na estrutura funcional das comunidades de árvores de florestas alagáveis amazônicas. Para isto, nós amostramos doze atributos funcionais em quarenta parcelas botânicas, distribuídas em florestas alagáveis de águas brancas (várzeas) e pretas (igapós). **No primeiro capítulo desta tese** nós comparamos a composição funcional das comunidades de árvores de várzea e igapó. Nós avaliamos a influência dos filtros ambientais alagamento periódico (altura e duração média da inundação) e das características edáficas na composição funcional (valores médios) e na variabilidade dos atributos (desvio padrão) destas comunidades, e como os atributos funcionais variam em relação à estes gradientes ambientais. Nós discutimos quais as principais estratégias ecológicas refletidas pela estrutura funcional de cada comunidade e a relação dos filtros ambientais nestas estratégias.

Como as barreiras geográficas são importantes fatores que determinam a composição de espécies das comunidades vegetais que, por sua vez, influenciamos atributos funcionais, **no segundo capítulo** nós buscamos entender melhor a importância do ambiente na variação dos atributos comparando espécies filogeneticamente próximas entre habitats com diferentes tipos de solo. Nós selecionamos sete pares congenéricos e doze famílias botâncias e avaliamos como onze atributos diferem entre as tipologias de várzea e igapó. Nós discutimos o papel do ambiente (habitat) na diferenciação dos atributos funcionais em espécies com uma história evolutiva comum. No **terceiro capítulo** nós selecionamos o atributo densidade da madeira, por ser uma característica integradora de diversas propriedades da madeira, e avaliamos sua variação entre diferentes partes da planta. Nós relacionamos a densidade da madeira do ramo e da madeira do caule em 96 espécies de árvores de florestas de várzea e igapó, e em 28 espécies de terra-firme, e avaliamos as possíveis relações ecológicas por trás desta relação.

OBJETIVOS

O principal objetivo desta tese foi revelar a importância de filtros hídricos e edáficos para o entendimento dos padrões funcionais de árvores de florestas alagáveis da Amazônia Central.

Capítulo 1. Avaliar como o alagamento sazonal e as propriedade do solo influenciam a composição funcional e a variabilidade dos atributos funcionais das comunidades arbóreas de várzea e igapó de águas pretas.

Capítulo 2. Avaliar se os atributos funcionais de espécies congenéricas diferem entre tipologias de florestas alagáveis com diferentes tipos de solo.

Capítulo 3. Avaliar como a densidade da madeira varia do caule para o ramo e sua relação com estratégias ecológicas de florestas alagáveis e de terra-firme.

ARTIGO 1

Flooding is not the major driver of functional composition of Amazonian floodplain forests

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Abstract

Questions: Amazonian floodplain forests are species-rich ecosystems with variable soil fertility, thought to be shaped by harsh anoxic environmental conditions that impose strong filters on species and trait composition of tree communities. How do functional trait composition differ between white- and black-water forests? How do environmental factors (flooding and soil resource availability) affect functional composition and functional variability?

Location: Central Amazonia floodplains, Brazil.

Methods: We evaluated the functional composition of tropical white-water and black-water floodplain forests. We measured mean and standard deviation (SD) tree functional traits related to flooding survival and nutrient uptake, and environmental factors (flooding and soil resource availability). We used principal component analysis and analysis of variance to evaluate how traits mean differ between forest types. We used redundancy analysis to evaluate how flooding and resource availability affect mean and SD functional traits composition and multiple linear regression analysis to understand how traits vary individually along environment gradients of flooding and resources.

Results: We found that white-water forests have higher values of traits related to resource acquisition while black-water forests have higher values of traits related to resource conservation, revealing a distinction between acquisitive and conservative strategies. Surprisingly, flooding do not have a strong effect on individual traits variation. And, functional trait composition was more related to soil resource availability, especially total exchangeable bases, indicating trait convergence linked to soil properties in these Amazonian flooded forests.

Conclusions: Flooding seem not to be the main driver of functional traits variability in floodplain trees, and we suggest that soil properties should be more important to explain differences in traits between floodplain communities.

Keywords: Central Amazonia, flooded forests, environmental filtering, plant traits, tree communities, trait-convergence, trait-divergence, plant strategies.

Introduction

Amazonian floodplain forests are the most species-rich floodplain forests worldwide (Wittmann et al. 2006) and are influenced by two major environmental filters: seasonal flooding and nutrient resource availability (Assis et al. 2014). Seasonal flooding, also called ‘floodpulse’(Junk et al. 1989) is thought to be the major force acting on species composition, resulting in a flood-adapted flora.

Differences in topography along the river margins give rise to gradients in flooding height and duration, resulting in a concomitant gradient in vegetation structure and composition (Wittmann et al. 2006; Assis & Wittmann 2011). Floodplain tree species possess a number of functional adaptations (i.e., traits) that enable them to survive, grow and reproduce in the anoxic conditions during flooding, instability caused by water dynamics, and drought stress after flooding (Junk et al. 1989; Junk 1997; Parolin & Wittmann 2010). Differences in nutrient resource availability and sediment load in floodplain forest lead to two contrasting floodplains: the white-water forests (‘várzea’) are flooded by nutrient-rich white-water rivers whereas the black-water forests (‘igapó’) are flooded by nutrient-poor black-water rivers (Prance, 1979; Sioli, 1984). Both forests have a very different structure and floristic composition sharing only 30% of the tree species (Wittmann et al., 2013). White-water forests are usually highly diverse compared to black-water, due to higher nutrient availability and higher sedimentation and erosion processes (Assis et al. 2015).

Plant functional traits reflect the ability of species to cope with abiotic and biotic conditions and can be used to understand how species are being selected by the environmental characteristics (Díaz & Cabido, 2001; Violle et al., 2007). When environmental filtering is strong, species within a community can have similar traits (trait-convergence) because they are functionally adapted to grow and survive under specific environmental conditions (Weiher & Keddy 1995; Díaz et al. 1999). By the other hand, competition, limiting resources and disturbance can lead to traits differentiation (trait-divergence), that allow species to compete and coexist, because they can occupy different niches and share resources (Macarthur & Levins 1967; Tilman et al. 1997; Grime 2006). The functional trait composition and diversity of communities is therefore an ideal way to assess the influence of environmental factors and environmental change on individuals and species (McGill et al. 2006; Santiago & Wright 2007; Lohbeck et al. 2015).

This study aims to compare the functional trait composition of white-water and black-water floodplain forests, and the effect of seasonal flooding and soil resource availability on community functional composition and variation. We addressed the following two questions and corresponding hypotheses: (1) How do white- and black-water forests differ in their functional trait composition? We predict that white-water forest communities have high values for traits related to resource acquisition and fast-growth (i.e., higher specific leaf area, leaf nutrient concentrations and plant size), because these forests grow on more fertile soils. Black-water forest communities have high values for traits related to resource conservation and slow-growth (i.e., lower specific leaf area and higher wood density), because these forests grow on nutrient-poor soils; (2) How do flooding and nutrient availability affect functional traits in seasonal flooded forests? We predict that flooding will be more correlated to trait variability (divergence) while soil fertility will be more related to trait mean values (convergence).

Methods

Study areas

Our study areas are located in the same sub-region of Central Amazonia (Fittkau et al. 1975) and are approximately 700 Km apart (Fig. 1). Central Amazonia has a typical hot and humid tropical climate. Mean annual temperature is 26.6 °C and mean annual precipitation is 2,100 mm/y, with a wet season occurring from December to April and a dry season from June to October. Amazonian soils are generally heavily leached, acidic and low in mineral nutrients, where Central Amazonia is especially nutrient poor due to higher cycles of erosion and sedimentation that occurred in this region (Quesada et al. 2011). This leads to a forest structure (i.e. biomass and stand level turnover rates) more similar compared to other sub-regions (Quesada et al. 2012), which makes the study areas comparable. The seasonal distribution of precipitation in the Amazon basin leads to large fluctuations of the water levels in streams and rivers. In large rivers this fluctuation is around 10 meters (Irion et al. 1997).

White-water forest. The white-water floodplain forests are located in the Jarauá river, inside the ‘Mamirauá Sustainable Development Reserve’ (2°51’S 64°55’W). The Mamirauá reserve has an area of 124,000 Km² of white-water floodplain forests, and is adjacent to the Japurá and Solimões river and the Auati-paranã channel (Wittmann et al., 2002).

Black-water forests. The black-water floodplain forests are located in the Abacate river, in the ‘Uatumã Sustainable Development Reserve” (1°48′S, 59°15′W) that has an area of 9,387,200Km² (Targhetta et al. 2015). The Abacate river is one of the main tributaries of Uatumã river (located at its left margin), draining the Abacate basin (Instituto de Conservação e Desenvolvimento Sustentável do Amazonas 2009).

Sampling design

In total, 40 research plots of 25x25 meters (625 m^2) were established; 20 plots in each forest type (white- and black-water), with 10 in each flooding level (low level of flooding and high level of flooding), classified according to water level in meters and flooding duration in days (Wittmann et al. 2002). The white-water forests had an average of high inundation of ~5.0 m and 246 days, and a low flooding of ~2.72 m and 180 days. The black-water forests had an average of high inundation of ~3.0 m and 100 days, and a low flooding of ~1.0 m and 50 days. The distance between plots varied from 100 to 1,500 m. To evaluate community level composition, we used an individual-based approach where we sampled every tree individual with ≥ 10 cm diameter at breast height (DBH) in the plots. In a total 1, 212 individuals were measured, 533 in white-water forest and 679 in black-water forest.

Functional trait measurements

For each tree, we measured 12 functional traits at the leaf, branch, trunk and whole-plant level that are important for nutrient acquisition and conservation, and for survival and growth in flooded conditions. The traits were Leaf area – LA (cm^2), Specific leaf area - SLA ($cm^2.g^{-1}$), Leaf dry matter content – LDMC ($g.g^{-1}$), Chlorophyll content – Chl (SPAD units), Leaf nitrogen concentration – LN ($g.kg^{-1}$), Leaf phosphorus concentration– LP ($g.kg$-^{1}), Leaf potassium concentration – LK ($g.kg^{-1}$), Leaf calcium concentration– LCa ($g.kg^{-1}$), Deciduousness (binary), Branch wood density – BWD ($g.cm^{-3}$), Lenticel density – LD (count of lenticel in 10 cm^{-2}), and height:diameter ratio– HD ($m.cm^{-1}$). Measurements were made following standardized trait protocols (Pérez-Harguindeguy et al., 2013; Table 1 and S1). Leaf traits were measured for 5 sun-exposed leaves per individual and BWD was measured for one branch per individual (bark included). Each species was classified as being (semi)deciduous (code 1) or evergreen (code 0) based on available data from literature (60% and 44% of species were classified in white-water and black-water forest, respectively (Lorenzi 1992; Lorenzi 1998; Lorenzi 2009; da Silva Marinho et al. 2010; Wittmann et al. 2010), and calculated the percentage of occurrence per plot. The measurements were conducted in the field and leaf nutrient analysis was done by Brazilian company of farming and research (Embrapa, Manaus, Brazil). To reduce sampling effort and damage to trees, we measured wood density at the branch level instead of the trunk level (Swenson & Enquist 2008).

Environmental gradients

We measured soil texture (sand, silt and clay), which is related to soil water retention capacity, and soil chemical variables (macro and micronutrients), which are related to resource availability, per plot. Three soil samples were collected from each plot (centre and two corners), at the first 10 cm from topsoil (excluding litter layer), and mixed to form a composite sample. Soil analyses were carried out by Brazilian company of farming and research (Embrapa Solos 1997, S1).

We measured flooding level (meters) and flooding duration (days per year) per plot. The mean flooding level was calculated from the height of the water marks left on the trunks of all tree individuals in the plots, a reference of the last flooding. For each plot the flooding duration was calculated by comparing flood levels (obtained in 2016) with water level data from hydrological stations (1982-2011 for várzea and 1974-2015 for igapó; Agência Nacional das Águas – ANA; Wittmann & Junk, 2003).

Data analyses

For both forest types we calculated the mean value and the standard deviation (SD) for each trait per plot to characterize community trait strategy and community trait variability, respectively (S2 and S3). All variables were tested for correlation using Pearson' coefficient of correlation.

To evaluate whether the two forest types differed in environmental conditions (soil resource availability and flooding) and in functional composition, we used Analyses of variance (ANOVA) with forest type as a factor. To describe the variation in functional composition across the plots we carried out a principal component analysis (PCA) using the 12 trait mean values. To evaluate variation in species composition we used a principal correspondence analysis (PCoA) using species occurrence in each plot, and Bray-Curtis distance because it is appropriate to evaluate species dissimilarity between two habitats (Legendre 1998). To evaluate whether species and functional composition are related we used a linear regression between the first axis of the PCA (dependent variable) and the first axis of the PCoA (independent variable).

We hypothesized that functional differences between and within forest types are mainly caused by environmental filters. We first selected the eight most ecologically relevant and least correlated environmental variables based on a PCA (average pair wise correlation of 0.56). These included soil physical variables (sand concentration), soil chemical variables (organic matter, nitrogen, total phosphorus, aluminum and total exchangeable bases) and flooding (level and duration). To analyse how environmental filters influence traits composition we carried out a redundancy analysis (RDA) using trait mean values, traits standard deviation and the eight environment variables, using a forward selection procedure (Legendre 1998). To analyse how traits vary individually along environment gradients of flooding and resources we carried out a series of forward multiple regression analysis. We used trait mean values and traits SD as dependent variables, and the 8 environmental factors as independent variables. We adjusted the p-values for ANOVA and multiple regression using Bonferroni correction (threshold of $p \leq 0.003$), to avoid errors for multiple comparisons (Gotelli & Elison 2010). All analyses were carried out using the R platform v 3.3.3 (R 2018).

Results

Environmental and functional differences between white-water and black-water forests

White- and black-water forests differ significantly in all environmental variables but soil pH. White-water forests had higher nutrient concentrations and flooding levels compared to black-water forests, especially higher concentrations of calcium (483.6), magnesium (31.5), and total exchangeable bases (92.3, S4).

White- and black-water forests differ significantly in all functional trait means but height:diameter ratio (Table 2). White-water forests had higher leaf area, specific leaf area, leaf nutrient concentrations, especially potassium (3.4 higher) and calcium (2.4), more deciduous species and taller plants, compared to black-water forests. In contrast, white-water forests had lower leaf dry mass content, chlorophyll content, branch wood density, lenticel density and less evergreen species.

The principal component analysis (Fig. 2) shows how plots vary in their functional composition. The first axis explains 49% of the variation with white-water forests and acquisitive traits (high values of SLA, LN, LP, LK, LCa and deciduousness) to the left, and black-water forests and conservative traits (high values of LDMC, Chl, evergreen trees, BWD, LD) to the right. Within each forest type, there is a continuum of functional composition along the second axis, explained by 11% of the variation, with plots with trees with larger leaves and diameter at the bottom. The white-water forests plots differed in species composition according to flooding level, whilst black-water forests did not (PCoA analysis, S5). A regression analysis between functional trait and species composition indicated that changes in functional trait composition are correlated with shifts in species' composition (slope=8.71, R^2 adjust=0.90, $P<0.001$, S6).

The effect of environmental conditions in functional composition and individual trait variability

The redundancy analysis showed that functional trait means were best explained by total phosphorus, organic matter, total exchangeable bases and flooding level, with the most important environmental factors being total phosphorus and total exchangeable bases (R^2adj=0.51, Table 3). Traits variation was best explained by sand, total phosphorus and flooding level, with the most important environmental factor being total phosphorus (R^2 adj=0.41, Table 3).

The multiple regression analysis indicate that trait mean values vary along the environmental gradients of flooding and soil properties, especially exchangeable bases and organic matter (Table 4 and Fig. 3). An increase in total exchangeable bases was related to an increase in specific leaf area and leaf nitrogen and potassium concentration, and a decrease in evergreen individuals, branch wood density and lenticel density. An increase in organic matter content had, in general, the opposite effect on specific leaf area and leaf nitrogen concentration, compared to those of total exchangeable bases, while aluminum had the same effect in leaf nitrogen concentration. An increase in flooding level led to an increase in specific leaf area, and an increase in flooding duration led to an increase in deciduous individuals. This environmental variables were good predictor of communities' means variation across environmental gradients within and among forest types.

The communities' standard deviation of three traits was related to flooding. An increase in flooding level lead to a lower variation of specific leaf area and leaf potassium, and an increase in flooding duration lead to a higher variation in specific leaf area, leaf postassium and deciduous trees (Table 5 and S7). The partial regression p-values and β-coefficients of all traits can be seen in the supplementary material (S8).

Discussion

We asked whether white- and black-water forests differ in community functional traits and how it is affected by seasonal flooding and soil resource availability. We found that white-water forests had higher values of acquisitive traits than black-water forests. Surprisingly, in these flooded forests, flooding level or duration was not a stronger driver of functional trait composition and variation.

How do white-water and black-water forests differ in environmental conditions and functional composition?

It is well-known that white-water forests have higher soil fertility than black-water forests (Sioli 1984). White-water forests in our study areas had higher soil water retention capacity (higher silt and clay concentrations), more fertile soils (higher macro- and micro-nutrient concentrations) and were subjected to higher water stress and dynamic (higher levels and longer flood duration). Specifically, we found higher concentrations of calcium, manganese and base cations, and moderately higher concentrations (2-3 times higher) of total phosphorus and nitrogen. In contrast, black-water forests had sandy and poorer soils (low macro- and micro-nutrient concentrations), and lower water stress (lower levels and shorter flooding duration) compared to white-water forests. These environmental differences between white- and black-water forests are found in other areas in Amazonia, and describe a similar general pattern for these forest types (S4).

We hypothesized that, because white-water forests grow on more fertile soils, they would have more acquisitive traits that enhance resource acquisition and growth. White-water forests had indeed larger leaf area, higher specific leaf area, leaf nutrient concentrations and larger trees, that enhance light capture, photosynthetic capacity, carbon gain and growth rate (Lavorel & Garnier 2002; Reich & Oleksyn 2004; Wright et al. 2004; Poorter et al. 2006; Lebrija-trejos et al. 2010). Leaf calcium concentration was higher in white-water, probably because of its higher concentrations in the soil (Table 2; Furch 1997). High calcium concentrations can also be related to the leaf short-life cycles in acquisitive species because calcium is associated to inhibition of leaf senescence (Ferguson 1984). Black-water forests had denser wood and higher leaf dry matter content that increase stem and leaf persistence and enhance resource conservation (Kitajima & Poorter, 2008; Parolin & Worbes, 2000). Chlorophyll content was higher in black-water forests.

Usually, leaf chlorophyll content is higher with less waterlogging because of leaf water supply and availability, but can also be a reflect of plant or leaf age (Parolin et al. 2010).

Because white-water forests in our study experience higher levels and longer flooding duration, they also possess different flooding traits compared to black-water forests. White-water forests had a larger proportion of deciduous trees. Deciduousness is an existing strategy in floodplain forests trees to reduce leaf transpiration and save water during the dry season, but it may imply a high production cost of new leaves when nutrient is limiting, as in black-water forests (Parolin & Wittmann, 2010; Parolin et al., 2002). Although deciduousness and sclerophyllous leaves (higher LDMC) are described as a response to flooding in both white- and black-water forests (Parolin et al., 2002), the differences we found in these traits are probably related to nutrients availability. Lenticels enhance oxygen uptake in flooding conditions and the formation of hypertrophied lenticels (very large lenticels that improve gas exchange during flooding periods), is a common response to flooding (Armstrong & Hull 1994; Lopez & Kursar 1999). Counterintuitively, lenticel density differ between forests and was higher in black-water forests that experience less flooding. Maybe a similar trade-off between density and size that occurs in stomata applies for stem lenticels (Franks & Beerling 2009; Wang et al. 2014). Higher stomatal density is important for a more flexible regulation of gas exchange, and larger stomata is important for the magnitude of gas exchange (Hetherington & Woodward 1979). This would mean that in longer and more deeply flooded white-water forests the lenticel density is lower, but perhaps their gas exchange is larger because of the higher size of the lenticels.

White-water forests are a more dynamic environment than black-water forests. Individuals that do not totally tolerate submergence have an ‘escape strategy’ (Parolin, 2012), that is, they have adaptations to grow fast and maintain at least some parts of the plant above the water surface. The combination of higher water dynamics and higher availability of nutrients in white-water forests led to the more acquisitive traits resulting in fast-growth and shorter life cycle in white-water communities and the opposite in black-water forests (Junk et al., 2015). The observed pattern for leaf and wood traits values reveals a distinction in resource acquisition and conservation strategies between white-and black-water forests, which agrees with patterns described for other terrestrial herbaceous and woody plant communities (Díaz et al., 2004; Sterck, Markesteijn, Schieving & Poorter, 2011; Wilfahrt, Collins & White, 2014; Wright et al., 2004).

How do environmental conditions affect functional composition and individual trait variability?

We hypothesized that, because flooding imposes stressful anoxic conditions, it would influence community trait variation leading to trait-divergence, and resources availability will influence community trait means, leading to trait-convergence. Most plant traits and strategies in floodplain forests are described as an adaptation to the stress caused by flooding, water dynamics and different flooding levels, resulting in different floristic composition (Wittmann et al. 2006b; 2013; Assis et al. 2015), forest structure and traits (De Simone, Junk & Schmidt, 2003; Maurenza, Marenco, Parolin & Piedade, 2012; Parolin, 2012). We found that functional composition showed a stronger association with soil variables and to a less extent to flooding level, especially total exchangeable bases and total phosphorus had a strong impact on community traits. Traits variation across environmental gradients of soil properties was also strong, with an increase in total exchangeable bases leading to more acquisitive traits. Base cations are important bioelements that accumulate in the vegetation and are related to biological processes, like photosynthesis and plant growth (Furch 1997). Calcium, for example, which is a limiting nutrient in the upland forest of the Amazon region, was especially higher in white-water forest and can be an important component driving trait variation. Aluminum, which is a toxic element, seems to be an important environmental attribute of white-water forests influencing trait composition.

Few traits showed association to flooding, with flooding duration leading to a decrease but not an increase in trait variation. We expected that functional traits will respond strongly to flooding as indicated by other studies (Assis et al. 2014; Fortunel et al. 2014), but in our results the variation in soil resource availability came out to be the most important environmental driver that gives rise to the conservative-acquisitive distinction observed among these Amazonian floodplain communities. To our knowledge, this is the first study that analyses the functional trait composition and variation of two contrasting floodplain forests at a fine-scale community level and to evaluate the influence of flooding in different soil conditions. Apparently, small-scale variation in soil nutrients can be a more important driver of variation in community functional composition than flooding levels of almost 4 m and more than 6 months of duration, which is supported by the little effect of flooding level and duration within the forests. Because of flooding disturbance, we expected a divergence of traits when positions in the flooding gradient were different (Grime 2006; Helsen et al. 2012). In contrast, we found that flooding and especially nutrient availability leads to a decrease in trait variation and resulting in trait-convergence.

