NATHALLE CRISTINE ALENCAR FAGUNDES

MORPHOANATOMICAL, FUNCTIONAL AND EVOLUTIONARY TRAITS CONDITIONING THE ADAPTABILITY OF LEGUMINOSAE IN AN EDAPHOCLIMATIC GRADIENT

LAVRAS – MG
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Prof. Dr. Rubens Manoel dos Santos

Orientador

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NATHALLE CRISTINE ALENCAR FAGUNDES

CARACTERÍSTICAS MORFOANATÔMICAS FUNCIONAIS E EVOLUTIVAS CONDICIONANDO A ADAPTABILIDADE DE LEGUMINOSAE EM UM GRADIENTE EDÁFO-CLIMÁTICO

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APROVADA em 29/03/2019

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LAVRAS – MG

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"Se fizermos abstração das florestas virgens, encontraremos em diversos tipos de vegetação, em particular na província das Minas, uma espécie de escala (...). As caatingas crescem nas partes mais baixas (...) e deve existir uma grande quantidade de exceções determinadas pela exposição, pela maior ou menor umidade, e, sobretudo pela natureza do solo"

Auguste de Saint-Hilaire

RESUMO

A tese teve como objetivo avaliar a relação entre a diversidade filogenética, as características funcionais e o sucesso adaptativo de Leguminosae, representado pelas variáveis estruturais e dinâmicas dessa família em um gradiente edafoclimático na direção norte / sul do estado de Minas Gerais. O gradiente compreendeu formações de floresta decidual, no norte de Minas, floresta semidecidual no Campo das Vertentes, e floresta ombrófila nebular, no sul de Minas Gerais. Para tal, utilizamos dois inventários de dinâmica florestal (15 anos e três mensurações), dados de estrutura das leguminosas nas parcelas amostradas, variáveis químicas e texturais de solo, as dezenove variáveis bioclimáticas segundo o WorldClim, a diversidade beta-filogenética e características funcionais relativas à hidráulica das leguminosas, coletadas nas espécies presentes nas parcelas. Foram construídos modelos lineares generalizados mistos com todas as variáveis supracitadas no primeiro capítulo, e com características funcionais hidráulicas da madeira, solos e utilizando apenas as formações de Floresta Tropical Sazonalmente Seca (FTSS) no segundo capítulo. Através dos resultados, observamos que a estrutura das leguminosas foi fortemente relacionada às variáveis ambientais amostradas, principalmente com a altitude, variável que sintetiza clima e umidade, e à distância filogenética. A distribuição da família mostrou-se condicionada a ambientes secos, quentes e de solos férteis. Uma grande especialização em termos de funcionalidade foi observada nas florestas decíduas, diminuindo em direção às semideciduais e com as ombrófilas apresentando espécies mais generalistas em termos de habitat. Os indivíduos presentes nas florestas decíduas apresentam menor vulnerabilidade à cavitação por déficit de pressão de vapor do que os presentes em semideciduais. Florestas deciduais apresentaram leguminosas com estratégia ecológica conservativa, porém crescimento rápido, enquanto as semideciduais apresentaram funcionalidade compatível com uma característica aquisitiva, porém crescimento lento. Assim, apesar de tratadas como um bioma homogêneo, as FTSS apresentam estratégias ecológicas distintas em resposta à sazonalidade. Em florestas semideciduais, apesar da predominância de espécies aquisitivas, ocorreram espécies conservativas e pioneiras de crescimento muito rápido. Porém, houve aumento das leguminosas de crescimento lento na dinâmica das florestas semideciduais, mostrando que as mudanças climáticas podem estar favorecendo espécies tolerantes à altas temperaturas e maior déficit hídrico, influenciando a composição florística das florestas semideciduais. Esses resultados, além de auxiliarem na compreensão dos padrões biogeográficos envolvidos na distribuição da família, podem ser utilizados para predizer as respostas de Leguminosae mediante as mudanças climáticas, e consequentemente, estabelecer estratégias de conservação das comunidades vegetais.

Palavras-chave: Floresta estacional decidual. Floresta estacional semidecidual. Floresta ombrófila. Traços funcionais. Diversidade beta-filogenética. Estratégia ecológica. Aquisição de recursos. Conservação de recursos.

ABSTRACT

This thesis aimed to assess relationships among phylogenetic diversity, functional traits and adaptive success of the family Leguminosae, represented by variables related to the structure and dynamics of this family in an edaphoclimatic gradient across the north / south direction of the Minas Gerais state. Said gradient comprises deciduous forest formations, in the northern portion of the state, semideciduous forests in the *Campo das Vertentes* mesoregion and ombrophilous nebular forests in southern Minas Gerais. To achieve our aim, we used data from two forest dynamics inventories (15 years and three measurements), structural data about the legumes in the sampled plots, chemical and textural soil variables, the nineteen bioclimatic variables from WorldClim, phylogenetic beta diversity and hydraulic-related functional traits collected from legume species within the forest plots. In the first chapter we fitted generalized linear mixed-effects models with all the aforementioned variables, and in the second chapter, with hydraulic-related wood functional traits, soils and using only data from Seasonally Dry Tropical Forest (SDTF) formations. From our results, we could observe that Leguminosae structure was strongly related to the sampled environmental variables, especially with altitude, which synthesizes climate and humidity, as well as to phylogenetic distance. This family distribution revealed conditioned to dry, hot and fertile environments. We found conspicuous functional specialization in the observed deciduous forests, with a decrease in specialization towards the semideciduous formations, and the presence of more generalist legume species, in terms of habitat, in the ombrophilous forests. The individuals collected in the deciduous forests presented lower vulnerability to cavitation by water vapour pressure deficit than those from semideciduous forests. Legume individuals from deciduous forests showed conservative ecological strategies, but with fast growth, while the individuals from the semideciduous formations revealed a functionality more compatible with an acquisitive strategy, but with slower growth. Thus, although usually regarded as a homogeneous biome, the SDTFs present distinct ecological strategies in response to seasonality. In semideciduous forests, despite the predominance of acquisitive species, we also found conservative and rapid-growth pioneer species. However, we recognised an increase in slow-growth legume species in the semideciduous forests dynamics, showing that climate change may be favouring species that are tolerant to high temperatures and water deficit, influencing the floristic composition of semideciduous forests. Beyond increasing the understanding of the biogeographic patterns involved in the Leguminosae distribution, these results can provide insights about the Leguminosae responses to climate change and, consequently, they can be used to establish plant community conservation strategies.

Keywords: Seasonal deciduous forest. Seasonal semideciduous forest. Ombrophilous forest. Functional traits. Phylogenetic beta diversity. Ecological strategy. Resource acquisition. Resource conservation.

SUMÁRIO

1 INTRODUÇÃO

O estímulo para investigar o que condiciona o sucesso adaptativo de Leguminosae e as possíveis mudanças nas estratégias ecológicas dessa família em um gradiente xérico-mésico veio de extensas observações em campo e dos diversos estudos conduzidos pelo Laboratório de Fitogeografia e Ecologia Evolutiva do Departamento de Ciências Florestais (DCF) da Universidade Federal de Lavras (UFLA). Integro o grupo desde 2016, mas os trabalhos com estrutura de comunidades e dinâmica florestal acontecem desde meados da década de 80. Para a tese, utilizei dados de nove áreas e cerca de 12 ha de parcelas permanentes, de um banco de dados que conta com mais 40 áreas e cerca de 100 ha de parcelas permanentes em florestas ombrófilas, semideciduais e deciduais no sudeste e nordeste brasileiros, mensuradas a cada cinco anos.

Na busca de melhor compreender os processos que culminam nos padrões de estruturação das comunidades vegetais, o grupo de pesquisa tem se voltado para a investigação funcional e evolutiva, proposta integrativa que apresento nesta tese. Uma vez que as características anatômico-funcionais das espécies refletem suas tolerâncias fisiológicas e tendem a ser conservadas evolutivamente, podem permitir avanços na compreensão da ecologia das comunidades como um todo. As leguminosas, grupo com grande diversidade e ampla ocorrência em gradientes ambientais é considerado como um excelente preditor do comportamento das comunidades vegetais, além de ser alvo de especulações no que tange às mudanças climáticas globais. Alguns artigos discorrem sobre a adaptabilidade e capacidade competitiva das leguminosas em ambientes xéricos, mas pouco se sabe sobre como as características funcionais e filogenéticas condicionam essa adaptabilidade na gama de condições diferenciadas onde as espécies ocorrem. Em face das mudanças climáticas globais, alguns autores esperam um aumento de Leguminosae em ambientes mésicos. Porém, as estratégias ecológicas que permitem às leguminosas ocorrer em ambientes xéricos e mésicos são pouco conhecidas. Estudos como este, que incluam parâmetros da dinâmica das leguminosas em gradientes ambientais permitem compreender seu papel na comunidade vegetal, encontrar modificações temporais e inferir com maior robustez sobre possíveis modificações. Assim, através dos resultados aqui apresentados, descortinamos processos que promovem os padrões estruturais e dinâmicos de Leguminosae, as estratégias ecológicas que permeiam esses padrões, e avançamos um passo importante para a compreensão da estruturação das comunidades em gradientes ambientais.

2 REFERENCIAL TEÓRICO

2.1 A família Leguminosae

Leguminosae (ou Fabaceae) é a terceira maior família de Angiospermas em riqueza, com aproximadamente 770 gêneros e cerca de 19.500 espécies (LPWG, 2013, 2017). Representa uma das linhagens mais bem sucedidas entre as Angiospermas, e são cosmopolitas em distribuição, abrangendo os maiores biomas, e constituindo um grupo de grande importância em florestas temperadas, tropicais, mediterrâneas, ombrófilas, sazonais secas e nas savanas (Koenen *et al.*, 2013; Lavin, Herendeen e Wojciechowski, 2005; LPWG, 2013). A primeira Leguminosa surgiu há cerca de 60 – 56 milhões de anos atrás (Mya), durante o final do Paleoceno, quando outras famílias de Angiospermas também surgiram (Lavin, Herendeen e Wojciechowski, 2005; Sprent, 2007). A hipótese inicial postulava o oeste da Gondwana como centro de origem (Oliveira-Filho *et al.*, 2013; Sprent, 2007), e atualmente acredita-se que esse centro tenha sido ao norte, na Laurásia, em condições semiáridas, em florestas estacionais secas semelhantes climaticamente às atuais (Sprent, 2007).

Há pouca diferença entre a idade estimada da origem das leguminosas e da sua diversificação (Lavin, Herendeen e Wojciechowski, 2005), e as taxas de diversificação são consideravelmente maiores que a média para as demais Angiospermas nos últimos 60 Mya (Hughes e Eastwood, 2006; LPWG, 2013). As leguminosas apresentam considerável diversidade morfológica, que vai desde árvores de florestas úmidas e lianas arbóreas até plantas aquáticas e arbustos (LPWG, 2017). Atualmente ocupam todos os biomas terrestres, constituindo elementos significativos em florestas tropicais úmidas na África, América do Sul e Ásia, ocorrendo no Mediterrâneo, em regiões desérticas e temperadas (Gei *et al.*, 2018; LPWG, 2013), e dominando as florestas secas e savanas através dos trópicos (Allen *et al.*, 2017; DRYFLOR, 2016; LPWG, 2013; Pennington, Lavin e Oliveira-Filho, 2009)

Nas florestas tropicais, principalmente em florestas secas, leguminosas são frequentemente a família mais rica e abundante (Gei e Powers, 2015; German, Werden e Powers, 2015; Pennington, Lavin e Oliveira-Filho, 2009), embora a abundância ainda não esteja bem sintetizada através dos gradientes sucessionais e climáticos que caracterizam as florestas tropicais (Gei *et al.*, 2018). Estudos anteriores envolvendo florística, estrutura ou dinâmica das áreas de florestas secas e úmidas amostradas no presente trabalho atestam a predominância de espécies de Leguminosae em florestas deciduais e semideciduais (Espírito-Santo *et al.* 2002; Machado *et al.* 2004; Santos *et al.* 2011; Oliveira-Filho *et al.* 2013; Apgaua *et al.* 2015). A abundância das leguminosas tende a diminuir em formações ombrófilas, principalmente de maior altitude (Oliveira-Filho *et al.* 2013; Gei *et al.* 2018). Florestas úmidas e sazonais secas experimentam diferenças substanciais na disponibilidade hídrica e de nutrientes, e portanto, variações sistemáticas na distribuição das leguminosas devem ocorrer ao longo do gradiente formado pela variação desses fatores (Gei *et al.*, 2018). De fato, as Leguminosas tendem a ser mais abundantes e dominantes nas Florestas Tropicais Sazonalmente Secas (FTSS) (Pennington *et al*. 2009; Oliveira-Filho *et al*. 2013; Allen *et al*. 2017; Gei *et al*. 2018). A diversificação dessa família em áreas de FTSS apoia a gama de adaptações que possuem para evitação e tolerância à seca (Gei *et al.*, 2018; German, Werden e Powers, 2015; Lavin *et al.*, 2004), e mesmo o conservadorismo de nicho em linhagens de leguminosas em FTSS é discutido em diversos estudos (Allen *et al.*, 2017; Gei *et al.*, 2018; Pennington, Lavin e Oliveira-Filho, 2009; Rodrigues *et al.*, 2015).

Os motivos do grande sucesso adaptativo de Leguminosae são amplamente discutidos no que concerne à fixação de nitrogênio (Chen *et al.*, 2007; Doyle, 2011; Faria *et al.*, 1984, 1987, 1989; Gei *et al.*, 2018; Gei e Powers, 2015; Houlton *et al.*, 2008; Powers *et al.*, 2015). Porém, German, Werden e Powers (2015) afirmam que características funcionais ligadas ao nicho regenerativo das espécies, como fecundidade, dispersão, dormência e germinação de sementes podem ser mais importantes para o sucesso das leguminosas na colonização dos ambientes do que a fixação de nitrogênio. Sementes de leguminosas germinam duas vezes mais rápido que sementes de espécies não leguminosas, o que pode ser uma adaptação importante em ambientes extremamente sazonais, como as FTSS (German, Werden e Powers, 2015). A rapidez com que a diversificação ocorre em alguns clados, e que os permite ocupar diferentes ambientes também é um fator citado como preponderante (Hughes e Eastwood, 2006; Koenen *et al.*, 2013). Estudos discutem ainda a importância das adaptações de leguminosas aos gradientes climáticos e o uso eficiente da água como características importantes para seu sucesso adaptativo (Adams, Simon e Pfautsch, 2010; Reyes-García *et al.*, 2012). Porém, os estudos com leguminosas são via de regra comparativos entre outras famílias, e não se tem conhecimento das diversas características funcionais que permitem a adaptação dessa família à amplitude do gradiente que ela ocupa.

2.2. Características funcionais: implicações adaptativas, na história de vida dos indivíduos e relações filogenéticas.

Características ou atributos funcionais (*Functional traits* em inglês) são quaisquer caractere morfológico, fisiológico, bioquímico, estrutural, fenológico ou comportamental expresso fenotipicamente, relacionado ao *fitness* (capacidade de crescimento, reprodução e sobrevivência) e mensurável a nível de indivíduo (Díaz *et al.*, 2013; Donovan *et al.*, 2011; Violle *et al.*, 2017). Características funcionais mediam a resposta e a tolerância de cada indivíduo ao ambiente, a estressores ambientais e distúrbios; e contribuem para propriedades e serviços do ecossistema (Díaz *et al.*, 2013; Violle *et al.*, 2007; Lavorel e Garnier, 2002). Assim, determinam a performance fisiológica, influenciando as taxas vitais e determinando o fitness e a história de vida dos organismos (Adler *et al.*, 2014). Por determinar a história de vida, e consequentemente, a história adaptativa dos indivíduos, a abordagem funcional tem sido bastante utilizada para predizer a estrutura e dinâmica das comunidades vegetais (Adler *et al.*, 2014; Boukili e Chazdon, 2017; Cadotte *et al.*, 2015; Díaz *et al.*, 2013). Os mecanismos que estruturam as comunidades e governam a substituição de espécies podem ser investigados através das respostas das características funcionais às mudanças (Auffret *et al.*, 2017), fazendo com que estas sejam amplamente utilizadas na busca do entendimento de padrões e processos em ecologia de comunidades (Adler *et al.*, 2014; Auffret *et al.*, 2017; Cadotte *et al.*, 2015; Cavender-Bares *et al.*, 2009; Chao *et al.*, 2008; Cianciaruso, Silva e Batalha, 2009; Costa *et al.*, 2017; Diaz *et al.*, 2004; Díaz *et al.*, 2013; Lavorel e Garnier, 2002; Sobral e Cianciaruso, 2012). No entanto, como as características funcionais variam ou covariam em gradientes ambientais de larga escala ainda é uma questão em aberto (Anderegg et al. 2015; Costa *et al.*, 2017).

A nível de indivíduo, as características funcionais estão relacionadas ao investimento na construção dos tecidos e manutenção das estratégias ecológicas, bem como ao retorno daquele investimento em fitness ao indivíduo, uma relação denominada de espectro econômico (“*economics spectrum*” em inglês) (Chave *et al.*, 2009; Donovan *et al.*, 2011; Westoby *et al.*, 2002; Wright *et al.*, 2004). A partir dessa relação econômica, as plantas estabelecem *trade-offs* para investimento em sobrevivência ou crescimento, de acordo com as restrições do ambiente onde se encontram (Markesteijn *et al.*, 2011; Reich *et al.*, 2003). Por exemplo, folhas com alta massa por área (LMA – *leaf mass per area* em inglês), implicam uma lâmina foliar espessa, com grande concentração de lignina, células pequenas e de parede celular espessa, com maior vida útil (LL – *Leaf lifespan* em inglês) (Westoby *et al.*, 2002; Wright *et al.*, 2004). LMA e LL possuem correlação positiva, e determinam se a planta vai investir na capacidade fotossintética e rápido crescimento (baixos LMA e LL), ou na longevidade foliar através do acúmulo de LMA. A área foliar (LA – *Leaf area* em inglês), a área foliar específica (SLA – *Specific leaf area*) e o conteúdo de massa seca da folha (LDMC – *Leaf dry matter content*) também estão diretamente relacionados ao LL. Porém, as características relacionadas à área foliar são inversamente proporcionais às relacionadas à massa, e à longevidade foliar (Cornelissen *et al.*, 2003; Pérez-Harguindeguy *et al.*, 2013). Ambos afetam diretamente a capacidade fotossintética liquida da folha, e portanto o crescimento relativo do indivíduo, com folhas de maior LL apresentando menor capacidade fotossintética, menor LA e SLA, porém maior resistência mecânica (altos LMA e LDMC), favorecendo a sobrevivência em detrimento do crescimento (Adler *et al.*, 2014; Westoby *et al.*, 2002).

O *trade-off* crescimento / sobrevivência relaciona ainda a eficiência na condutividade ou maior resistência mecânica e à embolia nos vasos do xilema (Markesteijn *et al.*, 2011). Quanto maior e mais largo o vaso condutor, menor é sua resistência ao fluxo de água, e menor tende a ser a frequência de vasos por mm², bem como a densidade da madeira (Chave *et al.*, 2009; Tng *et al.*, 2018). Assim, espécies com menor densidade da madeira (WD – *wood density*), densidade específica da madeira (WSD – *wood specific density*) e menor densidade de vasos por mm² tendem a ter vasos condutores maiores, investindo na eficiência da condutividade, crescimento e maior capacidade competitiva (Chave *et al.*, 2009; Cornelissen *et al.*, 2003; Markesteijn *et al.*, 2011; Perez-Harguindeguy *et al.*, 2013; Vico *et al.*, 2017). No entanto, transporte eficiente não significa transporte seguro, e as características supracitadas tornam a planta mais susceptível à embolia e cavitação (Markesteijn *et al.*, 2011; Tng *et al.*, 2018). Resistência à embolia e aos possíveis danos mecânicos implica vasos menores e com maior densidade por mm², alta lignificação e madeira densa (Chave *et al.*, 2009; Muscarella *et al.*, 2016). No geral, as espécies que investem em longevidade possuem crescimento lento, expresso pela alta lignificação, alta LMA e investimento em órgãos mais resistentes, com tendência a maximizar esse investimento retendo e / ou preservando esses órgãos (Chave *et al.*, 2009; Markesteijn *et al.*, 2011; Muscarella *et al.*, 2016; Wright *et al.*, 2004).

