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ESTRATÉGIAS ECOLÓGICAS DE PLANTAS EM FLORESTAS ESTACIONAIS E SAVANAS DO CERRADO

Orientador: Dr. Marcus Vinicius Cianciaruso

Coorientador: Dr. Marcos Bergmann Carlucci

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Tese apresentada à Universidade Federal de Goiás, como parte das exigências do Programa de Pós-graduação em Ecologia e Evolução para obtenção do título de doutor em Ecologia e Evolução.

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ATA DA SESSÃO PÚBLICA DE DEFESA DE TESE Nº 55

Aos treze dias do mês de abril de 2017 (13/04/2017), às oito horas (08h), no Auditório do ICB V, UFG, reuniram-se os componentes da banca examinadora: **Prof. Dr. Marcus Vinicius Cianciaruso, ICB-UFG; Prof. Dr. Paulo De Marco Júnior, ICB-UFG; Dra. Marcia Nunes Macedo, Woods Hole Research Center – Falmouth, EUA; Prof. Dr. Fabrício Barreto Teresa, UEG-Anápolis; Prof. Dr. José Roberto Rodrigues Pinto, UnB**; para, em sessão pública presidida pelo (a) primeiro(a) examinador(a) citado(a), procederem à avaliação da defesa de tese intitulada: **"Estratégias ecológicas de plantas em florestas estacionais e savanas do Cerrado"**, em nível de doutorado, área de concentração em Ecologia e Evolução, de autoria de **Leandro Maracahipes dos Santos**, discente do Programa de Pós-Graduação Ecologia e Evolução da Universidade Federal de Goiás. A sessão foi aberta pelo(a) presidente(a), que fez a apresentação formal dos membros da banca. A palavra, a seguir, foi concedida a(o) autor(a) da tese que, em cerca de 35 minutos, procedeu à apresentação de seu trabalho. Terminada a apresentação, cada membro da banca arguiu a(o) examinada(o), tendo-se adotado o sistema de diálogo sequencial. Terminada a fase de arguição, procedeu-se à avaliação da tese. Tendo-se em vista o que consta na Resolução nº 1127 de dezembro de 2012 do Conselho de Ensino, Pesquisa, Extensão e Cultura (CEPEC), que regulamenta o Programa de Pós-Graduação em Ecologia e Evolução, a tese foi APROVADA, considerando-se integralmente cumprido este requisito para fins de obtenção do título de Doutor(a) em Ecologia e Evolução pela Universidade Federal de Goiás. A conclusão do curso dar-se-á quando da entrega da versão definitiva da tese na secretaria do programa, com as devidas correções sugeridas pela banca examinadora, no prazo de trinta dias a contar da data da defesa. Cumpridas as formalidades de pauta, às 12 h e 02 min., encerrou-se a sessão de defesa e, para constar, eu, Suely Ana Ribeiro, secretária executiva da Universidade Federal de Goiás - UFG, lavrei a presente ata que, após lida e aprovada, será assinada pelos membros da banca examinadora em três vias de igual teor.

Prof. Dr. Marcus Vinicius Cianciaruso
Presidente da banca
ICB-UFG

Paulo de Marco Junior
Prof. Dr. Paulo De Marco Júnior
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Fabrício Barreto Teresa
Prof. Dr. Fabrício Barreto Teresa
UEG-Anápolis

José Roberto R. Pinto
Prof. Dr. José Roberto Rodrigues Pinto
UnB

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Sumário

Resumo – A adoção de diferentes estratégias ecológicas é um fator importante para determinar o estabelecimento e a persistência de espécies em comunidades locais. De maneira geral, o cerrado é caracterizado por uma alta frequência de fogo e solos pobres em nutrientes. Geralmente em condições de baixa fertilidade e alta frequência de fogo as espécies filtradas tendem a possuir características que representam adaptações a estes estresses ambientais. Considerando que as espécies de Cerrado se desenvolvem sob a atuação destes filtros ambientais, nosso objetivo foi avaliar como a adoção de diferentes estratégias ecológicas podem determinar a performance dos atributos funcionais, a estrutura das comunidades e a relação entre uma planta focal e sua vizinhança. Neste trabalho de tese, que está dividido em três capítulos, nós utilizamos três diferentes escalas para avaliar como estratégias ecológicas das espécies podem determinar seu desempenho e estabelecimento em comunidades locais. No primeiro capítulo que está baseado em uma escala de habitat, nós avaliamos como as estratégias ecológicas de espécies generalistas e especialistas de floresta estacional e cerrado sentido restrito são fundamentais para o estabelecimento e a persistência das espécies nestes habitats com diferenças marcantes em relação à frequência de fogo e disponibilidade de nutrientes. Neste capítulo, nós discutimos que as diferentes estratégias adotadas pelas espécies estão de acordo com os fatores limitantes da ocorrência de espécies em cada um destes ambientes. No segundo capítulo, que está baseado em escala de comunidades, nós buscamos compreender como os gradientes ambientais podem determinar diferentes estratégias ecológicas relacionadas aos atributos funcionais e a densidade de espécies. Nós demonstramos que as mudanças nos valores de atributos e densidade de espécies foram mais claras no gradiente de fertilidade do que toxicidade, e que comunidades de floresta estacional foram mais sensíveis a mudanças do que comunidades de cerrado sentido restrito em ambos os gradientes. Nós observamos também que espécies com atributos conservativos foram associados à solos pobres e espécies com atributos aquisitivos associado à solos mais férteis. Já no terceiro capítulo, que foi desenvolvido na escala de indivíduo, nós discutimos se as características e relação filogenética das plantas vizinhas influenciam o dano foliar em árvores e arbustos do cerrado. Neste capítulo, demonstramos que a distância ecológica e evolutiva entre plantas individuais e as plantas vizinhas não determina o nível de consumo foliar por herbívoros. Nós discutimos que a dominância de herbívoros generalistas, a co-evolução entre plantas e herbívoros especialistas, e o consumo preferencial de folhas jovens podem ser mais importante para determinar o nível de dano foliar do que o contexto de vizinhança em que uma dada planta está inserida.

Palavras-chave: preferência de habitats, plasticidade fenotípica, gradiente edáfico, estratégia aquisitiva e conservativa, dano foliar, distâncias ecológicas e evolutivas, contexto de vizinhança

Introdução Geral

A diversidade do reino vegetal vem fascinando o homem há muito tempo, desde os celebres naturalistas aos renomados ecólogos contemporâneos, proponentes de teorias que buscam compreender quais são os mecanismos estruturadores da riqueza e composição de espécies. A teoria do nicho e todos os seus princípios tem sido aquela mais frequentemente testada ao longo do desenvolvimento da ecologia, essencialmente no que diz respeito às interações competitivas entre espécies e à atuação de filtros ambientais (tais como fogo em savanas do Cerrado). Assim, em função da atuação de filtros ambientes, a adoção de diferentes estratégias ecológicas é um fator importante para determinar o estabelecimento e a persistência de espécies, bem como os valores dos atributos funcionais das espécies capazes de se estabelecer em uma comunidade local.

Breve histórico

Comunidade ecológica é definida como um grupo de espécies que co-ocorre em um dado tempo e lugar (McGill *et al.* 2006). Entender os padrões e os mecanismos reguladores da composição e diversidade das comunidades naturais é um dos principais objetivos da ciência ecológica. Já nos séculos XVIII e XIX, os trabalhos dos naturalistas Alexander von Humboldt e Eugenius Warming buscaram compreender a relação entre plantas, animais e clima, bem como inferir os padrões de diversidade de cada localidade (Hawkins 2001). Os trabalhos de Warming e Humboldt influenciaram notáveis naturalistas do passado, tais como Karl Philipp von Martius, Alfred Wallace e Charles Darwin. Neste sentido, em “A origem das espécies” Darwin postula que indivíduos com alto grau de parentesco tendem a apresentar fortes relações competitivas, introduzindo o conceito de “competição ecológica” como um dos principais mecanismos reguladores da diversidade e composição de comunidades naturais (Mayfield & Levine 2010).

Na década de 20 e 30, Vito Volterra, Alfred Lotka e Georgii Gause avançaram no entendimento dos mecanismos reguladores da riqueza e composição de espécies ao propor o conceito de nicho ecológico. Estes autores postularam o “princípio da exclusão competitiva” ao afirmarem que duas espécies competindo pelo mesmo recurso não podem coexistir ao longo do tempo em uma mesma comunidade (Volterra 1926; Lotka 1932; Gause 1934). Em meados do século XX, George Hutchinson redefiniu nicho ecológico como um espaço multidimensional composto pelos requerimentos bióticos e abióticos necessários à sobrevivência e reprodução das espécies (Hutchinson 1957). Na década de 60, Robert MacArthur e Edward O. Wilson formularam a “teoria do equilíbrio da biogeografia de ilhas”, a qual exerceu um papel primordial no desenvolvimento do “princípio da partição de nicho”. Na mesma década, MacArthur e Levins formularam a hipótese da similaridade limitante (MacArthur & Levins 1967), que prevê um limite máximo de semelhança morfológica para duas espécies coexistirem numa mesma comunidade. Em hipótese, a coexistência de duas ou mais espécies com diferentes características morfológicas seria possibilitada pela exploração de recursos distintos, resultando numa baixa sobreposição de nicho entre essas espécies.

Atualmente, os cientistas buscam compreender como os diferentes mecanismos reguladores da diversidade e composição de espécies atuam nas diferentes escalas espaciais. Neste sentido, se destacam os trabalhos de David Tilman e Peter Chesson (Tilman 1982, 1990, Chesson 2000), os quais buscam entender como atuam os principais mecanismos reguladores da composição e diversidade de espécies. Mais recentemente, uma nova abordagem baseada na “teoria de biogeografia de ilhas”, denominada “Teoria Neutra da Biodiversidade”, tem sido utilizada para explicar os padrões de diversidade e composição de espécies nos mais variados grupos de organismos (Hubbell 2001). A teoria neutra assume que as espécies dentro de uma comunidade são ecologicamente equivalentes e que as extinções são balanceadas pelas especiações, e por processos estocásticos de nascimento e imigração.

Teoria de Nicho

A teoria de nicho teve suas bases lançadas por Eugenius Warming ao observar que as plantas possuíam diferentes habilidades fisiológicas e que algumas espécies eram capazes de se estabelecer em determinados locais e incapazes de obter o mesmo sucesso em outros locais (Cavender-Bares *et al.* 2009). Partindo destas observações, Grinell e Elton foram os primeiros ecólogos a desenvolverem o conceito de nicho ecológico de espécie (Grinnell 1917; Elton 1927). Posteriormente, Hutchinson redefiniu o conceito de nicho (Hutchinson 1957), assumindo que espécies com elevada similaridade ecológica não poderiam coexistir, assim criou-se um paradigma onde processos evolutivos não possuíam qualquer influência na estruturação das comunidades (Cavender-Bares *et al.* 2009). No entanto, atualmente diversos estudos vêm demostrando à relevância da história evolutiva e das interações interespecíficas como processos fundamentais para compreender a coexistência das espécies (Webb *et al.* 2002; Cahill *et al.* 2008; Cavender-Bares *et al.* 2009; Vamosi *et al.* 2009; Mayfield & Levine 2010).

A teoria do nicho Hutchinsoniano basicamente é constituída de um conjunto de condições (abióticas - também chamado de nicho Grinnelliano) e de recursos (bióticos - nicho Eltoniano) que determinam a capacidade de uma espécie em se estabelecer e manter populações viáveis ao longo do tempo (Hutchinson 1957; Soberón 2007). A premissa básica desta teoria encontra-se fundamentada no Princípio da Exclusão

Competitiva proposto por Gause (Gause 1934). Dentro da teoria do nicho, a atuação de filtros ambientais também pode ser um importante processo regulador do nicho das espécies (Gómez *et al.* 2010). O filtro ambiental determina quais espécies são aptas a se estabelecer em cada local, e é provável que atue sobre escalas espaciais maiores (escala regional), o que resultaria na seleção de espécies mais semelhantes em atributos (Gómez *et al.* 2010; Sobral & Cianciaruso 2012). Enquanto que, após a seleção de determinado conjunto de espécies pelo filtro ambiental, em escala local a similaridade limitante entre as espécies é quem irá atuar e determinar quais espécies deverão coexistir (Gómez *et al.* 2010; Sobral & Cianciaruso 2012).

Entretanto, dentro da teoria de nicho outros processos importantes são a sobreposição e a diferenciação dos nichos (Gilbert 2012). Quando espécies possuem elevado grau de sobreposição de nicho (ou seja, alto compartilhamento de consumo de recursos) isso resulta em fortes interações competitivas que muitas vezes podem levar a exclusão competitiva, ou forçar as espécies a explorarem diferentes recursos (diferenciação de nicho) (Webb *et al.* 2002). A diferenciação de nicho pode ainda levar ao deslocamento de caracteres, caracterizado por uma alta similaridade morfológica quando duas espécies são distribuídas alopatricamente, mas há uma diferenciação em uma ou mais dessas características quando ocorrem simpatricamente (Connell 1980; Schmidt *et al.* 2000). Outra possibilidade é a divisão do recurso disponível entre os competidores (partição de nicho), que consiste em cada competidor ocupar uma porção do recurso disponível, evitando a competição e consequente exclusão de um dos competidores (Webb *et al.* 2002).

Estratégias ecológicas de plantas

Em ecologia funcional, diversos atributos funcionais têm sido utilizados para compreender a estruturação e a funcionalidade das comunidades naturais (atributos foliares, da madeira e regenerativos). Dentre estes, o sistema LHS (*leaf-height-seed*; folha-altura-semente) descreve o nicho funcional das plantas, usando estes três eixos fundamentais e independentes, resumindo todas as principais dimensões de variação na estrutura e funcionamento (Westoby 1998). A representação deste sistema, que consiste em um modelo de classificação tridimensional, é importante por representar demandas conflitantes fundamentais controlando as estratégias vegetais e pelo fato de que cada uma dessas características se correlaciona com outros atributos relevantes (Westoby 1998; Laughlin *et al.* 2010). A área foliar específica é o principal atributo envolvendo o espectro econômico foliar (Wright *et al.* 2004) e representa a demanda conflitante entre aquisição e a estratégia no uso de recurso pelas plantas. A altura máxima da planta indica a habilidade competitiva da planta por luz e, portanto, sua estratégia de assimilação de carbono (Westoby *et al.* 2002). Enquanto que a massa da semente indica a estratégia de regeneração das espécies por meio da demanda conflitante entre massa da semente, habilidade de dispersão e estabelecimento de plântulas (Westoby *et al.* 2002). O sistema LHS vem sendo testado em diversos ambientes e demonstrando ser capaz de prever a funcionalidade das comunidades (Lavergne, Garnier & Debussche 2003; Carly, Marcelo & Jaime 2009).

Em ambientes florestais, em que o acesso à luz é um fator limitante, o investimento de árvores em crescimento vertical é vantajoso, pois árvores que apresentam alturas maiores do que seus vizinhos possuem maior vantagem competitiva devido ao melhor acesso à luz. Ainda, a altura em que as flores e sementes são produzidas também pode influenciar o sucesso reprodutivo dos indivíduos, bem como a dispersão de sementes (Garnier & Navas 2012), uma vez que a altura da árvore possui uma relação positiva com a distância em que as sementes são dispersas. Por outro lado, plantas que produzem poucas sementes grandes são caracterizadas como espécies com alta habilidade competitiva, enquanto que espécies que produzem elevado número de pequenas sementes são vistas como espécies pioneiras devido à sua alta capacidade de dispersão (Garnier & Navas 2012). Outro importante mecanismo utilizado por plantas é o sistema de rebrota. Diversas plantas do Cerrado apresentam esta característica de resiliência, que permite com que o indivíduo possa rebrotar após um distúrbio (como fogo) a partir de estruturas basais ou subterrâneas (Medeiros & Miranda 2005).

Fogo, consumo foliar e propriedades do solo no Cerrado

O Cerrado é composto por um complexo mosaico vegetacional, com a ocorrência de vários tipos de vegetação (Eiten 1972), variando de savanas abertas a florestas de galeria, florestas secas e semideciduais. Muitas das espécies são capazes de se estabelecer em diferentes fisionomias (Ratnam *et al.* 2011; Hoffmann *et al.* 2012). No entanto, estratégias relacionadas principalmente a proteção contra o fogo (grande espessura da casca) podem ser cruciais para determinar o estabelecimento e permanência de espécies nos diferentes ambientes savânicos do Cerrado. Além disso, estratégias relacionadas a proteção contra herbívoros (folhas grossas, espinhos e tricomas) e perda de água (folhas grossas, e fechamento de estômatos e esporos) (Silva & Batalha 2011; Dantas, Batalha & Pausas 2013a).

Uma vez que os processos de dispersão e eventos estocásticos determinam o banco regional de espécies, este é composto pelo conjunto de espécies que possuem agentes dispersores que as tornem capazes de chegar a uma área (Lortie *et al.* 2004), possibilitando que um conjunto de espécies melhor adaptado as condições locais seja selecionado a partir do banco regional de espécies. Inicialmente, em maior escala poderá ser filtrado um conjunto de espécies com atributos funcionais mais similares (por exemplo, pelo clima), e posteriormente por fatores ambientais em menores escalas (por exemplo, características edáficas) e, por último as interações bióticas entre as espécies (tais como relação entre planta-planta e planta-herbívoros) irão determinar a abundância relativa e quais espécies poderão estabelecer e persistir em cada comunidade local (Cain, Milligran & Strand 2000; Dufour *et al.* 2006; Lessard *et al.* 2012; Bello *et al.* 2013).

O fogo é um dos principais fatores estruturadores de comunidades vegetais no cerrado (Hoffmann *et al.* 2012; Dantas *et al.* 2013b, 2016). Os focos de incêndio no cerrado ocorrem com elevada frequência e intensidade, principalmente em localidades em que ocorre grande acumulo de biomassa durante alguns anos sem fogo. No Cerrado, áreas de savanas possuem grande abundância de gramíneas, com arbustos e árvores coexistindo sobre a camada de herbácea. No momento da passagem do fogo as gramíneas atuam como uma grande fonte de combustível, promovendo um maior avanço do fogo em áreas com maior quantidade (Dantas *et al.* 2013a). Enquanto que, em áreas florestais a maior umidade relativa e a baixa quantidade de gramíneas dificultam a propagação do fogo nestes ambientes (Hoffmann *et al.* 2012).

O fogo atua como um filtro selecionando espécies com caraterísticas que confiram resistência contra os efeitos das queimadas ou que possuem estruturas de reserva que permita rebrotar após a passagem do fogo (Dantas *et al.* 2013a; Pausas, Keeley & Schwilk 2016). As espécies evoluíram com a presença constante de fogo, sendo assim diversas adaptações de resistência e resiliência ao fogo foram desenvolvidas ao longo do tempo evolutivo (Simon *et al.* 2009; Pausas *et al.* 2016). A espessura da casca é um dos principais atributos de resistência ao fogo em plantas

(Rosell *et al.* 2014). Hoffmann *et al.* (2012) propuseram um limiar de que espécies com espessura de casca superior à 5,9 mm tem alta probabilidade resistir a queimadas de baixa intensidade. Muitas das espécies exclusivas de savanas possuem espessura de casca igual ou superior a este limiar, no entanto espécies com habito florestal que ocorrem em áreas de savanas não possuem tais características, e muitas vezes são excluídas das comunidades locais após a passagem do fogo.

Considerando que habitats de florestas estacionais e savanas são contrastantes, e que ocorrem lado a lado em paisagens de Cerrado. Isto torna possível encontrar espécies com ocorrência em ambos habitats ou com ocorrência restrita à somente um destes habitas (floresta estacional ou savana). Sendo assim, avaliar como diferentes estratégicas ecológicas de espécies generalistas e especialistas de florestas estacional e cerrado sentido restrito é fundamental para compreender o estabelecimento e a persistência de espécies nestes habitats com diferenças marcantes em relação à frequência de fogo e disponibilidade de nutrientes. Nesse primeiro capítulo, nós discutimos como as diferentes estratégias adotadas pelas espécies estão de acordo com os fatores limitantes da ocorrência de espécies em cada um destes ambientes.

De maneira geral, os solos do cerrado são pobres em nutrientes e bem drenados (Furley & Ratter 1988). Desta forma, para que a coexistência de espécies torne-se possível, frequentemente as espécies adotam diferentes estratégias relacionadas ao crescimento e reprodução (Oliveras & Malhi 2016), que podem resultar em estratégias de rápida aquisição ou conservação de recursos. As propriedades edáficas influenciam fortemente a estrutura de comunidade de plantas. Assim, visto que mudanças ao longo de gradientes ambientais são capazes de alterar a composição funcional das comunidades, nós buscamos compreender neste segundo capítulo como o gradiente de fertilidade e toxicidade do solo dentro de cada um dos habitats (floresta estacional e savana) podem determinar a performance dos atributos funcionais e densidade de espécies. Logo, nós fomos hábeis em discutir se espécies com atributos conservativos foram associados à solos pobres e espécies com atributos aquisitivos associado à solos mais férteis.

Estas condições de baixa fertilidade dos em solos savanas e a alta frequência de fogo, fazem com que as espécies filtradas tenham características adaptativas à estresse ambiental, que também estão relacionadas a proteção contra o ataque por herbívoros. As plantas de savanas desenvolveram diversas estratégias que inibe ou acaba por reduzir o efeito dos herbívoros sobre as plantas (Silva & Batalha 2011). Entretanto, o nível de consumo foliar por herbívoros varia muitas entre as plantas coexistentes em um dado local. Diversos fatores podem explicar esta variação, aqui neste Capítulo 3 nós buscamos compreender se as características das plantas vizinhas poderiam determinar a taxa de consumo foliar de um indivíduo focal. Desta forma, nós buscamos entender como a distância ecológica e evolutiva entre uma planta individual e suas plantas vizinhas podem mediar a nível de consumo foliar.

Em suma, nesta tese nós usamos três diferentes escalas para avaliar como estratégias ecológicas de plantas podem determinar a performance dos atributos funcionais, a estrutura das comunidades e a relação entre uma planta focal e sua vizinhança. O Capítulo 1 está baseado em uma escala de habitat e busca compreender como a preferência de habitat pode determinar a performance dos atributos funcionais em diferentes habitats. Já o Capítulo 2 foi analisado em uma escala de comunidades e busca entender como gradientes ambientais podem determinar diferentes estratégias ecológicas relacionadas aos atributos funcionais e a densidade de espécies. E por fim, o Capítulo 3 foi desenvolvido em uma escala de indivíduo e nós buscamos compreender como as características e relação filogenética das plantas vizinhas poderiam influenciar na taxa de dano foliar de uma planta focal.

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CAPÍTULO I

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Plant ecological strategies in seasonal forests and savannas species

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Summary

- Seasonal forests and savannas are contrasting habitats that occur side by side in Neotropical savanna landscapes. Thus, it is possible to either find plant species common to both forests and savannas (generalists) or exclusive to one of these habitats (specialists). In this study, we aimed to unravel the ecological strategies that determine the occurrence of species in forests, savannas or in both habitats.
- We used data on habitat preference of 284 woody species of seasonal forest and savanna communities in six sites throughout the Brazilian Cerrado. We evaluated the ecological strategies of generalist and specialist species of forests and savannas using data on ecological traits at inter- and intraspecific level.
- We found that acquisitive traits were associated to forest habitat (forest specialist and forest generalist species), while conservative traits were related to savanna habitat (savanna specialist and savanna generalist species).
- Our results demonstrate how functional traits mediate species habitat preference in contrasting habitats. The different strategies adopted by species are in accordance with the limiting factors of species occurrence in each habitat. While acquisitive traits represent competitive ability and fast resource acquisition for forest-specialist species in an environment where light is a limiting resource, conservative traits promote resistance against fire and other environmental stresses for savanna specialists. Furthermore, phenotypic plasticity appears to underlie the ability of species to persist in the contrasting habitats of seasonal forests and savannas.

