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Efeitos da inundação e da antropização sobre padrões de diversidade de árvores na floresta de várzea amazônica

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Tese apresentada ao Programa de Pós-Graduação em Ecologia do convênio da Universidade Federal do Pará e Embrapa Amazônia Oriental, como requisito parcial para obtenção do título de Doutor em Ecologia.
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“*Even mild impacts and slow changes are cumulative, and in the long-term, the effects in the landscape can be dramatic when considered in geological scale*.”

(Carina Hoorn & Frank Wesselingh, 2010, *Amazonia landscape and species evolution*, Willey-Blackwell Pubs.)

“*American flora, fauna, and landscape were slowly Europeanized after 1492, but before that they had already been Indianized*.”

(William Denevan, 1972, *The Native Population of the Americas in 1492*, U. Wisconsin Press.).

Efeitos da inundação e da antropização sobre padrões de diversidade de árvores na floresta de várzea amazônica

RESUMO

A várzea amazônica é um ecossistema altamente heterogêneo e que abriga uma grande quantidade de espécies vegetais adaptadas a sua dinâmica sazonal. Os ambientes florestais de várzea sujeitos a inundação estão distribuídos ao longo de toda a extensão da calha principal do rio Amazonas e dos afluentes que possuem nascentes na cordilheira andina. A alta concentração de sedimentos carreados promove alta fertilidade por conta da dinâmica de deposição nos solos quando comparada a outros sistemas amazônicos e favorece uma alta produtividade primária apesar das condições anóxicas proporcionadas pela cheia dos rios. A fertilização natural das várzeas a tornou historicamente um hábitat propício para a colonização humana por seus benefícios à produção de alimentos. Nesse sentido, por atravessar quase todo o bioma, tem sido a principal rota de acesso de populações humanas atuais e pregressas aos mais distantes pontos da calha. Todos estes fatores contribuem para que as florestas de várzea sejam um importante modelo para se testar os padrões de diversidade ao longo de gradientes naturais e antropogênicos. Esta tese é apresentada em duas sessões que usam abordagens distintas, enfocando diferentes aspectos da diversidade e estrutura da floresta. A sessão 1 examina a estrutura filogenética do componente arbóreo de florestas de várzea nas macrorregiões Central e Leste da Amazônia brasileira e investiga como a presença humana atual tem a modificado, mais especificamente indagando como a ação humana interfere na diversidade das linhagens atuais destas florestas. A sessão 2 investiga como a diversidade taxonômica e os conjuntos de espécies locais e regionais foram afetados pelo histórico de densidade humana desde a chegada dos europeus na região. Para alcançar os objetivos, foram amostradas sete áreas distribuídas ao longo de 2.400 km de extensão da porção brasileira do Rio Amazonas que abrange diferentes regimes de inundação e tipos de influência humana. Foram amostrados os indivíduos arbóreos com DAP $\geq$ 10 cm e coletados dados disponíveis na literatura que foram utilizados como variáveis preditoras nas modelagens de diversidade em diferentes escalas. Os resultados demostraram que o regime de inundação é o principal fator que influencia a estrutura filogenética enquanto a densidade humana de quase três séculos atrás pode ser responsável por padrões de diversidade taxonômica encontrados atualmente. Assim, foram detectados padrões de diversidade em diferentes escalas espaciais e temporais, onde ficou evidenciado que a ação humana em tempos pregressos pode estar sendo refletida nos padrões de diversidade atuais muito tempo depois de terem ocorrido. Por ser um ecossistema de relativa facilidade de acesso na região e ter poucas áreas estritamente protegidas em unidades de conservação, aumenta-se a necessidade de entender como estas florestas são importantes para a manutenção de serviços ecossistêmicos essenciais e a sua dinâmica de regeneração diante da influência humana ao longo do tempo.

Palavras-chave: estrutura filogenética; diversidade taxonômica; ecologia histórica; influência humana.

Effects of inundation and anthropization over tree diversity patterns in Amazonian white-water floodplain forests

ABSTRACT

The white-water floodplain forest in Amazon (locally *várzea*) is a highly heterogeneous floodplain ecosystem that encompasses a large number of adapted species. It is distributed along the entire length of the main channel of the Amazon River and of tributaries of Andean origin. In addition, due to periodic flooding by waters with high sediment load, it has high fertility when compared to other Amazonian systems. What on the one hand is important for high primary productivity also makes it the target of human colonization for its benefits to food production. In this sense, because it presents continental dimensions and crosses almost all the biome from East to West, it has been the main access route of present and previous human populations to the most distant points of the basin. All these factors contribute to these forests being an important model for testing diversity patterns along natural and anthropogenic gradients. This thesis is presented in two chapters that use distinct approaches, focusing on different aspects of forest diversity and structure. Chapter 1 examines the phylogenetic structure of the arboreal component of floodplain forests in the Central and Eastern macro-regions and investigates whether the current human presence has modified it, specifically reducing the number of tree lineages present and leading to the phylogenetic homogenization of these forests. Chapter 2 investigates whether the taxonomic diversity and the local and regional tree species found today in the macro-regions of the study are associated with historical patterns of human density since the arrival of Europeans in the region. To reach the objectives, seven areas were sampled along the 2,400 km stretch of the Brazilian portion of the Amazon River, which covers different flood regimes and human influences. Thus, tree individuals with DBH $\geq$ 10 cm were sampled and data were collected *in situ* and in databases available to be used as predictors variables in modeling tree diversity at different scales. With the results, it was detected that the flood regime is the main factor that influences the phylogenetic structure whereas the human density of almost three centuries ago is responsible for the patterns of taxonomic diversity that are currently found. The diversity patterns were detected in the evolutionary and ecological scale, where it was shown that human influences may have a long-delayed response after they have occurred. Because *várzea* is a system of relatively easy access in the region and has few protected areas, it is necessary to understand how these forests are important for the maintenance of essential ecosystem services, even though they have been affected by human influence for a long period.

Keywords: phylogenetic structure; taxonomic diversity; historical ecology; human influence.

SUMÁRIO

1. INTRODUÇÃO GERAL

A floresta de várzea amazônica é um ecossistema único, tanto na riqueza de espécies quanto ao histórico evolutivo e de ocupação humana na paisagem. Nestes ambientes, coexistem espécies de plantas que toleram condições específicas devido a submersão e ao aporte de nutrientes pela inundação periódica de águas ricas em sedimentos de origem andina (Junk et al., 2011; Parolin e Wittmann, 2010). A ocupação da paisagem amazônica remonta a chegada de diversos grupos humanos que utilizaram as várzeas e suas terras férteis desde antes da chegada europeia na região (Barlow et al., 2012; Denevan, 1992). O conjunto de espécies de plantas que compõe a maior diversidade arbórea em florestas inundáveis no mundo (Luize et al., 2018; Slik et al., 2015; Wittmann et al., 2013) tem sofrido intensa pressão pelo desmatamento e pela sobre-exploração dos recursos naturais na atualidade. Como as florestas de várzea estão estruturadas e quais espécies as compõem é de interesse tanto ecológico quanto para a conservação. Nesse contexto, esta tese tem como foco o estudo da organização de comunidades de árvores na floresta de várzea amazônica em escala local e regional, considerando aspectos evolutivos e ecológicos para avaliar os efeitos da inundação e da pressão humana histórica e atual nos padrões de diversidade filogenética (SESSÃO I) e taxonômica (SESSÃO II) de árvores ao longo de mais de 2,4 mil km da calha principal do rio Amazonas.

1.1. A floresta de várzea no contexto da paisagem amazônica

A maior extensão de floresta tropical úmida contínua do mundo encontra-se no norte da América do Sul e, segundo estimativa mais conservadora, abriga cerca de um terço das espécies de seres vivos conhecidos, excluindo os microrganismos (Bar-On, Phillips e Milo, 2018; Slik et al., 2015). As principais hipóteses para explicar sua riqueza biológica atual apontam para a história geológica e climática da região (Antonelli et al., 2018; Haffer, 2008; Leite e Rogers, 2013). Na escala de tempo geológica, a paisagem amazônica passou por intensas transformações geomorfológicas (Hoorn et al., 2010), que culminaram, durante a última glaciação (últimos dez mil anos), com a estabilização no nível dos rios e o surgimento das várzeas como as conhecemos hoje (Irion et al., 2010). A diversidade de paisagens e ambientes favoráveis à manutenção de várias espécies (Zizka et al., 2018), mesmo em condições extremas como a inundação (Parolin e Wittmann, 2010; Wittmann et al., 2013).

As florestas tropicais da Amazônia são diversas em formação e origem e o aparente 'tapete' verde esconde hábitats únicos e heterogêneos que retroalimentam a manutenção da biodiversidade (Lovejoy e Nobre, 2018; Myster, 2016; Zizka et al., 2018). Nas zonas de transição entre os ambientes aquáticos e terrestres ocorrem formações vegetais que são permanentemente ou periodicamente inundáveis (Junk et al., 2011). O ritmo desta inundação ("pulso de inundação" *sensu* Junk et al 1989) é o principal fator de pressão seletiva das espécies de plantas nestes hábitats e moldam as respostas ecológicas e evolutivas da biota associada (Mori et al., 2019; Wittmann e Householder, 2016). Os grandes tipos de ambientes inundáveis na Amazônia derivam da origem das águas que os inundam e outros fatores hidrológicos, como acidez e material dissolvido, e são destaques os igapós e as várzeas (Junk et al., 2012).

Dentre as áreas alagáveis da Amazônia, a várzea (*Amazonian white-water floodplain*) é a mais representativa com aproximadamente 400.000 km² de extensão (Hess et al., 2015; Melack e Hess, 2010; Reis et al., 2019; Wittmann et al., 2013). Ela compõe o eixo principal do rio Amazonas e alguns de seus afluentes que têm origem nos Andes (Madeira, Purus, Juruá, Javari, Marañon-Ucayali, Içá e Japurá). As áreas inundáveis ao redor da calha principal do Amazonas, das cabeceiras até a foz no Atlântico, recebem influência de sedimentos de origem andina com altos níveis de fertilidade associados à deposição de nutrientes durante episódios de inundação (Junk et al., 2011). Isso torna a várzea amazônica um dos maiores e mais diversos ecossistemas inundáveis do planeta quando comparado a outros sistemas semelhantes no mundo (Arias et al., 2016; Junk et al., 2011; Park e Latrubesse, 2019; Parolin e Wittmann, 2010).

A disponibilidade e a frequência de deposição dos sedimentos e nutrientes dissolvidos determinam a formação de hábitats locais associados a pequenas mudanças topográficas (Junk et al., 2012; Wittmann, Junk e Piedade, 2004). No sentido da vazão da calha principal do Amazonas, as várzeas podem ser divididas em três macrorregiões: a Oeste no alto curso (150.000 km²), a Central no médio curso (250.000 km²) e a Leste no baixo curso (50.000 km²) (Wittmann et al., 2013). Esta divisão em macrorregiões é compatível com as características edáficas e hidrográficas descritas na literatura (Sombroek, 2009, 2000; ter Steege, et al., 2013; Wittmann et al., 2013), que refletem diferentes frequências as quais as florestas são submetidas a inundação. Apesar de não existir consenso sobre o limite geográfico entre as macrorregiões (Albernaz et al., 2012; Wittmann et al., 2013), esta divisão tem o potencial de auxiliar no entendimento de padrões macroecológicos que abordarei nesta tese. Na porção brasileira, onde esta tese tem foco, as várzeas estão inseridas nas macrorregiões Central e Leste, no médio e baixo curso da calha principal do rio Amazonas, respectivamente.

O desnível do terreno de oeste para leste ao longo de cerca de 4.000 km do eixo principal do rio Amazonas, nas condições geológicas atuais, tem uma pequena variação de relevo (100 metros de Iquitos, no Peru, à foz, na costa Atlântica) (Albert e Reis, 2011; Irion et al., 2010). Porém, essa declividade longitudinal é um fator importante para a formação de gradientes de inundação, e o histórico de desenvolvimento dos hábitats ao longo das últimas eras geológicas propiciou diferentes pressões seletivas às espécies que hoje persistem nelas (Konar et al., 2013; Wittmann et al., 2002; Wittmann, Junk e Piedade, 2004). O desenvolvimento da planície de várzea recente do rio

Amazonas data do último período glacial (15.000-10.000 anos atrás) (Irion et al., 2010), no entanto, vários estudos estratigráficos e paleobotânicos indicam que a vegetação da planície amazônica esteve sujeita a episódios de inundação por um longo período em diversas ocasiões (Albert, Val e Hoorn, 2018; Graham, 2009; Hoorn et al., 2010), justificando assim o possível surgimento de um conjunto de linhagens de espécies com adaptações à inundação (Mori et al., 2019; Luize et al., 2018; Wittmann e Householder, 2016). Nas várzeas há ocorrência de diversas fisionomias vegetais, de campos a florestas, que sofrem a influência da dinâmica hidrológica, sedimentar e da topografia local (Ayres, 1995; Junk et al., 2012).

1.2. A diversidade filogenética de árvores na floresta de várzea amazônica

A evolução biológica e o papel da filogenia na organização das comunidades são um dos grandes paradigmas da biologia moderna (Webb et al., 2002). Linhagens de espécies proximamente aparentadas tendem a competir mais fortemente entre si do que com espécies distantes devido a conservação de características ancestrais (Gerhold et al., 2018). O resultado é uma exclusão competitiva local e tem como provável consequência um padrão de repulsão filogenética (em inglês *phylogenetic overdispersion*) nas comunidades biológicas (Ackerly, Schwilk e Webb, 2006; Webb et al. 2002). Por outro lado, a ação local de filtros ambientais como a inundação sobre organismos aparentados poderia gerar um padrão de agrupamento filogenético (em inglês *phylogenetic clustering*) nestas mesmas comunidades (Webb et al. 2002). Diversos trabalhos têm sido realizados para avaliar a estrutura filogenética de comunidades em diversos ecossistemas ao redor do globo para entender quais os possíveis padrões (Emerson e Gillespie 2008; Gerhold et al., 2018). Nesse sentido, entender os processos e as causas que levam a um arranjo de linhagens em comunidades locais requer uma perspectiva histórica da construção dos hábitats disponíveis na região e do complexo banco de espécies (do inglês *species pool*) do qual derivam (Gerhold et al., 2018).

A conservação filogenética de nicho (do inglês *phylogenetic niche conservatism*) é uma importante generalização derivada de estudos da evolução das adaptações dos organismos e considera que os mesmos carregam informações genéticas que os restringem a hábitats para os quais estariam originalmente adaptados (Emerson e Gillespie 2008; Webb et al., 2002). Nesse sentido, as espécies tenderiam a se manter e persistir em hábitats semelhantes àqueles onde surgiram para os quais já apresentam adaptações (Ackerly 2003; Crisp et al., 2009; Donoghue 2008; Gerhold et al., 2018). Nas florestas inundáveis da Amazônia Ocidental, Aldana e colaboradores (2017) encontraram linhagens de espécies mais aparentadas entre si nas florestas inundáveis do que florestas de terra firme adjacentes. Este resultado foi similar ao encontrado por Umaña e colaboradores (2012) na Colômbia. Estes padrões mostram uma tendência de conservação de nicho em comunidades nos ambientes com características ecológicas estressantes (Guevara et al., 2017).

No entanto, considerando que no caso das várzeas amazônicas não há estudo precedente que indique relação da diversidade filogenética entre hábitats com diferentes gradientes de inundação, a SESSÃO I desta tese investiga a hipótese de que a estrutura filogenética das comunidades de plantas arbóreas é indiferente a intensidade de inundação mas que a pressão antropogênica atual tem o potencial de diminuir a diversidade filogenética. As comunidades locais seriam mais homogêneas e menos diversas filogeneticamente (maior proporção de espécies aparentadas ou em agrupamento filogenético) quanto maior a perturbação humana. A premissa é que as linhagens de espécies adaptadas ao alagamento têm ampla distribuição no banco de espécies regional (conservação filogenética de nicho), no entanto a exploração seletiva acaba fazendo com que as mesmas se tornem menos diversas filogeneticamente.

1.3. A diversidade taxonômica em florestas de várzea amazônica

O banco de espécies das áreas inundáveis da Amazônia é estimado em 3,6 mil espécies (Luize et al., 2018; Wittmann et al., 2013). E nesse caso, o tamanho do banco de espécies é um fator importante a ser considerado para estudos de montagem de comunidades biológicas e depende circunstancialmente da escala (resolução) no qual o estudo está sendo considerado (Zobel et al., 2016). Comunidades locais — a diversidade da comunidade em um mesmo tipo de hábitat de uma determinada região é chamada diversidade alfa (p. ex. diversidade de árvores em florestas alagadas do Alto Rio Negro) — estão necessariamente inseridas dentro de um banco maior de espécies regionais — a diversidade da comunidade global (continente) em vários tipos de hábitats é chamada diversidade gama (p.ex. diversidade de árvores entre florestas alagadas da Amazônia). Em um contexto de resolução intermediária ou mesoescala, pode-se incluir a diversidade beta — a dissimilaridade de espécies entre comunidades locais de uma região, tanto em termos de distância espacial quanto temporal, originada pela adição ou substituição de espécies (Magurran, 2011). A diversidade beta reflete a riqueza de hábitats em uma determinada região e pode ser mensurada em termos de “aninhamento” ou “dispersão” (Baselga, 2012; Baselga e Leprieur, 2015; Pärtel et al., 2016).

Há muita discussão na literatura científica e outras tantas formas de se medir a diversidade biológica das comunidades, além das mencionadas (Vellend, 2010; Pärtel et al., 2016). Quando se examina a ocorrência das espécies em hábitats locais em condições ambientais estressantes (ex. inundação, salinidade), não toleradas por todas as espécies do banco regional, mas que eventualmente ocorrem nestas comunidades, pode-se inserir o conceito de diversidade escura (do inglês *dark diversity*). Estas espécies ausentes têm o potencial de ocorrer nestas comunidades (Pärtel et al, 2011; Pärtel et al., 2016). A filtragem ambiental (do inglês *environmental filtering*) é um processo com raízes históricas e evolutivas e uma determinada espécie somente persiste neste ambiente se primeiro conseguir chegar a ele (Cornell e Harrison, 2014). Com a estimativa de quantas espécies estão ausentes de uma comunidade local mas que ocorrem no banco de espécies regional, através da métrica de diversidade escura, pode-se mensurar o quanto uma comunidade local está completa (do inglês *community completeness*) e formular hipóteses sobre quais os fatores que estão levando a esta ausência de espécies nas comunidades locais (Pärtel, Szava-Kovats e Zobel, 2013).

Além disso, pode-se considerar que existe um limite (saturação) entre a quantidade de espécies que podem ocupar uma comunidade local e que vêm de um banco de espécies regional por uma simples questão de espaço (Srivastava, 1999; Pärtel, 2011; Szava-Kovats, Ronk e Pärtel, 2013). A saturação pode ser interpretada como um equilíbrio dinâmico da riqueza de espécies em um contexto espaço-temporal, pois sempre há um número de espécies que pode coexistir num determinado local e este número pode variar tanto em função do tamanho do banco de espécies regional (aspectos históricos e evolutivos), quanto da disponibilidade de recursos e interações bióticas (aspectos ecológicos) (Mateo et al., 2017; Olivares et al., 2018). Nesse sentido, o conceito de diversidade escura é uma ferramenta promissora para avaliar a integridade de comunidades locais.

O desenvolvimento de hipóteses científicas sobre como ocorre a recuperação de comunidades biológicas após eventos de perturbação e como as comunidades biológicas são formadas ao longo do tempo têm tido importante papel no desenvolvimento da ecologia como ciência (Connel 1978; Diamond, 1975; Hubbell, 2001; Kraft et al., 2007; MacArthur e Levins, 1967). A questão de quais espécies ocuparão a comunidade (regras de montagem ou *assembly rules*) está no escopo de várias teorias ecológicas que têm como base os processos de seleção, deriva, especiação e dispersão (Vellend, 2010). As comunidades de árvores em hábitats de florestas de várzea amazônicas têm um subconjunto específico de espécies dentro do banco regional e são um bom modelo para testar hipóteses de como estas comunidades são montadas (incluindo as espécies presentes e ausentes) e esse será o foco da SESSÃO II desta tese. O objetivo é testar o efeito da inundação e da densidade humana histórica e atual na diversidade de comunidades arbóreas e avaliar quantitativamente a sua integridade em relação ao conjunto de espécies regional. Os resultados desta sessão complementam as informações da sessão anterior e ampliam o escopo da tese ao indicar possíveis áreas de floresta de várzea com maior influência humana e que necessitam de maior atenção de medidas de conservação. A premissa é que causas antropogênicas históricas e atuais podem ter influência nos padrões de riqueza de espécies das comunidades locais e causar a longo prazo um débito de extinção no banco de espécies regional~~.~~

1.4. A influência da antropização na várzea amazônica

Independentemente das discussões teóricas sobre a montagem e origem das comunidades biológicas e consequentemente das florestas de várzea, outro fator pouco considerado em estudos ecológicos, mas potencialmente relevantes, é o grau de pressão antropogênica histórica e atual que estas florestas de várzea passaram ou vêm passando ao longo do tempo. Devido a sua alta produtividade e fertilidade, os ambientes de várzea são apontados como uma das principais rotas de entrada para a colonização humana na Amazônia (Denevan, 1996; McMichael e Bush, 2019; Palace et al., 2017). Além disso, formam os hábitats mais extensos, produtivos e diversificados dentre as áreas úmidas da região (Junk et al., 2011). Atualmente e em um passado relativamente recente, um grande contingente humano tem vivido e utilizado as várzeas amazônicas de diferentes formas (Castello et al., 2013; Heckenberger e Neves, 2009; Levis et al., 2012; McMichael e Bush, 2019). Ao longo de toda a extensão do rio Amazonas no território brasileiro, as várzeas ocupam cerca de 8% do bioma, e formam uma zona de amortecimento (*buffer zone*) que auxilia na manutenção do equilíbrio ecológico e dos serviços ecossistêmicos da floresta como um todo (Affonso, Barbosa e Novo, 2011; Araújo Barbosa, Atkinson e Dearing, 2016; Flores et al., 2017; Jancoski et al., 2019; Schöngart et al., 2017; Wittmann et al., 2013).