Mas o que leva uma espécie a investir em determinada estratégia ecológica dentro do *trade off* crescimento / sobrevivência? A pressão seletiva do ambiente. As características funcionais são selecionadas evolutivamente de acordo com a restritividade (ou filtragem) ambiental, e apesar das respostas plásticas / elásticas das espécies, as mesmas estão condicionadas a colonizar e persistir apenas em locais que não superam seu limiar de tolerância fisiológica (Reich *et al.*, 2003). Espécies de ambientes ricos em nutrientes e / ou maior disponibilidade hídrica tendem a ter rápido crescimento, com rápida captação, pouca conservação interna de recursos e portanto rápida substituição de órgãos (Chave *et al.*, 2009;

Lavorel e Garnier, 2002; Markesteijn *et al.*, 2011; Muscarella *et al.*, 2015, 2016; Westoby *et al.*, 2002; Wright *et al.*, 2004). Assim, espécies de ambientes com maior disponibilidade de recursos tendem a histórias de vida rápidas, com maior plasticidade (quando a adaptação é irreversível) e / ou elasticidade (quando o órgão ou tecido adapta-se a determinada situação, mas pode voltar ao estado original) para o crescimento individual e recrutamento (Adler *et al.*, 2014; Chave *et al.*, 2009; Lavorel e Garnier, 2002). São espécies com estratégia ecológica aquisitiva, que investem em tecidos de baixo custo (folhas de vida curta e madeira leve), mas com altas taxas fotossintéticas e rápido crescimento, portanto, rápido retorno do investimento (Adler *et al.*, 2014; Boukili e Chazdon, 2017; Muscarella *et al.*, 2015).

Por outro lado, espécies de ambientes restritivos, com menor aporte nutricional e / ou água disponíveis, tendem a ter história de vida lenta, com maior elasticidade para a sobrevivência (Adler *et al.*, 2014; Lavorel e Garnier, 2002; Muscarella *et al.*, 2015; Wright *et al.*, 2004). Essas espécies possuem estratégia ecológica conservativa, com maximização do tempo médio de permanência dos nutrientes através da maior longevidade dos órgãos e da alta reabsorção de nutrientes de órgãos senescentes, além do investimento em defesas químicas e mecânicas (Adler *et al.*, 2014; Boukili e Chazdon, 2017; Lavorel e Garnier, 2002; Muscarella *et al.*, 2015). Embora sejam bastante discutidas na literatura, a maioria dos trabalhos considerando a resposta das estratégias ecológicas a gradientes ambientais foram realizados em florestas temperadas ou tropicais úmidas e considerando espécies sempre-verdes (Boukili e Chazdon, 2017; Carmona *et al.*, 2015; Costa *et al.*, 2017; Esquivel-Muelbert, Galbraith, *et al.*, 2017; Lasky, Jesse R *et al.*, 2014; Muscarella *et al.*, 2016; Purschke *et al.*, 2013; Simpson, Richardson e Laughlin, 2016; Turnbull *et al.*, 2016). Pouco se sabe sobre as adaptações de espécies deciduais, ou sobre o papel dos diferentes fatores de restritividade do habitat na seleção das espécies que compõem a comunidade. Investigações acerca do papel das características funcionais como preditoras da dinâmica florestal são poucas e recentes (Auffret *et al.*, 2017; Chauvet *et al.*, 2017; Xu *et al.*, 2016), e em sua maioria consideram a dinâmica sob a perspectiva da modelagem. Cadote e Tucker (2017) ressaltam a necessidade de realização de estudos em grandes escalas espaciais, que incluam uma gama maior de variáveis a fim de melhor compreender como as características funcionais se comportam e influenciam as comunidades vegetais em gradientes ambientais.

Uma perspectiva filogenética tem sido amplamente utilizada para integrar estudos com características funcionais (Batalha *et al.*, 2011; Cavender-Bares *et al.*, 2009; Cianciaruso, Silva e Batalha, 2009; Díaz *et al.*, 2013; Muscarella *et al.*, 2015, 2016; Sobral e Cianciaruso, 2012;

Webb *et al.*, 2002). Uma vez que as características funcionais, principalmente as mais relevantes, são conservadas filogeneticamente, estudos que utilizem a perspectiva filogenética / funcional conseguem inferir sobre o papel dessas na estruturação das comunidades de forma mais abrangente (Bergholz *et al.*, 2017; Cavender-Bares *et al.*, 2009; Cianciaruso, Silva e Batalha, 2009; Sobral e Cianciaruso, 2012). A composição de espécies muda e a diversidade funcional tende a aumentar ao longo de gradientes de viabilidade de recursos (Muscarella *et al.*, 2015, 2016). Apesar de estudos filogenéticos serem realizados há algum tempo (Díaz *et al.*, 2013; Faith, 1996), a investigação do papel evolutivo na manutenção de características fenotípicas e estruturação das comunidades é recente (Batalha *et al.*, 2011; Bergholz *et al.*, 2017; Boukili e Chazdon, 2017; Cavender-Bares *et al.*, 2009; Díaz *et al.*, 2013; Grigulis *et al.*, 2007; Muscarella *et al.*, 2015; Sobral e Cianciaruso, 2012). Para tal, estudos que investiguem as respostas funcionais e evolutivas em gradientes ambientais são primordiais (Bergholz *et al.*, 2017; Boukili e Chazdon, 2017), e permitem predizer o comportamento das comunidades em face das mudanças climáticas globais.

2.3 Gradiente ambiental de ombrófilas a estacionais: características das formações vegetais e inferências sobre as mudanças climáticas globais.

Um dos objetivos centrais da ecologia é determinar como os processos de estruturação das comunidades variam ao longo dos gradientes ambientais (Muscarella *et al.*, 2016). Antes da ecologia existir como ciência, naturalistas já observavam e registravam as diferenças nos padrões de distribuição de espécies nas comunidades naturais, objeto de estudo de ecólogos até a atualidade (Begon, Harper e Townsend, 1996; Bergholz *et al.*, 2017; Cianciaruso, Silva e Batalha, 2009; Daru *et al.*, 2016; Hubbell, 2001; Macarthur e Levins, 1967; Magurran, 2004). Trabalhos clássicos empenharam debates acerca do papel da sucessão ecológica na diversificação das comunidades (Clements, 1916; Gleason, 1927), da ubiquidade e da raridade das espécies (Macarthur, 1960; Preston, 1948) e do papel da competição e das características ecológicas na estruturação das comunidades (Grime, 1977; Tilman, 1982, 2004). Tais debates contribuíram consideravelmente para a compreensão espaço-temporal dos padrões de diversidade biológica (Magurran, 2004). Desde então, diversos estudos se dedicam a descrever padrões de riqueza e distribuição de espécies em gradientes latitudinais (Lamanna *et al.*, 2014; Pianka, 1966), sucessionais (Madeira *et al.*, 2009), topográficos e altitudinais (Baldeck *et al.*, 2013; Silva *et al.*, 2014), gradientes de temperatura (Allen et al 2002; Cassemiro & Diniz-Filho 2010), de precipitação e disponibilidade hídrica (Balvanera, Quijas e Pérez-Jiménez, 2011; Esquivel-Muelbert, Baker, *et al.*, 2017; Gei *et al.*, 2018; Negret *et al.*, 2013), entre outros (Giehl e Jarenkow, 2015; Kumordzi, Wardle e Freschet, 2015; Moro *et al.*, 2015; Muscarella *et al.*, 2016; Saiter *et al.*, 2016; Scheiner e Willig, 2005; Terra *et al.*, 2018)

A sobrevivência, a persistência e as interações competitivas entre as espécies variam ao longo de um gradiente ambiental, e portanto, a estruturação das comunidades vegetais é diretamente influenciada pelo gradiente (Cadotte e Tucker, 2017). Em Minas Gerais, o gradiente climático xérico-mésico e edáfico formado na direção norte-sul compreende Florestas Tropicais Sazonalmente Secas (FTSS) deciduais e semideciduais, e florestas ombrófilas, respectivamente. As Florestas Tropicais Sazonalmente Secas (FTSS) constituem um conjunto de formações heterogêneas que ocorrem em diversos domínios fitogeográficos, porém com propriedades únicas, conferidas principalmente pelo regime de sazonalidade das chuvas (Allen *et al.*, 2017). A precipitação média anual é menor que 1800 mm, com estação seca perdurando por 3 a 6 meses, quando ocorrem valores de precipitação menores que 100 mm mensais (Allen *et al.*, 2017; DRYFLOR, 2016; Pennington *et al.*, 2000; Pennington, Lavin e Oliveira-Filho, 2009). Ocorrem em núcleos disjuntos em solos calcários de alta fertilidade, distribuídos desde o norte da Argentina e nordeste do Brasil até o noroeste do México (Dexter *et al.*, 2015; Mogni, Oakley e Bsen, 2015; Pennington *et al.*, 2000; Santos *et al.*, 2012). Assim, estão compreendidas em um gradiente de porte da vegetação associado à sazonalidade climática e fertilidade do solo, que vai desde fisionomias arbustivas em locais xéricos e de menor fertilidade até florestas de grande porte em locais um pouco mais úmidos e férteis (Allen *et al.*, 2017; Pennington, Lavin e Oliveira-Filho, 2009). A proporção de deciduidade das plantas também responde a um gradiente de precipitação, com espécies semidecíduas nos locais de maior precipitação até decíduas nos locais mais xéricos, embora sempre verdes com adaptações para armazenamento de água também ocorram (Apgaua *et al.*, 2014; Pennington, Lavin e Oliveira-Filho, 2009; Reis *et al.*, 2017).

A diversidade beta nas FTSS é alta, devido à grande heterogeneidade relacionada à multiplicidade de filtros ambientais pela variação na precipitação e fertilidade dos solos (Allen *et al.*, 2017; Apgaua *et al.*, 2014; Powers *et al.*, 2018). Em virtude disto, a variedade de estratégias ecofisiológicas e características funcionais é grande, e ainda pouco conhecida (Powers *et al.*, 2018). Um sinal filogenético forte geralmente é encontrado nos estudos que envolvem FTSS na região neotropical, e sinaliza a importância das características funcionais ligadas à tolerância à seca nesses ambientes (Gei *et al.*, 2018; Pennington, Lavin e Oliveira-Filho, 2009). Pennington *et al.*, (2009) evidenciaram o conservadorismo de nicho em linhagens de Leguminosae nas FTSS como resultado de filtragem ambiental, e citam que outros trabalhos encontraram resultado semelhante para outras linhagens nesses ambientes. A alta representatividade de Leguminosae também é reportada, e diversos estudos ligam essa representatividade à capacidade de fixação de nitrogênio na maioria dos indivíduos dessa família (Allen *et al.*, 2017; Gei *et al.*, 2018; Waring *et al.*, 2016). No entanto, ainda não foram testadas outras características funcionais de Leguminosae e suas respostas a gradientes ambientais em maior escala, ou em gradientes dentro da heterogeneidade própria das FTSS, uma vez que ocorrem fisionomias com diferenças consideráveis na sazonalidade da precipitação e na temperatura, como as florestas decíduas e semidecíduas.

As Florestas Estacionais Deciduais (FEDs) fazem parte do domínio fitogeográfico das Caatingas (Santos *et al.*, 2012). Ocorrem em locais de solos férteis e bem drenados, oriundos da intemperização de rochas calcárias (Apgaua *et al.*, 2014; Santos *et al.*, 2012; Terra *et al.*, 2018), e apresentam maior estacionalidade na precipitação, além de temperaturas mais altas (Terra *et al.*, 2018). São habitats onde a filtragem ambiental exerce forte seleção, favorecendo uma maior dominância, menor área basal e menor densidade de indivíduos (Murphy e Lugo, 1986; Oliveira-Filho *et al.*, 2013; Terra *et al.*, 2018). Durante a estação seca há um aumento no déficit de pressão de vapor no ar, e para regular essa pressão internamente, a planta precisa fechar os estômatos, reduzir a transpiração, limitando assim a fotossíntese (Vico *et al.*, 2017). Portanto, a manutenção das áreas foliares em condições de aridez significa um alto custo de carbono para a planta, sendo mais vantajosa a perda das folhas (Vico *et al.*, 2017). Nas florestas deciduais, essa perda excede 60 % das folhas, enquanto que nas semideciduais ocorre entre 30 a 60 %, ambas na estação seca.

Formações semideciduais constituem ambientes com menor sazonalidade e mais favoráveis à colonização que as deciduais, e portanto, com maior riqueza de espécies (Terra *et al.*, 2018). Segundo o IBGE (1993), florestas semideciduais são habitats *sensu lato* do domínio Atlântico. Ocorrem em áreas de transição entre as formações ombrófilas atlânticas e o Cerrado, com precipitação entre 1500 e 2000 mm anuais, distantes da costa em até 700 km (Oliveira-Filho e Fontes, 2000). Estudos propuseram fatores chave que impedem a expansão das áreas ombrófilas do Domínio Atlântico para as demais fisionomias, inclusive as semideciduais, denominando as formações ombrófilas de core, e as demais de habitats marginais (Neves *et al*. 2017; Scarano 2009). Scarano (2009) cita o estresse hídrico como principal fator de diferenciação entre formações ombrófilas e semideciduais do domínio Atlântico. De fato, a sazonalidade da precipitação é um fator preponderante e provavelmente o fator-chave na redução e substituição de espécies de formações ombrófilas (sempre-verdes, com chuvas bem distribuídas durante o ano) para semideciduais (Oliveira-Filho *et al.*, 2013; Oliveira-Filho e Fontes, 2000).

As formações atlânticas ombrófilas ocorrem em uma faixa de precipitação de 2000 a 3600 mm anuais, com distribuição ao longo da costa brasileira até 300 km adentrando o continente, com chuvas influenciadas pelos ventos oceânicos e pelo lado marítimo das cadeias montanhosas (Oliveira-Filho e Fontes, 2000). Ocorrem também em florestas mistas com *Araucaria* e *Podocarpus* (floresta ombrófila mista) em áreas de maior elevação (Bertoncello *et al.*, 2011). Nessas áreas, o principal fator limitante para as espécies é o congelamento, embora a diminuição da pressão atmosférica, maior incidência de radiação solar e aceleração das massas de ar (aumentando a nebulosidade e incidência de chuvas) também sejam fatores que moldam a composição (Oliveira-Filho e Fontes, 2000) e consequentemente, a filogenia e a funcionalidade. Porém, estudos relacionando estrutura de comunidades, filogenia e caracteres funcionais são recentes (Bergholz *et al.*, 2017) e pouco expressivos em florestas ombrófilas. A maioria tem focado principalmente nos gradientes sucessionais (Boukili e Chazdon, 2017; Lasky, Jesse R *et al.*, 2014; Norden *et al.*, 2011; Turnbull *et al.*, 2016), e mesmo aqueles que integram um gradiente de variáveis ambientais de maneira mais ampla (Costa *et al.*, 2017; Muscarella *et al.*, 2016) não consideram o papel dessa gama na dinâmica das comunidades.

Estudos que compreendam gradientes ambientais de grande escala são urgentes, principalmente mediante as predições envolvendo as mudanças climáticas globais. Gradientes ambientais em grande escala geográfica abrangem grande heterogeneidade, onde as respostas da vegetação variam consideravelmente, principalmente quando englobam ambientes com situações de estresse hídrico (Wu *et al.*, 2015). Projeções climáticas apontam para um aumento na duração e severidade do período seco, e não se sabe como as comunidades vegetais vão responder a essas mudanças (Anderegg, 2015; Sperry e Love, 2015). Estudos apontam para uma alta mortalidade na Amazônia e / ou mudanças na composição das comunidades em decorrência de déficit hídrico (Brienen *et al.*, 2015; Condit, Hubbell e Foster, 1995; Doughty *et al.*, 2015; Esquivel-Muelbert *et al.*, 2018; Esquivel-Muelbert, Galbraith, *et al.*, 2017; Marengo *et al.*, 2008). Muitos taxas tropicais são fortemente limitados por restrições fisiológicas ligadas à disponibilidade hídrica, o que é predito pela distribuição desses táxons ao longo dos gradientes biogeográficos (Esquivel-Muelbert, Baker, *et al.*, 2017; Esquivel-Muelbert, Galbraith, *et al.*, 2017). Uma vez que a diminuição da precipitação, eventos de seca extrema e aumento geral da temperatura vem ocorrendo e são preditos para o futuro (Anderegg, 2015; Esquivel-Muelbert, Galbraith, *et al.*, 2017; Rodrigues *et al.*, 2015; Simpson, Richardson e Laughlin, 2016; Wu *et al.*, 2015), entender como essas mudanças podem afetar a diversidade funcional, filogenética e a composição das comunidades como um todo é fundamental. Estudos discorrem sobre a possibilidade de expansão de grupos típicos de florestas secas, como as leguminosas, sobre as áreas úmidas e as savanas (Allen *et al.*, 2017; Oliveira-Filho *et al.*, 2013; Rodrigues *et al.*, 2015). Uma vez que características funcionais hidráulicas podem constituir a base da separação ecológica entre florestas ombrófilas e sazonais, a quantificação do valor adaptativo dessas características pode permitir avanços na captura das dimensões críticas de vulnerabilidade e a resposta das espécies às modificações no ambiente (Anderegg, 2015; Wu *et al.*, 2015). As mudanças climáticas podem causar desde a morte de espécies não aclimatadas, até a mudanças nos padrões de estruturação das comunidades ao longo do gradiente (Cadotte e Tucker, 2017). Assim, estudos que englobem gradientes em larga escala podem prover informações sobre os níveis de tolerância dos táxons, permitindo inferências robustas sobre como as florestas tropicais responderão às mudanças climáticas globais.

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SEGUNDA PARTE – ARTIGOS SEGUNDO OECOLOGIA

ARTIGO 1: CLIMATE, SOIL, PHYLOGENY OR FUNCTIONAL TRAITS? WHAT VARIABLES BETTER EXPLAIN LEGUME SUCCESS IN A XERIC-MESIC ENVIRONMENTAL GRADIENT

Abstract: Leguminosae constitutes one of the most successful lineages of Angiosperms, widely distributed in a diversity of environments, but how environmental, evolutionary and functional attributes drive this success are poorly known. Thus, we investigated these variables using structural and temporal behaviour as proxies for adaptative success of Leguminosae in a gradient that comprises xeric, mesic and wet forests. Using linear mixed-effects models, we showed that the environmental variables had a strong effect over richness, stem proportion and aboveground biomass (ABG) proportion of legumes (structural variables). Altitude (or a range of conditions synthesized by it) are negatively associated with richness, stem, AGB proportion and biomass temporal loss. Phylogenetic distance was preponderant only for stem proportion, ABG and biomass temporal gain. Structural variables present a higher percentage of explanation, while the temporal parameters analysed (gain and loss in basal area) remained mostly unexplained. Leguminosae structure was conditioned by water deficit, warm temperatures and lower altitudes, temporal parameters mainly by phylogeny and functional traits, show us how legumes are structured spatial and temporally in our gradient.

Keywords: Fabaceae, deciduous forest, semideciduous forest, rain forest, plant dynamics

Introduction

Leguminosae (or Fabaceae) constitutes one of the most successful lineages of Angiosperms, the third botanical family in richness of species, with diversification rates considerably higher than the average for Angiosperms in the last 60 million years (Hughes e Eastwood, 2006; Lavin, Herendeen e Wojciechowski, 2005; LPWG, 2013, 2017). Although this family had a centre of origin in a semiarid region, with climatic conditions similar to the seasonally dry tropical forests (SDTFs) (Sprent, 2007), they currently occupy all major biomes, ranging from wet tropical forests in Africa, South America and Asia to the Mediterranean, in desertic and temperate regions (Gei *et al.*, 2018; LPWG, 2013). Thus, the Leguminosae composes a group of great importance in temperate, tropical, Mediterranean, wet and seasonal forests (Koenen *et al.*, 2013; Lavin, Herendeen e Wojciechowski, 2005; LPWG, 2013), dominating the dry forests and savannas across the tropics (Allen *et al.*, 2017; DRYFLOR, 2016; LPWG, 2013; Pennington, Lavin e Oliveira-Filho, 2009). This widespread distribution in a range of environmental conditions makes Leguminosae an ideal botanical family for plant community studies in environmental gradients. In face of climate change and given the Leguminosae widespread occurrence and representativity, this group can be treated as a proxy for tropical tree communities' responses to environmental changes (Allen et al. 2017).

The reasons of this great adaptative success of Leguminosae are largely discussed in the literature. The majority of studies on this family focuses on the nitrogen fixation capacity of some legume species (Chen *et al.*, 2007; Corby, 1988; Doyle, 2011, 2016, Faria *et al.*, 1984, 1987, 1989; James *et al.*, 1994), attributing to this feature an important explanation for the family's success (Gei *et al.*, 2018; Gei e Powers, 2015; Houlton *et al.*, 2008; Powers *et al.*, 2015). German et al. (2015) contradicts that, explaining that functional traits linked to regenerative niche can be more important than the nitrogen fixation capacity for the success of Leguminosae, mainly during colonisation of environments. The increase in altitude is cited as a factor that decreases the legume occurrence (Gei *et al.*, 2018; Oliveira-Filho e Fontes, 2000), mainly due to increasing humidity and decreasing temperature. Temperature and annual precipitation have been cited to explain the legume abundance (Adams, Simon e Pfautsch, 2010; Oliveira-Filho *et al.*, 2013), but adaptative success from structural and temporal behaviour have not yet been investigated. Studies yet discuss the importance of traits that confer efficient use of water in Leguminosae for the adaptative success in climatic gradients (Adams, Simon e Pfautsch, 2010; Reyes-García *et al.*, 2012), and these traits can allow legumes to colonise and survive in a range of conditions, from wet to dry forests.