Key words: habitat preference, specialist species, generalist species; functional diversity; ecological strategies, phenotypic plasticity

Introduction

Understanding the role of species traits on how species are sorted across habitats is an important question in community ecology (Hoffmann *et al.*, 2005, 2012; Ratnam *et al.*, 2011; Pellegrini *et al.*, 2015; Pellegrini, 2016). Habitats with low soil fertility or hard access to nutrients by plants low soil fertility [as African savannas (Wigley *et al.*, 2016)], high elevation [as French Alps, (de Bello *et al.* (2013)], and high fire frequency [as Australian savannas (Murphy *et al.*, 2010)] represent habitats with strong environmental filters to plants (see de Bello *et al.* (2013) for more details). Thus, plants with a conservation resource strategy are more likely to occur in such environments (Wigley *et al.*, 2016; Pellegrini, 2016). On the other hand, in environments with high resource availability plants with acquisition resource strategy are more likely to prevail (Pellegrini, 2016).

In savannas, recurrent fires and edaphic properties, such as low soil fertility and moisture deficits (Murphy & Bowman, 2012; Dantas *et al.*, 2013a,b), should favour species with conservative strategies (Pausas *et al.*, 2016). Indeed, the predominant strategies of savanna species are related to protection against fire (e.g., thick bark, Hoffmann *et al.*, 2009, 2012; Dantas *et al.*, 2013a) and drought (e.g., water storage in stem and root tissues, thick leaves with trichomes and high leaf carbon-nitrogen ratio, Scholz *et al.*, 2007; Schymanski *et al.*, 2013; Dantas *et al.*, 2013a). On the other hand, the predominant strategies of seasonal forest species are related to competition for light (taller plants, large leaves, and high specific leaf area), nutrient usage (high leaf nutrient content) and structural vigor (high wood density) (Hoffmann & Franco, 2003; Dantas *et al.*, 2013a; Pellegrini, 2016). Light is a limiting resource in forest interior, especially during the phase when tree juveniles grows toward the canopy (Hoffmann & Franco, 2003). These two strategies, rapid acquisition or conservation of resources, can be assessed through trade-offs in functional traits, thereby helping explain why a given species is able to occur in forests or in savannas (Table 1, Westoby, 1998; Lusk *et al.*, 2008; Ratnam *et al.*, 2011; Dantas *et al.*, 2013a).

Forest and savanna habitats occur intermingle, distributed as patches across Neotropical landscapes with savanna predominance. Given this close co-occurrence of habitats, the regional pool of these savanna-dominated landscapes should have species with traits that allow them to establish and persist in one of these environments (Hoffmann *et al.*, 2012; Pausas & Dantas, 2016) or in both of them (Ratnam *et al.*, 2011; Hoffmann *et al.*, 2012; Pausas & Dantas, 2016). Exclusive forest species are unable to establish in savanna habitats because they are not adapted to survive to frequent and intense fires, low soil water availability and low soil fertility (Goodland & Pollard, 1973; Hoffmann *et al.*, 2003; Dantas *et al.*, 2013a). On the other hand, exclusive savannas species are unable to establish in forest, especially due to shade intolerance and little invest in height growth (Hoffmann & Franco, 2003; Poorter, 2009; Rossatto *et al.*, 2013; Silva *et al.*, 2013). Thus, the establishment of forest species in savanna habitats require long intervals without fire, while disturbance and edge effects, like those caused by fire, may enable the persistence of savanna species in forest habitats (Hoffmann & Franco, 2003).

The boundary between forest and savanna is normally abrupt (Hoffmann *et al.*, 2003; Rossatto *et al.*, 2009) and few species are able to occur in both habitats (Hoffmann *et al.*, 2009, 2012). The capacity of some species occur in both habitats can be related to plastic responses of species to different biotic and abiotic factors (Turcotte & Levine, 2016), or because they have strategies that permit colonizing different habitat types (Hoffmann *et al.*, 2012; Silva *et al.*, 2013; Bowman *et al.*, 2015). The ability of species to exhibit different strategies according to the conditions imposed by the environment is defined as phenotypic plasticity (Miner *et al.*, 2005). Phenotypic plasticity plays a fundamental role on species interactions and coexistence (Violle *et al.*, 2012; Cianciaruso *et al.*, 2012). Many plant species are highly plastic and are able to establish and persist in various environments (Hoffmann *et al.*, 2009, 2012). Intraspecific variability can determine species persistence in environments with strong differences to plant establishment, as forest and savannas. We highlight that considering species habitat preference (habitat generalist versus specialist) and phenotypic plasticity is a new perspective in the quest to understand the distinct ecological strategies of species in seasonal forest and savannas. Several studies have sought to identify which mechanisms determine the species occurrence in forest and savanna habitats (Hoffmann *et al.*, 2003, 2005; Ratnam *et al.*, 2011; Rossatto *et al.*, 2013; Charles-Dominique *et al.*, 2015; Pellegrini *et al.*, 2015). However, information about how different ecological strategies relate to edaphic proprieties and fire disturbance determine the occurrence of species in forests or savannas is still missing, because the few existing studies evaluated a low number of species and just a few traits (Hoffmann *et al.*, 2003, 2004, 2005, 2012; Hao *et al.*, 2008; Rossatto *et al.*, 2009; Ratnam *et al.*, 2011; Silva *et al.*, 2013; Pellegrini, 2016)

Here we evaluated whether forest-specialist, savanna-specialist and generalist woody species (i.e., occurring in both seasonal forest and savannas) have distinct ecological strategies (Table 1). We aimed to answer the following questions: (i) Do trait values differ between habitat-specialist and habitat-generalist species (i.e. species restricted to either seasonal forest or savanna, and species common to seasonal forest and savanna, respectively)? (ii) Do generalist species exhibit intermediate functional traits values between forest- and savanna-specialist species? (iii) Do the same species occurring in forests and savannas show different functional traits values in each environment? We hypothesized that savanna-specialist woody species would have trait values more related to a conservative use of resource whereas forest-specialist woody species will have functional traits associated to competitive ability and resource acquisition (Table 1). Generalist species would present intermediate values of functional traits between forest- and savanna-specialist species. Additionally, using site-specific data we expect that when a species occurs at both habitats, its traits values will be plastic and respond to the general strategy of each environment, with acquisitive strategy in seasonal forest and conservative strategy in savanna.

Table 1 Functional significance of traits and basis of trait-based patterns predicted in relation to forest and savanna habitats.

Trait	Abbreviations	Unit	Functional significance	Prediction		Rationale
				Forest	Savanna	
Bark thickness	BT	mm	Protection of vital tissue against damage, like that caused by fire [1]	Low	High	Savannas are fire-prone environments and present many species with fire resistance characteristics
Stem-specific density	SSD	mg mm^{-3}	Resistance to physical damage, and consequent structural vigor [1,2,3]	Medium	High	Higher wood density in the savanna because stress tolerant plants have greater construction costs in poor soils, and need protection from fires or herbivores. Forest species have medium wood density due to the mixture of species with high wood density (climax species) and low (pioneer species)
Leaf thickness	LT	mm	Related to species strategies of resource acquisition and use, and resistance to physical damage. Every time is correlated with leaf toughness [4,5]	Low	High	Savanna species live under severe environmental stress and nutrient scarcity, so that they invest in leaf thickness to assure greater protection against herbivores and water loss
Leaf carbon/nitrogen ratio	C/N	(%) / g/kg (%)	Low values of the ratio indicate higher nutritional quality and palatability of leaves. Nitrogen is the major limiting macronutrient in plants [1,8]	Low	High	C/N ratio would be higher among savanna species because the assimilation of N would be lower in the savanna, leading to a higher C/N ratio. Higher C/N ratio can promote greater leaf toughness and protection against abiotic and biotic stress[11]
Maximum plant height	Hmax	m	Competitive plant fitness, plant fecundity, tolerance or resistance to disturbances [1]	High	Low	Forest species are taller due to the greater investment in vertical growth resulting from the strong competition for light in the forest canopy
Leaf area	LA	cm^2	Ecological strategy related to resource acquisition and use, responsible to environmental stress and disturbances. High stress tends to select small leaves [1]	High	Low	Forest species have higher leaf area because light is a limiting resource in forest interiors, and higher leaf laminas enable higher absorption of light per leaf
Specific leaf area	SLA	$cm^2\ g^{-1}$	Related to structural defense, resource uptake, resource use efficiency, and growth strategies. It is negatively correlated with leaf lifespan [1]	High	Low	Species from forest environments rich in nutrients can invest in a larger leaf surface per unit of leaf mass, which would improve their competitive ability in forest interiors
Leaf phosphorus content	LPC	g/kg (%)	Related to growth and productivity of plants [6]	High	Low	Forest environments have higher concentrations of these nutrients available in the soil than savanna environments and more efficient nutrient cycling processes arising from the litter
Leaf potassium content	LKC	g/kg (%)	Plays a critical role in plant growth and metabolism, and contributes to survival of plants that are under various biotic and abiotic stresses [7]	High	Low	Same rationale of leaf phosphorous content
Leaf calcium content	LCaC	g/kg (%)	Unique macronutrient with diverse but fundamental physiological roles in plant structure and signaling. Plays an important role in structure and increasing resistance of plants, and helps the leaves to grow strong and health [8,9]	High	Low	Same rationale of leaf phosphorous content
Leaf magnesium content	LMgC	g/kg (%)	Involved in photosynthetic processes, related with growth and health of plants [10]	High	Low	Same rationale of leaf phosphorous content

[1] Pérez-Harguindeguy *et al.* (2013); [2] Chave *et al.* (2009); [3] Larjavaara & Muller-Landau (2010); [4] Cianciaruso *et al.* (2012); [5] Vile *et al.* (2005); [6] Schachtman *et al.* (1998); [7] Tripler *et al.* (2006); [8] Chapin *et al.* (2011); [9] Gilliham *et al.* (2011); [10] Shaul (2002); [11] Silva & Batalha (2011).

Methods

Study region

The Cerrado domain (Savannas) is a region of approximately 2 x 10^6 km^2. The study region ranged from 12°S to 22°S. The soils are predominantly characterized as red-yellow latosol, with oxisols and dystrophic soils (Marimon Junior & Haridasan, 2005; Ruggiero *et al.*, 2006; Silva & Batalha, 2008; Pinheiro & Durigan, 2009). These soils show high water permeability and their water available capacity varies in accordance to texture and clay concentrations (Reatto *et al.*, 2008). For a better characterization of the climate and edaphic proprieties of the studied sites sampled see Table S1. The Cerrado is composed of several vegetation mosaics that are the result of the occurrence of various physiognomies (Eiten, 1972), ranging from open savannas to evergreen gallery forests along streams and upland forests of deciduous and evergreen species (Hoffmann *et al.*, 2012).

Sampling design

We selected six study sites throughout the Brazilian Cerrado phytogeographic domain (Fig. 1). The mean distance between pairs of sites was 12 km. The shortest distance between sites was 150 km (Emas National Park and City of Jataí). We adopted a paired sampling design, which consisted in one block of plots placed in savanna (*cerrado stricto sensu*) and another block of plots placed in seasonally dry forests. The shortest distance within site between a forest and a savanna block was 1 km (in Emas National Park). In each locality we sampled woody communities in 10 100-m^2 plots in each block. We recorded all individuals with diameter at breast ground height (DGH) ≥ 5 cm in all savanna plots, and all individuals with a diameter breast height (DBH) ≥ 10 cm in all forest plots. All individuals were identified to the species level. Nomenclature follows the Brazilian Flora (Forzza *et al.*, 2012).

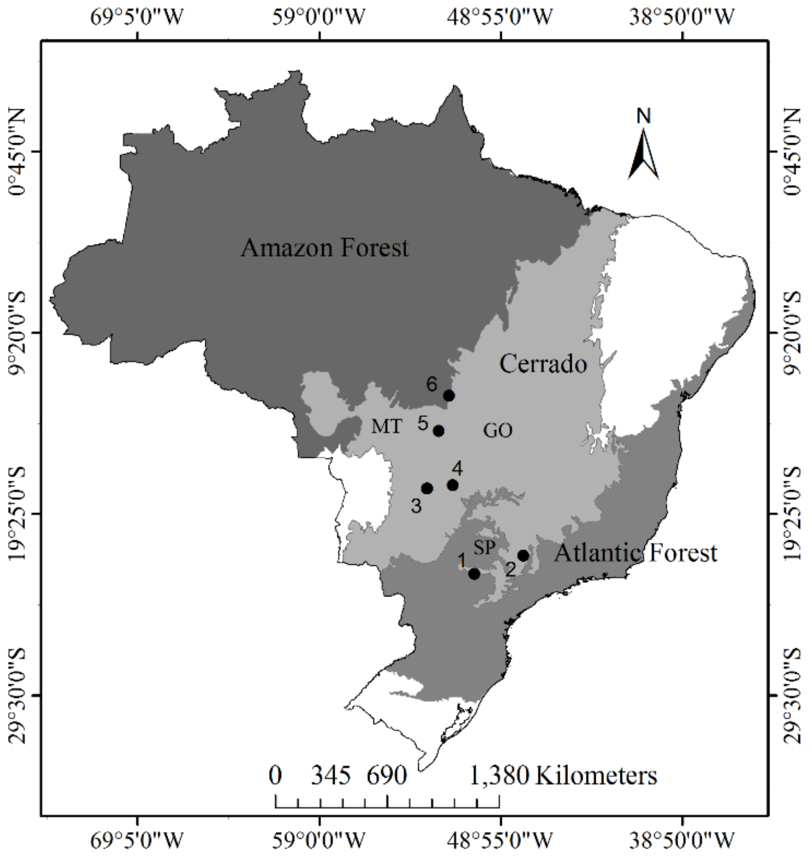

Figure 1. Location of six study sites of seasonal forests and savannas sampled in the Brazilian Cerrado. 1. Assis Ecological Station – SP, 2. Vassununga State Park – SP, 3. Emas National Park – GO, 4. Jataí – GO, 5. Bacaba Park – MT, 6. Ribeirão Cascalheira – MT.

Trait sampling

We sampled 11 functional traits of 284 species belonging to 57 families distributed in forest and savannas in six sites throughout the Cerrado (Table S2). The species richness ranged from 21 to 52 species in the forest blocks, and from 43 to 89 in the savanna blocks.

Following Pérez-Harguindeguy et al. (2013), we measured the following traits: bark thickness (BT), stem-specific density (SSD), leaf thickness (LT), leaf carbon/nitrogen ratio (C/N), maximum plant height (Hmax), leaf area (LA), specific leaf area (SLA), leaf phosphorous content (LPC), leaf potassium content (LKC) leaf calcium content (LCaC), and leaf magnesium content (LMgC) (see Table 1 for their ecological significance). Whenever possible we measured 10 individuals for each species in each site. When a given species had less than 10 individuals in our plots, we sampled individuals that were nearby the plot (see Table S3). Leaf nutrient concentration (phosphorous, potassium, calcium, magnesium) and leaf carbon/nitrogen ratio were measured for three individuals of each species in each site. Leaf nutrient concentrations were determined in the Laboratory of Soils of the University of Viçosa. All other traits were quantified in each site for all species by sampling individuals whenever possible. We did not measure stem-specific density for palm species because is impossible to collect it without injuring the whole plant.

To obtain leaf trait values, we scanned three to five leaves of each individual. We measured scanned leaf area through of a script that we build using the “EBImage” package (Pau et al., 2014) with R 3.2.1 (http://www.R-project.org). Then, we dried leaves at 70 °C for 48 h, and measured leaf dry mass. Leaf thickness of fresh leaves and bark thickness were measured using a digital micrometer. All traits were collected during the rainy season (December to March), which represents the peak of growth and is also the period of maximum leaf expansion and maturity for the studied species.

We classified species according to their habitat of occurrence according to Mendonça *et al.*, (2008) and the Brazilian Flora database (http://floradobrasil.jbrj.gov.br/). We considered as savanna specialists or forest specialists all species with restrict occurrence to savanna or forest, respectively. Species that occur in both habitats according to the literature, but that were sampled only in forest plots were considered “forest-generalist species”. Following the same rationale species that occurred only in savannas plots, but can also occur in forests according to the literature, were considered “savanna-generalist species”. In order to avoid misinterpretations due to potential sample bias we classified the species as “forest-generalist species” and “savanna-generalist species”, and not only like generalists, because we only found them in only one habitat at the field (Table S2). Only 19 species were sampled in both forest and savanna habitats. These species were analysed separately in order to evaluate the potential intraspecific variation in their ecological strategies (see below).

Statistical analyses

We performed ANOVA to test for differences in functional traits between habitat preferences of species (forest specialists, savanna specialists, forest generalist and savanna generalist) with Tukey’s post hoc comparisons, when appropriate. In order to control for type I error, P-values were based on Bonferroni’s correction. The ANOVAs were conducted using “aov” function in R (R Core Team, 2015).

Considering that different sources of variation can act on habitat preferences of species, we evaluated the role of variability among habitat preferences, within habitats and among species. This approach enabled us to assess whether the possible differences related to habitat preference in the ANOVA are a result of variation among different sites or changes in species composition. We fitted a general linear mixed model (GLMM) using site, habitat preference and species as nested random factor in the “lme” function in the “nlme” R package (Pinheiro *et al.*, 2016). We adopted this order, for the nested random factors for considering sites as the coarser and species as the finer factor.

To partition the variation among these three components we used the “varcomp” function in the “ape” R package (Paradis *et al.*, 2004).

For the 19 species sampled in both forest and savanna habitats we performed paired *t* test to evaluate how functional trait of these species respond to forest and savanna habitats.

Results

In general, forest specialists and forest generalists presented traits values representative of an acquisitive strategy, whereas savannas specialists and generalists had trait values more related to a conservative strategy. Forest species had higher maximum height, specific leaf area and leaf nutrient content than savanna species (Table 2; Fig. 2). Conversely, savanna species had ticker barks and leaves and higher leaf carbon/nitrogen ratio (Table 2; Fig. 2). Moreover, the traits of forest specialist and forest generalist species did not differed (Table 2; Fig. 2). However, savanna specialist species presented higher values of bark thickness and leaf thickness than savanna generalist species (Table 2; Fig. 2). We did not find any differences for stem-specific density and leaf area in relation to habitat type (Table 2; Fig. 2).

For all traits, the variation among species and habitats explained trait variability (Table 2). In general, the variability among sites was low, with only carbon/nitrogen, phosphorous and calcium presenting intermediate values of variability (Table 2; Fig. S1).

Table 2 Mean values of functional traits (± SD) and results of variance component analysis comparing the variability among sites, habitats and species for traits of seasonal forests and savannas in the Brazilian Cerrado. Tukey's post hoc comparisons with Bonferroni corrections ($\alpha = 0.05$ to 0.0045) reveals significant differences between functional traits of forest and savanna. Different letters indicate significant differences between habitat preferences (Tukey test, $p < 0.05$).

Trait	Forest	Generalist		Savanna			Variability			
		Sampled only in forest	Sampled only in savanna		F	*P*	Among sites	Among habitats	Among species	Residuals
Bark thickness (mm)	1.73 ± 1.77 ^{a}	2.37 ± 2.23 ^{a}	6.26 ± 5.33 ^{b}	8.19 ± 4.62 ^{c}	54.35	<0.001	0.00	0.35	0.65	0.00
Stem-specific density (mg mm^{-3})	0.54 ± 0.12	0.53 ± 0.14	0.54 ± 0.09	0.51 ± 0.08	1.95	0.121	0.12	0.12	0.66	0.10
Leaf thickness (mm)	0.17 ± 0.04 ^{a}	0.18 ± 0.05 ^{a}	0.22 ± 0.08 ^{b}	0.27 ± 0.08 ^{c}	37.78	<0.001	0.07	0.37	0.48	0.08
Leaf C/N ratio (g/kg(%))	2.55 ± 0.80 ^{a}	2.65 ± 0.79 ^{a}	3.18 ± 0.86 ^{b}	3.47 ± 0.84 ^{b}	22.34	<0.001	0.10	0.15	0.65	0.10
Maximum plant height (m)	15.8 ± 5.5 ^{a}	15.8 ± 5.5 ^{a}	6.7 ± 2.2 ^{b}	5.6 ± 1.8 ^{b}	134.6	<0.001	0.00	0.73	0.27	0.00
Leaf area (cm^{2})	175 ± 281	181 ± 360	111 ± 173	90 ± 120	2.50	0.059	0.01	0.04	0.84	0.11
Specific leaf area (cm^{2} g^{-1})	117 ± 39.0 ^{a}	119 ± 43.3 ^{a}	88 ± 26.55 ^{b}	81.3 ± 22.4 ^{b}	24.91	<0.001	0.00	0.46	0.53	0.01
Leaf phosphorous content (g/kg(%))	1.25 ± 0.53 ^{a}	1.30 ± 0.48 ^{a}	1.11 ± 0.34 ^{a,b}	1.01 ± 0.26 ^{b}	7.28	<0.001	0.29	0.22	0.42	0.07
Leaf potassium content (g/kg(%))	9.25 ± 6.23 ^{a}	9.10 ± 5.14 ^{a}	6.19 ± 3.57 ^{b}	5.48 ± 2.72 ^{b}	12.98	<0.001	0.00	0.49	0.47	0.04
Leaf calcium content (g/kg(%))	12.5 ± 11.7 ^{a}	9.57 ± 9.31 ^{a}	3.99 ± 2.86 ^{b}	3.44 ± 1.74 ^{b}	24.72	<0.001	0.26	0.48	0.21	0.05
Leaf magnesium content (g/kg(%))	3.05 ± 1.90 ^{a,b}	3.29 ± 1.93 ^{a}	2.43 ± 1.29 ^{b,c}	2.17 ± 1.02 ^{c}	7.69	<0.001	0.06	0.32	0.53	0.09

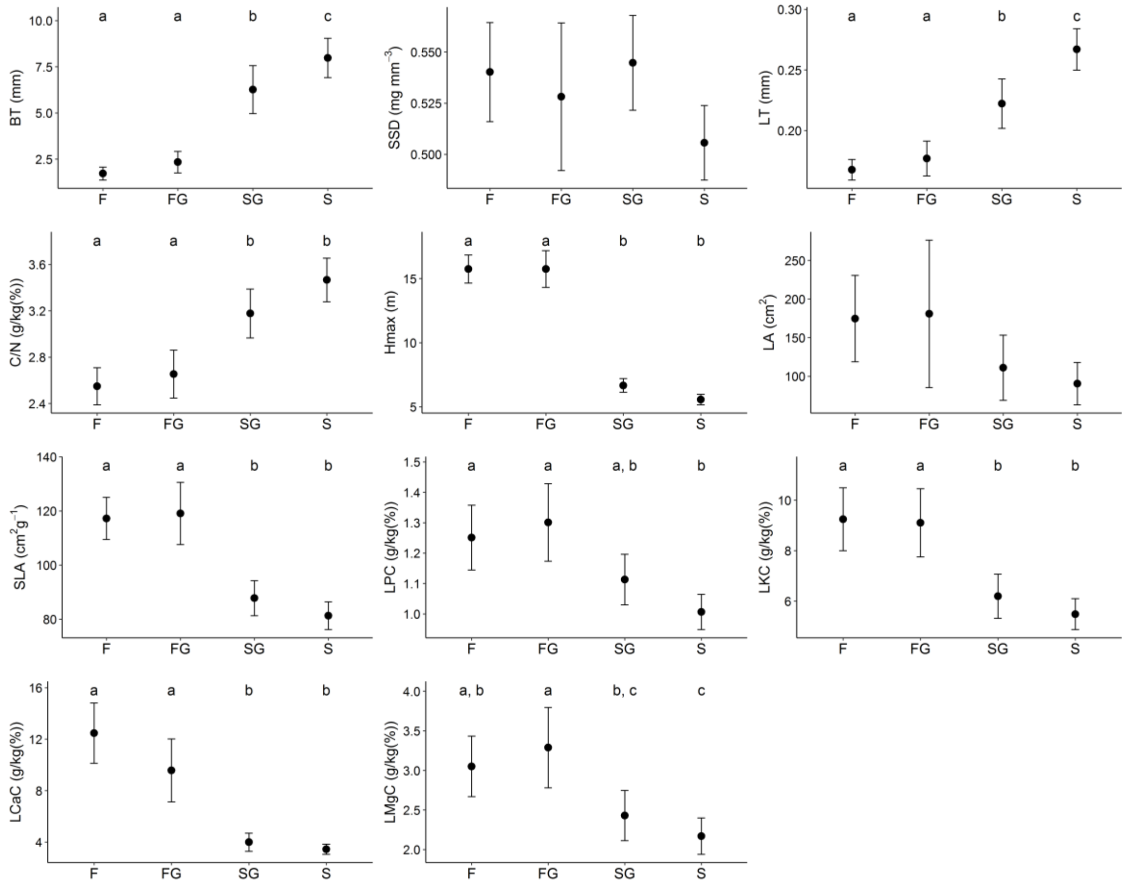

Figure 2 Mean value and confidence interval to species habitat preference - specialist of forest (F) and savanna (S), and generalist sampled only in forest (FG) and sampled only in savanna (SG) - for traits of seasonal forests and savannas in the Brazilian Cerrado. Different letters indicate significant differences between habitat preferences (Tukey test, $p < 0.05$).

