FELIPE DE CARVALHO ARAÚJO

ECOLOGIA DE FLORESTAS SAZONALMENTE ALAGADAS DOS RIOS TRIBUTÁRIOS DO MÉDIO SÃO FRANCISCO, MG

LAVRAS-MG

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Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Botânica Aplicada, área de concentração em Botânica Aplicada, para obtenção do título de Doutor.

Prof. Dr. Rubens Manoel dos Santos
Orientador

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**ECOLOGIA DAS FLORESTAS SAZONALMENTE ALAGADAS
DOS RIOS TRIBUTÁRIOS DO MÉDIO SÃO FRANCISCO, MG**

**SEASONALLY FLOODED FORESTS ECOLOGY OF THE
TRIBUTARY RIVERS FROM MIDLE SAN FRANCISCO, MG**

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Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Botânica Aplicada, para obtenção do título de Doutor.

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APROVADA em 02 de março de 2018

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Prof. Dr. Rubens Manoel dos Santos
Orientador

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*À minha família, pelo imenso carinho e amor demonstrado nesta fase da
minha vida;
à minha esposa, pelo companheirismo e força;
aos meus amigos da UFLA e da igreja, por toda a ajuda;
a Deus, pela incrível oportunidade concedida;
dedico.*

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"Em todo lugar por onde esse rio passar haverá todo tipo de animais e de peixes. O rio fará com que as águas do mar Morto fiquem boas e ele trará vida por onde passar."

Ezequiel

RESUMO

Atualmente, um dos ecossistemas que tem mais chamado a atenção de pesquisadores são os sistemas florestais sazonalmente alagados, devido à sua elevada biodiversidade, ao endemismo biológico, ecológico e funcional e a seus serviços ecossistêmicos. A frequência e a intensidade de alagamento por intermédio do sobrefluxo de grandes rios têm moldado ao longo do tempo sistemas adaptados a esse ciclo sazonal de acordo com a precipitação, e suas alterações podem ser determinantes na ecologia e diversidade de espécies vegetais, assim como demais organismos terrestres e aquáticos. O objetivo da presente tese é de esclarecer o comportamento da vegetação arbórea presente nessas zonas de alagamento em diferentes frequências, buscando compreender a ecologia das mesmas e sua relação com fatores ambientais. Por intermédio de um delineamento amostral capaz de abranger diferentes tipos de formações, conforme nosso objetivo, as análises estatísticas atuais nos permitiram inferir novas ideias e testar hipóteses consagradas a respeito dessas comunidades arbóreas e suas relações com fatores ambientais e outras fisionomias em seus aspectos ecológicos e evolutivos. Em um contexto do bioma das Florestas Tropicais Sazonalmente Secas, essas comunidades possuem características distintas em relação à frequência de alagamento, e os fatores ambientais são determinantes na sua caracterização. A utilização desses sistemas pelo homem e as mudanças climáticas globais podem alterar a realidade das florestas sazonalmente alagadas e levar à crescente perda de habitat e da biodiversidade, o que esperamos ajudar a diminuir ou reter através dos conhecimentos gerados pela presente tese.

Palavras-chave: Florestas Tropicais Sazonalmente Secas, Ecologia de Comunidades, Fatores ambientais

ABSTRACT

Currently one of the ecosystems that have most attracted the attention of researchers is the seasonally flooded forest systems due to their high biodiversity, biological, ecological and functional endemism and their ecosystem services. The frequency and intensity of flooding through the overflow of large rivers has shaped over time systems adapted to this seasonal cycle according to precipitation and their changes can be determinant in the ecology and diversity of plant species as well as other terrestrial and aquatic organisms. The aim of this thesis is to clarify the behavior of the arboreal vegetation present in these flood zones in different frequencies and intensity, trying to understand the ecology of the same and its relation with environmental factors. By means of a sampling design capable of covering different types of formations according to our objective and current statistical analysis allowed us to infer new ideas and test consecrated hypotheses about these tree communities and their relationships with environmental factors and other physiognomies in their ecological and evolutionary aspects. In a context of the biome of the Seasonally Dry Tropical Forests, these communities have different characteristics in relation to the frequency of flooding and the environmental factors are determinant in their characterization. The use of these systems by man and global climate change can alter the reality of seasonally flooded forests and lead to increasing loss of habitat and biodiversity, which we hope to help reduce or retain through the knowledge generated by this thesis.

Keywords: Seasonally Dry Tropical Forests, Community Ecology, Environmental factors

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO GERAL

A água é um dos grandes fatores abióticos e faz-se essencial para a vida das espécies, atuando como condição para alguns organismos e recurso para outros. Interligados ao ecossistema terrestre, corpos d'água como rios (artérias) são importantes na manutenção da biodiversidade terrestre, percorrendo desde sua nascente (coração) até o oceano (órgãos). Uma vez no oceano, essa água (sangue) é filtrada (evaporação - veias) e, em forma gasosa (nuvens - pulmão), é novamente lançada na superfície terrestre, que a absorve pelo solo até o lençol freático. Por fim, a água é disponibilizada em uma nascente (coração), novamente reiniciando o ciclo. Nesse percurso, a sua capacidade de transportar nutrientes, além de sua capacidade de deposição e erosão influenciam na distribuição das espécies aquáticas e terrestres, principalmente as adjacentes a esses rios, captando e fornecendo recursos na manutenção da vida biológica.

As planícies de inundação são áreas adjacentes a esses rios que periodicamente não comportam tamanha quantidade de água, principalmente devido à alta concentração de precipitação, provocando o sobrefluxo dos rios e promovendo alagamentos no seu entorno. Na literatura científica, esse habitat é chamado de "*floodplains*" quando se refere às planícies de inundação, e, de uma forma mais ampla, "*wetlands*" quando se refere a zonas úmidas, incluindo lagoas, charcos, mangues, salinas, restinga, pântanos e turfas.

O grupo de pesquisa de Fitogeografia e Ecologia Evolutiva liderado pelo Prof. Dr. Rubens Manoel dos Santos, na última década, vem desenvolvendo pesquisas de ecologia de comunidades vegetais e estudando como os fatores ambientais influenciam a distribuição das espécies de árvores. Recentemente, o

grupo tem focado nos sistemas alagadiços, porém, com uma pergunta ecológica para a qual até então ainda não existe uma resposta: como seria o comportamento das florestas sazonalmente alagadas em biomas como os das Florestas Tropicais sazonalmente secas? Levando em consideração que esses sistemas são bem estudados em biomas tropicais úmidos, um cenário de gradiente de disponibilidade de água, desde as florestas "secas" até as áreas alagadiças, nos levou a querer responder essa pergunta e a compreender os padrões que regem o comportamento ecológico destes sistemas alagadiços peculiares e seus padrões na estrutura e diversidade das comunidades arbóreas. Em 2012, o primeiro sistema foi amostrado no rio Carinhanha; o segundo, no rio Verde Grande, ambos no extremo norte de Minas Gerais, tributários do Rio São Francisco – pesquisa que resultou em duas dissertações de mestrado. No ano de 2015, dois rios foram amostrados também ao norte de Minas, Paracatu e Jequitaí, cujos resultados estão presentes numa dissertação e nesta tese.

Neste trabalho, em escala regional, são analisados os padrões das comunidades arbóreas das florestas sazonalmente alagadas, situadas no bioma das florestas tropicais sazonalmente secas, adjacentes aos quatro rios tributários do Médio São Francisco. Primeiro, procuramos avaliar a estrutura da vegetação ao longo do gradiente ambiental de acordo com a frequência de alagamento e a influência das propriedades do solo. Depois, procuramos avaliar a diversidade evolutiva ao longo desse mesmo gradiente ambiental. No gradiente constam áreas que alagam todo ano, em depressões topográficas com saturação hídrica sazonal; áreas que alagam aproximadamente a cada trinta anos; e áreas que não sofrem com o alagamento e que, com o estresse de déficit hídrico devido à sazonalidade marcante quanto ao clima, ficam na maior parte do ano expostas à seca.

2 REFERENCIAL TEÓRICO

2.1 Distribuição das planícies de inundação

Globalmente, as áreas que possuem período de inundação, dentre suas formas mais variadas, estão presentes em todos continentes, exceto na Antártica e quase todas as zonas climáticas dentro desse continente (VAN DER VALK, 2006). Junk et al. (2006), em conjunto com dados de outras revisões bibliográficas, discorrem sobre a diversidade de sete importantes áreas que sofrem alagamento ao redor do mundo: os continentes americanos possuem três áreas dentre as sete: as pradarias (*peatlands)* no extremo norte do Canadá; os *Everglades*, situados no sudeste americano, no Parque Nacional da Flórida; e o Pantanal brasileiro, na América do Sul, abrangendo regiões da Bolívia e Paraguai. No continente africano há o delta interno do rio Okavango. No sudeste asiático, as áreas alagadas abrangendo planícies, lagos e rios da região de *Tonle Sap.* No norte australiano de *Kakadu*, o sistema de savanas inundáveis e mangues, e as áreas alagadas de *Sudarban* associadas aos grandes sistemas hidrológicos dos rios Ganges e Brahmaputra, na baía da Bengala, Índia.

A vegetação correspondente às planícies de inundação recebe vários nomes como florestas ripárias, matas ciliares, mata de galerias, floresta de brejo, aluvial, entre outras, devido principalmente à sua característica com zona de conexão entre os ecossistemas aquáticos e terrestres (HUGHES, 1988).

No Brasil, bons exemplos são os sistemas fluviais que comportam a vegetação de áreas alagadas, como o rio Amazonas e a grande depressão do Pantanal. As florestas de inundação na Amazônia são divididas em dois grandes tipos quanto à sua composição, riqueza e estrutura: as florestas de várzeas e as florestas de igapó (PRANCE, 1979; WITTMANN; SCHONGART; JUNK, 2010). A diferença está na origem e na conformação hidrogeomorfológica de cada tipo de floresta. A floresta de várzea ocorre ao longo dos canais vindos das montanhas do Andes e recebe afluentes como Solimões, Juruá, Japurá, Purus e

Maderia (WITTMANN; SCHONGART; JUNK, 2010). Esses rios são ricos em sedimentos que são carregados ao longo do percurso e depositados, denominados de *white-waters*, devido à coloração provocada por toda essa carga, conferindo uma maior quantidade de nutrientes a essas florestas se comparadas às florestas de igapó (SIOLI, 1954 *apud* WITTMANN; SCHONGART; JUNK, 2010; PRANCE, 1979). As florestas de igapó ocorrem em rios provindos dos escudos paleozoicos e pré-cambrianos de Guyana e Brasil Central, como exemplo, rio Negro, Xingu e Tapajós, que são rios que carregam pouca sedimentação e, portanto, baixa quantidade de nutrientes, denominados de *black-water/clear-water* (PRANCE, 1979; WITTMANN; SCHONGART; JUNK, 2010).

Em escala menor, o Brasil possui o sistema de redes fluviais que convergem na bacia do São Francisco, no sudeste e nordeste do Brasil, além das formações ribeirinhas do Brasil Central, que são revestidas das matas de galerias do Cerrado brasileiro (OLIVEIRA-FILHO; RATTER, 1995). Devido à sua extensão e aos diferentes ambientes percorridos, a bacia do São Francisco se divide em quatro unidades fisiográficas: região do Alto São Francisco, correspondente a 19% da área da bacia; Médio São Francisco, que corresponde a 55%; Submédio São Francisco, (24%), e Baixo São Francisco, (7%) (PEREIRA et al., 2007). A nascente do rio começa na Serra da Canastra e tem os afluentes Piumhi, Pará, das Velhas, Paracatu, Urucuia, Pandeiros, Verde Grande e Carinhanha, além de outros rios tributários. A região conhecida como Médio São Francisco compreende o trecho que se estende de Pirapora, Estado de Minas Gerais (MG), até a cidade de Pilão Arcado, Estado da Bahia (BA). A cobertura vegetal é representada pelos domínios do Cerrado, Caatinga e Mata Atlântica (GOMES, 2008; SANTOS et al., 2012). No Médio São Francisco, o relevo pouco acidentado facilita o acúmulo de sedimentos, enquanto as depressões em áreas adjacentes aos cursos de água são onde ocorrem áreas sazonalmente

alagadas (CODEVASF, 2015). Como resultado, é comum a criação de áreas de inundação tanto ao longo do leito principal do Rio São Francisco quanto na junção deste com seus tributários, resultando na formação de várzeas, lagoas, diques aluviais e cicatrizes de leitos antigos (JUNK; BAYLEY; SPARKS, 1989; POMPEU; GODINHO, 2006).

Muitos estudos em florestas sazonalmente alagadas estão inseridos dentro do bioma das Florestas Tropicais Úmidas (Florestas Ombrófilas), como, por exemplo, as florestas alagadas no Domínio Amazônico, tratadas anteriormente. Em comunidades arbóreas, as Florestas Tropicais Sazonalmente Secas (FTSS) compõem um bioma com formações distribuídas em locais com precipitação média anual menor que 1800 mm e com um período de 3 a 6 meses, recebendo menos que 100 mm mensais, caracterizada por um longo período de seca (BANDA et al., 2016). Como consequência, 50 a 80% das espécies de árvores que compõem as florestas secas perdem suas folhas. A deciduidade está diretamente relacionada ao gradiente de precipitação (BULLOCK; MOONEY; MEDINA, 1995; PENNINGTON; RICHARDSON; LAVIN, 2006).

As FTSS possuem características distintas das florestas úmidas ou cerrados brasileiros por ocorrerem na forma de núcleos no neotrópico, em um caráter de metacomunidade (PENNIGNTON; LAVIN; OLIVEIRA-FILHO, 2009; BANDA et al., 2016). Sua ampla distribuição abrange o nordeste do Brasil com Domínio Caatinga, Brasil Central, sudeste do Paraguai, leste da Bolívia, nordeste da Argentina e Oeste do estado do Mato Grosso, nas regiões periféricas ao domínio do Chaco e aos Andes (vales interandinos do norte, costa do Andes Central e vales interandinos centrais), áreas disjuntas na costa Pacífica do continente, do Peru à Venezuela, na América Central e no México (BANDA et al., 2016).

Uma das maiores formações contínuas de FTSS se encontra no Domínio Fitogeográfico da Caatinga, no nordeste brasileiro (SANTOS et al., 2012;

BANDA et al., 2016), aonde a extremidade sul do domínio chega ao norte de Minas Gerais com grande influência nas florestas alagadas do rio São Francisco e seus tributários. Estas comunidades estão sujeitas a duas condições de disponibilidade hídrica. Por um lado, as florestas que não sofrem alagamento estão sujeitas ao déficit hídrico sazonal, por outro, essas florestas que recebem diferentes frequências de alagamento e conjuntamente com as características do solo, diferentes intensidades, estão sujeitas a extrema quantidade de água e condições de saturação hídrica por um breve período, como áreas que alagam todo ano e outras que alagam a cada 30 anos. Essas florestas sazonalmente alagadas de FTSS ainda são pouco estudadas e muito pouco se sabe sobre sua ecologia, como estrutura, diversidade, composição e comportamento diante do estresse hídrico (tanto o excesso quanto a escassez).

2.2 Adaptações morfológicas, fisiológicas e anatômicas na propagação das espécies em planícies de inundação.

As espécies arbóreas que conseguem se estabelecer nas áreas alagadas enfrentam o estresse periódico de pulsos de inundação (JUNK; BAILEY; SPARKS, 1989). Durante o período alagado, as espécies vegetais necessitam de estratégias para se manterem e sobreviverem nestes locais, uma vez que seus indivíduos juvenis encontram fatores limitantes no seu estabelecimento, como a escuridão provocada pela reflexão e absorção da luz pela água e a condição de anoxia provocada pelo déficit de oxigênio, afetando a fotossíntese e a respiração desses indivíduos, e assim, a energia para seu estabelecimento (FERREIRA et al., 2009). As plantas necessitam, simultaneamente, alocarem energia para a viabilidade da semente produzida e se programarem no tempo para o seu futuro estabelecimento.

Os pulsos de inundações regulares em florestas alagadas são importantes na determinação dessas estratégias adaptativas. A dispersão de diásporos (frutos e sementes) é fundamental para a estrutura de comunidades e sua composição,

além de compor uma etapa fundamental no nicho regenerativo de uma espécie (GRUBB, 1977). Em uma revisão recente, Parolin, Wittman e Ferreira (2013) discorreram que nas florestas alagadas existem semelhanças na síndrome de dispersão e nos tipos de diásporos comparado aos ambientes terrestres (*uplands)*, mas o uso da água como um vetor de dispersão é evidente para muitas espécies. Vários são os tipos encontrados como legumes, pixídios, cápsulas, drupas e bagas (PAROLIN; WALDHOFF; PIEDADE, 2010), mas muitas espécies são equipadas de estruturas vantajosas para os períodos de alagamentos, fazendo da hidrocoria (dispersão por água) e ictiocoria (dispersão por peixes) uns dos principais agentes de dispersão abiótica e biótica, respectivamente (KUBITZKI; ZIBURSKI, 1994; WALDHOFF; SAINT-PAUL; FURCH, 1996).