In a gradient represented by soil and climatic conditions, as occurs between rain and seasonally dry forests, substantial differences in water and nutrient availability promote systematic variations in the distribution of Leguminosae (Gei *et al.*, 2018). Despite the considerable morphological diversity that allows the cosmopolitan distribution of the Leguminosae (LPWG, 2017), its abundance and richness tend to decrease from wet formations to SDTF (Gei *et al.*, 2018). Gei et al. (2018) points out that the legume abundance has not yet been synthesized across climatic gradients in tropical forests. Studies cite legume abundance or possible factors that condition it in a broader context (Apgaua, Pereira, *et al.*, 2015; Espírito-Santo *et al.*, 2002; Neves *et al.*, 2015; Oliveira-Filho *et al.*, 2013; Pennington, Lavin e Oliveira-Filho, 2009; Rodrigues *et al.*, 2015), but few studies have focused on testing using only Leguminosae (Gei *et al.*, 2018; German, Werden e Powers, 2015). We are not aware of other studies that use structural and temporal parameters of Leguminosae as a proxy for the adaptative success of this family in an environmental gradient.

The fast diversification of some clades, which promotes a high morphological diversity (LPWG, 2017) and allows the Leguminosae to occupy different environments, is considered a preponderant factor for this family’s success (Hughes e Eastwood, 2006; Koenen *et al.*, 2013). Legumes are clearly conditioned to drought (Adams, Simon e Pfautsch, 2010), and phylogenetic relationships tend to be structured by the gradient between wet and dry forests (Hughes, Pennington e Antonelli, 2013; Oliveira-Filho *et al.*, 2013; Simon *et al.*, 2009). Phylogenetic signal and niche conservatism of Leguminosae in STDFs is cited in many studies (Allen *et al.*, 2017; Gei *et al.*, 2018; Pennington *et al.*, 2010; Pennington, Lavin e Oliveira-Filho, 2009; Rodrigues *et al.*, 2015; Simon *et al.*, 2009). Consequently, phylogenetic distances among sites could be used in studies aiming to understand the drivers of legume success (Oliveira-Filho *et al.*, 2013). These distances may reflect a range of ecological adaptations, with functional traits representing the basis of ecological divergence between wet and dry forests (Anderegg, 2015; Wu *et al.*, 2015). Modelling functional traits with phylogenetic distances and edaphoclimatic variables may provide an understanding of how these factors contribute to the widespread distribution of Leguminosae. We have not found studies with legumes that evaluate the relationships between phylogeny, functional traits and edaphoclimatic variables in a gradient that comprises wet to dry environments. These relationships also fit in discussions related to biogeographic patterns and ecosystem responses to climate change, wherein ecosystem resilience is related to species dynamics and functionality (Santos et al. 2012; Allen et al. 2017).

The environmental gradient that we sampled comprises a range between rain, semideciduous and deciduous forest. Deciduous forest occur in environments with high temperatures, high precipitation seasonality and with a lengthy dry period, where drought represents a strong environmental filter (Terra *et al.*, 2018). These forests are included in the Caatinga Domain (Santos et al 2012), and occur in highly fertile and well-drained soils in northern Minas Gerais state, in Brazil (Santos et al 2012; Apgaua et al 2014). The semideciduous and rain forests sampled are included in the Atlantic domain (Neves *et al.*, 2017; Oliveira-Filho e Fontes, 2000), with moist environments presenting weaker environmental filters (Terra *et al.*, 2018) and less fertile soils than deciduous forest. Temperature and mainly rainfall regimes separate between semideciduous and rain Atlantic forests (Oliveira-Filho e Fontes, 2000).

Semideciduous forests constitutes a less fertile, less warm and less seasonal environment than deciduous forest and more than rain forests. In environmental gradients like this, plant communities assembly according to their capacity to tackle the water deficit in seasonal areas, and invest in functional traits to improve competition for available resources in moist areas (Cadotte e Tucker, 2017; Kraft, Godoy e Levine, 2015; Muscarella *et al.*, 2016). Functional traits are related to an economics spectrum of plants, related to investments in tissue formation and the maintenance of ecological characteristics that offset the invested energy by an individual (Chave *et al.*, 2009; Donovan *et al.*, 2011; Westoby *et al.*, 2002; Wright *et al.*, 2004). From this economics relationship, plants establish trade-offs for investment in survival or growth, according to the constraints of the environment which they inhabit (Markesteijn *et al.*, 2011; Reich *et al.*, 2003), and these characteristics tend to be evolutionarily conserved (Reich *et al.*, 2003). However, the role of phylogeny and functional traits combined with edaphoclimatic conditions structuring the communities is not clearly known. Legume biodiversity has not been explored from this perspective. Although several works cites the high diversification and morphological variation of this family (Hughes e Eastwood, 2006; Koenen *et al.*, 2013; Lavin, Herendeen e Wojciechowski, 2005; LPWG, 2013, 2017; Oliveira-Filho *et al.*, 2013), they have not tested if this represents a strong driver of adaptative success of this family like some authors affirm (Hughes e Eastwood, 2006; Koenen *et al.*, 2013). Thus, this paper aims to investigate which variables – functional traits, phylogenetic distance, climatic and edaphic – best explain the adaptative success of Leguminosae (represented by structural and temporal parameters) in a gradient that comprises an edaphoclimatic range of seasonal to wet forests. We expect that phylogeny and functional traits will better explain the structural and temporal parameters of Leguminosae in this dry / wet gradient.

Material and Methods

Study area

The environmental gradient sampled comprises a range of dry to wet edaphoclimatic conditions across the north – south direction in Minas Gerais state, Brazil. Three forest types are comprised in this gradient: tropical deciduous forest, in the Caatinga Domain (Santos *et al.*, 2012) and tropical semideciduous forest and tropical rain forest, both physiognomies in the Atlantic Forest Domain (Neves *et al.*, 2017; Oliveira-Filho e Fontes, 2000). In each vegetation type, we selected three sites (Fig. 1) with permanent plots, where two previous inventories of forest dynamics had been carried out. We collected soil samples and hydraulic functional traits of Leguminosae in each plot. The three sites of rain forests sampled are nebular forests, with high influence of humidity conferred by clouds.

The dimensions of the permanent plots are 20 x 20 m (400 m²) (total area of each in Tab. 1). Within these plots, we recorded and numbered with aluminium tags all tree individuals within the inclusion criterion of DBH (diameter at breast height) ≥ 5 cm. These individuals were identified by specialists in the field, or otherwise a sample of botanical material was collected when necessary. The plots were measured every five years, and only the two last measurements were used in this analysis. The fragments of semideciduous forest, the deciduous VV and the rain forest Carr was sampled in 2010 and 2015. The deciduous forest AGP and BonM was sampled in 2009 – 2014 and 2012 – 2017 respectively, and the rain forest BocM and Itam was sampled in 2013 – 2018 and 2012 – 2017, respectively. In those years, all surviving tree individuals were measured again. The new individuals that reached the inclusion criterion (recruits) were identified in the field with the aid of specialists, marked with aluminium labels numbered and measured. The dead individuals were recorded. We considered only the Leguminosae individuals in data analysis.

Bioclimatic, soil and elevation variables

Soil chemistry and texture explanatory variables were obtained through samples composed of 1L of superficial soil (0-20 cm of depth) in each plot using the analysis methods described by the Embrapa (1997) protocol. The variables obtained were pH, phosphorus (mg/cm^3) (P), potassium (mg/cm^3) (K), calcium (cmol/dm^3) (Ca), magnesium (cmol/dm^3) (Mg), aluminum (cmol/dm^3) (Al), organic matter of soil (dag/kg) (OMS), sand percentage (dag/kg) (sand %), silt percentage (dag/kg) (silt %) and clay percentage (dag/kg) (clay %). To avoid collinearity, instead of using the variables Ca, Mg and K separately, they were synthesized in the variable sum of bases.

We obtained the 19 bioclimatic variables from the Worldclim Global Climate Data repository (Hijmans *et al.*, 2005). Due to the high collinearity (Pearson correlation: $r > |0.85|$) found between the bioclimatic variables in our dataset, we opted to use the variables Annual Mean Temperature, Annual Precipitation, Mean Diurnal Range, Isothermality and Temperature Annual Range. Only Annual Mean Temperature and Annual Precipitation have $r > |0.85|$ ($r = -0.94$), the other fourteen variables showed $r < |0.85|$ with Annual Mean Temperature and Annual Precipitation. We used BIOs data with 30 arc-second resolution (1-km spatial resolution), obtained using raster and sp R packages (Hijmans, Etten, van e Checg, 2012; Pebesma e Bivand, 2005). Altitude values were obtained through the elevatr package, with data from Mapzen Terrain Service (zoom was set to 9).

Structure and dynamics variables

To understand Leguminosae's adaptive success, we obtained its structural and temporal variables at each sample unit. For structural parameters, we calculated the proportion of Leguminosae species richness, stems and Above-Ground Biomass (AGB), obtained by the pantropical equation (Chave *et al.*, 2014) using the biomass package (Réjou-Méchain *et al.*, 2017). For the temporal behavior, we calculated gain and loss in biomass. For gain calculation, in plots with a negative ΔAGB/stem ratio, the negative values were set to zero, and for loss calculation, the positive ΔAGB/stem ratio values were also set to zero. When subtracting the Leguminosae AGB and stem gain/loss from the others species', we aim to evaluate growth success of Leguminosae in relation to others species present in the plant communities sampled. Our response variables were the following.

$$\text{Gain} = (((\text{AGBgainleg} - \text{AGBgainOS}) / \text{AGB1}) + ((\text{stemgainleg} - \text{stemgainOS}) / \text{stem1})) / 2$$

$$\text{Loss} = (((\text{AGBlossleg} - \text{AGBlossOS}) / \text{AGB1}) + ((\text{stemlossleg} - \text{stemlossOS}) / \text{stem1})) / 2$$

Where: AGBgainleg = ΔAGB gain of Leguminosae, AGBgainOS = ΔAGB gain of the others species, AGB1 = plot initial, AGB stemgainleg = Δstem gain of Leguminosae, stemgainOS = Δstem gain of the others species, stem1 = plot initial stems, AGBlossleg = ΔAGB loss of Leguminosae, AGBlossOS = ΔAGB loss of the others species, stemlossleg = Δstem loss of Leguminosae, stemlossOS = Δstem loss of the others species.

Functional traits

We collected the functional traits in the permanent plots of the study sites, in well-illuminated branches of three healthy mature individuals of each Leguminosae species, according to the protocol by Perez-Harguindeguy et al. (2013). In each branch, we collected a satisfactory number of leaves (to scan and perform measurements) in order to obtain the leaf area, measured one meter from the distal portion of the branches collected, and extracted two pieces (samples) of the branch for anatomy and measurements. A minimal number of five leaves was scanned in the resolution of 150 pp in grayscale, weighed in a digital balance accurate to 0.001 g (fresh weight). One of the branch samples was imbibed in water for three days, after bark and pith removal, where present. After imbibition, we obtained fresh weight and fresh volume through the Archimedes' Principle or water displacement method (Falster e

Westoby, 2005). After obtaining the fresh measurements, we placed the leaf and branch samples in a heating chamber at 70ºC for three days to obtain the dry weight. Throughout this process, we obtained the following leaf-related variables: leaf area (LA), leaf mass per area (LMA – dry weight in mg / leaf area in mm^2), specific leaf area (SLA – leaf area in mm^2 / dry weight in mg) and leaf dry matter content (LDMC – dry weight in mg / fresh weight in g). Additionally, we calculated the branch-related variables sapwood density (fresh weight – g / fresh volume – cm^3) and sapwood specific density (dry weight – mg / fresh volume – mm^3) (Pérez-Harguindeguy *et al.*, 2013).

We used the other branch sample to examine the vessel-related functional traits, carrying out the following approach: we sliced the branch sample using a GSL1 microtome (Gärtner, Lucchinetti e Schweingruber, 2014), stained the obtained sections with toluidine blue and mounted them into microscope slides with glycerine jelly. In a Zeiss optical microscope coupled to a digital camera (AxioCam ERc5s), we photographed the vessels at 100x magnification, producing three photos per slides (in the distal, middle and proximal regions of xylem, comprising all range of vessel sizes). Through the photographs, we stained and measured / counted the xylems' vessels using, respectively, digital square frames of a standardized area (1 mm^2) in the imaging software GIMP 2.8.10 (https://www.gimp.org/) and the imaging software Image J (National Institutes of Health, Bethesda, MD, USA). We calculated total vessel lumen areas (average of the three photos and three individuals per species in a square frame), vessel diameter (µm), vessel density (in number of vessels per square frame area), vessel fraction (vessel area – µm / vessel density – mm^2), vessel multiple fraction (amount of multiple vessels) and the vulnerability index of Carlquist (1977) (vessel diameter / vessel density) (Apgaua *et al.*, 2017; Pérez-Harguindeguy *et al.*, 2013; Scholz *et al.*, 2013). Vessel multiple fraction is a vessel grouping index that represents the percentage of vessels in direct contact with one another (multiple vessels) in total vessels per square frame, and this clustering of vessels may enhance hydraulic efficiency (Apgaua *et al.*, 2017; Scholz *et al.*, 2013). Values of vessel multiple fraction close to 01 denote a tendency for the existence of solitary vessels. The vulnerability index indicates a plant's susceptibility to cavitation, drought or induced frost (Carlquist, 1977; Scholz *et al.*, 2013).

With the trait-related information for the tree species collected in the sampled areas, we initially obtained a synthesis matrix of species traits (species x traits), by obtaining their means for each variable. When species had their traits measured in more than one location, we differentiate their means in this final matrix (for example, *Acosmium lentiscifolium* from AGP, *Acosmium lentiscifolium* from BonM) to account for possible intraspecific variability. This matrix with species synthesis values for each trait was submitted to Principal Component Analysis (PCA), from which we extracted the species scores in the first two axes (35.6% of variance explained for axis 1 and 14.3% for axis 2) to be used as a synthesis of species functional patterns. The resulting matrix (species x scores in the two axis) were then used as a traits matrix to obtain the community-weighted means (CWM) for the functional patterns synthesized by the two PCA axis, using the *functcomp* function of the *FD* package (Laliberté, Legendre e Maintainer, 2015). Weighting was performed using species abundance in sample units as measure of relative importance, where variations within the same species were logically only considered in sample units of each specific site.

Phylogenetic data

Based on the Leguminosae species pool of the study sites we built the phylogenetic tree through the *ComTreeOpt* function from the *ComTreeOpt* package (Gastauer *et al.*, 2018) in R environment (2018). We dated the tree using the *phylomatic* function from the PHYLOCOM 4.2 software based on the mega tree R20160415.new (Gastauer, Augusto e Meira-Neto, 2017) and adjusted the clade lengths with the *chronos* function from the *ape* package (Paradis e

Schliep, 2019). We subsequently calculated the UniFrac (Lozupone, Hamady e Knight, 2006) phylogenetic beta-diversity between the sample units using the *unifrac* function from the *picante* package (Kembel, 2010). Next, we used these distances to obtain an ordination of the sample units using Principal Coordinates Analysis (PCO). The scores obtained for each sample unit in the two more explicative axis (13.2 % of variance explained for the axis 1 and 7.2 % for the axis 2) were considered a synthesis of the phylogenetic composition of each sample unit to be used as an explanatory variable in the analysis elucidated below.

Data analysis

To evaluate phylogenetic, traits, soil, climate and altitude effects in Leguminosae success (structure and dynamics) we fitted generalized linear mixed-effects models. Random effects were incorporated due to the data's nested design and the repeated measures at the same sample unit in the structure data, in which we used two inventories. For the models of proportional species richness, stems and AGB of Leguminosae, fragments and sample units were coded as random factors, and for dynamics models only fragment was used as a random factor (Bolker *et al.*, 2009). Explanatory variables with Pearson correlation > |0.6| were not allowed in the same models (Dormann *et al.*, 2013; Magrach, Santamaría e Larrinaga, 2012), and selected models were checked for variance inflation factor (VIF) > 4. We attested residuals normality and variance homogeneity by residuals analyses, and when normality improvement was necessary, we applied cube-root transformation, since most of our responses contain zeros. For model selection we used an information theoretical approach based on the Akaike Information Criterion of second order (AICc), in which the best model was indicated by the lower AICc value (Burnham e Anderson, 2002). From the global models we obtained the best models (ΔAICc ≤ 2) for each response variable, where models' degrees of freedom were limited according to the number of observations for each response variable, ensuring at least 15 observations per degree of freedom. We submitted the best models to model averaging

(Burnham e Anderson, 2002) and then calculated the averaged coefficients and their respective 95% confidence intervals. We obtained the relative importance of each explanatory variable based on Akaike weights; however, relative importance will not be discussed since some variables were not contained in the same number of models. Effect size was assessed through the standardized coefficients. For each response variable we obtained an averaged R^2 from the selected models by the Nakagawa and Schielzeth (2013) method. We also checked for Spatial Autocorrelation (SAC) in model residuals through Moran’s I test, and found the models residuals are exempt of SAC.

We used the following packages to perform data analyses: lme4 for fitting the linear mixed-effects models (Bates *et al.*, 2015); lmerTest to calculate models’ degrees of freedom (Kuznetsova, Brockhoff e Christensen, 2017); MuMIn for model selection, model averaging (Bartón, 2009) and R^2 calculation (Nakagawa e Schielzeth, 2013) and ncf to test the presence of SAC (Bjornstad, 2018). All analyses were performed at R version 3.5.1 (R Core Team, 2018) with a significance level of 0.05. We opted to show and discuss only the statistically significant variables included in the averaged models (ΔAICc ≤ 2).

Results

CWM axis 1 synthesized investments in vessel fraction, vessel area and vulnerability positively, while it negatively synthesized vessel density, leaf mass per area, sapwood density and specific sapwood density, with negative correlations with organic matter, and positive with sand (table with correlations in supplementary material). This axis separated two groups (Fig. 2). One group characterised mainly by an investment in resource acquisition (higher vessel area and, consequently, higher vulnerability), formed by samples collected in semideciduous forests, although some plots of semideciduous forests aggregated with the second group. This second group was more closely clumped, with species negatively associated with the vulnerability-conditioning traits, and more associated with vessel density and sapwood density. Rain forests did not form a separate group, being representative in the entire axis gradient, suggesting higher specificity of Leguminosae species in seasonal environments and more generalized populations in moist environments. In turn, CWM axis 2 synthesized an investment in leaf mass per area, with strongly positive correlations with LMA and sapwood density. This axis correlated positively with organic matter and negatively with sum of bases, phosphorus and silt. However, CWM axis 2 did not clearly separate any groups.

UniFrac axis 1 synthesized phylogenetic distances between one of the semideciduous study areas (Mat) and all other sampled areas (Fig. 3). This axis had a negative correlation with clay, since Mat is the only area without riparian influence among our sampled semideciduous forests, and in which more genera from other domains (mostly from the Brazilian Savannas or Cerrado). UniFrac axis 2 separated two groups: one comprised of semideciduous forest, and the other of deciduous and rain forests together. Thus, the more evolutionarily stable areas were grouped together, while semideciduous, an ecotonal physiognomy with influence of Atlantic and Cerrado domains, presented larger phylogenetic distances. This axis had positive correlations with temperature seasonality and precipitation of the wettest quarter, and negative correlations with sum of bases, mean diurnal range and precipitation of the driest quarter.

The structural parameters of Leguminosae presents the altitude as an important factor in all analysed parameters. Altitude (estimate = - 0.0105, $p < 0.001$), percentage of sand (estimate = - 0.0093, $p < 0.001$), total annual precipitation (estimate = - 0.0104, $p < 0.001$) and annual mean temperature (estimate = - 0.0099, $p < 0.001$) had a negative effect on richness proportion of Leguminosae in the gradient studied. For annual mean temperature (estimate = 0.0099, $p < 0.001$), sum of bases (estimate = 0.0092, $p < 0.001$), clay (estimate = 0.0101, $p < 0.001$) and silt (estimate = 0.0006, $p < 0.001$), we found the opposite effect. The rise of these variables represents the rise of the Leguminosae richness in the studied sites (Fig. 4). All variables had a strong influence over richness, except silt. This model showed an average R^2 of 73%.

For stem proportion model, altitude (estimate = - 0.3584, $p < 0.001$), sand (estimate = - 0.1818, $p < 0.001$), temperature annual range (estimate = - 0.1027, $p = 0.003$), CWM axis 1 (estimate = - 0.0578, $p = 0.02$) and UniFrac axis 1 (estimate = - 0.2287, $p < 0.001$) had a negative effect, with strong effects caused by altitude and the UniFrac axis 1. Only CWM axis 2 had a positive effect on stem proportion (estimate = 0.1300, $p < 0.001$) (Fig. 5). Altitude and UniFrac axis 1 had the strongest effects over stem proportion. This model showed an average R^2 of 56 %.