For the 19 species that occurred in both forest and savanna habitats, we found intraspecific differences for only three traits (Fig. 3). Individuals occurring in forests presented higher values of maximum plant height, specific leaf area, while those occurring in savannas had higher carbon/nitrogen ratio (Fig. 3).

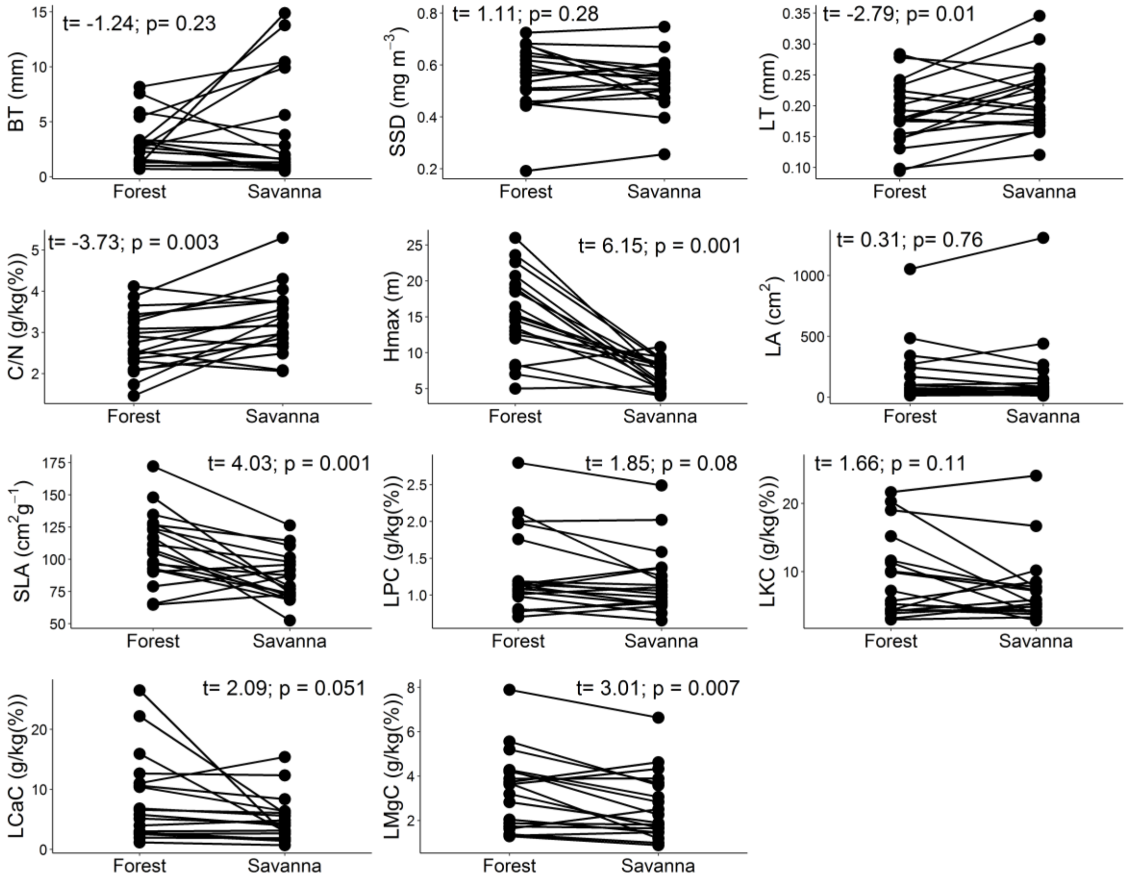

Figure 3 Ecological strategies of 19 species common to seasonal forests and savannas environments in the Brazilian Cerrado. Paired *t* test with Bonferroni corrections (α = 0.05 to 0.0045) reveals significant differences between functional traits of forest and savanna.

Discussion

In general, our results were in accordance to our predictions (see Table 1) and demonstrate that forest and savanna species have different ecological strategies. Forest species had higher values for traits related to competitive ability and fast resource acquisition, and savannas species had higher values for traits associated with physical and biological stress damage. We found evidence for fundamental trade-offs involving major plant traits in contrasting tropical habitats, in which a set of species invests in traits related to rapid acquisition of resources, while another group of species allocates more energy in traits that represent conservation of resources and protection against physical and biological damage (Diaz *et al.*, 2004; Wigley *et al.*, 2016). For example, plants with a resource acquisition strategy have leaves with high nutritional quality and fast growth, with higher plant height and specific leaf area, which represents better capture and use of light (Westoby, 1998; Diaz *et al.*, 2004; Hoffmann *et al.*, 2012; Pellegrini, 2016). Because light is a limited resource in the understory species that invest more in acquisitive strategies tend to be more successful in seasonal forests (Hoffmann *et al.*, 2012). On the other hand, species with traits related to conservative strategy tend to persist in savannas, under poor soils and higher effect of strong environmental filters (Westoby, 1998; Dantas *et al.*, 2013a; Pausas *et al.*, 2016).

The distinction between functional traits of forest and savanna species occurs because the species with different growth strategies respond differently to environments so contrasting as forests and savannas and adopt different strategies for persisting in an environment that is either light limiting or fire-prone (Hoffmann & Franco, 2003; Dantas *et al.*, 2016; Pausas *et al.*, 2016). The adoption of these different ecological strategies by species living in habitats drive by different limiting factors often determine their persistence or exclusion (Hoffmann & Franco, 2003; Laureto & Cianciaruso, 2015). Species that do not have fire-adaptive traits may be excluded from fire-prone habitats like savannas (Simon *et al.*, 2009; Pausas *et al.*, 2016). Likewise, species that not have fast growth or shade tolerance may not persist in light limiting habitats (Hoffmann & Franco, 2003; Ratnam *et al.*, 2011). For instance, savanna species presented higher values for traits related to defense against herbivores and water loss (leaf thickness and carbon/nitrogen ratio) and fire protection (bark thickness) (Silva & Batalha, 2011; Dantas *et al.*, 2013b,a; Pausas *et al.*, 2016), representing strategies of stress tolerance in savanna environments (Hoffmann *et al.*, 2012; Pellegrini *et al.*, 2015). On the other hand, forest species have strategies associated with competitive vigor (taller plants), efficiency in capture and use of the light resource (high specific leaf area), and fertility (high leaf concentrations of P, K, Mg, Ca). Thus, forest specialist species cannot establish in savannas because of the effects of environmental filters, and savanna specialist species are unable to establish in forests due to low competitive ability for light (Silva *et al.*, 2013).

We expected that stem-specific density and leaf area would be different between forest and savannas species (see Table 1). However, these traits did not differ between forest and savanna species. A similar wood density to forest and savanna species can be explained because forest species need a high wood density to support taller trees in an environment where height means competitive ability (Chave *et al.*, 2009; Pérez-Harguindeguy *et al.*, 2013). On their turn, savanna species slow growth in a stressful environment have high construction costs (Larjavaara & Muller-Landau, 2010), which leads to high wood density, that also confers higher advantage in persisting in under strong environmental stress, poor soils and high fire frequency [Dantas *et al.* (2013a); but see Hoffmann *et al.* (2009) and Brando *et al.* (2012)]. Even if some studies showed that leaf area is two times greater for forest than savanna species (Hoffmann *et al.*, 2012; Silva *et al.*, 2013), these studies were conducted with a restricted number of species. Savannas species have large root systems (Oliveira *et al.*, 2005) and lead habitat ranging from evergreens to deciduous species (Cianciaruso *et al.*, 2013). The deep roots make the savanna species able to have access to soil water and, therefore, to survive and grow even during the dry season (Oliveira *et al.*, 2005). Yet, many savannas species concentrate the loss of leaves during dry season whereas forest species generally produce and lose leaves throughout the year (Franco *et al.*, 2005; Lenza & Klink, 2006). However, for Neotropical savanna species, Cianciaruso *et al*. (2013) found a lack of differences in leaf traits (SLA and N) among species with distinct leaf habits. In fact, they found that even evergreens and deciduous have similar leaf life spans. This reinforces the idea that the more relevant trade-offs are in the root systems. Also, the similar leaf area between forest and savannas species (but distinct SLA) indicate that leaf dry mass content is main factor determining acquisitive strategy for forest (high SLA and low carbon/nitrogen rate) and conservative strategy for savannas (low SLA and high carbon/nitrogen rate).

When we evaluate the individuals of the same species inhabiting in seasonal forests and savannas, three out of the 11 functional traits differed between species of forest and savanna. Carbon/nitrogen that represent conservative strategy presented higher values in savanna habitat, while maximum plant height and specific leaf area that indicate acquisitive strategy were higher in forest habitat. These opposite responses of the same species in different environments show that the habitat has a strong influence on intraspecific trait variability of generalist species. Intraspecific variability is evident when a given species occurs in different environments expressing distinct trait values (Miner *et al.*, 2005), because non-plastic species can be removed from communities through environmental filters (as fire) and competition by light (Hoffmann & Franco, 2003; Jung *et al.*, 2010). Leaf traits and plant height are traits that have greater phenotypic plasticity and that can shift according to light and resource availability or environmental stress (Hoffmann & Franco, 2003; Hoffmann *et al.*, 2005, 2012; Nicotra *et al.*, 2010). Assuming that some "dominant plants tend to monopolize light and mineral nutrient capture by the development of extensive leaf canopies and root systems" (Campbell *et al.*, 1991), thus species ability to perform shifts in morphological and physiological leaf traits is key to determine the permanence of generalist species (Schlichting, 1986; Callaway *et al.*, 2003). Usually, savanna species have thicker barks than forest species, because bark promote protection of stem in fire-prone habitat (Hoffmann *et al.*, 2003). However, our results showed that the same species in savanna and forest had similar bark thickness.

Savanna species have thick barks as a fire resistance strategy (Dantas *et al.*, 2013a; Rosell *et al.*, 2014; Pausas *et al.*, 2016). Hoffmann *et al.* (2012) calculated a threshold bark thickness of 5.9 mm needed to survive in a low-intensity fire of forest and savanna species. In our study system, the species with individuals inhabiting in seasonal forests and savannas showed mean values below of threshold bar thickness in both habitats (see Table S4). These values below of threshold bark thickness can be explained by the fact that the most of the 19 species occurring in forest and savanna have the forest habitat as preferential habitat (see list of species in Table S4). Moreover, these 19 species present low percentage of occurrence in 376 areas analysed by Ratter et al. (2003) that also can be justified by forest preferential habitat these species, because no included forest areas in analyses. We highlight that the same species with individuals occurring in forest and savannas are not proper generalists, which would promote an adaptive advantage in a phytogeographic region with forests and savannas, and with distinct levels of fire. We verified that some traits respond to habitat preference at interspecific level, but such differences are lost when intraspecific variation is included. However, changes in SLA, plant height and leaf carbon/nitrogen ratio were similar at both inter and intraspecific levels. Therefore, these are likely to be key traits for adaptation of individuals in forest and savannas.

Concluding remarks

We showed that habitat preference determines the value of functional traits. Traits related to an acquisitive strategy were associated to and higher in the forest habitat, while traits with conservative strategy were related to and higher in the savanna habitat (Diaz *et al.*, 2004). We highlight that these different strategies are related to competitive ability and resource acquisition of forest-specialist species in an environment in which light is a limiting resource as forests, and related to defense against fire and physical and biological stress of savanna-specialist species in an environment with high fire frequency and poor-soils as savannas (Pellegrini, 2016; Pausas *et al.*, 2016). Generalist species with occurrence restrict to forest or savanna in our study generally presented values of functional traits intermediary between forest- and savanna-specialist species. However, generalist species of forests and savannas were more similar to specialist species of each habitat than each other. This indicates that the habitat play an important role on functional traits, determining values according to limiting factors of each environment. This pattern was also observed when we evaluated the same species occurring in forest and savanna, demonstrating that the habitat has also a strong influence on intraspecific trait variability of generalist species. Thus, the phenotypic plasticity of the species may confer ability to persistence in a habitat with stronger competition for light (forest) or in a habitat with strong environmental filters and stress (savanna).

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Supporting Information

Table S1. Climate characteristics and edaphic proprieties of the six sites sampled in Brazilian Cerrado. The values represented a range, when available, of 20 years of data collected in the nearest weather station of each site. The fire frequency applies only to savannas sites. A low fire frequency indicates an interval about of 5 years among fire events, and high fire frequency of 10 years.

Environmental characteristics	Assis Ecological State - SP	Vassununga State Park - SP	Emas National Park - GO	Jataí - GO	Bacaba Park - MT	Ribeirão Cascalheira - MT
Coordinates	50W 22’, 22S 35’	47W 37’, 21S 36’	52W 59’, 17S 54’	51W 32’, 17S 45’	52W 21’, 14S 42’	51W 46’, 12S 49’
Fire frequency	low	low	High	high	high	low
Climate Type	Cfa	Cwa	Aw	Aw	Aw	Aw
Altitude (m)	560	740	840	860	325	374
Mean Annual Temp. (°C)	23.6	22.3	24.6	22.6	24.8	25.4
Mean Minimum Temp. (°C)	19.0	16.6	18.9	17.0	18.9	20.1
Precipitation (mm yr^{-1})	1352	1437	1745	1605	1433	1822
Evapotranspiration (mm)	129	92	82	121	134	136
Relative Moisture (%)	64	70	69	69	77	71
Soil characteristics	Forest savanna	Forest savanna	Forest savanna	Forest savanna	Forest savanna	Forest savanna
N	0.32(0.14); 0.25(0.10)	0.22(0.06); 0.12(0.04)	0.26(0.09); 0.09(0.04)	0.18(0.03); 0.17(0.04)	0.11(0.02); 0.08(0.01)	0.10(0.01); 0.05(0.01)
P	8.39(4.26); 3.91(0.31)	4.51(4.58); 3.89(3.13)	1.79(0.65); 0.56(0.20)	1.57(0.66); 1.03(0.76)	1.15(0.57); 2.03(0.14)	1.75(0.25); 2.04(0.63)
K	46.3(16.9); 11.8(3.82)	11.2(39.8); 13.1(3.33)	42.4(7.43); 31.4(8.06)	28.4(12.0); 22.3(5.51)	46.7(10.1); 46.2(6.65)	17.7(3.20); 18.3(7.42)
SOM	3.10(1.12); 1.70(0.60)	5.13(0.96); 3.10(0.50)	5.87(1.64); 3.08(1.30)	6.22(1.13); 4.79(0.83)	1.07(0.56); 1.73(0.31)	2.49(0.28); 1.83(0.57)
Clay	11.2(2.64); 8.0(1.79)	44.7(10.8); 10.6(0.80)	26.1(7.13); 29.4(18.7)	54.6(7.32); 51.0(3.69)	20.1(3.42); 12.6(2.33)	16.7(2.10); 2.9(1.14)
pH	7.09(0.67);4.85(0.13)	6.16(0.65); 4.51(0.09)	4.20(0.42); 4.30(0.25)	5.26(0.15); 5.26(0.11)	4.65(0.09); 5.04(0.13)	4.10(0.08); 4.95(0.22)
Al	0; 0.88(0.15)	0.12(0.32); 1.70(0.20)	1.65(0.37); 1.19(0.27)	1.03(0.37); 0.65(0.26)	0.85(0.18); 1.16(0.13)	1.12(0.11); 0.77(0.11)

Table S2 List of species and families classified according to habitat preference. The species are ordered according to family. In bold the 19 species that occurred in both forest and savanna habitats in our study and for which we have intraspecific trait variability.

Species	Family	Habitat preference
Anacardium occidentale L.	Anacardiaceae	Generalist savanna
***Astronium fraxinifolium* Schott**	**Anacardiaceae**	**Generalist**
Astronium graveolens Jacq.	Anacardiaceae	Generalist forest
Myracrodruon urundeuva Allemão	Anacardiaceae	Generalist forest
***Tapirira guianensis* Aubl.**	**Anacardiaceae**	**Generalist**
Tapirira obtusa (Benth.) J.D.Mitch.	Anacardiaceae	Generalist forest
Tapirira sp.	Anacardiaceae	Forest
Annona cacans Warm.	Annonaceae	Generalist forest
Annona coriacea Mart.	Annonaceae	Savanna
Annona crassiflora Mart.	Annonaceae	Generalist savanna
Annona sylvatica A. St.-Hil.	Annonaceae	Generalist forest
Bocageopsis mattogrossensis (R.E.Fr.) R.E.Fr.	Annonaceae	Generalist forest
Duguetia marcgraviana Mart.	Annonaceae	Generalist forest
Ephedranthus parviflorus S.Moore	Annonaceae	Generalist forest
Guatteria blepharophylla Mart.	Annonaceae	Forest
Xylopia amazonica R.E.Fr.	Annonaceae	Forest
***Xylopia aromatica* (Lam.) Mart.**	**Annonaceae**	**Generalist**
Xylopia frutescens Aubl.	Annonaceae	Forest
Xylopia sericea A.St.-Hil.	Annonaceae	Generalist savanna
Aspidosperma desmanthum Benth. ex Müll.Arg.	Apocynaceae	Forest
Aspidosperma discolor A.DC.	Apocynaceae	Forest
Aspidosperma macrocarpon Mart.	Apocynaceae	Generalist savanna
Aspidosperma multiflorum A.DC.	Apocynaceae	Savanna
Aspidosperma nobile Müll.Arg.	Apocynaceae	Generalist savanna
Aspidosperma polyneuron Müll.Arg.	Apocynaceae	Generalist forest
Aspidosperma ramiflorum Müll.Arg.	Apocynaceae	Forest
Aspidosperma tomentosum Mart.	Apocynaceae	Generalist savanna
Hancornia speciosa Gomes	Apocynaceae	Savanna
Himatanthus obovatus (Müll.Arg.) Woodson	Apocynaceae	Savanna
Himatanthus sucuuba (Spruce ex Müll.Arg.) Woodson	Apocynaceae	Forest
Schefflera macrocarpa (Cham. & Schltdl.) Frodin	Araliaceae	Generalist savanna
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin	Araliaceae	Generalist forest
Schefflera vinosa (Cham. & Schltdl.) Frodin & Fiaschi	Araliaceae	Savanna
Euterpe edulis Mart.	Arecaceae	Forest
Oenocarpus distichus Mart.	Arecaceae	Generalist forest
Syagrus comosa (Mart.) Mart.	Arecaceae	Savanna
Syagrus flexuosa (Mart.) Becc.	Arecaceae	Savanna

Species	**Family**	**Habitat preference**
Moquiniastrum polymorphum (Less.) G. Sancho	Asteraceae	Generalist savanna
Piptocarpha rotundifolia (Less.) Baker	Asteraceae	Savanna
Vernonia sp.	Asteraceae	Savanna
Handroanthus heptaphyllus (Vell.) Mattos	Bignoniaceae	Forest
Handroanthus ochraceus (Cham.) Mattos	Bignoniaceae	Savanna
Handroanthus serratifolius (Vahl) S.O.Grose	Bignoniaceae	Generalist forest
Jacaranda copaia (Aubl.) D.Don	Bignoniaceae	Forest
Jacaranda micrantha Cham.	Bignoniaceae	Forest
Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex S.Moore	Bignoniaceae	Savanna
Zeyheria tuberculosa (Vell.) Bureau ex Verl.	Bignoniaceae	Forest
Cordia sellowiana Cham.	Boraginaceae	Generalist forest
Cordia trichotoma (Vell.) Arráb. ex Steud.	Boraginaceae	Generalist forest
Protium pilosissimum Engl.	Burseraceae	Forest
Protium spruceanum (Benth.) Engl.	Burseraceae	Forest
Protium unifoliolatum Engl.	Burseraceae	Forest
Tetragastris altissima (Aubl.) Swart	Burseraceae	Forest
Trattinnickia glaziovii Swart	Burseraceae	Forest
Trattinnickia sp.	Burseraceae	Forest
Kielmeyera coriacea Mart.	Calophyllaceae	Savanna
Kielmeyera rubriflora Cambess.	Calophyllaceae	Savanna
Jacaratia spinosa (Aubl.) A.DC.	Caricaceae	Forest
Caryocar brasiliense A.St.-Hil.	Caryocaraceae	Savanna
Cheiloclinium cognatum (Miers) A.C.Sm.	Celastraceae	Forest
Plenckia populnea Reissek	Celastraceae	Savanna
Salacia crassifolia (Mart. ex Schult.) G. Don	Celastraceae	Savanna
Couepia grandiflora (Mart. & Zucc.) Benth. ex Hook.f.	Chrysobalanaceae	Generalist savanna
***Hirtella glandulosa* Spreng.**	**Chrysobalanaceae**	**Generalist**
Hirtella racemosa Lam.	Chrysobalanaceae	Generalist forest
Licania apetala (E.Mey.) Fritsch	Chrysobalanaceae	Forest
Licania blackii Prance	Chrysobalanaceae	Forest
Licania gardneri (Hook.f.) Fritsch.	Chrysobalanaceae	Forest
Licania humilis Cham. & Schltdl.	Chrysobalanaceae	Savanna
Licania kunthiana Hook.f.	Chrysobalanaceae	Generalist forest
Licania minutiflora (Sagot) Fritsch	Chrysobalanaceae	Forest
Buchenavia tetraphylla (Aubl.) R.A.Howard	Combretaceae	Generalist forest
***Buchenavia tomentosa* Eichler**	**Combretaceae**	**Generalist**
Terminalia argentea Mart.	Combretaceae	Generalist savanna
Connarus perrottetii (DC.) Planch.	Connaraceae	Forest
Connarus suberosus Planch.	Connaraceae	Savanna
Rourea induta Planch.	Connaraceae	Savanna
Curatella americana L.	Dilleniaceae	Savanna
Davilla elliptica A.St.-Hil.	Dilleniaceae	Savanna
Diospyros hispida A.DC.	Ebenaceae	Generalist savanna