A atuação humana na Amazônia, cujo período de influência tem sido intensamente debatido (Clement et al., 2015; Denevan, 1992; Levis et al., 2017; McMichael et al., 2015, 2017), sobrepõe-se aos fatores ambientais e históricos da paisagem alagável e adicionam uma variável sobre os processos que permitem as comunidades de plantas nas várzeas persistirem. Alguns estudos sugerem que grande parte da floresta Amazônica, em especial a periferia do bioma e ao longo dos seus rios, devem estar em estado de recuperação por perturbações humanas ocorridas repetidamente durante o Holoceno (Barlow et al., 2012; McMichael e Bush, 2019). A organização de comunidades biológicas em ecossistemas é moldada pelo contexto ambiental ao longo da escala evolutiva e ecológica (Chave, 2013) e, portanto, podemos inferir que a diversidade de plantas nas várzeas amazônicas pode ser considerada o reflexo de causas distais e proximais (Antonelli et al., 2018; Antonelli e Sanmartín, 2011; Hoorn, C. et al., 2010).

Comunidades biológicas de ambientes dinâmicos, seja por perturbações previsíveis seja imprevisíveis, de natureza antrópica (ex. corte seletivo, queima, coleta de sementes etc.) somadas as naturais (ex. inundações, ciclones, terremotos etc.), apresentam alto valor para a biologia da conservação (Arroyo-Rodríguez et al., 2017; Barlow et al. 2012; Cavender-Bares et al., 2016; Rozendaal et al., 2019; Vieira, Toledo e Higuchi, 2018). Áreas degradadas ou antropizadas são repositórios da biodiversidade outrora existente e podem contribuir efetivamente para a manutenção de serviços ecossistêmicos importantes (Arroyo-Rodríguez et al., 2017). Elas proveem uma rede de fluxo gênico que pode, com a manutenção de estratégias de conservação (p. ex. reintrodução de espécies) e técnicas de recuperação florestal (p. ex. em áreas de nascentes), amenizar o clima e ainda gerar renda para as populações que tiram o sustento de produtos da floresta se houver o manejo sustentável (Chazdon, 2003; Malhi et al., 2014).

O fato é que nossa espécie, hoje globalmente dominante, tem causado inúmeras alterações no ambiente em curtos espaços de tempo e numa grande velocidade. A tomada de decisões relevantes para que cenários irreversíveis não ocorram no futuro depende de estudos básicos sobre a contribuição da diversidade destas comunidades na paisagem (Bellard et al., 2012; Díaz et al., 2015; Nolan et al., 2018). Estudos recentes consideram que o papel da espécie humana na história do planeta tem implicado na existência de uma nova era geológica, o Antropoceno (Corlett, 2015; Malhi, 2017; Mehrabi, Ellis e Ramankutty, 2018), muito embora seja discutida a sua data de início exata (Lewis e Maslin, 2015; Tarolli et al., 2019; Vieira, Toledo e Higuchi, 2018). A pressão humana sobre o ambiente e os ecossistemas naturais tem dimensões locais, regionais e globais e está associada a atividades econômicas, como a agricultura e outros usos da terra, ao nível de desenvolvimento tecnológico e mesmo ao contexto sócio-político de comunidades humanas contemporâneas e pregressas (Clement, 1999; Henderson e Loreau, 2019; Piperno, 2017; Weinberger, Quiñinao e Marquet, 2017). Todos estes efeitos parecem ser cumulativos e se intensificam à medida que a densidade dos agrupamentos humanos aumenta (Klein Goldewijk, 2001; Kaplan et al., 2017; Klein Goldewijk et al., 2016). Sem um controle efetivo dos danos ou medidas de remediação ambiental, a tendência preocupante é que ocorram mais extinções de espécies, que os serviços ecossistêmicos decaiam e percam grande parte de seu poder benéfico, e que possa ocorrer escassez de alimentos e movimentos migratórios em massa para regiões menos atingidas pelas mudanças (Díaz et al., 2019).

A investigação de fatores que levaram à formação dos ecossistemas amazônicos atuais é multidisciplinar e passa pelo entendimento de processos históricos, sejam eles evolutivos, ecológicos ou de ocupação humana (Bush et al., 2015; Hoorn et al., 2010; Levis et al., 2017; McMichael e Bush, 2019; Ritter et al., 2019). Deve-se considerar que há sinergia entre fatores, e que as influências ocorrem em várias escalas temporais e que pode haver uma defasagem entre um estímulo e a resposta do ecossistema (Kuussaari et al., 2009; Levin, 1992; Pärtel et al., 2017; Pavoine e Bonsall, 2011). Além da dimensão temporal, é preciso considerar a alta heterogeneidade espacial de um bioma de dimensões continentais como a Amazônia, incluindo ambientes pouco estudados e que apresentam alto grau de endemismo (Draper et al., 2018; Guevara Andino et al., 2017; Myster, 2016; Wittmann e Householder, 2016).

1.5. Questões delineadoras

O desmatamento e a fragmentação florestal podem levar à extinção local de espécies e a tendência é diminuir irreversivelmente a diversidade das comunidades biológicas. Entender o padrão de diversidade atual das florestas de várzea amazônicas requer uma abordagem macroecológica para entender como múltiplos fatores interagem. Da perspectiva do tempo de vida de um ser humano, nossa espécie parece ter uma longa história de dominância sobre o planeta, mas a existência do *Homo sapiens* é uma novidade (Ellis et al., 2013). É a civilização moderna que tem alterado significativamente o meio ambiente e provocado a formação de comunidades biológicas depauperadas ou homogeneizadas (Cadotte, 2013; Donaldson, Wilson e Maclean, 2016; Laurance et al., 2012).

Esta tese investiga como os regimes de inundação e a densidade humana nas macrorregiões estudadas influenciam os padrões de diversidade arbórea nas florestas de várzea ao longo da calha do rio Amazonas. O estudo é apresentado em duas sessões que usam abordagens distintas, com foco em diferentes métricas de diversidade. A SESSÃO 1 examina a diversidade filogenética do componente arbóreo de florestas de várzea e investiga duas hipóteses: i) a severidade da inundação é responsável por diminuir a diversidade filogenética em ambientais de várzea que permanecem alagados por mais tempo, mais especificamente diminuindo a quantidade de linhagens presentes e levando à homogeneização filogenética destas florestas; ii) a diversidade filogenética é semelhante em locais com maior pressão antropogênica. A SESSÃO 2 investiga os padrões de diversidade taxonômica e o efeito cumulativo da densidade humana histórica nos bancos de espécies locais e regionais desde a chegada dos europeus na região: i) o aumento da densidade humana diminui o banco de espécies regional e consequentemente a completude das comunidades arbóreas da floresta de várzea; ii) a diversidade de espécies é menor em locais com maior densidade populacional humana histórica. Ao final, os resultados apresentados nos dois capítulos são integrados e discutidos em conjunto, apontando os principais resultados e conclusões alcançados sobre a influência dos fatores naturais e antropogênicos examinados.

2. Sessão I

“Do flooding and human land use patterns affect phylogenetic structure of Amazonian *várzea* tree communities?”

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Do flooding regimes and current human land use patterns affect phylogenetic structureof Amazonian *várzea* tree communities?

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Abstract: The phylogenetic structure approach is widely used to assess the role of evolutionary and ecological processes that shapes tropical tree communities. Amazonian várzea forests are closely related to Amazon River origin where lineages of tree species have a filtered species pool with adaptations to flood tolerance. But current human disturbances are increasing and may have an influence on the phylogenetic diversity on theses landscapes by extirpating species. Towards contributing to the knowledge of the phylogenetic dimension of tree communities in the region, we seek to answer the following question: Do Amazonian *várzea* forest present distinct phylogenetic structures due to differences in their flooding regime and current human land use? In this way, we investigated macro-regions with distinct flood regimes and anthropization levels along 2,400 km of the main channel of Amazon River. The hypothesis that severity of flooding is a proxy to phylogentic filtering among macro-regions of várzea tree communities was not fully corroborated. The macro-regions studied showed a similar phylogenetic structure of distant related taxa in both macro-regions analyzed, with tree communities of both macro-regions represented by a wide range of lineages besides different flooding regimes. On the other hand, closely related taxa showed a pattern of phylogenetic homogenization when lineages tend be more similar (clustered) than expected by chance in locations with lower flood severity (Eastern macro-region). In this way, phylogenetic niche conservatism related to flood regime is widespread along distinct flood regimes and local communities may have distinct traits to cope flooding severity. Pivotally, therefore, even location in highly anthropized macro-regions could be a major reservoir of phylogenetic diversity and could represent important sources of seeds for evolutionarily distinct species to promote reforestation and restoration projects in várzea macro-regions.

Keywords: phylogenetic niche conservatism; flooded forest anthopization index; phylogenetic clustering; phylogenetic overdispersion; human influence.

INTRODUCTION

Tree lineages in Amazon tropical rain forests have a complex geo-ecological history (Honorio Coronado et al. 2015; Carlucci et al. 2017; Slik et al. 2018); diversification and extinction episodes may have been the rule over millions of years throughout landscape construction (Antonelli and Sanmartín 2011). When compared to other Amazonian habitats, white-water floodplain forests (locally called várzea) are closely related to Andean origin (Antonelli et al. 2009). The current extension of Amazon River (from Andean region to Atlantic Ocean) is relatively recent and current várzeas were formed within the Holocene (Irion et al. 2010). But before that, a long history of orogeny and geomorphologic events formed an extensive sedimentary basin that now occupies 400,000 km² (~8%) of the biome (Hess et al. 2015; Wittmann and Householder 2016). Lineages of tree species in these flooded habitats may have a filtered pool of species with adaptations distinct from that of other flooded or non-flooded habitats (Wittmann et al. 2013; Luize et al. 2018). Additionally, in an evolutionary scale the tree assemblages may have constraints amplified by current human disturbances (Tilman and Lehman 2001; Root-Bernstein and Svenning 2018). Here we search for macroecological patterns of phylogenetic structure on tree communities in the Brazilian part of the várzea forest system (Central and Eastern) within different flood regimes and current human influence.

Since the early Miocene (~25 Ma), increased Andean orogeny continually fed Amazon River in Western and Central macro-regions with high sediment load, but records of their arrival in Eastern macro-region date back from late Miocene (~7 Ma) to early Pliocene (~5 Ma) (Hoorn et al. 2010, 2017; Albert et al. 2018). In the period before transcontinental incision and connection with Atlantic Ocean, macro-regions of the Amazon River had different evolutionary settings that may be considered in the formation of their lineage pool (Gerhold et al., 2018). While the biota in the Western and Central macro-regions experienced submergence by extensive lake systems of Andean origin for a long time (Hoorn et al. 2010), Eastern macro-region biota might have had been affected by older Paleozoic (~250 Ma) formations of the eastern-most part of Guyana and Brazilian shields (Hoorn et al. 2017; Albert et al. 2018). The current Amazonian várzea habitats have an intermediate number of species when compared to richer adjacent upland (terra firme) forests in the same macro-region (Wittmann et al. 2013). Thus, it is reasonable to infer the formation of a filtered pool of species with different tolerances and adaptations to waterlogged conditions across the Amazon River (Luize et al. 2018; Mori et al. 2019).

Despite generalizations for environmental constraints, some studies reveal that different diversity patterns may arise at regional and local scales in várzea forests tree communities (Parolin et al. 2004; Wittmann et al. 2006; Albernaz et al. 2012). Flooding regime, seasonal amplitude of water level and sedimentation dynamics are correlated with different distribution patterns of species along macro-regions. At the regional scale, flooding regime is linked to monomodal and polimodal flood pulses in Central and Eastern macro-regions, respectively (Junk et al. 2012). The monomodal flood pulse is pervasive in the Amazonian várzea where it is associated to seasonal rainfall, and it can reach until 280 days of submergence in forest of low topographic level; but polimodal flood pulse occurs daily only in the Amazon River mouth where it is restricted to the tidal reach of ocean waves in the lower part of the River (Prance 1979). In these contrasting flood regimes, submergence period should be the main environmental filter (Junk et al. 2012) and at the local scale, topographic variation is linked to a zonation pattern of species with different tolerances and adaptations to submergence where water level amplitude promotes coexistence of different species (Cattanio et al. 2002; Wittmann et al. 2002). Also, in the local scale, sedimentation dynamics are linked to a mosaic of different successional stages within a limited area (Worbes et al. 1992; Wittmann et al. 2004).

In the context of conservation, community phylogenetics is a powerful tool to understand how biological communities respond to human disturbances of varying type, intensity, and frequency (Santos et al., 2014). Short-term human disturbance may affect várzea forest tree communities in a similar way by maintaining initial sucessional stages in areas where it has recent influence (Albernaz et al. 2012; Arias et al. 2016). While it is still debated how pervasive were pre-Columbian human interferences on inter-fluvial landscapes in the Amazon (Barlow et al. 2012; Piperno et al. 2015; McMichael et al. 2017; Levis et al. 2017), increasing evidence shows that large rivers and their surrounding high fertilized várzeas have had intense human presence since before European arrival (Denevan 1996; McMichael and Bush 2019). European colonization, including native human depopulation, their own establishment and the eventual development of major cities, may have profound effects on species composition and forest structure (Denevan 1996; Porro 1996; Zarin et al. 2001; Balée 2010; Fortini and Zarin 2011; Renó et al. 2011, 2016; Castello et al. 2013; McMichael and Bush 2019). In addition, a recent study showed that current human land use of the várzea forests differs between macro-regions (for instance, while cattle ranching is the major influential economic activity in the Central region, the extraction of non-timber forest products prevails in the Eastern region) leading to different anthropogenic influences in both macro-regions (Magalhães et al 2015).

Should both flood regime and current human land use be responsible for evolutionary patterns of Amazonian várzea tree communities? To our knowledge, no investigation has explicitly addressed this issue, while a number of studies have investigated the influence of environmental conditions on phylogenetic dimension of communities throughout the biome. For instance, some studies have compared tree communities phylogenetic structure between upland terra firme and flooded forests (Umaña et al. 2012; Honorio Coronado et al. 2015; Guevara et al. 2016; Carlucci et al. 2017; Guevara Andino et al. 2017; Aldana et al. 2017). In this scenario, phylogenetic niche conservatism may have an important role in the habitat specialization of the trees in the regional species pool (Antonelli et al. 2009; Pérez-Escobar et al. 2017). Angiosperm diversification on tree communities can be tracked back to the Miocene (~25 Ma) in várzea forests (Worbes et al. 1992; Wittmann et al. 2013; Albert et al. 2018), but current human disturbance may be skewing our understanding of the phylogenetic patterns we observe today (Arroyo-Rodríguez et al. 2012).

Towards contributing to the knowledge of the phylogenetic dimension of tree communities in the Amazonian várzea forests, we seek to answer the following question: Do Amazonian várzea forests show distinct phylogenetic structures due to differences in their flooding regime and current human land use? Here we proposed to test two hypotheses: First, communities of trees with adaptations to polimodal regime (Eastern macro-region) would have an overdispersed phylogenetic structure when compared to monomodal regime (Central macro-region). It should be similar, but not at the same level of difference, to what has been observed between a steeper gradient from upland terra firme to seasonal flooded forests in Western Amazon (Aldana et al. 2017), because flooding severity (higher number of days submerged) is by far more intense in Central várzea forests than in Eastern counterpart. Second, communities of trees occupying more anthropized areas, independent of macro-region, would have clustered structure when compared to less anthropized areas because the extirpation of selected lineages, similar to what was observed in other tropical regions (Matos et al., 2017; Kusuma et al. 2018), showing that human influence may have a role in phylogenetic homogenization (higher number of closely related species) in tree communities.

MATERIALS AND METHODS

Study areas and sampling design

A data set of 524 tree species (DBH ≥ 10 cm; ESM1) was recorded in 280 square plots (0.625 ha each and 17.5 ha in total) among seven locations (2.5 ha each) distributed across Central (four locations) and Eastern (three locations) macro-regions (*sensu* ter Steege *et al*. 2013) of the Amazon *várzea* forests (Figure 1). Table 1 summarizes species richness, number of individuals, species diversity (Fisher’s alpha), average flood height and current human influence index (FFAI, flooded forest anthropization index *sensu* Magalhães et al., 2015) in the seven locations sampled as well as the mean values for each macro-region. Both macro-regions have *várzea* forests with contrasting flooding regimes and water level amplitudes (Junk et al. 2012; Wittmann et al. 2013) and flood height is a consistent proxy to number of days submerged. It means that flood height is positively correlated with number of flooding days (Albernaz et al., 2012). Additionally, they had undergone through different, recent and historical, human land use patterns (Levis et al. 2012; Magalhães et al. 2015; McMichael and Bush 2019). We used a blocked sampling design in which each of the seven locations had 20 plots (1.25 ha) among one of two levels of anthropization (high= "A+", and low= "A-") (Table 1). Anthropization levels were confirmed by a standardized flooded forest anthropization index (FFAI) that ranges between 0 and 1 in an increasing scale of human land use severity. For instance, FFAI values close to zero means no current human land use and FFAI values close to one means multiple current human land uses. We maximized sampling effort in each location by scattering plots: i) along the local flooding gradient indicated from the maximum flood height in each plot; and ii) along different current human land uses measured in each plot with FFAI. For analysis, we grouped plots in Central and Eastern macro-regions within two levels of anthropization (ESM2). These sampling groups we used found adherence with longitudinal variance of maximum flood height and levels of human land use and categorical variables used (ESM3).

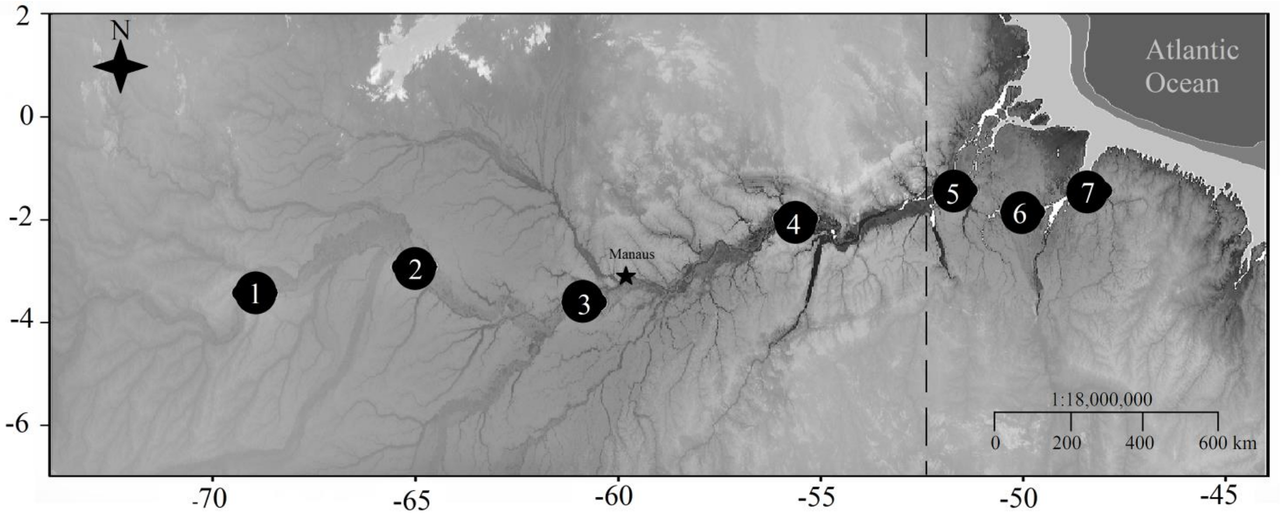

Figure 1: Study locations in Amazonian *várzea* forests along the main stem of the Amazon River. Locations 1-4 are situated in Central and 5-7 in Eastern macro-region. Dashed line splits macro-regions *sensu* ter Steege et al. (2013).

Building a phylogenetic tree of várzea forests tree communities

We built a phylogenetic tree of all tree species in várzea communities sampled based in a version with a consistent nomenclature revision of a previous published megaphylogeny of vascular plants (Zanne et al. 2014). This megaphylogeny (PhytoPhylo) was constructed by Qian and Jin (2016) and is well resolved in genera levels and includes more than 98% of the extant vascular plant families of APG III classification. This methodology is widely used in tropical forest and do not have known bias in relation to branch age estimation of the clades. The PhytoPhylo tree exceeds the number of total vascular plant families across lineages of the more recent version of angiosperm Phylocom/BLADJ-based super-tree (i.e. R20120829) (Qian and Jin 2016). Additionally, we used a proposed R function (S.PhyloMaker) to estimate phylogenetic structure in our study (Qian and Jin 2016). The phylogenetic structure generated with this tool is accessible and robust for studies of tropical community phylogenetic structure, particularly those interested in patterns of phylogenetic diversity along environmental gradients. Our resulting phylogenetic tree (ESM4) was consistent for deep as well as for terminal nodes and all species found in our *várzea* tree communities were included. Species names were standardized according to The Plant List (http://www.theplantlist.org/) using the R package ‘Taxonstand’ (Cayuela et al., 2012).

Table 1: Summary of descriptors and variables measured by levels of human influence on the seven locations and the means values of macro-regions with different levels of human influence in várzea forests tree communities in this study. Anthropization index (FFAI) follows Magalhães et al. (2015). Values hyphen separated indicate range within locations and the numbers followed by parenthesis indicate average and standard deviations, respectively.