Sand (estimate = - 4.3988, $p = 0.01$), phosphorus (estimate = - 2.9670, $p < 0.001$), UniFrac axis 1 (estimate = - 8.4808, $p < 0.001$), mean diurnal range (estimate = - 8.0781, $p < 0.03$) and altitude (estimate = - 8.9381, $p < 0.001$) had a negative effect on aboveground (ABG) biomass, with the strongest negative effects represented by UniFrac axis 1, mean diurnal range and altitude (Fig. 6). CWM axis 2 (estimate = 5.2260, $p < 0.001$) and annual mean temperature (estimate = 10.3687, $p < 0.001$) had positive effects over ABG biomass, with temperature accounting for the strongest positive effect. This model showed an average R^2 of 34 %.

For the variables related to temporal behaviour (dynamics), only two explanatory variables had a negative effect on biomass gain: CWM axis 1 (estimate = - 0.0081, $p = 0.04$) and UniFrac axis 1 (estimate = - 0.013, $p = 0.02$), with the latter variable exerting the strongest effect (Fig. 7). This model showed an average R^2 of 7 %.

Sand (estimate = - 0.0141, $p = 0.004$), annual precipitation (estimate = - 0.0175, $p < 0.001$), UniFrac axis 2 (estimate = - 0.0091, $p = 0.04$) and altitude (estimate = - 0.0170, $p < 0.001$) had a negative effect over the temporal loss in biomass. On the other hand, sum of bases (estimate = - 0.0106, $p = 0.01$), isothermality (estimate = - 0.0120, $p = 0.008$) and annual mean temperature (estimate = - 0.0166, $p < 0.001$) had a positive effect over loss in biomass. The variables with stronger effects were annual precipitation, altitude, temperature and Unifrac axis 2 (Fig. 8). This model showed an average R^2 of 14 %.

Discussion

Altitude was the most representative variable, influencing all analyzed parameters (except gain), probably because it synthesizes important biogeographic and climatic variables that encompass legumes preferences (Neves *et al.*, 2015; Oliveira-Filho e Fontes, 2000), as discussed below, refuting our hypothesis. The results show that the percentage of response is not the same for structure and temporal behavior of Leguminosae. The explanatory variables analyzed presented a higher percentage of explanation for the structural parameters, and a smaller explanation power for temporal parameters, suggesting that the temporal behavior of legume species may be more related with variables not considered in this study.

Leguminosae of the deciduous forests were the most cohesive group in the PCA and the PCO, related to functional traits that confer lower vulnerability to cavitation, as expected for areas that have water deficit as the main environmental filter driving community assembly (Adler *et al.*, 2014; Anderegg, 2015; Chauvet *et al.*, 2017; Chave *et al.*, 2009; Donovan *et al.*, 2011; Wright *et al.*, 2004). As precipitation seasonality decreases from deciduous to semideciduous forests, species presented traits more related to resource acquisition, which are positively related to increasing vulnerability (Anderegg, 2015; Chauvet *et al.*, 2017; Perez-Harguindeguy *et al.*, 2013). The larger and wider are the conducting vessels, the lower is their resistance to water flow, their density per mm² as well as the wood density (Apgaua *et al.*, 2017; Chave *et al.*, 2009; Tng *et al.*, 2018). Plants with these traits, investing in more conducting vessels, improve their growth and competitive efficiency, but efficient transportation does not necessarily mean safe transportation, and these plants are more susceptible to cavitation

(Cornelissen *et al.*, 2003; Markesteijn *et al.*, 2011; Pérez-Harguindeguy *et al.*, 2013; Tng *et al.*, 2018; Vico *et al.*, 2017). Despite the increasing vulnerability to cavitation from deciduous to semideciduous forests, the rain forests did not reveal a functional pattern, leading us to infer higher legume specificity in extremely drier environments (Allen *et al.*, 2017; Gei *et al.*, 2018; Pennington, Lavin e Oliveira-Filho, 2009), and an increase of the generalization of functional traits in moist and wet environments.

The well-structured phylogenetic relationships of wood legumes in deciduous physiognomies of STDFs, with niche conservatism and high adaptation to drought, has been documented in several papers (Allen *et al.*, 2017; Gei *et al.*, 2018; Neves *et al.*, 2015; Oliveira-Filho *et al.*, 2013; Pennington, Lavin e Oliveira-Filho, 2009; Werneck *et al.*, 2011). Previous studies have recognized the historical habitat stability of the core areas of deciduous forest in the Caatinga Domain (Prado e Gibbs, 1993; Werneck *et al.*, 2011), to which has been attributed in part the current patterns of spatial distribution and species richness in these forests (Werneck *et al.*, 2011). In turn, semideciduous are an ecotonal physiognomy under milder weather influenced by the Atlantic and Cerrado floras, representing a transition zone between these domains (Oliveira-Filho e Fontes, 2000; Terra *et al.*, 2018). Oliveira-Filho and Fontes (2000) highlighted that semideciduous forests near the Cerrado are floristically different than semideciduous forests elsewhere. In our study, we only sampled Cerrado species such as *Copaifera langsdorffii* Desf. in semideciduous forests, and typical Cerrado genera like *Bowdichia*, *Hymenaea* and *Platypodium* were sampled in only one area of semideciduous forest (Mat), supporting their phylogenetic distances to other semideciduous fragments. The riparian influence present in two other semideciduous areas, with more clayey soils, may act as a filter to legume species phylogenetically closer to deciduous forests, further supporting the phylogenetic distances to Mat.

Oliveira-Filho and Fontes (2000) found altitude and temperature to be the main variables promoting the transition between rain and semideciduous forests. In our study, altitude appears decreasing legume representativity in richness, stem and biomass proportion. These decreases are expected, given the decreasing temperature and increasing humidity promoted by raising altitude, conditions opposed to those preferred by the Leguminosae (Neves *et al.*, 2015; Oliveira-Filho e Fontes, 2000). The factors associated with richness proportion reflect the preferences of Leguminosae: warm and dry environments, with more fertile and clayey soils with lower proportion of sand. In general, the abundance representativity of legumes is higher in dry areas, owing to the legume capacity to thrive under water-deficit conditions, conferring a competitive advantage in these habitats (Adams, Simon e Pfautsch, 2010; Gei *et al.*, 2018; Oliveira-Filho *et al.*, 2013). Leguminosae diversified in dry areas and are clearly conditioned by drought (Adams, Simon e Pfautsch, 2010). In warm seasonally dry environments, legumes often present compound leaves with small leafleats that reduce transpiration-prone area and consequently reduce daily water use (Gei *et al.*, 2018; Reyes-García *et al.*, 2012).

Legumes have high transpiration and water use efficiency with water allocation in heartwood (Reyes-García *et al.*, 2012), high nitrogen metabolism through diverse systems for nitrogen acquisition (Oliveira-Filho *et al.*, 2013) and other traits for coping with drought (German, Werden e Powers, 2015), such as leaf deciduousness (Murphy e Lugo, 1986). These traits offer the Leguminosae advantages for growth and accumulation of reserves in the wet seasons, favouring survival during the dry periods (Reyes-García *et al.*, 2012). Leaf deciduousness in particular is directly linked to the occurrence of Leguminosae in fertile soils: high fertility is necessary for rapid post dry season leaf-flush in deciduous physiognomies. Traits related to drought tolerance that decrease the vulnerability and promote the persistence of deciduous species in dry habitats are energetically expensive (Chave *et al.*, 2009; Donovan *et al.*, 2011; Wright *et al.*, 2004), and fertile soils helps to promote the formation of high-cost organs with higher lifespan. Beyond the functional traits related to hydraulic conductance in plants, some traits have great importance in promoting the persistence of a species in highly filtered habitats, and are poorly studied on this perspective (Araújo *et al.*, 2017; Araújo e Santos, 2019).

Traits that allow species persistence in a certain habitat by recovering from or preventing physical damages determine the species ability for survival and competition (Bond e Midgley, 2001). In this sense, resprouting ability, also influenced by phylogeny, can be considered a key trait in allowing species persistence in harsh environments (Araújo *et al.*, 2017; Araújo e Santos, 2019), driving legume adaptative strategies in areas of low altitude and low sand percentage. The high correlation of legume stem proportion with Unifrac axis 1 reveals that this is a phylogenetically constrained trait. It is widely accepted that drought triggers resprouting in seasonally dry areas (Araújo *et al.*, 2017; Dunphy, Murphy e Lugo, 2000), and recent studies have associated resprouting to water stress by flooding (Araújo e Santos, 2019). In our study, the association of legume resprouting with lower altitude / annual temperatures, larger vessel areas and species vulnerability, as well as its positive relationship with organic matter in less fertile soils (CWM axis 2), allows us to infer that resprouting is more intense in riparian plots of semideciduous forests. Leguminosae is strongly related and adapted to water deficit, so water saturation may represent a stressful condition to this family. Hence, investing in sprouts can be a way to survive under regular stress regimes, like the floodings of the rainy seasons, preventing the death of entire individuals in cases of trunk breakage (Araújo *et al.*, 2017; Dunphy, Murphy e Lugo, 2000) by partitioning the biomass in several trunks.

Aboveground biomass proportion of Leguminosae was strongly negatively associated with altitude, but the main driver of biomass was the mean annual temperature in areas where the mean diurnal ranges were not highly variable. Aboveground biomass is an important component of net primary productivity, driven by growth and mortality and related to trade-offs between resource acquisition or survival and persistence in a habitat (Lasky, Jesse R. *et al.*, 2014). The positive association with CWM axis 2 allows an understanding that legumes with acquisitive ecological strategies allocate more biomass. This strategy was negatively associated with the phylogenetic distances synthesized by Unifrac axis 1, which occurs with the temporal biomass gain. Thus, acquisitive species under riparian influence in semideciduous forests, related to environments with larger clay and organic matter contents, allocate more aboveground biomass and present higher biomass gain. Investigating the forests communities of our study region, Terra et al. (2018) found that density of individuals and basal area are higher in the semideciduous in comparison with deciduous forests. In fact, plants under stressful conditions reduce stem growth. Dry seasons are more severe in deciduous forests (Terra *et al.*, 2018), so when species shed leaves, their growth is suppressed in order to survive the water deficit (Santos, Carvalho e Santos, 2018). Biomass loss decreases when altitude and climatic variables related to altitude (precipitation and temperature) increases. However, all temporal variables analyzed had a considerably lower percentage of explanation when compared to structural variables. Biomass was related to phylogeny and leaf traits, but also with diversity, successional stages and competition (Lasky, Jesse R. *et al.*, 2014; Lasky, Uriarte e Muscarella, 2016), and mainly with natural temporal dynamics fluctuations that we were unable to account for (Reis *et al.*, 2017).

Climatic and edaphic variables are the main drivers of vegetation patterns and turnover between plant communities, and consequently of legume occurrence and structure in space (Gei *et al.*, 2018; Neves *et al.*, 2015, 2017; Oliveira-Filho *et al.*, 2013), as our study has shown. However, few are the studies that tested these variables in temporal vegetation response, and in a context of climate change, they are highly required (Allen *et al.*, 2017). Studies have demonstrated that density-dependent mechanisms (Higuchi *et al.*, 2008), niche-based deterministic mechanisms (Swenson *et al.*, 2012) and successional stages (Lasky, Jesse R. *et al.*, 2014; Santos, Carvalho e Santos, 2018) are important drivers of the temporal behavior of tropical communities. However, we did not find studies investigating temporal behavior that explain Leguminosae success. Previous research has shown the importance of drought severity for driving species composition (Allen *et al.*, 2017; Muscarella *et al.*, 2016; Oliveira-Filho *et al.*, 2013; Santos, Carvalho e Santos, 2018; Terra *et al.*, 2018), and changes in composition that favors drought-related species, such as legumes (Allen *et al.*, 2017; Oliveira-Filho *et al.*, 2013; Rodrigues *et al.*, 2015). Our study shows that Leguminosae representativity in richness is related not only to water deficit and temperature, but also to fertile soils. Thus, the success of Leguminosae in colonizing and persisting in different habitats is linked to the evolutionary capacity of the species in this family to thrive under water-deficit conditions through functional traits, applying different types of ecological strategies related to the severity of environmental filters. These effects can be used to predict future responses of tree communities and ecosystems to environmental change and to understand biogeographic patterns, also being important for conservation strategies in these usually neglected formations (Allen *et al.*, 2017).

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Table 1. Physiognomies (P) and location of study sites, latitude (S) and longitude (W), mean altitude (Alt.), annual mean temperature in ºC (T) and rainfall, climate type according to Koppen, number of species with functional traits collected in each area (R) and total area of permanent plots (A). TDF = Tropical Deciduous Forest, TSF = Tropical Semideciduous Forest, TRF = Tropical rain Atlantic Forest.

P	Sites	Lat. (S)	Long. (W)	Alt.	T	Rainfall	Climate	R	A
TDF	AGP	15°36'29.4"	44°42'05.6"	500	23	1.000	Aw	10	1
TDF	BonM	15°18'00.75"	44°44'45.1"	670	23	1.086	Aw	10	1,5
TDF	VV	14°24'88.0"	44°09'79.0"	658	23	1.000	Bsh	09	0,8
TSF	Lagoa	21°13'11.0"	44°58'15.0"	875	19	1.493	Cwb	10	1,16
TSF	Mat	21°13'40.0"	44°57'50.0"	927	19	1.493	Cwb	09	2,23
TSF	Subest	21°13'17.0"	44°57'47.0"	925	19	1.493	Cwb	13	2,08
TRF	Carr	21º36’39.0”	44º36’39.1”	1200	17	1.632	Cwb	02	1
TRF	Itam	22º21’55.1”	44º48’32.0”	1500	14	1.652	Cwb	03	1
TRF	BocM	22º13’00.8”	44º32’23.3”	1500	15	1.607	Cwb	08	1

Figure 1. Study areas of Leguminosae in a in a xeric-mesic environmental gradient. The three sites in north of Minas Gerais state are fragments of deciduous forests, the three sites condensed in one point are the semideciduous forests located in the municipality of Lavras. The three sites in the south of Minas Gerais state are fragments of rain forests with nebular influence.

Figure 2. Community-weighted means (CWM) of the two PCA axis obtained through functional traits of Leguminosae in the sampled plots, when the dots represents each plot sampled (a); Correlation values between Leguminosae functional traits and each one of the two PCA axis used as synthesis variables (only traits with correlation values equal or greater than |0.6| are plotted) (b) in a xeric-mesic environmental gradient. Dry = deciduous forest, Semi = semideciduous forest, Rain = rain forests LMA = leaf mass *per* area, Specific SD = specific sapwood density.

Figure 3. Principal Coordinates Analysis obtained with values of phylogenetic beta-diversity calculated by UniFrac for Leguminosae sampled in a in a xeric-mesic environmental gradient. Dots represents each plot sampled.

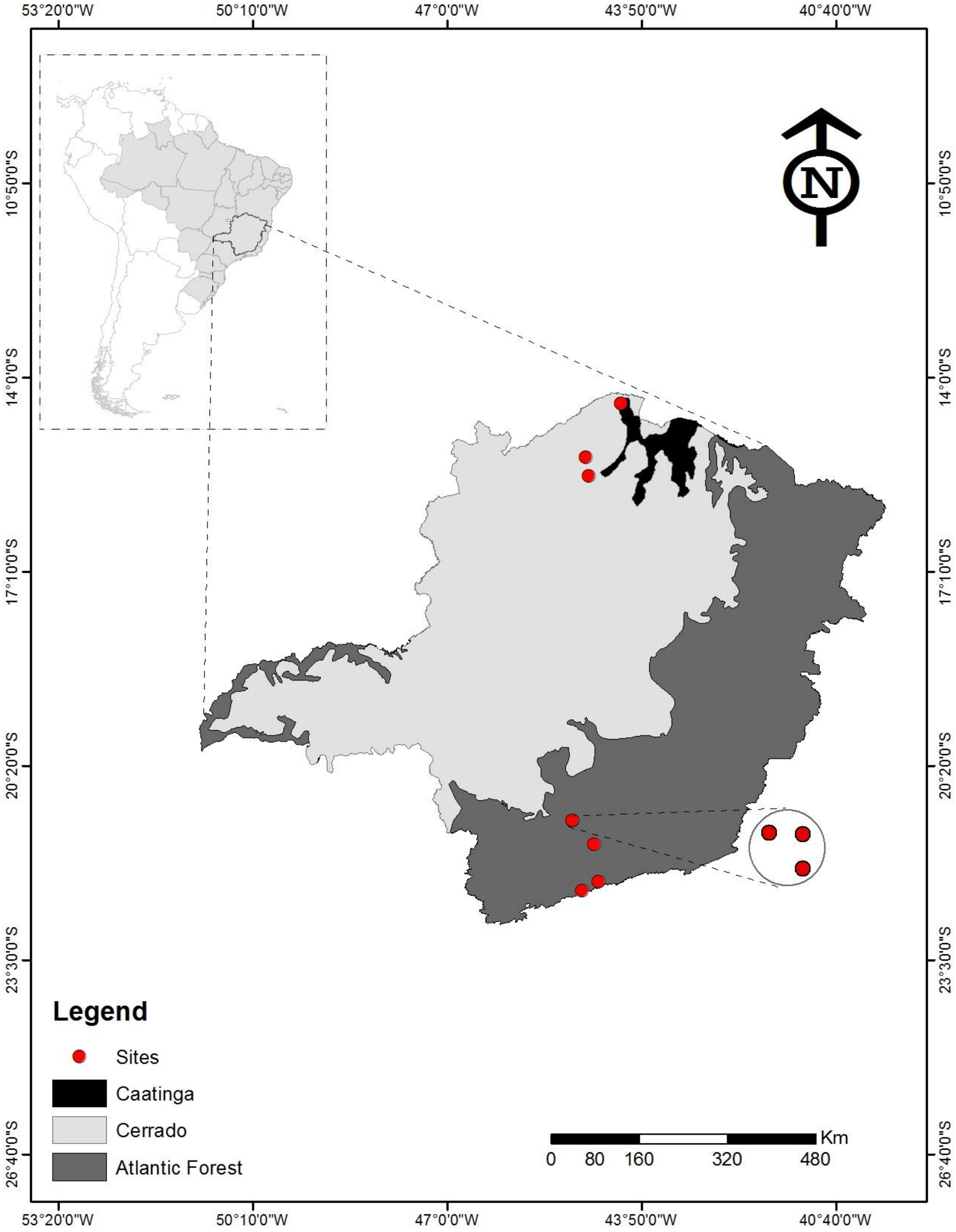
Figure 4. Explanatory variables (Model parameter) and their effects on richness proportion of Leguminosae sampled in a xeric-mesic environmental gradient. Length of bars represents the strength in which the explanatory variable influences the variable response. When the standard error touch the zero, the variable is not statistically significant. Plot obtained with ggplot2 (Wickham 2016).

Figure 5. Explanatory variables (Model parameter) and their effects on stem proportion of Leguminosae sampled in a xeric-mesic environmental gradient. Length of bars represents the strength in which the explanatory variable influences the variable response. When the standard error touch the zero, the variable is not statistically significant. Plot obtained with ggplot2 (Wickham 2016).

Figure 6. Explanatory variables (Model parameter) and their effects over aboveground (ABG) biomass of Leguminosae sampled in a xeric-mesic environmental gradient. Length of bars represents the strength in which the explanatory variable influences the variable response. When the standard error touch the zero, the variable is not statistically significant. Plot obtained with ggplot2 (Wickham 2016).

Figure 7. Explanatory variables (Model parameter) and their effects on temporal gain in biomass of Leguminosae sampled in a xeric-mesic environmental gradient. Length of bars represents the strength in which the explanatory variable influences the variable response. When the standard error touch the zero, the variable is not statistically significant. Plot obtained with ggplot2 (Wickham 2016).

Figure 8. Explanatory variables (Model parameter) and their effects on temporal loss in biomass of Leguminosae in a xeric-mesic environmental gradient. Length of bars represents the strength in which the explanatory variable influences the variable response. When the standard error touch the zero, the variable is not statistically significant. Plot obtained with ggplot2 (Wickham 2016).


53°20'0"W
50°10'0"W
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10°50'0"S
14°0'0"S
17°10'0"S
20°20'0"S
23°30'0"S
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N
Legend
Sites
Caatinga
Cerrado
Atlantic Forest
Km
0
80
160
320
480

Figure 1.