In this study we evaluated two forests only, and our results may partially reflect the particularities of these two areas. Changes in functional traits composition were correlated to changes in species' composition (S6), what could be explained by environmental filtering of traits, by a biogeography effect on the regional species pool (Higgins et al. 2011) or by the combination of both. We are not able to quantify the importance of differences in the regional species pool for these flooded forests. However, our results clearly show that flooding conditions are not the strongest filter influencing community trait composition or community trait divergence. Based on this, we suggest that soil conditions, rather than flooding, can be a more important environmental driver that differentiate functional composition and ecological strategies between floodplain tree communities. To better understand the influence of species pool and soil properties on functional strategies in floodplain forests, future studies should evaluate the traits variation within species or between closely related species occurring in these ecosystems.

Conclusions

White-water forests have more acquisitive traits and black-water forests more conservative traits. Flooding does not explain the major variation in functional composition and ecological strategies within or across these communities. We suggest soil resource availability, especially exchangeable bases, should be the more important environmental factor to understand the community functional composition of flooded forests.

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TABLES

Table 1. Overview of the plant functional traits included in this study, with the organizational level, trait name, abbreviations, units, their function and hypothesis related.

Plant functional trait	Function related	Reference	Hypothesis	
			Flooding	Increase in soil fertility
Leaf				
Leaf area, LA (cm²)	Light intercepting area, respiration, transpiration, gas exchange	Lebrija-trejos et al. 2010	Higher variability along flooding gradient, lower mean values at higher flooding level and duration	Higher mean values
Specific leaf area, SLA (cm².g^{-1})	Light capture economics, net assimilation rate, relative growth rate, leaf life span, photosynthetic capacity	Lavorel and Garnier 2002, Poorter and Bongers 2006	No effect	Higher mean values
Chlorophyll content, Chl (SPAD units)	Light uptake efficiency, photosynthetic rates	Poorter and Bongers 2006	Higher variability along flooding gradient, lower mean values at higher flooding level and duration	Higher mean values
Leaf dry matter content, LDMC (g.g^{-1})	Construction costs, nutrient retention, resistance against herbivory and physical damage, drought resistance	Lavorel and Garnier 2002, Lebrija-Trejos et al. 2010	Higher variability along flooding gradient, higher mean values at higher flooding level and duration	Lower mean values
Leaf nitrogen, LN and phosphorus, LP (g.kg^{-1})	Photosynthetic rates, CO_2 assimilation, leaf nutrients levels	Wright et al. 2004, Reich et al. 2014	No effect	Higher mean values
Leaf potassium, LK (g.kg^{-1})	Stomata control, turgor provision and water homeostasis	Maathuis 2009	No effect	Higher mean values
Leaf Calcium, LCa (g.kg^{-1})	Cellwall structure	Maathuis 2009	No effect	Higher mean values

Deciduousness, De (binary; 0-evergreen, 1-deciduous/semi-deciduous)	Drought avoidance	Lebrija-Trejos et al. 2010	Higher frequency of deciduousness at higher flooding level and duration	Higher frequency of deciduousness
Branch				
Branch wood density, BWD (g.cm^{-3})	Construction costs, growth rate, pathogen resistance, mortality rate	Swenson and Enquist 2008, Chave et al 2009	Higher variability along flooding gradient, lower mean values at higher flooding level and duration	Lower mean values
Trunk				
Lenticels density, LD (count cm^{-2})	Oxygen uptake, gas exchange	Parolin and Wittmann 2009	Higher variability along flooding gradient, higher mean values at higher flooding level and duration	No effect
Whole-plant				
Height:diameterratioplant, HDR (m.cm^{-1})	Stability, competitive strength	Chave et al 2009, Opio et al 2000	Higher variability along flooding gradient, higher mean values at higher flooding level and duration	Higher mean values

Table 2. Differences in 12 functional traits (leaf, branch, trunk and whole-plant levels) between white- and black-water forests studied here. The columns indicate the trait mean values per forest type, the ratio between the mean values of white-water and black-water forest, and the Anova results (*F* statistic and p-value).

Plant functional traits	Forest type mean values		White-water/ black-water	Anova test	
	White-water	Black-water		*F*	p-value
Leaf					
LA	69.0	47.7	1.45	15.1	<0.001
SLA	139.6	88.5	1.58	135.3	<0.001
LDMC	1.0	1.8	0.54	35.0	<0.001
Chl	50.6	55.4	0.91	11.7	<0.001
N	19.7	14.9	1.33	102.2	<0.001
P	1.9	1.0	1.80	44.0	<0.001
K	11.9	3.5	3.40	135.5	<0.001
Ca	5.6	2.4	2.40	44.6	<0.001
Evergreen	0.4	10.2	0.04	467.1	<0.001
Deciduous	0.3	0.2	1.97	11.6	<0.001
Branch					
BWD	0.5	0.7	0.72	129.8	<0.001
Trunk					
LD	1.8	3.3	0.55	80.5	<0.001
Whole-plant					
HD	0.6	0.5	1.06	1.7	0.19

Table 3. Redundancy analyses, showing how environmental variables sand, total phosphorous, organic matter, total exchangeable bases and flooding level affect multivariate trait mean values and standard deviation. The columns indicate *F* statistic and significance level (p-value).

Environmental variables	Mean-value		Standard deviation	
	F-statistic	p-value	F-statistic	p-value
Sand			9.05	0.001
Organic matter	5.47	0.015		
Total phosphorus	23.34	0.001	19.72	0.001
Exchangeable bases	18.62	0.001		
Flooding level	4.81	0.019	5.04	0.01

Table 4. Multiple regression analyses of 7 leaf, branch and whole-plant trait means on environmental variables soil organic matter, total exchangeable bases, aluminium, flooding level and flooding duration. The column values indicate the standardized β-coefficient of variation for each environment variable, R^2 adjusted and significance (p-value).

Plant functional traits	Organic matter	Total exchangeable bases	Aluminum	Flooding level	Flooding duration	R^2 adj	p-value
Leaf							
SLA	-0.57	0.9		0.35		0.72	<0.001
LN	-0.3	0.95	0.42			0.74	<0.001
LK		0.81				0.75	<0.001
Evergreen		-0.93				0.87	<0.001
Deciduous					0.97	0.63	<0.001
Branch							
BWD		-0.84				0.72	<0.001
Trunk							
LD		-0.86				0.62	<0.001

Table 5. Multiple regression analyses of three traits standard deviation on environmental variables flooding level and flooding duration. The columns values indicate the standardized β-coefficient of variation for each environment variable, R^2 adjusted and significance (p-value).

Plant functional trait	Flooding level	Flooding duration	R^2 adj	p-value
SLA	-1.65	2.98	0.66	<0.001
LK	-1.10	1.74	0.07	<0.001
Deciduous		3.33	0.47	<0.001

FIGURES

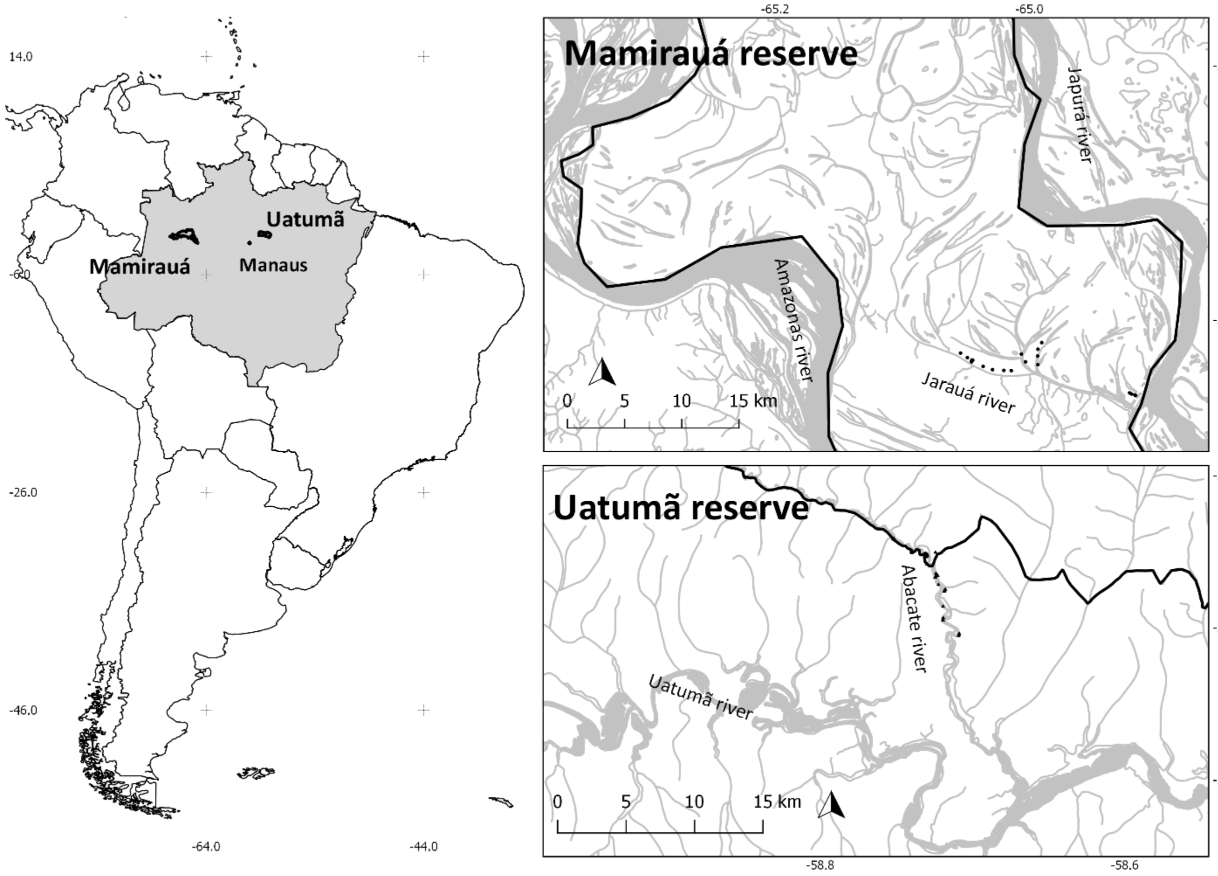


Figure 1. Location of study areas Mamirauá and Uatumã reserves (left side) and research plots (right side). Black dots indicate plots in white-water forests (upper right panel) and black triangles indicate plots in black-water forests (lower upper panel).

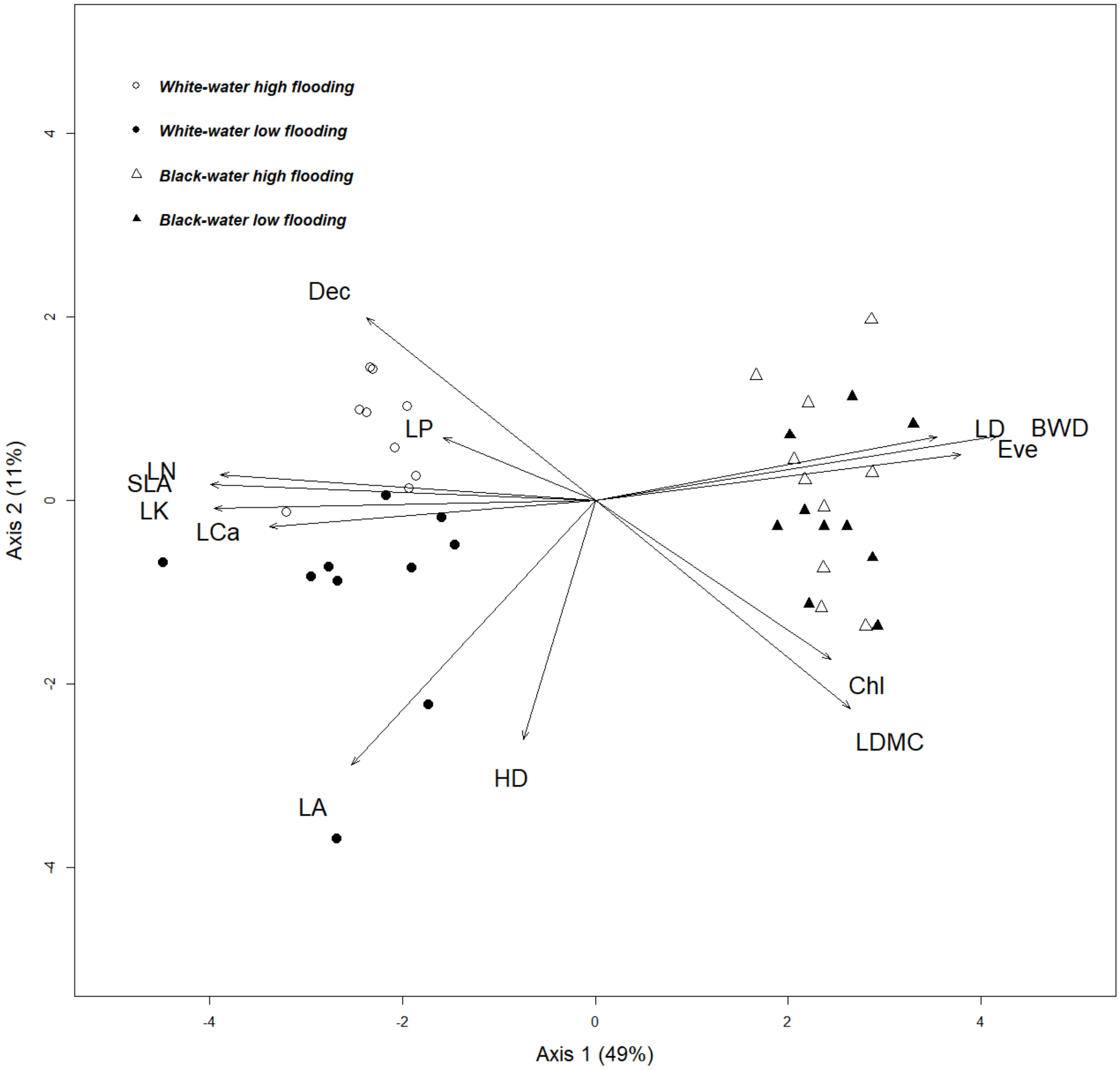


Figure 2. Principal component analysis (PCA) of 12 functional trait mean values of white-water forests (circles) and black-water forests (triangles) that experience high flooding level (open symbols) and low flooding level (filled symbols). The first PCA axis explains 49% of traits mean variation, and the second PCA axis explains 11%. For trait abbreviations see Table 1.

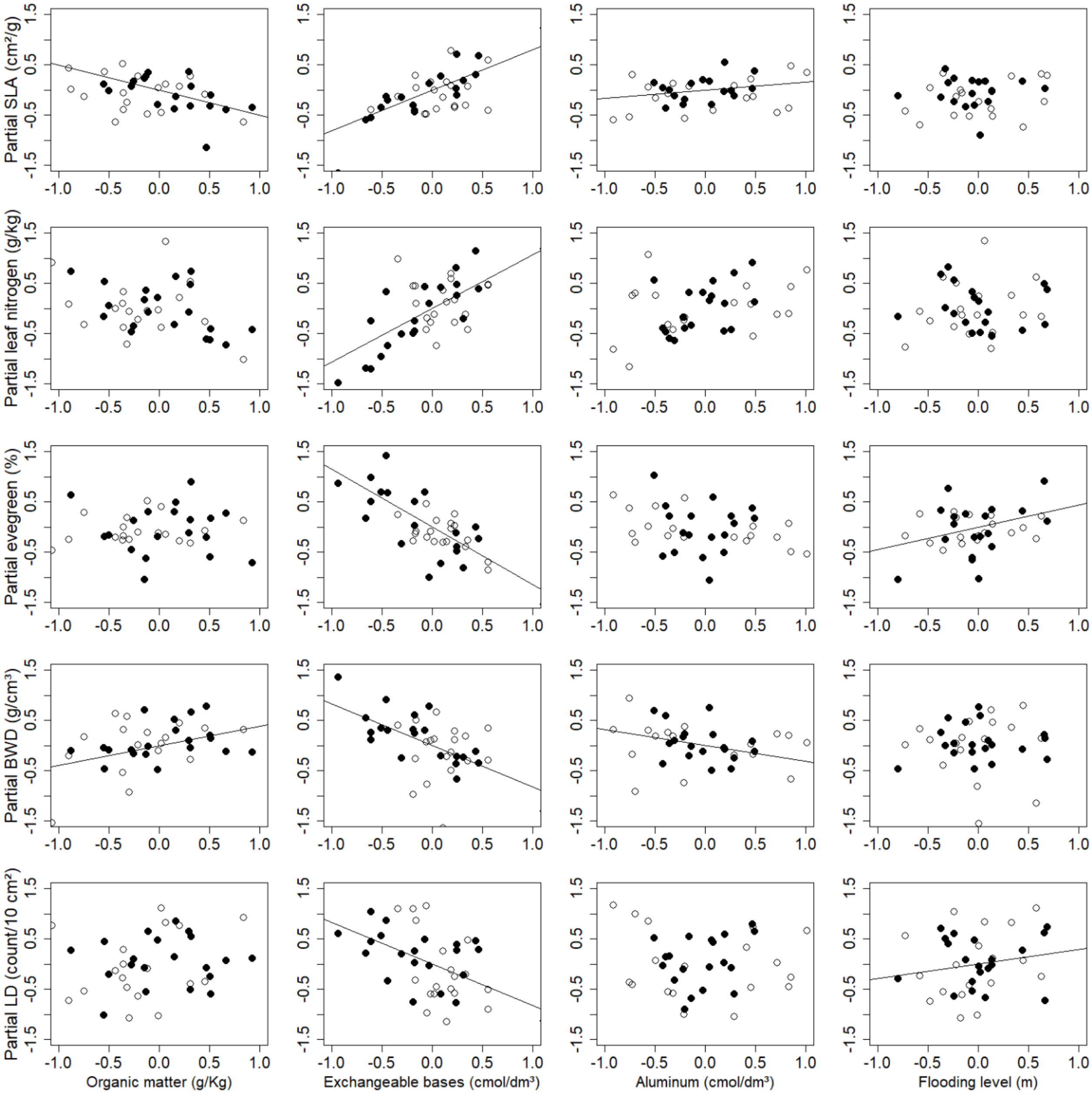


Figure 3. Partial regressions derived from multiple regression of five functional trait mean values that included different plant characteristics and responses to flooding and soil nutrients (specific leaf area –SLA, leaf nitrogen, evergreen, branch wood density – BWD and lenticel density - LD) with four environmental variables that had more influence on traits variation (organic matter, total exchangeable bases, aluminum, and flooding level) on white-water forests (open circles) and black-water forests (filled circles).

SUPPLEMENTARY MATERIAL

S1. Functional traits and soil properties measurements

Functional traits: Leaf traits, except chlorophyll index, were measured on 5 sun-exposed leaves (petiole excluded). For leaf area measurement, fresh leaves were scanned using a portable scanner, and the leaf area (cm) was calculated in the software ImageJ. Fresh leaves were weighed with an analytical balance to obtain fresh mass (g). After that, leaves were dried at 60°C during 48 hours, and weighed to obtain its oven-dry mass (g). Specific leaf area (cm.g^{-1}) was measured by the ratio of leaf area and its oven-dry mass. Leaf dry matter content (g.g^{-1}) was measured by oven-dry mass divided by its fresh mass. Dried leaves were stored and its nutrient content (g.kg^{-1}) was obtained by the Empresa Brasileira de Pesquisa Agropecuária (Embrapa, Manaus). Leaf nitrogen was obtained by Kjedahl method, leaf phosphorus was obtained by vanadate yellow spectrometry, leaf potassium was obtained by emission flame spectrometry and leaf calcium was obtained by atomic absorption spectrometry. Chlorophyll index was obtained in 3 sun-exposed leaves with a chlorophyll meter (SPAD-502) and calculated the average of the three measurements. Leaf deciduousness was classified by species as being (semi) deciduous (code 1) or evergreen (code 0), based on available data from literature (Lorenzi 1992; Lorenzi 1998; Lorenzi 2009; da Silva Marinho et al. 2010; Wittmann et al. 2010). We classified 60% and 44% of species in white-water and black-water forest, respectively. Branch wood density (g.cm^{-3}) was measured for one terminal branch per individual (bark included) as the oven-dry mass divided by its fresh volume. Fresh volume was obtained using the water displacement method and samples were dried at 105°C during 72 hours, and weighed using analytical balance to obtain the oven-dry mass. Lenticels density was measured using a 10 cm² templet positioned at 1.3 m height in the trunk. The plant height:diameter (m.cm^{-1}) ratio was measured by the estimated plant height divided by the diameter at breast height (at 1.30 m).

Soil properties: Three soil samples were collected from each plot at the first 10 cm from topsoil (excluding litter layer), to form a mixed sample per plot. Soil physical and chemical properties were analyzed by Empresa Brasileira de Pesquisa Agropecuária (Embrapa 1997, Manaus). The percentage of sand, silt and clay were obtained by total dispersion method. The hydrogen potential was obtained by combined electrode immersed in soil suspension:liquid (water). The organic carbon (g.kg^{-1}) was obtained by potassium dichromate in sulfuric solution. Total nitrogen (g.kg^{-1}) was obtained by kjedahl method. Total exchangeable bases (cmolc.dm^{-3}) was obtained by K Cl N method. Iron, manganese (mg.dm^{-3}), aluminium (cmolc.dm^{-3}) and total phosphorus (g.kg^{-1}) were obtained by sulfuric extract. Potassium, magnesium (mg.dm^{-3}), sodium and calcium (cmolc.dm^{-3}) were obtained in water solution.

S2. Twelve funtional traits of 40 research plots of white-water and black-water floodplain forests. The columns indicates the trait mean values per plot: leaf area, specific leaf area, leaf dry matter content, Chlorophyll content, leaf nitrogen, leaf phosphorus, leaf potassium, leaf calcium, deciduousness (evergreen/deciduous), branch wood density, lenticel density, and height:diameter ratio.