Region	Anthrop.level	Location	Area (ha)	Nº spp.	Nº ind.	Fisher's alpha	Flood height	FFAI*
Central	+A	1	1.25	8-27	17-36	23.31 (14.31)	2.12 (1.06)	0.10 (0.03)
		2	1.25	9-23	25-65	15.47 (8.69)	2.91 (0.72)	0.11 (0.03)
		3	1.25	10-24	25-85	9.22 (4.73)	3.20 (1.69)	0.14 (0.07)
		4	1.25	6-16	12-43	6.01 (2.82)	1.15 (0.59)	0.13 (0.05)
		Central+A	5	60-122	505-813	36.02(13.9)	2.34 (1.34)	0.12 (0.05)
	-A	1	1.25	10-25	23-46	16.92 (6.57)	2.62 (1.08)	0.01 (0.01)
		2	1.25	12-28	22-43	25.95 (14.54)	2.87 (1.14)	0
		3	1.25	11-29	24-59	17.04 (14.17)	2.95 (1.81)	0.04 (0.01)
		4	1.25	8-18	19-58	7.75 (4.6)	1.28 (0.36)	0.08 (0.02)
		Central-A	5	63-147	582-781	41.55 (20.4)	2.43 (1.37)	0.03 (0.04)
Eastern	+A	5	1.25	13-26	27-48	21.72 (7.75)	0.41 (0.10)	0.15 (0.04)
		6	1.25	6-27	24-51	9.56 (9.45)	0.24 (0.09)	0.11 (0.03)
		7	1.25	10-24	15-57	12.85 (8.74)	0.61 (0.07)	0.13 (0.05)
		Eastern+A	3.75	67-99	707-770	23.22 (7.2)	0.42 (0.18)	0.13 (0.05)
	-A	5	1.25	13-26	19-51	17.95 (8.54)	0.15 (0.05)	0.07 (0.02)
		6	1.25	5-23	22-53	7.24 (4.84)	0.26 (0.09)	0.11 (0.03
		7	1.25	10-26	25-57	13.16 (4.74)	0.48 (0.09)	0.03 (0.02)
		Eastern-A	3.75	70-90	680-781	23.7 (4.6)	0.30 (0.16)	0.07 (0.04)

*Flooded Forest Anthropization Index (FFAI) ranges from 0-1 in an increasing scale of current human land use.

Phylogenetic diversity and structure of tree communities in várzea forests

We assessed the phylogenetic diversity of *várzea* tree communities using two metrics that take into consideration standardized effect size (ses) to minimize effects of different species richness between macro-regions (Miller et al., 2017): i) mean pairwise distance (ses.MPD), and ii) mean nearest taxon distance (ses.MNTD). The former analyzes phylogenetic structure of distant related taxa (e.g., order) and the latter of closed related taxa (e.g., genera). Both metrics are modifications of the method proposed by Webb et al. (2002) and may be interpreted in terms of average distance and phylogenetic relatedness of distinct taxa to a null model (Kembel and Hubbell 2006; Pavoine et al. 2013). It means that by considering null model as no phylogenetic structure (zero values), phylogenetic overdispersion (positive values) would indicate high phylogenetic diversity (higher number of distant related taxa) and phylogenetic clustering (negative values) would indicate low phylogenetic diversity (higher number of closely related taxa) (Webb et al. 2002; Kembel 2009). In both cases, we used phylogeny.pool as the null model, which draws species at random with equal probability from the regional species pool while maintaining plot species richness (Miller et al. 2017). We computed both phylogenetic metrics using species abundances and the regional species pool was defined as the total species list for all locations, thereby including both Central and Eastern macro-regions of *várzea* tree communities.

Data analyses

We considered both phylogenetic structure metrics separately as our response variables (ses.MPD and ses.MNTD) to answer our main question. We utilized two-way ANOVA to examine the multiplicative effect of flood regime (Central and Eastern macro-regions) and level of current human land use (+A and -A) groups as predictor factors. We had independent predictor groups but with different sample sizes among each level and so we used unbalanced correction to compute statistics (Borcard et al. 2018). We used Tukey-Kramer HSD (honestly significance difference) posteriori tests to compare means. We performed all analyses within R environment (R Core Team 2018).

RESULTS

Species richness or alpha diversity was similar within locations but showed a small and weak decrease from west to east ($r = -0,23$, $R^2=0,05$). Tree species diversity was highly variable among locations (species per plot) but similar within different levels of current human land use (+A and -A categories) within the same location (Table 1). But when we compared number of species among macro-regions, Central had in average 30 more species than Eastern macro-region (Table 1). Another comparison is that besides the fact that flooding regime is more severe at Central Amazon várzea and that species composition is different, the most important families are well represented in both macro-regions (ESM 1).

To test our hypothesis, that Eastern macro-region (less severe inundation) has more phylogenetic diversity (overdispersion) and that more anthropized sites (+A) have less phylogenetic diversity (clustered), we compared different levels of anthropization among macro-regions. We also used two different metrics that analyzes phylogenetic structure of distant related taxa (ses.MPD) and closely related taxa (ses.MNTD). We found that independent of metric used, anthropization levels between macro-regions has a role in explaining differences in the phylogenetic structure ($F_{ses.MPD}(1,276)=29.85$, $p< 0.01$; $F_{ses.MNTD}(1,276)=23.97$, $p< 0.01$).

In relation to distant related taxa (ses.MPD), communities of trees in more anthopized Central macro-region (*+A.Central*) were phylogenetic clustered in relation to all other categories evaluated (Figure 2). All other locations evaluated in relation to distant related taxa were phylogenetic overdispersed and had similar values for this metric.

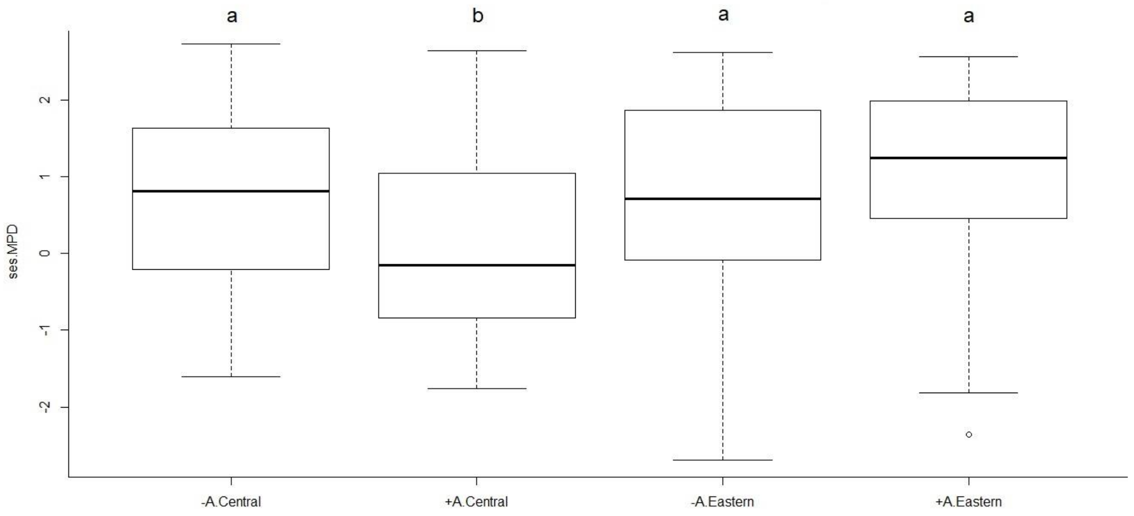

Figure 2: Phylogenetic structure of tree communities in different levels of anthropization (less and more anthropized, -A and +A) in Central and Eastern macro-regions of the várzea forests measured with average distance and phylogenetic relatedness of distinct taxa to a null model in relation to distant related taxa (ses.MPD). Significant differences were found only in relation to more anthropized Central macro-region (+*A.Central*). Letters above graphs are Tukey post-hoc and same letters do not differ, p < 0.05.

In relation to closely related taxa (ses.MNTD), communities of trees in less anthropizated Eastern macro-region (-*A.Eastern*) were clustered in relation to both levels of anthropization in Central macro-region. But, in the other hand, communities in more anthropized Eastern macro-region showed no difference in relation to more anthropized Central counterpart (Figure 3).

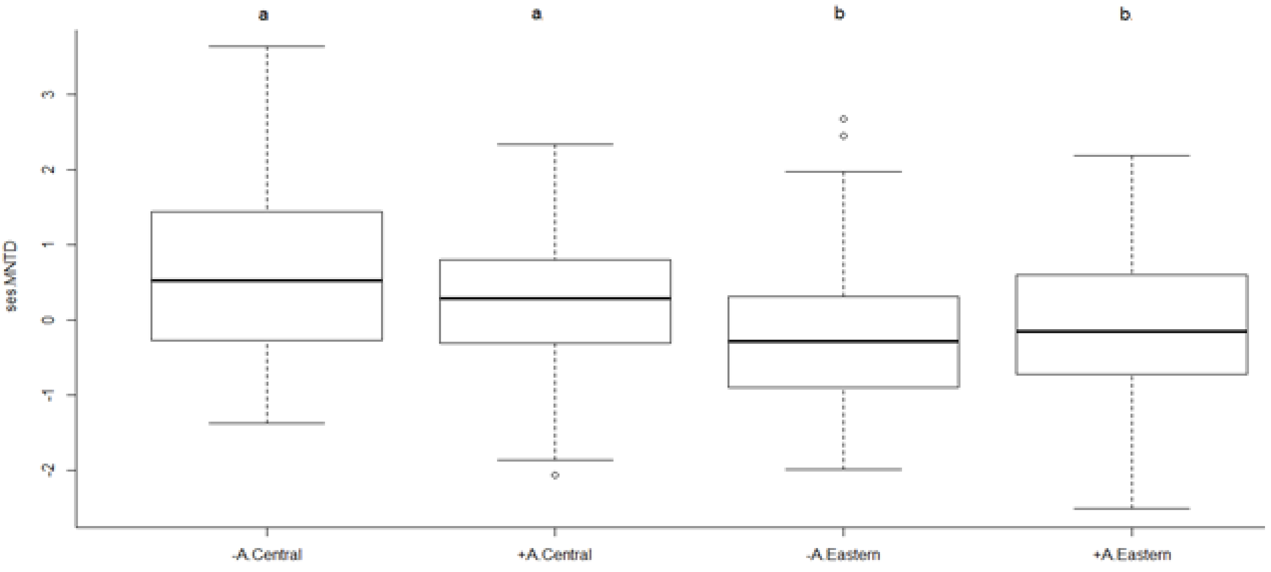

Figure 3: Phylogenetic structure of tree communities in different levels of anthropization (less and more anthropized, -A and +A) in Central and Eastern macro-regions of the várzea forests measured with average distance and phylogenetic relatedness of distinct taxa to a null model in relation to closely related taxa (ses.MNTD). Significant differences were found mainly in less anthropized Eastern macro-region (-*A.Eastern*). Letters above graphs are Tukey post-hoc and same letters do not differ.

DISCUSSION

The hypothesis that severity of flooding is a proxy to phylogentic filtering among macro-regions of várzea tree communities was not fully corroborated. The macro-regions studied showed a similar phylogenetic structure of distant related taxa in both macro-regions analyzed, with tree communities of both macro-regions represented by a wide range of lineages besides different flooding regimes. The exception was more anthropized locations in Central macro-region (+A.Central), that tended to have a clustered structure. It might mean that phylogenetic niche conservation is not the main driver in these lineages and that particular human disturbances in the Central macro-region is promoting the loss of more deep nodes lineages than in Eastern counterpart. On the other hand, closely related taxa showed a pattern of phylogenetic homogenization when lineages tend be more similar (clustered) than expected by chance in locations with lower flood severity (Eastern macro-region). This latter result was the opposite of what we hypothesized initially and may be explained by different adaptations of closely related lineages to cope with flooding severity.

We expected that higher submergence period in Central macro-region (monomodal flood pulse) should be related to a phylogenetic clustering in tree communities because less species should have time to evolve physiological adaptations to cope with these harsher conditions (Parolin & Wittmann, 2010). But according to Hoorn et al. (2010), Western and Central macro-regions in Amazon have had prolonged stable conditions of flooded environments since the Early Miocene in Northern South America, what has allowed for taxa to specialize and adapt to these particular habitats for long period of time (Wittmann et al. 2013). On the other hand, Eastern macro-region received sediments of Andes region from the Late Miocene to early Pleistocene (Albert et al., 2018; Hoorn et al., 2010) and has a limited time of flooding, mainly prone by daily or less frequent flooding period because of recurrent tides (Cattanio et al., 2002).

Phylogenetic niche conservatism predicts that closely related lineages are more ecologically similar than would be expected based on their phylogenetic relationships (Losos 2008). But according to our results, adaptations to submergence seems to be widespread in várzea tree lineages. Since evolutionary events of flooding occurred from early to late Miocene (Wittmann and Householder 2016; Albert et al. 2018), it is logical to suppose that the current distant related tree lineages have had a longer time to accommodate in the landscape as we observed in our study and a lineage pool of distant related species might the case in both macro-regions (Luize et al., 2018). In this sense, these flooded habitats seem to inherit diversification events from past epochs in which the equivalent habitat types were dominant (Gerhold et al., 2018)

It is the case for distant related species in our study, both flood regimes in the macro-regions tested showed phylogenetic overdispersion, except for more anthropized Central macro-region (+A.Central). It might show in these areas that humans or the type of impact they are promoting is extirpating more lineages than in the other areas. The Central macro-region várzea forests have a different land use pattern than Eastern macro-region. While the former has intense cattle ranching, the latter has human disturbances linked to the extraction of non-timber forest products (Fortini & Zarin, 2011; Magalhães et al., 2015). Other studies in tropical regions found that intensity of landscape fragmentation or human land use may be random in relation to extirpation of lineages of species in plant communities (Andrade et al., 2015; Arroyo-Rodríguez et al., 2012; Matos et al., 2017; Santos et al. 2010, 2014).

Várzea forests have species with adaptations to natural disturbance effects promoted by inundation and sedimentation dynamics (Wittmann et al. 2002), what might result in similar responses to current human land use, at least for Central macro-region where sedimentation is higher (Wittmann et al. 2004; Park and Latrubesse 2019). As both natural and anthropogenic disturbances open space in the sucessional gradient, várzea forest may have pre-adapted species of the species pool to occupy the new disturbed area as soon as new space is open. Early successional communities are dominated by closely related species, but relatedness declines in every case as succession proceeds (Letcher et al., 2012). In a conservational perspective, the extirpation of particular tree species with useful traits to humans (e.g. high wood density) may represent a permanent loss if not hampered by sustainable management techniques. It might be case for clustered structure in relation to closed related taxa in Eastern macro-region because historical human land use have a cumulative effect since species extirpation in these areas are longer and more chronic that in Central macro-region (Schaan 2010; McMichael and Bush 2019). Some studies speculate that large extent of Amazon rainforests today, including várzea forests, might be considered early to late sucessional stages originated on areas of past human disturbance (Barlow et al. 2012; Bush et al. 2015).

Additionally, the clustered phylogenetic structure related to closely related taxa in Eastern macro-region (polimodal flood pulse) should be linked to lower alpha diversity in this area when compared to Central region (Table 1). The phylogenetic metric we used (ses.MNTD) is expected to respond to taxonomic diversity (Webb et al. 2002; Emerson and Gillespie 2008; Honorio Coronado et al. 2015). However, despite we do not tested differences in turnover between macro-regions, we hypothesize that regional differences observed previously (Parolin et al. 2004; Wittmann et al. 2006; Albernaz et al. 2012), should be linked to local scale effects not measured in our study, for instance, sedimentation dynamics as proposed by Wittmann et al (2013). Therefore, both macro-regions should contain different species of the same lineage pool to cope with these constating flooding regimes.

Overall, the observed differences in our phylogenetic structures of anthropization levels should support the hypothesis of low phylogenetic conservatism associated with land use vulnerability in the Neotropics (Arroyo-Rodríguez et al. 2012). It is a favorable signal to the conservational status of fragmented or secondary forest in the region, since our results indicate that even high anthropized areas have a good representativeness in phylogenetic diversity. This interpretation follows similar results found in relation to taxonomic diversity on adjacent non-flooded areas in secondary forests in Amazonia (Solar et al. 2016; Coelho de Souza et al. 2016). And phylogenetic diversity in both macro-regions should be preserved to avoid permanent loss of genetic information since only 1% of current várzea forests in Brazilian Amazon are protected under regulation by public policies (Albernaz et al., 2012).

In summary, regional historical differences, both in the evolutionary and ecological scale, are important drivers of phylogenetic diversity in tree communities of várzea forest in Brazilian Amazon. Pivotally, therefore, even locations in highly anthropized macro-regions could be a major reservoir of phylogenetic diversity and could represent important sources of propagules for evolutionarily distinct species to promote reforestation and restoration projects in várzea macro-regions. The theory behind phylogenetic structure patterns along disturbance gradients (environmental or human based) relies on hypotheses about the retention of species with adaptations to survive the harsh conditions imposed and particular traits may be divergent to cope with these different flooding regimes. Future studies should focus on the phylogenetic signal of particular species and test whether phylogenetic impoverishment is linked to the loss of important information within the lineage pool of várzea.

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Electronic Supplementary Material (ESM)

ESM 1: List of tree species found in all locations used in this study with information to the phylogenetic group that each family belongs to according to APG III. Taxa names were standardized according to the The Plant List platform (www.theplantlist.org)

SPECIES	GENERA	FAMILY	GROUP
Trichanthera_gigantea	Trichanthera	Acanthaceae	Eudicots
Lindackeria_latifolia	Lindackeria	Achariaceae	Eudicots
Lindackeria_paludosa	Lindackeria	Achariaceae	Eudicots
Lindackeria_pauciflora	Lindackeria	Achariaceae	Eudicots
Anacardium_giganteum	Anacardium	Anacardiaceae	Eudicots
Astronium_lecointei	Astronium	Anacardiaceae	Eudicots
Mangifera_indica	Mangifera	Anacardiaceae	Eudicots
Spondias_mombin	Spondias	Anacardiaceae	Eudicots
Tapirira_guianensis	Tapirira	Anacardiaceae	Eudicots
Tapirira_peckoltiana	Tapirira	Anacardiaceae	Eudicots
Annona_cuspidata	Annona	Annonaceae	Magnoliids
Annona_exsucca	Annona	Annonaceae	Magnoliids
Annona_hypoglauca	Annona	Annonaceae	Magnoliids
Annona_montana	Annona	Annonaceae	Magnoliids
Annona_sericea	Annona	Annonaceae	Magnoliids
Annona_tenuipes	Annona	Annonaceae	Magnoliids
Duguetia_calycina	Duguetia	Annonaceae	Magnoliids
Duguetia_duckei	Duguetia	Annonaceae	Magnoliids
Duguetia_echinophora	Duguetia	Annonaceae	Magnoliids
Duguetia_quitarensis	Duguetia	Annonaceae	Magnoliids
Duguetia_spixiana	Duguetia	Annonaceae	Magnoliids
Duguetia_surinamensis	Duguetia	Annonaceae	Magnoliids
Guatteria_foliosa	Guatteria	Annonaceae	Magnoliids
Guatteria_inundata	Guatteria	Annonaceae	Magnoliids
Guatteria_poeppigiana	Guatteria	Annonaceae	Magnoliids
Guatteria_schomburgkiana	Guatteria	Annonaceae	Magnoliids
Onychopetalum_amazonicum	Onychopetalum	Annonaceae	Magnoliids
Oxandra_riedeliana	Oxandra	Annonaceae	Magnoliids
Pseudoxandra_leiophylla	Pseudoxandra	Annonaceae	Magnoliids
Pseudoxandra_lucida	Pseudoxandra	Annonaceae	Magnoliids
Pseudoxandra_polyphleba	Pseudoxandra	Annonaceae	Magnoliids
Unonopsis_duckei	Unonopsis	Annonaceae	Magnoliids
Unonopsis_floribunda	Unonopsis	Annonaceae	Magnoliids
Unonopsis_guatterioides	Unonopsis	Annonaceae	Magnoliids
Xylopia_aligustrifolia	Xylopia	Annonaceae	Magnoliids
Xylopia_amazonica	Xylopia	Annonaceae	Magnoliids
Xylopia_benthamii	Xylopia	Annonaceae	Magnoliids
Xylopia_calophylla	Xylopia	Annonaceae	Magnoliids
Xylopia_emaginata	Xylopia	Annonaceae	Magnoliids
Xylopia_nitida	Xylopia	Annonaceae	Magnoliids

SPECIES	GENERA	FAMILY	GROUP
Xylopia_ochrantha	Xylopia	Annonaceae	Magnoliids
Xylopia_sp.	Xylopia	Annonaceae	Magnoliids
Ambelania_acida	Ambelania	Apocynaceae	Eudicots
Aspidosperma_auriculatum	Aspidosperma	Apocynaceae	Eudicots
Aspidosperma_desmanthum	Aspidosperma	Apocynaceae	Eudicots
Aspidosperma_excelsum	Aspidosperma	Apocynaceae	Eudicots
Aspidosperma_macrocarpon	Aspidosperma	Apocynaceae	Eudicots
Aspidosperma_rigidum	Aspidosperma	Apocynaceae	Eudicots
Couma_macrocarpa	Couma	Apocynaceae	Eudicots
Himatanthus_sucuuba	Himatanthus	Apocynaceae	Eudicots
Himatanthus_tarapotensis	Himatanthus	Apocynaceae	Eudicots
Lacmellea_aculeata	Lacmellea	Apocynaceae	Eudicots
Malouetia_tamaquarina	Malouetia	Apocynaceae	Eudicots
Tabernaemontana_markgrafiana	Tabernaemontana	Apocynaceae	Eudicots
Astrocaryum_jauari	Astrocaryum	Arecaceae	Monocots
Astrocaryum_murumuru	Astrocaryum	Arecaceae	Monocots
Attalea_maripa	Attalea	Arecaceae	Monocots
Attalea_phalerata	Attalea	Arecaceae	Monocots
Bactris_maraja	Bactris	Arecaceae	Monocots
Euterpe_oleracea	Euterpe	Arecaceae	Monocots
Euterpe_precatoria	Euterpe	Arecaceae	Monocots
Manicaria_saccifera	Manicaria	Arecaceae	Monocots
Mauritia_flexuosa	Mauritia	Arecaceae	Monocots
Mauritiella_armata	Mauritiella	Arecaceae	Monocots
Oenocarpus_bacaba	Oenocarpus	Arecaceae	Monocots
Raphia_taedigera	Raphia	Arecaceae	Monocots
Socratea_exorrhiza	Socratea	Arecaceae	Monocots
Crescentia_cujete	Crescentia	Bignoniaceae	Eudicots
Jacaranda_copaia	Jacaranda	Bignoniaceae	Eudicots
Tabebuia_barbata	Tabebuia	Bignoniaceae	Eudicots
Tabebuia_fluviatilis	Tabebuia	Bignoniaceae	Eudicots
Tabebuia_serratifolia	Tabebuia	Bignoniaceae	Eudicots
Cochlospermum_orinocense	Cochlospermum	Bixaceae	Eudicots
Cordia_exaltata	Cordia	Boraginaceae	Eudicots
Cordia_nodosa	Cordia	Boraginaceae	Eudicots
Cordia_scabrifolia	Cordia	Boraginaceae	Eudicots
Cordia_sp.	Cordia	Boraginaceae	Eudicots
Cordia_tetrandra	Cordia	Boraginaceae	Eudicots
Crepidospermum_goudotianum	Crepidospermum	Burseraceae	Eudicots
Protium_decandrum	Protium	Burseraceae	Eudicots
Protium_giganteum	Protium	Burseraceae	Eudicots
Protium_heptaphyllum	Protium	Burseraceae	Eudicots
Protium_krukoffii	Protium	Burseraceae	Eudicots
Protium_pallidum	Protium	Burseraceae	Eudicots
Protium_spruceanum	Protium	Burseraceae	Eudicots