Os diásporos necessitam permanecer viáveis e tolerantes ao alagamento, pelo menos por um período. Existem pré-adaptações, como asas e pelos, que são dispersadas por ventos e ajudam na flutuação e câmaras de ar, formando um tecido flutuante e diminuindo sua densidade (PAROLIN; WITTMAN; FERREIRA, 2013). Em *Swartzia polyphylla* DC., Williamson, Costa e Minte Vera (1999) demonstraram que sua capacidade de flutuar estava positivamente correlacionada ao volume de ar entre os dois cotilédones, que apresentaram de 6 a 20 % do volume total da semente. Segundo Reddy e Kulkarni (1985), os frutos das palmeiras Cocosoídeas são drupas fibrosas derivadas de um gineceu sincárpico tricarpelar e ovário trilocular, caracterizado por um epicarpo resistente com células epidérmicas e hipodérmicas, mesocarpo fibroso esponjoso e volumoso compondo maior parte do pericarpo e endocarpo esquelético. Traços de frutos, que são adaptações que permitem a flutuação, incluem o mesocarpo esponjoso e a formação de cortiça no pericarpo (RIDLEY, 1930 *apud* COUSENS; DYTHAM; LAW, 2008). Até mesmo *Cocos nucifera* L. (coqueiro), um coqueiro adaptado a sistemas aquáticos marinhos, uma Arecaceae, possui

espaços preenchidos por ar entre as fibras da casca do fruto (coco) e na câmara central (COUSENS; DYTHAM; LAW, 2008).

Em diferentes populações de uma mesma espécie podem ocorrer plasticidade e modificações nas estruturas dos frutos. Na família de leguminosas, frutos indeiscentes de indivíduos de habitats alagados possuem tecidos com caráter flutuante, e em habitats terrestres os indivíduos produzem legumes que são dispersos pelo vento ou animal, como nos gêneros *Aldina, Cynometra, Pterocarpus, Vatairea, Machaerium, Diplotropis, Dalbergia* e *Hymenolobium* (KUBITZKI; ZIBURSKI, 1994). Linhagens de populações que se desenvolvem em habitats não alagáveis produzem frutos deiscentes que são dispersos por vento ou animal, em habitats sazonalmente alagáveis, produzem sementes hidrocóricas e frutos indeiscentes (KUBITZKI; ZIBURSKI, 1994). Em leguminosas, as espécies de *Ormosia (O. excelsa, O. coutinhoi* e *O. cinerea)* desenvolveram legumes indeiscentes capazes de se prolongarem flutuando nos períodos de alagamento (KUBITZKI; ZIBURSKI, 1994).

Outra alteração das espécies em relação aos habitats sazonalmente alagados de notável importância para sua sobrevivência e perpetuação é o período das fenofases, o que afeta diretamente a sobrevivência, envolvendo a dispersão e estabelecimento das sementes germinadas. Piedade, Parolin e Junk (2006), estudando a fenologia da palmeira *Astrocarium jauari,* encontraram que o período de floração ocorre na estação seca e a frutificação em períodos de maior pico de alagamento, correspondendo às suas necessidades de serem dispersas quando o nível da água está alto.

Um dos grandes problemas com a dispersão por água é sua unidirecionalidade, pois as sementes acompanham o fluxo d´água. Portanto, algumas espécies são adaptadas aos vetores indiretos como peixes (ictiocoria), tartarugas, entre outros – como no exemplo anterior de *A. jauari* que é dispersa por peixes, sendo encontradas várias sementes no trato digestivo desses animais

(PIEDADE; PAROLIN; JUNK, 2006). As adaptações das sementes em relação à dispersão de animais seguem principalmente seu tamanho, coloração e valor nutritivo (KUBITZKI; ZIBURSKI, 1994; GORDON, 1998, PAROLIN; WALDHOFF; PIEDADE, 2010). Para animais como aves, formigas, entre outros, as sementes são coloridas e possuem apêndices atrativos como o arilo comestível; já na água as sementes descolorem e há a perda desse arilo (KUBITZKI; ZIBURSKI, 1994), predominando a atração pelo valor nutritivo das sementes (PAROLIN; WALDHOFF; PIEDADE, 2010). Sementes atrativas são aquelas que possuem alto teor de proteínas e gorduras, conferindo alto valor energético, baixos níveis de carboidratos e baixa proporção de água (PAROLIN; WALDHOFF; PIEDADE, 2010). Exemplos desse *trade-off* são as espécies *Pseudobombax munguba* (Mart. & Zucc.) Dugand e *Psidium acutangulum* Mart. ex DC, que possuem diferenças na realocação dos recursos em sementes do conteúdo de água, teor de gordura e proteína (PAROLIN; WALDHOFF; PIEDADE, 2010). Waldhoff, Saint-Paul e Furch (1996), estudando frutos das espécies das planícies de inundação, encontraram 19 frutos que possuem sementes ricas em proteínas e gorduras e, em contrapartida, maior quantidade de carboidratos no pericarpo, o qual possui alta quantidade de tecido fibroso.

A capacidade das espécies de se adaptarem às planícies de inundação excede o universo morfológico, compreendendo também características anatômicas e fisiológicas. Uma vez que essas espécies tenham sido dispersadas, o próximo passo no ciclo de vida é sua germinação e estabelecimento. Estudos mostram que a alta reserva de nutrientes nas sementes é necessária para o rápido crescimento no período seco durante o estabelecimento de plântulas (PAROLIN; JUNK, 2002). As espécies de planícies de inundação, uma vez estabelecidas, necessitam sobreviver aos períodos alagados. O córtex da raiz é um tecido primário do meristema apical da raiz e o seu desenvolvimento leva à formação de espaços intercelulares, parênquima entre a endoderme e a hipoderme que

pode ser modificada, então, para formar câmaras de ar, cavidade ou espaços (SEAGO; MARSH; STEVENS, 2005).

Foi comprovado que a disponibilidade hídrica nas zonas alagadas em ciclos sazonais é a causa das alterações das estruturas anatômicas, fisiológicas e morfológicas das espécies nessas comunidades vegetais. O déficit hídrico, por outro lado, também é um fator determinante nas modificações fisiológicas de espécies vegetais em ambientes xéricos, como nas FTSS, como metabolismo fotossintético CAM e C4 potencializando a troca de gases (POREMBSKI, 2007) e adaptações morfológicas e anatômicas como folhas de menor área foliar, cilíndricos ou esféricos para reduzir transpiração, maior espessamento foliar com cutícula e epiderme sinuosa espessada, presença de hipoderme que pode armazenar água, parênquima paliçádico em maior quantidade em ambas as faces, atenuando a alta radiação, maior densidade de estômatos e tricomas concentrados em câmaras ou críptas estomáticas para o controle de água, além de um tecido vascular denso com maior quantidade de esclerênquima, típico de folhas escleroformas (JORDAAN; KRUGER, 1992; CASTRO; PEREIRA; PAIVA, 2009).

2.3 Padrões de estrutura e diversidade e comunidades sazonalmente alagadiças

Na seção anterior, vimos como ambientes estressantes exercem pressão seletiva em plantas submetidas a essas condições, em nível de espécie. Um breve histórico sobre uma parte dos padrões encontrados foi descrito com o objetivo de explorar como futuras pesquisas pelo grupo de Fitogeografia e Ecologia Evolutiva em ambientes sazonalmente alagados nas FTSS, como o gradiente ambiental de disponibilidade hídrica, afetaria essas características morfológicas, fisiológicas e anatômicas. Nesta seção buscamos abordar os padrões existentes nos sistemas alagados em nível de comunidade vegetal.

Em nível de organização de comunidade, uns dos frequentes padrões encontrados na distribuição de espécies estão relacionados à diferença existente

entre as comunidades vegetais no que diz respeito à sua diversidade, riqueza e abundância. Várias teorias ecológicas existem com a finalidade de explicar o porquê desses padrões, e muitas delas utilizam das condições ambientais como filtros ecológicos na diversificação dos padrões encontrados. O alagamento atua como um desses filtros ambientais, e estudos mostram a diferenciação entre comunidades devido a esse filtro. Carim et al. (2016), estudando as florestas de várzea e igapó, na Amazônia oriental, encontraram diferença entre as duas comunidades alagadiças, como previsto. Nas florestas de várzea, a composição florística foi mais representativa pelas famílias botânicas Fabaceae, Arecaceae, Malvaceae, Meliaceae e Rubiaceae, enquanto em Igapó as famílias mais representativas foram Lecythidaceae, Euphorbiaceae, Malvaceae e Arecaceae. Wittmann, Schongart and Junk (2010) encontraram maior riqueza nas florestas de várzea e em áreas com maior frequência de alagamento, que foram caracterizadas com alto número de espécies endêmicas. Os autores sugerem que a estabilidade desses ambientes desde o Palaeoceno faz dessas florestas um refúgio para a flora em períodos de clima seco.

A frequência de alagamento tem sido considerada um dos fortes fatores de caracterização da vegetação ao longo dos gradientes. Budke, Jarenkow e Oliveira-Filho (2010) encontraram ao longo do gradiente de uma floresta subtropical úmida diferenças de estrutura, diversidade e grupos funcionais, relacionadas ao regime de alagamento, às propriedades do solo e à autocorrelação espacial da vegetação e condições ambientais. Dois fatores podem explicar esse padrão. Primeiro, a variação topográfica – como níveis diferentes de depressões do relevo – e as características funcionais – como grupos funcionais relacionados a traços que permitem a ocupação em devidas condições ambientais (OLIVEIRA-FILHO et al., 1994; BUDKE; JARENKOW; OLIVEIRA-FILHO, 2007; BUDKE; JARENKOW; OLIVEIRA-FILHO, 2010).

Um traço funcional frequentemente associado às regiões alagadas é a capacidade de perfilhamento. Esse comportamento de produção de vários números de fustes é um traço relacionado à capacidade de persistir em ambientes instáveis, um *trade-off* entre reprodução e crescimento (BELLINGHAM; SPARROW, 2000; BOND; MIDGLEY, 2001). Em florestas subtropicais úmidas alagadiças, esse perfilhamento foi encontrado em linhagens filogenéticas distantemente relacionadas, o que trouxe maior diversidade evolutiva em áreas frequentemente alagadas (GIEHL; JARENKOW, 2015), contrário à diversidade taxonômica (BUDKE; JARENKOW; OLIVEIRA-FILHO, 2010). Recentemente, estudos relacionados ao regime de inundação em florestas tropicais e subtropicais úmidas na América do Sul encontraram modificações na diversidade evolutiva com padrões distintos. Por exemplo, Aldana et al. (2016) encontraram espécies filogeneticamente próximas em áreas frequentemente alagadas, resultado contrário ao de Giehl e Jarenkow (2015), que encontraram espécies filogeneticamente distantes. Se biomas com caráter climático semelhantes possuem padrões que se diferem, esperamos encontrar também, nas FTSS, padrões distintos do até então narrado em nosso referencial teórico.

3 CONSIDERAÇÕES FINAIS

Nosso trabalho, pioneiro em florestas sazonalmente alagadas nas FTSS, busca compreender os padrões da estrutura das comunidades vegetais ao longo desse gradiente de disponibilidade de água. Se as áreas alagadas são um dos fortes determinantes na estrutura da vegetação e sua diversidade, provocando padrões distintos em vários estudos, esperamos que dentro de nossas áreas possamos encontrar padrões diferentes dos comumente encontrados, vistas as diferenças nas características do bioma em que se encontra nossa área de estudo. Procuramos preencher a lacuna existente nos padrões de modificações das florestas sazonalmente alagadas (planícies de inundação) e contribuir para a

ecologia das florestas tropicais, avançando no conhecimento científico, corroborando ou refutando teorias consagradas na ecologia geral ao aplicá-las na conservação e preservação da biodiversidade desses ricos biomas, principalmente os das FTSS, frequentemente negligenciadas.

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SEGUNDA PARTE – ARTIGO 1

Artigo a ser submetido formatado nas normas da revista Journal of Vegetation Science

Flooding regime drives tree community structure changes in tropical dry forests in southeast Brazil

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Abstract

Flooding regime is a key environmental force shaping riverine and associated vegetation communities. However, there have been little quantitative studies on the structural and functional responses of plant communities to this perturbance, and none so far have examined these processes in semi-arid regions. Here we access the flooding gradient in seasonally flooded dry forests along river tributaries in the semi-arid region of southeast Brazil. We sampled 120 plots across four tributaries of the São Francisco River, southeast Brazil, of which 72 plots were situated in annually flooded forests, 24 in occasionally flooded forests and 24 in forests that were never subjected to flooding. We analyzed vegetation structure under flooding regime and soil properties (fertility and texture) effects accessing composition, diversity, richness and abundance besides functional response of community weight means traits of stem number and biomass. Seasonally flooded forests in dry biomes

had structural patterns shaped by flooding gradient and soil as expected. We wish to draw attention to the diverse adapted flora along water availability gradient with distinct floristic groups, the diversity of dry forests with high diversity patterns in never flooded forests and the different functional response promoted by flooding and soil properties. While persistence strategy were described by flooding regime with high stem number in annually flooded forests, productivity with biomass was not influenced by flooding frequency, but pH and aluminum variation. Neotropical seasonally flooded dry forests had distinct structural changes related with floodplains in moist biomes and an exhaustive management criterion it is necessary to cover these biodiversity forests.

Key-swords: Environmental filter, Disturbance gradient, Stress gradient, Soil fertility, Soil texture, Drought Stress, Caatinga Domain, Vegetation structure.

Abbreviations: CWM (community weight means)
AGB (above ground biomass)

Flooding regime drives dry forests community structure

Introduction

Community assembly processes across environmental filtering is a central goal in community ecology in predict species distribution, traits variation and diversity patterns (Ackerly & Cornwell, 2007). These links are partially explained by ecological niche partitioning related to these abiotic filters and environmental changes occur mainly due disturbance-

stress gradients (Grime, 1979). Plant community structure has received a lot of attention to have an effect on ecosystem functioning, in environment changed by disturbance such as fire, floods and land use (Chazdon et al., 2003; Araujo et al., 2017a) and soil related stress (De Jager et al., 2012; Araujo et al., 2017b). Understand how disturbance-stress gradients shape vegetation structure are underlying of ecosystems processes, management and ecological applications.

Seasonally-flooded forests are subject to periodically waterlogging and flood pulse impact due adjacent rivers overflow (Junk, 1989). These perturbances have the potential to damage or uproot plants, (Junk, 1989, Voesenek et al., 2004), reduce resource availability (De Jager et al., 2012), and therefore be a source of environmental stress for affected vegetation communities (Grime, 1979; Li & Shipley, 2018). For example, it is predicted that multi-stemmed trees are better able to persist in habitats subjected to flooding (Bellingham & Sparrow, 2000; Bond & Midgley, 2001). The frequency and intensity of this environmental pertubance can therefore play an important role in shaping the diversity (taxonomic, functional and phylogenetic), floristic composition, vegetation structure, and dynamics of forests growing in regions subjected to flooding (Capon, 2005; Wittmann et al., 2010; Violle et al., 2010; Wittmann et al., 2013; Giehl & Jarenkow; 2015, Aldana, 2016). Indeed, plant communities affected by floods are known to have a specialized flora with physiological, anatomical and morphological adaptations (Wittmann et al., 2010; Tanentzap et al., 2016). At community-level, high flooding frequency can decrease taxonomic diversity (Budke et al., 2008), increase endemic species (Wittman et al.,

2010) and has been shown to result in the assembly of a phylogenetically depauperate community comprising of closely related plant species in some regions (e.g. Aldana et al., 2016).

In vegetation systems subjected to flooding, soil properties may also play influence vegetation structure. These happen because flooding gradient is associated with topography variations as depressions and/or elevations and change chemicals and physicals soil properties (Oliveira-Filho et al., 1994; Budke et al., 2007). For example, fertility can be a strong factor determining vegetation structure (Weiher & Keddy, 1995) which can be reduced by flooding (Giehl & Jarenkow, 2015). Clay soils with high organic matter and flood tolerance species were found at lower elevations in floodplains (De Jager et al., 2012). These "cascade effect" lead to studies find indirect or secondary effects of soil properties in floodplains community structure where flooding led to soil texture and fertility changes (Junk, 1989; Koschorreck & Darwick, 2003; Burke et al., 2003; De Jager et al., 2012; Korol et al., 2016).