Plot	Forest type	Leaf area (cm^2)	Specific leaf area (cm^2.g-1)	Leaf dry matter content (g.g-1)	Chlorophyll content (SPAD units)	Leaf nitrogen (g.kg-1)	Leaf phosphorus (g.kg-1)	Leaf potassium (g.kg-1)	Leaf calcium (g.kg-1)	Branch wood density (g.cm^{-3})	Lenticel density (count/10 cm^2)	Height:diameter ratio (m.cm-1)	Evergreen (%)	Deciduous (%)
1	white-water	69.5	135.71	0.71	46.53	20.82	1.82	7.52	4.69	0.56	1.65	0.52	0.45	0.48
2	white-water	64.25	139.73	0.66	46.94	18.97	1.54	7.16	3.9	0.57	1.32	0.58	0.48	0.39
3	white-water	57.83	137.46	0.56	47.02	18.36	1.18	5.34	4.33	0.59	1.35	0.69	0.5	0.41
4	white-water	53.36	139.76	0.84	49.83	19.77	2.43	14.48	11.38	0.56	1.59	0.64	0.61	0.24
5	white-water	50.46	120.56	0.55	55.77	20.13	2.28	13.1	8.05	0.56	1.42	0.54	0.81	0.13
6	white-water	116.98	130.22	3.05	53.26	22.16	2.13	13.8	8.17	0.51	1.61	0.65	0.51	0.09
7	white-water	93.35	116.48	3.02	49.97	17.45	1.73	14.32	8.26	0.54	2.23	0.59	0.54	0.25
8	white-water	67.55	121.47	0.78	55.57	19.42	1.63	7.45	6.76	0.52	1.5	0.62	0.48	0.24
9	white-water	49.19	140.93	0.37	52.6	21.37	1.7	12.49	5.29	0.55	2.98	0.55	0.17	0.52
10	white-water	34.62	144.63	0.34	42.84	24	2.56	16.09	6.99	0.57	2.54	0.52	0.21	0.73
11	white-water	51.81	137.24	0.49	50.17	20.71	1.93	15.68	5.89	0.55	1.73	0.42	0.44	0.08
12	white-water	58.69	134.38	1.7	49.57	18.52	1.89	12.6	4.74	0.55	2.28	0.62	0.31	0.54
13	white-water	47.35	138.23	0.49	51.21	16.94	1.38	13.9	5.26	0.61	1.36	0.52	0.18	0.36
14	white-water	40.5	152.55	0.37	49.68	18.28	1.59	13.15	5.14	0.56	1.78	0.54	0.29	0.41
15	white-water	105.84	220.76	1.24	44.34	20.81	2.67	13.65	6.18	0.4	2.6	0.58	0.15	0.35
16	white-water	92.21	181.84	0.88	55.03	17.88	1.76	6.25	4.97	0.45	1.34	0.54	0.13	0.31
17	white-water	90.51	131.27	0.77	52.16	19.2	1.73	15.96	2.91	0.51	1.26	0.6	0.11	0.37
18	white-water	104.97	125.74	1.28	52.83	20.23	2.34	14.8	3.75	0.38	2.23	0.51	0.29	0.43
19	white-water	61.75	125.68	0.62	52.79	19.15	1.76	10.87	3.01	0.54	1.8	0.61	0.39	0.21
20	white-water	69.45	117.92	0.75	53.17	20.67	1.64	10.16	3.27	0.57	1.93	0.59	0.23	0.14
21	black-water	40.76	100.77	1.85	54.96	16.45	0.55	4.15	3.16	0.68	4.18	0.44	12.74	0.31
22	black-water	66.17	91.62	1.9	56.65	16.94	0.59	3.77	2.81	0.72	3.7	0.57	15.15	0.13
23	black-water	31.35	81.74	1.76	55.72	13.31	0.43	4.51	2.32	0.79	3.18	0.56	9.25	0.18
24	black-water	47.48	87.43	1.81	68.31	13.63	0.48	5.2	2.29	0.78	2.88	0.74	13.12	0.38
25	black-water	48.63	93.65	1.83	53.88	13.6	0.48	4.82	2.86	0.74	3.72	0.66	13.55	0.51

Cont. S2. Twelve funtional traits in 40 research plots of white-water and black-water floodplain forests. The columns indicates the trait mean values and standard deviation: leaf area, specific leaf area, leaf dry matter content, Chlorophyll content, leaf nitrogen, leaf phosphorus, leaf potassium, leaf calcium, deciduousness (evergreen/deciduous), branch wood density, lenticel density, and height:diameter ratio.

Plot	Forest type	Leaf area (cm^2)	Specific leaf area (cm^2.g-1)	Leaf dry matter content (g.g-1)	Chlorophyll content (SPAD units)	Leaf nitrogen (g.kg-1)	Leaf phosphorus (g.kg-1)	Leaf potassium (g.kg-1)	Leaf calcium (g.kg-1)	Branch wood density ($g.cm^{-3}$)	Lenticel density (count/10 cm^2)	Height:diameter ratio (m.cm-1)	Evergreen (%)	Deciduous (%)
26	black-water	51.01	93.91	1.92	51.53	14	9.67	1.27	4.26	0.74	2.42	0.48	21.16	0.28
27	black-water	41.23	83.66	1.9	50.52	13.46	0.51	4.39	3.14	0.73	3.92	0.29	14.46	0.29
28	black-water	51.26	88.25	1.8	72.19	15.17	0.79	2.99	2.23	0.72	2.79	0.54	9.75	0.1
29	black-water	43.69	96.81	1.72	51.03	14.63	0.57	2.45	1.92	0.75	4.07	0.63	7.5	0.02
30	black-water	56.44	71.52	1.59	53.17	12.89	0.58	3.39	2.31	0.75	2.61	0.68	7.31	0.03
31	black-water	54.08	82.67	1.94	52.83	15.14	0.85	3.04	2.78	0.67	3.89	0.52	7.23	0.14
32	black-water	39.71	90.74	1.9	49.84	13.45	0.71	3.47	2.24	0.73	3.31	0.57	6	0.03
33	black-water	62.58	97.17	1.89	54.92	15.01	0.63	4.47	1.71	0.72	3.92	0.68	9.06	0.14
34	black-water	45.74	94.22	1.8	53.84	15.56	0.52	3.4	2.08	0.72	2.61	0.54	5.54	0.06
35	black-water	44.94	77.61	1.67	51.01	13.54	0.5	3.84	2.72	0.74	3.27	0.52	5.53	0.33
36	black-water	42.93	93.96	1.8	54.79	15.35	0.52	3.51	4.58	0.85	3.13	0.47	3.96	0.17
37	black-water	43.86	83.29	1.64	53.75	14.32	0.59	2.44	0.8	0.76	3.06	0.65	10.09	0
38	black-water	45.4	81.76	1.66	55.8	16.13	0.6	3.18	1.08	0.73	2.67	0.56	9.25	0.07
39	black-water	43.66	85.55	1.78	58.3	16.86	0.65	2.29	0.86	0.77	4.28	0.37	10.09	0.09
40	black-water	53.28	93.86	1.8	55.31	17.72	0.66	3.59	0.99	0.76	3.34	0.3	14.13	0.13

S3. Twelve funtional traits of 40 research plots of white-water and black-water floodplain forests. The columns indicates the traits stadandard deviation per plot: leaf area, specific leaf area, leaf dry matter content, Chlorophyll content, leaf nitrogen, leaf phosphorus, leaf potassium, leaf calcium, deciduousness (evergreen/deciduous), branch wood density, lenticel density, and height:diameter ratio.

Plot	Forest type	Leaf area (cm^2)	Specific leaf area (cm^2.g-1)	Leaf dry matter content (g.g-1)	Chlorophyll content (SPAD units)	Leaf nitrogen (g.kg-1)	Leaf phosphorus (g.kg-1)	Leaf potassium (g.kg-1)	Leaf calcium (g.kg-1)	Branch wood density (g.cm-3)	Lenticel density (count/10 cm^2)	Height:diameter ratio (m.cm-1)	Evergreen (%)	Deciduous (%)
1	white-water	34.97	55.29	0.38	9.85	5.29	0.58	2.65	3.87	0.09	2.42	0.21	0.5	0.5
2	white-water	38.76	42.41	0.44	7.36	5.35	0.5	4.31	2.71	0.09	1.48	0.23	0.5	0.49
3	white-water	24.22	34.97	0.21	10.12	3.83	0.22	4.31	1.11	0.29	1.76	0.25	0.5	0.48
4	white-water	27.21	66.09	1.7	7.78	8.64	2.78	8.73	4.07	0.12	1.91	0.2	0.49	0.44
5	white-water	33.24	28.55	0.61	6.69	4.18	1.26	4.14	4.1	0.1	1.74	0.2	0.45	0.3
6	white-water	185.6	57.09	10.08	9.21	8.86	0.94	7.34	4.81	0.12	1.16	0.2	0.5	0.28
7	white-water	101.25	32.68	9.93	4.73	3.4	0.73	5.19	3.7	0.13	1.76	0.21	0.48	0.43
8	white-water	41.67	39.45	0.65	8.58	4.92	0.74	3.14	3.99	0.11	1.02	0.18	0.5	0.36
9	white-water	37.05	50.02	0.31	9.11	8.03	0.91	5.18	3.54	0.13	2.82	0.21	0.39	0.5
10	white-water	17.31	76.55	0.31	10.46	8.43	1.11	5.75	4.16	0.11	2.28	0.34	0.45	0.49
11	white-water	31.26	32.57	0.36	7.5	6.11	1.15	6.49	2.5	0.1	2.77	0.18	0.49	0.4
12	white-water	43.74	38.51	5.79	8.2	5.12	0.87	4.83	2.39	0.11	1.13	0.6	0.45	0.48
13	white-water	19.66	46.66	0.25	8.04	5.21	0.56	3.48	3.35	0.08	0.91	0.29	0.39	0.48
14	white-water	23.45	69.65	0.34	7.95	8.35	1.26	3.91	3.86	0.13	2.22	0.4	0.46	0.5
15	white-water	58.76	68.67	0.87	9.95	5.22	1.32	7.54	2.95	0.1	3.18	0.22	0.48	0.43
16	white-water	68.42	102.13	0.68	10.86	4.28	1.26	3.49	2.45	0.1	1.09	0.13	0.36	0.46
17	white-water	46.2	54.97	0.45	9.48	3.23	0.37	2.49	3.12	0.08	0.53	0.16	0.42	0.42
18	white-water	58.92	28.78	0.9	6.08	4.46	0.93	4.57	1.58	0.17	2.16	0.28	0.49	0.49
19	white-water	36.88	27.49	0.42	7.36	3.56	0.99	3.61	1.72	0.12	1.94	0.22	0.49	0.35
20	white-water	36.13	34.15	0.59	7.98	6.43	0.57	2.95	1.65	0.12	1.09	0.46	0.43	0.35
21	black-water	24.06	28.37	0.18	7.7	2.76	0.13	1.43	1.92	0.19	2.31	0.33	0.48	0.28
22	black-water	48.96	17.17	0.23	5.79	4.04	0.12	1.11	2.61	0.09	2.33	0.21	0.5	0.26
23	black-water	14.41	15.41	0.19	7.1	2.16	0.09	1.32	1.77	0.09	1.86	0.2	0.33	0.38
24	black-water	31.34	20.14	0.35	7.13	2.3	0.12	1.7	1.12	0.15	2.12	0.25	0.43	0.5
25	black-water	24.84	16.51	0.25	7.3	2.27	0.11	1.8	2.18	0.17	1.75	0.24	0.37	0.5

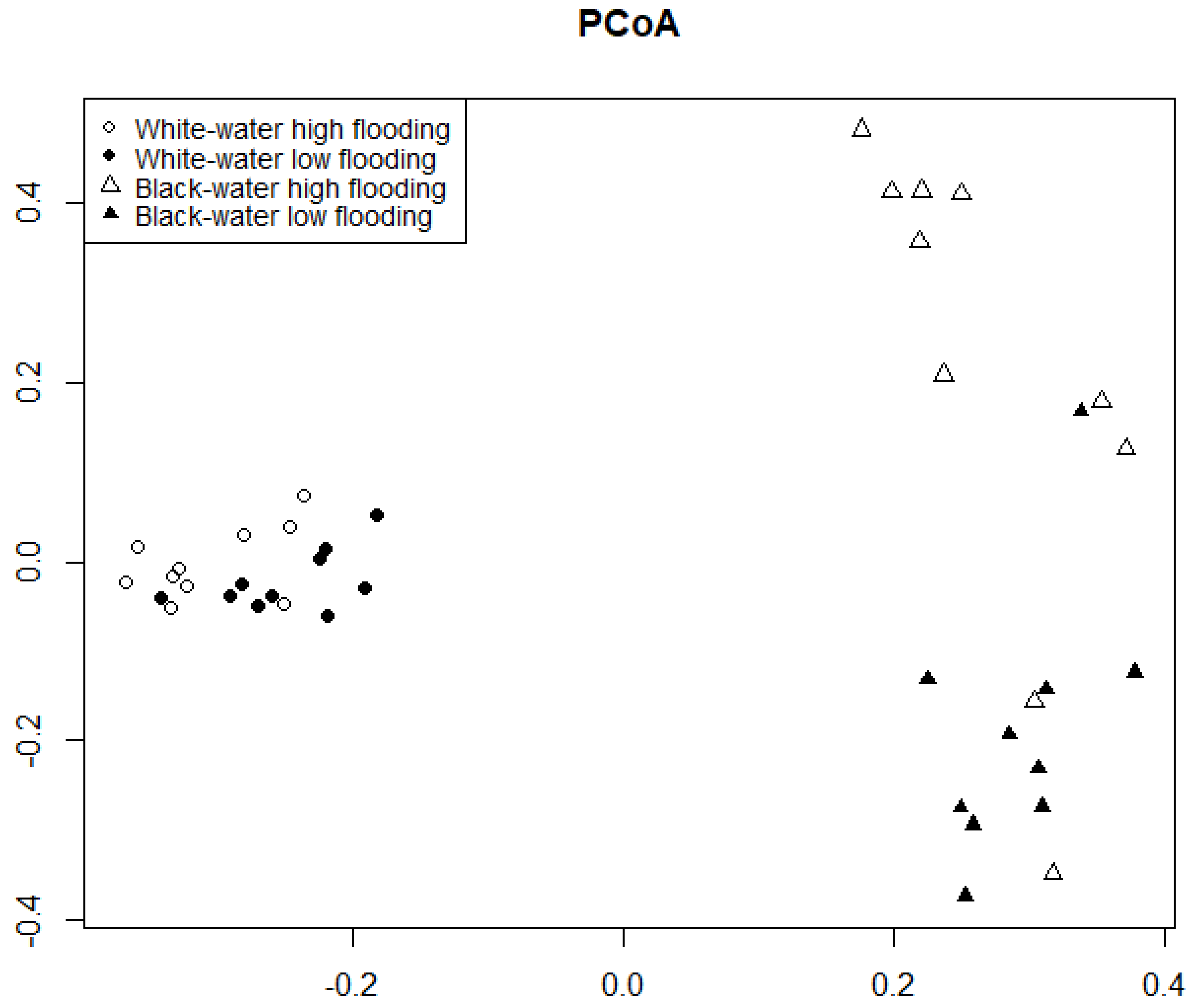
Cont. S3. Twelve funtional traits of 40 research plots of white-water and black-water floodplain forests. The columns indicates the traits stadandard deviation per plot: leaf area, specific leaf area, leaf dry matter content, Chlorophyll content, leaf nitrogen, leaf phosphorus, leaf potassium, leaf calcium, deciduousness (evergreen/deciduous), branch wood density, lenticel density, and height:diameter ratio.

Plot	Forest type	Leaf area (cm²)	Specific leaf area (cm².g-1)	Leaf dry matter content (g.g-1)	Chlorophyll content (SPAD units)	Leaf nitrogen (g.kg-1)	Leaf phosphorus (g.kg-1)	Leaf potassium (g.kg-1)	Leaf calcium (g.kg-1)	Branch wood density (g.cm-3)	Lenticel density (count/10 cm²)	Height:diameter ratio (m.cm-1)	Evergreen (%)	Deciduous (%)
26	black-water	18.84	11.2	0.25	6.04	1.97	6.56	1.2	3.62	0.07	1.54	0.23	0.5	0.45
27	black-water	16.43	21.26	0.43	7.45	2.59	0.11	1.68	2.11	0.14	1.95	0.33	0.34	0.45
28	black-water	27.98	15.44	0.32	110.44	2.77	0.21	1.18	2.27	0.09	2.18	0.22	0.49	0.25
29	black-water	21.53	24.08	0.28	9.86	4.09	0.18	1.44	1.41	0.11	3.86	0.19	0.44	0.15
30	black-water	42.63	24.12	0.37	7.57	4.14	0.39	3.35	1.13	0.08	2.63	0.23	0.44	0.16
31	black-water	24.81	16.26	0.2	7.94	3.91	0.35	1.15	1.9	0.08	1.82	0.2	0.42	0.34
32	black-water	21.03	23.06	0.54	7.06	3.77	0.28	1.46	2.03	0.09	1.82	0.2	0.38	0.16
33	black-water	30.06	24.29	0.33	8.33	3.32	0.12	2.18	1.28	0.07	1.77	0.37	0.3	0.36
34	black-water	31.4	22.08	0.35	7.46	4.28	0.17	1.16	1.27	0.12	1.48	0.16	0.48	0.25
35	black-water	21.6	18.39	0.38	8.7	3.23	0.15	1.43	1.57	0.09	1.34	0.15	0.46	0.47
36	black-water	22.98	19.23	0.17	6.2	2.96	0.11	1.04	2.65	0.94	1.51	0.17	0.46	0.37
37	black-water	21.82	15.37	0.2	8.44	2.65	0.13	0.84	0.6	0.06	2.14	0.17	0.4	0
38	black-water	31.34	24.45	0.33	6.26	3.36	0.12	1.45	0.9	0.11	2.24	0.23	0.44	0.26
39	black-water	25.46	29.57	0.4	8.66	4.32	0.14	0.92	0.5	0.07	3.45	0.19	0.46	0.28
40	black-water	28.37	20.85	0.5	6.05	5.32	0.23	2.54	0.49	0.07	1.42	0.04	0.49	0.33

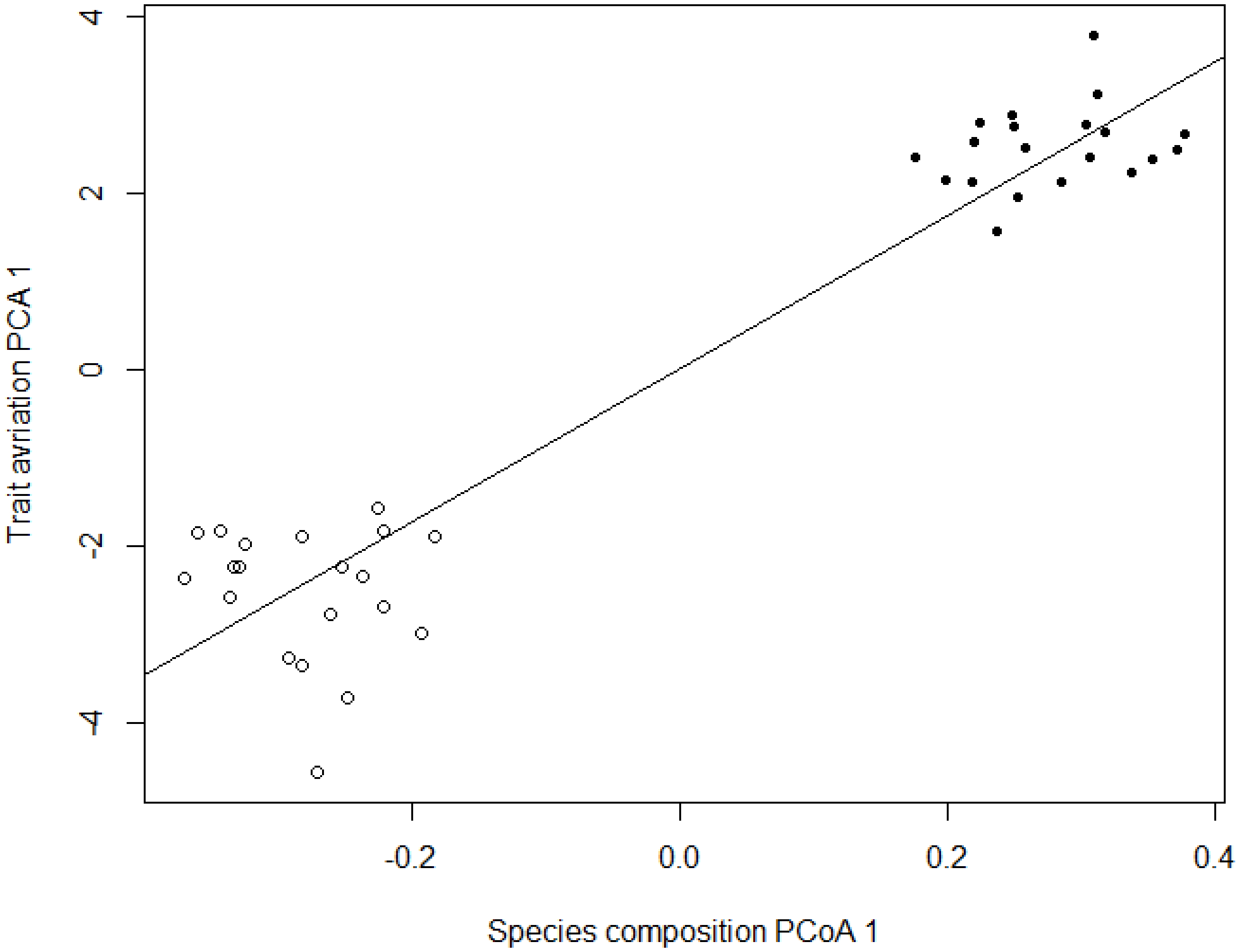
S4. Differences in soil physical and chemical variables between white- and black-water forests. The columns indicate the forest types mean values, the ratio between the mean values of white-water and black-water forest, and the Anova results (*F* statistic and p-value) of this study, and forest type mean values for different floodplains across the major tributaries of the Amazon basin white-water forests, Juruá, Jutaí, Purus, and black-water, Tarumã Mirím and Upper rio Negro.