SPECIES	GENERA	FAMILY	GROUP
Protium_strumosum	Protium	Burseraceae	Eudicots
Tetragastris_altissima	Tetragastris	Burseraceae	Eudicots
Calophyllum_brasiliense	Calophyllum	Calophyllaceae	Eudicots
Caraipa_grandifolia	Caraipa	Calophyllaceae	Eudicots
Caraipa_richardiana	Caraipa	Calophyllaceae	Eudicots
Connarus_angustifolius	Connarus	Cannaraceae	Eudicots
Crateva_tapia	Crateva	Capparaceae	Eudicots
Caryocar_microcarpum	Caryocar	Caryocaraceae	Eudicots
Maytenus_ebenifolia	Maytenus	Celastraceae	Eudicots
Maytenus_guyanensis	Maytenus	Celastraceae	Eudicots
Maytenus_macrocarpa	Maytenus	Celastraceae	Eudicots
Maytenus_myrsinoides	Maytenus	Celastraceae	Eudicots
Couepia_guianensis	Couepia	Chrysobalanaceae	Eudicots
Couepia_paraensis	Couepia	Chrysobalanaceae	Eudicots
Hirtella_bicornis	Hirtella	Chrysobalanaceae	Eudicots
Hirtella_eriandra	Hirtella	Chrysobalanaceae	Eudicots
Licania_apetala	Licania	Chrysobalanaceae	Eudicots
Licania_canescens	Licania	Chrysobalanaceae	Eudicots
Licania_guianensis	Licania	Chrysobalanaceae	Eudicots
Licania_heteromorpha	Licania	Chrysobalanaceae	Eudicots
Licania_laevigata	Licania	Chrysobalanaceae	Eudicots
Licania_licaniiflora	Licania	Chrysobalanaceae	Eudicots
Licania_longistyla	Licania	Chrysobalanaceae	Eudicots
Licania_macrophylla	Licania	Chrysobalanaceae	Eudicots
Licania_membranacea	Licania	Chrysobalanaceae	Eudicots
Licania_parviflora	Licania	Chrysobalanaceae	Eudicots
Licania_sp.	Licania	Chrysobalanaceae	Eudicots
Parinari_excelsa	Parinari	Chrysobalanaceae	Eudicots
Parinari_montana	Parinari	Chrysobalanaceae	Eudicots
Cleome_arborea	Cleome	Cleomaceae	Eudicots
Garcinia_brasiliensis	Garcinia	Clusiaceae	Eudicots
Garcinia_macrophylla	Garcinia	Clusiaceae	Eudicots
Garcinia_madruno	Garcinia	Clusiaceae	Eudicots
Moronobea_coccinea	Moronobea	Clusiaceae	Eudicots
Symphonia_globulifera	Symphonia	Clusiaceae	Eudicots
Tovomita_brevistaminea	Tovomita	Clusiaceae	Eudicots
Tovomita_speciosa	Tovomita	Clusiaceae	Eudicots
Buchenavia_macrophylla	Buchenavia	Combretaceae	Eudicots
Buchenavia_ochroprumna	Buchenavia	Combretaceae	Eudicots
Buchenavia_oxycarpa	Buchenavia	Combretaceae	Eudicots
Buchenavia_sp.	Buchenavia	Combretaceae	Eudicots
Terminalia_argentea	Terminalia	Combretaceae	Eudicots
Terminalia_dichotoma	Terminalia	Combretaceae	Eudicots
Tapura_guianensis	Tapura	Dichapetalaceae	Eudicots
Tapura_juruana	Tapura	Dichapetalaceae	Eudicots

SPECIES	GENERA	FAMILY	GROUP
Tapura_singularis	Tapura	Dichapetalaceae	Eudicots
Diospyros_artanthifolia	Diospyros	Ebenaceae	Eudicots
Diospyros_guianensis	Diospyros	Ebenaceae	Eudicots
Diospyros_poeppigiana	Diospyros	Ebenaceae	Eudicots
Sloanea_erismoides	Sloanea	Elaeocarpaceae	Eudicots
Sloanea_excelsa	Sloanea	Elaeocarpaceae	Eudicots
Sloanea_garckeana	Sloanea	Elaeocarpaceae	Eudicots
Sloanea_grandiflora	Sloanea	Elaeocarpaceae	Eudicots
Sloanea_guianensis	Sloanea	Elaeocarpaceae	Eudicots
Sloanea_parviflora	Sloanea	Elaeocarpaceae	Eudicots
Sloanea_porphyrocarpa	Sloanea	Elaeocarpaceae	Eudicots
Sloanea_robusta	Sloanea	Elaeocarpaceae	Eudicots
Sloanea_sp.	Sloanea	Elaeocarpaceae	Eudicots
Sloanea_terniflora	Sloanea	Elaeocarpaceae	Eudicots
Erythroxylum_citrifolium	Erythroxylum	Erythroxylaceae	Eudicots
Alchornea_fluviatilis	Alchornea	Euphorbiaceae	Eudicots
Alchornea_schomburgkii	Alchornea	Euphorbiaceae	Eudicots
Conceveiba_guianensis	Conceveiba	Euphorbiaceae	Eudicots
Croton_cuneatus	Croton	Euphorbiaceae	Eudicots
Croton_matourensis	Croton	Euphorbiaceae	Eudicots
Glycydendron_amazonicum	Glycydendron	Euphorbiaceae	Eudicots
Hevea_brasiliensis	Hevea	Euphorbiaceae	Eudicots
Hevea_spruceana	Hevea	Euphorbiaceae	Eudicots
Hura_crepitans	Hura	Euphorbiaceae	Eudicots
Mabea_caudata	Mabea	Euphorbiaceae	Eudicots
Mabea_nitida	Mabea	Euphorbiaceae	Eudicots
Mabea_paniculata	Mabea	Euphorbiaceae	Eudicots
Mabea_speciosa	Mabea	Euphorbiaceae	Eudicots
Pera_distichophylla	Pera	Euphorbiaceae	Eudicots
Sagotia_racemosa	Sagotia	Euphorbiaceae	Eudicots
Sapium_glandulosum	Sapium	Euphorbiaceae	Eudicots
Sapium_marmieri	Sapium	Euphorbiaceae	Eudicots
Acacia_loretensis	Acacia	Fabaceae	Eudicots
Acacia_polyphylla	Acacia	Fabaceae	Eudicots
Albizia_multiflora	Albizia	Fabaceae	Eudicots
Albizia_subdimidiata	Albizia	Fabaceae	Eudicots
Alexa_grandiflora	Alexa	Fabaceae	Eudicots
Andira_inermis	Andira	Fabaceae	Eudicots
Andira_surinamensis	Andira	Fabaceae	Eudicots
Batesia_floribunda	Batesia	Fabaceae	Eudicots
Campsiandra_comosa	Campsiandra	Fabaceae	Eudicots
Cassia_leiandra	Cassia	Fabaceae	Eudicots
Cedrelinga_cateniformis	Cedrelinga	Fabaceae	Eudicots
Chamaecrista_xinguensis	Chamaecrista	Fabaceae	Eudicots
Copaifera_officinalis	Copaifera	Fabaceae	Eudicots

SPECIES	GENERA	FAMILY	GROUP
Crudia_bracteata	Crudia	Fabaceae	Eudicots
Crudia_oblonga	Crudia	Fabaceae	Eudicots
Cynometra_bauhiniifolia	Cynometra	Fabaceae	Eudicots
Cynometra_hostmanniana	Cynometra	Fabaceae	Eudicots
Cynometra_spruceana	Cynometra	Fabaceae	Eudicots
Dialium_guianense	Dialium	Fabaceae	Eudicots
Diplotropis_martiusii	Diplotropis	Fabaceae	Eudicots
Enterolobium_schomburgkii	Enterolobium	Fabaceae	Eudicots
Eperua_glabra	Eperua	Fabaceae	Eudicots
Erythrina_fusca	Erythrina	Fabaceae	Eudicots
Etaballia_dubia	Etaballia	Fabaceae	Eudicots
Hydrochorea_corymbosa	Hydrochorea	Fabaceae	Eudicots
Hymenaea_intermedia	Hymenaea	Fabaceae	Eudicots
Hymenaea_oblongifolia	Hymenaea	Fabaceae	Eudicots
Inga_alba	Inga	Fabaceae	Eudicots
Inga_auristella	Inga	Fabaceae	Eudicots
Inga_bourgonii	Inga	Fabaceae	Eudicots
Inga_brachyrhachis	Inga	Fabaceae	Eudicots
Inga_brachystachys	Inga	Fabaceae	Eudicots
Inga_capitata	Inga	Fabaceae	Eudicots
Inga_cinnamomea	Inga	Fabaceae	Eudicots
Inga_disticha	Inga	Fabaceae	Eudicots
Inga_flagelliformis	Inga	Fabaceae	Eudicots
Inga_grandiflora	Inga	Fabaceae	Eudicots
Inga_laurina	Inga	Fabaceae	Eudicots
Inga_macrophylla	Inga	Fabaceae	Eudicots
Inga_marginata	Inga	Fabaceae	Eudicots
Inga_minutula	Inga	Fabaceae	Eudicots
Inga_nobilis	Inga	Fabaceae	Eudicots
Inga_obidensis	Inga	Fabaceae	Eudicots
Inga_paraensis	Inga	Fabaceae	Eudicots
Inga_punctata	Inga	Fabaceae	Eudicots
Inga_rubiginosa	Inga	Fabaceae	Eudicots
Inga_splendens	Inga	Fabaceae	Eudicots
Inga_stenoptera	Inga	Fabaceae	Eudicots
Inga_thibaudiana	Inga	Fabaceae	Eudicots
Inga_ulei	Inga	Fabaceae	Eudicots
Inga_umbellifera	Inga	Fabaceae	Eudicots
Inga_velutina	Inga	Fabaceae	Eudicots
Lecointea_amazonica	Lecointea	Fabaceae	Eudicots
Macrolobium_acaciifolium	Macrolobium	Fabaceae	Eudicots
Macrolobium_augustifolium	Macrolobium	Fabaceae	Eudicots
Macrolobium_bifolium	Macrolobium	Fabaceae	Eudicots
Macrolobium_pendulum	Macrolobium	Fabaceae	Eudicots
Macrolobium_sp.	Macrolobium	Fabaceae	Eudicots

SPECIES	GENERA	FAMILY	GROUP
Mora_paraensis	Mora	Fabaceae	Eudicots
Muellera_frutescens	Muellera	Fabaceae	Eudicots
Ormosia_coutinhoi	Ormosia	Fabaceae	Eudicots
Paramachaerum_ormosioides	Paramachaerum	Fabaceae	Eudicots
Parkia_multijuga	Parkia	Fabaceae	Eudicots
Peltogyne_venosa	Peltogyne	Fabaceae	Eudicots
Pentaclethra_macroloba	Pentaclethra	Fabaceae	Eudicots
Platymiscium_filipes	Platymiscium	Fabaceae	Eudicots
Platymiscium_trinitatis	Platymiscium	Fabaceae	Eudicots
Platymiscium_ulei	Platymiscium	Fabaceae	Eudicots
Pseudopiptadenia_psilostachya	Pseudopiptadenia	Fabaceae	Eudicots
Pterocarpus_officinalis	Pterocarpus	Fabaceae	Eudicots
Pterocarpus_rohrii	Pterocarpus	Fabaceae	Eudicots
Pterocarpus_santalinoides	Pterocarpus	Fabaceae	Eudicots
Schizolobium_parahyba	Schizolobium	Fabaceae	Eudicots
Senna_reticulata	Senna	Fabaceae	Eudicots
Stryphnodendron_guianense	Stryphnodendron	Fabaceae	Eudicots
Stryphnodendron_pulcherrimum	Stryphnodendron	Fabaceae	Eudicots
Swartzia_acreana	Swartzia	Fabaceae	Eudicots
Swartzia_acuminata	Swartzia	Fabaceae	Eudicots
Swartzia_arborescens	Swartzia	Fabaceae	Eudicots
Swartzia_corrugata	Swartzia	Fabaceae	Eudicots
Swartzia_laurifolia	Swartzia	Fabaceae	Eudicots
Swartzia_leptopetala	Swartzia	Fabaceae	Eudicots
Swartzia_panacoco	Swartzia	Fabaceae	Eudicots
Swartzia_polyphylla	Swartzia	Fabaceae	Eudicots
Swartzia_racemosa	Swartzia	Fabaceae	Eudicots
Tachigali_myrmecophila	Tachigali	Fabaceae	Eudicots
Tachigali_paniculata	Tachigali	Fabaceae	Eudicots
Taralea_oppositifolia	Taralea	Fabaceae	Eudicots
Vatairea_erythrocarpa	Vatairea	Fabaceae	Eudicots
Vatairea_guianensis	Vatairea	Fabaceae	Eudicots
Zollernia_paraensis	Zollernia	Fabaceae	Eudicots
Zygia_cataractae	Zygia	Fabaceae	Eudicots
Zygia_cauliflora	Zygia	Fabaceae	Eudicots
Zygia_juruana	Zygia	Fabaceae	Eudicots
Zygia_latifolia	Zygia	Fabaceae	Eudicots
Hernandia_guianensis	Hernandia	Hernandiaceae	Magnoliids
Sacoglottis_guianensis	Sacoglottis	Humiriaceae	Eudicots
Vantanea_parviflora	Vantanea	Humiriaceae	Eudicots
Vismia_baccifera	Vismia	Hypericaceae	Eudicots
Vismia_cayennensis	Vismia	Hypericaceae	Eudicots
Vismia_macrophylla	Vismia	Hypericaceae	Eudicots
Emmotum_acuminatum	Emmotum	Icacinaceae	Eudicots
Emmotum_sp.	Emmotum	Icacinaceae	Eudicots

SPECIES	GENERA	FAMILY	GROUP
Lacistema_aggregatum	Lacistema	Lacistemataceae	Eudicots
Vitex_cymosa	Vitex	Lamiaceae	Eudicots
Vitex_triflora	Vitex	Lamiaceae	Eudicots
Aniba_guianensis	Aniba	Lauraceae	Magnoliids
Aniba_hostmanniana	Aniba	Lauraceae	Magnoliids
Aniba_kappleri	Aniba	Lauraceae	Magnoliids
Endlicheria_anomala	Endlicheria	Lauraceae	Magnoliids
Endlicheria_formosa	Endlicheria	Lauraceae	Magnoliids
Endlicheria_sp.	Endlicheria	Lauraceae	Magnoliids
Licaria_armeniaca	Licaria	Lauraceae	Magnoliids
Mezilaurus_itauba	Mezilaurus	Lauraceae	Magnoliids
Mezilaurus_mahuba	Mezilaurus	Lauraceae	Magnoliids
Nectandra_amazonum	Nectandra	Lauraceae	Magnoliids
Nectandra_cuspidata	Nectandra	Lauraceae	Magnoliids
Nectandra_lucida	Nectandra	Lauraceae	Magnoliids
Nectandra_pulverulenta	Nectandra	Lauraceae	Magnoliids
Ocotea_aciphylla	Ocotea	Lauraceae	Magnoliids
Ocotea_canaliculata	Ocotea	Lauraceae	Magnoliids
Ocotea_cernua	Ocotea	Lauraceae	Magnoliids
Ocotea_cymbarum	Ocotea	Lauraceae	Magnoliids
Ocotea_longifolia	Ocotea	Lauraceae	Magnoliids
Ocotea_sp.1	Ocotea	Lauraceae	Magnoliids
Ocotea_sp.2	Ocotea	Lauraceae	Magnoliids
Ocotea_sp.3	Ocotea	Lauraceae	Magnoliids
Ocotea_sp.4	Ocotea	Lauraceae	Magnoliids
Ocotea_sp.5	Ocotea	Lauraceae	Magnoliids
Ocotea_sp.6	Ocotea	Lauraceae	Magnoliids
Allantoma_lineata	Allantoma	Lecythidaceae	Eudicots
Bertholletia_excelsa	Bertholletia	Lecythidaceae	Eudicots
Couratari_guianensis	Couratari	Lecythidaceae	Eudicots
Couratari_tenuicarpa	Couratari	Lecythidaceae	Eudicots
Couroupita_guianensis	Couroupita	Lecythidaceae	Eudicots
Couroupita_subsessilis	Couroupita	Lecythidaceae	Eudicots
Eschweilera_albiflora	Eschweilera	Lecythidaceae	Eudicots
Eschweilera_amazonica	Eschweilera	Lecythidaceae	Eudicots
Eschweilera_collina	Eschweilera	Lecythidaceae	Eudicots
Eschweilera_coriacea	Eschweilera	Lecythidaceae	Eudicots
Eschweilera_grandiflora	Eschweilera	Lecythidaceae	Eudicots
Eschweilera_ovalifolia	Eschweilera	Lecythidaceae	Eudicots
Eschweilera_parviflora	Eschweilera	Lecythidaceae	Eudicots
Eschweilera_pedicellata	Eschweilera	Lecythidaceae	Eudicots
Gustavia_augusta	Gustavia	Lecythidaceae	Eudicots
Gustavia_hexapetala	Gustavia	Lecythidaceae	Eudicots
Lecythis_lurida	Lecythis	Lecythidaceae	Eudicots
Lecythis_pisonis	Lecythis	Lecythidaceae	Eudicots

SPECIES	GENERA	FAMILY	GROUP
Lecythis_poiteaui	Lecythis	Lecythidaceae	Eudicots
Hebepetalum_humiriifolium	Hebepetalum	Linaceae	Eudicots
Byrsonima_arthropoda	Byrsonima	Malpighiaceae	Eudicots
Byrsonima_frondosa	Byrsonima	Malpighiaceae	Eudicots
Byrsonima_japurensis	Byrsonima	Malpighiaceae	Eudicots
Apeiba_burchellii	Apeiba	Malvaceae	Eudicots
Apeiba_echinata	Apeiba	Malvaceae	Eudicots
Ceiba_pentandra	Ceiba	Malvaceae	Eudicots
Eriotheca_longipedicellata	Eriotheca	Malvaceae	Eudicots
Guazuma_crinita	Guazuma	Malvaceae	Eudicots
Guazuma_ulmifolia	Guazuma	Malvaceae	Eudicots
Luehea_cymulosa	Luehea	Malvaceae	Eudicots
Luehea_speciosa	Luehea	Malvaceae	Eudicots
Lueheopsis_duckeana	Lueheopsis	Malvaceae	Eudicots
Matisia_paraensis	Matisia	Malvaceae	Eudicots
Matisia_sp.	Matisia	Malvaceae	Eudicots
Pachira_aquatica	Pachira	Malvaceae	Eudicots
Pachira_insignis	Pachira	Malvaceae	Eudicots
Pachira_paraensis	Pachira	Malvaceae	Eudicots
Pseudobombax_munguba	Pseudobombax	Malvaceae	Eudicots
Pseudomedia_murure	Pseudomedia	Malvaceae	Eudicots
Quararibea_guianensis	Quararibea	Malvaceae	Eudicots
Quararibea_ochrocalyx	Quararibea	Malvaceae	Eudicots
Sterculia_elata	Sterculia	Malvaceae	Eudicots
Sterculia_excelsa	Sterculia	Malvaceae	Eudicots
Sterculia_pruriens	Sterculia	Malvaceae	Eudicots
Sterculia_speciosa	Sterculia	Malvaceae	Eudicots
Theobroma_cacao	Theobroma	Malvaceae	Eudicots
Theobroma_speciosum	Theobroma	Malvaceae	Eudicots
Theobroma_subincanum	Theobroma	Malvaceae	Eudicots
Bellucia_grossularioides	Bellucia	Melastomataceae	Eudicots
Henriettea_succosa	Henriettea	Melastomataceae	Eudicots
Miconia_affinis	Miconia	Melastomataceae	Eudicots
Mouriri_acutiflora	Mouriri	Melastomataceae	Eudicots
Mouriri_ficoides	Mouriri	Melastomataceae	Eudicots
Mouriri_grandiflora	Mouriri	Melastomataceae	Eudicots
Mouriri_nigra	Mouriri	Melastomataceae	Eudicots
Carapa_guianensis	Carapa	Meliaceae	Eudicots
Cedrela_odorata	Cedrela	Meliaceae	Eudicots
Guarea_guidonia	Guarea	Meliaceae	Eudicots
Guarea_kunthiana	Guarea	Meliaceae	Eudicots
Guarea_subsessiliflora	Guarea	Meliaceae	Eudicots
Trichilia_lecointei	Trichilia	Meliaceae	Eudicots
Trichilia_micrantha	Trichilia	Meliaceae	Eudicots
Trichilia_quadrijuga	Trichilia	Meliaceae	Eudicots