Species	**Family**	**Habitat preference**
Sloanea monosperma Vell.	Elaeocarpaceae	Forest
Sloanea pubescens Benth.	Elaeocarpaceae	Forest
Sloanea sinemariensis Aubl.	Elaeocarpaceae	Forest
Erythroxylum engleri O.E.Schulz	Erythroxylaceae	Savanna
Erythroxylum suberosum A.St.-Hil.	Erythroxylaceae	Savanna
Erythroxylum testaceum Peyr.	Erythroxylaceae	Savanna
Erythroxylum tortuosum Mart.	Erythroxylaceae	Savanna
Alchornea glandulosa Poepp.	Euphorbiaceae	Generalist forest
***Chaetocarpus echinocarpus* (Baill.) Ducke**	**Euphorbiaceae**	**Generalist**
Croton floribundus Spreng.	Euphorbiaceae	Generalist forest
Croton piptocalyx Müll.Arg.	Euphorbiaceae	Forest
Mabea fistulifera Mart.	Euphorbiaceae	Generalist forest
Mabea paniculata Spruce ex Benth.	Euphorbiaceae	Forest
Maprounea guianensis Aubl.	Euphorbiaceae	Generalist savanna
Micrandra elata (Didr.) Müll.Arg.	Euphorbiaceae	Forest
Pera coccinea (Benth.) Müll.Arg.	Euphorbiaceae	Forest
Pera glabrata (Schott) Poepp. ex Baill.	Euphorbiaceae	Generalist savanna
Pera bicolor (Klotzsch) Müll.Arg.	Euphorbiaceae	Forest
Albizia niopoides (Spruce ex Benth.) Burkart	Fabaceae	Forest
Anadenanthera peregrina (L.) Speg.	Fabaceae	Generalist savanna
Andira cujabensis Benth.	Fabaceae	Generalist savanna
Andira vermifuga Benth.	Fabaceae	Generalist savanna
Apuleia leiocarpa (Vogel) J.F.Macbr.	Fabaceae	Forest
Bowdichia virgilioides Kunth	Fabaceae	Generalist savanna
***Copaifera langsdorffii* Desf.**	**Fabaceae**	**Generalist**
Dalbergia miscolobium Benth.	Fabaceae	Savanna
Dimorphandra mollis Benth.	Fabaceae	Savanna
Diplotropis purpurea (Rich.) Amshoff	Fabaceae	Forest
Dipteryx alata Vogel	Fabaceae	Generalist savanna
Diptychandra aurantiaca Tul.	Fabaceae	Generalist savanna
Enterolobium gummiferum (Mart.) J.F.Macbr.	Fabaceae	Savanna
Holocalyx balansae Micheli	Fabaceae	Forest
Hymenaea courbaril L.	Fabaceae	Forest
Hymenaea stigonocarpa Hayne	Fabaceae	Savanna
Inga heterophylla Willd.	Fabaceae	Forest
Inga striata Benth.	Fabaceae	Forest
Inga thibaudiana DC.	Fabaceae	Forest
Leptolobium dasycarpum Vogel	Fabaceae	Savanna
Leptolobium elegans Vogel	Fabaceae	Savanna
Luetzelburgia praecox (Harms) Harms	Fabaceae	Generalist savanna
Machaerium acutifolium Vogel	Fabaceae	Generalist savanna
Machaerium brasiliense Vogel	Fabaceae	Generalist savanna
Mimosa laticifera Rizzini & A.Mattos	Fabaceae	Savanna
Myroxylon peruiferum L.f.	Fabaceae	Forest

Species	Family	Habitat preference
Ormosia arborea (Vell.) Harms	Fabaceae	Forest
Ormosia fastigiata Tul.	Fabaceae	Forest
Ormosia paraensis Ducke	Fabaceae	Forest
Peltogyne confertiflora (Hayne) Benth.	Fabaceae	Generalist savanna
Piptadenia gonoacantha (Mart.) J.F.Macbr.	Fabaceae	Forest
Plathymenia reticulata Benth.	Fabaceae	Savanna
Platypodium elegans Vogel	Fabaceae	Generalist savanna
Pterodon emarginatus Vogel	Fabaceae	Generalist savanna
Pterodon pubescens (Benth.) Benth.	Fabaceae	Generalist savanna
Senegalia polyphylla (DC.) Britton	Fabaceae	Generalist forest
Stryphnodendron adstringens (Mart.) Coville	Fabaceae	Savanna
Stryphnodendron rotundifolium Mart.	Fabaceae	Savanna
Tachigali aurea Tul.	Fabaceae	Savanna
***Tachigali vulgaris* L.F. Gomes da Silva & H.C. Lima**	**Fabaceae**	**Generalist**
Vatairea macrocarpa (Benth.) Ducke	Fabaceae	Savanna
Sacoglottis guianensis Benth.	Humiriaceae	Generalist forest
Emmotum nitens (Benth.) Miers	Icacinaceae	Generalist savanna
Aegiphila sellowiana Cham.	Lamiaceae	Forest
Cryptocarya moschata Nees & Mart.	Lauraceae	Forest
Endlicheria paniculata (Spreng.) J.F.Macbr.	Lauraceae	Forest
Mezilaurus crassiramea (Meisn.) Taub. ex Mez	Lauraceae	Generalist savanna
Nectandra cuspidata Nees & Mart.	Lauraceae	Generalist forest
Nectandra megapotamica (Spreng.) Mez	Lauraceae	Forest
Ocotea corymbosa (Meisn.) Mez	Lauraceae	Generalist savanna
Ocotea dispersa (Nees & Mart.) Mez	Lauraceae	Forest
Ocotea guianensis Aubl.	Lauraceae	Forest
Ocotea indecora (Schott) Mez	Lauraceae	Forest
Ocotea leucoxylon (Sw.) Laness.	Lauraceae	Forest
Cariniana legalis (Mart.) Kuntze	Lecythidaceae	Forest
Antonia ovata Pohl	Loganiaceae	Savanna
Strychnos pseudoquina A. St.-Hil.	Loganiaceae	Savanna
Lafoensia pacari A. St.-Hil.	Lythraceae	Savanna
Byrsonima basiloba A.Juss.	Malpighiaceae	Savanna
Byrsonima coccolobifolia Kunth	Malpighiaceae	Savanna
Byrsonima intermedia A.Juss.	Malpighiaceae	Generalist forest
Byrsonima pachyphylla A.Juss.	Malpighiaceae	Savanna
Byrsonima verbascifolia (L.) DC.	Malpighiaceae	Generalist savanna
Heteropterys byrsonimifolia A.Juss.	Malpighiaceae	Generalist savanna
Ceiba speciosa (A.St.-Hil.) Ravenna	Malvaceae	Forest
Eriotheca candolleana (K.Schum.) A.Robyns	Malvaceae	Forest
Eriotheca globosa (Aubl.) A.Robyns	Malvaceae	Generalist forest
Eriotheca gracilipes (K.Schum.) A.Robyns	Malvaceae	Savanna
Eriotheca pubescens (Mart. & Zucc.) Schott & Endl.	Malvaceae	Generalist savanna

Species	**Family**	**Habitat preference**
Guazuma ulmifolia Lam.	Malvaceae	Forest
Luehea grandiflora Mart.	Malvaceae	Generalist savanna
Mollia lepidota Spruce ex Benth.	Malvaceae	Forest
***Pseudobombax longiflorum* (Mart. & Zucc.) A.Robyns**	**Malvaceae**	**Generalist**
Bellucia grossularioides (L.) Triana	Melastomataceae	Forest
Miconia albicans (Sw.) Steud.	Melastomataceae	Savanna
Miconia latecrenata (DC.) Naudin	Melastomataceae	Forest
Miconia ligustroides (DC.) Naudin	Melastomataceae	Generalist savanna
Miconia pyrifolia Naudin	Melastomataceae	Forest
Miconia rubiginosa (Bonpl.) DC.	Melastomataceae	Savanna
Miconia sp.	Melastomataceae	Forest
Mouriri apiranga Spruce ex Triana	Melastomataceae	Forest
Mouriri elliptica Mart.	Melastomataceae	Savanna
Mouriri pusa Gardner ex Gardner	Melastomataceae	Savanna
Cabralea canjerana (Vell.) Mart.	Meliaceae	Forest
Cedrela fissilis Vell.	Meliaceae	Forest
Guarea guidonia (L.) Sleumer	Meliaceae	Forest
Guarea kunthiana A.Juss.	Meliaceae	Forest
Trichilia casaretti C.DC.	Meliaceae	Forest
Trichilia catigua A.Juss.	Meliaceae	Forest
Trichilia claussenii C.DC.	Meliaceae	Forest
Trichilia elegans A.Juss.	Meliaceae	Forest
Trichilia micrantha Benth.	Meliaceae	Forest
Trichilia pallida Sw.	Meliaceae	Forest
Mollinedia widgrenii A.DC.	Monimiaceae	Forest
Brosimum gaudichaudii Trécul	Moraceae	Savanna
Brosimum rubescens Taub.	Moraceae	Forest
Ficus eximia Schott	Moraceae	Forest
Pseudolmedia laevigata Trécul	Moraceae	Forest
***Virola sebifera* Aubl.**	**Myristicaceae**	**Generalist**
Campomanesia adamantium (Cambess.) O.Berg	Myrtaceae	Savanna
Campomanesia xanthocarpa (Mart.) O.Berg	Myrtaceae	Generalist forest
Eugenia aurata O.Berg	Myrtaceae	Savanna
Eugenia blastantha (O.Berg) D.Legrand	Myrtaceae	Forest
Eugenia dysenterica DC.	Myrtaceae	Generalist savanna
Eugenia florida DC.	Myrtaceae	Generalist forest
Eugenia gemmiflora O.Berg	Myrtaceae	Savanna
Eugenia livida O.Berg	Myrtaceae	Savanna
Eugenia punicifolia (Kunth) DC.	Myrtaceae	Generalist savanna
Eugenia ternatifolia Cambess.	Myrtaceae	Savanna
Eugenia uniflora L.	Myrtaceae	Generalist forest
Myrcia bella Cambess.	Myrtaceae	Savanna
Myrcia camapuanensis N.Silveira	Myrtaceae	Savanna

Species	**Family**	**Habitat preference**
Myrcia guianensis (Aubl.) DC.	Myrtaceae	Savanna
Myrcia lanuginosa O.Berg	Myrtaceae	Savanna
Myrcia multiflora (Lam.) DC.	Myrtaceae	Generalist savanna
Myrcia rimosa Cambess.	Myrtaceae	Savanna
Myrcia sp.	Myrtaceae	Savanna
Myrcia splendens (Sw.) DC.	Myrtaceae	Generalist savanna
Myrcia tomentosa (Aubl.) DC.	Myrtaceae	Generalist forest
Myrcia uberavensis O.Berg	Myrtaceae	Savanna
Myrcia variabilis Mart. ex DC.	Myrtaceae	Savanna
Myrcia venulosa DC.	Myrtaceae	Generalist savanna
Myrciaria delicatula (DC.) O.Berg	Myrtaceae	Savanna
Myrciaria floribunda (H.West ex Willd.) O.Berg	Myrtaceae	Generalist forest
Neomitranthes glomerata (D.Legrand) Govaerts	Myrtaceae	Forest
Plinia cauliflora (Mart.) Kausel	Myrtaceae	Forest
Psidium firmum O.Berg	Myrtaceae	Savanna
Psidium laruotteanum Cambess.	Myrtaceae	Savanna
Psidium sp.	Myrtaceae	Forest
Guapira graciliflora (Mart. ex J.A.Schmidt) Lundell	Nyctaginaceae	Generalist savanna
Guapira noxia (Netto) Lundell	Nyctaginaceae	Savanna
Neea theifera Oerst.	Nyctaginaceae	Savanna
Ouratea discophora Ducke	Ochnaceae	Forest
Ouratea hexasperma (A. St.-Hil.) Baill.	Ochnaceae	Savanna
Ouratea spectabilis (Mart. ex Engl.) Engl.	Ochnaceae	Savanna
Quiina florida Tul.	Ochnaceae	Forest
Heisteria ovata Benth.	Olacaceae	Generalist savanna
Minquartia guianensis Aubl.	Olacaceae	Forest
Agonandra brasiliensis Miers ex Benth.	Opiliaceae	Generalist savanna
Savia dictyocarpa Müll.Arg.	Phyllanthaceae	Generalist forest
Gallesia integrifolia (Spreng.) Harms	Phytolaccaceae	Forest
Cybianthus sp.	Primulaceae	Forest
Myrsine guianensis (Aubl.) Kuntze	Primulaceae	Generalist forest
***Myrsine umbellata* Mart.**	**Primulaceae**	**Generalist**
Euplassa inaequalis (Pohl) Engl.	Proteaceae	Generalist savanna
***Roupala montana* Aubl.**	**Proteaceae**	**Generalist**
Colubrina glandulosa G.Perkins	Rhamnaceae	Forest
***Prunus myrtifolia* (L.) Urb.**	**Rosaceae**	**Generalist**
Amaioua guianensis Aubl.	Rubiaceae	Generalist forest
***Cordiera sessilis* (Vell.) Kuntze**	**Rubiaceae**	**Generalist**
Ferdinandusa rudgeoides (Benth.) Wedd.	Rubiaceae	Forest
Genipa americana L.	Rubiaceae	Forest
Tocoyena formosa (Cham. & Schltdl.) K.Schum.	Rubiaceae	Savanna
Metrodorea nigra A. St.-Hil.	Rutaceae	Forest
Zanthoxylum monogynum A. St.-Hil.	Rutaceae	Forest
Casearia gossypiosperma Briq.	Salicaceae	Generalist forest

Species	**Family**	**Habitat preference**
Casearia grandiflora Cambess.	Salicaceae	Generalist forest
Casearia lasiophylla Eichler	Salicaceae	Generalist savanna
***Casearia sylvestris* Sw.**	**Salicaceae**	**Generalist**
Prockia crucis P.Browne ex L.	Salicaceae	Forest
Xylosma pseudosalzmanii Sleumer	Salicaceae	Forest
Cupania vernalis Cambess.	Sapindaceae	Generalist forest
Magonia pubescens A. St.-Hil.	Sapindaceae	Generalist savanna
***Matayba guianensis* Aubl.**	**Sapindaceae**	**Generalist**
Matayba sp.	Sapindaceae	Forest
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	Sapotaceae	Forest
Micropholis venulosa (Mart. & Eichler ex Miq.) Pierre	Sapotaceae	Generalist forest
***Pouteria ramiflora* (Mart.) Radlk.**	**Sapotaceae**	**Generalist**
Pouteria sp.	Sapotaceae	Forest
***Pouteria torta* (Mart.) Radlk.**	**Sapotaceae**	**Generalist**
***Schoepfia brasiliensis* A.DC.**	**Schoepfiaceae**	**Generalist**
Simarouba versicolor A. St.-Hil.	Simaroubaceae	Generalist savanna
Styrax ferrugineus Nees & Mart.	Styracaceae	Savanna
Styrax sp.	Styracaceae	Forest
Cecropia pachystachya Trécul	Urticaceae	Generalist forest
Urera baccifera (L.) Gaudich. ex Wedd.	Urticaceae	Generalist forest
Callisthene fasciculata Mart.	Vochysiaceae	Generalist savanna
Qualea cordata Spreng.	Vochysiaceae	Generalist savanna
Qualea grandiflora Mart.	Vochysiaceae	Savanna
Qualea multiflora Mart.	Vochysiaceae	Savanna
Qualea parviflora Mart.	Vochysiaceae	Savanna
Salvertia convallariodora A. St.-Hil.	Vochysiaceae	Savanna
Vochysia cinnamomea Pohl	Vochysiaceae	Savanna
Vochysia rufa Mart.	Vochysiaceae	Savanna
Vochysia tucanorum Mart.	Vochysiaceae	Savanna
Vochysia vismiifolia Spruce ex Warm.	Vochysiaceae	Forest

Table S3 Number of species sampled to each site of seasonal forests and savannas environments in the Brazilian Cerrado. Density ≤ 3 represents the number and percentage of species with individual density equal or less that three individuals in each site, and density ≥ 4 denotes the number and percentage (in parentheses) of species with individual density equal or greater that four individuals in each site.

Site	Number of species	density ≤ 3	density ≥ 4
Forest			
Assis Ecological State - SP	39	31 (79)	8 (21)
Vassununga State Park - SP	31	18 (58)	13 (42)
Emas National Park - GO	21	15 (71)	6 (29)
Jataí – GO	29	12 (41)	17 (59)
Bacaba Park - MT	28	16 (57)	12 (43)
Ribeirão Cascalheira - MT	52	20 (38)	32 (62)
Savanna			
Assis Ecological State - SP	44	16 (36)	28 (64)
Vassununga State Park - SP	47	16 (34)	31 (66)
Emas National Park - GO	51	34 (67)	17 (33)
Jataí – GO	43	7 (16)	36 (84)
Bacaba Park - MT	90	15 (17)	74 (83)
Ribeirão Cascalheira - MT	66	24 (36)	42 (64)

Table S4 Percentage of occurrence in 376 areas evaluated by Ratter et al. (2003) and bark thickness of the 19 species that occurred in both seasonal forest and savanna habitats in the Brazilian Cerrado. Bold indicate the species that were more important (38 species) in Ratter et al. (2003), and threshold bark thickness of 5.9 mm in Hoffmann *et al*. (2012).

Species	Family	Percentage of occurrence in Ratter et al. (2003)	Bark thickness (mm)	
			Forest	Savanna
Astronium fraxinifolium	Anacardiaceae	**47.3**	0.7	0.60
Tapirira guianensis	Anacardiaceae	28.5	1.4	0.78
Xylopia aromatica	Annonaceae	**49.2**	**5.9**	3.8
Hirtella glandulosa	Chrysobalanaceae	16.5	**7.6**	2.0
Buchenavia tomentosa	Combretaceae	21.5	3.3	2.8
Chaetocarpus echinocarpus	Euphorbiaceae	1.0	2.7	1.6
Copaifera langsdorffii	Fabaceae	39.1	2.6	**10.4**
Tachigali vulgaris	Fabaceae	42.3	3.1	0.52
Pseudobombax longiflorum	Malvaceae	39.6	2.7	5.6
Virola sebifera	Myristicaceae	15.2	2.3	1.7
Myrsine umbellata	Primulaceae	5.3	1.0	0.9
Roupala montana	Proteaceae	**57.4**	**8.2**	**10.4**
Prunus myrtifolia	Rosaceae	0.8	1.3	1.3
Cordiera sessilis	Rubiaceae	10.6	1.5	0.66
Casearia sylvestris	Salicaceae	**58.0**	1.1	**14.9**
Matayba guianensis	Sapindaceae	26.9	3.3	1.6
Pouteria ramiflora	Sapotaceae	**55.9**	5.4	**9.9**
Pouteria torta	Sapotaceae	24.2	3.1	**13.8**
Schoepfia brasiliensis	Schoepfiaceae	0	1.4	1.1

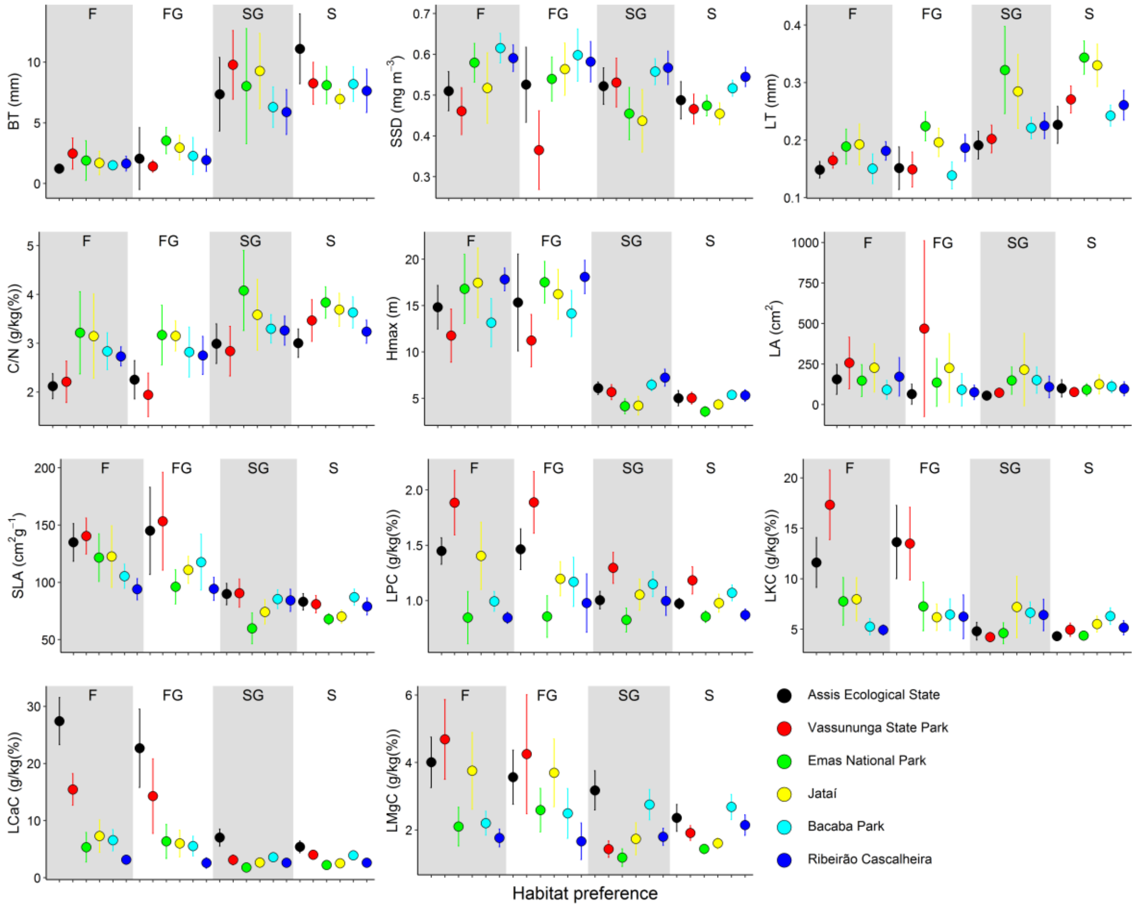

Figure S1 Mean values of functional traits to each group of habitat preference - specialist of forest (F) and savanna (S), and generalist sampled only in forest (FG) and sampled only in savanna (SG) - for the sites of seasonal forests and savannas in the Brazilian Cerrado.

CAPÍTULO II

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Edaphic properties drive functional trait patterns in savannas and seasonal forests plant communities of the Cerrado

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Key-words

acquisitive strategies, conservative strategies, soil nutrients, edaphic gradients, leaf nutrient content

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Abstract

Question: Do gradients in soil fertility and toxicity drive shifts in density of individuals and community trait means in savannas and seasonal forests? Are communities with conservative traits associated with poor soils and communities with acquisitive traits associated with more fertile soils?

Location: Savannas and seasonal forests plant communities in the Cerrado phytogeographic domain, in Brazil.

Methods: We measured seven functional traits from 286 species occurring in 120 plots distributed in six forest and savanna sites throughout the Cerrado. In each vegetation, we recorded tree and shrub species and collected surface soil samples in 10 200-m^2 plots. We measured maximum plant height (Hmax), leaf area (LA), specific leaf area (SLA), leaf phosphorous content (LPC), stem-specific density (SSD), leaf thickness (LT), and leaf carbon-nitrogen ratio (C/N) to compute community-weighted means for each trait. We used linear regressions to model community trait means and density of individuals by edaphic gradients.

Results: We found lower density of individuals in more fertile soils in forests and savannas. In forests communities, our results suggest that an acquisitive strategy is related to toxicity (lower LA, SLA and PLC in more toxic soils) and fertility (high Hmax and LA in richer soils) gradients, and that a conservative strategy is related to toxicity gradient (high SSD and C/N in more toxic soils). In savanna communities, the patterns were less evident, with fewer traits indicating a strategy of resource acquisition (high LA in richer soils) or a strategy of resource conservation (high LT in toxic soil).

Conclusions: We brought evidence that forest and savanna species indeed adopt different strategies related to resource use in contrasting communities of the Cerrado

domain. We highlighted that density of individuals and community trait means shift along edaphic gradients in savannas and seasonal forest plant communities in the Cerrado domain. We show a stronger negative relationship of density of individuals with fertility and toxicity gradient, that could be result of dominance of some species with high competitive ability. For community trait mean, we demonstrate that in plots with fertile soils and less toxic have species with traits related to fast acquisitive strategy of resources, while in soil more toxic and with low fertility have species with traits related to conservative strategy.

Introduction

Understanding what are the processes and factors determining ecological strategies plants use to respond to abiotic and biotic factors and their consequences to community composition, structure and functioning is a fundamental goal in vegetation science (McGill et al. 2006; Vellend 2010). In order to coexist, species often adopt different strategies of growth and reproduction (Oliveras & Malhi 2016) leading to a trade-off between rapid acquisition and resource conservation strategies (Diaz et al. 2004; Poorter 2009). Such a trade-off may be assessed by evaluating the distribution of traits along environmental gradients at the community scale (Goodland & Pollard 1973; Furley & Ratter 1988; Ordoñez et al. 2009; Baxendale et al. 2014). Therefore, exploring the role of environmental gradients on different traits (Lavorel & Garnier 2002; Carvalho & Batalha 2013; Wigley et al. 2016) is key to understanding vegetation dynamics in contrasting environments such as forests and savannas.