Environmental factors	Forest type mean values		White-water/ black-water	Anova test		Juruá (white-water; Assis et al 2018)	Jutaí (white-water; Assis et al. 2018)	Purus (white-water; Assis et al. 2018)	Tarumã Mirím (black-water; Furch, 1997)	Upper Rio Negro (black-water; Mafra et al. 2006)
	White-water	Black-water		F	p-value					
Soil physical variables										
Sand (%)	15.54	56.96	0.3	52.6	<0.001	2.31	13.45	3.84	-	75
Silt (%)	46.77	15.61	3	114	<0.001	47.23	42.32	41.81	-	21
Clay (%)	37.68	27.44	1.4	4.9	0.03	50.45	44.22	54.34	-	4
Soil chemical variables										
pH	4.58	4.42	1	3.2	0.07	4.79	4.24	4.48	3.7	4.2
Carbon (g.kg^{-1})	27.01	16.81	1.6	10.6	0.002	14.24	24	22.26	39.5	-
Organic matter (g.kg^{-1})	46.6	28.91	1.6	10.7	0.002	-	-	-	-	-
P (g.kg^{-1})	27.5	8	3.4	23.2	<0.001	2.13	5	4.2	0.15	-
N (g.kg^{-1})	2.51	1.1	2.3	26.1	<0.001	2.13	1.88	2.41	3.1	1.8
K (mg.dm^{-3})	93.15	19.25	4.8	113	<0.001	145.5	56.9	95.7	70.2	-
Na (mg.dm^{-3})	31	3.2	9.7	359	<0.001	28.17	6.3	45.7	0.08	-
Fe (mg.dm^{-3})	402.25	21	19.2	56.2	<0.001	596.1	316.1	680.1	-	-
Zn (mg.dm^{-3})	4.93	0.33	14.8	149	<0.001	9.04	2.97	6.75	-	-
Mn (mg.dm^{-3})	65.29	0.45	144.1	5.7	0.02	111.7	6.78	39.8	-	-
Ca (cmolc.dm^{-3})	11.61	0.02	483.6	142	<0.001	15.18	0.13	6.99	0.14	-
Al (cmolc.dm^{-3})	1.68	1.06	1.6	5	0.03	3.9	0.27	3.03	-	1.6
Mg (cmolc.dm^{-3})	2.05	0.07	31.5	195	<0.001	5.45	9.97	7.07	-	-
Total exchangeable bases (cmolc.dm^{-3})	14.03	0.15	92.3	152	<0.001	36.3	10.55	17.52	-	0.3
Cu (cmolc.dm^{-3})	9.43	0.14	67.6	190	<0.001	3.86	1.71	5.47	-	-
Flooding										
Level (m)	3.88	2.02	1.9	17.8	<0.001	-	-	-	-	-
Duration (days/y)	203.75	77.47	2.6	62.1	<0.001	114.15	120.41	128.34	-	-

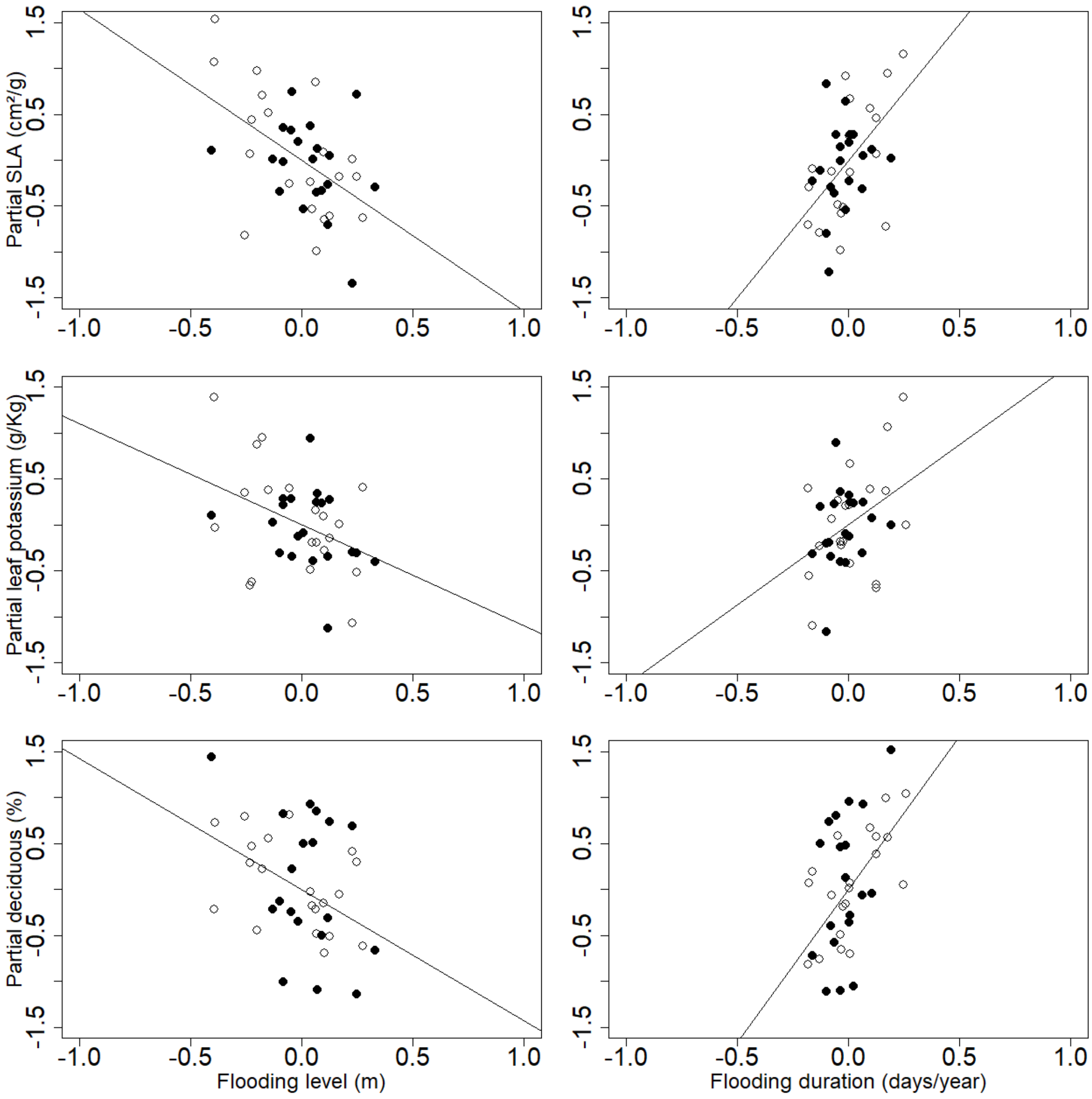
S5. Supplementary material: principal correspondence analysis (PCoA) of species 'composition of white-water forests (circles) and black-water forests (triangles) that experience high flooding level (open symbols) and low flooding level filled symbols. The goodness of fit is 0.29.



S6. Relationship between functional trait variation (first PCA axis) and species composition (first PCoA axis) of white-water forests (white circles) and black-water forests (black circles); R^2 adj = 0.9, $p<0.001$.



S7. Partial regressions derived from multiple regression of three functional traits standard deviation that included different plant characteristics and responses to flooding and soil nutrients (specific leaf area –SLA, leaf potassium and deciduous trees) with environmental variables that had more influence on traits variation (flooding level and flooding duration) on white-water forests (open circles) and black-water forests (filled circles).



S8. Partial multiple regression analyses of 12 leaf, branch and plant trait mean values and standard deviation (SD) on environmental variables related to soil sand content, organic matter, nitrogen, phosphorus, total exchangeable bases, aluminum, flooding level and flooding duration. The columns indicate the standardized β-coefficient of variation for each environment variable. When significant (p-value<0.03), the β- coefficient is highlighted in bold and p-value are indicated (*).

Plant trait	β-coefficient	Sand	Organic matter	Nitrogen	Phosphorus	Exchangeable bases	Aluminum	Flooding level	Flooding duration
Leaf area	mean	-0.46	-0.22	-0.49	0.24	0.63	0.33	-0.44	-0.01
	SD	-0.41	0.19	-0.35	0.22	0.14	0.26	-1.05	0.61
Specific leaf area	mean	-0.07	**-0.5 *<0.03**	-0.12	0.05	**0.81 *<0.03**	0.16	0.28	0.16
	SD	0.23	0.36	0.15	0.12	-1.04	-0.38	-1.65	**2.98 *0.02**
Leaf dry matter content	mean	-0.38	0.38	-0.19	-0.1	-0.7	-0.11	**-0.6*0.02**	0.05
	SD	-0.22	0.67	-0.12	0.00	-0.24	0.04	-1.65	1.39
Chlorophyll content	mean	-0.38	0.38	-0.19	-0.1	-0.7	-0.11	-0.6	0.05
	SD	-0.27	-0.21	0.04	-0.02	-0.21	-0.13	-0.06	0.14
Leaf nitrogen	mean	-0.08	-0.25	-0.14	-0.03	**1.07 *<0.03**	**0.49 *<0.03**	-0.03	-0.12
	SD	0.40	0.16	-0.04	0.14	0.82	0.24	-0.23	0.16
Leaf phosphorus	mean	0.05	-0.39	-0.08	0.11	0.8	0.19	0.22	0.02
	SD	0.15	-0.20	0.00	0.28	0.30	-0.06	-0.09	0.61
Leaf potassium	mean	-0.15	0.04	-0.16	0.1	**0.75 *<0.03**	0.3	-0.01	-0.01
	SD	-0.19	0.25	0.23	0.27	-0.62	-0.29	**-1.09 *0.02**	**1.74 *0.02**
Leaf calcium	mean	-0.26	-0.1	0.08	-0.01	0.35	0.09	0.06	0.14
	SD	-0.15	-0.15	-0.12	-0.08	0.41	0.21	0.31	0.04
Evergreen	mean	-0.29	-0.02	0.04	-0.1	**-1.15 *<0.03**	-0.26	0.44	-0.17
	SD	-0.59	-0.41	-0.39	0.06	1.29	0.22	0.69	-1.57
Deciduous	mean	-0.04	-0.01	0.43	-0.01	-0.59	-0.27	0.22	**0.84 *<0.03**
	SD	-0.03	0.38	0.37	-0.31	-1.89	-0.52	-1.43	3.33
Branch wood density	mean	0.07	0.39	0.15	-0.2	**-0.82 *<0.03**	-0.32	-0.03	-0.08
	SD	-0.25	0.05	0.11	-0.42	-0.85	0.01	-0.54	1.23
Lenticel density	mean	0.13	0.18	0.02	-0.12	**-0.83 *<0.03**	-0.06	0.29	-0.14
	SD	0.08	0.00	-0.28	0.12	0.63	0.05	1.19	-1.57
Height:diameter ratio	mean	0.10	-0.10	0.05	0.05	0.13	-0.12	-0.42	0.51
	SD	0.32	-0.22	-0.12	-0.39	0.30	0.18	0.54	0.31

ARTIGO 2

Trait divergence and habitat specialization in tropical floodplain forests trees

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Abstract

Habitat heterogeneity of tropical forests is thought to lead to specialization in plants and contribute to the high diversity of tree species in Amazonia. One prediction of habitat specialization is that species specialized for resource-rich habitats will have traits associated with high resource acquisition and fast growth while species specialized for resource-poor habitats will have traits associated with high resource conservation and persistence but slow growth. We tested this idea for seven genera and for twelve families from nutrient-rich white-water floodplain forest (várzea) and nutrient-poor black-water (igapó) floodplain forest. We measured 11 traits that are important for the carbon and nutrient balance of the trees, and compared trait variation between habitat types (white- and black-water forests), and the effect of habitat and genus/family on trait divergence. Functional traits of congeneric species differed between habitat types, where white-water forest species invested in resource acquisition and productive tissues, whereas black-water forest species invested in resource conservation and persistent tissues. Habitat specialization is leading to the differentiation of floodplain tree species of white-water and black-water forests, thus contributing to a high diversity of plant species in floodplain forests.

Introduction

Habitat filtering is a key mechanism underlying assembly of plant communities as it determinates whether species are able to establish, grow and reproduce under specific abiotic conditions[1]. Species are filtered out based on their functional traits, and habitat filtering usually explains the co-occurrence of species under similar abiotic conditions as a result of shared traits and ecological similarity. Ecological similarity though, is often caused by phylogenetic relatedness between species [2,3], meaning that related species tend to have more similar trait values. Therefore, comparing phenotypic differences in plant traits between related species is a simple way to control for phylogenetic relatedness, and to test whether different habitat selecting pressures have led to species trait differentiation [4,5].

Habitat heterogeneity is thought to be an important cause of tree species diversity in Amazonian forests [6–8]. Few Amazonian tree species are dominant while many are rare [9], and it is assumed that the majority of coexisting species are habitat generalists [10]. Yet, the high turnover of tree species across local environmental gradients suggests that species do specialize to specific habitat conditions, thus promoting species diversity and coexistence [7,11,12].

Many plant traits diverge as an adaptation to environmental conditions, for instance, topography, soil nutrients and water availability, leading to species preference for different habitat types [13–16]. The occurrence of phylogenetically closely related species in contrasting habitats, and the co-occurrence of unrelated species in the same habitat with similar abiotic conditions, indicates that species have specialized for different habitats [8]. Trait divergence between closely related species that occur in different habitats is therefore an indication of how habitat specialization occurs [4,17].

Rather than single traits, it is a suite of different traits that allow species to specialize for a certain habitat condition [4,14]. In combination, this suite of traits forms a plants strategy. For example, large leaves, high specific leaf area and high leaf nutrient concentrations are usually associated with fast-growth which is advantageous in high-resource environments, whereas low specific leaf area and high leaf dry matter content reflect investment in strong and persistent tissues that increase nutrient conservation, water use efficiency and plant survival in low-resource environments [18–20]. Habitat specialization is, therefore, an important ecological process that leads to the development of different ecological strategies in plant communities, thus contributing to species diversity [21–23].

Amazonian floodplain forests provide a unique ecosystem to evaluate the influence of habitat specialization. These forests face seasonal flooding dynamics [24,25] which allows only species with specific traits and strategies to survive under these anoxic conditions [26–28]. One important strategy to deal with flooding is to slow down the metabolism to save energy and resources, which is reflected in the sclerophyllous leaves, lower plant height and diameter and higher wood density. Another strategy, is the development of lenticels in roots and trunks, which are responsible for the gas exchange in flooded soils that have low oxygen available [26,28]. Different floodplain forest types are recognized based on their contrasting soil nutrient availability, the nutrient-rich white-water forests (várzea) and the nutrient-poor black-water forests (igapó; [24,29]). Although many species occur in floodplain forests, white- and black-water forests share only 30% of the species [30]. Because of the low floristic similarity between white- and black-water forests, habitat specialization is likely to be the main process underlying the floristic differences between these two forest types.

In this study, we evaluated how functional traits diverge between congeneric tree species of two floodplain forests of Central Amazonia that have contrasting soil resource conditions [31]. We addressed the following questions and hypotheses: (1) Do functional traits diverge between congeneric species living in different floodplain forest with different soil types? We hypothesized that congeneric species that occur in nutrient-rich white-water forests will have acquisitive trait values (i.e., higher specific leaf area and leaf nutrients) and fast-grow, whereas congeners inhabiting nutrient-poor black-water forests will have conservative trait values (i.e., higher wood density and leaf dry matter content) that increase persistence under nutrient poor conditions but lead to slow-growth. Variation in trait values will be lower in black-water species compared to white-water species because strong limitation of nutrient resources [31]; (2) Can variation in trait values between congeneric species be attributed to differences among genera or to forest types? We hypothesized that habitat (forest types) will be more important for trait differentiation, and will lead to the divergence of traits between white- and black-water forest species within the same genus.

Material and methods

Study sites and sample design

Research was carried out in Central Amazonia which is characterized by a hot and humid tropical climate. Mean annual temperature is 26.6 °C. Mean annual precipitation is 2,100 mm/y, with a wet season occurring from December to April and a dry season from June to October. White-water forests have higher soil water retention capacity (higher silt and clay concentrations), and higher macro- and micro-nutrient concentration, especially calcium, manganese and base cations. Black-water forests have sandy soils and low macro- and micro-nutrient concentrations compared to white-water forests [31,32].

Trees from white-water and black-water forests species were sampled in 25x25m plots previously established and inventoried in two reserves, the Mamirauá Sustainable Development Reserve (RDS Mamirauá) and the Uatumã Sustainable Development Reserve (RDS Uatumã). The flooding regime varies from 2 to 5 meters, during 180-240 days in the white-water forests; and from 1 to 3 meters, during 50-100 days in black-water forests. The RDS Mamirauá (2°51'S 64°55'W) has an area of 124,000 km² of white-water floodplain forests, and is adjacent to the Japurá and Solimões river and the Auati-paranã channel [33]. The Uatumã RDS (1°48′S, 59°15′W) has an area of 4,244.300 km², and is located between Itapiranga and São Sebastião do Uatumã cities [34]. Field work was carried out under collecting permits 015/2016-DEMUC/SEMA and SISBIO 52109-1, provided by Departamento de Mudanças Climáticas e Gestão de Unidades de Conservação da Secretaria Estadual de Meio Ambiente of Amazonas State and Instituto Chico Mendes de Conservação da Biodiversidade, respectively.

To evaluate whether habitat specialization occurs, we carried out our analysis at the genus and also at the family level, to verify if an older evolutionary split is causing specialization. We selected seven genera that occur in both white- and black-water forests along the flooding gradient that have at least 5 individuals per genus in each forest type, to estimate the average trait value of a genus (Table 1). The threshold of 5 individuals was chosen because of the low co-occurrence of species between these forest types [30]. The individuals within a genus belong from 1 to 4 species. In total we sampled 70 individuals (35 individuals per forest type, and 5 individuals per genus). These individuals belonged to 29 species, with 14 species occurring only in white-water forest, 10 species occurring only in black-water forest, and 5 species occurring in both forest types (S1 Table). The criteria for family selection was the same as for genus (i.e. 5 individuals per family per forest type), leading to a total of 12 families that occurred in both forest types (Table 1). We sampled 120 individuals (50 individuals per forest type) and 54 genera, with 22 genera occurring only in white-water forest, 14 genera occurring only in black-water forest, with 18 occurring in both forest types (S1 Table).

Table 1. Seven genera and 12 families of the study. The columns indicate the genus/family, and the species/genus number belonging to each genus/family in white-water and black-water forests. The number of individuals sampled for each genus/family per forest type is 5 (n=5).

Phylogenetic level	species number	
Genus	White-water forest	Black-water forest
Eschweilera (Lecythidaceae)	3	3
Guatteria (Annonaceae)	2	1
Licania (Chrysobalanaceae)	3	5
Mouriri (Melastomataceae)	2	2
Ocotea (Lauraceae)	3	2
Pouteria (Sapotaceae)	2	1
Zygia (Fabaceae)	4	1
Family	genus number	
Annonaceae	5	1
Apocynaceae	3	2
Chrysobalanaceae	3	2
Euphorbiaceae	5	4
Fabaceae	5	5
Lauraceae	1	1
Lecythidaceae	4	3
Malvaceae	5	1
Melastomataceae	1	2
Moraceae	4	2
Myrtaceae	2	5
Sapotaceae	3	4

Functional traits

For each tree we measured eleven functional traits that are related to resource acquisition and growth (S2 and S3 Table). The traits were Leaf area – LA (cm^2), Specific leaf area - SLA ($cm^2.g^{-1}$), Leaf dry matter content – LDMC ($g.g^{-1}$), Chlorophyll content – Chl (SPAD units), Leaf nitrogen – N ($g.kg^{-1}$), Leaf phosphorus – P ($g.kg^{-1}$), Leaf Potassium – K ($g.kg^{-1}$), Leaf Calcium – Ca ($g.kg^{-1}$), Branch wood density – BWD ($g.cm^{-3}$), Lenticel density – LD (count in 10 cm^{-2}), and the Height:diameter ratio - HDR ($m.cm^{-1}$) of the tree. Measurements were made following standardized trait protocols [35] (Table 2). Leaf traits were measured in 5 sun-exposed leaves per individual. Chlorophyll content was measured with a chlorophyll meter (SPAD-502) on 3 sun-exposed leaves. Lenticel density was measured in the trunk of the trees using a 10 cm^2 templet. To reduce sampling effort and tree damage, we measured wood density at the branch level instead of the trunk level [36]. BWD was measured in one branch per individual (bark included) using the water displacement method [36]. The measurements of LA, SLA, LDMC, Chl, BWD, LD and HDR were conducted in the field and leaf nutrient analysis was done by Empresa Brasileira de Pesquisa e Agropecuária (Embrapa, Manaus, Brazil).

Table 2. Overview of the plant functional traits included in this study, with the trait name, abbreviations, units and their function.

Plant functional trait	Function related	Reference
Leaf area, LA (cm^2)	Light intercepting area, respiration, transpiration, gas exchange	[37]
Specific leaf area, SLA ($cm^2.g^{-1}$)	Light capture economics, net assimilation rate, relative growth rate, leaf life span, photosynthetic capacity	[38,39]
Chlorophyll content, Chl (SPAD units)	Light uptake efficiency, photosynthetic rates	[39]
Leaf dry matter content, LDMC ($g.g^{-1}$)	Construction costs, nutrient retention, resistance against herbivory and physical damage, drought resistance	[37,38]
Leaf nitrogen (N) and phosphorus (P) concentration ($g.kg^{-1}$)	Photosynthetic rates, CO_2 assimilation, leaf nutrients levels	[19,20]
Leaf potassium, K ($g.kg^{-1}$)	Stomatal control, turgor provision and water homeostasis	[40]
Leaf Calcium, Ca ($g.kg^{-1}$)	Cellwall structure	[40]
Branch wood density, BWD ($g.cm^{-3}$)	Construction costs, growth rate, pathogen resistance, mortality rate	[36,41]
Lenticel density, LD (count of lenticels/10 cm^{-2})	Oxygen uptake, gas exchange	[26]
Height:diameter ratio of the plant, HDR ($m.cm^{-1}$)	Stability, competitive strength	[42,43]

Data analysis

To analyse how functional traits values vary within habitat types we calculated the mean value for each genera, and also the coefficient of variation for each forest type as the standard deviation multiplied by 100. To evaluate how functional traits vary between congeners in different habitat types (white- and black-water forests) we made for each trait a graph where the trait mean values of white- and black-water genera were paired. To evaluate if functional trait values diverge between forest types and genera we used a Linear mixed model for each functional trait, using forest type as a fixed effect and genus as a random effect [44]. For each trait, we compared models considering both habitat and genus ($model_1$) and considering only habitat ($model_2$) using likelihood ratio test, which indicates if models differ with the addition of genus effect [45]. To assess the importance of genus for trait variation we calculated the marginal and conditional R squared of each linear mixed model. The marginal R^2 describes the proportion of variance explained by the fixed effect (habitat), while the conditional R^2 describes the proportion of variance explained by both fixed and random effect (habitat + genus; [46]). When the conditional R^2 value is similar to marginal R^2, it indicates that the factor genus is not affecting plant traits. To verify whether an older evolutionary split would show the same pattern, we carried out the same analysis at the family level and compared the results. All analyses were carried out using the R platform [47].

Results

Traits divergence between forest types

All traits diverged between white- and black-water congeneric tree species (genus level comparison), except leaf chlorophyll content. White-water species had, on average, 1.2-3.0 times higher values of leaf area, specific leaf area and leaf nutrient concentrations, than congeneric black-water species. In contrast, black-water congeneric species had 1.2-2.7 times higher values of leaf dry matter content, branch wood density, lenticel density and height:diameter ratio (Table 3 and Fig 1). At the family level, the same traits had higher values for white-water or for black-water, maintaining the same patterns of trait variation for comparisons at an older phylogenetic level (family) as for comparisons at a more recent phylogenetic level (genus) (Table 4 and Fig 2). Frequently, trait variation among species within forest type was higher in the white-water forest than in the black-water forest, both when species comparisons were made at the genus level and the family level, indicated by the coefficient of variation (Tables 3 and 4). For some traits (especially leaf potassium and calcium), trait variation was larger in black-water forest than in white-water forest.