The biology and ecology of flooded forests such as those in the Neotropics have been relatively intensively studied. For instance, the annually flooded forests (várzea and igapó) from Amazon Basin have been relatively well-characterized in terms of structure and floristics (Worbe et al., 1992; Klinge et al., 1995; Ferreira et al., 2005; Haugaasen & Peres, 2006; Carim et al., 2016), their soil biology and chemistry (Furch, 1997, Junk et al., 2010) and ecological characteristics (Parolin & Ferreira, 1998; Parolin, 2001). In contrast, the flooded forests in the north- and south-eastern regions have received much less attention (but see Scarano 2002; Neves et al., 2017). In particular, forests in drier

tropical regions such as the semiarid zones of southeast and northeast Brazil are also affected by seasonal flooding, but these have received disproportionally less scientific attention. Indeed, tropical dry forests are considered a distinct biome from rainforests (Prado, 2000; Sarkinen et al., 2011), with a different in origin, evolutionary history, and species distribution patterns and diversity (Pennington et al. 2009; Eisenhardt et al., 2017).

We attempt to fill this knowledge gap about the influence of flooding regime on the community composition, vegetation structure, and functional ecology of river-associated dry forest communities in southeast Brazil with the current work. We hypothesize that flooding regime is the main driver of vegetation community composition and structure. Specifically, we predict that a high flooding regime will lead to lowered tree diversity, reduced aboveground biomass, and a higher abundance multi-stem formation. In addition, we predict that floods act as the main driver of soil chemical and physical properties, which in turn determine vegetation structure where we expected acidic and poor soils in contrast with fertile soils in dry forests.

Methods

Study site and vegetation sampling

Our study was conducted in dry forests in the semi-arid region of the southeast Brazil (Fig. 1). In South America, dry forests are concentrated in "nuclei" areas (Linares-Palomino et al., 2011), and attain their greatest extent and continuity in semiarid region in northeast and

southeast Brazil (locally encompassed by a province known as the "Caatinga Domain"; Fernandes, 2003, Santos et al., 2012). These forests are typically seasonally deciduous with a discontinuous and uneven canopy cover, occurring over fertile soils (Eiten, 1983; Pennington et al., 2009).

The study sites were situated along four tributaries of the São Francisco river: Carinhanha, Jequitaí, Paracatu and Verde Grande. The São Francisco river is the forth longest river in South America and traverses five states in Brazil. These four tributary rivers are situated the region of the Middle São Francisco, which stretches from the city of Pirapora in the State of Minas Gerais to the city of Arcados in the State of Bahia (Fig 1A-B). Due to the low relief and depressions adjacent to the watercourse, certain regions are affected by flooding in high rainfall periods between November to January. These flood events also facilitate the accumulation of sediments, and lead to the formation of temporary wetlands, which may remain well into the dry season in mid-July and August (CODEVASF, 2002).
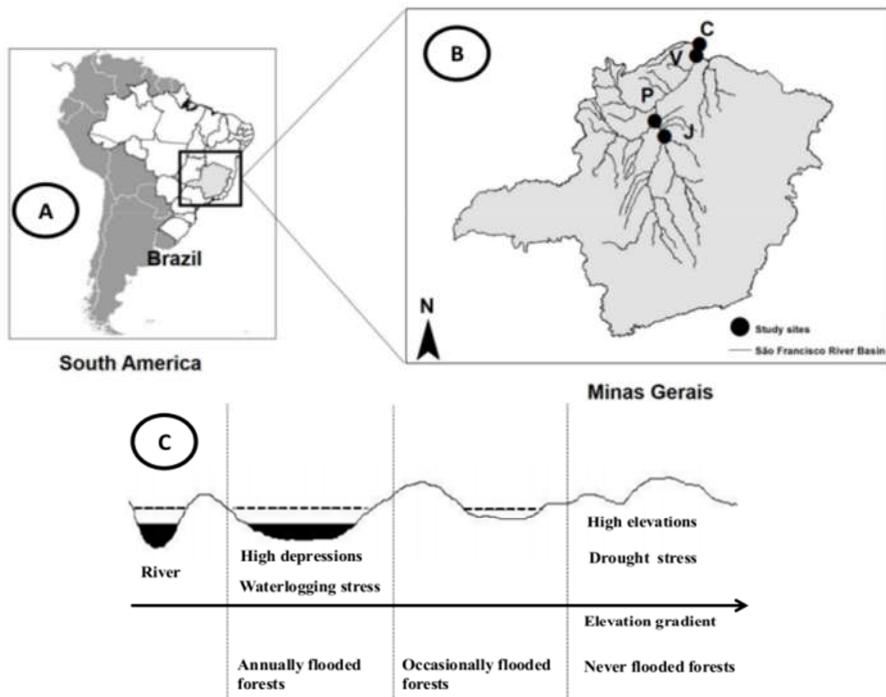
Figure 1 – Map of the study sites situated in the State of Mina Gerais, southeast Brazil (A). The four tributaries of the São Francisco River basin (B) sampled were Verde Grande (V), Carinhanha (C), Paracatu (P) and Jequitaí (J). Sampling sites comprising of forests with different flooding regimes (C), whereby annually flooded forests occurred in riparian settings or in landform depressions adjacent to the river tributaries; occasionally flooded forests in shallow depressions away from the tributaries, and: never flooded forests on raised ground above the highest watermark (see Methods). Figure 1-c was adapted from Pereira, 2013.

At each tributary area we established thirty 20 x 20 m or 10 x 40 m (400 m²: plots configurations depending on the width of the vegetation), totalling 120 plots (4.8 ha) across the four tributaries. We located study plots across sites representing three flooding regimes: flooded annually during the wet season (72 plots); occasionally flooded (24 plots), and; never flooded (24 plots). Our classification of flooding

regime of each site was based on local knowledge, and also observable landscape signs. For instance, our annually flooded forest sites are located by riparian habitats or depressions (Fig 1) and have evidence of sedimentation deposits and also short-lived ponds of standing water. The occassionally flooded sites are characterised by shallow depressions and are flooded at a frequency of about once every 30 years. Finally, the sites that are never flooded are typically 500-1900m from watercourses, with no evidence of temporary ponds. All plot censuses were performed during the dry seasons (July to November 2012, 2013 and 2015).

Within each plot, we tagged, measured, and identified to species all tree stems with diameter at breast height (DBH) $\geq$ 3.2 cm. Individual stems of multi-stemmed trees were measured whenever they fell within the measurement criteria. We also estimated the heights of all tree individuals.

Soil sampling

To determine the relationships between soil factors and vegetation, three 500ml soil surface samples (up to 20 cm depth) per plot were collected for quantitative analyses. The soil samples from each plot were bulked, homogenized, stored in plastic bags and transported to the Laboratory of Soil Analysis at the Federal University of Lavras for analysis. At the laboratory, we carried out soil analyses to quantify the following variables: pH, K, P, Ca, Mg, Al, t (cation exchange capacity) and OM (organic matter) as a proxy of soil fertility. We also applied a

categorical classification of soil texture on our samples by classifying each sample into sandy soils, sandy/clay soils, or clay soils.

Diversity indices, vegetation structure and community weighted traits

We calculated plot diversity in terms of species richness (number of species), Shannon-Wiener Index (H'), and Pielou's Evenness (J) (Brower & Zar, 1984).

To parameterize community structure, we used number of individuals, stem number, and aboveground biomass (AGB). We calculated AGB using the equation of Chave et al. (2014) for tropical forests: AGB = 0.0673 x 0.01 x (D^2 x H x WD)$^{0.976}$, where D is stem diameter, H is stem height and WD is wood density. We obtained wood density values from the Global Wood Density database (Zanne et al., 2009), with the exception of *Myracroduon urundeuva* Allemão, for which we used values reported in Silva et al. (2017). For some species we used genus-level values. Finally, we also calculated the community-weighted means (CWM) for the trait of being multistemmed (CWM$_{ms}$) based on the number of stems originating from the same individual. Because CWM is a plot-level functional measure weighted by individual species abundance, it is a more reflective of trait strategies within a forest stand than merely counting the number of multiple-stemmed individuals (e.g. Cornwell & Ackerly, 2009; Muscarella & Uriarte, 2016).

Data analysis

To examine how flooding regime shapes community composition, first, we ordinated the plot-level species abundance data using non-metric

multidimensional scaling (NMDS) ordination, using the "metaMDS" function of the "vegan" package (Oksanen et al., 2016) with abundance distance "Bray-Curtis" to visualize potential floristic units across the four river tributaries and across our gradient of site flooding.

We use a one-way ANOVA to test whether flooding regime led to significantly difference in CWM_{ms}, AGB, stem number, abundance and H′ and *post-hoc* Tukey tests to determine significantly different groups. For species richness and J, we used Kruskall-Wallis to and *post-hoc* Dunn tests due to non-normal distributions in these variables. CWM_{ms}, AGB and stem number were log-transformed.

We examined the soil composition of our 120 sites with a Principal Component Analysis (PCA) using the PC-ORD 5 software for Windows. Due to variable intercorrelation, we removed Ca, Mg and t from analysis (Appendix S1).

To test how flooding regime and soil properties affect community structure we fitted linear mixed models using richness, abundance, AGB, and CWM_{ms} as response variables; flooding regime (annually flooded, occasionally flooded and never flooded), and soil fertility (PCA axis 1 and PCA axis 2) as a fixed effect and river tributary (Verde Grande, Carinhanha, Paracatu and Jequitaí) as random effect. Then, to test soil properties (fertility and texture) only, without flooding frequency effects on vegetation structure, we fitted another set of linear mixed models using the same response variables but only soil fertility (PCA axis 1 and PCA axis 2) as a fixed effect and river tributary as random effect. We computed negative binomial family error for richness and abundance, since our data showed significant overdispersion and Gaussian family

error to CWM$_{ms}$ and AGB. The top five best models were selected based on Akaike information criterion based on small samples (AICc) until ΔAICc < 2 with "dredge" function in "MuMIn" package (Barton, 2017). All models were fitted with "lmer" function (Gaussian error) in lme4 package (Bates et al., 2015) in *R*, version 3.3.1 (R Development Core Team 2016).

Results

Species composition and diversity

We recorded a total of 13,474 stems and 5,778 individuals representing 146 genera and 223 species from our 120 sites. The never flooded forests had the highest tree species richness (130 spp.), followed by the annually flooded forests (114 spp.) and occasionally flooded forests (112 spp.) (Fig. 2a). Thirty-four tree species (15.2% of all the species) were common across all three forests types (Fig 2a). Occasionally flooded forests represented an intermediate floristic group sharing more species with each area than between them and was the lowest value of exclusive species with 20 (9%) (Fig 2a). Our NMDS ordination (Fig 2b; Appendix S2) segregated three main floristic groups which accorded well with our a priori vegetation categories of annually flooded, occassionally flooded and never flooded forests. Nevertheless, it was also possible to observe a divergence in species composition between the Paracatu and Jequitaí river tributaries (P and J) and the Carinhanha and Verde Grande rivers (C and V). This was due to the Paracatu and Jequitaí river tributaries having elements from both the Brazilian savanna (Cerrado) and rainforest (Atlantic forest), while the Carinhanha and

Verde Grande rivers (C and V) had a predominant influence from Brazilian savanna.

Annually flooded forests from Carinhanha and Verde Grande rivers (C and V) was characterized for exclusive species like *Casearia commersoniana* Cambess., *Geoffroea spinosa* Jacq., *Maytenus rigida* Mart., *Prosopis ruscifolia* Griseb., *Senegalia langsdorffii* (Benth.) Seigler & Ebinger and *Tocoyena bullata* (Vell.) Mart. and in never flooded forests from these rivers the *Acosmium lentiscifolium* Schott, *Aspidosperma polyneuron* Müll.Arg., *Dalbergia acuta* Benth., *Handroanthus heptaphyllus* (Martius) Mattos and *Ptilochaeta bahiensis* Turcz. At Paracatu and Jequitaí rivers, annually flooded forests housed exclusive species like *Bauhinia rufa* (Bong.) Steud., *Casearia gossypiosperma* Briq., *Cecropia pachystachya* Trécul, *Croton urucurana* Baill. and *Eugenia florida* DC. and in never flooded forests *Copaifera coriacea* Mart., *Dimorphandra mollis* Benth., *Machaerium opacum* Vogel, *Pterodon emarginatus* Vogel and *Qualea grandiflora* Mart.

On a plot level, the difference in tree species richness (X^2_{117} = 38.576, $p < 0.001$), Shannon's diversity ($F_{117} = 23.92$, $p < 0.001$) and Pielou's Evenness (J – X^2_{117} = 21.17, $p < 0.001$) was also significant higher in never flooded forests (Fig. 3).
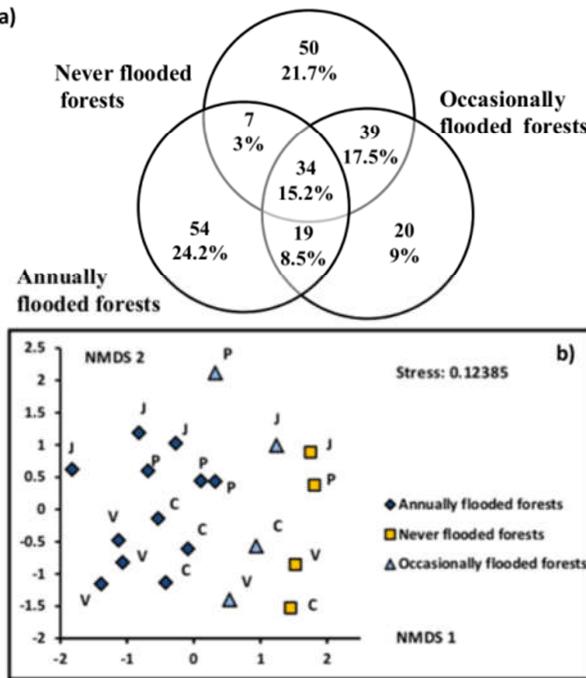
Figure 2 – Floristic groups of seasonally flooded dry forests. a) Venn Diagram with shared species richness across flooding frequency with absolute values and respective percentage and b) non-metric multidimensional scaling (NMDS) showing three floristic units across flooding gradient and the four tributaries of São Francisco river – Carinhanha (C), Verde Grande (V), Paracatu (P) and Jequitaí (J).

Community structure and traits

For community structure, log stem number had higher significant value in annually flooded forests ($F_{117} = 7.535$, $p < 0.001$) while abundance no difference was found ($F_{117} = 0.26$, $p = 0.771$) (Fig 4, a-b). For CWM$_{ms}$ and AGB we found distinct differences across plots under different flooding regimes. Annually flooded forests had the highest CMW$_{ms}$ values ($F_{117} = 7.535$, $p < 0.001$), while AGB was not significantly different ($F_{117} = 0.377$, $p = 0.687$) (Fig. 4 c-d). Some

individuals located in annually flooded forests showed 47-90 sprouts as in the species *Ruprechtia apetala* Weddell (POLYGONACEAE) in only one individual in the J and P rivers, 15-30 sprouts in *Annona spinescens* Mart. (ANNONACEAE), *Senegalia langsdorffii* (Benth.) Seigler & Ebingerem (FABACEAE), *Licania rigida* Benth. (CHRYSOBALANACEAE) and *Triplaris gardneriana* Weddell (POLYGONACEAE) in C and V rivers.
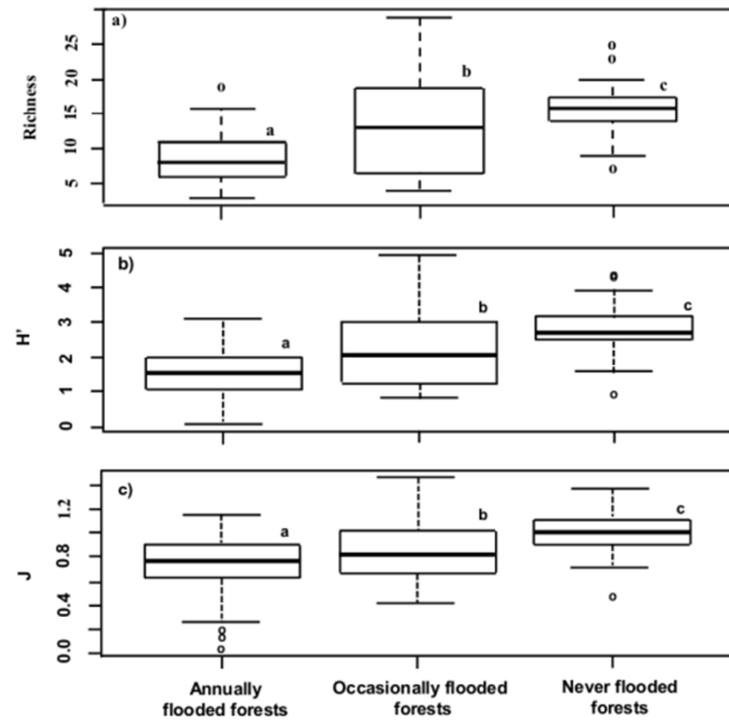
Figure 3 – Diversity metrics boxplots variation of vegetation structure across flooding frequency. Richness values (a), Shannon index (H') (b) and Pielou evenness (J) (c). Letters "a", "b" and "c" represent *post-hoc* Tuckey and Dunn tests when analysis of variance was significant between areas.