SPECIES	GENERA	FAMILY	GROUP
Trichilia_rubra	Trichilia	Meliaceae	Eudicots
Trichilia_sp.	Trichilia	Meliaceae	Eudicots
Batocarpus_amazonicus	Batocarpus	Moraceae	Eudicots
Brosimum_acutifolium	Brosimum	Moraceae	Eudicots
Brosimum_guianense	Brosimum	Moraceae	Eudicots
Brosimum_lactescens	Brosimum	Moraceae	Eudicots
Clarisia_ilicifolia	Clarisia	Moraceae	Eudicots
Ficus_citrifolia	Ficus	Moraceae	Eudicots
Ficus_gomelleira	Ficus	Moraceae	Eudicots
Ficus_guianensis	Ficus	Moraceae	Eudicots
Ficus_insipda	Ficus	Moraceae	Eudicots
Ficus_mathewsii	Ficus	Moraceae	Eudicots
Ficus_maxima	Ficus	Moraceae	Eudicots
Ficus_nymphaeifolia	Ficus	Moraceae	Eudicots
Ficus_obtusifolia	Ficus	Moraceae	Eudicots
Ficus_paraensis	Ficus	Moraceae	Eudicots
Ficus_pertusa	Ficus	Moraceae	Eudicots
Ficus_trigona	Ficus	Moraceae	Eudicots
Helicostylis_pedunculata	Helicostylis	Moraceae	Eudicots
Helicostylis_scabra	Helicostylis	Moraceae	Eudicots
Helicostylis_tomentosa	Helicostylis	Moraceae	Eudicots
Maclura_tinctoria	Maclura	Moraceae	Eudicots
Maquira_calophylla	Maquira	Moraceae	Eudicots
Maquira_coriacea	Maquira	Moraceae	Eudicots
Maquira_guianensis	Maquira	Moraceae	Eudicots
Naucleopsis_caloneura	Naucleopsis	Moraceae	Eudicots
Sorocea_duckei	Sorocea	Moraceae	Eudicots
Trymatococcus_amazonicus	Trymatococcus	Moraceae	Eudicots
Iryanthera_juruensis	Iryanthera	Myristicaceae	Magnoliids
Iryanthera_laevis	Iryanthera	Myristicaceae	Magnoliids
Iryanthera_tessmannii	Iryanthera	Myristicaceae	Magnoliids
Virola_calophylla	Virola	Myristicaceae	Magnoliids
Virola_michelii	Virola	Myristicaceae	Magnoliids
Virola_mollissima	Virola	Myristicaceae	Magnoliids
Virola_multinervia	Virola	Myristicaceae	Magnoliids
Virola_pavonis	Virola	Myristicaceae	Magnoliids
Virola_surinamensis	Virola	Myristicaceae	Magnoliids
Eugenia_egensis	Eugenia	Myrtaceae	Eudicots
Eugenia_feijoi	Eugenia	Myrtaceae	Eudicots
Eugenia_flavescens	Eugenia	Myrtaceae	Eudicots
Eugenia_florida	Eugenia	Myrtaceae	Eudicots
Eugenia_gomesiana	Eugenia	Myrtaceae	Eudicots
Eugenia_ochrophloea	Eugenia	Myrtaceae	Eudicots
Eugenia_omissa	Eugenia	Myrtaceae	Eudicots
Eugenia_patens	Eugenia	Myrtaceae	Eudicots

SPECIES	GENERA	FAMILY	GROUP
Eugenia_patrisii	Eugenia	Myrtaceae	Eudicots
Eugenia_ramiflora	Eugenia	Myrtaceae	Eudicots
Eugenia_sp.	Eugenia	Myrtaceae	Eudicots
Eugenia_tapacumensis	Eugenia	Myrtaceae	Eudicots
Myrcia_bracteata	Myrcia	Myrtaceae	Eudicots
Myrcia_eximia	Myrcia	Myrtaceae	Eudicots
Myrcia_paivae	Myrcia	Myrtaceae	Eudicots
Myrciaria_floribunda	Myrciaria	Myrtaceae	Eudicots
Myrciaria_glomerata	Myrciaria	Myrtaceae	Eudicots
Psidium_acutangulum	Psidium	Myrtaceae	Eudicots
Guapira_venosa	Guapira	Nyctaginaceae	Eudicots
Neea_aeruginosa	Neea	Nyctaginaceae	Eudicots
Neea_floribunda	Neea	Nyctaginaceae	Eudicots
Neea_oppositifolia	Neea	Nyctaginaceae	Eudicots
Neea_spruceana	Neea	Nyctaginaceae	Eudicots
Lacunaria_crenata	Lacunaria	Ochnaceae	Eudicots
Ouratea_paraensis	Ouratea	Ochnaceae	Eudicots
Quiina_paraensis	Quiina	Ochnaceae	Eudicots
Quiina_rhytidopus	Quiina	Ochnaceae	Eudicots
Aptandra_tubicina	Aptandra	Olacaceae	Eudicots
Cathedra_acuminata	Cathedra	Olacaceae	Eudicots
Chaunochiton_kappleri	Chaunochiton	Olacaceae	Eudicots
Dulacia_candida	Dulacia	Olacaceae	Eudicots
Heisteria_acuminata	Heisteria	Olacaceae	Eudicots
Minquartia_guianensis	Minquartia	Olacaceae	Eudicots
Agonandra_brasiliensis	Agonandra	Opiliaceae	Eudicots
Amanoa_guianensis	Amanoa	Phyllanthaceae	Eudicots
Discocarpus_essequeboensis	Discocarpus	Phyllanthaceae	Eudicots
Hieronyma_alchorneoides	Hieronyma	Phyllanthaceae	Eudicots
Margaritaria_nobilis	Margaritaria	Phyllanthaceae	Eudicots
Picramnia_latifolia	Picramnia	Picramniaceae	Eudicots
Piranhea_trifoliata	Piranhea	Picrodendraceae	Eudicots
Coccoloba_densifrons	Coccoloba	Polygonaceae	Eudicots
Coccoloba_latifolia	Coccoloba	Polygonaceae	Eudicots
Coccoloba_lehmannii	Coccoloba	Polygonaceae	Eudicots
Coccoloba_mollis	Coccoloba	Polygonaceae	Eudicots
Ruprechtia_tangarana	Ruprechtia	Polygonaceae	Eudicots
Symmeria_paniculata	Symmeria	Polygonaceae	Eudicots
Triplaris_surinamensis	Triplaris	Polygonaceae	Eudicots
Stylogyne_orinocensis	Stylogyne	Primulaceae	Eudicots
Roupala_sp.	Roupala	Proteaceae	Eudicots
Drypetes_variabilis	Drypetes	Putranjivaceae	Eudicots
Cassipourea_guianensis	Cassipourea	Rhizophoraceae	Eudicots
Rhizophora_racemosa	Rhizophora	Rhizophoraceae	Eudicots
Alibertia_edulis	Alibertia	Rubiaceae	Eudicots

SPECIES	GENERA	FAMILY	GROUP
Amaioua_guianensis	Amaioua	Rubiaceae	Eudicots
Calycophyllum_spruceanum	Calycophyllum	Rubiaceae	Eudicots
Chomelia_pohliana	Chomelia	Rubiaceae	Eudicots
Cordiera_myrciifolia	Cordiera	Rubiaceae	Eudicots
Duroia_duckei	Duroia	Rubiaceae	Eudicots
Faramea_capillipes	Faramea	Rubiaceae	Eudicots
Faramea_stenopetala	Faramea	Rubiaceae	Eudicots
Ferdinandusa_rudgeoides	Ferdinandusa	Rubiaceae	Eudicots
Genipa_americana	Genipa	Rubiaceae	Eudicots
Genipa_spruceana	Genipa	Rubiaceae	Eudicots
Posoqueria_longiflora	Posoqueria	Rubiaceae	Eudicots
Psychotria_barbiflora	Psychotria	Rubiaceae	Eudicots
Simira_rubescens	Simira	Rubiaceae	Eudicots
Zanthoxylum_compactum	Zanthoxylum	Rutaceae	Eudicots
Zanthoxylum_rhoifolium	Zanthoxylum	Rutaceae	Eudicots
Zanthoxylum_riedelianum	Zanthoxylum	Rutaceae	Eudicots
Banara_guianensis	Banara	Salicaceae	Eudicots
Banara_nitida	Banara	Salicaceae	Eudicots
Casearia_aculeata	Casearia	Salicaceae	Eudicots
Casearia_manauensis	Casearia	Salicaceae	Eudicots
Casearia_pitumba	Casearia	Salicaceae	Eudicots
Casearia_sylvestris	Casearia	Salicaceae	Eudicots
Casearia_ulmifolia	Casearia	Salicaceae	Eudicots
Homalium_guianense	Homalium	Salicaceae	Eudicots
Homalium_sp.	Homalium	Salicaceae	Eudicots
Laetia_corymbulosa	Laetia	Salicaceae	Eudicots
Allophylus_punctatus	Allophylus	Sapindaceae	Eudicots
Cupania_latifolia	Cupania	Sapindaceae	Eudicots
Cupania_scrobiculata	Cupania	Sapindaceae	Eudicots
Matayba_arborescens	Matayba	Sapindaceae	Eudicots
Matayba_guianensis	Matayba	Sapindaceae	Eudicots
Talisia_cerasina	Talisia	Sapindaceae	Eudicots
Talisia_cupularis	Talisia	Sapindaceae	Eudicots
Toulicia_guianensis	Toulicia	Sapindaceae	Eudicots
Chrysophyllum_auratum	Chrysophyllum	Sapotaceae	Eudicots
Chrysophyllum_brasiliense	Chrysophyllum	Sapotaceae	Eudicots
Chrysophyllum_cuneifolium	Chrysophyllum	Sapotaceae	Eudicots
Chrysophyllum_sparsiflorum	Chrysophyllum	Sapotaceae	Eudicots
Manilkara_amazonica	Manilkara	Sapotaceae	Eudicots
Manilkara_paraensis	Manilkara	Sapotaceae	Eudicots
Micropholis_acutangula	Micropholis	Sapotaceae	Eudicots
Micropholis_egensis	Micropholis	Sapotaceae	Eudicots
Pouteria_anibifolia	Pouteria	Sapotaceae	Eudicots
Pouteria_bilocularis	Pouteria	Sapotaceae	Eudicots
Pouteria_elegans	Pouteria	Sapotaceae	Eudicots

SPECIES	GENERA	FAMILY	GROUP
Pouteria_glomerata	Pouteria	Sapotaceae	Eudicots
Pouteria_gongrijpii	Pouteria	Sapotaceae	Eudicots
Pouteria_guianensis	Pouteria	Sapotaceae	Eudicots
Pouteria_krukovii	Pouteria	Sapotaceae	Eudicots
Pouteria_macrocarpa	Pouteria	Sapotaceae	Eudicots
Pouteria_oppositifolia	Pouteria	Sapotaceae	Eudicots
Pouteria_procera	Pouteria	Sapotaceae	Eudicots
Pouteria_robusta	Pouteria	Sapotaceae	Eudicots
Pouteria_venosa	Pouteria	Sapotaceae	Eudicots
Pradosia_cochlearia	Pradosia	Sapotaceae	Eudicots
Simaba_guianensis	Simaba	Simaroubaceae	Eudicots
Simaba_orinocensis	Simaba	Simaroubaceae	Eudicots
Simaba_polyphylla	Simaba	Simaroubaceae	Eudicots
Simarouba_amara	Simarouba	Simaroubaceae	Eudicots
Solanum_sp.	Solanum	Solanaceae	Eudicots
Discophora_guianensis	Discophora	Stemonuraceae	Eudicots
Ampelocera_edentula	Ampelocera	Ulmaceae	Eudicots
Cecropia_distachya	Cecropia	Urticaceae	Eudicots
Cecropia_latiloba	Cecropia	Urticaceae	Eudicots
Cecropia_membranacea	Cecropia	Urticaceae	Eudicots
Cecropia_obtusa	Cecropia	Urticaceae	Eudicots
Cecropia_palmata	Cecropia	Urticaceae	Eudicots
Cecropia_sciadophylla	Cecropia	Urticaceae	Eudicots
Coussapoa_nitida	Coussapoa	Urticaceae	Eudicots
Pourouma_bicolor	Pourouma	Urticaceae	Eudicots
Pourouma_cecropiifolia	Pourouma	Urticaceae	Eudicots
Pourouma_guianensis	Pourouma	Urticaceae	Eudicots
Pourouma_mollis	Pourouma	Urticaceae	Eudicots
Citharexylum_macrophyllum	Citharexylum	Verbenaceae	Eudicots
Leonia_glycycarpa	Leonia	Violaceae	Eudicots
Rinorea_racemosa	Rinorea	Violaceae	Eudicots
Qualea_sp.	Qualea	Vochysiaceae	Eudicots
Vochysia_guianensis	Vochysia	Vochysiaceae	Eudicots
Vochysia_sp.	Vochysia	Vochysiaceae	Eudicots

ESM 2: Detailed information for each 280 (0.0625 ha) plots used in this study: location numbers are related to Central (L1-L4) and Eastern (L5-L7) macro-regions with respective anthropization levels, flood height, latitude (lat), longitude (lon), number of species (n.spp), number of individuals (n.ind), plot size, and phylogenetic metrics in relation to distant (ses.MPD) and closely related (ses.MNTD) lineages.

location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L1	Central	+A	1	3.572	0.031	-0.275	0.546	-3.419	-69.018	22	28	0.0625
L1	Central	+A	2	2.799	0.111	1.637	0.972	-3.421	-69.017	20	29	0.0625
L1	Central	+A	3	3.431	0.124	-1.762	-0.771	-3.422	-69.014	22	26	0.0625
L1	Central	+A	4	3.200	0.091	-0.136	0.702	-3.424	-69.014	13	17	0.0625
L1	Central	+A	5	3.377	0.168	-0.396	-0.512	-3.416	-69.010	17	27	0.0625
L1	Central	+A	6	3.384	0.091	0.703	-2.059	-3.418	-69.010	20	29	0.0625
L1	Central	+A	7	2.644	0.094	-0.006	-0.442	-3.420	-69.010	19	29	0.0625
L1	Central	+A	8	2.778	0.109	1.029	-0.753	-3.422	-69.011	15	20	0.0625
L1	Central	+A	9	3.096	0.055	1.953	1.152	-3.412	-69.039	20	30	0.0625
L1	Central	+A	10	2.858	0.102	1.062	-0.821	-3.414	-69.040	18	26	0.0625
L1	Central	+A	11	1.833	0.135	2.014	0.861	-3.417	-69.042	24	36	0.0625
L1	Central	+A	12	1.058	0.083	1.583	0.126	-3.424	-69.042	17	27	0.0625
L1	Central	+A	13	1.083	0.111	2.298	0.605	-3.427	-69.028	15	29	0.0625
L1	Central	+A	14	1.419	0.164	2.639	-0.012	-3.425	-69.036	14	21	0.0625

location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L1	Central	+A	15	1.041	0.109	2.132	2.239	-3.423	-69.002	12	24	0.0625
L1	Central	+A	16	1.159	0.072	2.104	0.679	-3.423	-68.999	11	17	0.0625
L1	Central	+A	17	0.777	0.144	0.373	-1.251	-3.422	-68.997	11	18	0.0625
L1	Central	+A	18	1.188	0.112	2.060	-0.066	-3.417	-68.986	14	27	0.0625
L1	Central	+A	19	0.934	0.033	-0.158	0.856	-3.421	-68.988	8	28	0.0625
L1	Central	+A	20	0.771	0.086	0.348	0.208	-3.421	-68.992	11	17	0.0625
L1	Central	-A	21	3.940	0.000	0.676	-0.099	-3.427	-68.895	18	46	0.0625
L1	Central	-A	22	3.978	0.000	1.181	-0.589	-3.427	-68.899	20	43	0.0625
L1	Central	-A	23	4.059	0.000	0.423	-0.304	-3.429	-68.896	22	40	0.0625
L1	Central	-A	24	3.962	0.000	1.364	-0.795	-3.428	-68.893	21	40	0.0625
L1	Central	-A	25	3.017	0.000	0.575	-0.239	-3.426	-68.888	14	23	0.0625
L1	Central	-A	26	3.444	0.000	0.904	-0.510	-3.427	-68.886	18	32	0.0625
L1	Central	-A	27	2.804	0.000	1.397	0.614	-3.418	-68.888	22	44	0.0625
L1	Central	-A	28	2.784	0.022	0.090	1.520	-3.433	-68.896	25	42	0.0625
L1	Central	-A	29	2.777	0.000	0.773	1.109	-3.434	-68.898	17	36	0.0625
L1	Central	-A	30	4.729	0.000	-0.745	0.144	-3.435	-68.897	20	32	0.0625

location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L1	Central	-A	31	1.416	0.000	2.326	-0.009	-3.425	-68.897	17	30	0.0625
L1	Central	-A	32	1.962	0.008	1.964	0.949	-3.428	-68.890	23	34	0.0625
L1	Central	-A	33	1.417	0.031	2.515	0.087	-3.424	-68.890	15	29	0.0625
L1	Central	-A	34	2.398	0.022	1.340	0.577	-3.421	-68.890	20	33	0.0625
L1	Central	-A	35	1.270	0.022	2.276	-1.194	-3.424	-68.887	13	24	0.0625
L1	Central	-A	36	1.670	0.000	1.605	0.776	-3.437	-68.896	18	27	0.0625
L1	Central	-A	37	1.708	0.000	2.243	-0.964	-3.437	-68.894	10	30	0.0625
L1	Central	-A	38	1.700	0.055	2.436	1.499	-3.437	-68.891	16	43	0.0625
L1	Central	-A	39	1.708	0.052	1.912	-0.304	-3.439	-68.890	14	34	0.0625
L1	Central	-A	40	1.763	0.008	1.127	-1.290	-3.440	-68.898	19	29	0.0625
L2	Central	+A	1	3.770	0.055	2.434	1.496	-3.065	-64.999	16	45	0.0625
L2	Central	-A	1	2.170	0.000	1.102	-0.561	-2.843	-64.929	18	44	0.0625
L2	Central	+A	2	3.220	0.105	1.553	1.148	-3.063	-65.002	19	25	0.0625
L2	Central	-A	2	3.880	0.000	-1.293	-1.340	-2.828	-64.951	18	45	0.0625
L2	Central	+A	3	2.030	0.055	1.449	-1.185	-3.062	-65.004	16	45	0.0625
L2	Central	-A	3	3.850	0.000	-0.077	0.958	-2.831	-64.951	17	45	0.0625

location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L2	Central	+A	4	3.410	0.112	2.533	1.910	-3.057	-65.008	23	38	0.0625
L2	Central	-A	4	3.600	0.000	-0.902	0.217	-2.802	-65.069	22	41	0.0625
L2	Central	+A	5	3.050	0.105	1.338	0.013	-3.054	-65.010	23	32	0.0625
L2	Central	-A	5	4.030	0.000	-1.603	-0.079	-2.800	-65.065	19	41	0.0625
L2	Central	+A	6	3.230	0.187	0.805	2.333	-3.056	-65.010	12	26	0.0625
L2	Central	-A	6	2.280	0.000	-0.195	-0.085	-2.794	-65.056	19	65	0.0625
L2	Central	+A	7	2.260	0.112	-0.367	0.828	-3.062	-65.005	17	38	0.0625
L2	Central	-A	7	1.928	0.000	-0.557	-0.488	-2.792	-65.053	19	52	0.0625
L2	Central	+A	8	2.390	0.187	-0.144	0.574	-3.063	-65.004	19	33	0.0625
L2	Central	-A	8	1.630	0.000	-0.716	1.835	-2.709	-65.098	18	29	0.0625
L2	Central	+A	9	2.160	0.091	0.693	0.174	-3.064	-65.003	9	36	0.0625
L2	Central	-A	9	4.190	0.000	-0.831	1.502	-2.706	-65.097	21	47	0.0625
L2	Central	+A	10	3.710	0.091	-1.194	-0.691	-3.067	-65.006	14	25	0.0625
L2	Central	-A	10	1.250	0.000	1.577	0.322	-2.722	-65.088	21	40	0.0625
L2	Central	+A	11	3.770	0.134	-0.950	0.237	-3.068	-65.005	23	35	0.0625
L2	Central	-A	11	2.500	0.000	1.080	0.527	-2.784	-64.892	13	22	0.0625

location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L2	Central	+A	12	3.630	0.134	-0.632	0.020	-3.069	-65.003	15	23	0.0625
L2	Central	-A	12	4.190	0.000	-0.575	1.374	-2.795	-64.890	18	29	0.0625
L2	Central	+A	13	3.610	0.091	-0.844	0.886	-3.067	-65.004	15	25	0.0625
L2	Central	-A	13	3.700	0.000	0.157	0.635	-2.826	-64.897	19	23	0.0625
L2	Central	+A	14	3.940	0.099	-0.506	0.342	-3.066	-65.003	22	28	0.0625
L2	Central	-A	14	4.200	0.000	-0.320	0.537	-2.734	-65.100	19	29	0.0625
L2	Central	+A	15	3.250	0.112	1.270	2.058	-3.065	-65.001	15	27	0.0625
L2	Central	-A	15	1.270	0.000	0.759	0.575	-2.739	-65.099	19	26	0.0625
L2	Central	+A	16	1.810	0.134	0.282	0.628	-3.045	-65.023	16	24	0.0625
L2	Central	-A	16	1.780	0.000	0.935	-0.923	-2.805	-65.011	16	25	0.0625
L2	Central	+A	17	2.080	0.134	0.021	0.358	-3.043	-65.024	20	30	0.0625
L2	Central	-A	17	4.030	0.000	0.390	-0.512	-2.831	-65.003	15	34	0.0625
L2	Central	+A	18	2.500	0.091	0.668	0.587	-3.043	-65.026	12	33	0.0625
L2	Central	-A	18	1.760	0.000	0.602	0.670	-2.808	-65.010	28	43	0.0625
L2	Central	+A	19	2.000	0.099	-0.004	0.575	-3.046	-65.019	17	23	0.0625
L2	Central	-A	19	3.750	0.000	-0.919	0.534	-2.827	-65.003	18	27	0.0625