Several studies have highlighted that edaphic properties strongly influence plant community structure (Wright et al. 2004; de Bello et al. 2006; Dantas & Batalha 2011; Zava & Cianciaruso 2014; Laureto & Cianciaruso 2015; Barros et al. 2015; Moraes et al. 2015). Functional traits influence directly the responses of plants to the environment as well as plant-plant interactions (Díaz & Cabido 2001; Lavorel & Garnier 2002). Soil properties can determine the performance and distribution of functional traits, directly affecting the growth and reproduction of plants (Wright et al. 2004; Swenson & Enquist 2007; Freschet et al. 2011; Moles et al. 2014). Low stem density, high maximum height, high specific leaf area, and leaves of high nutritional quality characterize plants with an acquisitive strategy, typical of nutrient-rich environments. On the other hand, plants with a conservative strategy, typical nutrient-poor environments, can be characterized by thick and tough leaves, low specific leaf area, and leaves of low nutritional quality (Wright et al. 2004; Diaz et al. 2004; Ordoñez et al. 2009). Therefore, functional trait-based approaches enable us to evaluate the responses of plants to environmental conditions and interactions among species (Lavorel & Garnier 2002; Götzenberger et al. 2012).

One way to evaluate the dominant strategies in plant communities, is with community trait means weighted by abundance (CWM, Garnier et al. 2004). Ecosystem processes are mainly determined by dominant species (Grime 1998; Garnier et al. 2004), thus, CWM is useful to account the effect of dominant species on environmental change and ecosystem processes (Garnier et al. 2004; Pakeman & Quested 2007; Garnier et al. 2007; Garnier & Navas 2012). Because it is expected that CWM vary along environmental gradients (Diaz et al. 2004; Garnier et al. 2004) this approach should allow us to understand how changes in the functional composition along of environmental gradients reflect in acquisitive and conservative strategies in forest and savanna communities. Furthermore, trait mean values can provide insights on different trait compositions across environmental gradients.

In Neotropical savannas different habitats, such as savannas and seasonal forests, occur side by side under the same climate (Oliveras & Malhi 2016). The occurrence of such contrasting environments under the same climatic conditions has been identified as an effect of spatial variation in soil nutrient availability (Ruggiero et al. 2002). Several nutrients play important roles in the structure and composition of these communities (Furley & Ratter 1988; Ruggiero et al. 2002; Dantas & Batalha 2011; Pellegrini 2016). In savannas, an important determinant of the structure and composition of communities is related to the ability of acquisition of soil nutrients and water by plants (Oliveira et al. 2005). Many savanna species have a root system that enable them to extract nutrients and water from great depths (Goedert 1983). While high soil aluminum concentration may inhibit nutrients absorption by plants, being toxic for many forest species, savanna species are usually adapted to high levels of aluminum and some are even aluminum accumulators (Furley & Ratter 1988). Soil moisture, fire, and competition for nutrients determine plant density in savannas (Furley & Ratter 1988; Marimon Junior & Haridasan 2005). High frequency of fire can turn savannas into grasslands, while fire exclusion may lead to the development of seasonal forests (Hoffmann et al. 2012). On the other hand, forest habitats often have higher soil nutrient availability that favours tree growth, because plants with strategy of fast growth can avoid light limitation in the understory (Ruggiero et al. 2002; Hoffmann et al. 2012; Oliveras & Malhi 2016). Moreover, resource availability together with disturbance regimes have been appointed as a determining factor for the occurrence of forest and savanna habitats under same climate (Dantas et al. 2016).

We answered the following questions to each study habitat (forest and savanna): (i) Do gradients in soil fertility and toxicity reduce the number of individuals in seasonal forests and savannas? (ii) Do gradients in soil fertility and toxicity drive shifts in community trait means? Our expectation is that communities with higher soil fertility and lower toxicity will have higher mean values of maximum plant height (Hmax), leaf area (LA), specific leaf area (SLA), leaf phosphorous content (LPC), but lower mean values of stem-specific density (SSD), leaf thickness (LT) and leaf carbon-nitrogen ratio (C/N), reflecting a dominance of species with rapid acquisition strategy (Westoby 1998; Pérez-Harguindeguy et al. 2013; Wigley et al. 2016). On the other hand, communities in soils with low fertility and high toxicity, we expect to observe lower mean values of Hmax, LA, SLA and LPC, but high mean values of SSD, LT and C/N, reflecting a conservative strategy (Table 1). Furthermore, forest environments with high fertility and low toxicity may promote the establishment of species with fast growth and better competitive ability, reducing the number of individuals by competitive exclusion (Mayfield & Levine 2010; Dantas & Batalha 2011; Carvalho & Batalha 2013).

Table 1. Functional significance of traits and trait-based patterns predicted in relation to edaphic gradients in forests and savannas of the Cerrado.

Trait	Acronym	Functional significance	Prediction	References
Maximum plant height	Hmax	Competitive plant fitness, plant fecundity, tolerance or resistance to disturbances.	We expected that trees in more fertile soil will be taller. Considering that soils richer in nutrients support higher plant biomass, the variation of Hmax along soil gradients may be related to a trade-off between resource conservation and competitive ability.	(Westoby 1998; Pérez-Harguindeguy et al. 2013; Laureto & Cianciaruso 2015)
Leaf area	LA	Strategies of resource acquisition and use. Ecological strategy adopted with respect to environmental nutrients stress and disturbances.	Leaf area has consequences for the leaf energy and water balance. We expected that plants present high leaf area in more fertile habitats than infertile habitats. The slower growth of plants on infertile soils can favor a smaller investment in leaf area, which minimizes water loss.	(McDonald et al. 2003; Pérez-Harguindeguy et al. 2013)
Specific leaf area	SLA	Related to structural defense, resource uptake and use efficiency and growth strategies; negatively correlated with leaf lifespan.	We expected that communities in resource-rich environments have higher SLA than in poor habitats. This reflects the trade-off between fast growth and nutrient conservation, and is related with leaf nitrogen concentration. This indicate that environments with fertile soils provide rapid resource capture and high relative growth, while the opposite is expected for a conservative strategy.	(Wright et al. 2004; Pérez-Harguindeguy et al. 2013)
Leaf phosphorus content	LPC	Phosphorous is a limiting resource related to growth and productivity in plants.	We expected that plants in more fertile soils show higher nutrients concentrations in their leaves. Fertile soils are generally associated with high nutritional quality and plant growth due to higher soil phosphorous availability.	(Schachtman et al. 1998; Lloyd et al. 2009; Ordoñez et al. 2009; Pérez-Harguindeguy et al. 2013)
Stem-specific density	SSD	Structural vigor, and consequent resistance to physical damage.	We expected to find a negative relationship between SSD and soil fertility. This relation is associated to the growth-survival trade-off, in which low stem density (with large vessels) leads to a fast growth, because of large hydraulic capacity and conductive tissue is less expensive to construct, whereas a high stem density (with small vessels) leads to a high survival by providing a stronger defense against physical and biological damage.	(Baker et al. 2004; Chave et al. 2006; Lloyd et al. 2009; Chave et al. 2009; Pérez-Harguindeguy et al. 2013)
Leaf thickness	LT	Related to species strategies of resource acquisition and use, and with resistance to physical damage, correlated with leaf toughness.	LT is one of the key components of SLA and photosynthetic capacity, and predict that LT should be higher in less fertile habitats, because balancing photosynthetic benefits against C costs of respiration and transpiration. Besides, LT indicates the largest relative carbon investment in structural protection of photosynthetic tissues.	(Vile 2005; Pérez-Harguindeguy et al. 2013)
Leaf carbon-nitrogen ratio	C/N	Nutritional quality and palatability of plant, leaf decomposition rate, N is the major limiting macronutrient in plants.	We expected a negative relationship between C/N ratio and soil fertility. In less-fertile soils high values of this ratio suggest a resource conservation strategy. Moreover, more fertile soils tend to present soil organic matter, and this might enhance the nitrogen absorption by plants, thereby increasing the nitrogen content in the leaves of plants in more fertile soils.	(Ordoñez et al. 2009; Pérez-Harguindeguy et al. 2013; Apaza-Quevedo et al. 2015)

Material and Methods

Study region

The Cerrado is a phytogeographical domain characterized by complex vegetational mosaics (Ribeiro & Walter 2008) composed by savannas, seasonal forests and tropical grasslands (Batalha 2011; Dantas et al. 2016). The Cerrado receives strong floristic influence of the neighboring phytogeographical domains of Amazônia, Mata Atlântica and Caatinga (Méio et al. 2003; Souza-Neto et al. 2016). The great variety of habitats, ranging from grasslands to forests, can result from the diverse climatic conditions, edaphic properties and fire frequency registered throughout the phytogeographical domains (Oliveira-Filho & Ratter 2002; Dantas et al. 2013).

Sampling design

We surveyed six regions located throughout the Cerrado domain in order to capture a great range of phytogeographical variation. We adopt a paired design sampling one savanna (cerrado *stricto sensu*) and one forest (seasonally dry forest) site in each region (Fig. 1). Average distance between sites was 12 km, and the latitudinal range varied from 12°S to 22°S (Fig. 1 and Table S1). The smallest distance between regions was 150 km (between Emas National Park and Jataí), while the smallest distance within pairs of forest and savanna blocks was 1 km (in Emas National Park). In general, the mean values and coefficient of variation of the edaphic characteristics varied little between the plots of either forests or savannas at each site (Table S2).

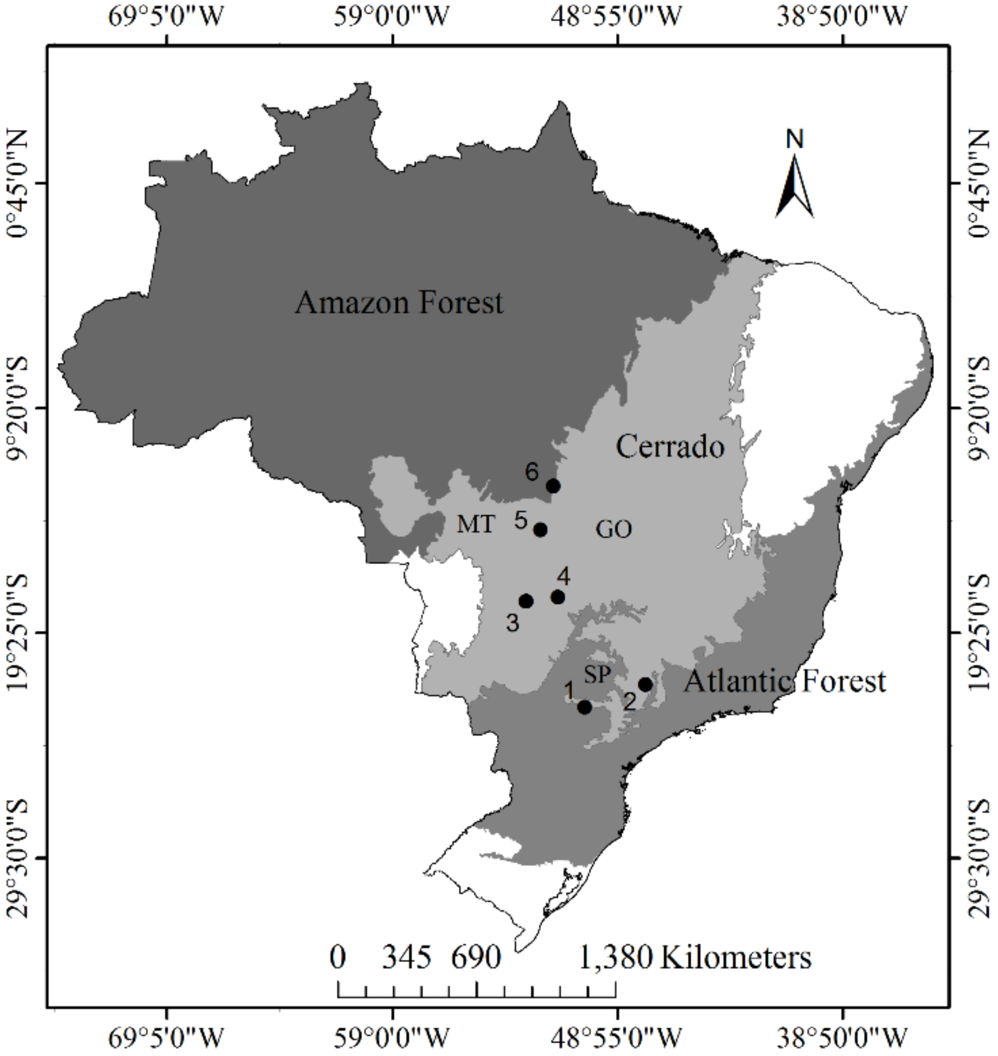

Figure 1. Location of six study regions with seasonal forest and savanna sites in the Brazilian Cerrado. 1. Assis Ecological Station (lat/long: 22°35'S/50°22'W), 2. Vassununga State Park (21°36'S/47°37'W), 3. Emas National Park (17°54'S/52°59'W), 4. Jataí (17°45'S/51°32'W), 5. Bacaba Park (14°42'S/52°21'W), 6. Ribeirão Cascalheira (12°49'S/51°46'W).

In each savanna and forest site we sampled all tree- and shrubs in 10 100-m^2 plots. In savanna plots we recorded all individuals with diameter at ground height ≥ 5 cm, whereas in forest plots all individuals with diameter at breast height ≥ 10 cm were sampled. All individuals were identified following the Angiosperm Phylogeny Group classification (APG-IV 2016). Additionally, we revisited the species names in the Brazilian Flora (Forzza et al. 2012).

Trait sampling

We measured the following traits at species-level according to Pérez-Harguindeguy et al. (2013): maximum plant height (Hmax), leaf area (LA), specific leaf area (SLA), leaf nutrient content of phosphorous (LPC), leaf thickness (LT), stem specific density (SSD) and carbon/nitrogen ratio (C/N) (see Table 1 for their ecological significance). Whenever possible we measured 10 individuals for each species in each site. When a given species had less than 10 individuals in our plots, we sampled individuals that were nearby the plot. When that was not possible we included all individuals that were available (see Table S3). LPC and C/N were measured for three individuals of each species in each site. To obtain the values of leaf traits, first we scanned five leaves of each individual, and posteriorly calculated area leaf through of a script that we build using the "EBImage" package (Pau et al., 2014) with R 3.2.1 (http://www.R-project.org). After scanning, the leaves were dried at 80 °C for 48 h to acquire leaf dry mass. Other five leaves were utilized to calculate the leaf thickness values using a digital micrometer. All traits were collected during the rainy season (December to March 2011-2012), which represents the period of maximum leaf expansion and maturity and growth and reproductive peak for most of the studied plants (Lenza & Klink 2006).

Edaphic variables

Composite soil samples (0-10 cm depth) were collected in all forest and savanna plots (three samples per plot). We obtained the following soil variables (Embrapa 1999): clay concentration, pH, soil organic matter (SOM), phosphorus concentration (P), nitrogen concentration (N), exchangeable contents of K^+ and Al^{3+}.

Spatial autocorrelation

Our aim was to evaluate the role of fertility gradient on community trait means of plant communities. Communities at short distances from one another tend to be more similar than distant communities (Hawkins 2012) due to shared historical processes and spatially-structured biological processes such as dispersal and species interactions (Peres-Neto & Legendre 2010). Therefore, response variables such as community trait means may be structured in the space, which affect statistical assumptions such as independence of residuals (Legendre 1993).

In order to take the spatial autocorrelation into account in our analysis we used the method of principal coordinates of neighbourhood matrices (PCNM) (Borcard & Legendre 2002). The PCNM is based on a PCoA of geographical coordinates truncated by distance in order to generate axes (spatial filters) representing vectors of spatial variation at increasing scales. Here, we used the spatial filters as explanatory variables together with the environmental predictors to minimize the residual autocorrelation (Rangel et al. 2006). These analyses were conducted at the plot level and the truncation distance that represent the maximum distance connecting all communities, which defines the neighbourhood boundaries (Rangel et al. 2006), was 5.5 km for forest plots and 2.5 km for savanna plots. We conducted the PCNM analyses in software SAM 4.0 (Rangel et al. 2006).

Statistical analyses

All analyses were performed separately at the plot level for each of communities of forests (60 plots) and savannas (60 plots). To reduce the dimensionality of edaphic parameters we computed principal component analysis (PCA). The number of components retained for further analyses was determined on the basis of the broken stick criteria, in which the eigenvalue must be greater than the values of broken stick eigenvalue (Frontier 1976). Moreover, we evaluated the effect of each variable on each principal component (PC) through bootstrap randomization in the software Past (Hammer et al. 2001). These analyses were conducted separately for forest (Fig. S1) and savanna plots (Fig. S2).

Initially, we seek to understand if the fertility and toxicity gradients determine the density of individuals of the communities of forest and savannas. We related the density of individuals with edaphic gradients controlling the spatial autocorrelation of predictors variables through spatial filters.

In order to evaluate shifts of trait means at the community level along the gradient, we computed community-weighted trait means (CWM), defined as the mean traits values present in the community weighted by the relative abundance of species (Garnier et al. 2004).

To investigate the shifts of community trait means along the edaphic gradient, we fitted a linear regression analysis (ordinary least squares - OLS) with PC1, PC2 and PCNM (spatial filters) as predictors variables (Rangel et al. 2006; Peres-Neto & Legendre 2010). Spatial filters were used as predictor variables to account for spatial autocorrelation in residuals. When necessary, we used an algorithm that added the spatial filter that accounted for the most of the spatial autocorrelation in the residuals remaining in the model, repeating this process until the autocorrelation in the residuals reached its minimum (Rangel et al. 2010; Peres-Neto & Legendre 2010). All response variables of community trait means were spatially structured. Thus, we accounted for spatial autocorrelation in the residuals of the models by including spatial filters as predictors (Table 2 and Appendix 1).

Results

Environmental gradients - For the forests, the first two principal components (PC) together accounted for 70.4% of the variance in the edaphic variables (Fig. 2). PC1 accounted for 42.3% of the explained variance and represents mainly a soil toxicity gradient, characterized mostly by Al and low pH (Fig. 2 and S1A). PC2 accounted for 28.1% of the explained variance and represents a soil fertility gradient, characterized mostly by SOM and clay (Fig. 2 and S1B). For savannas, the first two principal components together accounted for 54.5% of the variance in the edaphic variables (Fig. 3). The PC1, accounted for 30.3% explained variance and represented a soil fertility, characterized mostly by clay and SOM (Fig. 3 and S2A). On the other hand, PC2 accounted for 24.2% of the explained variance and represented a toxicity gradient, characterized by pH and Al (Fig. 3 and S2B).

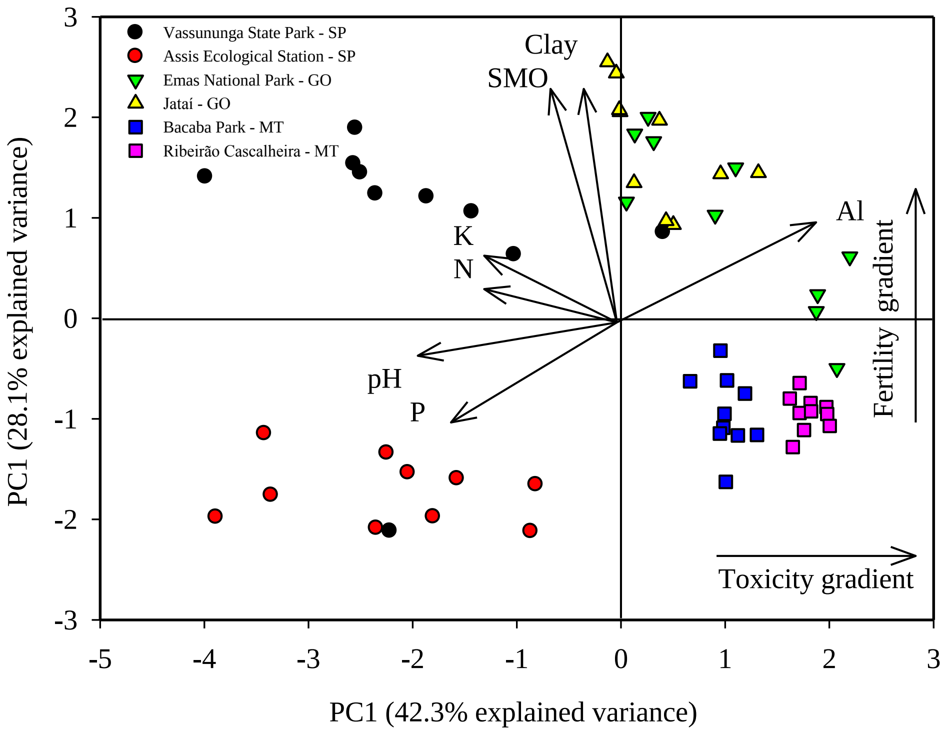

Figure 2. Distribution of the plots and sites of seasonal forests along the two axes of a principal component analysis (PCA) based on ten edaphic properties. Each principal component represents a soil gradient: PC1, toxicity gradient, and PC2, fertility gradient. Different symbols and colors represent different sites.

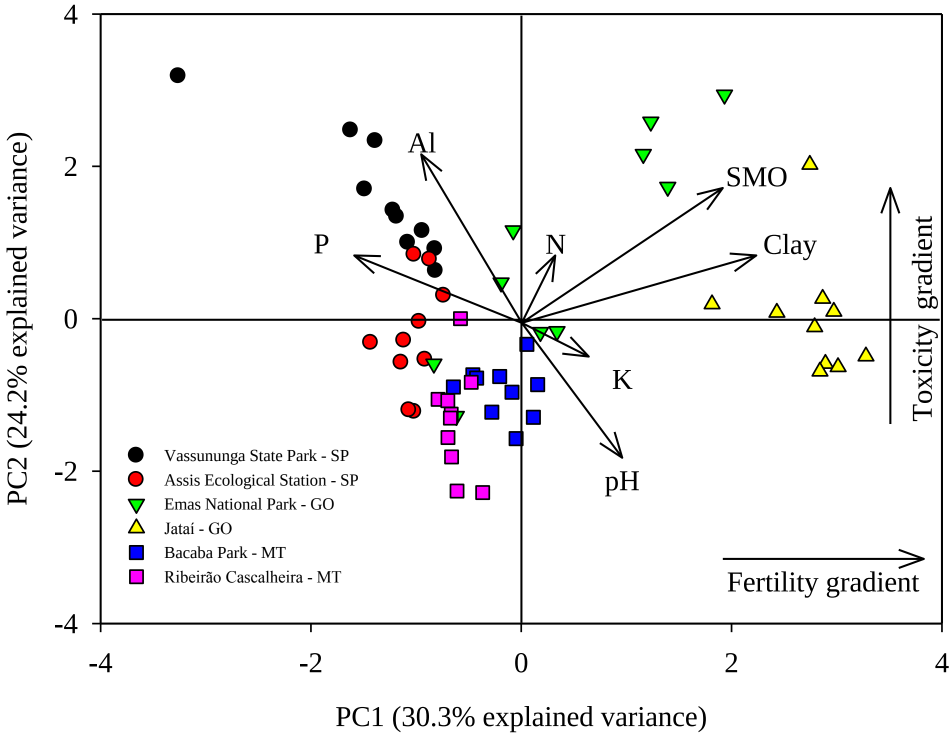

Figure 3. Distribution of the plots and sites of savannas along the two axes of a principal component analysis (PCA) based on ten edaphic properties. Each principal component represents a soil gradient: PC1, fertility gradient, and PC2, toxicity gradient. Different symbols and colors represent different sites.

Density of individuals – The density of individuals decreased along the toxicity and fertility gradients in the forests (Table 2, Fig. S3). In savannas, the density of individuals decreased only with fertility, however spatial filters showed high explanatory power for this model (Table 2, Fig. S3).