Effects of flooding and soil properties over vegetation structure

Soil variables (pH, Al, P, K and OM) played key role in separate rivers, not flooding gradient as expected (Fig 5; Appendix S3). PCA axis 1 and PCA axis 2 jointly explained 57.6 % of total variation (Fig 5; 999 randomizations $p < 0.001$ for axis 1 and 2). Axis 1 was strongly negative correlated with pH and positively correlated with Al (acidic gradient) and axis 2 was negatively correlated with OM and K (organic matter gradient). P showed no expressive correlation with these two axis.
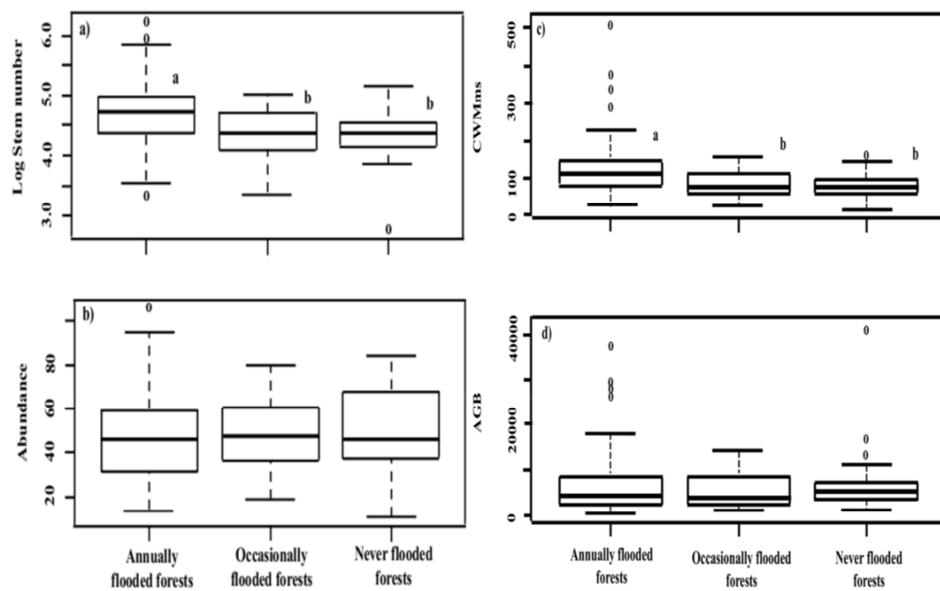
Figure 4 - Boxplots variation of vegetation structure across flooding frequency. Log stem number (a), abundance (b), CWM_{ms} (c) and AGB (d) changes with significant p values by *post-hoc* Tukey and Dunn tests represented by letters "a" and "b".

Among vegetation structure responses tested with models, CWM_{ms} and richness was significantly predicted by flooding frequency, while AGB was supported by significant relationships with high flood frequency and PCA axis 1 (acidic gradient) (Table 1; Appendix S4). Only

soil properties effects, significant difference was lacking in the model for CWM$_{ms}$, abundance and richness, only AGB was predicted for sandy soils and PCA axis 1 relationships (Table 2; Appendix S5). Top five best models using AICc of criterion information (delta < 2) demonstrated strong relationships with flood and soil fertility for CWM$_{ms}$ and richness response variables, while acidic and organic matter gradient seems to be a better predictor than soil texture, with exception in CWM$_{ms}$ (Table 3).
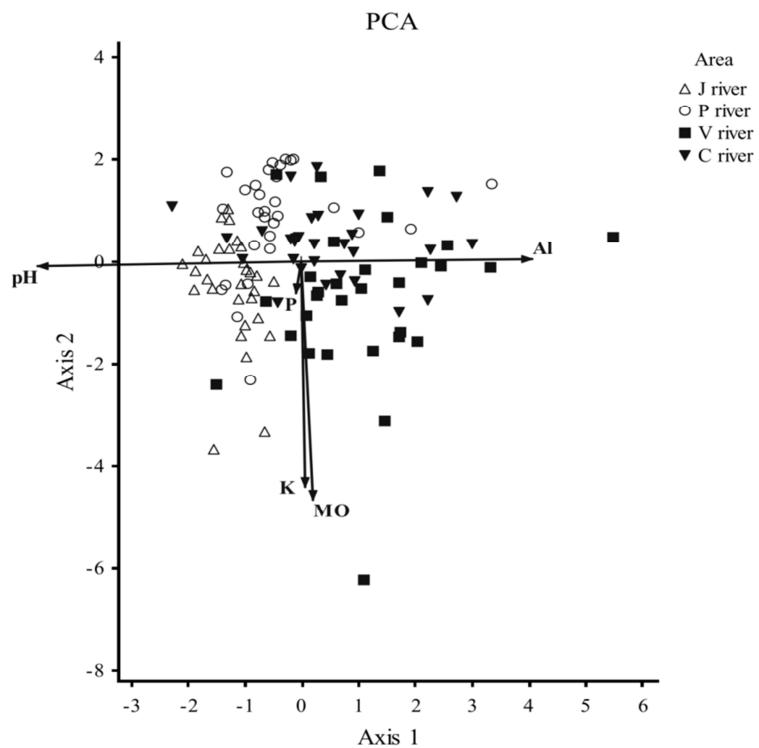
Figure 5 – Soil fertility characterizing rivers. C and V rivers were characterized by acid soils with high aluminum content and P and J rivers alkaline soils with exceptions. The J and V river tributaries have higher OM and K values than the C and P tributaries. First axis explained 30.2 % of the total variation and axis two explained 27.4% of the variation.

Discussion

Seasonally flooded forests in dry biomes had structural patterns shaped by flooding gradient and soil as expected, but in different ways, once soil factors were not conditioned by flooding, contrary to our expectation. We found overall differences with more structure parameters related to high flooding frequency and more diversity patterns related to never flooded forests, in contrast of biomass explained better from soil acidic gradient. In addition, results indicate that occasionally flooded forests act as a transition zone between the two extreme environments of water availability.

Table 1 – Significant results of generalized linear mixed effects models. Here we demonstrated values of community weight means (CWM) structural trait (stem number) and above ground biomass fitted to flooding frequency and soil fertility (PCA axis 1 and 2) as fixed effects and rivers as random effects in flooded dry forests, Minas Gerais, southeast Brazil. CWM : community weight means; ms : multi-stems; AGB : above ground biomass; OF : Occasionally flooded; NF : Never flooded; N : abundance; R : richness; SE : standard error; AIC : Akaike information criterion. * represents significant p values. All values were described in Appendix S4.

	Estimate	SE	t/z-value	p-value	Random residual	AIC
CWM$_{ms}$	.	.	.	.	.	.
Intercept	1.425	0.082	17.515	<0.001*	0.312	217.6
OF	0.65	0.132	4.9	<0.001*	.	.
NF	1.03	0.132	7.747	<0.001*	.	.
AGB (g/cm³)	.	.	.	.	.	.
Intercept	8.494	0.102	82.802	<0.001*	0.718	315.1
PCA axis 1	0.145	0.06	2.469	0.023*	.	.

	Estimate	SE	t/z-value	p-value	Random residual	AIC
N	.	.	.	.	.	.
Intercept	3.85	0.059	64.64	<0.001*	0.005	1053
R	.	.	.	.	.	.
Intercept	2.13	0.078	27.491	<0.001*	0.015	698.7
OF	0.43	0.088	4.911	<0.001*	.	.
NF	0.626	0.084	7.462	<0.001*	.	.

Table 2 – Siginificant results of generalized linear mixed effects models. Here we demonstrated values of community weight means (CWM) structural trait (stem number) and above ground biomass fitted to soil fertility (PCA axis 1 and 2) and soil texture as fixed effects and rivers as random effects in flooded dry forests, Minas Gerais, southeast Brazil. CWM : community weight means; ms : multi-stems; AGB : above ground biomass; *N* : abundance; *R* : richness; AIC : Akaike information criterion. * represents significant *p* values. All values were described in Appendix S5.

	Estimate	SE	t/z-value	p-value	Random residual	AIC
CWM$_{ms}$	.	.	.	.	.	.
Intercept	1.751	0.141	12.443	0.001*	0.489	268.8
AGB (g/cm³)	.	.	.	.	.	.
Intercept	8.724	0.175	49.640	0.001*	0.706	313.9
PCA axis 1	0.207	0.073	2.814	0.013*	.	.
N	.	.	.	.	.	.
Intercept	3.916	0.088	44.27	<0.001*	0.005	1052.6
R	.	.	.	.	.	.
Intercept	2.384	0.111	21.401	<0.001*	0.012	737.2

Table 3 – Results of model selection for the impact of flooding frequency and soil factors and results of model selection of soil fertility and texture over CWM_{ms}, AGB, R and N. Chemicals variables were summarized into two PCA axes (See Fig 4) and physical variables as sandy, sandy/clay and clay soils. We presented models with delta ($\Delta AICc$) < 2. CWM: community weight means; AGB : above ground biomass; AICc : Akaike information criterion of small sample size; AICcWt : Weight of AICc; ST : Soil Texture; w/ : with; N : abundance; R : richness.

Response variables w/ flooding	Model variables	AICc	ΔAICc	AICcWt
CWM_{ms}	Flooding	216.2	0	0.390
	Flooding+PCA axis 2	216.9	0.68	0.277
	Flooding+PCA axis 1	217.4	1.21	0.213
AGB (g/cm³)	PCA axis 1	311.8	0	0.422
	PCA axis 1+PCA axis 2	312.7	0.90	0.270
N	Intercept(annually flooded)	1047.1	0	0.387
	PCA axis 2	1047.9	0.76	0.264
R	Flooding	688.6	0	0.402
	Flooding+PCA axis 1	689.7	1.09	0.233
	Flooding+PCA axis 2	689.8	1.11	0.231
Response variables w/ ST	.	.	.	.
CWM_{ms}	ST	266.2	0	0.264
	Intercept (sandy soils)	267.4	1.14	0.149
	PCA axis 2	267.4	1.24	0.142
	PCA axis 2+ST	267.5	1.33	0.136
	PCA axis 1	268.1	1.89	0.102
AGB (g/cm³)	PCA axis 1	311.8	0	0.339
	PCA axis 1+ST	312.7	0.85	0.222
	PCA axis 1+ PCA axis 2	312.7	0.90	0.217
N	Intercept(sandy soil)	1047.1	0	0.362
	PCA axis 2	1047.9	0.76	0.248

R	Intercept(sandy soil)	734.1	0	0.212
	PCA axis 1	734.2	0.15	0.197
	PCA axis 2	734.7	0.58	0.159
	PCA axis ½	734.8	0.74	0.147
	ST	735	0.87	0.137

Floristic composition was strongly zoned across flooding gradient and domains matrix. The Neotropical dry forests are inserted in a context of a seasonally marked climate, with a long period of drought, which is a delimiting factor of their floristic and physiognomic composition (Santos et al., 2012; Dryflor, 2016). Drought stress impose a selective pressure over vegetation, so do floods (waterlogging stress) (Pennington et al., 2009; Tanentzap et al., 2016). In both extreme side of the gradient, exclusive plant species represented almost half of total floristic composition, which indicate replacement of a specialized flora in seasonally flooded forests at Caatinga Domain. Beyond flooding frequency, proximity of moist biomes like tropical rainforests (Atlantic Forest Domain), would explain compositional changes of J and P rivers from C and V rivers. Precipitation acts as strong environmental filter on Atlantic Domain (Oliveira-Filho & Fontes, 2000; Eisenlohr & Oliveira-Filho, 2015). Overall changes of water availability, from floods (local scale) to domains borders related to precipitation (regional scale) seem to be a driver factor filtering vegetation composition as well as structure (Appendix S6).

In high floods frequency, significant changes in structure and diversity patterns were found (Budke et al., 2010) and, in particular, high flooding frequency associated with resprouting ability (Giehl & Jarenkow, 2015). Indeed, frequency could explain why flooded forests

housed the greatest stem number (resprouting strategy) values and were affected by flooding frequency. The ability to form multiple stems can increase the persistence in unstable environments (Flinn et al., 1992; Bond & Midgley, 2001). In tropical dry forests, natural occurrence of multi-stemmed trees was recorded from Puerto Rico and drought stress as a key driver of multi-stems stands (Dunphy et al., 2000). In contrast, our results demonstrated that floods trigger stem formation instead water shortage on seasonally flooded dry forests at Caatinga Domain.

Some studies reported higher values in species richness, and diversity and evenness indices in intermediate flooding frequency in moist subtropical flooded forests (Budke et al, 2010; Giehl & Jarenkow, 2015). Seasonally flooded dry forests of Caatinga Domain under disturbance-stress gradient showed different pattern of diversity, evenness and richness with highest values in never flooded forests (dry forests core) in contrast of these studies and what is expected from Intermediary Disturbance Hypotheses or unimodal richness patterns (Connell, 1978; Sheil, 2001). In other words, the richest sites were found where drought stress is predominant filter. In our flooding systems, diversity pattern seems to be more sensitive to waterlogging and flood pulse than drought stress. In dry forests, it is expected that species would be better adapted under seasonally dry climate than floods. Wittmann et al., (2010) proposed that high flooding forests from Amazon Basin act as a refuge for moist-sensitive flora in dry marked climate periods. Indeed, in a proportional scale, our riverine forests house group of species adapted from waterlogging stress, like *Geoffroea spinosa* (Appendix S6).These groups so could persist in a marked dry environment with more annual

water supplying increasing diversity of Tropical dry forests at Caatinga Domain and also refugees by these riverine forests.

In terms of biomass however, models showed no influence of flooding frequency, but soil properties did being pH the main factor. In the Amazon floodplains, flooding is considered the main driver of diversity and biomass changes, with lower values compared to uplands forests (Wittmann et al., 2010; Schonhgart et al., 2010). In our study on seasonally flooded tropical dry forests, disturbance gradient had no effect on biomass (the same for abundance). Here, productivity was determined by: (i) -limiting biomass production factors or stress related to soil properties (Grime, 1979) and (ii) overall patterns on regional scale (climate and soil variation), not local scale (flooding frequency). This could happen due to disparate impact of the rivers size, once in our dry biome they account with tiny proportion of the landscape. Here, at regional scale, without flood effects, biomass increase where pH decrease and become more acidic and soils tended to be more clayey as in C and V rivers. Thus, soil acidic stress gradient was the main driver of productivity on the studied system. This pattern also was found for functional response of productivity along stress gradient increasing functional dissimilarity when stress increased, but not the same for perturbance (Li & Shipley, 2018).

Studying vegetation structure of seasonally dry forests across flooding frequency and soil properties effects brought intriguing patterns about community structure response to disturbance-stress gradient, which are not yet included in studies of this magnitude from tropical dry forests at Caatinga Domain. Although flooding and soil properties determined

structural changes on composition, diversity and stand patterns, we highlight ecological differences of these patterns in our study region relative to flooded forests in other moist biomes. Overall, we wish to draw attention to the diverse adapted flora along water availability gradient, the diversity of dry forests and the different functional response promoted by flooding and soil properties. Neotropical dry forests at Caatinga Domain already proved to be a distinct structure pattern from the world (Sarkinen et al., 2011; Santos et al., 2012) being important to conservation efforts, but now, especially from these floodable systems, exhaustive management criterion it is necessary to cover these biodiversity forests.

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Author contributions

RMS designed the research, FDCA, DMGA and RMS collected the data and FDCA, DYPT, DMGA and RMS wrote the manuscript.

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Supporting information to the paper

Araújo et al. Flooding regime drives tree community structure changes in tropical dry forests in southeast Brazil. *Journal of Vegetation Science*

Appendix S1. Spearman correlation analysis in soil fertility.
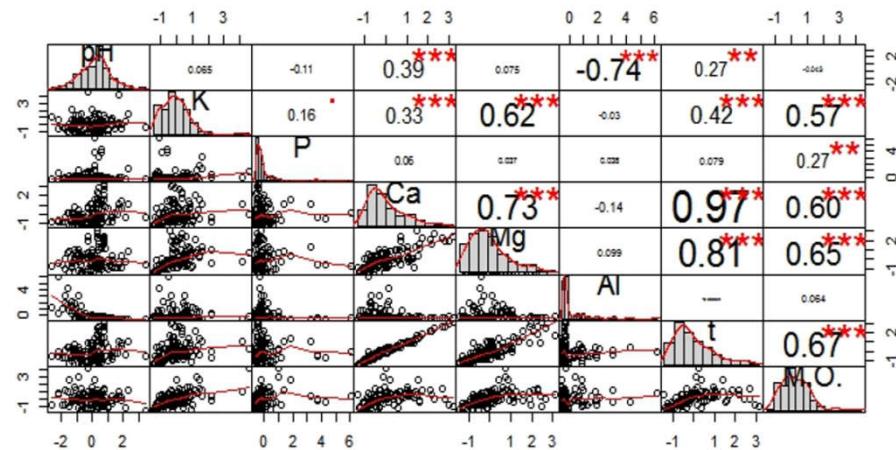
Supporting information to the paper

Araújo et al. Flooding regime drives tree community structure changes in tropical dry forests in southeast Brazil.