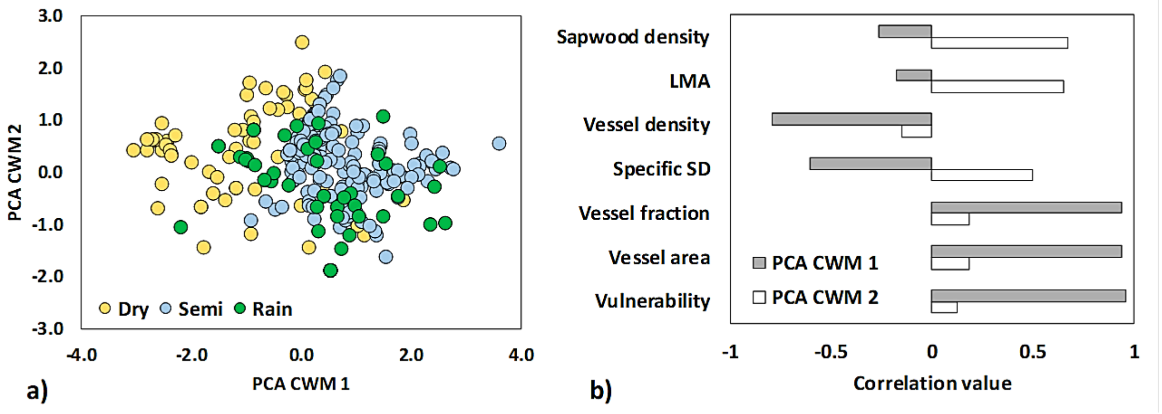
3.0
2.0
1.0
0.0
-1.0
-2.0
-3.0
PCA CWM 2
● Dry ● Semi ● Rain
-4.0
-2.0
0.0
2.0
4.0
PCA CWM 1
a)
Sapwood density
LMA
Vessel density
Specific SD
Vessel fraction
Vessel area
Vulnerability
▨ PCA CWM 1
☐ PCA CWM 2
-1
-0.5
0
0.5
1
Correlation value
b)

Figure 2.

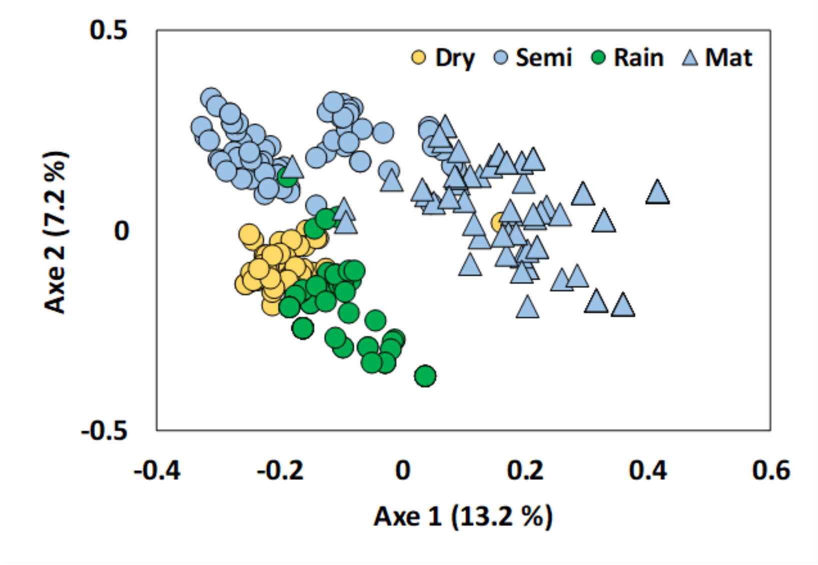

Figure 3.

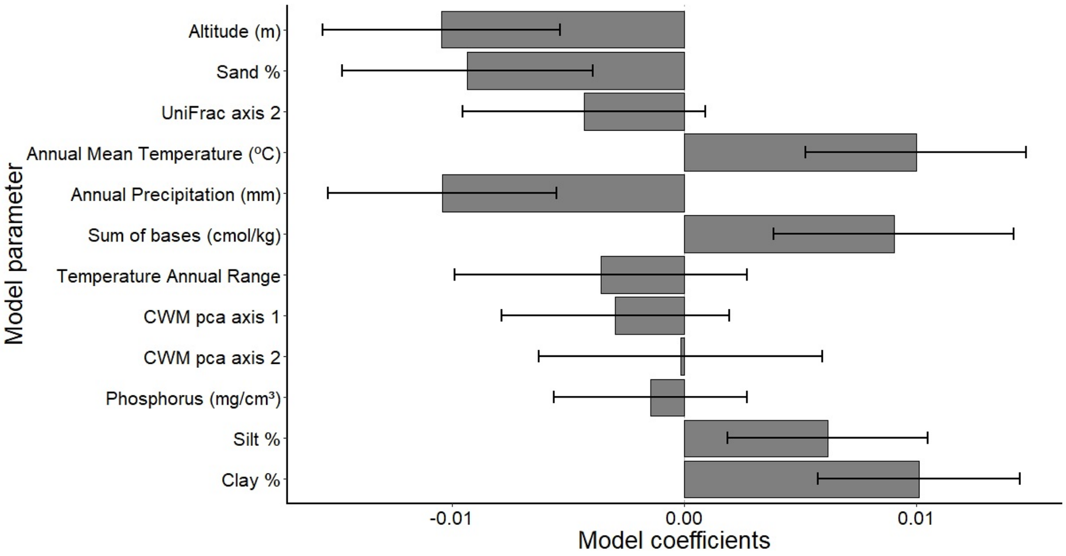
Model parameter
Altitude (m)
Sand %
UniFrac axis 2
Annual Mean Temperature (ºC)
Annual Precipitation (mm)
Sum of bases (cmol/kg)
Temperature Annual Range
CWM pca axis 1
CWM pca axis 2
Phosphorus (mg/cm³)
Silt %
Clay %
-0.01
0.00
0.01
Model coefficients

Figure 4.

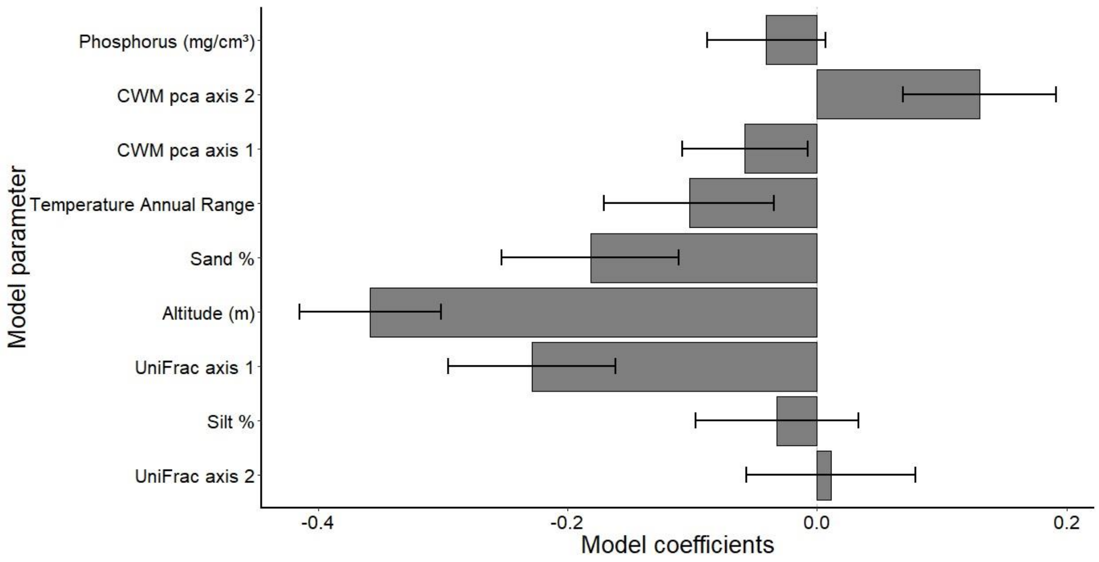
Model parameter
Phosphorus (mg/cm³)
CWM pca axis 2
CWM pca axis 1
Temperature Annual Range
Sand %
Altitude (m)
UniFrac axis 1
Silt %
UniFrac axis 2
-0.4
-0.2
0.0
0.2
Model coefficients

Figure 5.

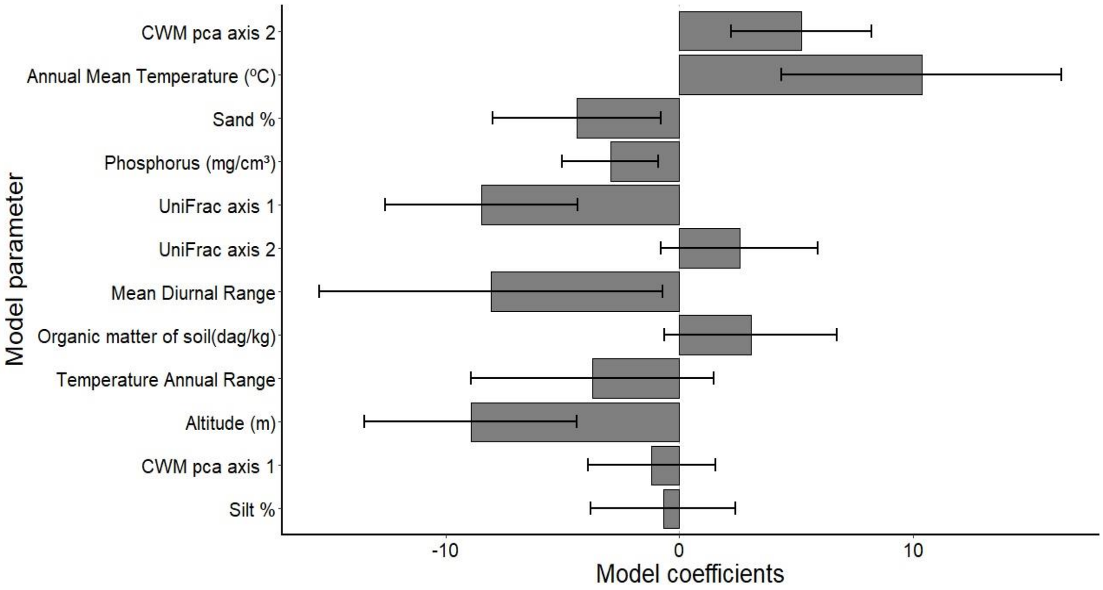
CWM pca axis 2
Annual Mean Temperature (ºC)
Sand %
Phosphorus (mg/cm³)
UniFrac axis 1
UniFrac axis 2
Mean Diurnal Range
Organic matter of soil(dag/kg)
Temperature Annual Range
Altitude (m)
CWM pca axis 1
Silt %
Model parameter
-10
0
10
Model coefficients

Figure 6.

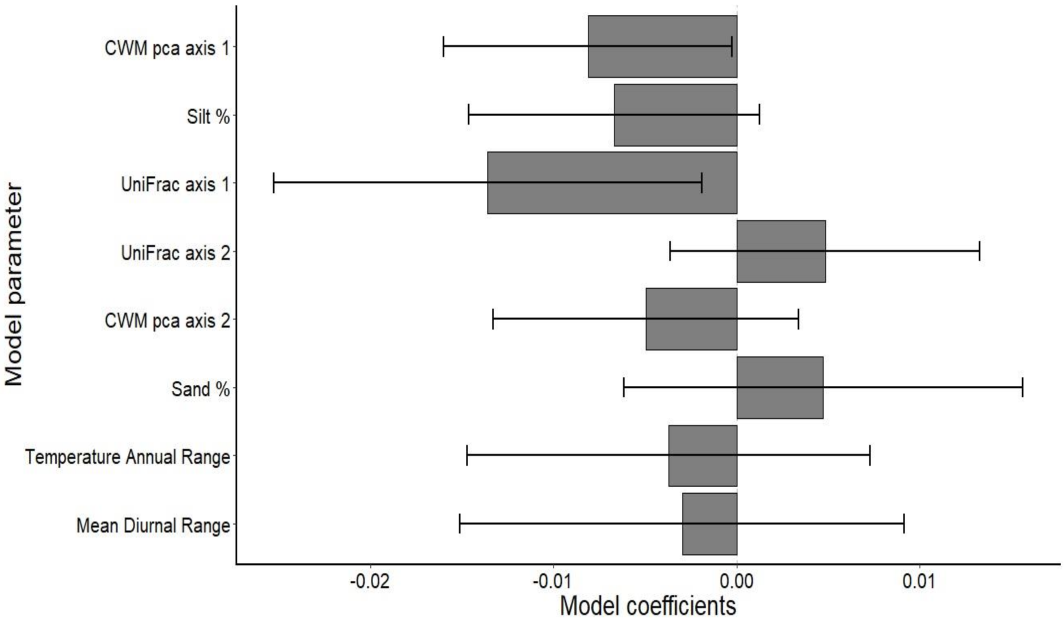
Model parameter
CWM pca axis 1
Silt %
UniFrac axis 1
UniFrac axis 2
CWM pca axis 2
Sand %
Temperature Annual Range
Mean Diurnal Range
-0.02
-0.01
0.00
0.01
Model coefficients

Figure 7.

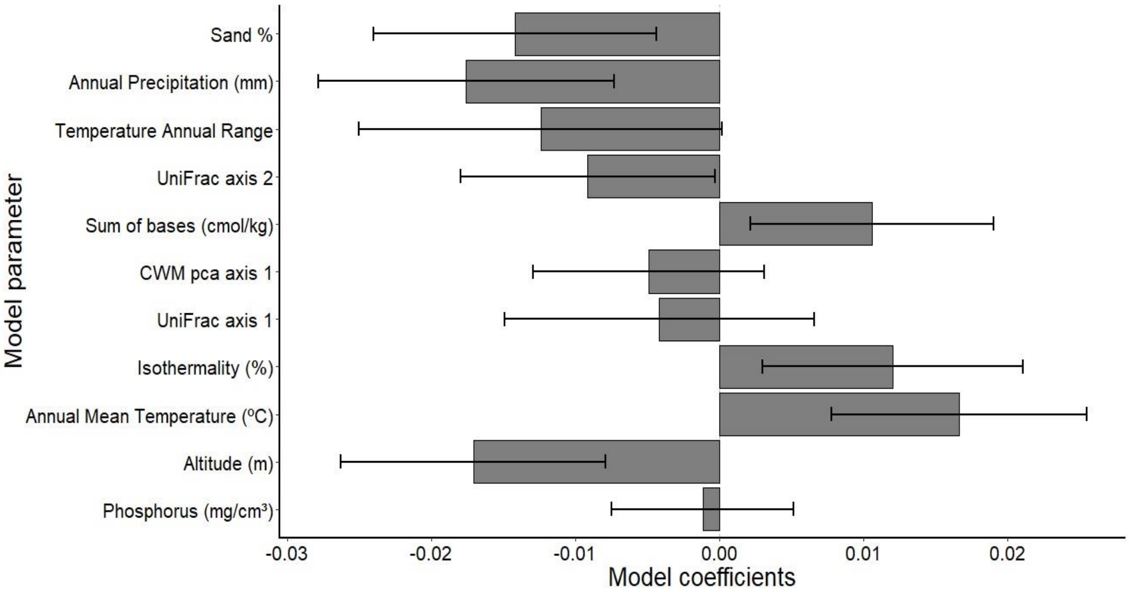
Sand %
Annual Precipitation (mm)
Temperature Annual Range
UniFrac axis 2
Sum of bases (cmol/kg)
CWM pca axis 1
UniFrac axis 1
Isothermality (%)
Annual Mean Temperature (°C)
Altitude (m)
Phosphorus (mg/cm³)
Model parameter
-0.03
-0.02
-0.01
0.00
0.01
0.02
Model coefficients

Figure 8.

Supplementary table 1. Correlations between variables of functional traits, phylogenetic distance, soil and bioclimatic variables of Wordclim in a xeric-mesic environmental gradient, part one. CWM = Community-weighted means for the functional patterns of Leguminosae synthesized by Principal Components Analysis axis 1 (CWM1) and axis 2 (CWM2); UF = phylogenetic beta-diversity between sampled units using UniFrac and synthesized by Principal Coordinates Analysis axis 1 (UF1) and axis 2 (UF2); Alt = altitude; p = phosphorus; Sb = sum of bases; Al = Aluminum; Om = organic matter; Bio 1 = Annual Mean Temperature; Bio2 = Mean Diurnal Range (Mean of monthly (max temp - min temp)); Bio3 = Isothermality (BIO2/BIO7) (* 100); Bio4 = Temperature Seasonality (standard deviation *100); Bio5 = Max Temperature of Warmest Month; Bio6 = Min Temperature of Coldest Month; Bio7 = Temperature Annual Range (BIO5-BIO6); Bio8 = Mean Temperature of Wettest Quarter; Bio9 = Mean Temperature of Driest Quarter; Bio10 = Mean Temperature of Warmest Quarter; Bio 11 = Mean Temperature of Coldest Quarter; Bio12 = Annual Precipitation; Bio13 = Precipitation of Wettest Month; Bio14 = Precipitation of Driest Month; Bio15 = Precipitation Seasonality (Coefficient of Variation); Bio16 = Precipitation of Wettest Quarter; Bio17 = Precipitation of Driest Quarter; Bio18 = Precipitation of Warmest Quarter; Bio19 = Precipitation of Coldest Quarter.

	CWM1	**CWM2**	**UF1**	**UF2**	**Alt**	**ph**	**p**	**Sb**	**Al**	**Om**	**Sand**	**Silt**	**Clay**	**Bio1**	**Bio2**	**Bio3**
CWM1	1,000	-0,195	-0,025	0,377	0,326	-0,397	-0,052	-0,403	0,205	-0,047	0,021	-0,304	0,159	-0,384	-0,396	-0,455
CWM2	-0,195	1,000	0,414	-0,153	-0,343	0,086	-0,045	-0,021	-0,165	0,005	-0,205	-0,024	0,219	0,310	0,139	-0,075
UF1	-0,025	0,414	1,000	-0,001	0,142	-0,532	-0,088	-0,438	0,408	0,576	-0,530	-0,288	0,702	-0,164	-0,458	-0,338
UF2	0,377	-0,153	-0,001	1,000	-0,269	-0,051	-0,111	-0,021	-0,260	-0,135	-0,212	0,057	0,183	0,185	-0,449	-0,107
Alt	0,326	-0,343	0,142	-0,269	1,000	-0,752	-0,190	-0,607	0,799	0,431	-0,078	-0,379	0,292	-0,987	-0,469	-0,608
ph	-0,397	0,086	-0,532	-0,051	-0,752	1,000	0,264	0,802	-0,840	-0,541	0,307	0,527	-0,609	0,782	0,733	0,682

p	-0,052	-0,045	-0,088	-0,111	-0,190	0,264	1,000	0,183	-0,144	-0,139	0,243	-0,042	-0,224	0,223	0,348	0,240
Sb	-0,403	-0,021	-0,438	-0,021	-0,607	0,802	0,183	1,000	-0,656	-0,273	0,061	0,616	-0,412	0,637	0,473	0,633
Al	0,205	-0,165	0,408	-0,260	0,799	-0,840	-0,144	-0,656	1,000	0,637	-0,133	-0,436	0,378	-0,773	-0,467	-0,427
Om	-0,047	0,005	0,576	-0,135	0,431	-0,541	-0,139	-0,273	0,637	1,000	-0,601	-0,030	0,623	-0,412	-0,558	-0,216
Sand	0,021	-0,205	-0,530	-0,212	-0,078	0,307	0,243	0,061	-0,133	-0,601	1,000	-0,309	-0,833	0,129	0,635	0,299
Silt	-0,304	-0,024	-0,288	0,057	-0,379	0,527	-0,042	0,616	-0,436	-0,030	-0,309	1,000	-0,262	0,385	0,144	0,420
Clay	0,159	0,219	0,702	0,183	0,292	-0,609	-0,224	-0,412	0,378	0,623	-0,833	-0,262	1,000	-0,345	-0,722	-0,537
Bio1	-0,384	0,310	-0,164	0,185	-0,987	0,782	0,223	0,637	-0,773	-0,412	0,129	0,385	-0,345	1,000	0,535	0,715
Bio2	-0,396	0,139	-0,458	-0,449	-0,469	0,733	0,348	0,473	-0,467	-0,558	0,635	0,144	-0,722	0,535	1,000	0,535
Bio3	-0,455	-0,075	-0,338	-0,107	-0,608	0,682	0,240	0,633	-0,427	-0,216	0,299	0,420	-0,537	0,715	0,535	1,000
Bio4	0,508	-0,103	0,298	0,014	0,815	-0,789	-0,245	-0,707	0,627	0,316	-0,233	-0,448	0,485	-0,889	-0,573	-0,939
Bio5	-0,385	0,318	-0,190	0,141	-0,981	0,803	0,246	0,633	-0,779	-0,453	0,187	0,360	-0,389	0,996	0,602	0,705
Bio6	-0,331	0,277	-0,080	0,308	-0,968	0,687	0,169	0,595	-0,724	-0,307	0,005	0,394	-0,224	0,976	0,347	0,707
Bio7	-0,248	0,194	-0,379	-0,484	-0,247	0,528	0,289	0,250	-0,335	-0,544	0,600	-0,029	-0,590	0,273	0,914	0,146
Bio8	-0,343	0,331	-0,130	0,245	-0,995	0,750	0,203	0,607	-0,779	-0,408	0,090	0,368	-0,296	0,996	0,480	0,662
Bio9	-0,368	0,289	-0,157	0,219	-0,983	0,766	0,213	0,633	-0,764	-0,392	0,108	0,391	-0,327	0,998	0,492	0,729
Bio10	-0,378	0,314	-0,170	0,197	-0,991	0,786	0,217	0,639	-0,789	-0,424	0,122	0,387	-0,339	0,999	0,529	0,692
Bio11	-0,399	0,290	-0,185	0,172	-0,979	0,792	0,225	0,654	-0,770	-0,408	0,139	0,399	-0,363	0,999	0,539	0,745
Bio12	0,505	-0,283	0,310	0,060	0,909	-0,879	-0,264	-0,714	0,756	0,473	-0,269	-0,427	0,511	-0,944	-0,747	-0,756
Bio13	0,565	-0,275	0,372	0,214	0,801	-0,881	-0,249	-0,725	0,707	0,471	-0,292	-0,452	0,551	-0,834	-0,813	-0,682
Bio14	0,430	-0,249	0,265	-0,069	0,949	-0,846	-0,266	-0,679	0,765	0,459	-0,245	-0,395	0,467	-0,983	-0,660	-0,788
Bio15	-0,479	0,230	-0,379	-0,118	-0,853	0,882	0,304	0,690	-0,720	-0,527	0,400	0,369	-0,610	0,904	0,824	0,791
Bio16	0,500	-0,298	0,292	0,038	0,922	-0,872	-0,250	-0,713	0,762	0,462	-0,236	-0,440	0,486	-0,950	-0,723	-0,740