Community trait means – In seasonal forests, considering species with traits with acquisitive strategy, only maximum height increased along the toxicity gradient, while leaf area, specific leaf area and leaf phosphorous content decreased along the same gradient (Table 2, Fig. S4). On fertility gradient, maximum height and leaf area increased along the fertility gradient, while specific leaf area and leaf phosphorous content decreased along the same gradient (Table 2, Fig. S4). Considering species with traits with conservative strategy, stem-specific density and carbon/nitrogen ratio increased along the toxicity gradient (Table 2, Fig. S4). While, stem-specific density, leaf thickness and carbon/nitrogen ratio also increased along the fertility gradient (Table 2, Fig. S4).

In savannas, the fertility gradient was more important than toxicity to community trait mean. Only leaf thickness increased along the toxicity gradients considering conservative strategy (Table 2, Fig. S5). Considering traits with acquisitive strategy, maximum height increased along the fertility gradient, while leaf area decreased along the same gradient (Table 2, Fig. S5). While considering conservative strategy, only leaf thickness increased along the fertility gradient (Table 2, Fig. S5). The others traits were significant with edaphic gradient (Table 2, Fig. S5).

Table 2. Models of linear regression analysis for toxicity and fertility gradients in seasonal forests and savannas in the Brazilian Cerrado. Spatial filters (F) were computed using principal coordinates of neighbourhood matrices (PCNM; Peres-Neto & Legendre 2010) and were included in each model as predictors to account for spatial autocorrelation in the residuals. The variables toxicity and fertility are principal component from PCA computed separately for seasonal forest and savannas. Numbers stressed in bold indicate significant regression coefficients (β) with $p < 0.05$ and with explanatory power of predictors ≥ 0.19.

	Model	toxicity - β	fertility - β	R^2	P model	predictors	shared	filters
Density of individuals								
Forest	density ~ toxicity + fertility + F1 + F5	**-0.31**	**-0.73**	0.52	0.001	**0.45**	-0.09	0.18
Savanna	density ~ fertility + toxicity + F2 + F3 + F4 + F5 + F6	0.11	**-0.69**	0.80	0.001	**0.27**	0.16	0.40
Community-weighted means								
Forest - acquisitive strategy	Hmax ~ toxicity + fertility + F1 + F2	**0.60**	**0.34**	0.36	0.001	**0.23**	-0.07	0.23
	LA ~ toxicity + fertility + F1	**-0.35**	**0.33**	0.38	0.001	**0.23**	-0.04	0.21
	SLA ~ toxicity + fertility + F3	**-0.48**	**-0.25**	0.64	0.001	**0.29**	0.20	0.16
	LPC ~ toxicity + fertility + F3 + F4 + F5	**-0.58**	**-0.21**	0.91	0.001	**0.27**	0.44	0.21
Forest - conservative strategy	SSD ~ toxicity + fertility + F3	**0.44**	**0.15**	0.82	0.001	**0.21**	0.36	0.26
	LT ~ toxicity + fertility + F1 + F2 + F3	0.27	**0.73**	0.52	0.001	**0.43**	-0.17	0.29
	C/N ~ toxicity + fertility + F2 + F3	**0.71**	**0.59**	0.75	0.001	**0.48**	0.16	0.11
Savanna - acquisitive strategy	Hmax ~ fertility + toxicity + F2 + F3 + F5	-0.16	**-0.71**	0.84	0.001	**0.45**	0.19	0.21
	LA ~ fertility + toxicity + F2 + F4	-0.15	**0.43**	0.51	0.001	**0.19**	0.06	0.29
	SLA ~ fertility + toxicity + F2 + F4 + F5	-0.05	-0.38	0.81	0.001	0.13	0.18	0.51
	LPC ~ fertility + toxicity + F2 + F3 + F5	-0.04	0.16	0.90	0.001	0.02	0.16	0.74
Savanna - conservative strategy	SSD ~ fertility + toxicity + F1	-0.29	0.14	0.74	0.001	0.10	0.40	0.25
	LT ~ fertility + toxicity + F2 + F4 + F5	**0.22**	**0.53**	0.86	0.001	**0.28**	0.30	0.29
	C/N ~ fertility + toxicity + F2 + F3	-0.01	0.02	0.86	0.001	0.01	0.25	0.63

Discussion

In general, our results support that forest and savanna plants have different strategies related to rapid acquisition and conservative strategy of resources. We showed that communities with more toxic soil determined lower density of individuals in forest. In contrast, more fertile soils determined lower density of individuals in forest and savanna environments. For community trait mean, traits values were more sensible to shift in fertility gradient than toxicity gradient, mainly in forest environments. These different strategies (rapid acquisitive and conservative) observed are responses of traits in relation to resources acquisition for establish and develop in environments with different light and soil resources availability as seasonal forest and savanna (Reich et al. 1999; Diaz et al. 2004; Svenning et al. 2004; Apaza-Quevedo et al. 2015; Wigley et al. 2016).

Density of individuals

Density of individuals decreased with the increasing in soil fertility and toxicity in forest communities. This could be related to high competitive ability of some species, that on fertile soils become dominant producing a larger canopy cover, avoiding the establishment or excluding others species (Carvalho & Batalha 2013; Martorell et al. 2015). In theory, a greater resource available in the soil tend to promote species coexistence through resources partitioning (Barot 2004; Dantas & Batalha 2011), as even forest species are adapted to experience habitats with certain nutrient limitation conditions (Furley & Ratter 1988), which would lead sites with more richer soils for have high competitive effect resulting in low density of individuals. Neri *et al.* (2012) also showed a negative relationship between density of individuals and aluminium in the soil from savanna-woodland. Al is the main element indicator of toxicity in our study system (Goodland & Pollard 1973) because it compete with other essential elements for absorption sites (Wagatsuma 1983). Thus, even with many Al-tolerant species, in general the aluminium toxicity may act on establishment of species, determining a lower density of plants.

Community-level trait shifts

Generally, higher values of leaf nutrient content, SLA, large leaves (Ruggiero et al. 2002; Carvalho & Batalha 2013; Wigley et al. 2016), and tall plants (Westoby 1998; Schamp & Aarssen 2009) grow fast and have a great competitive ability, thus being related to rapid acquisition of resources. On the other hand, large values of wood density, leaf thickness and C/N ratio are related to conservative strategy, protection against fire and water loss (Table 1) (Baker et al. 2004; Hoffmann et al. 2005; Chave et al. 2006; Wigley et al. 2016). Based on such strategies, our expectations were that the soil fertility and toxicity would influence the trait mean values along these gradients (Ruggiero et al. 2002; Silva et al. 2010; Carvalho & Batalha 2013; Baxendale et al. 2014; Wigley et al. 2016). However, our results showed that trait related to acquisitive strategies tended to have larger values in more benign environments (high fertility and low toxic soil), while trait related for conservative strategies tended to have larger values in more stressful environments (low fertility and high toxic soil). Additionally, our results showed that these strategies were more evident in the seasonal forests than on the savannas of Cerrado.

In general, we demonstrate that seasonal forest in richer soils have higher leaf phosphorous content and tall plants, while that low leaf area, specific leaf area and leaf phosphorous content, high woody density, carbon/nitrogen ratio and leaf thickness in soils with higher toxicity. Likewise, the savanna plots with richer soils have higher leaf area, while that high leaf thickness in toxic soils. These findings are according for the fast acquisitive strategy of resources adopted by plants in conditions of large resource available and lesser environmental stress (Diaz et al. 2004; Wigley et al. 2016; Pellegrini 2016). This is possible because more fertile soils support higher plant biomass due to higher resource available, making possible that species with strategy of fast growing, that consequently have larger nutrient demand, may have an investment in traits related to fast growth (Chapin III et al. 1993; Westoby 1998; Pellegrini 2016), and produce litter with high-quality, that is quickly recycled (Baxendale et al. 2014).

In fact, the nutrient available is an important environmental driver involving the rapid acquisition of nutrients and conservation of resources in plant, determining functional traits and community composition (Wright et al. 2004; Lloyd et al. 2009; Ordoñez et al. 2009; Baxendale et al. 2014; Wigley et al. 2016; Oliveras & Malhi 2016). Plants that explore water- and nutrient stress tend to have convergent traits that indicate better use and conservation of resources, promoting defences and long leaf lifespans (Chapin III et al. 1993; Diaz et al. 2004), and are represented by small, thick and tough leaves, low SLA and leaf nutrient content, and lower plant (Diaz et al. 2004; Pérez-Harguindeguy et al. 2013), and high woody density, leaf thickness and carbon/nitrogen ratio (Table 1). Strikingly, for some leaf traits and wood density the results were opposite to our predictions. We registered low SLA and LPC and high SSD, LT and C/N (in forest), and lower plants and high LT (in savannas) on more fertility soils. These results appoint to conservative strategy on fertile soils, in which normally is expected strategy related to rapid acquisition of resources (Diaz et al. 2004; Liu et al. 2012; Jager et al. 2015; Wigley et al. 2016). We expected that communities in resource-rich environments would have higher SLA than in poor habitats (Knops & Reinhart 2000; Wright et al. 2004). However, our results were the opposite and can be related to access to light in forests because there is evidence that plants decrease SLA as they increase in height (in order to reach the canopy where light is fully available) (Fahey et al. 1998; Klooster et al. 2007). Thus, more richer soils promoting higher growth of plants, as seen in maximum height in forest, leading to greater light available in taller plants. Like the solar radiation is intense during most of the year (Miranda et al. 1997), when plants reaches the top of the canopy they adopt strategies that prevents water loss altering yours morphological characteristics (low SLA, high LT and C/N). Some studies have showed that SLA generally increase with increasing foil fertility in response to soil nutrient availability and related to rapid acquisition strategy (Ordoñez et al. 2009; Wang et al. 2012; Li et al. 2015).

Plant height is related with the nutrient transport capacity, and maximum plant height is limited by hydraulic and mechanical constraints (Koch et al. 2004; Niklas 2007), moreover the costs with nutrients transports in taller trees can resulting reduction in leaf photosynthesis (Ryan & Yoder 1997). Thus, we expected that plants in less productive and more toxic environment tend to be smaller (Laureto & Cianciaruso 2015; Sfair et al. 2016). Our results indicate that soil more fertile and less toxic promotes in taller plants in forest and savanna, which can reflect in high competitive vigor and tolerance or avoidance of environmental stress (as fire) (Westoby 1998). However, in this study the poor soil supported tall trees on savannas, this may be related to disturbance regime (fire) in savannas (Jager et al. 2015). In savanna communities, the grass are often tall, but in richer soils can accumulate large herbaceous layer increasing the frequency and intensity of fires and decreasing the plant height (Dantas, Pausas, et al. 2013; Dantas, Batalha, et al. 2013), because fertile soils can result in more heterogeneous canopy height (Jager et al. 2015). On the other hand, poor soils can result in more varied plant height, thus fire events often cause damage mainly on herbaceous layer, favoring the taller plants (Dantas, Pausas, et al. 2013; Jager et al. 2015). Likewise, seasonal forest registered taller plant on more toxicity soil, and its can be negatives effects from fragmentation, because the sites of seasonal forest from São Paulo State showed smaller toxicity and presented small plants, since that fragmentation makes the forest more susceptible to falling trees (Ferreira & Laurance 1997).

Conclusion

We highlighted that density of individuals and community trait means shift along edaphic gradients in savannas and seasonal forest plant communities in the Cerrado domain. We show a stronger negative relationship of density of individuals with fertility and toxicity gradient, that could be result of dominance of some species with high competitive ability. For community trait mean, we showed that the changes were more clear on fertility gradient than toxicity gradient, and that forest environments was more sensible to shift in both gradients than savannas. We demonstrate that in plots with fertile soils and less toxic have traits related to fast acquisitive strategy of resources reflecting in traits related to fast growth competitive ability, and that the plants adopt this strategy in conditions of large resource available and lesser environmental stress (Diaz et al. 2004; Wigley et al. 2016; Pellegrini 2016). On the other hand, soil more toxic and with low fertility have species with traits related to conservative strategy, indicating better use and conservation of resources and promoting defences and long leaf lifespans (Diaz et al. 2004; Pérez-Harguindeguy et al. 2013). However, the relation of some traits with the edaphic gradient were contrary to our expeditions, mainly on fertility gradient.

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Supplementary Material

Supplementary table 1. Climate characteristics of the six sites sampled in Brazilian Savanna. The values represented a range, when available, of 20 years of data collected in the nearest weather station of each site. The fire frequency is related only to savannas sites. A low fire frequency indicates an interval about of five years among fire events, and high fire frequency of 10 years.

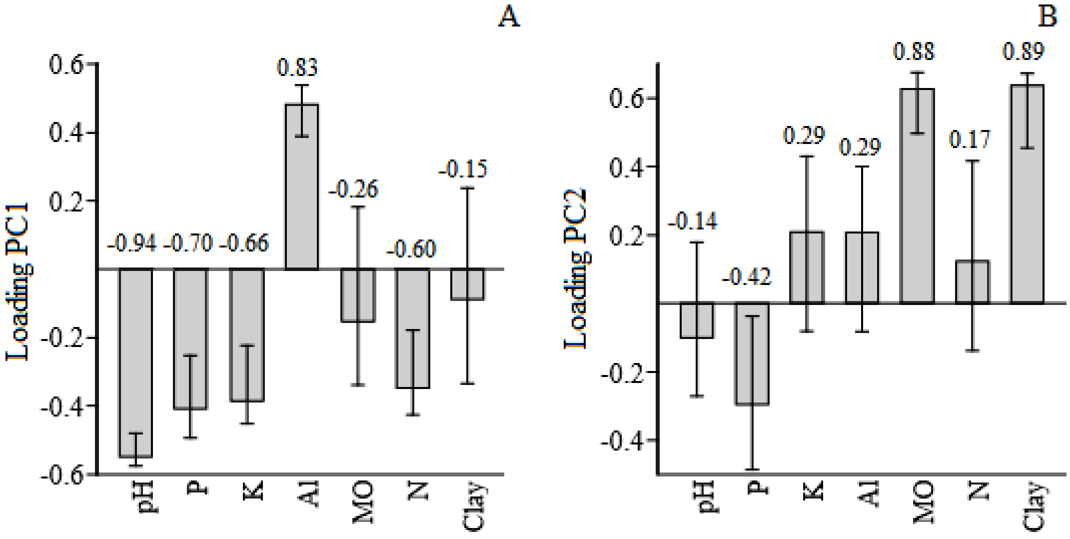
Environmental characteristics	Assis Ecological State - SP	Vassununga State Park - SP	Emas National Park - GO	Jataí - GO	Bacaba Park - MT	Ribeirão Cascalheira - MT
Coordinates	50W 22’, 22S 35’	47W 37’, 21S 36’	52W 59’, 17S 54’	51W 32’, 17S 45’	52W 21’, 14S 42’	51W 46’, 12S 49’
Fire frequency	low	low	high	high	high	low
Climate Type	Cfa	Cwa	Aw	Aw	Aw	Aw
Altitude (m)	560	740	840	860	325	374
Mean Annual Temp. (°C)	23.6	22.3	24.6	22.6	24.8	25.4
Mean Minimum Temp. (°C)	19.0	16.6	18.9	17.0	18.9	20.1
Precipitation (mm yr^{-1})	1352	1437	1745	1605	1433	1822
Evapotranspiration (mm)	129	92	82	121	134	136
Mean Monthly Relative Humidity (%)	64	70	69	69	77	71

Supplementary table 2. Mean values and coefficient of variation (in parentheses) of the soil variables to sites of seasonal forests and savannas environments in the Brazilian Cerrado. These values were calculated based in values of parameters in ten plots each site.

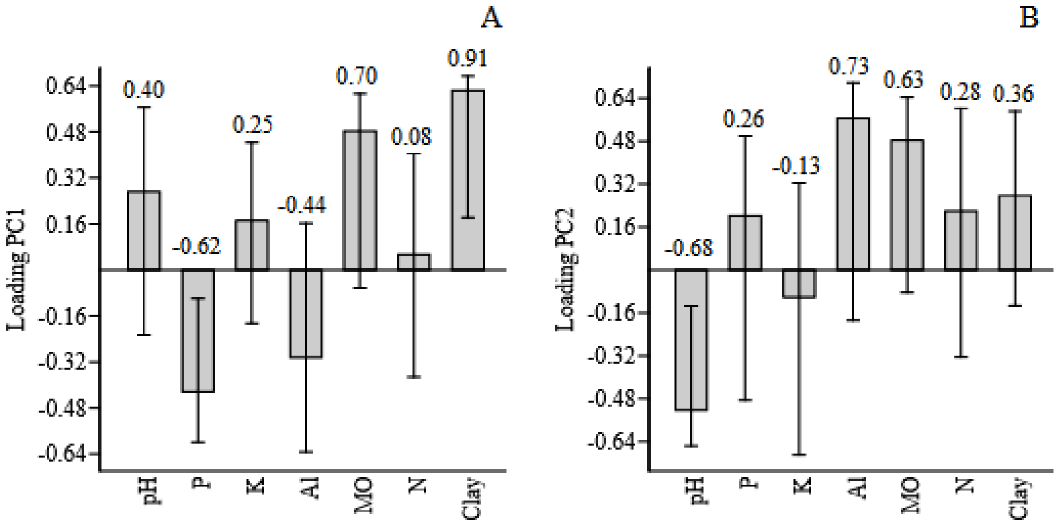
Soil characteristics	Assis Ecological State - SP		Vassununga State Park - SP		Emas National Park - GO		Jataí - GO		Bacaba Park - MT		Ribeirão Cascalheira - MT	
	Forest	Savanna	Forest	Savanna	Forest	Savanna	Forest	Savanna	Forest	Savanna	Forest	Savanna
N	0.32 (0.46)	0.25 (0.40)	0.22 (0.29)	0.12 (0.36)	0.26 (0.36)	0.09 (0.45)	0.18 (0.15)	0.17 (0.25)	0.11 (0.23)	0.08 (0.18)	0.10 (0.14)	0.05 (0.31)
P	8.39 (0.54)	3.91 (0.83)	4.51 (1.07)	3.89 (0.85)	1.79 (0.38)	0.56 (0.37)	1.57 (0.44)	1.03 (0.78)	1.15 (0.53)	2.03 (0.07)	1.75 (0.15)	2.04 (0.33)
K	46.3 (0.38)	11.8 (0.34)	11.2 (0.37)	13.1 (0.27)	42.4 (0.18)	31.4 (0.27)	28.4 (0.44)	22.3 (0.26)	46.7 (0.23)	46.2 (0.15)	17.7 (0.19)	18.3 (0.43)
SMO	3.10 (0.38)	1.70 (0.37)	5.13 (0.20)	3.10 (0.17)	5.87 (0.29)	3.08 (0.44)	6.22 (0.19)	4.79 (0.18)	1.07 (0.55)	1.73 (0.19)	2.49 (0.12)	1.83 (0.33)
pH	7.09 (0.10)	4.85 (0.03)	6.16 (0.11)	4.51 (0.02)	4.20 (0.11)	4.30 (0.06)	5.26 (0.03)	5.26 (0.02)	4.65 (0.02)	5.04 (0.03)	4.10 (0.02)	4.95 (0.05)
Al	0	0.88 (0.18)	0.12 (2.87)	1.70 (0.12)	1.65 (0.24)	1.19 (0.24)	1.03 (0.38)	0.65 (0.42)	0.85 (0.22)	1.16 (0.12)	1.12 (0.10)	0.77 (0.15)
Clay	11.2 (0.25)	8.0 (0.24)	44.7 (0.25)	10.6 (0.08)	26.1 (0.29)	29.4 (0.67)	54.6 (0.14)	51.0 (0.08)	20.1 (0.18)	12.6 (0.20)	16.7 (0.13)	2.9 (0.41)

Supplementary table 3. Mean traits and number of species sampled to each sites of the soil variables to sites of seasonal forests and savannas environments in the Brazilian Cerrado. Density ≤ 3 represents the number and percentage of species with individual density equal or less that three individuals in each site, and density ≥ 4 denotes the number and percentage (in parentheses) of species with individual density equal or less that four individuals in each site.

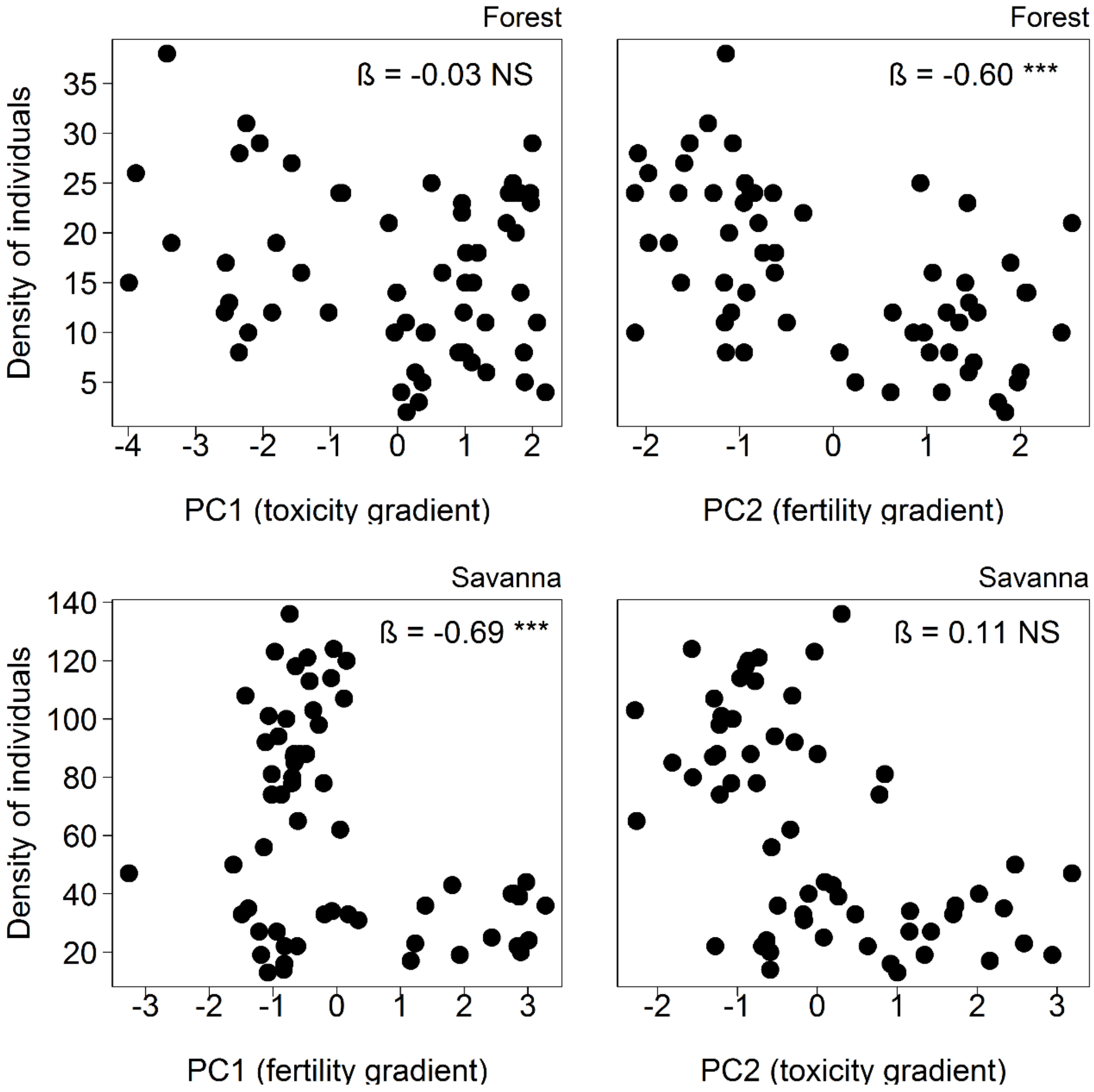
Site	Number of species	density ≤ 3	density ≥ 4	Height	LA	SLA	LPC	SSD	LT	C/N
Forest										
Assis Ecological State - SP	39	31 (79)	8 (21)	13.0	132.2	133.8	1.48	0.51	0.16	2.13
Vassununga State Park - SP	31	18 (58)	13 (42)	9.5	276.1	159.3	1.99	0.42	0.15	2.07
Emas National Park - GO	21	15 (71)	6 (29)	15.7	128.9	105.8	0.84	0.57	0.20	3.36
Jataí - GO	29	12 (41)	17 (59)	13.1	200.6	113.6	1.28	0.59	0.19	3.07
Bacaba Park - MT	28	16 (57)	12 (43)	11.6	78.1	110.8	1.06	0.62	0.15	2.78
Ribeirão Cascalheira - MT	52	20 (38)	32 (62)	14.6	138.7	95.6	0.86	0.59	0.18	2.73
Savanna										
Assis Ecological State - SP	44	16 (36)	28 (64)	4.5	76.8	85.3	0.98	0.51	0.21	2.83
Vassununga State Park - SP	47	16 (34)	31 (66)	4.3	71.2	80.9	1.22	0.48	0.25	3.30
Emas National Park - GO	51	34 (67)	17 (33)	2.7	70.0	68.4	0.83	0.48	0.34	3.92
Jataí - GO	43	7 (16)	36 (84)	3.1	125.2	71.0	0.99	0.46	0.32	3.73
Bacaba Park - MT	90	15 (17)	74 (83)	4.3	139.3	84.7	1.10	0.53	0.23	3.55
Ribeirão Cascalheira - MT	66	24 (36)	42 (64)	5.0	81.8	78.0	0.91	0.56	0.24	3.32