Appendix S2. Non-metric multidimensional scaling (NMDS) in 120 plots across flooding frequency in southeast Brazil. *Journal of Vegetation Science*
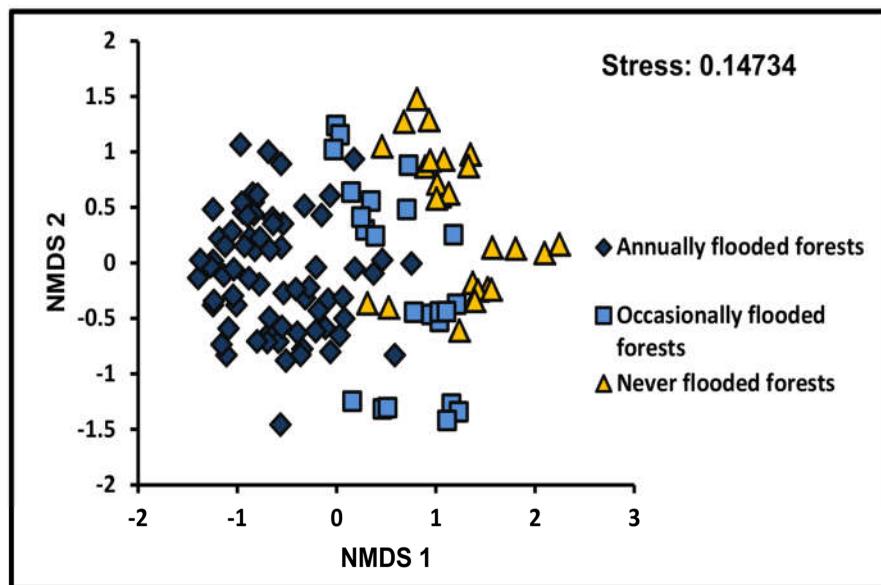
Supporting information to the paper

Araújo et al. Flooding regime drives tree community structure changes in tropical dry forests in southeast Brazil. *Journal of Vegetation Science*

Appendix S3. Principal Component Analysis (PCA) of soil fertility across flooding frequency in southeast Brazil.
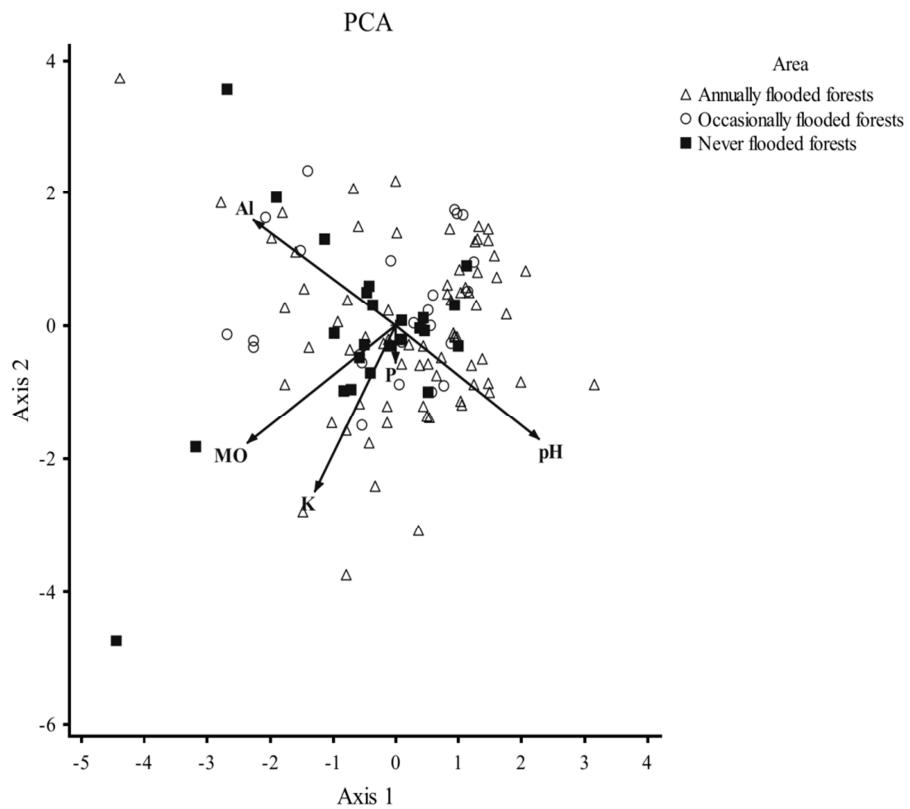
Appendix S4 – Results of generalized linear mixed effects models of community weight means (CWM) structural traits (stem number and above ground biomass) fitted to flooding frequency and soil factors as fixed effects and rivers as random effects in flooded dry forests, Minas Gerais, southeast Brazil. CWM : community weight means; ms : multi-stems; AGB : above ground biomass; OF : Occasionally flooded; NF : Never flooded; N : abundance; R : richness; SE : standard error; AIC : Akaike information criterion. * represents significant p values.

CWM_{ms}	Estimate	SE	t/z-value	p-value	Random residual	AIC
Intercept	1.425	0.082	17.515	<0.001*	0.312	217.6
OF	0.65	0.132	4.9	<0.001*	.	.
NF	1.03	0.132	7.747	<0.001*	.	.
PCA axis 1	0.042	0.043	0.99	0.331	.	.
PCA axis 2	-0.048	0.042	-1.116	0.268	.	.
AGB (g/cm³)	.	.	.	.	.	.
Intercept	8.494	0.102	82.802	<0.001*	0.718	315.1
OF	-0.105	0.201	-0.522	0.603	.	.
NF	0.15	0.201	0.743	0.46	.	.
PCA axis 1	0.145	0.06	2.469	0.023*	.	.
PCA axis 2	0.087	0.061	1.424	0.161	.	.
N	.	.	.	.	.	.
Intercept	3.85	0.059	64.64	<0.001*	0.005	1053
OF	0.028	0.094	0.30	0.761	.	.
NF	0.068	0.094	0.73	0.468	.	.
PCA axis 1	-0.001	0.031	-0.02	0.981	.	.
PCA axis 2	0.039	0.032	1.19	0.233	.	.
R	.	.	.	.	.	.
Intercept	2.13	0.078	27.491	<0.001*	0.015	698.7
OF	0.43	0.088	4.911	<0.001*	.	.
NF	0.626	0.084	7.462	<0.001*	.	.
PCA axis 1	0.034	0.032	1.072	0.284	.	.
PCA axis 2	-0.032	0.03	-1.077	0.282	.	.

Supporting information to the paper
Araújo et al. Flooding regime drives tree community structure changes in tropical dry forests in southeast Brazil. *Journal of Vegetation Science*

Appendix S5 - Results of generalized linear mixed effects models of community weight means (CWM) structural traits (stem number and above ground biomass) fitted to chemicals (PCA axis 1 and 2) and physicals soil properties as fixed effects and rivers as random effects in flooded dry forests, Minas Gerais, southeast Brazil. CWM : community weight means; s/c soil : sandy/clay soils; ms : multi-stems; AGB : above ground biomass; N : abundance; R : richness; AIC : Akaike information criterion. * represents significant *p* values.

CWM$_{ms}$	Estimate	SE	t/z-value	p-value	Random residual	AIC
Intercept	1.751	0.141	12.443	0.001*	0.489	268.8
s/c soil	-0.143	0.178	-0.804	0.423	.	.
Clay soil	0.170	0.210	0.808	0.420	.	.
PCA axis 1	0.008	0.057	0.134	0.894	.	.
PCA axis 2	-0.055	0.058	-0.944	0.347	.	.
AGB g/cm³	.	.	.	.	.	.
Intercept	8.724	0.175	49.640	0.001*	0.706	313.9
s/c soil	-0.213	0.215	-0.990	0.324	.	.
Clay soil	-0.396	0.256	-1.543	0.126	.	.
PCA axis 1	0.207	0.073	2.814	0.013*	.	.
PCA axis 2	0.018	0.071	0.259	0.796	.	.
N	.	.	.	.	.	.
Intercept	3.916	0.088	44.27	<0.001*	0.005	1052.6
s/c soil	-0.092	0.101	-0.92	0.359	.	.
Clay soil	-0.043	0.13	-0.33	0.742	.	.
PCA axis 1	0.003	0.041	0.08	0.938	.	.
PCA axis 2	0.029	0.035	0.79	0.429	.	.
R	.	.	.	.	.	.

Intercept	2.384	0.111	21.401	<0.001*	0.012	737.2
s/c soil	-0.07	0.121	-0.581	0.561	.	.
Clay soil	0.061	0.153	0.399	0.69	.	.
PCA axis 1	0.029	0.051	0.575	0.565	.	.
PCA axis 2	-0.043	0.04	-1.068	0.286	.	.

AppendixS6 – Floristic list with relative abundance across flooding gradient from four tributaries of São Francisco River Basin (Carinhanha, Jequitaí, Paracatu and Verde Grande). AF: Annually flooded; OF: Occasionally flooded; NF: Never flooded. Presence was marked as "x" and ausence by ".".

Species composition	Carinhanha			Jequitaí			Paracatu			Verde Grande		
	AF	OF	NF	AF	OF	NF	AF	OF	NF	AF	OF	NF
Acosmium lentiscifolium Schott	.	.	x	.	.	.	.	.	.	.	.	x
Albizia inundata (Mart.) Barneby & J.W.Grimes	x	.	.	x	.	.	x	.	.	x	x	.
Albizia niopoides (Spruce ex Benth.) Burkart	x	.	.	x	x	.	x	.	.	.	.	.
Allophylus racemosus Sw.	.	.	x	.	.	.	.	.	.	.	.	.
Alseis pickelii Pilger & Schmale	.	.	.	.	.	.	.	.	.	.	x	.
Amburana cearensis (Allemão) A.C.Sm.	.	.	.	.	.	.	.	.	x	.	.	x
Anadenanthera colubrina (Vell.) Brenan	.	x	x	x	x	x	.	.	x	.	.	x
Annona coriacea Mart.	.	.	.	.	.	.	.	x	.	.	.	.
Annona leptopetala (R.E.Fr.) H.Rainer	.	x	x	.	.	.	.	.	.	.	x	x
Annona montana Macfad.	x	.	.	.	.	.	.	.	.	.	.	.
Annona spinescens Mart.	x	.	.	.	.	.	.	.	.	x	x	.
Annona sylvatica A.St.-Hil.	.	.	.	.	.	.	x	.	.	.	.	.
Annona vepretorum Mart.	.	.	.	.	.	.	.	.	.	.	.	x

Species	1	2	3	4	5	6	7	8	9	10	11	12
Aralia warmingiana (Marchal) J.Wen	.	x	x	.	.	.	.	.	.	.	.	.
Aspidosperma cuspa (Kunth) S.F.Blake ex Pittier	.	.	.	.	.	.	.	.	x	.	.	x
Aspidosperma macrocarpon Mart.	.	.	.	.	.	x	.	.	.	.	.	.
Aspidosperma polyneuron Müll.Arg.	.	.	x	.	.	.	.	.	.	.	.	x
Aspidosperma pyrifolium Mart.	.	.	x	.	.	.	.	.	.	.	.	.
Aspidosperma subincanum Mart. ex A.DC.	.	.	.	.	x	x	.	.	.	.	.	x
Astronium fraxinifolium Schott ex Spreng.	x	x	.	x	x	x	.	x	x	.	.	.
Auxemma oncocalyx (Allemão) Taub. oncocalyx Allemão	.	.	x	.	.	.	.	.	.	.	.	.
Bauhinia acuruana Moric.	.	.	.	.	.	.	x	.	.	x	.	.
Bauhinia catingae Harms	.	.	.	.	.	.	.	.	.	x	.	.
Bauhinia rufa (Bong.) Steud.	.	.	.	x	.	.	x	.	.	.	.	.
Blanchetiodendron blanchetii (Benth.) Barneby & J.W.Grimes	.	.	x	.	.	.	.	.	.	.	.	.
Blepharocalyx salicifolius (Kunth) O.Berg	x	.	.	.	.	.	x	.	.	.	.	.
Bougainvillea praecox Griseb.	.	.	x	.	.	.	.	.	.	.	x	.
Bowdichia virgilioides Kunth	.	.	.	.	.	.	.	.	x	.	.	.
Brosimum gaudichaudii Trécul	.	.	.	.	x	x	x	.	x	.	.	.
Buchenavia tomentosa Eichler	.	.	.	.	.	x	.	.	.	.	.	.
Byrsonima chrysophylla Kunth	.	.	.	.	.	.	.	.	x	.	.	.
Calliandra depauperata Benth.	.	x	.	.	.	.	.	.	.	.	.	.
Calliandra foliolosa Benth.	x	.	.	.	.	.	.	.	.	.	.	.
Callisthene fasciculata (Spreng.) Mart.	.	.	.	x	x	x	x	x	x	.	.	.
Campomanesia sessiliflora (O.Berg) Mattos	.	.	.	.	.	.	.	.	.	.	.	x
Campomanesia velutina (Cambess.) O.Berg	.	.	.	.	x	.	.	.	.	.	.	.

Species	1	2	3	4	5	6	7	8	9	10	11	12
Capparis flexuosa (L.) L	.	.	.	x	.	.	.	.	.	.	.	.
Capsicum parviflorum Sendtn.	.	.	x	.	.	.	.	.	.	.	.	.
Caryocar brasiliense Cambess.	.	.	.	.	x	.	.	.	.	.	.	.
Casearia commersoniana Cambess.	x	.	.	.	.	.	.	.	.	x	.	.
Casearia gossypiosperma Briq.	.	.	.	x	.	.	x	.	.	.	.	.
Casearia rupestris Eichler	.	.	.	.	.	.	.	.	x	.	.	.
Casearia selloana Eichl.	.	.	.	.	.	.	.	.	.	.	.	x
Casearia sylvestris Sw.	.	.	.	.	x	.	x	.	x	.	.	.
Cecropia pachystachya Trécul	.	.	.	x	.	.	x	.	.	.	.	.
Cedrela fissilis Vell.	.	.	.	.	.	.	.	.	.	.	x	.
Celtis brasiliensis (Gardner) Planch.	.	x	.	.	x	x	.	.	.	.	x	.
Celtis ehrenbergiana (Klotzsch) Liebm.	x	.	.	x	.	.	x	.	.	x	.	.
Centrolobium microchaete (Mart. ex Benth.) H.C.Lima	.	.	.	.	.	.	.	.	.	x	.	.
Cereus jamacaru DC.	x	x	x	.	.	.	.	.	.	x	x	x
Cestrum axillare Vell.	x	.	.	.	.	.	.	.	.	.	.	.
Chloroleucon acacioides (Ducke) Barneby & J.W.Grimes	.	.	.	.	.	.	.	.	.	x	.	.
Chloroleucon dumosum (Benth.) G.P.Lewis	x	.	.	.	x	.	.	.	.	.	.	.
Chloroleucon foliolosum (Benth.) G.P.Lewis	x	x	x	.	.	.	.	.	.	.	.	x
Chomelia brasiliana A.Rich.	x	.	.	.	.	.	x	x	.	x	x	.
Chomelia pohliana Müll.Arg.	x	.	.	.	.	.	.	.	.	.	.	.
Chomelia sericea Müll.Arg	.	.	.	x	.	.	.	.	.	.	.	.
Coccoloba acuminata Kunth	.	.	.	.	.	.	.	.	.	x	.	.
Coccoloba schwackeana Lindau	.	.	x	.	.	.	.	.	.	.	x	x