location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L2	Central	+A	20	2.410	0.112	-1.182	0.792	-3.050	-65.013	21	41	0.0625
L2	Central	-A	20	1.500	0.000	1.332	-0.066	-2.806	-65.012	28	35	0.0625
L3	Central	+A	1	3.811	0.088	-0.965	0.773	-3.648	-60.796	16	40	0.0625
L3	Central	+A	2	5.274	0.124	-1.636	-1.103	-3.651	-60.797	10	30	0.0625
L3	Central	+A	3	4.711	0.079	-0.888	-0.169	-3.646	-60.795	12	39	0.0625
L3	Central	+A	4	4.104	0.052	-0.464	-0.430	-3.639	-60.795	15	85	0.0625
L3	Central	+A	5	4.344	0.063	0.465	0.801	-3.637	-60.799	15	50	0.0625
L3	Central	+A	6	5.078	0.122	-0.610	-0.022	-3.635	-60.804	16	59	0.0625
L3	Central	+A	7	4.673	0.153	-1.116	0.725	-3.633	-60.808	15	41	0.0625
L3	Central	+A	8	4.756	0.074	-0.791	0.733	-3.629	-60.806	19	57	0.0625
L3	Central	+A	9	5.889	0.072	-1.293	-0.806	-3.625	-60.809	13	29	0.0625
L3	Central	+A	10	4.178	0.044	-0.705	0.452	-3.632	-60.812	14	55	0.0625
L3	Central	-A	11	1.146	0.051	1.750	-0.352	-3.633	-60.816	13	31	0.0625
L3	Central	-A	12	0.743	0.033	2.557	0.007	-3.634	-60.817	18	34	0.0625
L3	Central	-A	13	0.617	0.033	-0.585	-0.223	-3.631	-60.817	13	25	0.0625
L3	Central	-A	14	1.036	0.041	0.225	0.106	-3.632	-60.818	10	26	0.0625

location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L3	Central	-A	15	1.811	0.061	0.844	-0.883	-3.630	-60.819	17	59	0.0625
L3	Central	-A	16	2.961	0.044	-0.233	-0.072	-3.629	-60.821	24	39	0.0625
L3	Central	-A	17	1.833	0.041	0.611	-0.168	-3.632	-60.819	12	28	0.0625
L3	Central	-A	18	0.646	0.048	0.591	1.331	-3.635	-60.819	12	28	0.0625
L3	Central	-A	19	1.492	0.015	0.973	-1.125	-3.636	-60.820	13	25	0.0625
L3	Central	-A	20	1.006	0.044	-0.380	-0.797	-3.636	-60.822	13	33	0.0625
L3	Central	+A	21	0.571	0.343	0.873	-0.990	-3.597	-60.816	12	40	0.0625
L3	Central	+A	22	0.403	0.222	2.098	-0.070	-3.593	-60.811	21	39	0.0625
L3	Central	+A	23	1.728	0.126	-1.152	-1.735	-3.588	-60.813	17	35	0.0625
L3	Central	+A	24	1.014	0.171	1.907	1.147	-3.585	-60.814	23	28	0.0625
L3	Central	+A	25	1.486	0.137	2.500	1.997	-3.579	-60.811	19	24	0.0625
L3	Central	+A	26	2.633	0.134	-1.277	-1.537	-3.575	-60.810	16	36	0.0625
L3	Central	+A	27	2.684	0.203	-1.073	-0.165	-3.573	-60.812	28	56	0.0625
L3	Central	+A	28	2.198	0.221	-1.065	-0.143	-3.569	-60.812	29	51	0.0625
L3	Central	+A	29	2.360	0.147	1.049	-0.893	-3.565	-60.811	21	32	0.0625
L3	Central	+A	30	2.027	0.122	-0.615	0.140	-3.557	-60.807	19	28	0.0625

location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L3	Central	-A	31	5.718	0.033	1.466	2.037	-3.582	-60.845	18	55	0.0625
L3	Central	-A	32	5.429	0.033	2.043	2.465	-3.585	-60.845	13	59	0.0625
L3	Central	-A	33	5.119	0.050	-0.224	0.675	-3.588	-60.845	13	26	0.0625
L3	Central	-A	34	4.617	0.033	-0.063	0.679	-3.591	-60.843	16	31	0.0625
L3	Central	-A	35	4.196	0.042	2.650	2.544	-3.593	-60.843	12	49	0.0625
L3	Central	-A	36	3.477	0.066	1.680	2.112	-3.594	-60.849	16	37	0.0625
L3	Central	-A	37	3.957	0.033	1.710	2.775	-3.595	-60.853	13	42	0.0625
L3	Central	-A	38	3.938	0.033	1.935	2.532	-3.596	-60.857	13	43	0.0625
L3	Central	-A	39	4.369	0.033	1.361	1.113	-3.593	-60.856	17	31	0.0625
L3	Central	-A	40	5.014	0.042	1.212	1.173	-3.593	-60.854	11	39	0.0625
L4	Central	+A	1	0.952	0.206	-0.785	0.062	-1.974	-55.423	10	29	0.0625
L4	Central	+A	2	0.253	0.132	-0.580	0.143	-1.975	-55.428	6	35	0.0625
L4	Central	+A	3	1.829	0.127	-0.692	0.661	-1.945	-55.435	14	27	0.0625
L4	Central	+A	4	1.632	0.138	-0.150	0.767	-1.946	-55.429	14	30	0.0625
L4	Central	+A	5	1.527	0.207	-1.489	-0.552	-1.945	-55.431	16	36	0.0625
L4	Central	+A	6	1.829	0.054	-1.027	0.239	-1.943	-55.433	11	37	0.0625

location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L4	Central	+A	7	0.346	0.168	-0.933	-0.063	-1.943	-55.515	7	18	0.0625
L4	Central	+A	8	0.184	0.097	0.137	1.408	-1.942	-55.517	11	29	0.0625
L4	Central	+A	9	1.111	0.128	-0.796	-0.015	-1.942	-55.522	9	42	0.0625
L4	Central	+A	10	0.993	0.153	0.732	0.873	-1.942	-55.526	13	32	0.0625
L4	Central	+A	11	1.753	0.114	0.930	1.839	-1.942	-55.528	10	39	0.0625
L4	Central	+A	12	1.042	0.074	-0.694	0.642	-1.940	-55.519	8	22	0.0625
L4	Central	+A	13	0.550	0.133	-0.839	0.335	-1.919	-55.543	7	12	0.0625
L4	Central	+A	14	0.806	0.082	-1.178	-1.861	-1.944	-55.517	6	30	0.0625
L4	Central	+A	15	0.759	0.128	-0.829	-1.155	-1.943	-55.516	7	25	0.0625
L4	Central	+A	16	0.814	0.110	-1.042	0.029	-1.941	-55.519	14	35	0.0625
L4	Central	+A	17	1.999	0.274	-0.915	-0.759	-1.941	-55.471	15	43	0.0625
L4	Central	+A	18	1.829	0.213	-0.173	1.438	-1.941	-55.469	10	32	0.0625
L4	Central	+A	19	1.424	0.102	0.954	1.187	-1.942	-55.468	10	35	0.0625
L4	Central	+A	20	1.298	0.052	-0.399	0.613	-1.943	-55.464	10	40	0.0625
L4	Central	-A	21	0.871	0.044	0.005	0.301	-2.006	-55.725	11	22	0.0625
L4	Central	-A	22	1.089	0.095	0.660	0.566	-2.009	-55.725	9	26	0.0625

location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L4	Central	-A	23	0.867	0.109	1.736	2.036	-2.011	-55.724	9	28	0.0625
L4	Central	-A	24	1.139	0.109	2.009	2.224	-2.012	-55.726	8	28	0.0625
L4	Central	-A	25	0.901	0.109	2.729	2.346	-2.010	-55.728	9	22	0.0625
L4	Central	-A	26	1.651	0.093	-0.544	-0.776	-2.011	-55.731	10	35	0.0625
L4	Central	-A	27	1.233	0.093	-1.339	-0.917	-2.012	-55.732	12	24	0.0625
L4	Central	-A	28	1.159	0.060	1.649	2.551	-2.013	-55.733	18	28	0.0625
L4	Central	-A	29	0.906	0.060	0.542	0.901	-2.016	-55.733	13	30	0.0625
L4	Central	-A	30	1.121	0.082	2.424	2.438	-2.014	-55.731	14	22	0.0625
L4	Central	-A	31	1.360	0.033	0.691	1.548	-2.010	-55.723	10	19	0.0625
L4	Central	-A	32	1.531	0.082	0.915	1.615	-2.012	-55.722	12	37	0.0625
L4	Central	-A	33	1.748	0.071	-1.109	0.031	-2.013	-55.720	11	36	0.0625
L4	Central	-A	34	1.693	0.093	-1.426	-1.372	-2.014	-55.719	17	42	0.0625
L4	Central	-A	35	1.948	0.093	-0.637	0.299	-2.014	-55.721	12	58	0.0625
L4	Central	-A	36	1.328	0.082	1.100	1.867	-2.013	-55.724	9	37	0.0625
L4	Central	-A	37	1.609	0.093	0.869	2.005	-2.013	-55.726	12	41	0.0625
L4	Central	-A	38	1.481	0.071	-0.179	0.837	-2.013	-55.728	13	38	0.0625

location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L4	Central	-A	39	1.368	0.109	2.553	3.644	-2.009	-55.726	14	29	0.0625
L4	Central	-A	40	0.543	0.077	-0.277	0.044	-2.007	-55.727	8	30	0.0625
L5	Eastern	-A	1	0.472	0.049	-0.348	-0.285	-1.389	-51.590	12	47	0.0625
L5	Eastern	-A	2	0.445	0.030	-0.306	0.147	-1.390	-51.589	19	31	0.0625
L5	Eastern	-A	3	0.298	0.022	-0.197	-0.459	-1.391	-51.590	18	33	0.0625
L5	Eastern	-A	4	0.284	0.030	-1.645	-1.099	-1.389	-51.590	13	28	0.0625
L5	Eastern	-A	5	0.410	0.022	0.047	0.378	-1.388	-51.592	18	49	0.0625
L5	Eastern	-A	6	0.474	0.033	2.618	0.574	-1.386	-51.592	18	41	0.0625
L5	Eastern	-A	7	0.509	0.022	2.032	-1.265	-1.386	-51.591	13	15	0.0625
L5	Eastern	-A	8	0.513	0.022	0.558	-0.430	-1.385	-51.591	17	41	0.0625
L5	Eastern	-A	9	0.481	0.022	2.034	0.749	-1.383	-51.591	16	47	0.0625
L5	Eastern	-A	10	0.464	0.033	0.349	-0.090	-1.383	-51.591	16	57	0.0625
L5	Eastern	-A	11	0.528	0.082	1.902	-0.485	-1.388	-51.595	16	44	0.0625
L5	Eastern	-A	12	0.546	0.022	-2.234	-1.529	-1.391	-51.595	10	18	0.0625
L5	Eastern	-A	13	0.452	0.008	1.757	-0.039	-1.389	-51.596	24	52	0.0625
L5	Eastern	-A	14	0.453	0.000	2.298	0.332	-1.388	-51.597	15	38	0.0625

location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L5	Eastern	-A	15	0.527	0.085	2.429	0.272	-1.386	-51.597	16	37	0.0625
L5	Eastern	-A	16	0.413	0.000	2.041	-0.043	-1.386	-51.595	15	27	0.0625
L5	Eastern	-A	17	0.523	0.049	-2.692	-1.536	-1.396	-51.593	17	41	0.0625
L5	Eastern	-A	18	0.663	0.049	-1.296	-0.889	-1.394	-51.594	15	57	0.0625
L5	Eastern	-A	19	0.591	0.000	0.765	-1.391	-1.393	-51.595	17	39	0.0625
L5	Eastern	-A	20	0.598	0.022	0.220	-0.254	-1.392	-51.595	14	28	0.0625
L5	Eastern	+A	21	0.707	0.140	0.946	1.619	-1.484	-51.745	10	25	0.0625
L5	Eastern	+A	22	0.626	0.140	0.404	1.931	-1.483	-51.745	17	30	0.0625
L5	Eastern	+A	23	0.586	0.027	0.816	-0.880	-1.482	-51.746	19	35	0.0625
L5	Eastern	+A	24	0.577	0.000	1.653	-0.991	-1.481	-51.746	15	33	0.0625
L5	Eastern	+A	25	0.516	0.076	1.670	-0.127	-1.480	-51.746	17	45	0.0625
L5	Eastern	+A	26	0.539	0.165	2.161	-0.805	-1.479	-51.746	18	41	0.0625
L5	Eastern	+A	27	0.583	0.217	0.949	0.652	-1.478	-51.746	26	55	0.0625
L5	Eastern	+A	28	0.469	0.182	0.829	-0.588	-1.477	-51.746	20	47	0.0625
L5	Eastern	+A	29	0.562	0.168	2.316	-0.436	-1.475	-51.746	20	57	0.0625
L5	Eastern	+A	30	0.526	0.224	2.431	0.327	-1.475	-51.747	22	39	0.0625

location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L5	Eastern	+A	31	0.803	0.092	0.389	-0.533	-1.470	-51.741	14	42	0.0625
L5	Eastern	+A	32	0.661	0.139	2.060	0.043	-1.471	-51.742	20	36	0.0625
L5	Eastern	+A	33	0.659	0.143	2.285	0.517	-1.472	-51.743	18	38	0.0625
L5	Eastern	+A	34	0.628	0.143	-0.791	-1.092	-1.472	-51.745	22	53	0.0625
L5	Eastern	+A	35	0.656	0.093	2.558	1.475	-1.472	-51.746	13	33	0.0625
L5	Eastern	+A	36	0.602	0.143	2.341	0.678	-1.474	-51.746	17	46	0.0625
L5	Eastern	+A	37	0.667	0.135	1.512	0.430	-1.473	-51.747	14	30	0.0625
L5	Eastern	+A	38	0.690	0.178	1.672	2.189	-1.473	-51.748	18	27	0.0625
L5	Eastern	+A	39	0.627	0.102	2.179	-0.118	-1.475	-51.749	16	33	0.0625
L5	Eastern	+A	40	0.659	0.130	-1.211	-0.723	-1.476	-51.749	15	36	0.0625
L6	Eastern	+A	1	0.423	0.055	2.005	1.284	-1.863	-49.916	14	31	0.0625
L6	Eastern	+A	2	0.147	0.105	-2.359	-1.886	-1.863	-49.921	15	49	0.0625
L6	Eastern	+A	3	0.121	0.112	2.511	2.013	-1.861	-49.926	8	36	0.0625
L6	Eastern	+A	4	0.232	0.187	1.054	-0.665	-1.864	-49.926	6	40	0.0625
L6	Eastern	+A	5	0.244	0.091	2.334	1.667	-1.856	-49.931	8	38	0.0625
L6	Eastern	+A	6	0.221	0.134	1.816	-0.171	-1.857	-49.932	8	37	0.0625

location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L6	Eastern	+A	7	0.201	0.134	2.220	0.741	-1.846	-49.939	7	42	0.0625
L6	Eastern	+A	8	0.214	0.091	1.964	-0.125	-1.842	-49.941	7	29	0.0625
L6	Eastern	+A	9	0.220	0.099	1.791	1.239	-1.842	-49.943	10	38	0.0625
L6	Eastern	+A	10	0.303	0.112	1.747	-0.559	-1.847	-49.946	10	39	0.0625
L6	Eastern	+A	11	0.229	0.055	1.204	0.062	-1.854	-49.978	18	51	0.0625
L6	Eastern	+A	12	0.151	0.105	1.097	-1.166	-1.856	-49.974	25	40	0.0625
L6	Eastern	+A	13	0.068	0.112	0.720	-2.504	-1.858	-49.974	15	25	0.0625
L6	Eastern	+A	14	0.203	0.187	1.579	0.115	-1.862	-49.983	16	25	0.0625
L6	Eastern	+A	15	0.176	0.091	0.820	0.124	-1.869	-49.979	27	39	0.0625
L6	Eastern	+A	16	0.308	0.134	-1.686	-0.830	-1.867	-49.981	11	24	0.0625
L6	Eastern	+A	17	0.386	0.134	2.032	0.545	-1.866	-49.980	14	35	0.0625
L6	Eastern	+A	18	0.241	0.091	2.142	-0.462	-1.862	-49.979	15	41	0.0625
L6	Eastern	+A	19	0.324	0.099	1.273	-0.333	-1.860	-49.979	11	50	0.0625
L6	Eastern	+A	20	0.403	0.112	1.828	1.601	-1.859	-49.976	11	45	0.0625
L6	Eastern	-A	21	0.253	0.055	1.748	0.178	-1.842	-50.049	8	52	0.0625
L6	Eastern	-A	22	0.243	0.105	2.257	0.480	-1.837	-50.042	9	44	0.0625

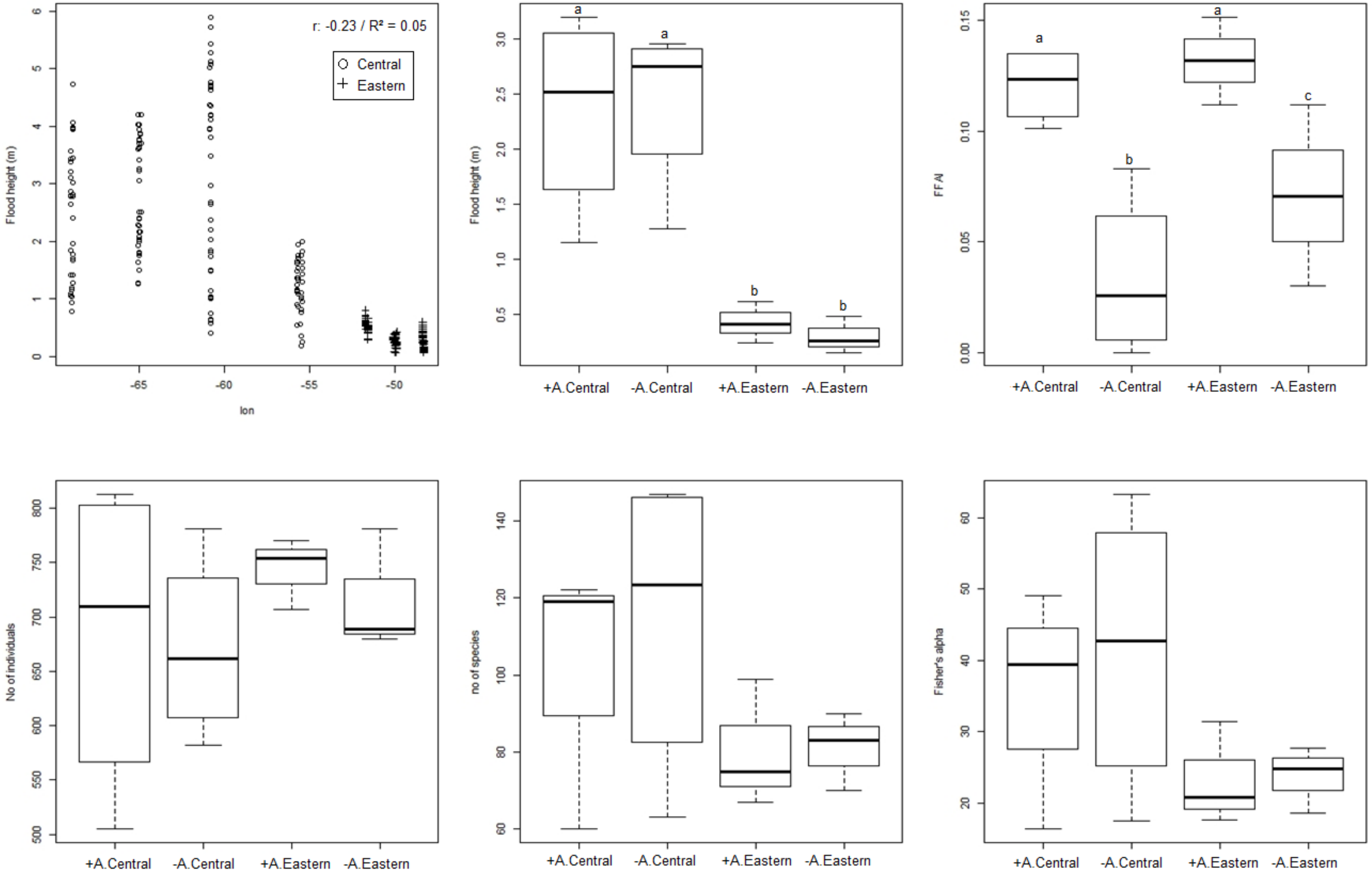
location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L6	Eastern	-A	23	0.338	0.112	2.413	0.310	-1.824	-49.997	11	46	0.0625
L6	Eastern	-A	24	0.363	0.187	2.196	0.285	-1.821	-50.000	11	22	0.0625
L6	Eastern	-A	25	0.318	0.091	1.850	-0.171	-1.820	-50.003	11	36	0.0625
L6	Eastern	-A	26	0.270	0.134	2.295	0.699	-1.819	-50.008	5	24	0.0625
L6	Eastern	-A	27	0.139	0.134	1.683	-0.535	-1.821	-50.014	9	34	0.0625
L6	Eastern	-A	28	0.082	0.091	1.082	-0.077	-1.823	-50.018	10	22	0.0625
L6	Eastern	-A	29	0.081	0.099	1.880	1.964	-1.826	-50.023	6	34	0.0625
L6	Eastern	-A	30	0.072	0.112	2.136	1.548	-1.829	-50.028	6	22	0.0625
L6	Eastern	-A	31	0.244	0.055	0.636	-0.539	-1.880	-50.063	18	33	0.0625
L6	Eastern	-A	32	0.254	0.105	-0.053	-0.854	-1.882	-50.063	13	33	0.0625
L6	Eastern	-A	33	0.288	0.112	0.512	-1.993	-1.883	-50.063	14	35	0.0625
L6	Eastern	-A	34	0.229	0.187	0.511	-1.168	-1.883	-50.065	14	32	0.0625
L6	Eastern	-A	35	0.333	0.091	0.998	-1.152	-1.882	-50.067	20	35	0.0625
L6	Eastern	-A	36	0.381	0.134	0.798	-0.714	-1.884	-50.069	23	53	0.0625
L6	Eastern	-A	37	0.307	0.134	-0.075	-0.495	-1.857	-50.098	12	31	0.0625
L6	Eastern	-A	38	0.323	0.091	0.074	-1.207	-1.857	-50.098	11	33	0.0625