Bio17	0,453	-0,235	0,281	-0,029	0,931	-0,849	-0,274	-0,685	0,746	0,455	-0,275	-0,394	0,498	-0,972	-0,682	-0,816
Bio18	0,504	-0,244	0,331	0,087	0,887	-0,883	-0,291	-0,704	0,742	0,485	-0,324	-0,395	0,548	-0,932	-0,777	-0,785
Bio19	0,521	-0,238	0,358	0,123	0,864	-0,890	-0,291	-0,710	0,740	0,498	-0,344	-0,397	0,569	-0,910	-0,799	-0,770

Supplementary table 1. Correlations between variables of functional traits, phylogenetic distance, soil and bioclimatic variables of Wordclim in a xeric-mesic environmental gradient, part two. CWM = Community-weighted means for the functional patterns of Leguminosae synthesized by Principal Components Analysis axis 1 (CWM1) and axis 2 (CWM2); UF = phylogenetic beta-diversity between sampled units using UniFrac and synthesized by Principal Coordinates Analysis axis 1 (UF1) and axis 2 (UF2); Alt = altitude; p = phosphorus; Sb = sum of bases; Al = Aluminum; Om = organic matter; Bio 1 = Annual Mean Temperature; Bio2 = Mean Diurnal Range (Mean of monthly (max temp - min temp)); Bio3 = Isothermality (BIO2/BIO7) (* 100); Bio4 = Temperature Seasonality (standard deviation *100); Bio5 = Max Temperature of Warmest Month; Bio6 = Min Temperature of Coldest Month; Bio7 = Temperature Annual Range (BIO5-BIO6); Bio8 = Mean Temperature of Wettest Quarter; Bio9 = Mean Temperature of Driest Quarter; Bio10 = Mean Temperature of Warmest Quarter; Bio 11 = Mean Temperature of Coldest Quarter; Bio12 = Annual Precipitation; Bio13 = Precipitation of Wettest Month; Bio14 = Precipitation of Driest Month; Bio15 = Precipitation Seasonality (Coefficient of Variation); Bio16 = Precipitation of Wettest Quarter; Bio17 = Precipitation of Driest Quarter; Bio18 = Precipitation of Warmest Quarter; Bio19 = Precipitation of Coldest Quarter.

	Bio4	**Bio5**	**Bio6**	**Bio7**	**Bio8**	**Bio9**	**Bio10**	**Bio11**	**Bio12**	**Bio13**	**Bio14**	**Bio15**	**Bio16**	**Bio17**	**Bio18**	**Bio19**
CWM1	0,508	-0,385	-0,331	-0,248	-0,343	-0,368	-0,378	-0,399	0,505	0,565	0,430	-0,479	0,500	0,453	0,504	0,521
CWM2	-0,103	0,318	0,277	0,194	0,331	0,289	0,314	0,290	-0,283	-0,275	-0,249	0,230	-0,298	-0,235	-0,244	-0,238
UF1	0,298	-0,190	-0,080	-0,379	-0,130	-0,157	-0,170	-0,185	0,310	0,372	0,265	-0,379	0,292	0,281	0,331	0,358
UF2	0,014	0,141	0,308	-0,484	0,245	0,219	0,197	0,172	0,060	0,214	-0,069	-0,118	0,038	-0,029	0,087	0,123

Alt	0,815	-0,981	-0,968	-0,247	-0,995	-0,983	-0,991	-0,979	0,909	0,801	0,949	-0,853	0,922	0,931	0,887	0,864
ph	-0,789	0,803	0,687	0,528	0,750	0,766	0,786	0,792	-0,879	-0,881	-0,846	0,882	-0,872	-0,849	-0,883	-0,890
P	-0,245	0,246	0,169	0,289	0,203	0,213	0,217	0,225	-0,264	-0,249	-0,266	0,304	-0,250	-0,274	-0,291	-0,291
Sb	-0,707	0,633	0,595	0,250	0,607	0,633	0,639	0,654	-0,714	-0,725	-0,679	0,690	-0,713	-0,685	-0,704	-0,710
Al	0,627	-0,779	-0,724	-0,335	-0,779	-0,764	-0,789	-0,770	0,756	0,707	0,765	-0,720	0,762	0,746	0,742	0,740
Om	0,316	-0,453	-0,307	-0,544	-0,408	-0,392	-0,424	-0,408	0,473	0,471	0,459	-0,527	0,462	0,455	0,485	0,498
Sand	-0,233	0,187	0,005	0,600	0,090	0,108	0,122	0,139	-0,269	-0,292	-0,245	0,400	-0,236	-0,275	-0,324	-0,344
Silt	-0,448	0,360	0,394	-0,029	0,368	0,391	0,387	0,399	-0,427	-0,452	-0,395	0,369	-0,440	-0,394	-0,395	-0,397
Clay	0,485	-0,389	-0,224	-0,590	-0,296	-0,327	-0,339	-0,363	0,511	0,551	0,467	-0,610	0,486	0,498	0,548	0,569
Bio1	-0,889	0,996	0,976	0,273	0,996	0,998	0,999	0,999	-0,944	-0,834	-0,983	0,904	-0,950	-0,972	-0,932	-0,910
Bio2	-0,573	0,602	0,347	0,914	0,480	0,492	0,529	0,539	-0,747	-0,813	-0,660	0,824	-0,723	-0,682	-0,777	-0,799
Bio3	-0,939	0,705	0,707	0,146	0,662	0,729	0,692	0,745	-0,756	-0,682	-0,788	0,791	-0,740	-0,816	-0,785	-0,770
Bio4	1,000	-0,880	-0,871	-0,216	-0,852	-0,896	-0,877	-0,911	0,904	0,823	0,930	-0,905	0,894	0,944	0,918	0,906
Bio5	-0,880	1,000	0,953	0,357	0,989	0,989	0,995	0,993	-0,959	-0,860	-0,989	0,929	-0,963	-0,979	-0,951	-0,931
Bio6	-0,871	0,953	1,000	0,057	0,981	0,987	0,974	0,976	-0,861	-0,717	-0,932	0,805	-0,871	-0,917	-0,845	-0,813
Bio7	-0,216	0,357	0,057	1,000	0,234	0,217	0,278	0,264	-0,506	-0,623	-0,387	0,580	-0,486	-0,400	-0,528	-0,561
Bio8	-0,852	0,989	0,981	0,234	1,000	0,995	0,997	0,992	-0,917	-0,797	-0,964	0,869	-0,926	-0,948	-0,900	-0,875
Bio9	-0,896	0,989	0,987	0,217	0,995	1,000	0,996	0,998	-0,926	-0,806	-0,976	0,886	-0,933	-0,965	-0,915	-0,890

Bio10	-0,877	0,995	0,974	0,278	0,997	0,996	1,000	0,997	-0,942	-0,836	-0,980	0,899	-0,949	-0,967	-0,929	-0,908
Bio11	-0,911	0,993	0,976	0,264	0,992	0,998	0,997	1,000	-0,948	-0,841	-0,987	0,912	-0,953	-0,978	-0,939	-0,918
Bio12	0,904	-0,959	-0,861	-0,506	-0,917	-0,926	-0,942	-0,948	1,000	0,966	0,979	-0,983	0,999	0,982	0,995	0,992
Bio13	0,823	-0,860	-0,717	-0,623	-0,797	-0,806	-0,836	-0,841	0,966	1,000	0,894	-0,949	0,964	0,904	0,957	0,971
Bio14	0,930	-0,989	-0,932	-0,387	-0,964	-0,976	-0,980	-0,987	0,979	0,894	1,000	-0,963	0,977	0,998	0,978	0,963
Bio15	-0,905	0,929	0,805	0,580	0,869	0,886	0,899	0,912	-0,983	-0,949	-0,963	1,000	-0,973	-0,972	-0,992	-0,991
Bio16	0,894	-0,963	-0,871	-0,486	-0,926	-0,933	-0,949	-0,953	0,999	0,964	0,977	-0,973	1,000	0,979	0,988	0,984
Bio17	0,944	-0,979	-0,917	-0,400	-0,948	-0,965	-0,967	-0,978	0,982	0,904	0,998	-0,972	0,979	1,000	0,985	0,972
Bio18	0,918	-0,951	-0,845	-0,528	-0,900	-0,915	-0,929	-0,939	0,995	0,957	0,978	-0,992	0,988	0,985	1,000	0,997
Bio19	0,906	-0,931	-0,813	-0,561	-0,875	-0,890	-0,908	-0,918	0,992	0,971	0,963	-0,991	0,984	0,972	0,997	1,000

Artigo 2: Ecological strategies and drought predicts Leguminosae functional responses and vulnerability in Seasonally Dry Tropical Forests habitats

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Abstract: Seasonally Dry Tropical Forests (SDTF) constitutes a heterogeneous biome, but many studies treated their ecological strategies and functional responses homogeneously. Since Leguminosae are the most representative family in this biome, we separated the legume species in ecological groups according to their growth rates and evaluated the hydraulic functional traits in two SDTF vegetation types (semideciduous and deciduous forests, differently mainly in water availability). Growth rates were obtained through de community dynamics data. The growth rates formed three ecological groups (very fast, fast and slow growth). Functional traits showed differences in growth groups and vegetation types, depending on the trait. Very fast group presented more vulnerability to cavitation, and fast group more representativeness in deciduous forests. Deciduous forests had a conservative strategy, but with higher growth rate species, while semideciduous forests had an acquisitive strategy, but with lower growth rates species. These results contradict what literature traditionally have proposed for plant functional groups. Leguminosae representativeness have not differed between vegetation types, but slow growth rate species increase in semideciduous forests in the second dynamics interval. Semideciduous forests are more vulnerable than deciduous forests in a climate change scenario, and these functional changes reflect this vulnerability.

Key words: acquisitive strategy, conservative strategy, functional traits, deciduous forest, semideciduous forest

Introduction

Over 40% of tropical forests are subject to seasonal water stress, and multiple strategies are required for plant survival under these conditions (Miles *et al.*, 2006; Xu *et al.*, 2016). Beyond the climate changes and the predicted precipitation extremes for future scenarios, tropical forests are under a situation of more severe and frequent droughts (Apgaua, Pereira, *et al.*, 2015; Esquivel-Muelbert *et al.*, 2018; Sherwood e Fu, 2014). Despite some species tolerance to water stress, this aridity scenario may increase tree hydraulic stress levels (Apgaua, Pereira, *et al.*, 2015; Esquivel-Muelbert *et al.*, 2018; Xu *et al.*, 2016). This situation is aggravated due the lack of knowledge in how plant communities will respond to these changes (Anderegg, 2015; Sperry e Love, 2015; Xu *et al.*, 2016). Climatic changes may affect biodiversity, ecosystem process and species distribution through species biological traits (Esquivel-Muelbert *et al.*, 2018; Rodrigues *et al.*, 2015). Thus, species traits adapted to locals with more water stress can provide an overview of the adaptations required for species resilience and persistence in future aridity scenarios. In face of future increase in aridity predictions; understand the ecological requirements and define critical dimensions of species vulnerability to drought are crucial. Future forecasts predict species adapted to Seasonally Dry Tropical Forests (SDTFs), like Leguminosae, that are able to expand their distribution to habitats currently covered by wet forests (Allen *et al.*, 2017; Enquist e Enquist, 2011; Rodrigues *et al.*, 2015). Leguminosae are a high adapted and dominant family in the tropical dry forests, with high level of niche conservatism at these regions (Allen *et al.*, 2017; Gei *et al.*, 2018; Pennington, Lavin e Oliveira-Filho, 2009; Santos *et al.*, 2012). However, few studies focused on climate changes impacts in SDTF, and how species will respond to drought and temperature increases (Allen *et al.*, 2017).

The tropical forests resistance and resilience relies on strategies in which trees will respond to water deficit, and how anatomical traits support water transport (Apgaua *et al.*, 2017;

Tng *et al.*, 2018). Drought-induced tree mortality effects is documented in several studies (Anderegg *et al.*, 2012; Esquivel-Muelbert *et al.*, 2018; Phillips *et al.*, 2009; Rita *et al.*, 2016; Rodrigues *et al.*, 2015), these effects leads to changes in species distribution and community structure. Future predictions of climatic extremes scenarios and some studies predicts the potential of Leguminosae to expand their distribution for less drier areas than seasonally ones (Allen *et al.*, 2017; Enquist e Enquist, 2011; Rodrigues *et al.*, 2015). However, seasonally dry tropical forests (SDTF) are not a homogeneous biome, and present a range of climatic and environmental conditions, from semideciduous with lower seasonality to deciduous forest with great precipitation seasonality (Allen *et al.*, 2017). Due to environmental filtering and ecological responses to these effects, Leguminosae representativeness (in abundance) may vary along rainfall and soil nutrient gradients (Gei *et al.*, 2018). Finally, not all species respond similarly, because plants groups presents different ecological strategies and respond in different ways to water deficit (Apgaua *et al.*, 2017; Chauvet *et al.*, 2017; Powney *et al.*, 2014).

Associations between anatomical traits with plant groups with similar ecological strategies and requirements are usually strong (Adler *et al.*, 2014; Apgaua *et al.*, 2017; Chaturvedi, Raghubanshi e Singh, 2011). Trade-offs between efficiency or stability in water conductivity differ between these ecological groups (Apgaua *et al.*, 2017), and can be correlated with light requirements, growth rates and site conditions (Adler *et al.*, 2014; Chauvet *et al.*, 2017). To predict plant adaptations and their implications at ecosystem level, it is necessary to understand water conductivity mechanisms and the ecological strategies from distinct plant ecological groups (Apgaua *et al.*, 2017). Growth rates are a good predictor of trade-offs between resource acquisition and survival investment presented by most species (Adler *et al.*, 2014; Chao *et al.*, 2008). Plant traits, especially those related to xylem hydraulic conductivity can show the critical dimensions of vulnerability to embolism due to higher vapor pressure deficit in dry conditions (Anderegg, 2015). Stem vessel size, vessel area, density and vessels fractions are important in modulating water transport and tree growth, since they affect xylem conductivity (Apgaua, Ishida, *et al.*, 2015; Chave *et al.*, 2009) and may reflect the different strategies used by ecological groups to capture and use water in situations of aridity.

Generally, plant ecological groups are mediated by a trade-off between functional traits, such as species groups that presents acquisitive or conservative life histories (Adler *et al.*, 2014; Chao *et al.*, 2008). These different strategies will yield their growth rates and survival. Slow growth species reflect a resource conservative trade-off, with investment in survival, resistance and longevity, while fast growth species reflect a resource acquisition trade-off, with fast resources acquisition, but low internal conservation of these resources (Adler *et al.*, 2014; Diaz *et al.*, 2004; Lavorel e Garnier, 2002). The differences are strongly mediated by site conditions, especially by nutrients and water availability (Lavorel e Garnier, 2002; Xu *et al.*, 2016). Lower vessels diameter for xylem conductance, for example, may be an adaptative strategy in drier environments (Chave *et al.*, 2009; Díaz *et al.*, 2013). Through functional traits, species differ in ecological strategies, which enable (or not) their survival and persistence in the habitats. However, most of these studies are realized in rainforests, being dry formations neglected (Apgaua *et al.*, 2017; Boukili e Chazdon, 2017; Kraft e Ackerly, 2010; Phillips *et al.*, 2009; Powell *et al.*, 2013b; Tng *et al.*, 2018). Plant ecological strategies and trait adaptability to water deficit are also less studied in SDTF than in other formations (Xu *et al.*, 2016), with a lack of studies that used species and community dynamic growth rates to classify ecological groups. Although studies have cited water and nutrient stress as very important plant trade-offs environmental drivers (Diaz *et al.*, 2004; Díaz *et al.*, 2013; Powell *et al.*, 2013a; Xu *et al.*, 2016), most of these studies were conducted in evergreen formations. That lack of knowledge regarding dry formations hinders the understanding of how dry forests plant communities will respond to climatic changes.

In order to fill this gap, we collected hydraulic functional traits of sapwood branches and separated the species in growth rates groups. These collections were performed in two STDF vegetation types, both with permanent plots and forest dynamics data. The first vegetation type is the tropical deciduous forest, characterized by a leaf deciduousness higher than 60% in the dry season (Rezende *et al.*, 2017), included in the Caatinga domain (Santos *et al.*, 2012). They occur in high fertile and well-drained soils in north of Minas Gerais state (Apgaua *et al.*, 2014; Santos *et al.*, 2012), with a marked dry period, where drought is their strongest environmental filtering (Terra *et al.*, 2018). The second type is the tropical semideciduous forest, characterized by 30 – 60 % of leaf deciduousness in the dry season (Rezende *et al.*, 2017), and considered a vegetation type of Atlantic Forest Domain (Neves *et al.*, 2017; Oliveira-Filho e Fontes, 2000). Semideciduous forests have a less marked seasonality than the deciduous, being usually more diverse than the deciduous. Semideciduous counts with higher basal area, density and lower dominance of species than the deciduous forest (Terra *et al.*, 2018). As described above, SDTF occurs in different domains, under different soils and climate conditions (Allen *et al.*, 2017; Neves *et al.*, 2017; Pennington, Lavin e Oliveira-Filho, 2009). The mechanisms underlying species responses to water deficit are still poorly understood in dry environments (Xu *et al.*, 2016). According to Allen et al. (2017), no studies have tested if SDTF with different rainfall regimes respond similarly (or not) to climate changes, being this issue treated as priority for future research.

This study aimed to understand how SDTF possible responses to a climate change scenario, thus, our objective was to evaluate differences between hydraulic functional traits associated to tree species de Leguminosae with different growth rates and vegetation type (semideciduous and deciduous forest). We tested if legume functional traits differ between growth rate ecological groups and vegetation types, and if the vegetation type mediate by growth rates groups' effects. We also tested if Leguminosae representativeness (total and for each growth rate group) differ between vegetation types and intervals of measurement, and if vegetation types mediate the temporal effects. These data allow understanding how different strategies between ecological groups enable the persistence of Leguminosae in these forests. Thus, we hypothesized that: (1) Leguminosae species ecological strategies (expressed by functional traits) differ between vegetation types, growth rates and their interactions; (2) vegetation types with more water deficit (deciduous forest) tends to present conservative strategies; (3) representativeness of legumes will be greater in deciduous forest.

Materials and methods

Study area

We selected six SDTF sites, three in tropical semideciduous forest (TSF) and three in tropical deciduous forest (TDF), in south and north of Minas Gerais State, Brazil, respectively (Figure 1, Table 1). All sites have permanent plots with two forest dynamic inventories, and with compound soil samples, according to EMBRAPA (1997) protocol. These vegetation types are under different rainfall regime, both are affected by seasonal drought in the winter, but in TSF, the period of drought is smaller than in TDF (Table 1).

Soil samples were collected in a compound sample per plot (collected in each corner, in the middle of plot, and mixed). The variables measured were: pH in water, potassium, phosphorus, residual phosphorus (P-res), calcium, magnesium, aluminium, hydrogen plus aluminium (H + Al), sum of bases (SB), base saturation (V), effective cation exchange capacity (t), Al saturation (m), cation exchange capacity at pH 7.0 (t), organic matter, the proportions of coarse sand (2 to 0,2 mm), fine sand (0.2 to 0.05 mm), silt (0.05 to 0.02 mm) and clay (<0.02 mm) (EMBRAPA, 1997).

Forest dynamics

The areas were sampled in permanent plots of 20 x 20 m (400 m²) (total area of each one are found in Tab. 1). Inside the plots, all tree individuals which met the inclusion criterion of DBH (diameter at breast height) ≥ 5 cm were sampled, numbered with aluminium tags and identified by specialists, or collected a botanical material when it is necessary. Plots were measured again after five. The fragments of semideciduous forest (Lagoa, Matinha e Subest) and the deciduous florest fragment VVerde was sampled in 2010 and 2015. The deciduous forest Agropop and BMinas was sampled in 2009 – 2014 and 2012 – 2017 respectively. In these years, all surviving tree individuals were measured again. The new individuals who reached the inclusion criterion (recruits) were identified in the field with the aid of specialists, measured and marked with aluminium labels. Dead individuals were also recorded.