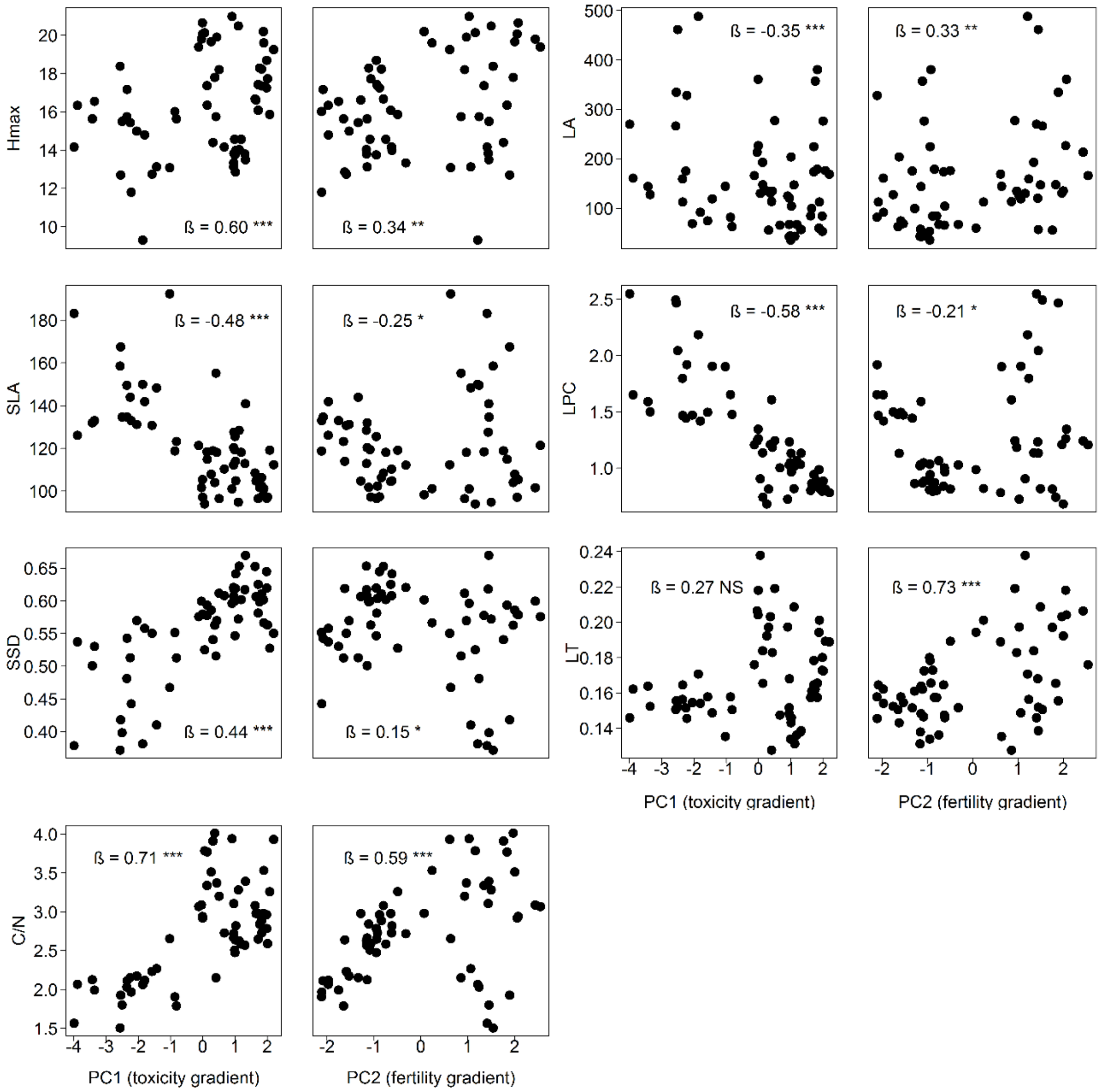
Supplementary figure 1. Contribution of edaphic parameters for the toxicity (PC1) and fertility (PC2) gradients in seasonal forest in the Brazilian Cerrado. Bootstrap confidence intervals when do not overlap zero indicates significant relationship (positive or negative) with the component principal. The numbers on the bars indicates the correlation values of each variable with the PCs.



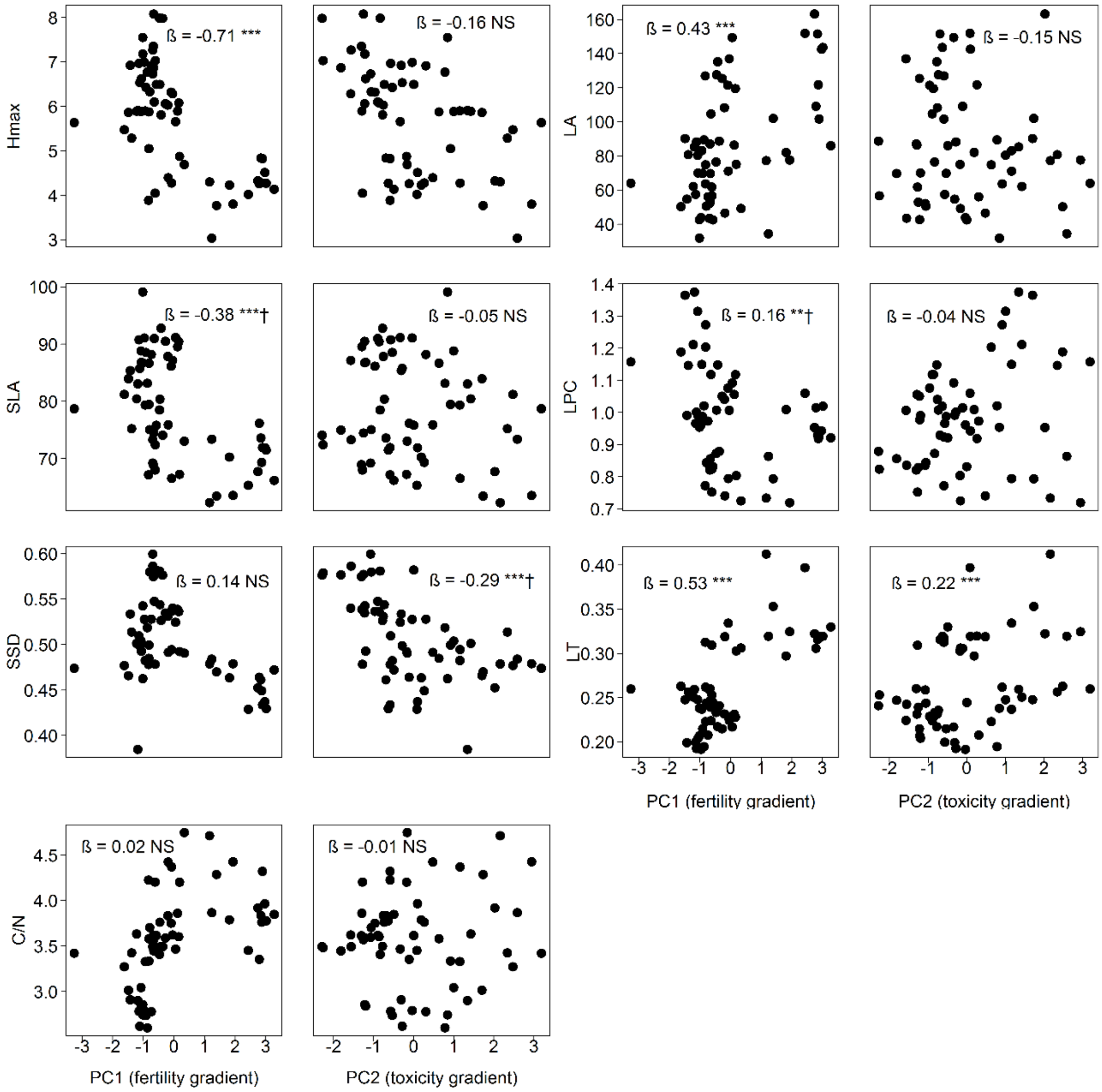
Supplementary figure 2. Contribution of edaphic parameters for the fertility (PC1) and toxicity (PC2) gradients in savannas in the Brazilian Cerrado. Bootstrap confidence intervals when do not overlap zero indicates significant relationship (positive or negative) with the component principal. The numbers on the bars indicates the correlation values of each variable with the PCs.



Supplementary figure 3. Relationship between individual density and soil proprieties of seasonal and savanna in Brazilian Savanna. Positive values in the PCs indicates greater levels of toxicity or fertility on the gradient.



Supplementary figure 4. Shifts in community-weighted trait means along soil toxicity (PC1) and fertility (PC2) gradients in seasonal forests in the Brazilian Cerrado. Beta regression coefficient (β) indicates the intensity and direction of each regression with the gradients. The β coefficients were derived from linear regression analyses. Hmax = maximum plant height (m); LA = leaf area (cm^2); SLA = specific leaf area (cm^2); LPC = leaf phosphorous content (g/kg(%)); SSD = Stem-specific density (mg mm^{-3}); LT = leaf thickness (mm); C/N = leaf carbon-nitrogen ratio. * $P < 0.05$, ** $P < 0{,}01$, *** $P < 0{,}001$, NS non-significant. Positive values in the PCs indicates greater levels of toxicity or fertility on the gradient.



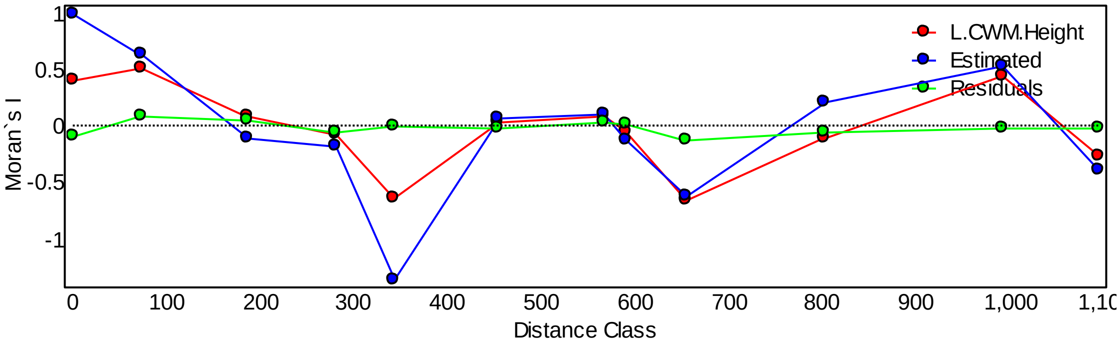
Supplementary figure 5. Shifts in community-weighted trait means along soil fertility (PC1) and toxicity (PC2) gradients in savannas in the Brazilian Cerrado. Beta regression coefficient (β) indicates the intensity and direction of each regression with the gradients. The β coefficients were derived from linear regression analyses. Hmax = maximum plant height (m); LA = leaf area (cm^2); SLA = specific leaf area (cm^2); LPC = leaf phosphorous content (g/kg(%)); SSD = Stem-specific density (mg mm^{-3}); LT = leaf thickness (mm); C/N = leaf carbon-nitrogen ratio. * P < 0.05, ** P < 0,01, *** P < 0,001, NS non-significant, † indicate low explanatory power of predictors. Positive values in the PCs indicates greater levels of toxicity or fertility on the gradient.

Appendix 1. Set of graphics representing the spatial patterns of all the predictor variables sampled in savanna and seasonal forests environments, displayed according to acquisitive or conservative strategy of resources. Spatial autocorrelogram of the patterns in the observed (red lines), expected (blue lines), and residuals (green lines).