Table 3. Mean values of 11 functional traits of seven genera in white-water and black-water forests. The columns indicate trait mean values per genus: leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen (N), leaf phosphorus (P), leaf potassium (K), leaf calcium (Ca), branch-wood density (BWD), lenticel density (LD), height:diameter ratio (HDR). Trait mean values are based on 5 individuals per genera and coefficient of variation (*CV*) is based on all 33 species per forest type (see Table 2 for trait units).

Forest type	Genus level	LA	SLA	LDMC	Chl	N	P	K	Ca	BWD	LD	HDR
White-water	*Guatteria*	94.8	139.7	0.8	60.6	19.8	2.0	9.7	4.6	0.4	3.2	0.8
	Licania	47.0	127.5	0.3	45.4	15.5	1.3	10.3	7.6	0.6	1.7	0.7
	Zygia	43.1	135.5	0.3	50.9	26.8	1.7	11.4	4.9	0.7	1.6	0.7
	Ocotea	125.7	114.7	1.1	56.7	19.0	1.8	12.4	1.5	0.5	0.8	0.7
	Eschweilera	37.7	116.7	0.4	51.4	21.3	2.8	14.6	7.3	0.6	2.7	0.6
	Mouriri	67.4	96.2	1.2	59.4	16.6	1.2	11.0	6.4	0.7	0.7	0.7
	Pouteria	66.3	74.0	0.6	61.7	22.8	2.0	13.3	5.6	0.6	2.4	0.9
	mean	68.9	114.9	0.7	55.1	20.3	1.8	11.8	5.4	0.6	1.9	0.7
	CV	65	26	78	14	37	62	36	65	18	100	25
Black-water	*Guatteria*	82.0	66.4	2.1	52.5	12.8	0.8	3.9	6.0	0.6	3.0	1.5
	Licania	47.8	87.2	1.9	52.6	15.0	0.6	3.9	1.2	0.8	2.7	1.4
	Zygia	40.2	118.0	1.6	57.7	21.4	0.7	3.0	3.8	0.8	3.3	1.7
	Ocotea	51.7	83.2	1.7	51.0	13.8	0.5	2.8	1.5	0.6	1.0	1.3
	Eschweilera	38.9	80.8	2.0	57.2	17.1	0.6	3.2	2.4	0.7	4.4	1.5
	Mouriri	31.0	66.2	1.8	55.8	17.9	0.5	5.8	1.1	0.9	2.0	1.6
	Pouteria	35.5	74.1	1.7	52.0	13.2	0.4	4.8	1.1	0.8	1.8	1.5
	mean	46.7	82.3	1.8	54.1	15.9	0.6	3.9	2.4	0.8	2.6	1.5
	CV	45	31	13	10	23	36	40	89	15	78	25

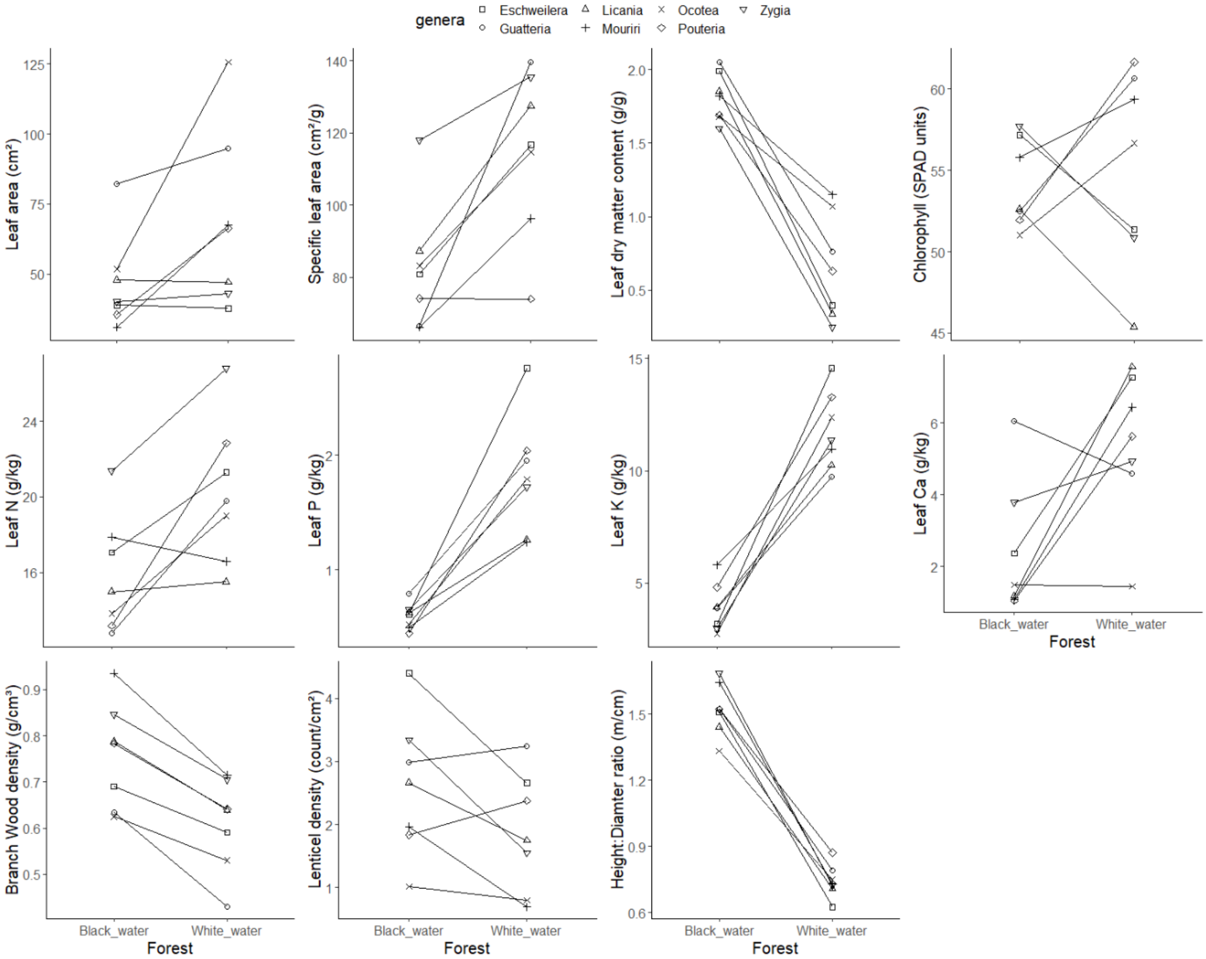

Fig 1. Mean values of leaf area, specific leaf area, leaf dry matter content, leaf chlorophyll, leaf nitrogen (N), leaf phosphorus (P), leaf potassium (K), leaf calcium (Ca), branch-wood density, lenticel density and height:diameter ratio for seven pairs of congeneric species of white-water and black-water forests. Lines connect the congeneric pairs. Mean values were based on 5 individuals per genus and forest type.

Table 4. Mean values of 11 functional traits of twelve families in white-water and black-water forests. The columns indicate trait mean values per family: leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen (N), leaf phosphorus (P), leaf potassium (K), leaf calcium (Ca), branch-wood density (BWD), lenticel density (LD), height:diameter ratio (HDR). Trait mean values are based on 5 individuals per family and coefficient of variation (*CV*) is based on all 54 genera per forest type (see Table 2 for trait units).

Forest type	Family	LA	SLA	LDMC	Chl	N	P	K	Ca	BWD	LD	HDR
White-water	Annonaceae	55.3	140.8	0.5	49.5	18.0	1.3	10.0	5.8	0.5	1.7	0.6
	Apocynaceae	70.7	148.0	0.8	54.7	19.6	1.5	12.2	5.2	0.5	2.3	0.6
	Chrysobalanaceae	45.3	127.3	0.3	49.5	18.0	1.6	10.1	9.2	0.6	1.6	0.6
	Euphorbiaceae	78.0	164.7	0.8	47.3	24.1	2.3	12.9	6.5	0.5	1.8	0.4
	Fabaceae	50.4	167.7	0.5	48.0	20.9	1.6	12.2	6.1	0.6	1.8	0.7
	Lauraceae	93.5	133.9	0.8	52.7	20.5	1.7	11.2	1.3	0.6	0.8	0.8
	Lecythidaceae	80.7	100.4	1.1	47.8	19.5	1.8	9.7	4.9	0.5	2.0	0.5
	Malvaceae	82.0	199.4	0.8	40.1	20.6	2.1	12.3	7.3	0.3	1.6	0.3
	Melastomataceae	65.0	98.5	1.1	60.7	16.9	1.3	11.9	6.0	0.7	0.9	0.6
	Moraceae	40.5	114.4	0.4	40.3	20.2	2.2	15.6	9.4	0.4	2.4	0.7
	Myrtaceae	54.2	119.8	0.6	53.4	16.3	1.3	10.9	7.1	0.6	1.2	0.6
	Sapotaceae	51.3	104.9	0.5	48.2	19.3	2.0	10.5	6.6	0.7	1.3	0.6
	mean-value	65.3	134.7	0.6	52.2	20.0	1.8	12.1	6.4	0.5	1.6	0.7
	CV	0.7	0.4	0.8	0.1	0.3	0.5	0.4	0.7	0.3	0.8	0.3
Black-water	Annonaceae	84.4	72.6	2.0	52.3	12.9	0.7	4.1	6.2	0.6	2.7	1.5
	Apocynaceae	69.6	132.5	2.7	57.0	20.1	0.9	5.1	4.0	0.7	4.5	2.6
	Chrysobalanaceae	31.7	95.7	6.1	48.9	12.7	0.5	3.4	1.2	0.8	3.6	1.8
	Euphorbiaceae	7.4	78.8	1.5	53.0	10.6	0.4	1.2	2.2	0.7	4.0	1.4
	Fabaceae	36.9	105.5	9.5	58.7	20.1	0.8	3.2	2.5	0.8	4.4	2.4
	Lauraceae	38.3	72.5	1.8	51.9	14.1	0.6	3.9	1.1	0.6	1.2	1.5
	Lecythidaceae	53.1	97.9	2.9	52.1	17.3	2.1	3.9	2.4	0.7	2.6	2.6
	Malvaceae	60.5	103.0	1.8	52.2	18.1	0.7	3.9	3.4	0.6	3.6	1.6
	Melastomataceae	55.0	75.9	1.7	60.0	17.0	0.5	3.2	1.4	1.0	2.0	1.4
	Moraceae	38.7	118.4	1.8	52.8	17.9	0.7	5.3	7.8	1.2	5.0	9.0
	Myrtaceae	35.2	95.0	1.7	54.3	12.4	0.7	2.7	1.8	0.8	4.2	2.3
	Sapotaceae	35.5	69.8	7.5	53.0	13.4	0.5	4.5	1.3	0.8	2.7	2.8
	mean-value	45.0	91.5	1.8	53.7	15.6	0.7	4.3	2.8	0.7	3.3	1.8
	CV	0.6	0.3	0.2	0.1	0.2	0.7	0.9	0.9	0.2	0.6	0.4

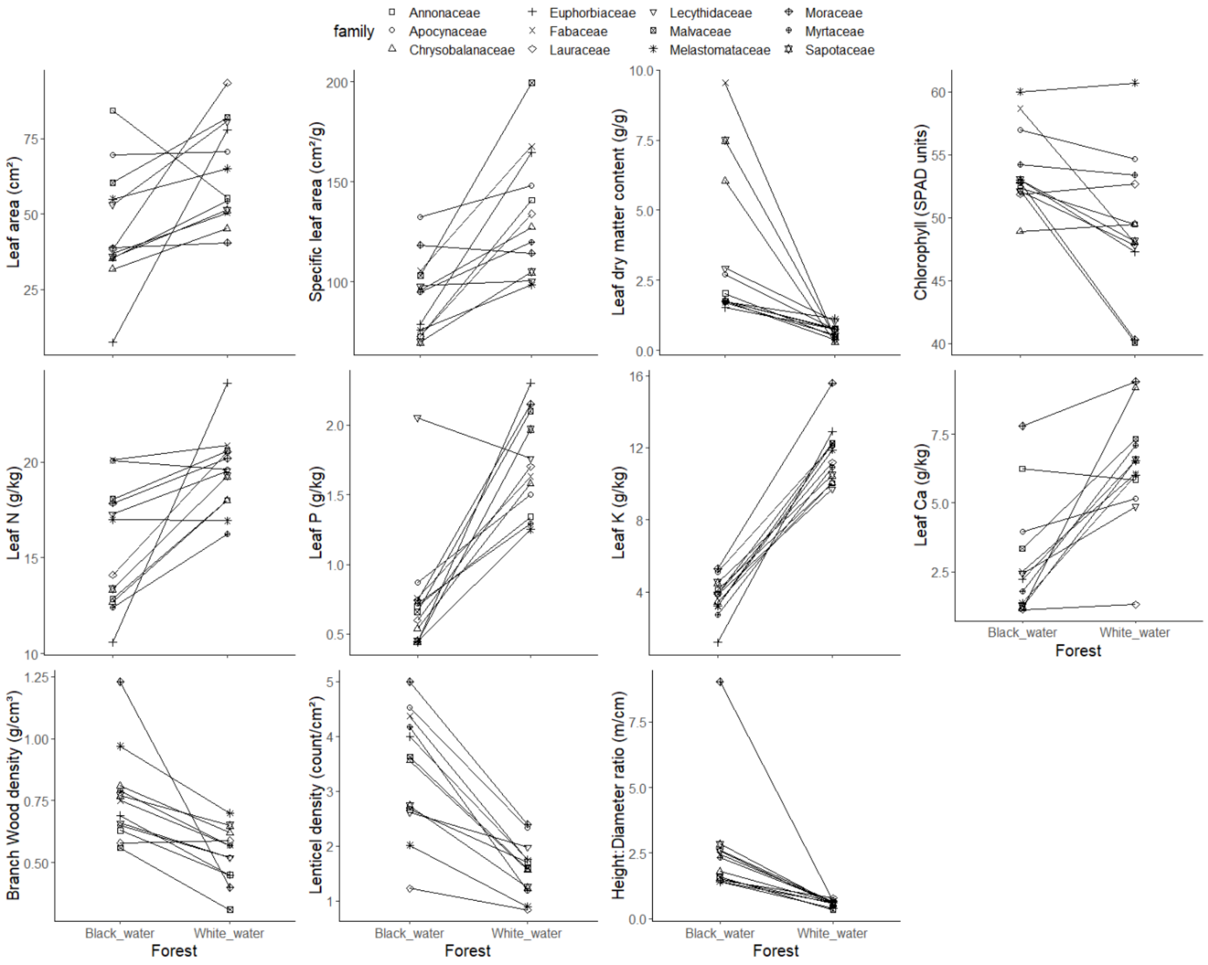

Fig 2. Mean values of leaf area, specific leaf area, leaf dry matter content, leaf chlorophyll, leaf nitrogen (N), leaf phosphorus (P), leaf potassium (K), leaf calcium (Ca), branch-wood density, lenticel density and height:diameter ratio for twelve pairs of families of white-water and black-water forests. Lines connect the family pairs. Mean values are based on 5 individuals per family and forest type.

The influence of habitat on trait divergence

All functional traits except leaf chlorophyll content and lenticel density varied significantly between forest types. The likelihood ratio test was not significant for leaf phosphorus, potassium, calcium and height:diameter, indicating that both models have the same support. This means that genus does not have a strong effect on trait values (Table 5) and that habitat has a stronger effect on trait values than genus. Leaf area, specific leaf area, leaf dry matter content, leaf nitrogen and branch wood density had higher likelihood values of models considering habitat and genus effect, which indicates that the variance was explained by both habitat and genus. The marginal and conditional R^2 differed little, especially for leaf nutrient concentration, leaf dry matter content and height:diameter ratio, which indicates that genus is not strongly affecting plant traits. A similar pattern was observed at the family level, but most of traits were explained by both habitat and family effect. The likelihood ratio test was not significant for leaf area, leaf dry matter content, leaf nitrogen and height:diameter ratio, indicating a strong effect of habitat. Specific leaf area, leaf calcium, phosphorus, potassium and lenticel density were best explained by the model considering habitat and family. The differences between marginal and conditional R^2 differed little too, suggesting that family, as well as genus, is not strongly influencing plant trait variation beyond habitat.

Table 5. Variation in 11 functional traits of white- and black-water flooded forests considering pairing at genus and family level. The columns indicate β-coefficient, p-value, marginal R squared (variance explained by the fixed effect (habitat); r^2m), conditional R squared (variance explained by the fixed effect + random effect (habitat + genus/family); r^2c) and likelihood ratio test (p-value indicates if models differ; ratio was calculated as model$_1$ (habitat + genus/family)/model$_2$ (habitat)).

Plant	Genus						Family					
trait	β-coefficient	p-value	r^2 m	r^2 c	likelihood		β-coefficient	p-value	r^2 m	r^2 c	likelihood	
					ratio	p-value					ratio	p-value
LA	22.12	0.003	0.09	0.34	5.4	0.001	20.28	0.002	0.07	0.12	0.6	0.26
SLA	32.62	<0.001	0.24	0.46	5.7	<0.001	43.22	<0.01	0.20	0.32	3.4	<0.001
LDMC	-1.15	<0.001	0.67	0.72	1.9	0.05	-1.21	<0.01	0.69	0.71	0.4	0.37
Chl	1.02	0.51	0.01	0.09	0.8	0.21	-1.44	0.24	0.01	0.13	2.3	0.03
N	4.39	0.001	0.11	0.25	1.9	0.04	4.4	<0.01	0.16	0.24	1.7	0.06
P	1.23	<0.001	0.36	0.37	0	0.85	1.11	<0.01	0.33	0.43	3.7	0.006
K	7.87	<0.001	0.60	0.60	0	0.99	7.82	<0.01	0.40	0.50	4.1	0.004
Ca	2.97	<0.001	0.20	0.27	0.7	0.22	3.55	<0.01	0.20	0.32	3.6	0.007
BWD	-0.15	<0.001	0.28	0.81	33	<0.001	-0.16	<0.01	0.23	0.52	16.1	<0.001
LD	-0.73	0.1	0.00	0.15	1.4	0.09	-1.67	<0.01	0.17	0.33	5.4	0.001
HDR	-0.78	<0.001	0.62	0.62	0	0.99	-1.14	<0.01	0.48	0.49	1.7	0.06

Discussion

We asked whether functional traits of tree species diverge between habitats differing in soil nutrient availability, and if habitat conditions are driving trait differentiation despite differences amongst genera in their evolutionary history. We found that white-water species have traits related to resource acquisition and fast-growth, while black-water species have traits related to resource conservation and persistence. Habitat effect was important to cause traits variation, even for less plastic traits.

Traits divergence between habitat types

Plant species show different strategies to deal with rich and poor soils [48,49]. The trade-off in tissue investment that we observed in our study reflect different strategies to deal with the differences in soil nutrient availability between the two habitats. We hypothesized that congeneric species from white-water would have acquisitive trait values associated with fast-growth in a resource-rich environment whereas congeneric species from black-water would have more conservative trait values associated with persistence in a resource-poor environment. Congeneric species from white-water had indeed higher leaf area, specific leaf area and leaf nutrient concentrations which are related to high light capture, photosynthetic rates and carbon gain [19,20,38,39,50]. These characteristics result in productive plants with a short-life cycle [19,39]. White-water species had a lower height:diameter ratio. A low HDR increases plant stability against water and wind [43] and may allow white-water species to resist to disturbance from the higher water movement that is typical for white-water forests [30,51].

Congeneric species from black-water had, in contrast, higher leaf dry matter content and branch wood density. When resources are limiting, as in black-water forest, species tend to invest in strong tissues and plant longevity [36,38,41]. A small leaf area and high leaf dry matter content allow black-water species to adapt to low nutrient availability, by increasing longevity and reducing growth rate [49]. These traits are indirectly influenced by flooding and more related to plant age [52].

We also hypothesized that trait variation within forests would differ, and that in white-water forests it would be higher than in black-water forests because black-water forest is a resource-limited habitat, which imposes a strong selection filter. Trait variation in white-water forest was indeed higher than black-water forest for most traits (Table 3 and Fig 1). This result can be related to the stronger habitat filtering in black-water forest that leads to similar traits and strategies [1], or because it has a lower number of species than white-water forest, resulting in a lower trait variation. The larger variation in leaf nutrient concentrations in black-water forests may be related to stronger niche differentiation for nutrients and, hence, a larger variation in nutrient strategies in this nutrient-poor environment [53].

The influence of habitat on trait divergence

We hypothesized that trait divergence between white- and black-water forest would be related to abiotic conditions (habitat types), indicating habitat specialization by white- water and by black-water species. Habitat type is indeed important for the divergence of labile traits between the two forests types, such as leaf dry matter content, leaf nutrient concentration and height:diameter ratio, leading to species adaptation for different habitats.

Some traits are phylogenetically conserved, but still show to some extent phenotypic plasticity. Wood density, for instance, is considered to be more conserved [54–56], but can vary in relation to environmental conditions, as flooding and soil nutrients [57–59]. Specific leaf area is very plastic in response to light availability [60], but varies very little in response to water availability [61]. In our study, wood density and specific leaf area were both affected by habitat (i.e., forest type) and by phylogeny (i.e., genus). These traits values diverged between forest types, but maintained a similar pattern within the same taxa, especially for branch wood density. For example, the genus *Mouriri* was the genus with denser wood in white-water forests (0.71 g.cm^{-3}) and also the genus with denser wood in black-water forests

(0.93 g.cm^{-3}). When you compare the genus *Mouriri* between forest types black-water species have denser wood, but when you compare genera within habitats *Mouriri* was the genus with denser wood in both habitats (Fig 1). This result suggest that differences between habitat leads to trait variation among forests, but there is also a variation within forest type caused by differences amongst co-occurring genera.

Other traits are more labile and can respond faster to selective pressures adapting to environmental conditions, such as leaf nitrogen and leaf dry matter content [62,63]. Leaf nutrient concentration, leaf dry matter content and height:diameter ratio are related to plant growth, resource acquisition and competition [20,42], and were mainly related to habitat type (Table 5). Variation in these traits was not caused by genus identity. The convergence of these traits values within habitat, independent of genus, suggests that there is an environmental selection of these traits, and can be an ecological adaptation in response to the differences in soil conditions between black- and white-water floodplain forests.

The divergence of traits between habitats in related species can be an indication of habitat specialization to soil properties [4,12,64]. The increasing evidence of the importance of local abiotic conditions and habitat diversity for traits and species variation in the Amazonian forests [6,8], suggests that habitat specialization is an important process driving plant communities, and that trait lability probably contributes to this specialization, because it improves species adaptation to the environment [61]. Even for less labile traits, the habitat soil conditions seem to be influencing trait differentiation. The trait divergence between the congeners in theses floodplain forests seems to be, therefore, a result of habitat specialization, contributing to floristic differentiation between these areas and, hence, increasing overall species diversity.