Plant Ecological Groups (PEG)

Only species from Leguminosae botanical family were sampled (to decrease evolutionary variation within similar strategies). Species were sampled when at least five individuals of the species were found at the site. For each species studied, we quantified the basal area gain of their populations (Sheil et al. 1995). The gain data were submitted to k-means group selection algorithm, in order to determine the optimal number of species groups based on the Elbow Method (Kodinariya & Makwana, 2013), which considers the inflection point of the sum of squares in the groups as the optimal point.

Functional traits

Functional traits are collected in well-illuminated branches of three healthy mature individuals of each Leguminosae species' in the permanent plots. All samples were collected according to Perez-Harguindeguy et al. (2013) protocol. We measured one meter from the distal portion of branches collected, and extract two pieces (samples) for anatomy and measurements.

One part of the sample was placed in water for three days to imbibition, after bark and pith removal when it was present. After the imbibition, fresh weight and fresh volume was obtained through the Principle of Archimedes (ASTM 2002) or water displacement method (Falster e Westoby, 2005). Samples was dried in a heating chamber at 70ºC for three days to obtain the dry weight. Through this process, sapwood density (fresh weight – g / fresh volume – cm^3), and sapwood specific density (dry weight – mg / fresh volume – mm^3) were obtained (Perez-Harguindeguy *et al.*, 2013).

From the other sample of branches, we obtained sections using a GSL1 microtome (Gärtner, Lucchinetti e Schweingruber, 2014), stained with toluidine blue and mounted them into microscope slides with glycerine jelly for examine the functional traits relative to vessels. In a Zeiss optical microscope coupled to a digital camera (AxioCam ERc5s), we photographed the vessels in a magnification of 100x, three photos per slides (in the distal, middle and proximal regions of xylem, comprising all range of vessel sizes). Through the photographs, the xylems' vessels were coloured using digital square frames of a standardized area (1 mm^2) in the imaging software GIMP 2.8.10 (https://www.gimp.org/) and measured / counted using the imaging software Image J (National Institutes of Health, Bethesda, MD, USA). We calculated total vessel lumen areas (average of the three photos and three individuals per specie in a square frame - μm^2), vessel diameter (μm^2), vessel density (in number of vessels per square frame area), vessel fraction (vessel area – μm^2 / vessel density), vessel multiple fraction (amount of multiple vessels) and the vulnerability index of Carlquist (vessel diameter / vessel density) (Apgaua *et al.*, 2017; Carlquist, 1977; Perez-Harguindeguy *et al.*, 2013; Scholz *et al.*, 2013). Vessel multiple fraction are a vessel grouping index that represent the percentage of vessels in direct contact with one another (multiple vessels) in total of vessels per square frame, this clustering of vessels may enhance hydraulic efficiency (Apgaua *et al.*, 2017; Scholz *et al.*, 2013). Values of vessel multiple fraction close to 01 denotes a tendency for solitary vessels.

Vulnerability index indicates a susceptibility of a plant to drought or frost induced cavitation (Carlquist, 1977; Scholz *et al.*, 2013). For high correlation, we excluded vessel diameter (correlated to vessel area) and vessel fraction (correlated to vulnerability index) from the analysis.

Representativeness

Leguminosae representativeness were obtained at each plot and at both inventories. For representativeness in plant ecological groups, we count only the legumes sampled (abundance per plot).

Data analysis

We used generalized linear mixed models (GLMM) to test differences in traits as function of vegetation type and growth rate groups and their interactions, being both coded as factor. Soil variables (continuous) were also included as control variables, ensuring that Pearson ($r \geq |0.6|$) correlated variables does not be included at the same model (Dormann *et al.*, 2013). GLMM were also used to test Leguminosae and PEGs representativeness differences between vegetation types, dynamics intervals and their interactions. To deal with the expected spatial autocorrelation (SAC) between fragments and with data’s nested design we used fragment and species as random factor on traits models. Individuals (observation level) are nested in species and fragments, for Leguminosae and PEGs representativity, both fragments and plots were used as random, dealing with the SAC and the repeated measures at the same plot (Bolker *et al.*, 2009). Normality was accessed by residuals inspection, to improve normality natural logarithmic transformation was used when necessary. Vessels density (count data) was ran through Poisson error distribution family, Pearson chi-square goodness of fit test was used to validate Poisson models fitting. We also checked for variance inflation factor (VIF > 4) at the models before adding interactions. Model selection was based in a theoretical information criterion, Akaike Information Criterion of second order (AICc, which is indicated for small sample sizes), being the best model the one with lower AICc value (Burnham e Anderson, 1998). Statistical significance was considered at the models with delta AICc ≤ 2, being after submitted to Wald type II chi-square deviance test. When the selected models just add control variables, only the best model (delta AICc = 0) was considered. Analysis of contrasts between factor levels were accessed through least square means pairwise contrasts, adopting tukey adjust method. We test the presence of SAC between fragments through Moran’s I test, and found the models residuals are spatially independent.

GLMM were obtained with lme4 library (Bates *et al.*, 2015) and lmerTest library was used to access denominator degrees of freedom (Kuznetsova, Brockhoff e Christensen, 2017). Wald chi-square tests were performed with car package (Fox e Weisberg, 2010), and the contrasts through emmeans package (Lenth *et al.*, 2019). Model selection and R^2 were realized through MuMIn package (Bartón, 2018; Nakagawa e Schielzeth, 2013). Moran’s I test was performed through ncf package (Bjørnstad 2016). All analysis were performed at R version 3.3.1. (R Core Team 2016), with significance level of 5%.

Results

Based on Kmeans group selection algorithm results we divided the species of Leguminosae into three mainly groups: Slow Growth with 19 or 51 % of species sampled (with 1.48 $m^2\ ha^{-1}$ of gain in basal area), Fast Growth with (with 3,32 $m^2\ ha^{-1}$ of gain in basal area) and Very Fast Growth (with 13.40 $m^2\ ha^{-1}$ of gain in basal area) (Table in supplementary material).

Significant interactions were not found or they are not included at the selected models by AICc. This indicates growth rate effects on functional traits are independent of vegetation type and vice versa. Sapwood density and sapwood specific density not differ between vegetation types or between PEGs. Although the AICc method have included PEG at the vessel area selected model, vessel area did not show significant differences between PEG and vegetation type, which was not even included at the selected models. Interactions was not included at the best models too, instead of sum of bases, which were included but without significant effect. This model fixed effects showed a $R^2 = 8.5$ %.

Vessel density showed significant difference in relation to both vegetation type and PEG, without significant interactions (Figure 2). Vessel density showed to be higher in deciduous forest than semideciduous ($p < 0.001$). Regarding PEGs, vessel density was higher at fast growth PEG, which showed significant difference only with the lower mean from the very fast growth PEG ($p = 0.0067$). The low growth group is between both fast and very fast groups, being not statically different from the other groups. Sand % was included at the best model, but without significant effect. The best model fixed effects explained 39.7 % of the variance.

Vessel multiple fraction was not related with vegetation type, neither by interactions with PEGs. Meanwhile, PEGs have effect at VMF, being found significance between the higher mean from fast group with the lower mean from very fast group ($p = 0.0380$) (Figure 3). The low group is between the others, without significant differences with both. The soil control variable related to phosphorus showed negative effect in VMF ($p = 0.0232$). The used models fixed effects explained 7.8 % of the variance.

Vulnerability index showed to be higher in semideciduous than in deciduous forests ($p < 0.001$). Vulnerability index also have significant differences concerning PEGs, being higher in the very fast group and smaller at the fast group, being significantly different ($p = 0.042$) (Figure 4). The slow group have not showed statistical differences with both other levels.

Interaction terms was not included at these models by AICc criteria, which included sand %, lacking significant effect. This model fixed effects have explained 37.7% of the variance.

Legume representativeness has showed to be higher in semideciduous forest at the second interval when compared to the first interval ($p < 0.0001$) (Figure 6). Due to high intra-deciduous variability (random effects explained 78 % of the variance), they not showed significant differences in this vegetation or even between vegetation types, where they tend to be more representative in deciduous forests. The fixed effects explained 12 % of the variance.

The very fast PEG has not presented significant differences, neither significant interactions, being the null model the one with the lower AICc. The fast PEG showed to be more representative at deciduous forests than in semideciduous forests ($p = 0.0181$), without significant interactions, the interval variable was dropped by the Wald test, then, the vegetation type fixed effect explained 31 % of the variance (Figure 6). The slow PEG showed to be more representative at the semideciduous second interval when compared with the semideciduous first interval ($p < 0.0001$) (Figure 7), without another significant difference, at this model, the random factors explained 70% of the variance while the fixed (both factors and their interactions) explained 9%.

Discussion

The trade-off between slow growth rate and conservative strategy or fast growth rate and acquisitive strategy are largely discussed, but for different formations - especially comparisons between wet and dry forests (Adler *et al.*, 2014; Boukili e Chazdon, 2017; Chao *et al.*, 2008; Diaz *et al.*, 2004; Lavorel e Garnier, 2002). Although the third hypothesis (representativeness of legumes will be greater in deciduous forest) not corroborated, and the representativeness of Leguminosae not differ between vegetation types, we corroborated the other hypotheses (the first – ecological strategies differ, and the second – deciduous forest presents conservative strategy). Different vegetation types (deciduous and semideciduous forest) comprises the same biome (SDTF) but their species ecological strategies do not operate in the same way at each formation, according to what we proposed at the first hypothesis. The deciduous forest tends to present conservative strategy, but presents more species with fast growth rates, contradicting what is proposed by the abovementioned literature. The wood economic spectrum (Chave *et al.*, 2009; Donovan *et al.*, 2011; Westoby *et al.*, 2002; Wright *et al.*, 2004) studies are focused in adaptations mechanisms for dry or wet conditions, and to discuss dry environments ecological strategies and functional traits as if they are a homogeneous formation. However, not: SDTFs can be as variable as rainforests, or even more, the range of environmental conditions and ecological strategies (like deciduousness) from semideciduous to deciduous forest indicates this (Allen *et al.*, 2017; Reis *et al.*, 2017; Santos *et al.*, 2012).

Despite environmental conditions variability, the range of ecological and functional adaptations in habitats within SDTFs are poorly understood (Allen *et al.*, 2017). In face of pedoclimatic differences in a gradient formed by SDTFs, species adopted different ecological strategies that shape their performance according to the restrictiveness level from environmental filters. For example, the formation of three ecological groups shows this. Fast growth species constitute the extremes in acquisitive ecological strategies, when we expected that slow and fast grows would present these extremes behaviour. However, fast species are abundant in deciduous forest, while slow predominates in semideciduous forest. Allen et al. (2017) highlighted in dry forests habitats when rainfall decreases fast growth drought-deciduous species are favoured, like the results we found. On other hand, decreases in rainfall seasonality, as in semideciduous forests, may favour slow-growing species, as observed in our study. Our sampled deciduous forests are a peculiar environment, being often associate with limestone outcrops on very high fertile soils (Rezende *et al.*, 2017; Santos *et al.*, 2012).

Species of rich-nutrient habitats tends to present fast growth rates, with fast resources capitation and fast organ replacement (Chao *et al.*, 2008; Chave *et al.*, 2009; Lavorel e Garnier, 2002). Phosphorus and vessel multiple fraction negative correlation is probably related to this strategy. Phosphorus is linked with higher soil fertility, and greater amount of this nutrient tends to be found in soils derived from limestone rocks (Gurevitch, Scheiner e Fox, 2009), like our sampled deciduous forests soils. Although vessel multiple fraction did not differ between vegetation types, it has differed between plant ecological groups. Solitary vessels can be a conservative strategy plants characteristic, since the xylem network connectivity increases the vulnerability to embolism (Apgaua *et al.*, 2017). Vessel area and vessel multiple fraction also did not differ between vegetation types, but how the vessel area is distributed between them have differed, and affects directly the cavitation vulnerability on these forests. While deciduous forest presents more density of small vessels per area, the opposite occurs in semideciduous forest.

Vessel area (or diameter) is the most important parameter correlated to hydraulic safety, because the larger is the vessel, the lower is their water flow resistance, which enhance embolism (Chave *et al.*, 2009; Scholz *et al.*, 2013). Species with larger vessels tends to present an acquisitive strategy, and fast growth rates: priory investments in resources acquisition for growth and reproduction in detriment of survival (Adler *et al.*, 2014; Boukili e Chazdon, 2017; Chao *et al.*, 2008; Díaz *et al.*, 2013). Narrow vessels species have high hydraulic efficiency and are less vulnerable to drought-induced cavitation (Scholz *et al.*, 2013); these strategies prioritize survival and present slow growth rates (Boukili e Chazdon, 2017; Chao *et al.*, 2008). However, our slow, fast and very fast growth species do not present integrally those characteristics. Growth rates and functional trade-offs are proposed based on wet formations and consider woody density as a key functional trait defining the slow or fast growth trade-offs (Adler *et al.*, 2014; Boukili e Chazdon, 2017; Chao *et al.*, 2008; Phillips *et al.*, 2009), but between different families. In our study, we found between related species sampled in forests under seasonal water stress, wood density (sapwood density and sapwood specific density) not varies because these traits are strongly phylogenetically conserved between genera or even plant families (Adler *et al.*, 2014; Chave *et al.*, 2009). Despite this, others traits varies, corroborating the first hypothesis, and thus, showing that traits in SDTF plant ecological groups not have the expected behaviour predicted by previous studies (Adler *et al.*, 2014; Apgaua *et al.*, 2017; Boukili e Chazdon, 2017; Chave *et al.*, 2009; Díaz *et al.*, 2013; Xu *et al.*, 2016).

Very fast growth rate group are acquisitive species, with the abovementioned characteristics of acquisitive strategy, which include the high vulnerability to cavitation. This group comprises four pioneer species, r strategists, with short life cycles (Begon, Townsend e Harper, 2006; Boukili e Chazdon, 2017). In the other extreme and corroborating our second hypothesis, fast species, despite the very fast, present a conservative strategy, with vessel area distributed in a great density of vessels and lower vulnerability index than slow growth rate species. Deciduous-fast species presents low internal resources conservation, with short-lived leaves and rapid leaves replacement (Lavorel e Garnier, 2002). Fertile soils may provide the conditions required to rapid resprouting and growth in the rainy season. Deciduous forest restrictivity seems to select species with fast growth, but conservative characteristics which allow the survival in water deficit conditions (in dry season, mainly). On other hand, semideciduous forest has lower water deficit than deciduous forests, mainly due to the smaller precipitation seasonality, but poor soils in general (Terra *et al.*, 2018). These conditions grant the slow-growth species characteristics predominance in semideciduous forest, and the higher availability of water enables functional adaptations to optimize resources use. We have not found studies that have tested ecological groups and functional traits in a same botanical family, and our results shows that, in this situation, they not behave in the same way. Even in species with high-similar woody density, a range of diverse ecological requirements enables species to colonize and persist in a range of different habitats.

Leguminosae is recognized as a botanical family with great abundance and competitive success, and even niche conservatism in SDTFs (Gei *et al.*, 2018; Pennington, Lavin e Oliveira-Filho, 2009; Rodrigues *et al.*, 2015). Although other study showed the representativeness of Leguminosae strongly negatively related to water availability (Gei *et al.*, 2018), our third hypothesis not corroborate, because the representativeness of legumes not differ between vegetation types. However, the abundance of legumes remained constant in deciduous forest and increase in semideciduous forest in the last dynamic inventory, which may indicate a legumes increase in this forest type in face of climatic changes, like suggested by other studies (Allen *et al.*, 2017; Enquist e Enquist, 2011; Rodrigues *et al.*, 2015). Leguminosae is a group related with success in drier conditions (Gei *et al.*, 2018), and other studies infer drought-deciduous species will benefit in face of aridity increase (Rodrigues *et al.*, 2015; Vico *et al.*, 2017). According to Vico et al. (2017), lengthening of dry season may turn the evolutionary unstable drought-deciduous communities in stable ones. Deciduous forests are an evolutionary stable vegetation type (Pennington e Lavin, 2016; Vieira *et al.*, 2015; Werneck *et al.*, 2011), and according to our results, it tend to still stable. However, in face of aridity increase, semideciduous forest may experience changes in compositional and functional character, and consequently, in ecosystem services and processes changes.

Paleo studies cite SDTF as a strongly drought tolerant (Meir e Pennington, 2011), although variabilities in drought intensity and length may affects ecological processes in STDF (Allen *et al.*, 2017). Deciduous forests have a majority of species with fast ecological strategy, and semideciduous have an equilibrium in quantity of fast, very fast and slow species, fact that have changed in the last inventory, when the slow plant ecological group became the majority.

Changes in forest dynamics and composition can occur in face of climatic changes, and more diverse communities with distinct ecological strategies (like the semideciduous) may reduce species richness only if certain combinations of traits are favoured (Allen *et al.*, 2017). In our sampled semideciduous forest, this reduction already started. Deciduous forests have a legumes population composed mainly by fast species, plant ecological group of lower vulnerability in our study. Despites the legumes deciduous species adaptations to drought conditions (Allen *et al.*, 2017; Gei *et al.*, 2018), these species tolerance limits are not known.

Dry forests species composition shows strongly correlated with water storage capacity (Santos *et al.*, 2012) and water deficit (Neves *et al.*, 2015). Thus, there is a sensitive biome to climate changes (Allen *et al.*, 2017), and this sensitivity does not operates at the same way between the SDTF range of water and soil conditions. Our study shows that semideciduous have a great vulnerability in face of climatic changes, showing shifts in legumes representativity across time. Seasonally dry tropical forests are among the most threatened and unique ecosystems in the world (Allen *et al.*, 2017; Miles *et al.*, 2006; Pennington, Lavin e Oliveira-Filho, 2009), but plants ecological strategies in the SDTF range of different conditions are poorly studied (Allen *et al.*, 2017). According to Allen et al. (2017), knowledge about how SDTF forest types are vulnerable in face of climatic changes and the mechanisms underlying their responses are a priority research to the future, and must provide a better understanding in how climatic changes will affect these forests.

Although some studies have been focusing in the diversity of habitats and different forms of life in SDTFs (Allen *et al.*, 2017; Apgaua *et al.*, 2014, 2017; Apgaua, Ishida, *et al.*, 2015; Pennington, Lavin e Oliveira-Filho, 2009), species ecological strategies from an important family and with the same life form are not similar, and varies between the SDTF distinct habitats. In this work, we found ecological strategies in SDTF species not operates in the same way that's' described for wood economics spectrum or for the theories about plant functional / ecological types in restrictive habitats. Even the vulnerability of these SDTF habitats are not homogeneous, and the semideciduous forests higher vulnerability needs to lead in consideration in seasonally dry forests future researches.

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Table 1. Characteristics of study sites of Seasonally Dry Tropical Forests in the southeastern Brazil, with latitude (S) and longitude (W), mean altitude (Alt.) in meters, annual mean of temperature (T) in ºC and rainfall in mm, climate type according to Koppen, number of species with functional traits collected in each area (S) and permanent plots total area (A) in ha.

Sites	**Lat. (S)**	**Long. (W)**	**Alt.**	**T**	**Rainfall**	**Climate**	**S**	**A**
Agropop	15°36'29.4"	44°42'05.6"	500	23	1.000	Aw	10	1
BMinas	15°18'00.75"	44°44'45.1"	670	23	1.086	Aw	10	1,5
VVerde	14°24'88.0"	44°09'79.0"	658	23	1.000	Bsh	09	0,8
Lagoa	21°13'11.0"	44°58'15.0"	875	19	1.493	Cwb	10	1,16
Matinha	21°13'40.0"	44°57'50.0"	927	19	1.493	Cwb	09	2,23
Subest	21°13'17.0"	44°57'47.0"	925	19	1.493	Cwb	13	2,08

Figure 1. Seasonally Dry Tropical Forests sampled areas in the southeastern Brazil and biogeographic domains.

Figure 2. Differences in vessel density between vegetation types (A), and between Plant Ecological Groups (B) of Leguminosae sampled in Seasonally Dry Tropical Forests of southeastern Brazil.

Figure 3. Differences in vessel multiple fraction between three Plant Ecological Groups of Leguminosae sampled in Seasonally Dry Tropical Forests of southeastern Brazil.

Figure 4. Differences in vulnerability index between vegetation types (A), and between Plant Ecological Groups (B) of Leguminosae sampled in Seasonally Dry Tropical Forests of southeastern Brazil.

Figure 5. Differences in representativity of Leguminosae in two dynamic inventories (1 and 2) and two vegetation types (Deciduous and Semideciduous forest) sampled in Seasonally Dry Tropical Forests of southeastern Brazil.

Figure 6. Differences in representativity of Plant Ecological Groups of Leguminosae with fast growth rates in two vegetation types of Seasonally Dry Tropical Forests in southeastern Brazil.

Figure 7. Differences in representativity of Plant Ecological Groups of Leguminosae with slow growth rates in in two dynamic inventories (1 and 2) and two vegetation types (Deciduous and Semideciduous forest) of Seasonally Dry Tropical Forests in southeastern Brazil.