Species												
Combretum duarteanum Cambess.	.	.	x	.	x	x	x	.	.	.	.	x
Commiphora leptophloeus (Mart.) J.B.Gillet	.	x	x	.	.	.	.	.	.	.	x	x
Connarus suberosus Planch.	.	.	.	.	x	x	.	.	.	.	.	.
Copaifera coriacea Mart.	.	.	.	.	.	x	.	.	x	.	.	.
Copaifera langsdorffii Desf.	.	.	.	.	x	x	x	.	x	.	.	.
Cordia glabrata (Mart.) A.DC.	x	x	.	x	x	x	.	.	x	.	.	.
Cordia trichotoma (Vell.) Arrab. ex Steud.	.	.	x	.	.	.	.	.	.	.	.	.
Cordiera sessilis (Vell.) Kuntze	.	.	.	.	x	x	.	.	.	.	.	.
Croton urucurana Baill.	.	.	.	x	.	.	x	.	.	.	.	.
Curatella americana L.	.	.	.	.	x	.	x	x	x	.	.	.
Cybistax antisyphilitica (Mart.) Mart.	.	.	.	.	.	x	.	.	.	.	.	.
Cynophalla flexuosa (L.) J.Presl	x	.	.	.	.	.	.	.	.	x	x	.
Cyrtocarpa caatingae J.D.Mitch. & Daly	.	.	x	.	.	.	.	.	.	.	x	x
Dalbergia acuta Benth.	.	.	x	.	.	.	.	.	.	.	.	x
Dalbergia cearensis Ducke	.	x	.	.	.	.	.	.	.	.	.	x
Dilodendron bipinnatum Radlk.	.	x	.	.	x	x	.	.	x	.	.	.
Dimorphandra mollis Benth.	.	.	.	.	.	x	.	.	x	.	.	.
Diospyros burchellii Hiern	.	.	.	x	x	x	.	.	.	.	.	.
Diospyros hispida A.DC.	.	.	.	.	.	.	x	.	.	.	.	.
Dipteryx alata Vogel	.	.	.	.	x	x	.	.	x	.	.	.
Enterolobium contortisiliquum (Vell.) Morong	.	.	.	.	x	.	.	.	.	.	.	x
Enterolobium timbouva Mart. Mart.	.	.	.	.	.	.	.	.	.	.	x	.
Erythroxylum betulaceum Mart.	.	.	.	.	.	x	.	.	.	.	.	.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Erythroxylum caatingae Plowman	x	.	x	.	.	.	.	.	.	.	.	x	x
Erythroxylum nummularia Peyr.	.	.	.	.	.	.	.	.	x	.	.	.	.
Erythroxylum revolutum Mart.	x	x	.	.	.	.	.	.	.	.	.	.	.
Eugenia dysenterica DC.	.	.	.	.	x	x	.	.	x	.	.	.	.
Eugenia florida DC.	.	.	.	x	.	.	x	.	.	.	.	.	.
Eugenia ligustrina (Sw.) Willd.	.	.	.	.	.	.	x	.	.	.	.	.	.
Eugenia uniflora L.	x	x	.	.	.	.	x	.	.	.	.	.	x
Fridericia bahiensis (Schauer ex. DC.) L.G.Lohmann	.	.	x	.	.	.	.	.	.	.	.	.	.
Galipea ciliata Taub.	.	.	.	.	.	.	.	.	.	.	.	.	x
Genipa americana L.	x	.	.	x	.	.	x	x	.	.	.	.	.
Geoffroea spinosa Jacq.	x	.	.	.	.	.	.	.	.	x	.	.	.
Goniorrhachis marginata Taub.	.	.	x	.	.	.	.	.	x	.	.	x	x
Guapira tomentosa (Casar.) Lundell	.	.	.	.	.	.	.	.	.	.	.	.	x
Guazuma ulmifolia Lam.	.	.	.	x	x	.	x	.	.	.	.	.	.
Handroanthus heptaphyllus (Martius) Mattos	.	.	x	.	.	.	.	.	.	.	.	.	x
Handroanthus impetiginosus (Mart. ex DC.) Mattos	.	.	.	.	.	x	.	.	x	.	x	.	.
Handroanthus ochraceus (Cham.) Mattos	.	.	x	.	x	x	.	.	x	.	.	.	x
Handroanthus spongiosus (Rizzini) S.O.Grose	.	.	.	.	.	.	.	.	.	.	.	.	x
Heteropterys byrsonimifolia A.Juss.	.	.	.	.	.	x	x	.	x	.	.	.	.
Himatanthus obovatus (Müll.Arg.) Woodson	.	.	.	.	x	.	.	.	.	.	.	.	.
Hirtella gracilipes (Hook.f.) Prance	.	.	.	.	.	.	.	.	x	.	.	.	.
Hymenaea courbaril L.	x	.	.	.	.	.	.	.	.	.	.	.	.
Hymenaea martiana Hayne	x	x	.	x	x	x	.	.	x	.	.	.	.

Species												
Hymenaea stigonocarpa Mart. ex Hayne	.	.	.	.	.	x	.	.	.	.	.	.
Inga laurina (Sw.) Willd.	x	.	.	.	.	.	.	.	.	.	.	.
Inga vera Willd.	x	.	.	x	.	.	x	.	.	.	.	.
Jacaranda brasiliana (Lam.) Pers.	.	x	.	.	.	x	.	.	.	.	.	.
Jatropha mollissima (Pohl) Baill.	x	.	x	.	.	.	.	.	.	.	.	.
Jatropha palmatifolia Ule	.	.	.	.	.	.	.	.	.	.	x	x
Lafoensia pacari A.St.-Hil.	.	.	.	.	.	x	.	.	.	.	.	.
Libidibia ferrea (Mart. ex Tul.) L.P.Queiroz	x	x	x	.	.	.	.	.	.	.	.	x
Licania rigida Benth.	x	.	.	.	.	.	.	.	.	.	.	.
Lonchocarpus campestres Mart. ex Benth.	.	.	.	.	.	.	.	.	.	.	x	.
Lonchocarpus montanus A.M.G.Azevedo ex M.J.Silva & A.M.G.Azevedo	.	.	x	.	.	.	.	.	.	.	.	.
Luehea paniculata Mart. & Zucc.	.	.	.	.	x	x	.	x	.	.	.	.
Luetzelburgia bahiensis Yakovlev	.	.	.	.	.	.	.	.	x	.	.	.
Machaerium acutifolium Vogel	.	x	x	.	.	.	x	.	x	.	.	x
Machaerium floridum (Mart. ex Benth.) Ducke	x	.	.	.	x	.	.	.	.	.	.	.
Machaerium opacum Vogel	.	.	.	.	.	x	.	.	x	.	.	.
Machaerium punctatum (Poir.) Pers.	.	.	x	.	.	.	.	.	.	.	.	.
Machaerium scleroxylon Tul.	x	x	.	.	x	.	.	.	x	.	x	x
Machaerium villosum Vogel	.	.	.	.	x	x	.	.	.	.	.	.
Machaonia brasiliensis (Hoffmanss. ex Humb.) Cham. & Schltdl.	x	.	x	.	.	.	.	.	.	.	.	.
Maclura tinctoria (L.) D.Don ex Steud.	x	.	.	.	x	.	x	.	.	.	.	.
Magonia pubescens A.St.-Hil.	.	.	.	.	x	x	.	.	x	.	.	.
Manihot caerulescens Pohl	.	.	.	.	.	.	.	.	.	.	.	x

Species												
Manihot tripartita (Spreng.) Müll. Arg.	.	x	.	.	.	.	.	.	.	.	.	.
Manilkara salzmannii (A.DC.) H.J.Lam.	x	.	.	.	.	.	x	.	.	x	.	.
Margaritaria nobilis L.f.	.	.	.	.	.	.	x	.	.	x	.	.
Maytenus rigida Mart.	x	.	.	.	.	.	.	.	.	x	.	.
Maytenus robusta Reissek	.	.	.	.	x	x	.	.	.	.	.	.
Maytenus robustoides Loes.	.	.	.	.	.	.	x	.	.	.	.	.
Mimosa arenosa (Willd.) Poir.	x	.	.	.	.	.	.	.	.	x	x	.
Mimosa tenuiflora (Willd.) Poir.	x	.	x	.	.	.	.	.	.	.	x	x
Mouriri pusa Gardner	x	.	.	.	.	.	x	.	.	.	.	.
Myracrodruon urundeuva Allemão	x	x	x	.	x	x	x	.	x	.	.	x
Myrcia hebepetala DC.	.	.	.	.	.	.	x	.	.	.	.	.
Myrcia splendens (Sw.) DC.	.	.	.	x	.	.	.	.	.	.	.	.
Myrcia tomentosa (Aubl.) DC.	.	.	.	.	x	.	.	.	.	.	.	.
Myrciaria tenella (DC.) O.Berg	x	.	.	.	.	.	.	.	.	.	.	.
Nectandra megapotamica (Spreng.) Mez	.	.	.	.	.	.	x	.	.	.	.	.
Ouratea castaneifolia (DC.) Engl.	.	.	.	.	.	.	.	.	x	.	.	.
Parapiptadenia rigida (Benth.) Brenan	.	.	.	.	x	x	.	.	.	.	.	.
Peltophorum dubium (Spreng.) Taub.	.	x	.	x	.	.	x	.	.	.	x	.
Phyllanthus chacoensis Morong	x	x	.	.	.	.	.	.	.	x	.	.
Pilosocereus gounellei (F.A.C.Weber) Byles & G.D.Rowley	.	x	.	.	.	.	.	.	.	.	.	.
Pilosocereus pachycladus F.Ritter	.	.	x	.	.	.	.	.	.	.	.	.
Piper aduncum L.	.	.	.	.	.	.	x	.	.	.	.	.
Piper arboreum Aubl.	.	.	.	x	.	.	.	.	.	.	.	.

Species	1	2	3	4	5	6	7	8	9	10	11	12
Piptadenia stipulacea (Benth.) Ducke	.	.	.	.	.	.	.	.	.	x	.	.
Piptadenia viridiflora (Kunth) Benth.	.	x	x	.	.	.	.	.	.	x	x	x
Pisonia tomentosa Casar.	.	x	.	.	.	.	.	.	.	.	.	.
Pithecellobium diversifolium Benth.	x	.	x	.	.	.	.	.	.	.	.	.
Plathymenia reticulata Benth.	.	.	.	.	.	x	.	.	.	.	.	x
Platymiscium floribundum Vogel	.	.	x	.	.	.	.	.	x	.	x	x
Platypodium elegans Vogel	.	.	.	.	x	.	x	.	.	.	.	.
Poeppigia procera C.Presl.	.	.	.	x	.	.	.	.	.	.	.	.
Poincianella pluviosa (DC.) L.P.Queiroz	.	x	x	.	.	.	.	.	.	.	.	x
Pouteria gardneri (Mart. & Miq.) Baehni	x	.	.	.	x	x	.	.	.	.	.	.
Prockia crucis P.Browne ex L.	.	x	x	.	.	.	.	.	.	.	.	.
Prosopis ruscifolia Griseb.	x	.	.	.	.	.	.	.	.	x	.	.
Protium ovatum Engl.	.	.	.	x	x	x	.	.	.	.	.	.
Pseudobombax grandiflorum (Cav.) A.Robyns	.	.	.	.	.	x	.	.	.	.	.	.
Psidium acutangulum DC.	x	.	.	.	.	.	.	.	.	.	.	.
Psidium firmum O. Berg	.	.	.	x	.	.	.	.	.	.	.	.
Psidium guajava L.	.	.	.	x	.	.	.	.	.	.	.	.
Psidium salutare (Kunth) O.Berg	.	.	.	x	x	x	.	.	.	.	x	x
Pterocarpus zehntneri Harms	.	.	x	.	.	.	.	.	.	.	x	x
Pterodon emarginatus Vogel	.	.	.	.	.	x	.	.	x	.	.	.
Ptilochaeta bahiensis Turcz.	.	.	x	.	.	.	.	.	.	.	.	x
Qualea grandiflora Mart.	.	.	.	.	.	x	.	.	x	.	.	.
Qualea multiflora Mart.	.	.	.	.	.	.	.	x	x	.	.	.

Species	1	2	3	4	5	6	7	8	9	10	11	12
Qualea parviflora Mart.	.	.	.	.	.	.	.	x	.	.	.	.
Randia armata (Sw.) DC.	x	x	x	.	.	.	x	.	.	.	x	x
Roupala montana Aubl.	.	.	.	.	x	.	.	.	.	.	.	.
Ruprechtia apetala Weddell	x	.	.	x	.	.	x	.	.	.	x	x
Ruprechtia laxiflora Meisn.	x	x	.	.	.	.	.	.	.	.	.	.
Salacia crassifolia (Mart. ex Schult.) G.Don	x	.	.	.	.	.	.	.	.	.	.	.
Salacia elliptica (Mart. ex Schult.) G.Don	.	.	.	x	.	.	.	.	.	.	.	.
Sapium laurifolium (A. Rich.) Griseb.	.	.	.	.	.	.	.	x	.	.	.	.
Schinopsis brasiliensis Engl.	.	x	x	.	.	.	x	.	.	x	x	.
Schoepfia brasiliensis A.DC.	.	.	.	.	x	x	.	.	.	.	.	.
Seguieria americana L.	x	.	.	.	.	.	.	.	.	.	.	.
Senegalia langsdorffii (Benth.) Seigler & Ebinger	x	.	.	.	.	.	.	.	.	x	.	.
Senegalia martii (Benth.) Seigler & Ebinger	.	.	.	.	.	x	.	.	.	x	.	.
Senegalia polyphylla (DC.) Britton & Rose	x	x	x	.	x	.	x	.	x	.	.	.
Senna macranthera (DC. ex Collad.) H.S.Irwin & Barneby	x	.	.	.	.	.	.	.	.	.	.	.
Senna spectabilis (DC.) H.S.Irwin & Barneby	.	x	.	.	.	.	x	.	x	.	.	x
Sideroxylon obtusifolium (Roem. & Schult.) T.D.Penn.	x	x	x	.	.	.	.	.	.	.	x	.
Simarouba versicolor A.St.-Hil.	.	.	.	.	x	x	.	.	x	.	.	.
Simira sampaioana (Standl.) Steyerm.	.	.	.	.	.	.	.	.	x	x	x	x
Spondias tuberosa Arruda	.	x	.	.	.	.	.	.	.	.	.	x
Sterculia excelsa Mart.	.	x	.	.	.	.	.	.	.	.	.	.
Stillingia saxatilis Müll.Arg.	.	x	.	.	.	.	.	.	.	.	.	x
Swartzia flaemingii Vogel	.	.	.	.	.	.	.	.	x	.	.	.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Swartzia macrostachya Benth.	.	.	.	.	x	x	.	.	.	.	.	.	.
Sweetia fruticosa Spreng.	.	.	.	.	.	.	.	.	.	.	.	.	x
Tabebuia aurea (Manso) Benth. & Hook.f. ex S.Moore	.	.	.	.	.	.	.	x	.	.	.	.	.
Tabebuia reticulata A.H.Gentry	.	.	.	.	x	x	.	.	.	.	.	.	x
Tachigali paniculata Aubl.	.	.	.	.	x	x	.	.	x	.	.	.	.
Talisia esculenta (A.St.-Hil.) Radlk.	.	.	.	x	x	.	.	.	.	x	.	.	.
Terminalia argentea (Cambess.) Mart.	.	.	.	.	x	x	.	.	.	.	.	.	.
Terminalia phaeocarpa Eichler	.	.	.	.	x	.	.	.	.	.	.	.	.
Tocoyena bullata (Vell.) Mart.	x	.	.	.	.	.	.	.	.	x	.	.	.
Tocoyena formosa (Cham. & Schltdl.) K.Schum.	.	.	.	.	x	x	x	x	x	.	.	.	.
Trichilia casaretti C.DC.	.	.	.	.	.	.	.	.	.	.	.	.	x
Trichilia hirta L.	x	x	x	.	.	.	x	.	.	.	x	.	x
Trichilia pallens C.DC.	.	.	.	x	.	.	.	.	.	.	.	.	.
Triplaris gardneriana Weddell	x	x	.	x	.	.	x	.	.	x	x	.	.
Vachellia farnesiana (L.) Wight & Arn.	x	.	.	.	.	.	x	.	.	.	.	.	.
Vatairea macrocarpa (Benth.) Ducke	.	.	.	.	.	.	.	.	x	.	.	.	.
Warszewiczia coccinea (Vahl.) Klotzsch	.	.	.	.	.	.	.	.	.	.	.	x	.
Ximenia americana L.	.	x	x	.	.	.	.	.	.	.	.	x	x
Xylosma ciliatifolia (Clos) Eichler	x	.	.	.	.	.	x	.	.	.	.	.	.
Zanthoxylum monogynum A.St.-Hil.	x	.	x	.	.	.	.	.	.	.	.	.	.
Zanthoxylum riedelianum Engl.	.	.	.	x	.	.	.	.	.	.	.	.	.
Zanthoxylum stelligerum Turcz.	x	x	.	.	.	.	.	.	.	.	.	.	.
Ziziphus cotinifolia Reissek	x	x	x	.	.	.	.	.	.	.	.	x	.

Ziziphus joazeiro Mart.	x	.	.	.	.	.	.	.	.	.	.	x
Zygia latifolia (L.) Fawc. & Rendle	x	.	.	x	.	.	.	.	.	.	.	.

SEGUNDA PARTE – ARTIGO 2

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Riverine forests house the greatest evolutionary diversity in tropical dry biomes

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[1]**DECLARATION OF AUTORSHIP**

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[1] **AUTHORS' CONTRIBUTIONS**

FDCA and RMS conceived and designed the experiments. FDCA and RMS performed the experiments. FDCA, DMN analyzed the data. FDCA, DMN, RMS wrote the manuscript.