Conclusions

Functional traits of floodplain congeneric tree species diverge between forest types with different soil resource availability, resulting in a trade-off in tissue investment in resource acquisition and productive tissues in white-water species versus resource conservation and persistent tissues in black-water species. Both phenotypic plasticity and lability of traits are leading to habitat specialization and differentiation of floodplain tree species of white-water and black-water forests, thus contributing to a high diversity of plant species in floodplain forests.

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Supporting Information

S1 Table. Species of white-water and black-water forest belonging to seven genus and to twelve families. The columns indicate the phylogenetic level (genus and family) and the species belonging to each genus/ family in white-water and black-water forests.

Phylogenetic level	Species	
Genus	White-water forest	black-water forest
Eschweilera (Lecythidaceae)	*Eschweilera albiflora*	*Eschweilera albiflora*
	Eschweilera ovalifolia	*Eschweilera parviflora*
	Eschweilera parviflora	*Eschweilera tessmannii*
Guatteria (Annonaceae)	*Guatteria inundata*	*Guatteria guianensis*
	Guatteria sp.	
Licania (Chrysobalanaceae)	*Licania apetala*	*Licania apetala*
	Licania heteromorpha	*Licania heteromorpha*
	Licania micranta	*Licania macrophylla*
		Licania hypoleuca
		Licania longistyla
Mouriri (Melastomataceae)	*Mouriri guianensis*	*Mouriri brevipes*
	Mouriri sp. *A*	*Mouriri* sp. *B*
Ocotea (Lauraceae)	*Ocotea matogrossensis*	*Ocotea aciphylla*
	Ocotea cymbarum	*Ocotea adenotrachelium*
	Ocotea sp.	
Pouteria (Sapotaceae)	*Pouteria elegans*	*Pouteria pachyphylla*
	Pouteria glomerata	
Zygia (Fabaceae)	*Zygia ampla*	*Zygia cataractae*
	Zygia cataractae	
	Zygia latifolia	
	Zygia sp.	
Family		
Annonaceae	*Duguetia spixiana*	*Guatteria guianensis*
	Guatteria inundata	
	Oxandra riedeliana	
	Unonopsis guaterioides	
	Xylopia sp.	
Apocynaceae	*Aspidosperma guianensis*	*Aspidosperma excelsum*
	Aspidosperma rigidum	*Himatanthus articulatus*
	Malouetia sp.	
	Malouetia tamaquarina	
Chrysobalanaceae	*Couepia paraensis*	*Gaulettia parillo*
	Licania apetala	*Licania apetala*
	Licania heteromorpha	*Licania gracilipes*
	Licania micranta	*Licania heteromorpha*
	Parinari excelsa	*Licania macrophylla*
Euphorbiaceae	*Alchornea shomburkiana*	*Alchornea discolor*

	Hevea spruceana	*Hevea benthamiana*
	Hura crepitans	*Mabea nitida*
	Mabea nitida	*Maprounea guianensis*
	Piranhea trifoliolata	
Fabaceae	*Acosmium nitens*	*Campsiandra comosa*
	Campsiandra comosa	*Eperua duckeana*
	Inga splendens	*Macrolobium angustifolium*
	Swartzia laurifolia	*Swartzia polyphylla*
	Zygia cataractae	*Zygia cataractae*
Lauraceae	*Ocotea cymbarum*	*Ocotea aciphylla*
		Ocotea adenotrachelium
Lecythidaceae	*Couroupita guianensis*	*Couratari tenuicarpa*
	Eschweilera albiflora	*Eschweilera albiflora*
	Eschweilera parviflora	*Eschweilera parvifolia*
	Gustavia augusta	*Lecythis lurida*
	Lechytis lurida	
Malvaceae	*Apeiba echinata*	*Mollia lepidota*
	Ceiba pentandra	
	Luehea cymulosa	
	Pseudobombax munguba	
	Theobroma cacao	
Melastomataceae	*Mouriri grandifolia*	*Miconia argyrophylla*
	Mouriri guianensis	*Mouriri brevipes*
	Mouriri sp. A	*Mouriri* sp. B
Moraceae	*Batocarpus amazonicus*	*Brosimum guianense*
	Ficus maxima	*Brosimum sp.*
	Maquira coriacea	*Ficus maxima*
	Sorocea duckei	
Myrtaceae	*Calypthrantes multiflora*	*Blepharocalyx eggersii*
	Calyptranthes sp.	*Calyptranthes forsteri*
	Eugenia inundata	*Eugenia* sp. B
	Eugenia sp. A	*Myrcia amazonica*
		Plinia sp.
Sapotaceae	*Chrysophyllum argentum*	*Elaeoluma schomburgkiana*
	Micropholis egensis	*Manilkara bidentata*
	Micropholis guianensis	*Micropholis melinoniana*
	Pouteria elegans	*Pouteria pachyphylla*
	Pouteria glomerata	

S2 Table. Eleven functional trait measured of 5 individuals in seven genera at white-water and black-water forests. The columns indicate forest type, family, genera, species and functional trait values: leaf area (cm^2), specific leaf area (cm^2.g^{-1}), leaf dry matter content (g.g^{-1}), chlorophyll content (SPAD units), leaf nitrogen (g.kg^{-1}), leaf phosphorus (g.kg^{-1}), leaf potassium (g.kg^{-1}), leaf calcium (g.kg^{-1}), branch wood density (g.cm^{-3}), lenticel density (count in 10 cm^{-2}), and the Height:diameter ratio (m.cm^{-1}).

Forest type	Family	Genera	Species	Leaf area (cm^2)	Specific leaf area (cm^2.g^{-1})	Leaf dry matter content (g.g^{-1})	Chlorophyll content (SPAD units)	Leaf nitrogen (g.kg^{-1})	Leaf phosphorus (g.kg^{-1})	Leaf potassium (g.kg^{-1})	Leaf calcium (g.kg^{-1})	Branch wood density (g.cm^{-3})	Lenticel density (count/10 cm^2)	Height:diameter ratio (m.cm^{-1})
Black-water	Annonaceae	*Guatteria*	*Guatteria guianensis*	63.08	56.94	2.03	56.40	13.69	0.68	4.89	4.92	0.66	4.5	2.2
				94.48	58.85	1.98	58.50	13.30	0.66	3.09	5.10	0.64	1.8	1.4
				58.06	73.57	2.27	48.00	12.12	0.63	4.82	5.76	0.60	4.0	1.1
				99.29	69.02	2.10	51.00	12.57	1.56	2.67	7.86	0.65	3.6	1.5
				95.20	73.69	1.89	48.50	12.15	0.40	4.00	6.57	0.62	1.0	1.4
	Chrysobalanaceae	*Licania*	*Licania apetala*	20.26	87.55	1.64	55.20	15.43	0.50	3.20	1.19	0.81	4.0	1.2
			Licania heteromorpha	76.72	70.71	1.92	59.50	15.20	0.53	3.09	0.62	0.67	4.0	1.1
			Licania macrophylla	22.67	42.61	1.79	54.20	13.50	0.69	3.14	0.14	0.79	0.0	1.7
			Licania hypoleuca	47.70	141.45	2.08	38.30	14.14	0.84	8.27	1.34	0.82	4.0	1.3
			Licania longistyla	71.47	93.77	1.83	55.80	16.63	0.52	1.97	2.62	0.84	1.3	1.8
	Fabaceae	*Zygia*	*Zygia cataractae*	31.26	127.05	1.64	53.40	23.04	0.76	2.67	2.00	0.78	3.0	1.2
				42.26	135.29	1.60	59.80	24.14	0.82	3.24	1.40	0.88	5.0	1.7
				50.65	108.03	1.66	62.80	22.48	0.42	4.10	7.92	0.80	0.7	1.7
				39.76	102.42	1.58	58.40	17.44	0.63	2.52	4.11	0.84	4.0	1.6
				37.00	117.24	1.53	54.20	19.80	0.61	2.44	3.52	0.93	4.0	2.3
	Lauraceae	Ocotea	*Ocotea aciphylla*	37.91	67.77	1.73	47.00	13.41	0.57	2.54	1.34	0.66	1.3	1.2
				53.28	61.88	1.45	56.70	12.15	0.43	1.85	2.03	0.62	1.5	1.0
				66.82	69.96	1.49	41.80	11.42	0.43	2.02	1.47	0.61	1.2	0.9
			Ocotea adenotrachelium	37.51	57.77	1.57	58.30	12.01	0.51	1.97	0.62	0.66	0.0	2.2
				63.04	158.71	2.14	51.30	20.16	0.66	5.43	1.97	0.58	1.1	1.4
	Lecythidaceae	*Eschweilera*	*Eschweilera albiflora*	41.60	75.72	2.49	57.20	18.62	0.45	2.39	1.26	0.74	1.7	1.5
				49.58	91.81	1.98	60.10	13.24	0.52	2.94	6.18	0.60	11.2	1.1
			Eschweilera parviflora	30.40	72.11	1.71	54.10	19.71	0.83	2.02	0.64	0.63	2.6	2.4
				19.73	72.95	1.77	50.90	15.48	0.56	3.97	2.08	0.75	4.0	1.5
			Eschweilera tessmannii	53.11	91.44	2.01	63.60	18.20	0.71	4.59	1.68	0.73	2.5	1.1

	Melastomataceae	*Mouriri*	*Mouriri brevipes*	32.69	68.19	1.82	51.30	15.51	0.44	6.84	1.83	0.93	1.1	2.3
				24.17	60.28	1.55	56.20	14.36	0.37	4.96	1.48	0.92	1.2	1.4
				38.72	70.13	1.91	51.90	15.71	0.45	6.08	1.02	0.99	5.0	1.2
			Mouriri sp. *B*	28.28	64.45	1.91	63.10	21.81	0.60	6.06	0.55	0.91	1.3	1.9
				31.16	67.76	1.89	56.40	22.01	0.60	5.11	0.57	0.92	1.3	1.5
	Sapotaceae	Pouteria	*Pouteria pachyphylla*	49.44	77.55	1.67	57.10	14.78	0.43	3.97	0.93	0.76	2.1	1.2
				27.26	76.23	1.69	49.20	15.37	0.47	3.64	0.95	0.77	2.2	1.7
				28.28	69.31	1.78	50.00	12.26	0.41	6.07	1.42	0.84	1.8	1.7
				33.83	66.75	1.71	53.60	11.28	0.34	5.43	1.31	0.74	1.7	1.4
				38.87	80.65	1.62	49.90	12.21	0.53	5.00	0.66	0.82	1.3	1.6
White-water	Annonaceae	Guatteria	*Guatteria inundata*	97.52	196.61	0.64	52.20	13.80	1.07	13.20	9.64	0.38	1.1	0.7
				104.21	124.02	1.10	61.70	20.92	4.87	14.40	4.85	0.41	0.9	0.8
				139.81	124.78	0.86	68.00	19.10	1.20	4.18	4.09	0.47	0.7	0.8
			Guatteria sp.	49.58	108.59	0.55	60.40	24.25	1.28	8.80	1.78	0.49	10.0	0.9
				82.78	144.32	0.65	60.90	20.86	1.31	8.00	2.58	0.39	3.6	0.8
	Chrysobalanaceae	Licania	*Licania apetala*	18.56	113.19	0.11	41.30	16.66	1.38	5.23	1.09	0.56	0.0	0.4
				26.33	172.51	0.11	53.20	19.15	1.24	15.60	10.18	0.59	1.5	0.3
			Licania heteromorpha	54.19	102.52	0.16	40.50	13.50	1.19	10.80	11.96	0.71	3.0	0.6
				68.69	134.21	0.74	42.20	13.24	1.69	11.20	5.45	0.60	2.4	1.1
			Licania micranta	67.37	115.20	0.55	49.60	15.04	0.79	8.40	9.14	0.73	1.8	1.2
	Fabaceae	Zygia	*Zygia ampla*	23.47	135.01	0.16	45.00	51.24	1.54	10.00	4.39	0.75	2.3	0.8
			Zygia cataractae	25.67	120.84	0.10	47.60	21.45	2.30	9.20	2.42	0.78	1.5	0.9
			Zygia latifolia	86.63	148.08	0.54	56.60	12.68	1.46	12.80	4.02	0.63	1.5	0.7
				61.41	153.23	0.32	49.00	25.37	2.25	18.00	6.21	0.68	0.4	0.8
			Zygia sp.	18.15	120.54	0.15	56.10	23.27	1.07	6.80	7.63	0.69	2.0	0.5
	Lauraceae	Ocotea	*Ocotea matogrossensis*	75.46	74.68	0.86	73.20	16.52	1.58	4.24	3.88	0.43	0.6	0.6
			Ocotea cymbarum	169.32	116.70	1.43	51.90	16.21	1.82	13.60	1.26	0.57	0.9	0.8
				117.71	134.22	0.91	55.20	20.83	1.70	13.60	0.63	0.58	0.8	0.8
				119.68	121.13	1.02	55.70	20.19	2.15	16.40	0.60	0.53	1.1	0.8
			Ocotea sp.	146.12	126.54	1.11	47.30	21.25	1.72	14.00	0.88	0.54	0.6	0.7
	Lecythidaceae	Eschweilera	*Eschweilera albiflora*	31.17	150.60	0.30	55.30	18.65	3.25	15.20	6.58	0.60	2.1	0.5
				30.93	141.21	0.27	43.40	30.24	6.21	19.20	3.81	0.58	6.2	0.7
			Eschweilera ovalifolia	37.15	101.84	0.45	50.30	18.48	1.56	13.60	13.02	0.55	0.5	0.5
				42.75	101.22	0.47	54.40	19.24	1.18	11.60	9.05	0.53	2.4	0.8

		Eschweilera parviflora	46.60	88.70	0.50	53.40	19.88	1.58	13.20	3.85	0.69	2.2	0.6
Melastomataceae	Mouriri	*Mouriri guianensis*	98.96	87.84	1.68	60.70	13.78	0.84	12.40	11.47	0.64	0.8	0.5
			25.15	107.39	0.21	58.80	20.19	1.66	10.40	2.95	0.84	0.0	0.7
			149.63	99.49	2.57	58.80	16.60	1.41	8.85	6.56	0.70	1.3	0.6
			32.95	91.94	0.64	60.20	14.36	0.72	12.40	6.25	0.72	0.8	0.8
		Mouriri sp. *A*	30.33	94.48	0.63	58.30	18.03	1.56	10.80	4.90	0.68	0.6	1.1
Sapotaceae	Pouteria	*Pouteria elegans*	50.90	69.03	0.54	69.00	35.14	3.12	20.80	2.29	0.77	2.8	0.9
			26.00	72.22	0.26	59.00	33.60	3.30	21.20	6.18	0.65	2.5	0.7
			39.76	68.33	0.44	58.20	17.14	0.84	7.60	12.75	0.59	1.4	1.0
			49.03	66.55	0.53	63.00	13.30	0.88	7.20	3.58	0.66	0.9	0.9
		Pouteria glomerata	165.79	93.74	1.36	59.10	15.01	2.07	9.60	3.31	0.54	4.3	0.9

S3 Table. Eleven functional trait measured in 5 individuals of twelve families at white-water and black-water forests. The columns indicate forest type, family, genera, species and functional trait values: leaf area (cm^2), specific leaf area ($cm^2.g^{-1}$), leaf dry matter content ($g.g^{-1}$), chlorophyll content (SPAD units), leaf nitrogen ($g.kg^{-1}$), leaf phosphorus ($g.kg^{-1}$), leaf potassium ($g.kg^{-1}$), leaf calcium ($g.kg^{-1}$), branch wood density ($g.cm^{-3}$), lenticel density (count in 10 cm^{-2}), and the Height:diameter ratio ($m.cm^{-1}$).

Forest type	Family	Genera	Species	Leaf area (cm^2)	Specific leaf area ($cm^2.g^{-1}$)	Leaf dry matter content ($g.g^{-1}$)	Chlorophyll content (SPAD units)	Leaf nitrogen ($g.kg^{-1}$)	Leaf phosphorus ($g.kg^{-1}$)	Leaf potassium ($g.kg^{-1}$)	Leaf calcium ($g.kg^{-1}$)	Branch wood density ($g.cm^{-3}$)	Lenticel density (count/10 cm^2)	Height:diameter ratio ($m.cm^{-1}$)
Black-water	Annonaceae	*Guatteria*	*Guatteria guianensis*	63.08	56.94	2.03	56.40	13.69	0.68	4.89	4.92	0.66	4.5	2.2
				94.48	58.85	1.98	58.50	13.30	0.66	3.09	5.10	0.64	1.8	1.4
				58.06	73.57	2.27	48.00	12.12	0.63	4.82	5.76	0.60	4.0	1.1
				99.29	69.02	2.10	51.00	12.57	1.56	2.67	7.86	0.65	3.6	1.5
				95.20	73.69	1.89	48.50	12.15	0.40	4.00	6.57	0.62	1.0	1.4
	Apocynaceae	*Aspidosperma*	*Aspidosperma excelsum*	25.87	95.61	2.04	59.70	13.55	0.42	5.97	6.83	0.85	9.0	3.0
				38.72	80.23	2.02	63.50	15.85	0.69	4.70	2.97	0.82	4.0	2.5
				30.22	76.43	1.87	52.10	13.89	0.59	5.67	3.42	0.82	4.0	1.8
				38.72	80.23	2.02	63.50	15.85	0.69	4.70	2.97	0.82	4.0	2.5
		Himatanthus	*Himatanthus articulatus*	103.25	180.94	3.44	51.70	26.01	1.22	5.08	3.08	0.48	4.5	3.5
	Chrysobalanaceae	*Gaulettia*	*Gaulettia parillo*	17.79	120.87	1.72	35.90	10.19	0.53	5.25	1.11	0.84	0.0	1.5
		Licania	*Licania apetala*	20.26	87.55	1.64	55.20	15.43	0.50	3.20	1.19	0.81	4.0	1.2
			Licania gracilipes	12.26	126.68	1.60	53.30	14.64	0.26	3.16	1.57	0.92	4.0	2.7
			Licania heteromorpha	48.62	79.88	1.79	48.50	10.67	0.57	2.19	0.86	0.83	7.0	0.9
			Licania macrophylla	25.30	94.54	1.98	50.20	15.88	1.36	3.78	0.34	0.78	1.9	1.8
	Euphorbiaceae	*Alchornea*	*Alchornea discolor*	66.82	86.11	1.80	45.30	13.38	0.71	2.23	3.14	0.74	3.8	1.4
		Hevea	*Hevea benthamiana*	85.96	124.61	2.06	59.20	14.34	0.40	3.20	1.23	0.56	1.5	1.1
		Mabea	*Mabea nitida*	64.14	99.63	1.92	52.70	18.40	0.67	3.74	2.23	0.65	0.0	1.2
				37.50	76.58	1.70	59.50	9.63	0.38	3.81	1.23	0.87	6.0	1.7
		Maprounea	*Maprounea guianensis*	7.42	78.75	1.54	53.00	10.58	0.44	1.19	2.24	0.69	4.0	1.4
	Fabaceae	*Campsiandra*	*Campsiandra comosa*	50.29	128.68	1.95	45.10	18.68	0.65	3.72	1.07	0.75	8.0	2.1
		Eperua	*Eperua duckeana*	52.45	67.95	1.73	56.30	14.42	0.66	6.10	1.06	0.78	1.6	1.4

	Macrolobium	*Macrolobium angustifolium*	10.35	99.11	1.87	65.10	18.12	0.86	4.04	3.67	0.70	6.0	1.9
	Swartzia	*Swartzia polyphylla*	51.44	73.53	2.21	63.80	25.68	1.87	4.99	1.68	0.57	5.0	3.7
	Zygia	*Zygia cataractae*	28.11	93.01	1.44	55.40	21.42	0.71	1.60	2.38	0.76	2.5	2.5
Lauraceae	Ocotea	*Ocotea aciphylla*	52.99	89.30	1.83	54.40	14.31	0.56	2.99	1.38	0.59	0.6	1.3
			37.91	67.77	1.73	47.00	13.41	0.57	2.54	1.34	0.66	1.3	1.2
		Ocotea a denotrachelium	37.86	72.80	1.76	52.50	13.89	0.57	4.99	1.81	0.55	2.4	1.7
			31.76	66.19	1.78	54.60	14.56	0.66	4.93	0.40	0.53	0.0	1.7
			30.81	66.69	1.69	50.90	14.34	0.62	4.07	0.74	0.56	1.9	1.3
Lecythidaceae	*Couratari*	*Couratari tenuicarpa*	43.39	114.25	2.12	58.80	17.56	0.48	5.27	5.16	0.63	2.4	2.3
			38.92	59.84	2.10	67.90	19.01	0.77	5.01	2.21	0.58	2.0	1.1
	Eschweilera	*Eschweilera albiflora*	42.13	90.33	1.79	50.10	16.24	0.75	1.64	0.66	0.69	1.5	2.7
		Eschweilera parvifolia	47.16	79.88	1.82	52.10	17.39	0.51	3.26	1.62	0.74	2.8	1.5
	Lecythis	*Lecythis lurida*	109.65	60.70	1.49	66.40	16.80	0.54	1.52	0.32	0.73	5.0	3.1
Malvaceae	*Mollia*	*Mollia lepidota*	50.61	113.17	1.99	46.10	17.39	0.50	4.67	5.45	0.59	1.1	0.9
			35.03	91.46	2.00	56.10	17.28	0.62	3.27	5.09	0.57	5.0	0.9
			66.42	91.97	1.62	46.20	14.73	0.63	3.38	5.76	0.65	3.8	0.8
			68.68	191.41	2.09	46.20	19.88	0.75	6.56	2.60	0.52	4.2	1.2
			78.41	139.82	1.82	44.20	18.17	0.81	5.20	7.70	0.00	3.0	4.7
Melastomataceae	Miconia	*Miconia argyrophylla*	68.22	87.35	1.73	63.20	16.86	0.42	2.14	1.55	1.04	1.8	1.3
	Mouriri	*Mouriri brevipes*	32.69	68.19	1.82	51.30	15.51	0.44	6.84	1.83	0.93	1.1	2.3
			24.17	60.28	1.55	56.20	14.36	0.37	4.96	1.48	0.92	1.2	1.4
		Mouriri sp. B	30.45	62.70	1.75	48.80	17.64	0.43	4.38	1.14	0.91	4.0	1.5
			70.99	46.77	1.57	65.70	16.80	0.46	2.37	0.84	0.91	0.0	1.3
Moraceae	*Brosimum*	*Brosimum guianense*	27.70	116.89	1.81	55.90	25.37	0.89	4.06	3.19	0.70	5.0	2.9
			18.44	131.55	1.61	58.10	20.33	0.79	2.12	6.59	0.81	5.0	2.0
			24.55	99.22	1.48	59.70	17.08	0.62	4.09	7.24	0.71	4.0	1.9
		Brosimum sp.	25.77	77.42	1.88	47.50	20.64	1.03	4.75	0.68	0.65	7.0	2.2
	Ficus	*Ficus maxima*	101.77	179.04	1.11	41.00	20.10	3.93	32.40	12.76	0.46	2.8	0.4
Myrtaceae	*Blepharocalyx*	*Blepharocalyx eggersii*	6.96	94.53	1.92	56.20	12.07	0.15	1.58	0.47	0.69	4.0	1.5
	Calyptranthes	*Calyptranthes forsteri*	19.08	116.21	1.81	62.00	13.66	0.41	3.45	2.33	0.90	3.6	3.9