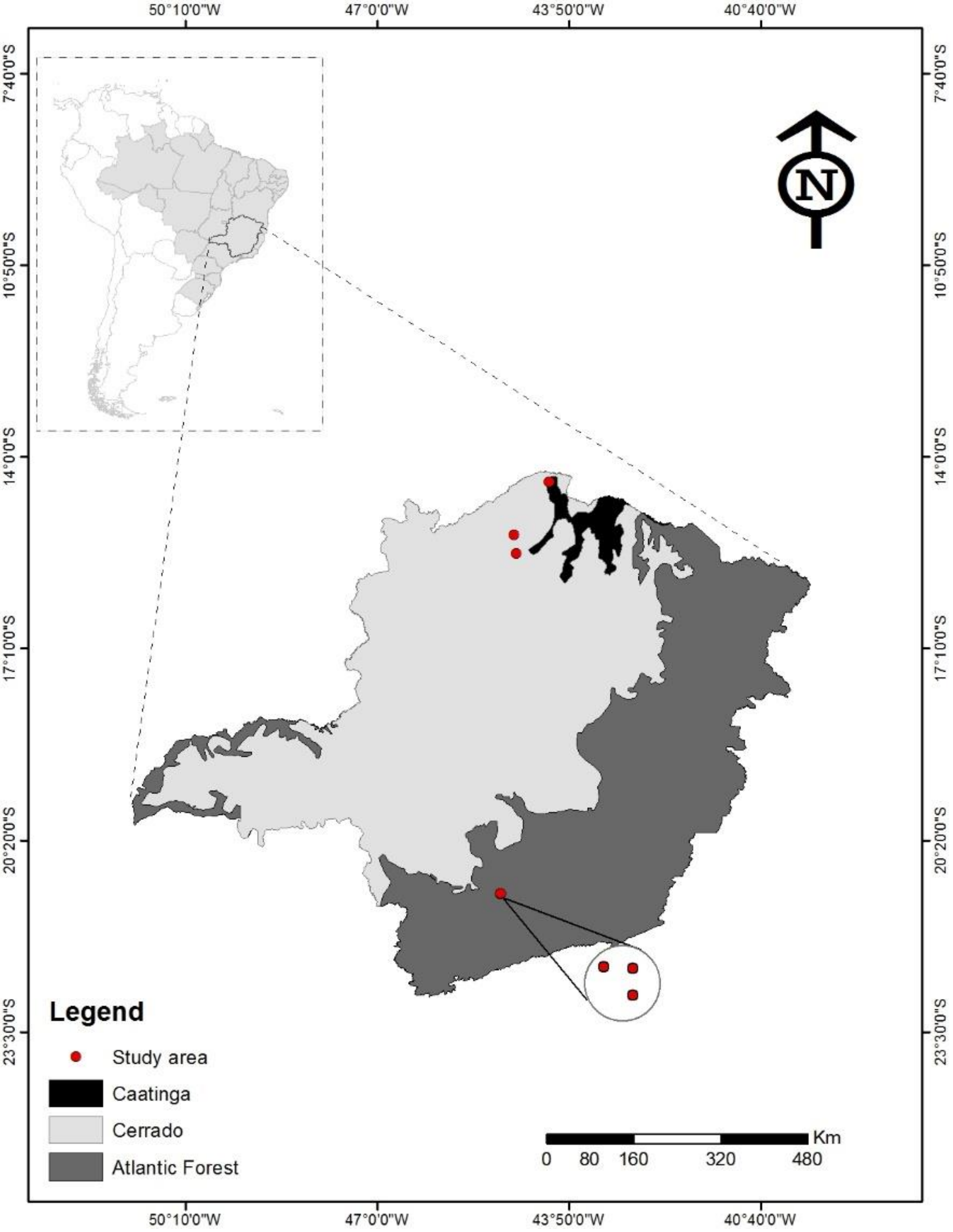
50°10'0"W
47°0'0"W
43°50'0"W
40°40'0"W
7°40'0"S
10°50'0"S
14°0'0"S
17°10'0"S
20°20'0"S
23°30'0"S
N
Legend
Study area
Caatinga
Cerrado
Atlantic Forest
Km
0
80
160
320
480

Figure 1.

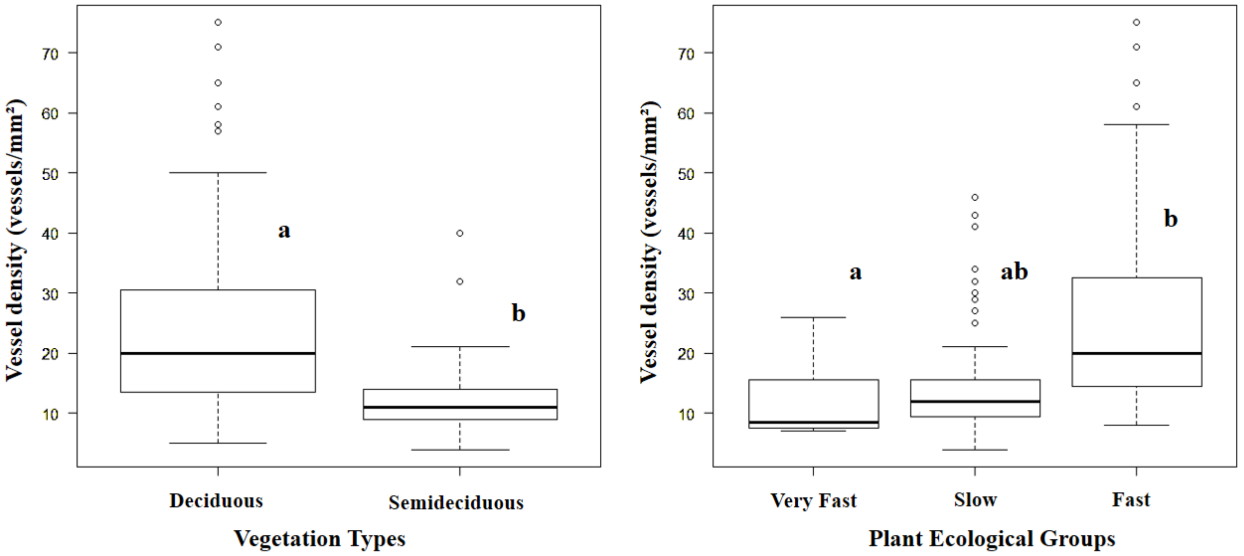
Vessel density (vessels/mm²)
70
60
50
40
30
20
10
a
b
Deciduous
Semideciduous
Vegetation Types
Vessel density (vessels/mm²)
70
60
50
40
30
20
10
a
ab
b
Very Fast
Slow
Fast
Plant Ecological Groups

Figure 2.

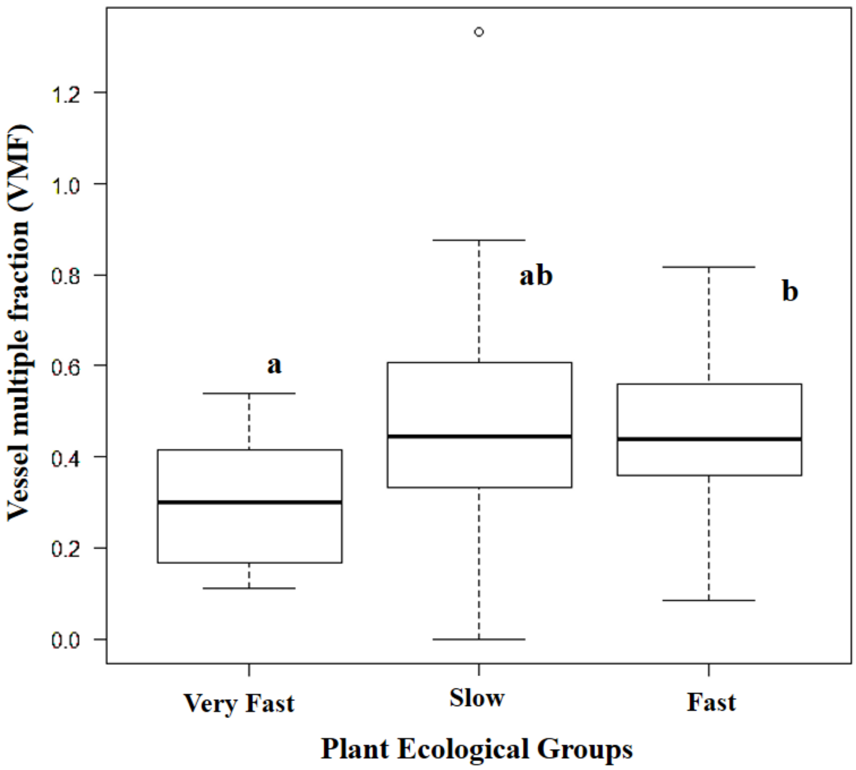
Vessel multiple fraction (VMF)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
a
ab
b
Very Fast
Slow
Fast
Plant Ecological Groups

Figure 3.

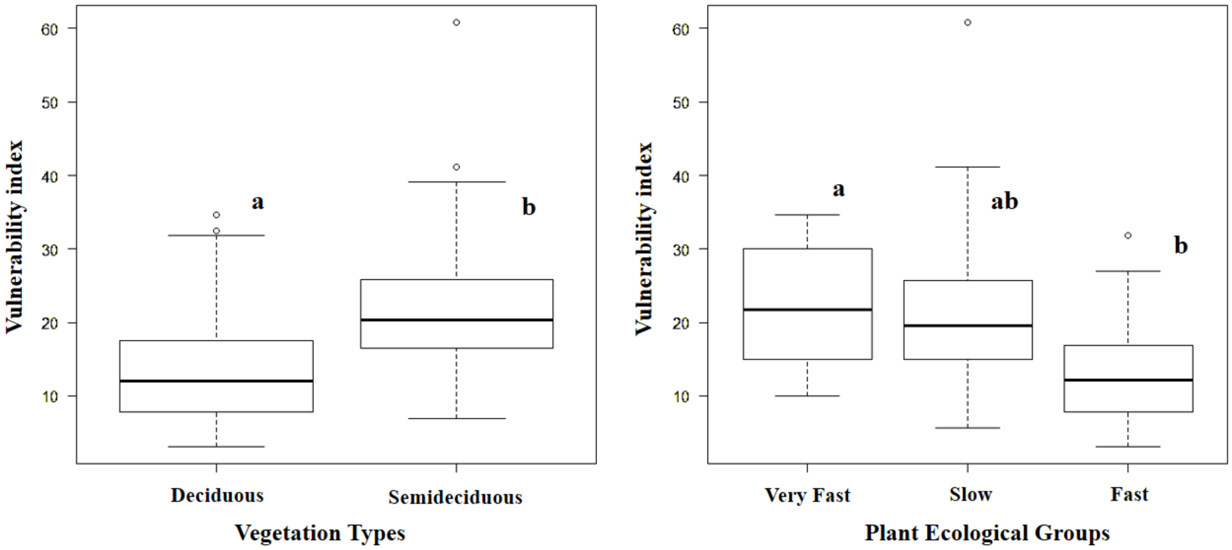
Vulnerability index
60
50
40
30
20
10
a
b
Deciduous
Semideciduous
Vegetation Types
Vulnerability index
60
50
40
30
20
10
a
ab
b
Very Fast
Slow
Fast
Plant Ecological Groups

Figure 4.

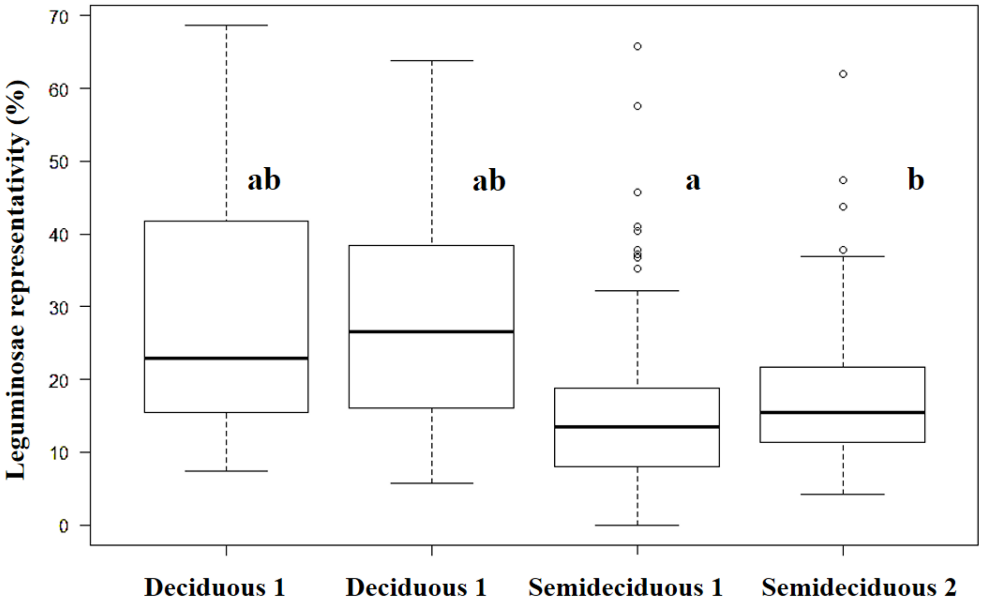
Leguminosae representativity (%)
0
10
20
30
40
50
60
70
ab
ab
a
b
Deciduous 1
Deciduous 1
Semideciduous 1
Semideciduous 2

Figure 5.

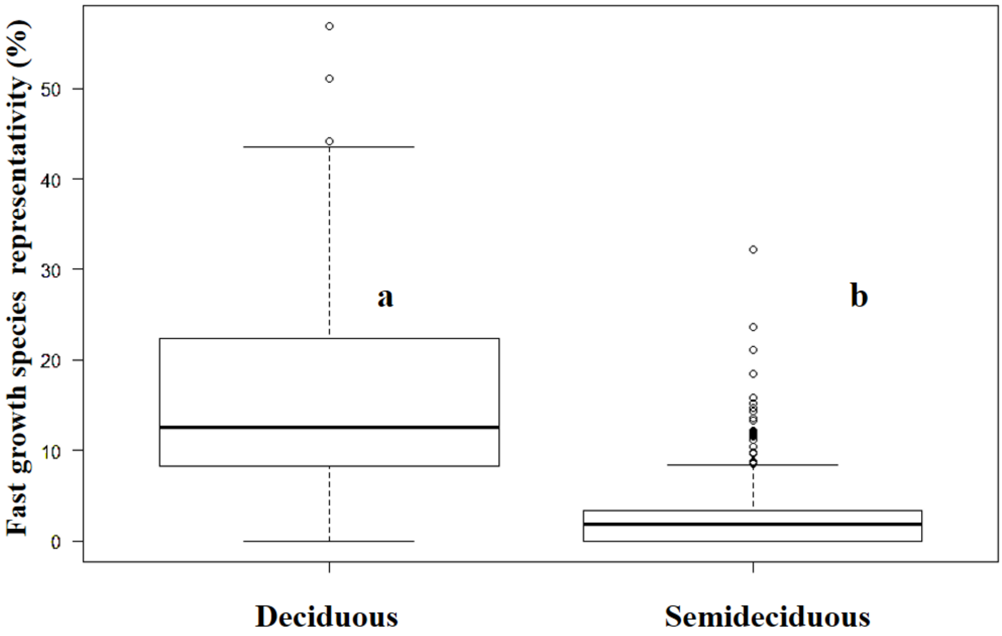
Fast growth species representativity (%)
0
10
20
30
40
50
a
b
Deciduous
Semideciduous

Figure 6.

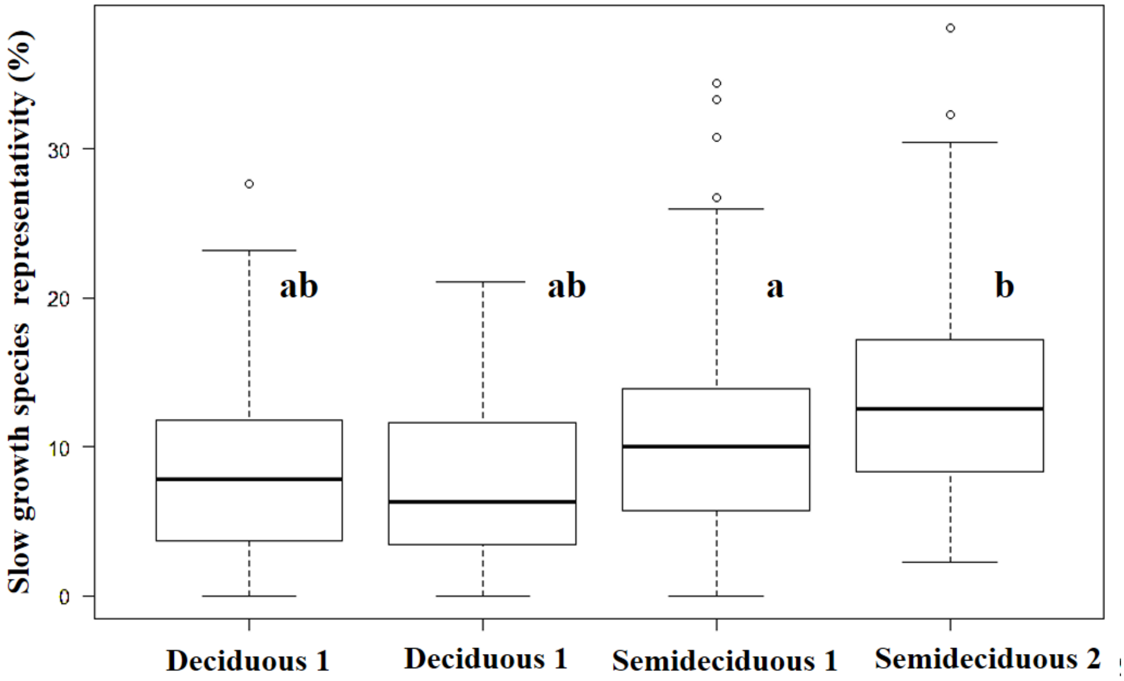
Slow growth species representativity (%)
0
10
20
30
ab
ab
a
b
Deciduous 1
Deciduous 1
Semideciduous 1
Semideciduous 2

Figure 7.

Supplementary table 1. Ecological groups formed by Leguminosae species sampled in two types of Seasonally Dry Tropical Forests in southeastern Brazil, through their growth rates. PEGs = Plant Ecological Groups.

Species	Vegetation types	PEGs
Acosmium lentiscifolium Schott	Deciduous	Fast
Amburana cearensis (Allemão) A.C.Sm.	Deciduous	Low
Anadenanthera colubrina (Vell.) Brenan	Deciduous	Low
Bauhinia rufa (Bong.) Steud.	Deciduous	Fast
Cenostigma pluviosa DC.	Deciduous	Fast
Centrolobium sclerophyllum H.C.Lima	Deciduous	Fast
Dalbergia cearensis Ducke	Deciduous	Fast
Goniorrhachis marginata Taub.	Deciduous	Low
Leucochloron limae Barneby & J.W.Grimes	Deciduous	Fast
Machaerium acutifolium Vogel	Deciduous	Fast
Machaerium leucopterum Vogel	Deciduous	Low
Machaerium punctatum (Poir.) Pers.	Deciduous	Low
Machaerium scleroxylon Tul.	Deciduous	Fast
Mimosa tenuiflora (Willd.) Poir.	Deciduous	Very Fast
Parapiptadenia rigida (Benth.) Brenan	Deciduous	Fast
Platymiscium blanchetii Benth.	Deciduous	Fast
Poeppigia procera C.Presl	Deciduous	Fast
Pterocarpus zehntneri Harms	Deciduous	Low

Senegalia martii (Benth.) Seigler & Ebinger	Deciduous	Very Fast
Senna spectabilis (DC.) H.S.Irwin & Barneby	Deciduous	Very Fast
Sweetia fruticosa Spreng.	Deciduous	Low
Albizia polycephala (Benth.) Killip ex Record	Semideciduous	Low
Bauhinia longifolia (Bong.) Steud.	Semideciduous	Fast
Bowdichia virgilioides Kunth	Semideciduous	Low
Copaifera langsdorffii Desf.	Semideciduous	Low
Dalbergia villosa (Benth.) Benth.	Semideciduous	Low
Hymenaea courbaril L.	Semideciduous	Low
Inga striata Benth.	Semideciduous	Low
Machaerium hirtum (Vell.) Stellfeld	Semideciduous	Low
Machaerium nictitans (Vell.) Benth.	Semideciduous	Low
Machaerium stipitatum Vogel	Semideciduous	Low
Machaerium villosum Vogel	Semideciduous	Low
Piptadenia gonoacantha (Mart.) J.F.Macbr.	Semideciduous	Fast
Platycyamus regnellii Benth.	Semideciduous	Low
Platypodium elegans Vogel	Semideciduous	Low
Senegalia polyphylla (DC.) Britton & Rose	Semideciduous	Very Fast
Tachigali rugosa (Mart. ex Benth.) Zarucchi & Pipoly	Semideciduous	Fast