ABSTRACT

The amount of evolutionary diversity in plant communities is positively associated with key aspects of ecosystem function, such as primary productivity. Yet we have little understanding of how evolutionary diversity is distributed across environmental gradient, especially in tropical forests. Here we assessed patterns of evolutionary diversity across a flooding gradient in the Caatinga Domain of South America, the largest continuous extent of the dry forest biome. We established 120 plots across four tributaries of the São Francisco River, eastern Brazil, being 72 plots in flooded forests, 24 in occasionally flooded forests and 24 in unflooded forests. We computed species diversity and metrics of phylogenetic diversity (PD, MNTD and MPD), with their equivalents standardized for species richness. Flooding frequency leads to different patterns of phylogenetic diversity and, contrary to expectations, higher evolutionary diversity was found in areas with higher flooding frequency. Quantifying evolutionary diversity across flooding gradients in seasonally dry environments brought new insights on how the same environmental filters may lead to disparate patterns of evolutionary diversity in distinct

biomes. We further argue that designing protected areas based on just species richness or raw phylogenetic diversity will miss evolutionarily important areas, such as the neglected and highly degraded riverine forests of the Caatinga Domain.

Keywords: Phylogenetic diversity, stress gradients, Caatinga, flooding, dry forests.

INTRODUCTION

Environmental gradients act as filters on the distribution of biodiversity across multiple spatial scales (Carvajal-Endara et al., 2017). In seasonally flooded environments, gradients associated to the frequency and intensity of flooding are known to shape the structure and dynamics of seasonally flooded plant communities, its floristic composition, edaphic conditions, plant species richness, and functional diversity in the Amazon (Wittmann et al., 2010; Wittmann et al., 2013), southern Brazil (Budke et al., 2007, 2008 and 2010), Central Brazil (Moreira et al., 2015), Central Australia (Capon et al., 2005), China (Luo et al., 2016) and Europe (Kotowski et al., 2010; Violle et al., 2010; Moor et al., 2015). A

prediction of the stress gradient hypothesis for seasonally flooded environments is that increased flooding decreases taxonomic diversity (Budke et al., 2008), selecting for a subset of species that comprise the traits necessary to thrive under higher flooding-stress (Giehl and Jarenkow, 2015). More recently, studies have shown that stress gradients also affect another dimension of biodiversity: the evolutionary. The influence of stress gradients on overall patterns of evolutionary diversity is documented in seasonally dry tropical forests (drought-stress; Pennington et al., 2009), savannas in Central Brazil and white-sand forests in the Amazon (edaphic-related stress, Guevara et al., 2016; Meira-Neto et al., 2017), zooplankton metacommunities (anthropogenic disturbances; Gianuca et al., 2017), sponges (light availability gradients; Quattrini et al., 2017) and in seasonally flooded forests (water saturation stress; Giehl and Jarenkow, 2015; Aldana et al., 2016).

In South America, studies that addressed patterns of evolutionary diversity in flooded forests took place in subtropical and tropical moist forests (Giehl and Jarenkow, 2015; Aldana et al., 2016; respectively), and showed contrasting results. For example, Aldana et al. (2016) found more closely related lineages in seasonally flooded areas relative to unflooded

(*terra firme*) forests in the Amazon, supporting the idea of flooding acting as a strong environmental filter in eudicot lineages. Giehl and Jarenkow (2015), however, found higher evolutionary diversity (richness) under higher levels of water saturation, attributing such patterns to the phylogenetic overdispersion (convergence) of traits that are associated with flooding tolerance. While both studies showed a robust, yet controversial relationship between flooding and evolutionary diversity in South American moist biomes, no study to date has assessed the importance of flooding as environmental filtering in seasonally dry biomes. While a wide net of large rivers and alluvial beds represent a major component of the landscape in moist biomes, and are often considered the main drivers of variation in biodiversity patterns in these biomes, such as in the Amazon (Wittmann et al., 2013), they account for only a tiny proportion of the landscape in seasonally dry biomes, and might, therefore, have distinct importance in controlling overall patterns of variation in biodiversity.

Because the amount of evolutionary diversity in plant communities is known to be tightly associated to key aspects of ecosystems services - evolutionarily diverse communities supply greater

ecosystem service (e.g., carbon cycling per unit area; Cadotte et al., 2008; Cadotte et al., 2009) - it is imperative to improve our understanding of how evolutionary diversity is distributed across geographical and environmental space. Therefore, here we aim to assess the influence of flooding gradients on evolutionary diversity across the South American Caatinga Domain, the largest continuous extent of the tropical dry forest biome (henceforth TDF) (Fernandes, 2003; Santos et al., 2012). While dry forests and woodlands, the predominant vegetation type in the Caatinga Domain and in TDFs as a whole, have natural constraints related to water shortage, seasonally flooded forests in TDFs are also potentially affected by soil waterlogging. Thus, we have a natural scenario for testing hypothesis associate with stress gradients as environmental filters shaping patterns of evolutionary diversity. Here we hypothesize that flooding frequency imposes a strong environmental filter, thus leading to significantly distinct patterns of evolutionary diversity across the flooding gradient. More specifically, we hypothesize that traits associated with seasonally flooded environments are phylogenetically conserved, and thus environments with harsher conditions (higher soil water saturation) impose a selective pressure that can decrease evolutionary diversity. We

further test whether resprouting, a trait usually associated with flooding frequency, is phylogenetically conserved.

METHODS

Study area and sampling

Sampling units in this study are tree communities across flooding gradients in four tributaries of the São Francisco River basin, eastern Brazil (Fig. 1). In each area we established 30 plots of 20 x 20 m (400 m^2), totaling 120 plots and 4.8 ha. In some cases, plots were 10 x 40 m (400 m^2) due to narrower vegetation bands. The plots were then classified into three vegetation types, according to their distance to the river channel, being 72 plots in the floodable environments, 24 plots in occasionally flooded and 24 plots in environments without flooding. All the tree individuals with diameter at breast height (DBH) $\geq$ 3.2 cm were sampled and identified at the species level. The tree species were identified during sampling at species level.

Phylogenetic diversity metrics

A phylogenetic tree of the whole species pool was generated using Phylomatic in Phylocom version 4.2 (Webb et al., 2008). This tool provides a phylogenetic hypothesis for the relationships among taxa by matching the list of species, with up-to-date family and genus names, and tip labels of a provided megatree (Webb and Donoghue, 2005). In this case, the topology of R20120829.new provided at http://phylodiversity.net/phylomatic/ was used. An ultrametric phylogeny including branch length in millions of years (Ma) was obtained using the branch length adjustment (bladj) in Phylocom. This function fixes the root node (angiosperms, 179 Ma) and other nodes to specified ages based on Wikstrom et al. (2001). We then used the Phylocom phylogeny, which includes all genera in our dataset, to calculate six metrics that evaluate the evolutionary history present in communities: (1) the total phylogenetic branch length of all species occurring in a given community, i.e. phylogenetic diversity *sensu stricto* (PD; Faith, 1992); (2) mean pairwise phylogenetic distance between species in terms of branch length (MPD; Webb, 2000; Webb et al., 2002); (3) mean nearest taxon distance (MNTD; Webb, 2000; Webb et al., 2002); and (4, 5 and 6) their equivalents standardized for species richness (ses.PD, ses.MPD, and

ses.MNTD). For each community, these standardizations were accomplished by randomly drawing the same number of species from the phylogeny as present in the community, repeating this 1000 times, calculating PD, MPD and MNTD for each randomization, taking the difference between the observed value of PD, MPD, and MNTD and the mean of the random values, and dividing these differences by the standard deviation across the randomizations. These derived metrics therefore represent standardized effect sizes (ses). Because these metrics are standardized (with an expected value of 0 and an SD of 1), values < 1.96 or >1.96 represent communities that show lower or higher phylogenetic diversity than would be expected by chance, respectively (Kembel et al., 2010), while values between this range indicate that phylogenetic diversity is no different than random expectation; i.e., communities are assembled from random draws of the phylogeny (Kembel et al., 2010)

We consider the total phylogenetic branch length (PD) in communities (Faith, 1992; Forest et al., 2007) and its deviation from expectation given species richness (ses.PD) to be the most straightforward measures of evolutionary diversity in communities with respect to conservation prioritization, but included the MPD, MNTD, ses.MPD, and

ses.MNTD results because of their history of use in the literature (e.g. Forest et al., 2007; Gonzalez et al., 2010; Fine and Kembel, 2011, Honorio Coronado et al., 2015). Because flooded environments have more sampling units, which could potentially hamper analyses and interpretation, we applied the same analysis using an even number of sampling units per flooding category, and found the same results (Online Resource 1). We computed the phylogenetic diversity analyses using the picante package (Kembel et al., 2010) in R.

Data analysis

We tested whether different flooding frequencies lead to significantly distinct amounts of phylogenetic diversity by applying Kruskal Wallis tests to non-normally distributed residuals, followed by *post-hoc* Dunn tests with Bonferroni correction (Dinno, 2017). We tested whether using an unresolved phylogeny affects the overall results found for phylogenetic diversity by generating one thousand randomly resolved phylogenies, using the ape package (Paradis *et al.*, 2004) in R. We then calculated ses.PD values using all fully resolved phylogenies and correlated the mean values with the ses.PD values found for the

unresolved phylogeny. We also used the fully resolved phylogenies to estimate phylogenetic signal in resprouting ability, a trait associated with flooding tolerance, by using Blomberg's *K* (Blomberg *et al.*, 2003), which quantify the amount of variance in an observed trait in relation to the expected variance under a Brownian motion model of evolution. We assessed the significance of the phylogenetic signal results by recalculating *K* a thousand times on phylogenies with randomly permuted tips. Finally, we mapped relative abundance in seasonally flooded sites on to the unresolved phylogeny by interpolating states at internal branches through a maximum likelihood ancestral state reconstruction (Schluter *et al.*, 1997). We then tested whether the relative abundance of lineages found in seasonally flooded sites is associated with resprouting ability by using a phylogenetic generalised least squares approach available in the nlme package (Pinheiro *et al.*, 2017) in R. We conducted the trait mapping and phylogenetic signal analyses using the phytools package (Revell, 2012) in R.

RESULTS

Taxonomic and Phylogenetic Diversity

Unflooded forests have the highest species richness, followed by flooded and occasionally flooded forests (Kruskal-Wallis $X^2_{38.77}$, $P <$ 0.001). The highest phylogenetic diversity (PD), the sum of phylogenetic branch lengths in a community, was also found in unflooded and occasionally flooded forests (Kruskal-Wallis $X^2_{31.75}$, $P <$ 0.001), mirroring overall patterns of species richness (Online Resource 2, Fig 2). Mean nearest taxon distance (MNTD), the mean phylogenetic distance in myrs of each taxon to its closest relative, was higher in flooded forest (Kruskal-Wallis $X^2_{25.47}$, $P <$ 0.001). Mean pairwise distance (MPD), the mean pairwise distance between communities in terms of branch length, was not different amongst the three groups (Fig 2).

Lineage Diversity and resprouting ability

The highest lineage diversity (i.e., PD standardised for species richness; ses.PD), was found in flooded and occasionally flooded forests (sesPD; F_{9279}, $P <$ 0.001) (Fig.3a). These results are robust to accounting for phylogenetic uncertainty; the correlation between average ses.PD (from randomly generating one thousand fully bifurcating trees) and ses.PD of the original tree, indicates that the lack of phylogenetic

resolution in the phylogenetic tree does not affect the overall results (Online Resource 3). Flooded forests have the highest amounts of both neighbour lineage diversity (MNTD standardised for species richness; ses.MNTD), (Kruskal-Wallis $X^2_{17.20}$, $P < 0.001$; Fig. 3b) and clade lineage diversity (MPD standardised for species richness; ses.MPD, Fig. 3c). Over 7% of the species in flooded forests belong to basal angiosperm lineages (magnoliids), with much lower proportions in occasionally (1,83%) and unflooded forests (2,32%). The PGLS showed higher lineage abundance in seasonally flooded environments for lineages with resprouting ability (Fig. 4; Delta AIC = -14.6171), but there is no phylogenetic signature for resprouting ability. This result is robust to calculate phylogenetic signal after randomly generating one thousand fully bifurcating trees (Online Resource 4).

DISCUSSION

Flooding gradients in seasonally dry environments do influence the distribution of evolutionary diversity, but contrary to the most intuitive expectation: higher amounts of evolutionary diversity are found under higher levels of seasonal flooding. Higher flooding frequency

promoted greater evolutionary diversity compared to unflooded or occasionally flooded areas, and this is likely related to both (i) phylogenetic niche conservatism for more mesic environments, and (ii) the importance of resprouting ability, an ecological relevant trait that is randomly distributed across the phylogeny used in this study.

On the one hand, there is compelling evidence in the literature supporting Phylogenetic Niche Conservatism for warm environments: only a small subset of lineages was able to colonize frost-affected environments over evolutionary time (Latham and Ricklefs, 1994; Jablonski and Valentine, 2006; Wiens and Donoghue, 2004; Wiens et al., 2010; Zanne et al., 2014; Kerkhoff et al., 2014; Augusto et al., 2014). On the other hand, patterns of Phylogenetic Niche Conservatism for mesic, moist environments are still unclear and poorly explored (Qian et al., 2017; Qian and Sandel, 2017), and our results bring further support to the idea that seasonally dry environments are mainly assembled from a subset of plant lineages that can tolerate marked drought. While tree communities in seasonally flooded forests are found under the same precipitation conditions as unflooded, dry forests (six months with less than 100mm of total rainfall), a higher level of soil moisture during the

dry season, due to proximity to the river channel, seems to provide a suitable environment for most plant lineages in the phylogeny, thus leading to the observed patterns of higher lineage diversity. This phylogenetic impoverishment in unflooded, dry forests is even more evident in basal lineages (magnoliids), which are known to conserve mesic habitat preferences (c.f., results; Honorio Coronado, 2015; Carlucci et al. 2016).

Another factor that is potentially driving the (unexpected) patterns of higher evolutionary diversity in seasonally flooded forests is associated with our results showing that resprouting, a trait associated with high flooding frequency, is not phylogenetically structured, but randomly distributed across the phylogeny. This contrasts the phylogenetic overdispersion (convergence) for resprouting ability in tree communities found across flooding gradients in the Atlantic Forest Domain (Giehl and Jarenkow, 2015), and suggest that the mechanisms driving the patterns of community assembly are overall distinct in seasonally dry environments. In our study, because flooding is filtering for plant lineages that have the ability to resprout after flooding disturbance, and resprouting is not a phylogenetically conserved trait, plant communities in seasonally flooded

environments are likely assembled from random draws of the resprouting lineage pool, leading to patterns of evolutionary diversity that are not different than random expectation (see Fig. 2 and Methods), but overall higher than in unflooded, dry forests, which are assembled from an impoverished lineage pool that can tolerate harshness associated with water shortage.

Quantifying evolutionary diversity across flooding gradients in seasonally dry environments brought new insights on how the same environmental filters may lead to disparate patterns of evolutionary diversity in distinct biomes, namely moist and seasonally dry biomes. Furthermore, if conservation strategies are to prioritise the protection of lineages, our study show that riverine forests in seasonally dry environments host more lineages per unit area relative to unflooded forests. On the one hand, the total phylogenetic diversity (i.e., sum of phylogenetic branch lengths) in communities is highly correlated with species richness, so designating species-rich protected areas will protect phylogenetically diverse communities, such as the unflooded, dry forests from our studied areas. Here we have shown, however, that many communities have higher phylogenetic diversity than expected based on

species richness alone, meaning that designing protected areas based on just species richness or raw phylogenetic diversity will miss evolutionarily important areas, such as the often neglected and highly degraded riverine forests of the Caatinga Domain.

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Caption

Fig 1 – A - Distribution of the sampling areas across the São Francisco River basin, Minas Gerais and Bahia states, Brazil. C – Carinhanha river; V – Verde Grande river; P – Paracatu river; J – Jequitaí river. **B –** Vegetation types found across the flooding gradients; classified according to the flooding frequency (see Methods). Dashed lines show water level during the flooding season (Adapted from Pereira, 2013).

Fig 2 - Distribution of species richness and phylogenetic diversity values (PD, MNTD and MPD) in tree communities found across flooding gradients of the São Francisco River basin, eastern Brazil. Same letters in two or more groups (flooding frequencies) indicate that means are no different than random expectation (i.e., $P > 0.05$ in Kruskall-Wallis and *post-hoc* Dunn test with *Bonferroni* correction).

Fig 3 - Distribution of phylogenetic diversity values standardised for species richness (ses.PD, ses.MNTD and ses.MPD) in tree communities found across flooding gradients in the São Francisco River basin, eastern Brazil. Same letters in two or more groups (flooding frequencies) indicate that means are no different than random expectation (i.e., *P* > 0.05 in Kruskall-Wallis and *post-hoc* Dunn test with *Bonferroni* correction).