		Eugenia	*Eugenia* sp. B	20.42	95.59	1.83	53.80	11.31	0.50	1.99	1.13	0.84	4.0	1.5
		Myrcia	*Myrcia amazonica*	23.30	96.27	1.61	49.20	11.23	0.46	0.70	1.00	0.84	10.0	1.8
		Plinia	*Plinia* sp.	68.43	98.32	1.64	53.70	14.11	0.50	3.70	2.02	0.76	4.2	1.9
	Sapotaceae	*Elaeoluma*	*Elaeoluma schomburgkiana*	14.23	82.43	1.89	61.70	11.28	0.38	2.13	1.77	0.73	2.4	1.5
		Manilkara	*Manilkara bidentata*	34.12	87.97	2.16	44.50	13.89	0.62	11.02	1.86	0.72	1.4	1.6
		Micropholis	*Micropholis melinoniana*	41.55	70.64	1.49	55.00	11.12	0.35	0.44	2.03	0.91	1.6	1.7
		Pouteria	*Pouteria pachyphylla*	27.26	76.23	1.69	49.20	15.37	0.47	3.64	0.95	0.77	2.2	1.7
				25.07	61.76	1.64	41.70	11.82	0.41	4.87	1.05	0.76	1.1	2.0
White-water	Annonaceae	*Duguetia*	*Duguetia spixiana*	49.14	128.10	0.37	60.60	22.85	1.69	12.00	5.19	0.65	0.0	0.6
		Guatteria	*Guatteria inundata*	97.52	196.61	0.64	52.20	13.80	1.07	13.20	9.64	0.38	1.1	0.7
		Oxandra	*Oxandra riedeliana*	36.45	131.38	0.36	67.80	21.78	1.55	13.20	10.57	0.48	2.0	0.7
		Unonopsis	*Unonopsis guaterioides*	49.20	107.15	0.35	58.40	15.99	2.07	6.80	6.56	0.50	0.8	0.6
		Xylopia	*Xylopia* sp.	12.19	153.50	0.06	57.10	22.46	1.45	10.80	2.99	0.43	3.0	1.1
	Apocynaceae	*Aspidosperma*	*Aspidosperma guianensis*	44.72	129.63	0.48	55.00	23.18	2.21	16.40	4.73	0.67	5.0	0.7
			Aspidosperma rigidum	28.11	131.09	0.28	54.80	18.56	0.88	10.00	3.47	0.52	0.7	0.8
		Malouetia	*Malouetia* sp.	61.39	134.22	0.70	62.90	20.22	1.61	18.40	7.39	0.49	0.6	0.5
			Malouetia tamaquarina	86.72	119.02	1.19	56.20	20.10	1.44	15.60	2.22	0.51	2.7	0.5
				62.03	170.69	0.80	45.50	15.90	1.86	8.00	14.81	0.46	3.5	0.7
	Chrysobalanaceae	*Couepia*	*Couepia paraensis*	113.32	130.68	0.73	44.20	13.78	0.91	12.40	2.27	0.59	3.0	0.5
		Licania	*Licania apetala*	33.28	132.59	0.30	41.70	16.32	1.19	6.08	1.72	0.61	0.2	0.6
			Licania heteromorpha	54.19	102.52	0.16	40.50	13.50	1.19	10.80	11.96	0.71	3.0	0.6
			Licania micranta	67.37	115.20	0.55	49.60	15.04	0.79	8.40	9.14	0.73	1.8	1.2
		Parinari	*Parinari excelsa*	20.83	125.33	0.08	56.00	14.98	0.91	6.40	14.38	0.57	1.9	0.6
	Euphorbiaceae	*Alchornea*	*Alchornea schomburkiana*	139.09	195.79	0.93	58.60	31.33	2.18	5.13	5.33	0.44	0.1	0.5
		Hevea	*Hevea spruceana*	157.59	144.58	1.39	47.60	17.58	2.12	11.52	4.50	0.34	1.2	0.6
		Hura	*Hura crepitans*	223.56	387.05	1.18	46.40	25.00	4.14	9.24	4.69	0.49	1.1	0.4
		Mabea	*Mabea nitida*	34.36	112.28	0.29	49.90	22.37	2.32	7.60	10.28	0.58	3.0	0.7

	Piranhea	*Piranhea trifoliolata*	17.97	106.95	0.05	41.70	32.03	5.31	22.40	12.25	0.67	2.2	0.5
Fabaceae	*Acosmium*	*Acosmium nitens*	16.15	173.29	0.12	45.30	28.50	1.76	17.20	3.62	0.63	3.8	0.8
	Campsiandra	*Campsiandra comosa*	40.22	298.34	0.58	45.90	12.74	0.82	8.80	4.47	0.44	0.8	1.0
	Inga	*Inga splendens*	72.05	132.79	0.78	53.90	7.73	1.46	14.10	3.64	0.56	1.5	0.8
	Swartzia	*Swartzia laurifolia*	49.64	161.89	0.41	51.40	24.61	1.46	6.60	2.76	0.57	0.7	0.8
	Zygia	*Zygia cataractae*	25.67	120.84	0.10	47.60	21.45	2.30	9.20	2.42	0.78	1.5	0.9
Lauraceae	*Ocotea*	*Ocotea cymbarum*	31.15	150.65	0.21	49.50	25.26	1.27	6.76	1.31	0.63	0.4	0.9
			29.85	146.89	0.21	51.10	20.13	1.57	5.52	2.79	0.67	1.0	0.6
			169.32	116.70	1.43	51.90	16.21	1.82	13.60	1.26	0.57	0.9	0.8
			117.71	134.22	0.91	55.20	20.83	1.70	13.60	0.63	0.58	0.8	0.8
			119.68	121.13	1.02	55.70	20.19	2.15	16.40	0.60	0.53	1.1	0.8
Lecythidaceae	*Couroupita*	*Couroupita guianensis*	81.79	149.97	1.29	38.70	18.09	1.25	8.80	1.82	0.39	1.0	0.6
	Eschweilera	*Eschweilera albiflora*	31.17	150.60	0.30	55.30	18.65	3.25	15.20	6.58	0.60	2.1	0.5
		Eschweilera parviflora	46.60	88.70	0.50	53.40	19.88	1.58	13.20	3.85	0.69	2.2	0.6
	Gustavia	*Gustavia augusta*	102.44	114.17	1.00	68.20	26.63	2.55	10.80	19.96	0.62	0.7	0.5
	Lechytis	*Lechytis lurida*	104.50	79.84	1.41	35.80	18.09	1.34	5.88	3.59	0.44	2.3	0.5
Malvaceae	*Apeiba*	*Apeiba echinata*	92.55	150.49	1.21	57.70	24.64	2.26	16.00	5.20	0.35	1.1	0.6
	Ceiba	*Ceiba pentandra*	31.76	150.08	0.26	53.00	24.14	1.86	5.11	7.09	0.34	0.6	0.8
	Luehea	*Luehea cymulosa*	66.59	201.06	0.33	52.70	17.86	1.46	16.40	14.42	0.32	3.1	0.8
	Pseudobombax	*Pseudobombax munguba*	50.14	112.28	0.72	33.80	22.32	2.50	21.60	4.20	0.45	0.7	0.6
	Theobroma	*Theobroma cacao*	130.72	184.58	0.67	46.90	24.02	4.74	9.20	7.98	0.37	2.3	0.7
Melastomataceae	*Mouriri*	*Mouriri grandifolia*	98.96	87.84	1.68	60.70	13.78	0.84	12.40	11.47	0.64	0.8	0.5
		Mouriri guianensis	25.15	107.39	0.21	58.80	20.19	1.66	10.40	2.95	0.84	0.0	0.7
		Mouriri sp. A	149.63	99.49	2.57	58.80	16.60	1.41	8.85	6.56	0.70	1.3	0.6
			32.95	91.94	0.64	60.20	14.36	0.72	12.40	6.25	0.72	0.8	0.8
			30.33	94.48	0.63	58.30	18.03	1.56	10.80	4.90	0.68	0.6	1.1
Moraceae	*Batocarpus*	*Batocarpus amazonicus*	46.51	97.35	0.28	53.20	12.29	1.10	14.80	11.09	0.51	0.5	0.8
	Ficus	*Ficus maxima*	101.77	179.04	1.11	41.00	20.10	3.93	32.40	12.76	0.46	2.8	0.6

	Maquira	*Maquira coriacea*	19.40	71.57	0.18	49.50	16.77	1.14	14.80	13.32	0.45	2.7	0.4
	Sorocea	*Sorocea duckei*	38.83	208.09	0.14	43.60	41.24	4.11	23.60	6.83	0.52	6.3	0.7
			23.34	109.39	0.19	45.10	22.15	2.19	18.80	1.33	0.47	3.8	0.9
Myrtaceae	*Calypthrantes*	*Calypthrantes multiflora*	70.32	80.48	0.78	59.70	17.02	0.97	9.20	2.89	0.59	1.5	0.6
		Calyptranthes sp.	88.84	146.64	0.80	56.70	17.86	1.33	6.82	4.70	0.62	0.0	1.4
	Eugenia	*Eugenia inundata*	57.10	142.11	0.51	53.40	15.96	1.09	12.00	12.15	0.56	0.2	0.5
			16.99	96.87	0.06	51.80	26.91	2.15	10.40	5.58	0.68	0.4	0.4
		Eugenia sp. A	31.92	109.67	0.24	56.30	12.91	0.88	12.80	2.90	0.00	5.1	0.6
Sapotaceae	*Chrysophyllum*	*Chrysophyllum argentum*	27.64	86.16	0.34	55.00	14.20	1.11	3.38	5.52	0.59	0.0	0.5
	Micropholis	*Micropholis egensis*	41.63	93.12	0.41	46.00	12.46	0.90	7.60	14.21	0.58	1.2	0.5
		Micropholis guianensis	55.22	110.30	0.54	46.30	26.96	1.09	18.80	6.10	0.44	1.0	0.7
	Pouteria	*Pouteria elegans*	50.90	69.03	0.54	69.00	35.14	3.12	20.80	2.29	0.77	2.8	0.9
		Pouteria glomerata	113.29	107.85	1.04	59.70	16.63	0.92	8.80	6.05	0.56	1.3	0.8

ARTIGO 3

Branch wood density is a proxy of stem wood density in tropical forest trees?

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Short communication em preparação

Abstract

Wood density (*ρ*) is a key functional trait because it integrates different wood properties and is largely used to biomass estimation. Usually, *ρ* is obtained from a section of a wood core, but the use of a branch sample is a less destructive method and can be easier to sample in the field, especially when leaf samples are also collected for botanical vouchers or functional trait studies. The comparability of these two methods remain unclear, especially in floodplain forests. Here we evaluated (i) if branch *ρ* is a good predictor of stem *ρ*, and (ii) how *ρ* change from stem to branch level. We analyzed branch and stem wood density data from 124 tree species of white-water and black-water floodplain and terra-firme forests. Branch *ρ* was not a good predictor for stem *ρ* at species level. Interestingly, branch wood is denser than stem wood in lighter trunks (<0.55 g/cm^3), and we suggest that this change along plant axis, can be related to differences in reserve tissues and water storage capacity in the trunk, and to plant growth in response to flooding.

Keywords: functional trait, wood properties, hydraulic system, flooding, tropical forests

Introduction

The incorporation of plant traits in plant community research is improving the comprehension of how species adapt to specific abiotic conditions selecting tree species assemblages by environmental filters. Wood density (*ρ*) is a key plant trait because it is an integrative characteristic of wood properties, as plant sustainability, growth and mortality (Enquist et al. 1999, Muller-Landau 2004, Chave et al. 2009). It is largely used to estimate plant biomass allocation, being important to estimate carbon stocks and sequestration in biomass and to understand forest dynamics, especially under global climate change scenarios (Fearnside 1997, Chave et al. 2005). Species with lighter woods tend to have a faster volumetric growth and shorter life spans, while heavier wood species tend to have a slower volumetric growth and longer life-spans, because stronger tissues confer more protection against pathogens and physical damage (Enquist et al. 1999, Poorter et al. 2008, Schöngart 2008, Baraloto et al. 2010). Wood density has been associated to tree hydraulic system, being related to plant water storage capacity and water transport efficiency. Lighter woods are usually associated with a more efficient hydraulic system, but with a higher embolism taxa, by the other hand, the heavier woods are less efficient but tend to be more resistant to cavitation (Hacke et al. 2001, Cosme et al. 2017).

Although wood density is important to understand woody plant dynamics, there is a lack of information about ρ, especially at community level. This is a consequence of the difficulty of sampling this trait. Wood density is obtained usually by the relation of oven dry mass and fresh volume of a wood sample (Chave et al. 2005), and a less destructive method commonly used is sampling stem cores (thin cylinders of wood taken perpendicular to the stem axis). Branch ρ is a measurement even less destructive and relatively easier to sample in the field, especially when leaf samples are also collected for botanical vouchers or functional trait studies, but the use of this attribute demands further investigation about the relationship between branches and stem woods. The possibility to estimate stem wood density (ρ_S) from branch (ρ_B) was pointed out by Swenson and Enquist (2008), who found a strong and positive relationship between ρ_S and ρ_B at the individual level, where ρ_S were15% higher than ρ_B in tree species from Costa Rica terra-firme forest. Intuitively, we expect that stems will have denser woods than branches, because it is a stronger and older tissue that sustain the whole plant. We also expect that branches and stem woods will be positively correlated, because they both reflect plant mechanic, physiologic and hydraulic strategies. Contrary, (Yeboah 2004) found that branch woods were denser than stems in two species. The relationship of ρ_S and ρ_B is, therefore, not clear, (Gurau et al. 2008, Sarmiento et al. 2011), and further studies are necessary.

Amazonian floodplain forests are subjected to floods that last for several months, which have impacts on tree structural and physiological traits (Junk et al. 1989, Parolin et al. 2010, Parolin 2012), including wood characteristics as ρ (Parolin and Ferreira 1998, Parolin and Worbes 2000, Wittmann et al. 2006, Schöngart et al. 2010, Hawes et al. 2012). Two major floodplain systems are differentiated by the physical and chemical properties of the rivers that inundate them. The white-water forests called 'várzea' are nutrient-rich systems that occur along rivers with sediments originated from Andes and pre-Andean regions. The black-water forests called 'igapó' nutrient-poor systems that occur along rivers with sediments from the Guyana and Brazilian Shields (Junk et al. 2010). Wood density of these floodplain trees are associated with environmental conditions, especially edaphic properties and hydroperiod (Parolin and Ferreira 1998, Schöngart et al. 2005, 2010, Mori et al. 2019). Black-water species usually have higher ρ and lower growth increment, which is a result of a poor nutrient supply. White-water species usually have lighter woods compared to black-water species, because the high nutrient supply allow species to growth faster and, also, allow a higher presence of pioneers (Parolin and Ferreira 1998). Flooding duration affect ρ because it reduce plant growth during the flooding period, restricting it to the terrestrial phase, which leads to the formation of annual growth rings and, consequently, denser woods (Worbes 1997, Schöngart et al. 2002). Until now, the studies that evaluate the relation of ρ_S and ρ_B did not included floodplain trees (Patino et al. 2009), and this information remains unknown. In this study, we evaluated if ρ_B is a good predictor for ρ_S at species level and how ρ change from stem to branch level across tree of floodplain and terra-firme forests and its relation to ecological strategies.

Material and Methods

Data collection

We combined data from fieldwork and literature obtained from different Amazon floodplain and terra-firme forests. Our dataset totalized 124 species, 96 floodplain species with 56 occurring only in white-water forests, 35 occurring only in black-water forests, and 5 occurring in both forest types, and 28 species of terra-firme.

Branch wood density was obtained from trees in várzea and igapó forests species sampled in 25x25m plots previously established and inventoried in two reserves, the Mamirauá Sustainable Development Reserve (RDS Mamirauá) and the Uatumã Sustainable Development Reserve (RDS Uatumã) (for more details see Mori et al. 2019). Stem wood density was mainly obtained by literature, and for some black-water species was obtained on fieldwork in RDS Uatumã. Terra-firme ρ_S and ρ_B were obtained from literature (Cosme et al. 2017). Branch samples were obtained from terminal branches (bark included) and stem samples were obtained form cores of the trunks at 1.3 m height. Wood density was calculate as oven-dry wood over green volume (g/cm^3), fresh volume was obtained using the water displacement method and samples were dried at 105 °C (Chave et al. 2005, Swenson and Enquist 2008). Tree species, location and reference (when extracted from literature) are listed in the supplementary material.

Data analysis

We calculated averages for ρ_B and ρ_S on the species, genus and family levels. To verify if ρ_B differ from ρ_S at species level in the forest types, we applied an Analysis of variance (ANOVA). To analyze if ρ_B is a good predictor for ρ_S, we used linear regression with ρ_B as independent variable and ρ_S as a dependent variable at the species level. To evaluate how ρ_B change in relation to ρ_S, we calculate the ratio of both parameters (ρ_S:ρ_B) that indicates if ρ_S is higher than ρ_B (ρ_S:ρ_B >1), equal (ρ_S:ρ_B =1), or lower (ρ_S:ρ_B <1). We used linear regression to relate the ratio (independent variable) with ρ_S (dependent variable) on species, genus and family levels.

Results

Stem wood density (ρ_S) was, in general, higher than ρ_B for várzea (68% of species) and upland species (85% of species, Table 1). In contrary, ρ_B was generally higher than stem ρ for igapó tree species (57% of species). Stem ρ was 6% and 10% higher than ρ_B in várzea and terra-firme, respectively, and ρ_B was 4% higher than ρ_S in igapó. Stem wood density was higher in upland species, while ρ_B was higher in igapó species. In várzea, both ρ_S and ρ_B were lighter compared to the other forest types. ρ_S had a positive relationship with ρ_B (Table 2 and Figure 1), indicating that an increase in ρ_B leads to an increase in ρ_S. This relationship was, although significant for all three environments, strong only for upland species (R^2adj = 0.69).

Table 1. Stem and branch wood density (ρ) of tree species occurring in different forest types. The columns indicate number of species (n), ρ mean values (g/cm^3), the standard deviation, and ANOVA results (F-statistic and significance, p-value) of várzea, igapó and upland forests.

Forest type	Species (*n*)	Wood density (ρ)		Anova	
		Branch	Stem	F-statistic	p-value
várzea	61	0.54 ± 0.10	0.60 ± 0.16	40.77	<0.01
igapó	40	0.68 ± 0.08	0.64 ± 0.14	15.01	<0.01
upland	24	0.64 ± 0.1	0.74 ± 0.12	63.34	<0.01

Table 2. Relationship between stem and branch wood density (ρ) in várzea, igapó and upland forests. The columns indicate intercepts, regression coefficients, R^2 adjusted and significance (p-value).

Forest type	Regression			
	intercept	β-coefficient	R^2 adj	p-value
várzea	0.07	0.98	0.39	<0.001
igapó	0.01	0.91	0.26	<0.001
upland	0.05	1.06	0.69	<0.001

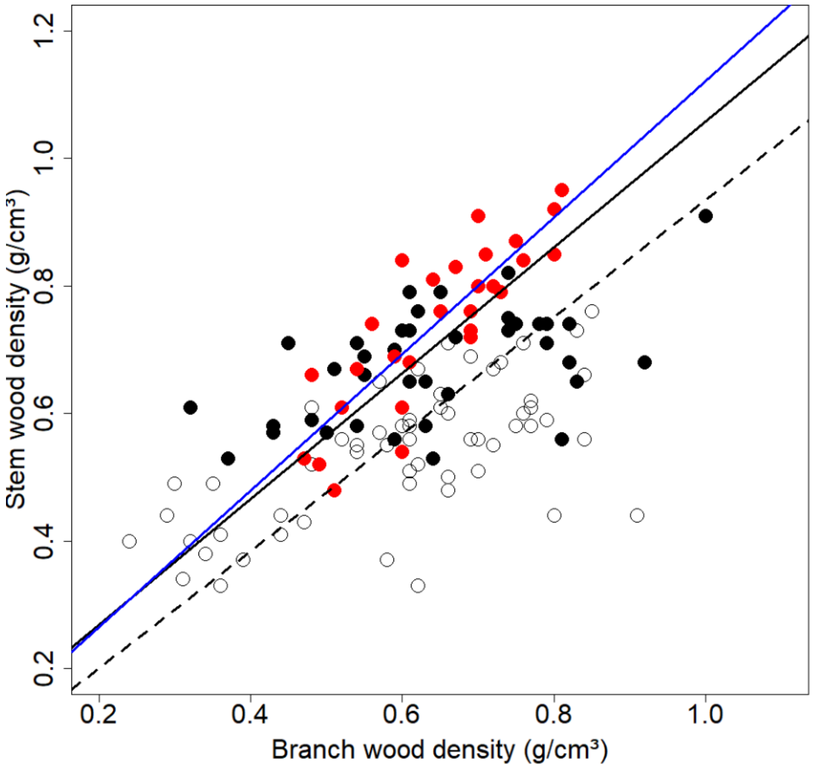

Figure 1. Relationship of stem and branch wood density (ρ) of white-water (várzea, white dots), black-water (igapó, black dots) and upland (terra-firme, red dots) forests species. Black line show the model for várzea species (R^2_{adj} = 0.39, β=0.98), dashed line show the model for igapó species (R^2_{adj} = 0.26, β=0.91), and blue line show the model for upland species (R^2_{adj} = 0.69, β=1.06).

The Stem:branch wood ratio had a positive relationship with ρ_S , indicating that denser trunks had a relative low ρ_B and that lighter trunks had relatively higher ρ_B (Table 3, Figure 2) with a threshold of about 0.6 g/cm³ (ρ_S), interestingly similar for species, genera and family levels, as well as for the three forest types. Comparing the studied environments the releationships on the species and genus levels are stronger in the igapó, followed by the várzea and were lowest in terra firme forests, although significant.

Table 3. Relationship between stem:branch wood density ratio and stem wood density in várzea, igapó and upland forests. The columns indicate intercept, regression coefficients, R^2 adjusted and significance (p-value) per level in each forest type.