location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L6	Eastern	-A	39	0.332	0.099	-1.348	-1.644	-1.856	-50.097	11	26	0.0625
L6	Eastern	-A	40	0.282	0.112	-0.667	-1.207	-1.857	-50.095	10	33	0.0625
L7	Eastern	+A	1	0.541	0.143	-1.822	-0.775	-1.437	-48.390	19	32	0.0625
L7	Eastern	+A	2	0.425	0.188	1.140	0.055	-1.436	-48.389	23	37	0.0625
L7	Eastern	+A	3	0.533	0.098	1.933	-0.458	-1.437	-48.390	19	35	0.0625
L7	Eastern	+A	4	0.594	0.147	1.112	-0.357	-1.437	-48.389	23	39	0.0625
L7	Eastern	+A	5	0.465	0.181	0.435	-0.767	-1.437	-48.388	23	35	0.0625
L7	Eastern	+A	6	0.371	0.145	1.415	-0.471	-1.438	-48.387	21	29	0.0625
L7	Eastern	+A	7	0.513	0.134	0.273	-0.454	-1.437	-48.386	25	43	0.0625
L7	Eastern	+A	8	0.500	0.161	1.740	-0.723	-1.438	-48.389	19	43	0.0625
L7	Eastern	+A	9	0.431	0.076	-1.093	-0.127	-1.434	-48.379	20	30	0.0625
L7	Eastern	+A	10	0.396	0.022	1.398	0.686	-1.433	-48.380	20	48	0.0625
L7	Eastern	+A	11	0.338	0.149	0.472	-1.401	-1.431	-48.381	21	32	0.0625
L7	Eastern	+A	12	0.349	0.199	0.031	-0.906	-1.432	-48.382	18	31	0.0625
L7	Eastern	+A	13	0.335	0.174	2.489	0.995	-1.434	-48.383	22	38	0.0625
L7	Eastern	+A	14	0.465	0.206	-1.082	-0.970	-1.434	-48.381	20	34	0.0625

location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L7	Eastern	+A	15	0.237	0.160	-1.011	-0.751	-1.435	-48.380	21	33	0.0625
L7	Eastern	+A	16	0.283	0.173	0.640	0.359	-1.435	-48.382	16	27	0.0625
L7	Eastern	+A	17	0.410	0.201	0.711	0.188	-1.435	-48.381	15	36	0.0625
L7	Eastern	+A	18	0.240	0.198	-0.397	-0.400	-1.437	-48.381	26	37	0.0625
L7	Eastern	+A	19	0.320	0.146	0.218	0.775	-1.431	-48.378	13	31	0.0625
L7	Eastern	+A	20	0.413	0.125	0.533	-0.644	-1.436	-48.379	22	37	0.0625
L7	Eastern	-A	21	0.158	0.066	0.474	-0.279	-1.453	-48.330	15	23	0.0625
L7	Eastern	-A	22	0.207	0.047	1.376	-0.742	-1.451	-48.330	22	42	0.0625
L7	Eastern	-A	23	0.144	0.066	0.503	-0.800	-1.452	-48.334	19	37	0.0625
L7	Eastern	-A	24	0.270	0.077	1.013	0.312	-1.446	-48.317	17	38	0.0625
L7	Eastern	-A	25	0.064	0.056	0.815	-0.119	-1.446	-48.317	27	48	0.0625
L7	Eastern	-A	26	0.244	0.044	-0.226	-0.960	-1.445	-48.316	20	40	0.0625
L7	Eastern	-A	27	0.164	0.086	-1.002	-0.452	-1.448	-48.318	20	29	0.0625
L7	Eastern	-A	28	0.154	0.078	1.074	1.321	-1.446	-48.319	19	40	0.0625
L7	Eastern	-A	29	0.119	0.105	1.502	-0.284	-1.452	-48.335	15	33	0.0625
L7	Eastern	-A	30	0.106	0.086	0.219	-1.271	-1.448	-48.320	16	19	0.0625

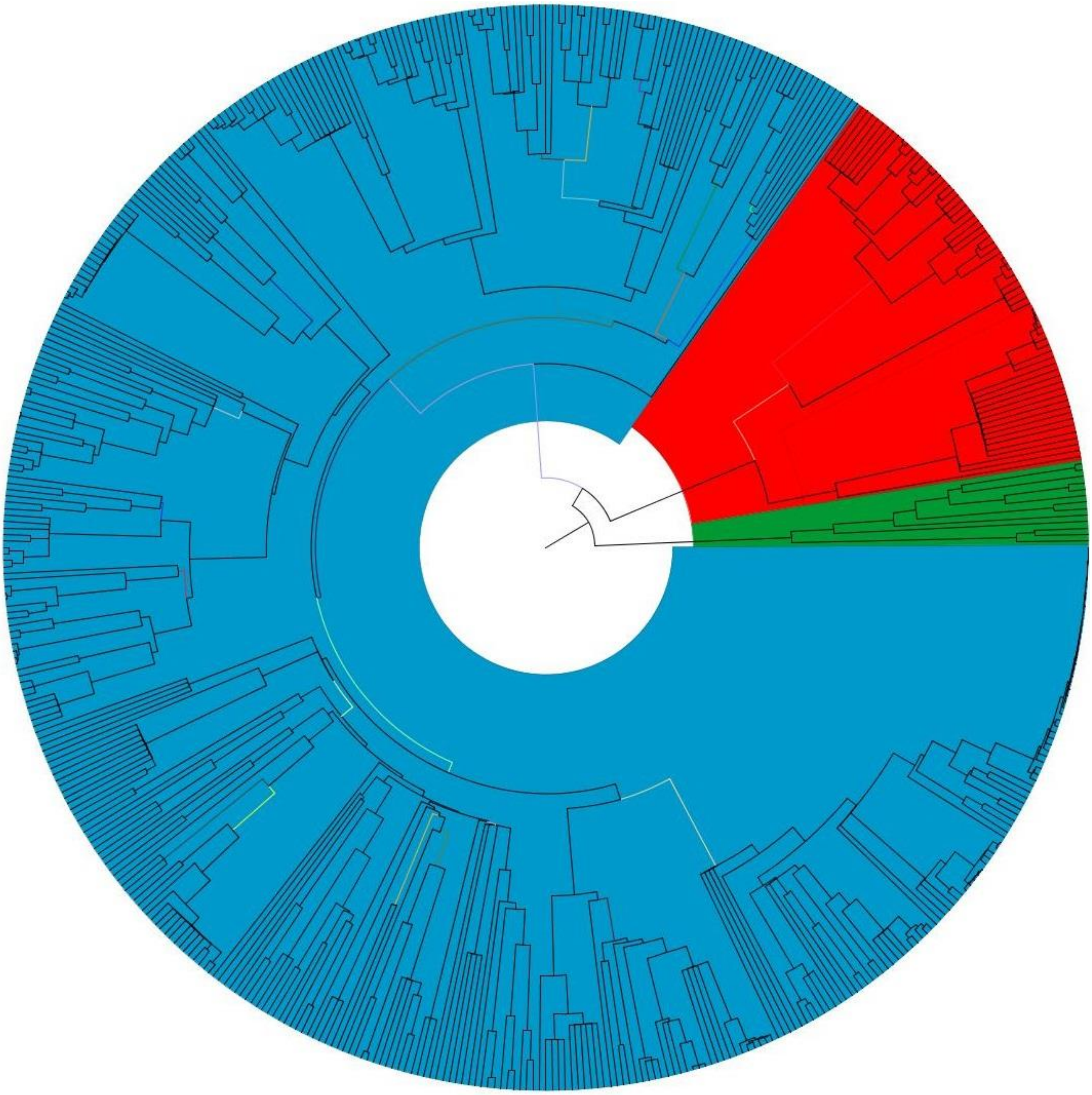
location	macro_region	anthropization_level	plot	flood.height	ffai	ses.MPD	ses.MNTD	lat	lon	n. spp	n.ind	plot.size (ha)
L7	Eastern	-A	31	0.160	0.063	1.733	0.263	-1.450	-48.336	14	27	0.0625
L7	Eastern	-A	32	0.203	0.097	0.883	-0.762	-1.450	-48.338	15	23	0.0625
L7	Eastern	-A	33	0.166	0.033	-0.502	-1.580	-1.456	-48.317	18	34	0.0625
L7	Eastern	-A	34	0.121	0.056	-0.093	1.109	-1.455	-48.319	15	37	0.0625
L7	Eastern	-A	35	0.113	0.056	2.231	2.445	-1.453	-48.319	18	41	0.0625
L7	Eastern	-A	36	0.081	0.055	0.655	1.126	-1.453	-48.322	19	32	0.0625
L7	Eastern	-A	37	0.148	0.097	2.134	2.668	-1.455	-48.322	16	32	0.0625
L7	Eastern	-A	38	0.162	0.111	-1.788	-0.904	-1.453	-48.328	21	51	0.0625
L7	Eastern	-A	39	0.136	0.055	-1.348	-0.560	-1.453	-48.325	17	27	0.0625
L7	Eastern	-A	40	0.094	0.074	0.403	0.627	-1.452	-48.332	20	36	0.0625

ESM3



ESM3: Relation between variable descriptors among macroregions of the várzea tree communities of Brazilian Amazon in this study. Letters above boxplot mean Tukey post-hoc ($p < 0.05$); same letters do not differ.

ESM4



ESM4: Phylogenetic tree containing 524 angiosperm tree species from tree communities of Amazon várzea forests. Blue are eudicots; red are magnoliids; and green are monocots.

3. Sessão II

“Centuries-long legacy effect of human influence on tree diversity along the Amazon River forests”

O segundo capítulo desta tese foi elaborado e formatado conforme as normas da publicação científica *Proceedings of the National Academy of Science (PNAS)*, disponível em: https://www.pnas.org/page/authors/authors

BIOLOGICAL SCIENCES, Ecology

Centuries-long legacy effect of human influence on tree diversity along the Amazon River forests

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Keywords: Brazilian Amazon; flooded forests; human population density; dark diversity, sustainable development

ABSTRACT

Amazonian flooded forests represent an important extension of the biodiversity realm of the region. Tree composition and diversity is conspicuous and adapted to seasonal and frequent inundations. Along the past centuries, it has been the main pathway to human movements across the biome and their alterations may represent one of the oldest human footprints on the landscape. Here we combine in situ observations of current tree diversity with historical human densities after European colonization to show that tree diversity patterns may be linked to decrease in tree diversity at the landscape in the region. The human prone lag-effect might be imprinted in the diversity of long-living trees and it is supported by our models where historical human density of 1700-1800 has a previous unsuspected effect on current tree diversity patterns by decreasing the number of species available in the current local pool of species. Although floodable habitats cover 400,000 km² of the landscape in Amazon basin, their high-fertilized areas may have subsidized important conditions for early cultural activities as land management and agriculture in the region. Unsustainable development, if not regulated by conservation practices and public policies, may bring generalized biodiversity impoverishment in an irreversible way to future generations.

SIGNIFICANCE STATEMENT

Humans have been altering Amazon rainforest since their first arrival and European colonization brought clear effects on the native population. Most of cities along the Amazon River are surrounded by flooded forests close to large rivers and human presence is increasing in a way never seen before. Here we argue that past human disturbance has a lag effect on current patterns of tree diversity within Amazon flooded forests. The growing rates of local human populations might accelerate biodiversity loss leading to impoverishment of the tree diversity of these landscapes.

INTRODUCTION

The floodplain forest of Amazon has been depauperated by intense human use in the last few decades and tree diversity impoverishment is the rule in recent inventories. Additionally, the environmental disturbances induced by ancient human populations and their implications for current biodiversity of Amazon is widely debated in the international scientific community in recent years (1–5). Human presence in Amazon is widespread and continuous for at least 12,000 years (6, 7). While the influence of pre-Colombian populations on interfluvial landscapes remains an open question, areas along rivers have been important settlement sites since first arrival of humans (3, 4, 8). Different uses of floodplain landscapes in the region, before and after European colonization, have guided human dissemination everywhere in the biome (6, 9–11).

The pattern of human occupation is especially significant for the white water flooplains (locally called várzeas, more details in SI Flooded ecosystems in Amazon), which are intensively used because of the proximity to the main channel of the Amazon River and their high soil fertility promoted by seasonal inundation of waters rich in sediments (7, 9, 12). The várzea habitats, their land portion and the rivers themselves, are shelter and source of abundant food when compared to non-flooded terra firme landscapes or other flooded environments (e.g. clear or black water – locally called "igapós") (13). Tree diversity in várzea is considered intermediate when compared to high diversity terra firme or low diversity igapós (14). Although várzea habitats cover approximately 50% of the 400,000 km² of the flooded landscape in Amazon basin, their high-fertilized areas provides important conditions for cultural and economic activities as land management and agriculture in the region but only 1% remain under protection by conservation units in Brazil (15).

Our study consisted in modelling tree diversity patterns among locations with different historical, current human densities and land use at multiple scales along 2,400 km of naturally occurring várzea habitats in the main course of Amazon River (locations 1-7 in Fig. 1A, Methods). Here we ask whether century-long legacy of human influence is the main driver of current tree diversity along the várzea communities in Amazon forests. The rationale for investigating historical and current human influence is that recurrent and frequent disturbances may disrupt regional species pool in the long term and permanently affect the distribution of species. Our main hypothesis is that current tree diversity decreased over centuries after European arrival and it could be detected thorough the different floodplain forested habitats of Amazon. In all communities, both natural and human-driven disturbances can alter species composition at multiple scales (16, 17). Sometimes decades or even centuries after a disturbance is needed until a new community equilibrium is reached for long-living organisms as trees (18, 19). In this way, both current and historical human disturbance as well as environmental constraints are potential important variables to explain tree community diversity in spatiotemporal scales (6, 20, 21).

Although the extent of disturbances promoted by native pre-Columbian human population remains in dispute (3, 22, 23), the combined influences of historical and current human influences might have a lag-effect on current diversity of várzea tree communities that is not apparent at first and the extinction debt is still being paid (8, 24). Community diversity responses to disturbances are dependent on the spatial scales and are often not immediate after the episode (24, 25). However, both scale and time delay issues can be disentangled when both observed and dark diversity are considered (26, 27). Dark diversity includes those species in a location that can potentially establish and thrive in the same habitat conditions but because of multiple reasons (e.g. dispersal limitation, selective logging) are currently locally absent. Effectively, dark diversity connects biodiversity at the studied location to the regional scales and defines the habitat-specific species pool (observed and dark diversity together). Here we access historical and current human influences after European arrival (i.e. 1500-2000, see Methods) to verify how diversity patterns in the Amazon várzea tree communities.

Despite the undoubted relevance of natural causes for landscape heterogeneity and community assembling of tree species throughout the várzea extension (14, 28, 29), here we focused on how current and historical human disturbances affected tree diversity. We used a multi-model approach (30) with both environmental and human-driven disturbances as variables to extract the proportion of explanation of their effect on the current patterns of tree diversity. We argue that the longevity of individual trees of our sampled species pool is sufficient to enable strong correlations (25, 31). We avoid the possible lack of independence in our sample design by using dimensionless diversity parameters to compare locations at the local and regional scales (26). This approach has been used to show diversity patterns of biological communities around the globe (32–35) and the main drivers indicate that human disturbance has a role in explain species diversity. Now we use the same metrics to infer how current and historical human influence may affect patterns of tree diversity in várzea forests in the Brazilian Amazon. The high number of species absent in a habitat specific species pool might indicate species impoverishment in an irreversible way if conservation practices in a climatic change scenario were not accomplished.

RESULTS AND DISCUSSION

Historical human occupation in floodplain várzeas in Amazon were different within locations studied, with decreasing patterns after European arrival and slow increase in subsequent centuries. In some locations (e.g. location 7 in figure 1A), the current human density level is still recovering and do not reached the same level observed in 1500 (Figure 2A). We found that current diversity of tree communities has a significant difference between pairs of locations we sampled along the várzea forests in the Brazilian Amazon (Fig. 1 B-G). When we modeled historical human influence from 1500 to 2000 period, the revealing result is that current tree diversity is mostly influenced (>80% explanation power) by 1500-1800 period where larger fluctuations on human densities occurred (Fig. 2B). Native human populations living along the basin have been estimated to be relatively large (estimates between 5 and 20 million people in previous studies), but they were widely dispersed throughout the basin (7, 36–38), except for two large groups that occupied specific areas around the rim of the Tapajós River and Marajó island (7). Currently, they are concentrated in scattered reserves called Indigenous Lands and high levels of human densities are associated with cumulative migration and miscegenation. While the native indigenous population decreased substantially, there has been an increase in migrants, mainly from other parts of Brazil, and the current population is highly concentrated in large cities at the margins of Amazon River and its large tributaries (39). However, human population density has changed along the past centuries (Fig. 2 A).

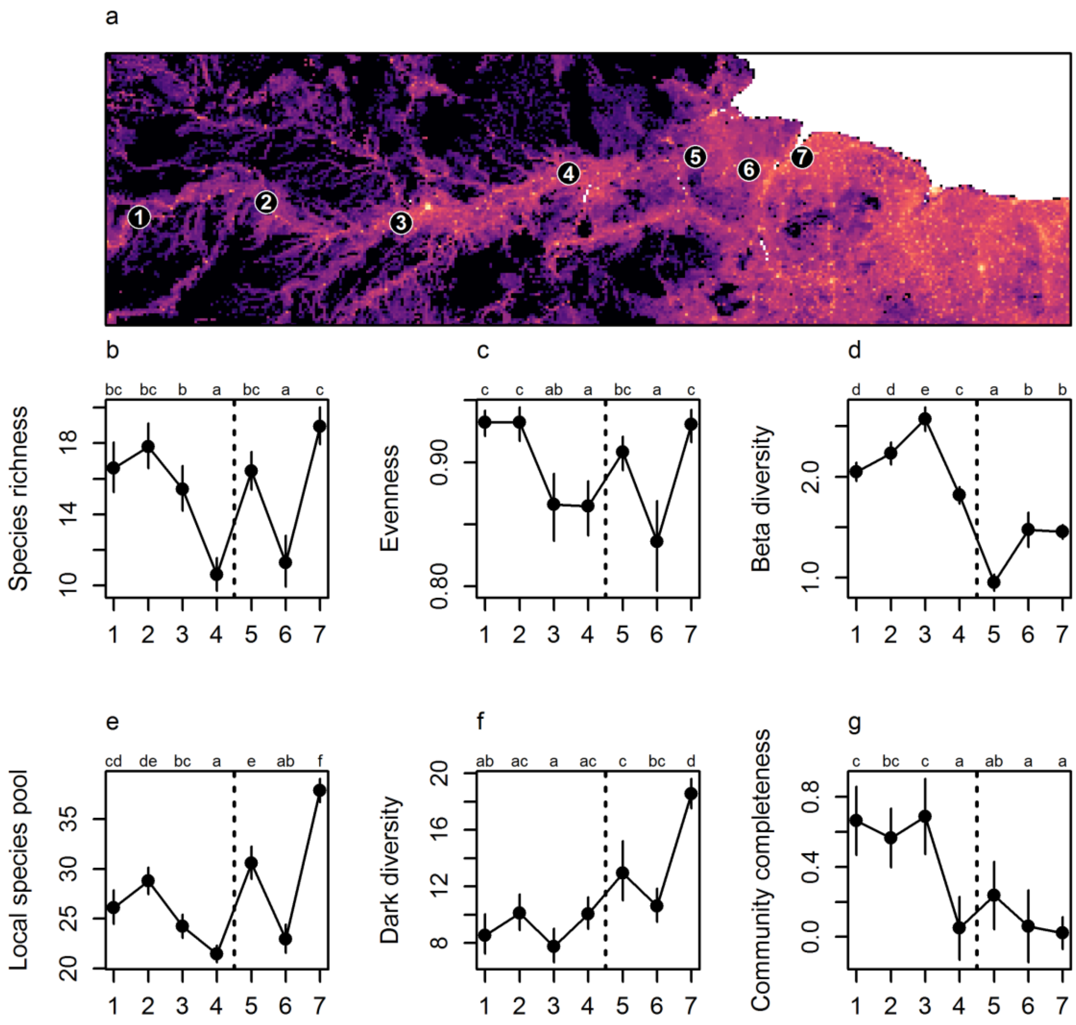
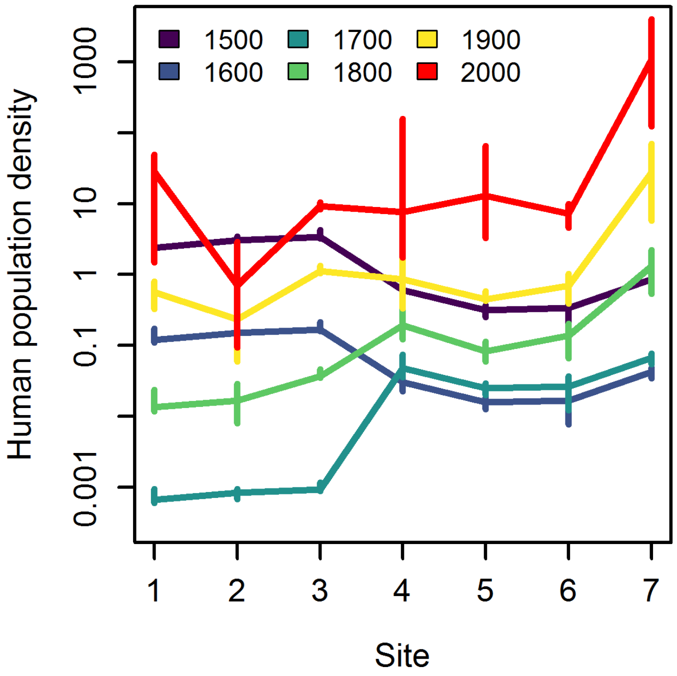


Figure 1. Panel showing map of the study region and diversity metrics used. A. Colors in the map indicate current human population density (2000), lighter colors indicate strong human density. Panels B-G are diversity measures with error bars at 95% confidence intervals. Letters above graphs are Tukey post-hoc (same letters do not differ, p<0.05).

Models with historical and current human population described much more current tree diversity patterns than the model with current human influence only (Fig. 2 B). Thus, current biodiversity patterns have an important historical human influence when compared to human population densities from the present only (Fig. 3). Current human impact had negative relationships with species richness and community completeness (Fig 3. A,C,I) and related positive effects on dark diversity metrics (Fig. 3 G,H).