Fig 4 - Time-calibrated phylogeny of angiosperm species in tree communities found across flooding gradients of the São Francisco River basin, eastern Brazil. Colours represent the relative abundance of lineages found in seasonally flooded sites (AF), and warmer colours indicate higher values. The figure illustrates the phylogenetic overdispersion of lineages that are abundant in seasonally flooded sites. Bars represent a resprouting index and larger bars indicate higher resprouting ability. Scale (length) is in myrs and is equivalent to branch lengths in the phylogeny (50 myrs).
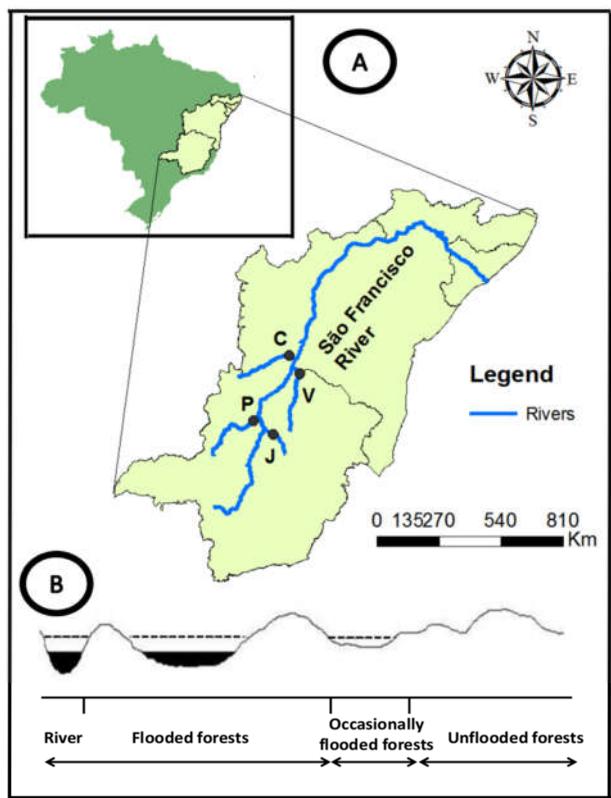
Figure 1
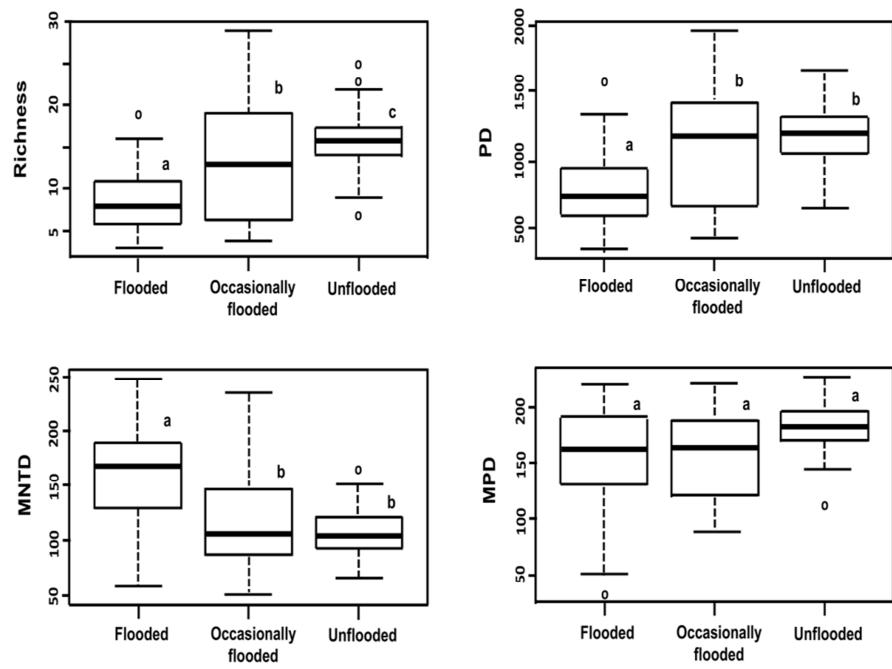
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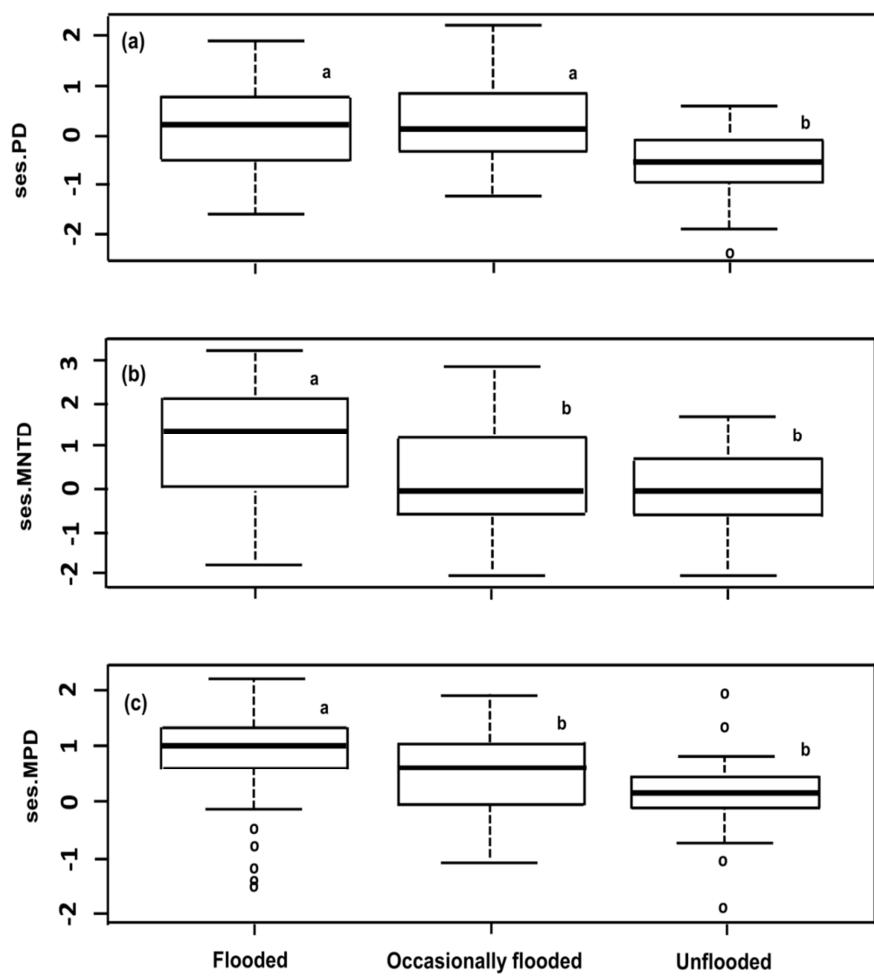
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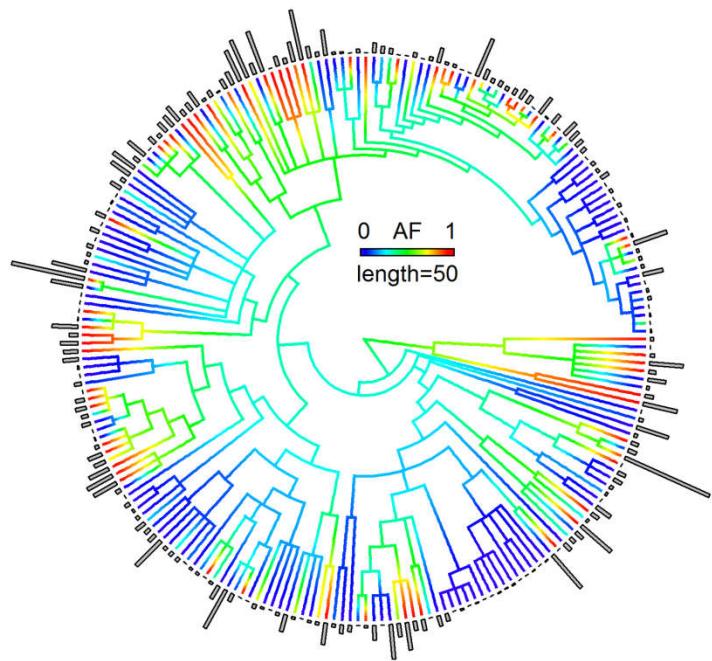
**Figure 4**

Riverine forests house the greatest evolutionary diversity in tropical dry biomes

Felipe de Carvalho Araújo [1]*, Danilo M. Neves[2], Rubens Manoel dos Santos[3]

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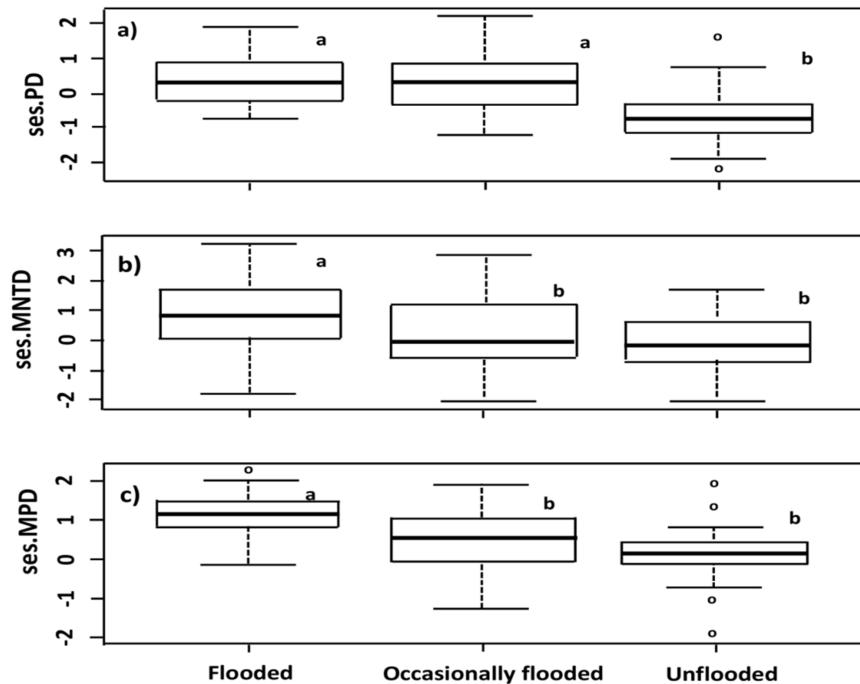
Online Resource 1 - Distribution of phylogenetic diversity values standardised for species richness (ses.PD, ses.MNTD and ses.MPD) in tree communities found across flooding gradients in the São Francisco River basin, eastern Brazil. This is equivalent to the analyses in Figure 3, but with identical number of sampling units for all groups of flooding frequency. Same letters in two or more groups (flooding frequencies) indicate that means are no different than random expectation (i.e., $P > 0.05$ in Kruskall-Wallis and *post-hoc* Dunn test with *Bonferroni* correction).

Online Resource 2 – Pearson correlations between richness (R), phylogenetic diversity (PD), mean nearest taxon distance (MNTD), MPD metrics and their equivalents standardised for species richness (ses). ($P < 0.05$ in all cases).

	R	PD	MNTD	MPD	ses.PD	ses.MNTD	ses.MPD
R	*	0.96	-0.61	0.5	-0.31	-0.32	-0.32
PD		*	-0.5	0.58	-0.05	-0.16	-0.16
MNTD			*	-0.3	0.59	0.89	0.74
MPD				*	0.11	0.25	0.36
sesPD					*	0.62	0.61
sesMNTD						*	0.8
sesMPD							*
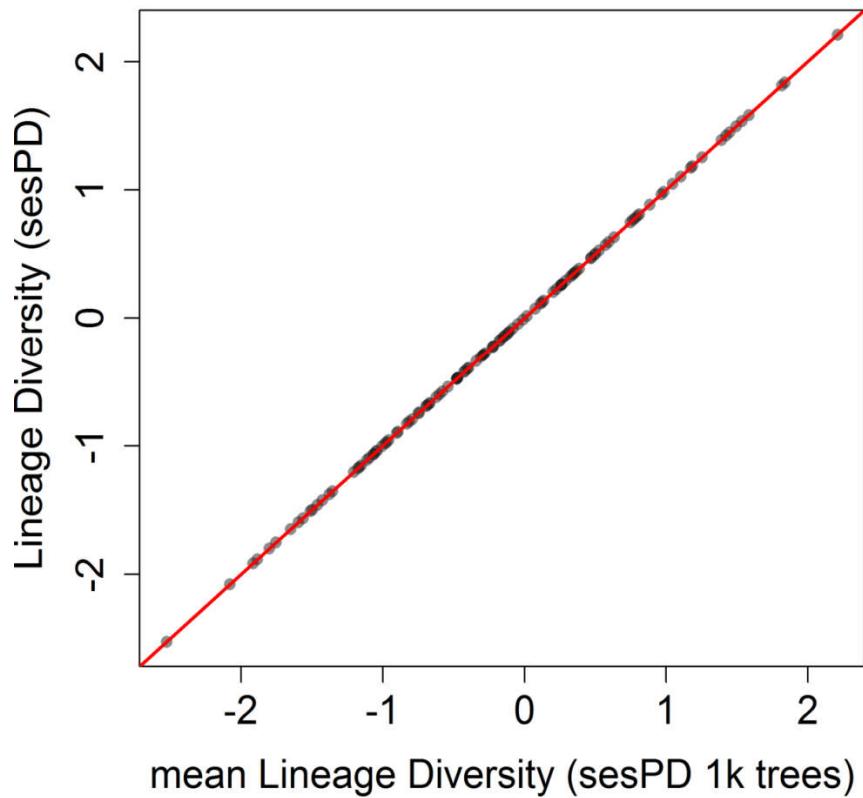
Online Resource 3 - Relationship between standardized effect size of lineage diversity (sesPD) using the unresolved phylogeny and mean values across one thousand fully resolved phylogenies (see Methods). The red line represents the identity line.

K = 0.21
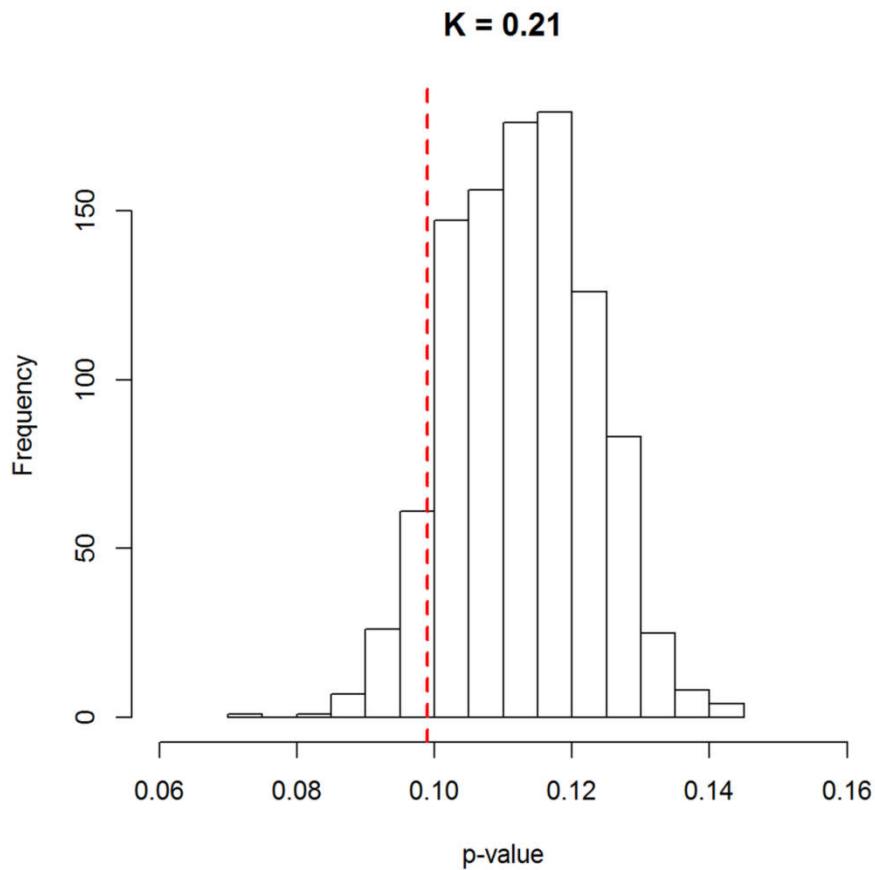
Online Resource 4 - Phylogenetic signal in resprouting ability for angiosperm lineages in tree communities found across flooding gradients of the São Francisco River basin, eastern Brazil. Phylogenetic signal was calculated for the unresolved phylogeny and for all the fully resolved phylogenies (one thousand; see Methods). Red dashed line represents the p-value in phylogenetic signal found for the unresolved phylogeny. The phylogenetic

randomness in resprouting ability is supported by its low phylogenetic signal ($K = 0.21$; $P > 0.05$ in all cases); i.e., the level of resprouting ability amongst close relatives is randomly distributed across the phylogeny used in this study.