Level	Regression			
várzea	Intercept	β-coefficient	R^2 adj	p-value
Specie	0.42	1.14	0.46	<0.001
Genera	0.39	1.21	0.48	<0.001
Family	0.56	0.9	0.40	<0.001
Igapó				
Specie	0.25	1.07	0.66	<0.001
Genera	0.25	1.06	0.69	<0.001
Family	0.52	0.67	0.43	0.001
Upland				
Specie	0.83	0.44	0.16	0.01
Genera	0.74	0.57	0.33	0.02
Family	0.52	0.67	0.43	0.001

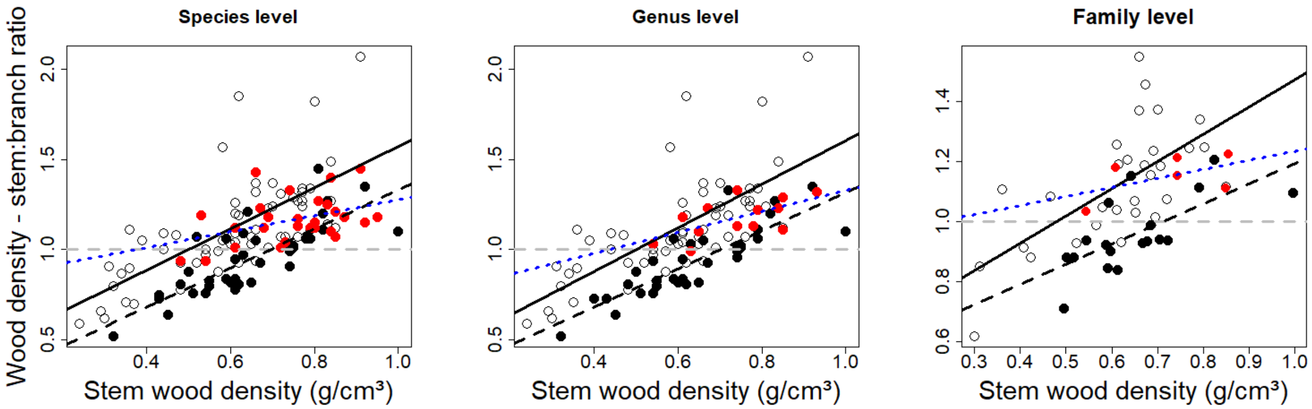

Figure 2. Relationship of the stem:branch wood density ratio and stem wood density of várzea (white dots), igapó (black dots) and upland (red dots) forests species on species, genera and family levels. Dashed horizontal line indicate 1:1 ratio, when stem and branch wood density are equal. Black line show the model for várzea species, dashed line show the model for igapó species, and blue line show the model for upland species.

Discussion

We evaluated if ρ_B is a good predictor for ρ_S and how it relate to each other among tree species from different floodplain forest types. We did not find a strong relationship between ρ_B and ρ_S indicating that ρ_B is not a good predictor to ρ_S, and the differences in ρ between stem and branch of these trees may reflect different ecological strategies. Stem wood density is usually lower in floodplain forests trees compared to upland trees, because flood-pulse dynamics limit the period of plant growth, resulting in lower ρ (Schöngart et al. 2005, Hawes et al. 2012). Indeed, we found that upland tree species have denser ρ_S than várzea and igapó species. We found a weak relationship between ρ_B and ρ_S in floodplain forests, which indicates that ρ_B is not a good predictor for ρ_S, especially in the igapó. Our results differ from Swenson and Enquist (2008), who found a very strong relationship between these attributes ($R^2 = 0.89$). For upland species, although, the relationship was stronger, which can indicate that a different pattern can occur in floodplain trees.

Interestingly, ρ_B was not always lower than ρ_S, especially in the igapó. Gurau et al. (2008) found the same result for two species, while Swenson and Enquist (2008) and Sarmiento et al. (2011), found that ρ_S is higher than ρ_B for most of species. In our study, stem wood had higher density for most of várzea and upland species, while for igapó, species tended to have denser branches. In both várzea and igapó, tree species with ρ_S below 0.6 g/cm^3 had denser branch wood than stem wood. Upland species seem to follow this pattern, but few species with low ρ were present in the dataset which also might result in the relatively low relationship on the species and genus level in the terra-firme. Variation in stem and branch woods are probably related to anatomical structures and ecological strategies, leading to wood variation along plant tissues. Here, we propose some hypothesis to explain these results: (1) Trunks usually store reserves tissues, which decrease overall wood density. In this sense, lighter trunks may have a higher proportion of reserve tissues stored, leading to lighter stems in relation to branches. This can apply especially for igapó species, because nutrient supply is low and individuals tend to store more reserves and transport it to the roots during anaerobic respiration (Schöngart et al. 2005); (2) Lighter trunks have a higher water transport capacity than branches and, consequently, lighter woods (McCulloh et al. 2011). (3) Flooding influence trees' metabolism. Some floodplain trees grow fast to escape flooding (Parolin 2002), and the fast development of the trunk results in lower stem density than ρ_B.

Few information is available regarding the relationship between ρ_S and ρ_B, which seems to be very variable among different species and influenced by environmental condition. Further studies are necessary to better understand plant dynamics and physiological processes which might explain the evidenced patters. Our results have also strong implications for estimates of carbon storage in wood biomass based on allometric models which nowadays use diameter, tree height and ρ as independent parameters, however, not accounting for the variation of ρ in stems and branches of trees and between environments.

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Supplementary material. Species of the study. The columns indicate family, species name, forest type, sampling location, reference (when no collected in this study).

Family	Specie	Forest type	Local	Reference
Annonaceae	*Guatteria citriodora*	Black-water	RDS Uatumã	-
	Guatteria guianensis	Black-water	RDS Uatumã	-
	Guatteria inundata	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
	Oxandra riedeliana	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
	Xylopia barbata	Black-water	RDS Uatumã	-
	Xylopia benthamii	Black-water	RDS Uatumã	-
	Xylopia calophylla	White-water	RDS Mamirauá/Jarauá	Wittmann et al. (2006)
Apocynaceae	*Malouetia tamaquarina*	White-water	RDS Mamirauá/Jarauá	Leoni et al. (2011), Schöngart (2003), Wittmann et al. (2006)
Bignoniaceae	*Handoanthus barbata*	White-water	RDS Mamirauá/Jarauá	Wittmann et al. (2006)
Brassicaceae	*Crataeva tapia*	White-water	RDS Mamirauá/Jarauá	Wittmann et al. (2006)
Burseraceae	*Protium heptaphyllum*	Black-water	RDS Uatumã	-
	Protium nitidifolium	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Protium opacum	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Protium klugii	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Protium trifoliolatum	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
Calophyllaceae	*Caraipa richardiana*	Black-water	RDS Uatumã	-
Chrysobalanaceae	*Couepia paraensis*	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
	Gaulettia parillo	Black-water	RDS Uatumã	-
	Licania apetala	White-water/ Black-water	RDS Mamirauá/Jarauá, Rio Tarumã-mirím, Parque Nacional do Jaú, rio Negro (Barcelos), RDS Amanã	Schöngart (2003), Parolin & Ferreira (1998), Parolin et al. (1998), Parolin & Worbes (2000), Schöngart (unpubl.), Stadtler (2007)
	Licania heteromorpha	White-water/ Black-water/Upland	RDS Mamirauá/Jarauá, Rio Branco, Rio Jufarís, Rio Negro (Barcelos), RDS Amanã, rio tarumã-mirím, Ducke Reserve	Schöngart (2003), Schöngart (unpubl.), Stadtler (2007),Worbes (1994)
	Licania hypoleuca	Black-water	RDS Uatumã	
	Licania macrophylla	Black-water/Upland	RDS Uatumã, Ducke Reserve	Cosme et al. (2017)
	Licania micranta	White-water	Rio Japurá	Cintra & Schöngart (unpubl.)
	Licania Octandra	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Licania longistyla	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
Clusiaceae	*Calophyllum brasiliensis*	Black-water	Rio Branco, rio Negro (Barcelos)	Schöngart (unpubl.)
	Garcinia brasiliensis	White-water	RDS Mamirauá/Panauã	Cintra & Schöngart (unpubl.)

	Tovomita spruceana	White-water/ Black-water	RDS Mamirauá/Jarauá, RDS Uatumã	Wittmann et al. (2006)
Combretaceae	*Terminalia dichotoma*	White-water	RDS Mamirauá/Jarauá	Wittmann et al. (2006)
Dichapetalaceae	*Tapura juruana*	White-water	RDS Mamirauá/Jarauá	Wittmann et al. (2006)
Elaeocarpaceae	*Sloanea floribunda*	White-water	RDS Mamirauá/Panauã, rio japurá	Cintra & Schöngart (unpubl.)
Euphorbiaceae	*Alchornea discolor*	Black-water	Rio Negro (Barcelos), RDS Amanã	Schöngart (unpubl.), Stadtler (2007)
	Alchornea shomburgkiana	White-water	Baixo Rio Solimões	Martius (1989)
	Croton cuneatus	White-water	RDS Mamirauá/Panauã	Cintra & Schöngart (unpubl.)
	Hevea spruceana	White-water	RDS Mamirauá/Jarauá	Schöngart (2003), Wittmann et al. (2006)
	Hura crepitans	White-water	RDS Mamirauá/Jarauá	Wittmann et al. (2006)
	Mabea nitida	White-water/ Black-water	RDS Mamirauá/Jarauá, Parque Nacional do Jaú, rio Tarumã-mirím	Schöngart (2003), Schöngart (unpubl.), Worbes (1994)
	Maprounea guianensis	Black-water	Parque Nacional do Jaú, rio Negro (Barcelos)	Parolin & Worbes (2000), Schöngart (unpubl.)
Fabaceae	*Campsiandra comosa*	White-water	Rio Japurá	Cintra & Schöngart (unpubl.)
	Cynometra bauhiniifolia	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
	Dicorynia paraensis	Black-water	RDS Uatumã	-
	Eperua duckeana	Black-water	RDS Uatumã	-
	Etabalia dubia	White-water	RDS Mamirauá/Jarauá	Schöngart (2003), Wittmann et al. (2006)
	Hymenolobium pulcherrimum	Black-water	RDS Uatumã	-
	Inga splendens	White-water	RDS Mamirauá/Jarauá	Wittmann et al. (2006)
	Peltogyne venosa	Black-water	RDS Uatumã	-
	Pterocarpus amazonum	White-water	RDS Mamirauá/Jarauá	Wittmann et al. (2006)
	Vatairea guianensis	White-water	RDS Mamirauá/Jarauá	Schöngart (2003), Wittmann et al. (2006)
	Zygia ampla	White-water	RDS Mamirauá/Jarauá	Schöngart (2003), Wittmann et al. (2006)
	Zygia cataractae	Black-water	RDS Uatumã	-
	Dipteryx punctata	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Dipteryx magnifica	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Swartzia lamellata	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Swartzia recurva	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
Humiriaceae	*Humiriastrum cuspidatum*	Black-water	RDS Uatumã	-
Lauraceae	*Aniba panurensis*	Black-water	RDS Uatumã	-
	Endlicheria anomala	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
	Nectandra hihua	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
	Ocotea aciphylla	Black-water	RDS Uatumã	-

	Ocotea adenotrachelium	Black-water	RDS Uatumã	-
	Ocotea cymbarum	White-water	RDS Mamirauá/Jarauá	Wittmann et al. (2006)
Lecythidaceae	*Couratari tenuicarpa*	Black-water	RDS Uatumã	-
	Couroupita guianensis	White-water	Alto Solimões	Schöngart (unpubl.)
	Lecythis lurida	White-water	Mamirauá/Jarauá	-
	Eschweilera albiflora	White-water	RDS Mamirauá/Jarauá	Schöngart (2003), Wittmann et al. (2006)
	Eschweilera ovalifolia	White-water	Baixo Rio Solimões	Worbes (1994)
	Eschweilera parviflora	White-water/ Black-water	RDS Mamirauá/Jarauá, Rio Branco, Parque Nacional do Jaú	Schöngart (2003), Wittmann et al. (2006), Schöngart (unpubl.)
	Gustavia augusta	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
	Lecythis poiteaui	Black-water	RDS Uatumã	-
	Lecythis pisonis	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Eschweilera laevicarpa	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Eschweilera truncata	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Lecythis prancei	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Cariniana integrifolia	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Couratari stellata	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Cariniana micrantha	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Couratari guianensis	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
Malpighiaceae	*Burdachia sphaerocarpa*	Black-water	RDS Uatumã	-
Malvaceae	*Ceiba pentandra*	White-water	Alto Solimões	Schöngart (unpubl.)
	Luehea cymulosa	White-water	RDS Mamirauá/Jarauá	Schöngart (2003), Wittmann et al. (2006)
	Mollia lepidota	Black-water	RDS Uatumã	-
	Pseudobombax munguba	White-water	RDS Mamirauá/Jarauá	Schöngart (2003), Wittmann et al. (2006)
Melastomataceae	*Mouriri brevipes*	Black-water	RDS Uatumã	
	Mouriri guianensis	White-water	Baixo Rio Solimões	Worbes (1994)
Meliaceae	*Cedrela odorata*	White-water	RDS Mamirauá/Jarauá	Wittmann et al. (2006)
	Trichilia lecointei	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
Moraceae	*Sorocea duckei*	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
Myristicaceae	*Virola calophylla*	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
	Virola venosa	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Virola pavonis	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
Myrtaceae	*Blepharocalyx eggersii*	Black-water	RDS Uatumã	-
	Calyptranthes forsteri	Black-water	RDS Uatumã	-
	Myrciaria dubia	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
Nyctaginaceae	*Neea spruceana*	White-water	RDS Mamirauá/Panauã	Cintra & Schöngart (unpubl.)
Phyllantaceae	*Discocarpus essequeboensis*	White-water	RDS Mamirauá/Jarauá	Schöngart (2003), Wittmann et al. (2006)

Polygonaceae	*Symmeria paniculata*	White-water	RDS Mamirauá/Jarauá	Schöngart (2003), Wittmann et al. (2006)
	Triplaris weigeltiana	White-water	Baixo Rio Solimões	Martius (1989), Parolin & Ferreira (1998), Parolin et al. (1998), Worbes (1994)
Rubiaceae	*Duroia duckei*	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
	Stachyarrhena acuminata	Black-water	RDS Uatumã	-
Rutaceae	*Zanthoxylum compactum*	White-water	Baixo Rio Solimões	Martius (1989)
Salicaceae	*Casearia aculeata*	White-water	Baixo Rio Solimões	Martius (1989), Parolin & Ferreira (1998), Parolin et al. (1998)
	Laetia corymbulosa	Black-water	RDS Uatumã	-
	Laetia corymbulosa	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
Sapindaceae	*Matayba arborencens*	White-water	RDS Mamirauá/Panauã	Cintra & Schöngart (unpubl.)
Sapotaceae	*Chrysophyllum argentum*	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
	Elaeoluma schomburgkiana	Black-water	RDS Uatumã	-
	Manilkara bidentata	Black-water	RDS Uatumã	-
	Micropholis egensis	White-water	RDS Mamirauá/Panauã, rio japurá	Cintra & Schöngart (unpubl.)
	Micropholis melinoniana	Black-water	RDS Uatumã	-
	Pouteria elegans	White-water	RDS Mamirauá/Jarauá	Schöngart (2003), Wittmann et al. (2006)
	Pouteria glomerata	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
	Pouteria pachyphylla	Black-water	RDS Uatumã	-
	Chrysophyllum	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Pouteria flavilatex	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Chrysophyllum sanguinolentum	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Pouteria williamii	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Micropholis williamii	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
	Micropholis splendens	Upland	Duck Reserve, Manaus	Cosme et al. (2017)
Simaroubaceae	*Simaba orinocensis*	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
Urticaceae	*Cecropia latiloba*	White-water	RDS Mamirauá/Jarauá	Schöngart (2003)
Violaceae	*Leonia glycycarpa*	White-water	RDS Mamirauá/Panauã, rio Juruá	Cintra & Schöngart (unpubl.)
Vochysiaceae	*Qualea dinizii*	Black-water	RDS Uatumã	-

SÍNTESE

As florestas alagáveis amazônicas são sujeitas a um alagamento sazonal e previsível que é considerado como a força motriz que estrutura a composição florística, a estrutura da vegetação e diversas características e estratégias ecológicas das árvores. As diferenças nas características do solo entre as tipologias de várzea e igapó, atuam como fator importante diferenciando estes ambientes, que é visto, principalmente, pelas diferenças na composição e diversidade florística entre elas. Esta tese, discutiu o papel destes dois importantes filtros ambientais, o alagamento sazonal e as características edáficas, na estrutura funcional da comunidade de árvores de várzea e igapó de águas pretas, na Amazônia Central.

Os atributos funcionais refletem as respostas dos organismos ao ambiente e, por esta razão, são fudamentais para se entender a dinâmica das comunidades vegetais em relação a condições abióticas específicas e/ou em relação à mudanças ambientais. No capítulo 1, mostramos que a composição funcional das árvores das comunidades de várzea e igapó diferem. As comunidades de várzea possuem valores de atributos relacionados à um crescimento rápido e uma aquisição de recursos mais eficiente, como maior área foliar específica e maior conteúdo de nutrientes nas folhas, enquanto as árvores das comunidades de igapó possuem valores de atributos relacionados à um crescimento mais lento e uma melhor conservação dos recursos, como maior densidade da madeira e maior conteúdo de massa seca na folha. O nível e a duração do alagamento pouco influenciaram a variação dos atributos, mesmo entre as comunidades com o mesmo tipo de solo. As propriedades do solo, por outro lado, foram bons preditores da variação dos atributos resultando em uma convergência dos valores nas comunidades dentro de cada tipologia, que está relacionada às diferentes disponibilidades de recursos. Ao longo deste gradiente de recursos, os valores médios dos traços variaram, revelando uma troca de estratégias relacionadas à alta versus baixa disponibilidade de nutrientes do solo. Isto é, em ambientes com maior disponibilidade de recursos, como as várzeas, os indivíduos investem em crescimento e em tecidos aquisitivos, enquanto nos ambientes com menor disponibilidade de recursos, como nos igapós, os indivíduos investem em persistência e longevidade, e na conservação de recursos, resultando em diferentes comunidades.

A importância do ambiente na diferenciação dos atributos funcionais em várzea e igapó ficou ainda mais evidente quando usamos um controle filogenético. No segundo capítulo, encontramos que espécies pertencentes a um mesmo gênero (pares congenéricos) ou a mesma família, diferem em seus atributos quando em habitas com diferentes tipos de solo. Encontramos uma convergência de valores de atributos dentro de cada tipo de floresta, que indica o mesmo *trade-off* de estratégias aquisição versus conservação de recursos, encontrados no primeiro capítulo. Neste capítulo, também verificamos que o papel do habitat foi importante na diferenciação de todos os atributos, especialmente nos atributos mais plásticos e lábeis. Alguns traços foram influenciados pelo tipo de habitat independente do gênero, como o conteúdo de nutrientes da folhas, enquanto outros atributos foram influenciados por ambos gênero e habitat, como a densidade da madeira do ramo. A variação dos atributos funcionais entre espécies filogenticamente próximas nos diferentes tipos de solo das várzeas e igapós, indica a ocorrência de especialização do habitat. Este processo de especialização leva a diferenciação das espécies entre as florestas de várzea e igapó, contribuindo para o aumento da diversidade de espécies em florestas alagáveis. No capítulo 3 nós encontramos que a densidade da madeira do ramo e a densidade da madeira do caule de espécies de florestas alagáveis não possuem uma relação linear forte, e este resultado parece ser diferente comparado às espécies de terra-firme. Espécies com troncos mais leves desenvolvem ramos mais densos, e isto pode ser um reflexo da influência do alagamento e das propriedades do solo no metabolismo e crescimento das árvores.

A convergência nos valores dos atributos dentro de cada tipo de floresta, mesmo em espécies com uma história evolutiva comum, e a forte relação desta convergência com as características solo, indicam que as propriedades edáficas são o filtro ambiental mais forte que determina a composição e a diferenciação funcional nestas áreas. E que a especialização do habitat, pode ser o processo por trás da diferenciação e manuntenção da diversidade das florestas alagáveis. Um atributo integrador, como a densidade da madeira, que reflete processos importantes de desenvolvimento da planta, ressaltou a importância do ambiente na determinação das estratégias ecológicas no nível de toda a planta.

As florestas alagáveis são importantes ambientes de interface entre o ambiente aquático e o ambiente terrestre, que carregam uma grande diversidade de espécies. Por estarem intimamente ligadas ao ciclo hidrológico são vulneráveis à suas alterações, o que é influenciado pelas mudanças climáticas e pelo desmatamento. Nossos resultados mostram que a composição funcional e as estratégias ecológicas das árvores destas florestas são determinadas principalmente pelo filtro ambiental de características do solo, o que implica em diferentes repostas das comunidades das várzea e dos igapós frente às mudanças ambientais. Esta diferença é relevante e deve ser incorporada no estabelecimento de estratégias e planos de manejo e conservação das florestas alagáveis.

GLOSSÁRIO

Biodiversidade	A variedade de tudo que é vivo, incluindo plantas, animais e microorganismos, suas interrelações, os genes que eles contém, e os ecossistemas que eles formam (EOL, [s.d.]).
Assembleia de comunidade	O processo ecológico pelo qual uma comunidade se forma, seguindo certos mecanismos que selecionam a favor ou contra certas espécies, a partir de um pool regional de espécies (KEDDY, 1992). A assembleia de comunidade é influenciada pelo limite de dispersão, filtros locais e interações bióticas (competição).
Ecossistema	Uma comunidade de plantas, animais ou microorganismos que são ligados pela energia e fluxo de nutrientes e que interagem uns com os outros e com o ambiente físico (EOL, [s.d.]).
Diversidade de espécies	Variação nas espécies (número ou diversidade) dentro de uma comunidade.
Atributos funcionais	Qualquer medida das características das plantas que afetam a aquisição e uso de recursos e, consequentemente, determinam deu crescimento, reprodução e/ou sobrevivência (VIOLLE et al., 2007). Considera-se que os atributos funcionais refletem as adaptações às condições bióticas e abióticas e *trade-offs* (ecofisiológicos e evolutivos) entre diferentes funções dentro do organismos.
Composição funcional	Valores médios dos atributos dentro de uma comunidade.
Diversidade funcional	Variação nos valores dos atributos dentro de uma comunidade (VAN DER SANDE et al., 2017).
Teoria da razão de massa	As espécies dominantes e seus atributos determinam a maioria dos processos ecossistêmicos (GRIME, 1998). Isto é, a média ponderada dos valores dos atributos determinam mais fortemente os processos ecossistêmicos do que a diversidade (em espécies ou valores de atributos) em uma comunidade.
Teoria da complementariedade de nicho	As espécies são complementares na aquisição e uso de recursos. Assim, uma alta diversidade (de espécies ou atributos) resultam em uma eficiente aquisição e uso de recursos no nível de comunidade, e com isso em um maior estoque e dinâmica de biomassa (TILMAN, 1999).
Florestas alagáveis	Florestas sujeitas a um alagamento periódico sazonal e previsível pelo estravazamento lateral da água dos rios, devido à alta pluviosidade e sazonalidade da precipitação e baixa elevação do terreno (JUNK et al., 2015b).
Pulso de inundação	Variação anual do nível da água dos rios. É considerada a principal força motriz que controla a biota da planície de inundação (JUNK; BAYLEY; SPARKS, 1989).

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