A)



B)

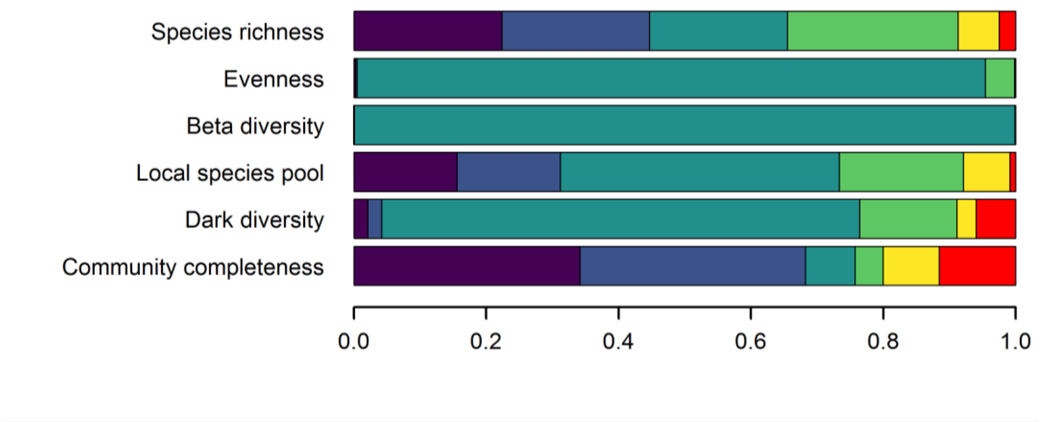


Figure 2. Panel showing human density estimates for different centuries in the past 500 years and average model explanation to each diversity metric evaluated. A.- Human population density (log10 scale) across sites from Hyde database (57). B – Relative weight for model interactions with diversity metrics in different historical human densities. Colors are related to the same time period in both panels.

In contrast, historical human population density had opposite effects: human population density in1700 was positively related to current species richness and evenness (Fig. 3 B,D), but negatively correlated to beta diversity (Fig. 3 E), and human population density in1800 was positively related to local species pool size (Fig. 3 F). These correlations seem to be associated with specific periods of Amazon human history. Following a massive decrease in indigenous human population after European arrival, exploitation cycles of forest goods for regional demanding or international markets characterized Amazon human occupation in the last three centuries (7, 38, 40–42). While the “rubber boom” brought thousands of immigrants in the beginning of 1800-1900 (43, 44), the exploitation of natural resources intensified after 1900, and current Amazonian landscapes (flooded and non-flooded) are being extensively deforested and substituted for other land uses to attend a growing national and international economic demand for food and other resources (e.g. timber, forest fruits) (39, 45–48).

Species richness is the outcome of both local and regional factors of currents human influence measured with an anthropization index (Fig 3 A, C). When we compared tree diversity with historical human influence, it was related to human density on 1700 (Fig 3 B). Evenness was also positively related to human population density during 1700 (Fig 3 D). During those times, humans likely enhanced diversity by intentionally or not controlling dominant or carrying useful species to other areas, so widening their original distribution (7, 49, 50). Such activities, however, made local sites also more similar and thus had caused homogenization of species distribution in some extent (Fig 3E). Local species pool size, characterizing suitable potential biodiversity habitats within surrounding landscapes, was positively related to human densities on 2000 (Fig 3F). This could mean that the absence or decreased number of indigenous people managing the forest made local conditions favorable for a larger number of tree species even with human population starting to increase after the initial period of colonization (4, 49).

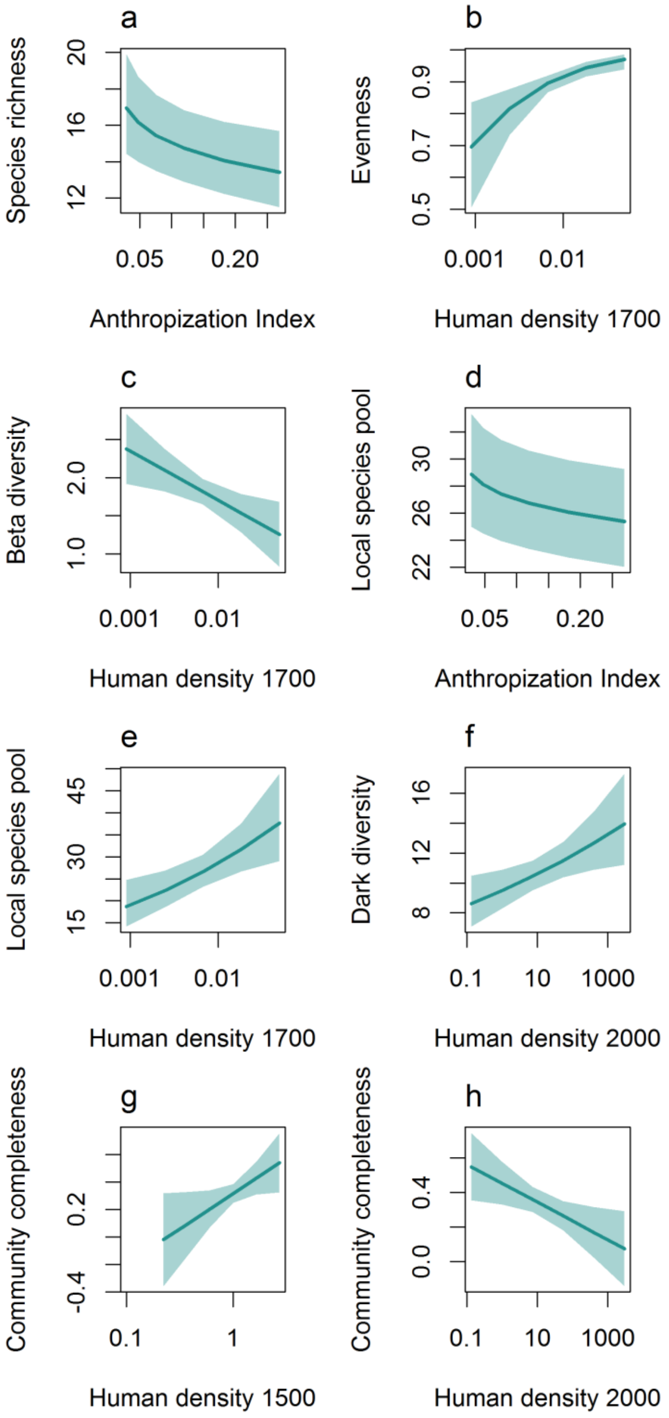


Figure 3. Effects of predictor variables on diversity metrics that showed significant values for our models (AIC). Human population density is in log-scale. The significant correlations were mainly associated with current human influence (measured in situ with an anthropization index): A Species Richness and D) local species pool; or with different periods of historical human population densities: B) Evenness, C) Beta diversity, E) local species pool; F) Dark diversity; E, G-H) Community completeness.

Dark diversity was positively related to both local and regional current human factors (Fig 3 F). Current human influence at the small and large scale have had caused local extinctions but suitable species are still present within locations (in the dark diversity) (51). These suitable species would allow biodiversity restoration if human pressure become lower in the future. However, if current human influence continues, the cascading local extinctions will finally result decrease of local species pool and ultimately global extinctions (52–54). Community completeness is an index showing how much the species pool has realized locally. This correlation is not surprising and means that while management practices of indigenous people enhanced tree species dispersion, current inhabitants had the opposite effect, decreasing the number of species in a location, even though species may survive somewhere else in the surroundings of the area.

In summary, the results showed that human population in the forests close to mainstream of Amazon River have had a strong influence on tree diversity patterns. The way várzea ecosystems were used in the recent past, reinforcing the already known importance of the nutrient-rich soils to historical human occupation patterns, may reflected land use legacies that we observed in our study (9, 10). This lag effect is hidden or diluted in some areas that have been out of use for long time, but other studies have pointed out that a high proportion of hyper-dominant tree species in Amazon basin are domesticated or were handled by native populations (4, 6), and the species pools we measured might be an evidence of this phenomena. Current non-urban riverine populations (cablocos) are descendant of indigenous, European and Afro-American populations and have a cultural heritage of past human populations (50, 55). Obviously, there are many uncertainties attached in historical human population estimates, but the growth rates would give us an acceptable surrogate of the reconstruction of historical population trends in the region (56, 57). In addition, the diversity patterns of várzeas may be linked to regional pool diversity on adjacent uplands and to evolutionary geographical and climatic process as well (58, 59).

In conclusion, the crescent demand by a growing human population for timber and other forest goods can prone substantial modifications in the tree diversity patterns in Amazon rainforest, especially over the easily accessible floodplains. While forest transitions are an important pattern in developing countries (60, 61), future research concerning biodiversity of tropical forests should take into consideration the impacts that human activities may have on tropical diversity loss. Our historical broad-scale patterns can be corroborated by extending field measurements to other flooded forests sites, habitats or biological groups using the species pool concept to compare different communities. Current human pressure is large but the cumulative influence from previous centuries make várzea forests good models to explore potential historical legacy effects of human influence in Amazon region.

METHODS

To access historical human influence, we utilized a detailed database with estimates of historical human density (57) and collected in situ information about local anthropization levels (62) in each location sampled. Historical records and archaeological evidence indicate that density of useful tree species is greater around sites located where indigenous populations used to live in Amazon floodplain (6, 7). Throughout the colonization process, contact with Europeans led to depopulation of native human people mainly by diseases or slavery (63). Thus, subsequent immigration and miscegenation with remnant native populations maintained a considerable human contingent in the region throughout the last centuries (8, 43, 49). The position of the main Amazonian cities today reflects these colonization patterns and posits rivers as the main route traveled by humans along Amazon basin human occupation (6, 8, 10). Summing up 500 years of history and the current pressures of globalization, the Amazon region is currently under intense human pressure (45, 64).

We collected data of tree communities in seven locations from January 2011 to October 2015. In all locations, we established 40 plots of 25 x 25 m with a minimum distance of 200 m each other, where we measured and identified all tree individuals with DBH ≥ 10 cm. In all plots we sampled several natural and anthropogenic gradients in situ (e.g., maximum flood height and anthropization index – FFAI (62) or collected data available on electronic datasets like Hyde (57) (Fig. S1). For diversity metrics, we worked with number of species in a single plot (species richness); equality in the number of individuals of species in a same plot (evenness); compositional difference between plots (beta diversity – Jaccard index). We also calculated four related diversity metrics: habitat specific species pool size (observed diversity and dark diversity), dark diversity (the locally absent fraction of the species pool), and community completeness (the ratio of local and dark diversities) (SI Methods).

We predicted species diversity of the different diversity measures using generalized additive models (GAMs) and we used an information theoretical approach and selected average models using an Akaike information criterion corrected for sample size (AICc) (30). We selected the predictor variables for which the model resulted in the lowest AICc values. In a second step, we examined all models with all predictors. Model assumptions were verified by plotting residuals versus fitted values and each independent variable (Fig. S2). We calculated the importance of each diversity metric as the sum of Akaike weights from models where the human density was included (Fig. 2B). Natural logarithm transformation was used in some cases to express relative differences, but we back transformed them to graphic representation (Fig. 3). It should be noted that several of these diversity measures are inherently related (e.g. local and dark diversities are additive components of the species pool), and patterns from these measures are expected to covary. At the same time, the pairs local-dark diversity and species pool size-community completeness are mathematically independent (65). All analyses in this study were performed using R software (66).

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SUPPORTING INFORMATION

SI Methods

Dark diversity was estimated using species co-occurrence patterns (1). This approach defines taxa as belonging to dark diversity when they are absent from a site but otherwise frequently co-occur with those species present at the site. Thus, species that are locally present are used as indicators for absent species: if there are frequent co-occurrences, it is assumed that the species share similar ecological requirements. A co-occurrence index, also known as Beals index, was calculated for each plot in each location. Threshold values for assigning species to the dark diversity were determined as the co-occurrence index depends on species frequency (2). For each species, we examined co-occurrence index values for all plots where it was present and recorded the minimum. Then, if the species was absent from a site, but its co-occurrence index exceeded the minimum observed in sites where it was present, the species was considered part of the dark diversity. For methodological details and working examples see (1). Community completeness was calculated as the log-ratio of local and dark diversities (3). Species pool size and community completeness were calculated on the assumption that local and dark diversity estimates represent distinct sets of taxa, that is, without many overlapping taxa.

SI Flooded ecosystems in Amazon

In general terms, the current system of classification of Amazonian rivers and floodplains adopt criteria that make them comparable, in structural and functional terms, regardless of geographic location (4). Taking this into account, the Amazonian rivers are divided into: (i) white-water rivers, rich in fertile sediments of recent geological origin from Andean origin, are locally called várzeas (e.g., Amazon River); (ii) the clear-water rivers derived from the Brazilian tertiary plateau (e.g., Tapajós River) and; (iii) black-water rivers, derived from the Guianas shield (e.g., Negro River). The two latter are called igapós, occupy a smaller proportion of the plain, with sandy sediments coming from geologically older tertiary basins, relatively more acidic and richer in organic matter. This classification still adopts the oscillation (stable or oscillating) and predictability (predictable or unpredictable) of the waters that inundate them (4).

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SI Figures

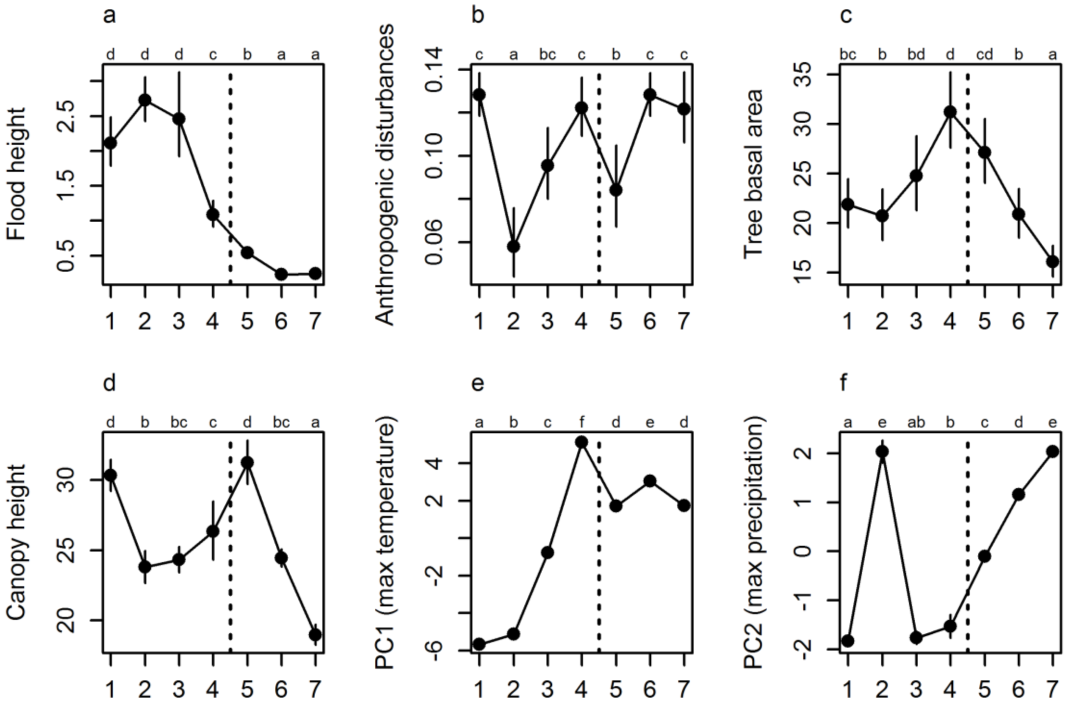

Fig. S1 Distribution of descriptors variables used or evaluated for model averaging (except human population density) across locations. Letters above graphs are Tukey post-hoc (same letters do not differ, $p<0.05$).

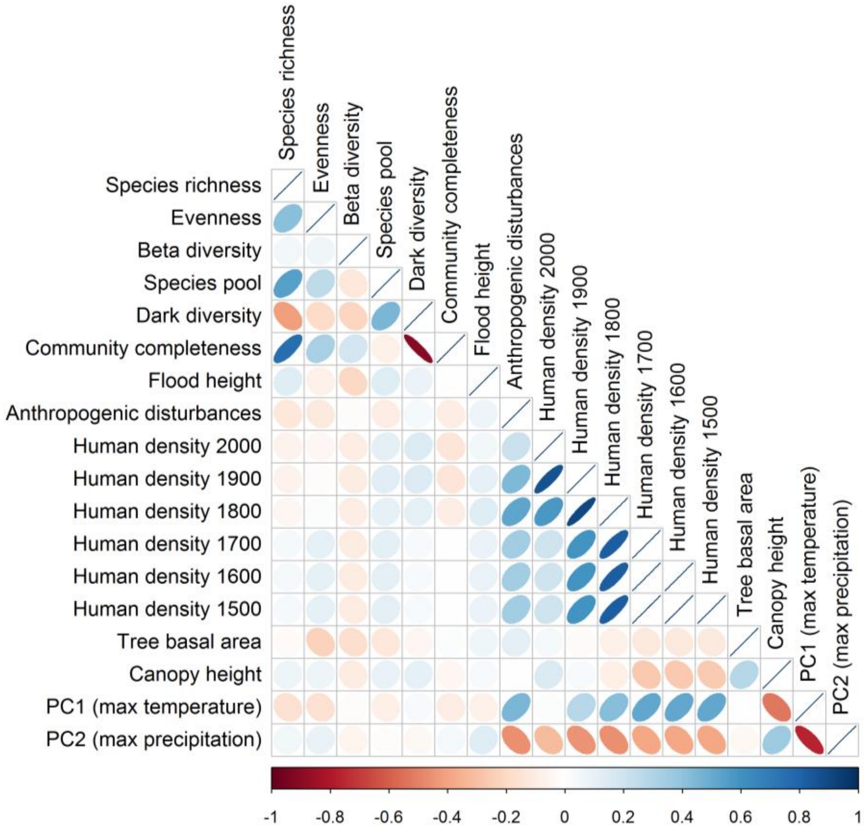

Figure S2. Partial correlations between all study variables used to modelling current diversity after the effect of locations has been removed (residuals). Blue colors indicate strong positive correlations while red colors indicate negative correlations. As strongest the correlation is, brighter is the color.

4. CONCLUSÃO GERAL

A floresta de várzea compõe a paisagem amazônica de maneira transversal, pois é um ambiente onde, tanto do ponto de vista evolutivo quanto ecológico, ocorrem múltiplos eventos dinâmicos e interativos. Nos locais investigados nesta tese, ocorrem diferentes regimes de inundação que estão relacionados com o tempo de imersão ao qual as árvores estão submetidas. Além disso, o rio Amazonas, como via histórica de deslocamento de pessoas na paisagem, tem sofrido com a influência de populações humanas ao longo do tempo. Nesta tese foram avaliadas as influências destes fatores tanto na estrutura filogenética (Capítulo 1) quanto na diversidade taxonômica (Capítulo 2) em comunidades arbóreas na floresta de várzea Amazônica.

No primeiro capítulo, foi observado que a estrutura filogenética é dispersa (*overdispersed*) com relação aos grupos taxonômicos mais basais (p.ex. famílias) independentemente do tempo que as árvores ficam submersas em diferentes regimes de inundação; ou seja, estes resultados indicam que o tempo de submersão não é a causa da conservação filogenética nas comunidades de espécies entre os diferentes regimes de inundação avaliados. As linhagens basais parecem estar adaptadas a estas condições há bastante tempo. Foi encontrado agrupamento (*clustering*) de linhagens basais apenas em locais com maior impacto antropogênico nos ambientes de várzea da Amazônia Central. Os clados mais derivados (p.ex. gêneros) apresentaram maior agrupamento apenas no regime que sofre influência de inundações diárias, na região Leste, indicando possivelmente que os diferentes regimes atuam por selecionar espécies com adaptações diferentes em cada região. De maneira geral, constatamos que a influência da perturbação humana está sendo ocasionada por usos diferentes da floresta de várzea. Na região Central há o predomínio de pecuária extensiva, enquanto na região Leste há maior extração de produtos florestais não-madeireiros (p.ex., manejo de açaizais). Nesse sentido, há indicação de que o tipo de influência antrópica não está diretamente ligado a diversidade das linhagens de espécies que lá ocorrem. Esse resultado é um bom sinal, pois as florestas de várzea continuam sendo um reservatório de importantes espécies que geram potenciais e importantes serviços ambientais. Promover ações de recuperação florestal e utilizar o banco genético disponível é um caminho viável diante deste cenário.

No segundo capítulo, foram utilizadas várias métricas de diversidade taxonômica para avaliar a influência humana histórica e recente exercida nos últimos 500 anos de ocupação das várzeas. Utilizamos uma base de dados com estimativas de densidade humana para testar se flutuações da presença humana estariam relacionados com a diversidade atual das árvores. Além disso, foram utilizadas métricas de diversidade adimensionais, ainda pouco difundidas, mas com potencial para explicar as influências humanas históricas que poderiam não ser detectadas com as métricas tradicionais. O principal resultado encontrado é que a presença humana de três séculos atrás explica melhor a diversidade taxonômica arbórea encontrada hoje do que a presença humana atual. Este resultado é relevante, pois parece estar relacionado a um atraso na resposta da presença humana passada no conjunto das espécies encontradas hoje. O ciclo de vida de árvores individuais ultrapassa várias gerações humanas e a maneira como utilizamos os recursos que elas provêm pode, em uma escala de tempo de médio a longo prazo, refletir no que estará disponível para as futuras gerações de habitantes da Amazônia.

Em suma, avaliar os padrões de diversidade nas florestas de várzea é essencial para entender o papel de fatores naturais e antropogênicos nestes sistemas. Abordar influências tanto em escalas espaciais locais e regionais quanto em escalas temporais longas pode gerar conhecimento sobre a estrutura destas florestas e uma visão geral dos padrões de diversidade de árvores encontrados nestes ambientes. Contribuir com a conservação destas florestas de várzea, que apresentam grande importância na paisagem amazônica, seja para a manutenção de serviços ecossistêmicos, seja para a utilização pelas populações que delas dependem é de suma importância. Considerar os aspectos evolutivos e históricos da paisagem amazônica e o papel da diversidade de suas comunidades biológicas é, além de tudo, respeitar o planeta em que se vive, pois do contrário, não haverá recursos suficientes no mundo para restaurar algo que foi construído ao longo de milhões de anos no processo de evolução.

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