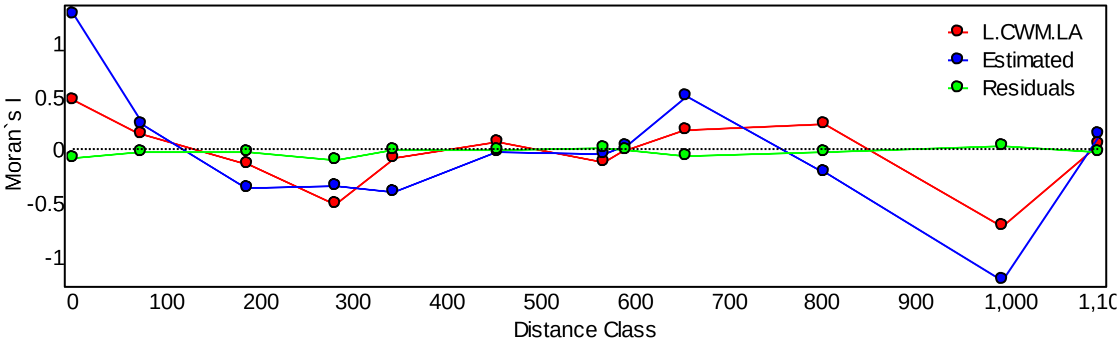
Community-weighted means

Forest – acquisitive strategy

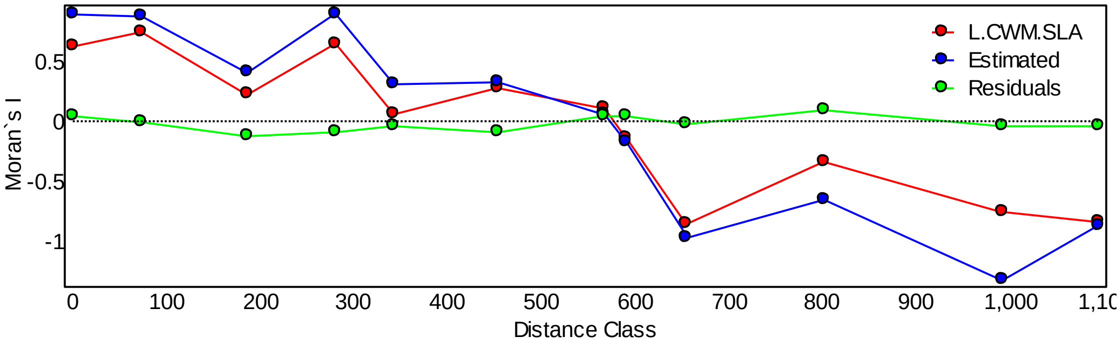
Hmax – maximum plant height



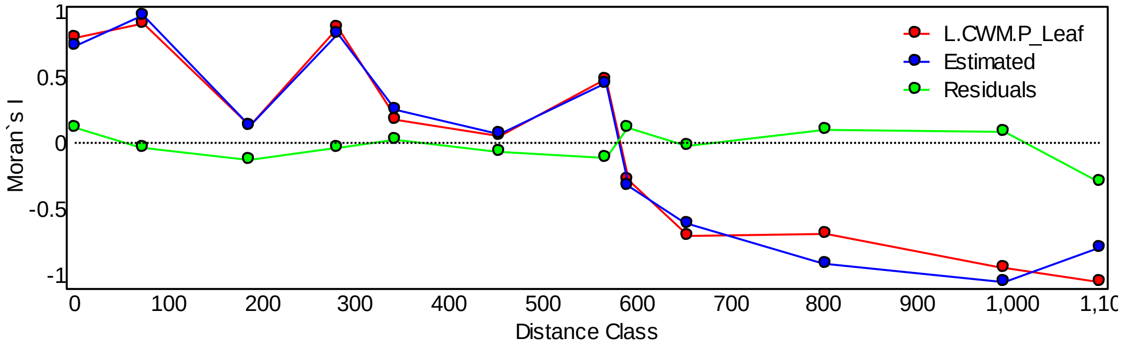
LA – leaf area



SLA – specific leaf area

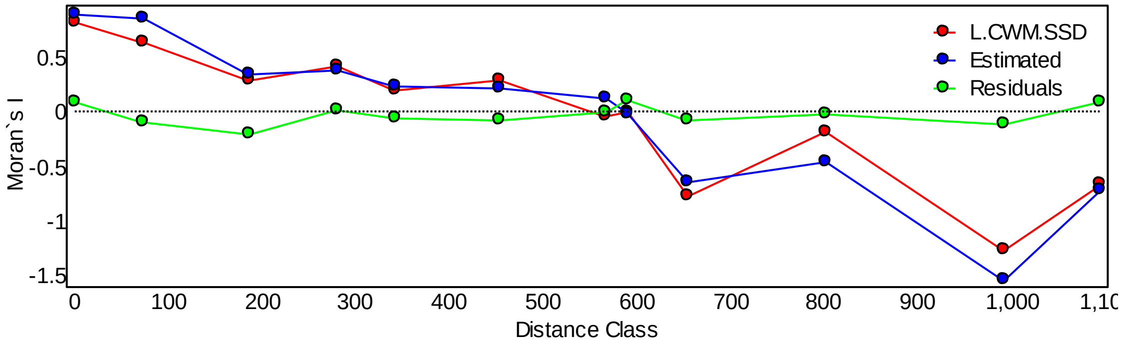


LPC – leaf phosphorous content

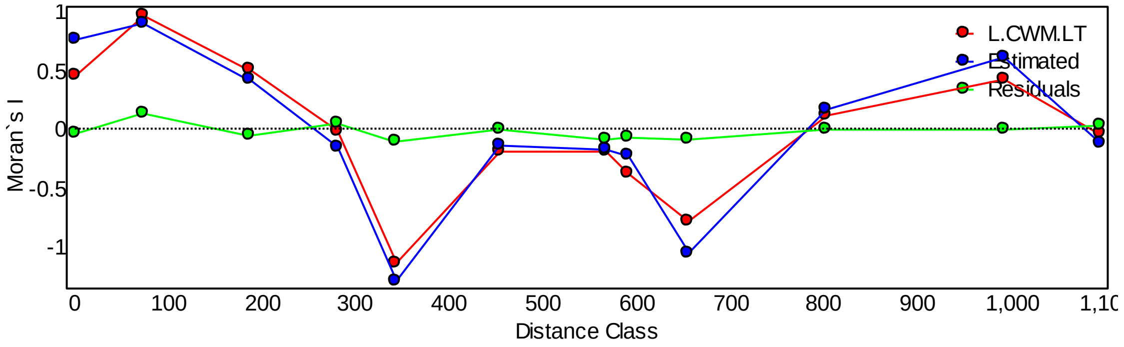


Forest – conservative strategy

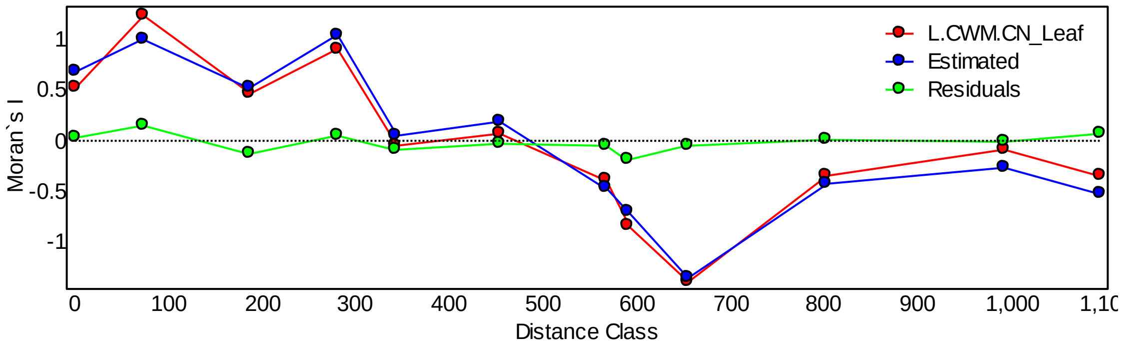
SSD – stem-specific density



LT – leaf thickness

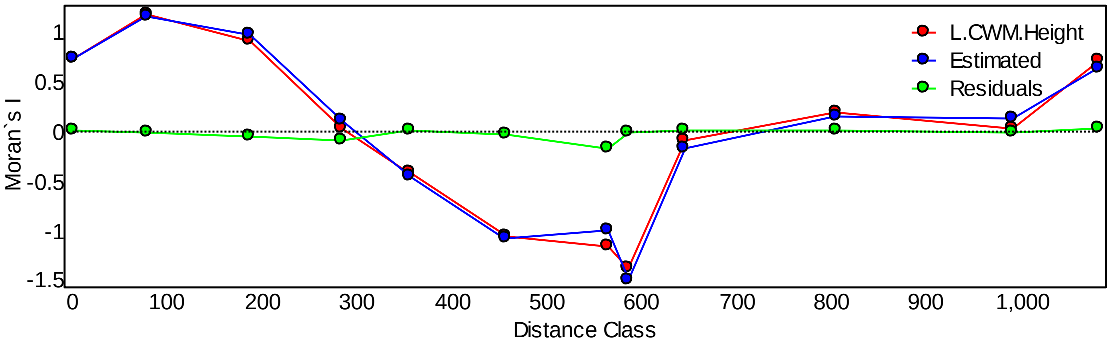


C/N – leaf carbon-nitrogen ratio

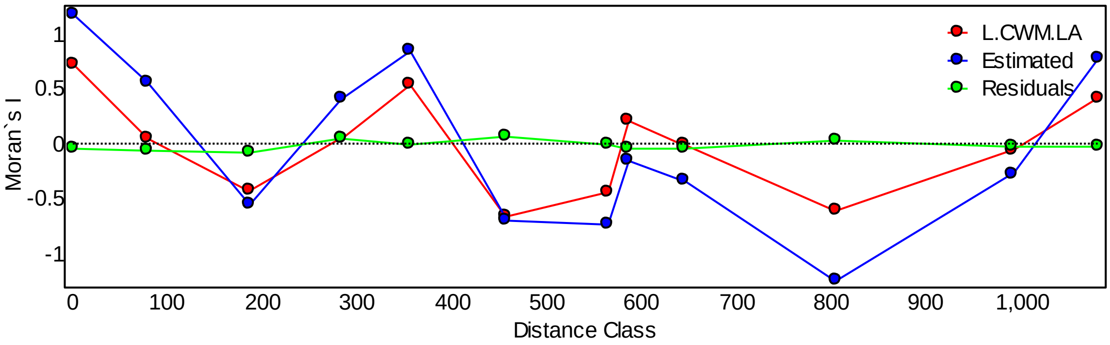


Savanna – acquisitive strategy

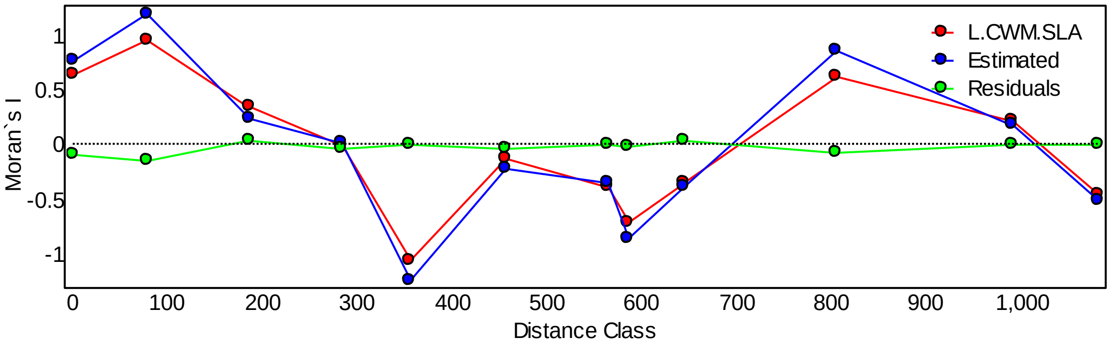
Hmax – Maximum plant height



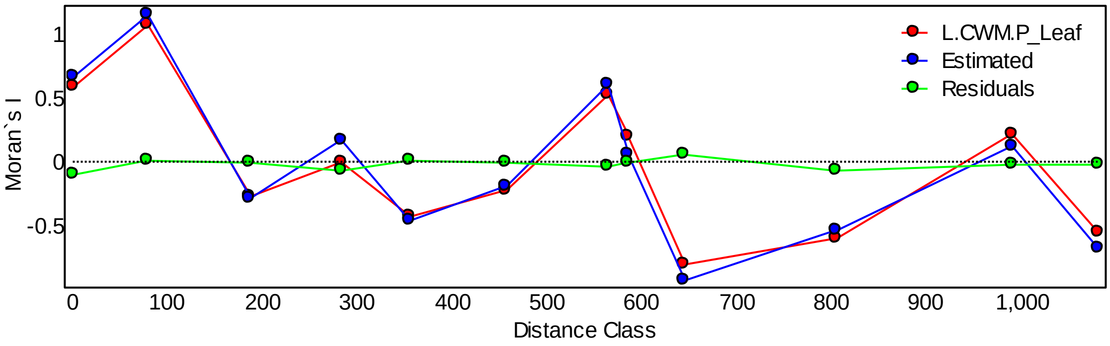
LA – leaf area



SLA – specific leaf area

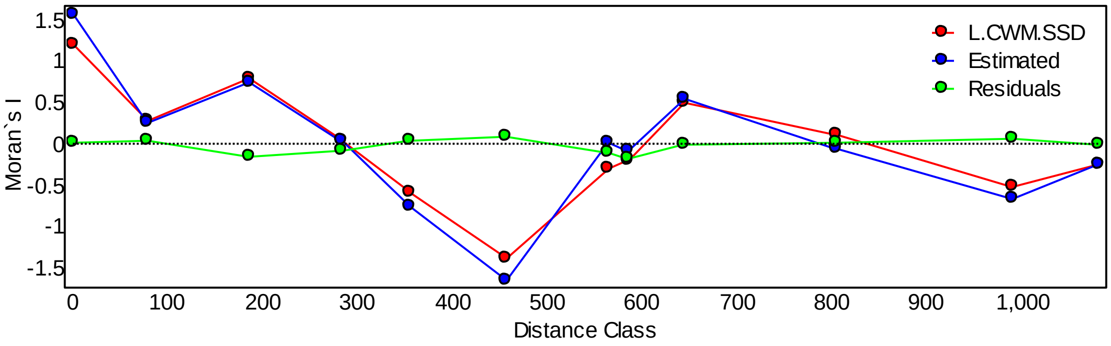


LPC – leaf phosphorous content

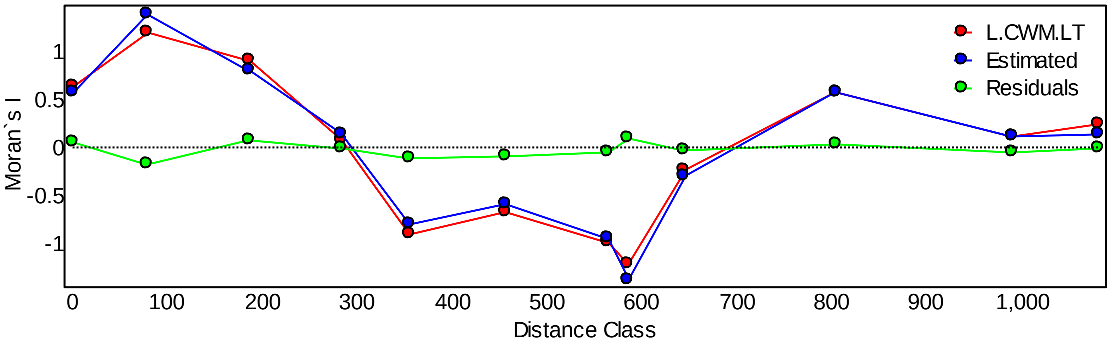


Savanna – conservative strategy

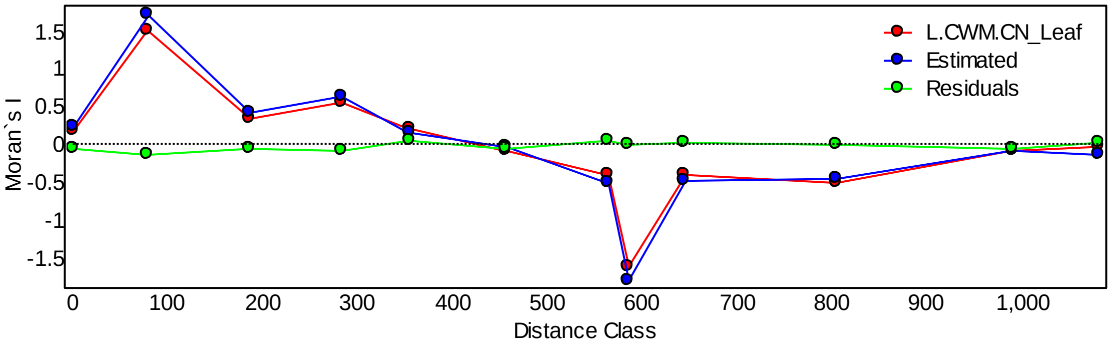
SSD – stem-specific density



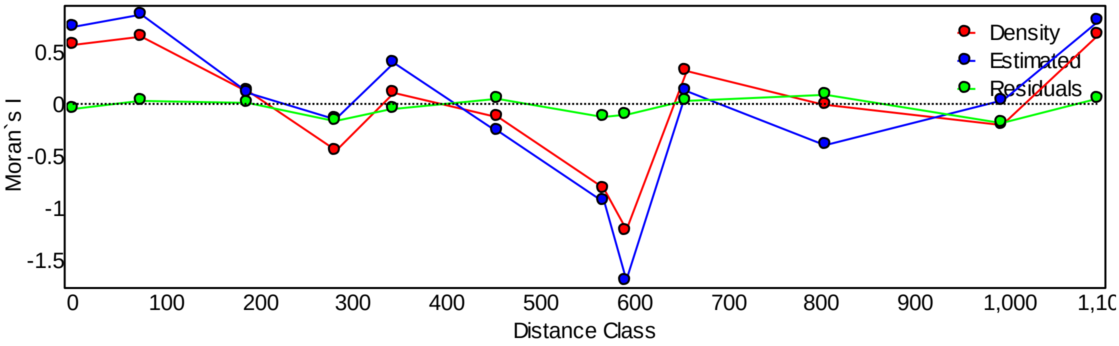
LT – leaf thickness



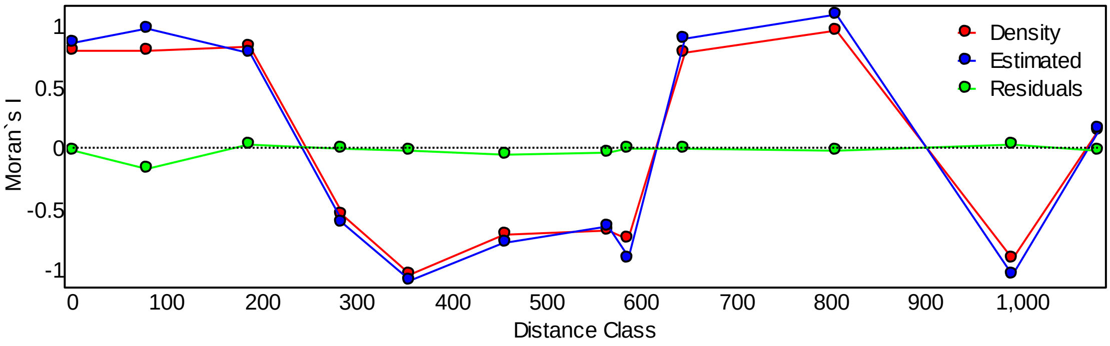
C/N – leaf carbon-nitrogen ratio



Density forest



Density savanna



CAPÍTULO III

Formatado nas normas da revista:

Journal of Ecology

Insect herbivore damage is not related with host plant ecological and evolutionary distances

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Summary

1. The spatial distribution and the identity of co-existing plants individuals should play an important role to herbivory levels. There is a growing interest in understand how the variation on functional traits and phylogenetic relationship in the neighboring affects the herbivory on focal plants.

2. To investigate whether ecological and evolutionary distances between individual plants and their neighbouring plants mediates leaf herbivory levels, we sampled 815 individuals belonging to 27 woody plant species in 49 savanna plots. For each individual, we quantified data on leaf damage (%), specific leaf area (cm^2 g^{-1}), leaf toughness (mm), plant height (cm), and abundance. To evaluate the herbivory effects at the individual level, we quantified relative trait values for each individual and the phylogenetic isolation of each individual in relation to the neighboring plants.

3. Contrary to our predictions, we found that ecological and evolutionary distances between focal plants and their neighbouring plants did not mediate leaf herbivory levels in the studied plants.

4. We showed that that the phylogenetic isolation, specific leaf area, leaf toughness, plant height and plant abundance did not influence the herbivore damage on the woody plants of Neotropical savannas, both in the individual context as at neighboring plants. Our results suggest that dominance of herbivore generalists, coevolution between plant and specialist herbivores and preferential consume of young leaves can be more important for determine the leaf damage level of the focal plant in savanna woody species, than the neighboring context.

5. *Synthesis*. We demonstrated that ecological and evolutionary distances between individual plants and their neighbouring plants did not mediates leaf herbivory levels in savanna woody species. These findings suggest that dominance of herbivore generalists, coevolution between plant and specialist herbivores and preferential consume of young leaves can be more important than the neighboring context for determine the leaf damage by herbivores in savanna woody species. Furthermore, we suggest that this approach be replicated to other plant groups and environments.

Key-words: neighboring plants, herbivory damage, plant functional trait, phylogenetic and ecological isolation, Janzen-Connell hypothesis, Neotropical savanna, cerrado

Introduction

Variation in leaf herbivory levels is a common phenomenon among co-occurring plant species (Cornelissen, Wilson Fernandes & Vasconcellos-Neto 2008; Carmona, Lajeunesse & Johnson 2011; Schuldt *et al.* 2012; Cárdenas *et al.* 2014). Potential explanations to such variation include differences in plant defensive traits, such as type and amount of secondary metabolites and leaf toughness, as well as differences in leaf nutritional content (Agrawal 2007; Carmona *et al.* 2011; Ali & Agrawal 2012; Loranger *et al.* 2012; Cárdenas *et al.* 2014). For example, leaves with high nitrogen concentration and high specific leaf area are more palatable to herbivores (Hanley *et al.* 2007) than leaves with high carbon-nitrogen ratio (Coley & Barone 1996). At the individual scale height influences the accessibility and localization of the plant by herbivores (Loranger *et al.* 2012) whereas at the assemblage level plant density is a signal of resource concentration (Hambäck & Englund 2005). Yet several studies investigated the direct effect of these factors on herbivory (Janzen 1970; Twigg & Socha 1996; Coley & Barone 1996; Agrawal 2007; Hanley *et al.* 2007) there is a growing interest in understand how the variation of these factors in the neighboring affects the herbivory on focal plants (Barbosa *et al.* 2009; Underwood *et al*. 2014; Kim & Underwood 2015).

Because plants are sessile organisms their spatial distribution and the identity of co-existing individuals should play an important role to herbivory levels. Neighboring plants can attract, retain or repulse herbivores (Root 1973; Hambäck & Englund 2005; Hakes & Cronin 2011) affecting the damage that a focal plant may experience. Damage to neighboring plants can also promote volatile emissions that elicit the induction of defenses in a given focal plant, leading to a reduction in herbivory (Barbosa *et al.* 2009). On the other hand, neighboring proprieties, such as plant abundance and identity may facilitate the survival of a focal plant by altering its conspicuity (Barbosa *et al.* 2009; Kim & Underwood 2015; Champagne, Tremblay & Côté 2016; Murphy, Xu & Comita 2016). The Janzen-Connell hypothesis predict that herbivore pressure should be positively correlated with conspecific neighbor abundance because specialist insect herbivores can be attract to high-density patches with preferred resource (Janzen 1970; Comita *et al.* 2014; Murphy *et al.* 2016). Palatable plants in an assemblage of unpalatable plants can remain undetected by herbivores and thereby escape from consumption (Callaway, Kikvidze & Kikodze 2000; Baraza, Zamora & Hódar 2006). Thus, studies of this nature are important because the neighboring effects on focal plant may influences their growth and survival, and determine species coexistence and diversity patterns in the local communities (Queenborough *et al.* 2007; Kim & Underwood 2015; Champagne *et al.* 2016).

The phylogenetic relationship between a given plant individual and its neighbors can act as an important mediator of plant–herbivore interactions (Gilbert *et al.* 2012; Lebrija-Trejos *et al.* 2014). This is because key plant functional traits can be phylogenetically conserved (Lebrija-Trejos *et al.* 2014) and closely related plant species often share more coevolutionary relationships with herbivore consumers and other natural enemies (Cavender-Bares *et al.* 2009; Futuyma & Agrawal 2009; Pearse & Hipp 2009; Gilbert *et al.* 2012). Thus, herbivores may limit the co-existence of closely related plants (Becerra 2007; Futuyma & Agrawal 2009). In this context, focal plants co-occurring with phylogenetically distant neighbors are expected to show lower herbivory levels than those co-occurring with closely related plants (Gilbert & Webb 2007; Chen *et al.* 2016).

In this study, we investigated whether ecological and evolutionary distances between individual plants and their neighbouring plants mediates leaf herbivory levels. We hypothesized that functionally and phylogenetically more similar neighbouring plants will show higher herbivore damage than functionally and phylogenetically less similar neighbouring focal plants. Specifically, we answered the following questions: (1) Does herbivory damage level in a focal plant is mediate by specific neighbour plant functional traits? (2) Do focal plants with leaf traits similar to neighbors plants (specific leaf area and leaf toughness) have higher herbivory damage levels than focal plants with distinct leaf traits to neighbouring? (3) Do focal plants larger than their neighbor plants have higher herbivory damage levels than focal plants smaller than neighborhood plants? (4) Do focal plants closely related to neighbouring plants have higher herbivory damage levels than focal plant distantly related to neighbouring plants?

Material and methods

STUDY SITE

The Cerrado is the largest savanna region of South America (Ratter, Ribeiro & Bridgewater 1997), and one of the richest savanna in the world, with a high habitat diversity and a large number of endemic plants and animals species (Klink & Machado

2005). The predominant vegetation of the Cerrado is a Neotropical savanna (cerrado *stricto sensu*) that is composed by shrubs, tree and grasses coexisting with the herbaceous layer (Ratter *et al.* 1997). The soils of the savannas of the Cerrado are nutrient-poor and well-drained and act as an environmental filter on species establishment (Furley & Ratter 1988). Another important filter is fire, that through time has selected species with traits of resistance or resilience to stresses caused by burning (Simon *et al.* 2009). The low soil fertility and high fire frequency filters species with adaptive traits to environmental stress and with anti-herbivore characteristics (Silva & Batalha 2011). Environments with high environmental stress, as the Cerrado, offer an under explored opportunity to understand how ecological and evolutionary relationships between neighboring species may determine the damage level caused by herbivores.

We conducted this study in the Emas National Park (ENP; 17°54’S, 52°59’W) in central Brazilian plateau, a region included predominantly in the Cerrado domain. The ENP occupies an area of 133,000 ha of mixed formations of savannas, and with elevations ranging between 720 to 890 m. The climate of the region is defined as Aw of Köppen (Peel *et al.* 2007), characbterized by a mean annual temperature of 24.6 °C and a mean annual precipitation ranging from 1,200 to 2,000 mm (Ramos-Neto & Pivello 2000). The soils are predominantly characterized as oxisols and dystrophic (Silva & Batalha 2008). The vegetation in the park comprises forest formations (e.g., *semidecidual and riparian forest*) and savannic formations (e.g., dense and open savannas) (Ribeiro & Walter 2008), wherein the last occupy 78.5% of the area of the park (Ramos-Neto & Pivello 2000).

ECOLOGICAL DISTANCES AND PHYLOGENETIC ISOLATION

We used data from 49 plots of 10 x 10 m where all woody plant individuals with a stem circumference larger than 10 cm at soil level were sampled (Zava & Cianciaruso 2014). These plots were randomly distributed in a gradient of open to dense savannas (39 plots in open savannas and 10 plots in dense savannas). We used only those species with at least ten individuals and that occurred in at least five plots. Overall, we analyzed 815 individuals of the 27 most abundant plant species (Table S1). *Anadenanthera peregrina* (Fabaceae) was excluded from the analysis due to its tiny folioles, which makes virtually impossible to measure leaf damage for this species. For each individual we sampled data on leaf damage (%), specific leaf area (cm^2 g^{-1}), leaf toughness (mm), and plant height (cm). Additionally, we calculated plant abundance per plot. For each individual we collected 10 mature leaves, of which five leaves were used to calculate leaf toughness, and the other five to calculate leaf damage, leaf area and specific leaf area. All trait measurements followed the protocols presented in Pérez-Harguindeguy *et al*. (2013).

To evaluate the herbivory effects at the level of individual, we quantified relative trait values for each individual (Table S2). Thus, for example, positive values for height indicate a higher-than-average individual and probably should be more attacked by herbivores, whereas negative values indicate lower-than-average ones and less attacked. To estimate phylogenetic isolation that is, the phylogenetic distance between each focal individual and the other co-occurring individuals, we used a dated phylogeny recently constructed by Zanne *et al*. (2014). From this phylogeny, we extracted the phylogenetic relationships of all 27 plants species analyzed (Fig. 1). However, 20 species were absent of the original phylogeny, we included these species in the phylogeny as polytomies at the genus (18 species) and family (2 species) level.

We quantified the phylogenetic isolation of each individual in relation to the neighboring plants as the sum of the branch lengths in the phylogeny connecting the focal individual and all the others plant individuals co-occurring in the same plot. Conspecific individuals had their phylogenetic distance set to zero. Therefore, this measure included the abundance of the neighboring plants at each plot, given that every single individual contributed to the sum. Individuals inserted in a local community comprising distantly-related plants will have high values of phylogenetic isolation.

STATISTICAL ANALYSIS

To investigate the factors that influence the leaf herbivore damage in each individual we built a model including SLA, relative SLA, LT, relative LT, conspecific abundance, height, relative height and phylogenetic isolation (Table 1). We build a random intercept linear mixed model relating the percentual herbivory of each individual and its trait values, as well as various measures of neighborhood context (Supporting Information Table S2), with plant species nested by plot identity as a random effect. Random effects structure was tested by likelihood ratio tests. We then computed the standardized coefficients with ±1.96*SE confidence intervals to assess the relative contribution of each variable to the differences in herbivory. Degrees of freedom for the *t-values* p computations were computed using the Satterthwaite's approximation (Satterthwaite 1946). The models were fit with the "lmer" function in the "lme4 package in R (R Core Team 2016).

Results

Leaf damage *per* plant individual ranged from 0.005% to 29.6%, with 95% of plant individuals having up to 10% of their leaf surface consumed by herbivores (Fig. 1). We found that the leaf toughness and relative leaf toughness were related to differences in leaf herbivory (Table 1, Fig. S1). However, the explanatory power of the global mixed effects model was very low. The marginal R^2 that are associated with fixed effects was of 0.07, while the conditional R^2 that considers both fixed and random effects was 0.42. Due to the low explanatory power of the fixed variables, we consider that all the predictor variables were not related to leaf damage (Table 1, Fig. 2).

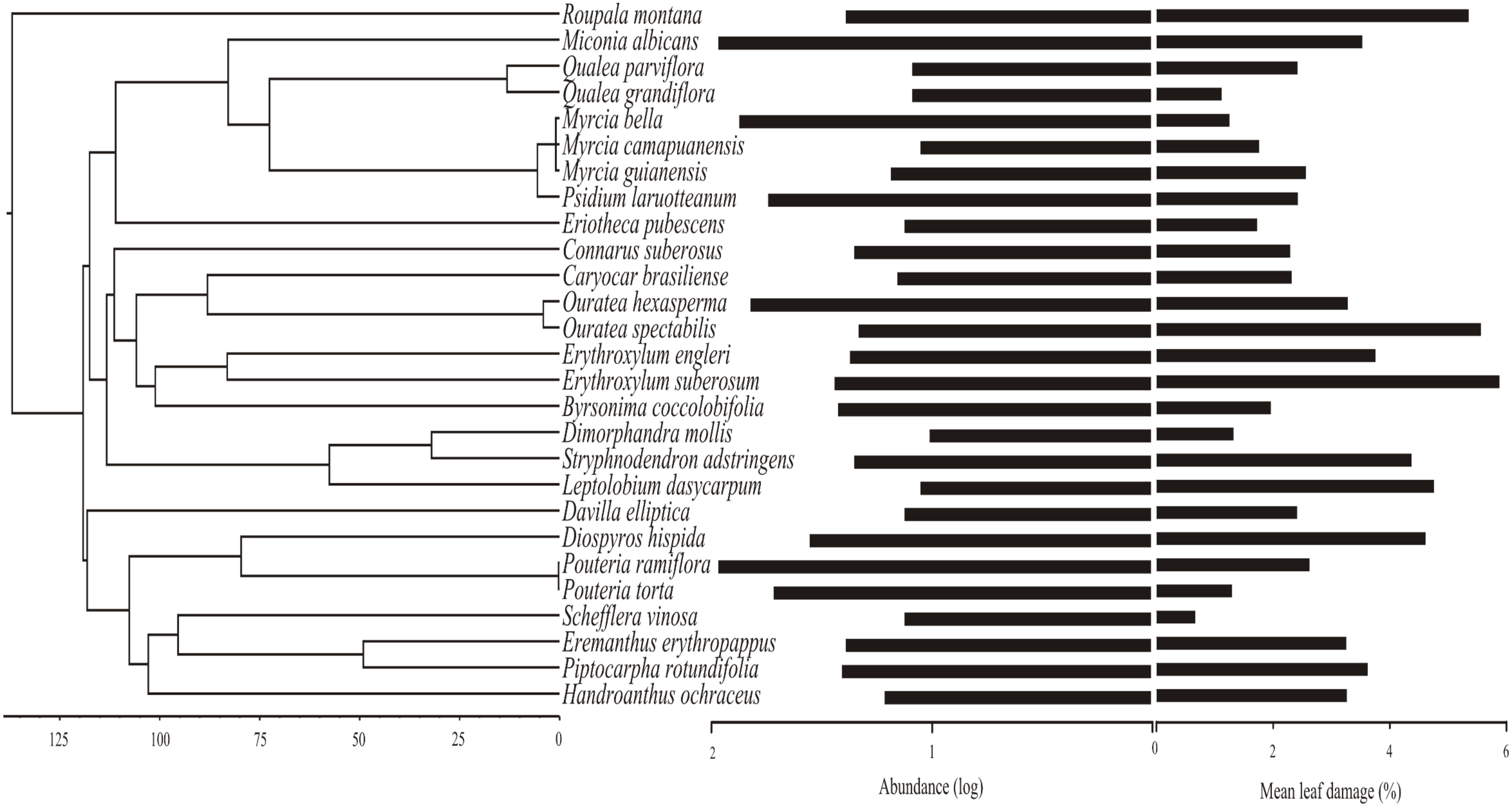

Fig. 1. The phylogenetic tree assembled for 27 cerrado species, with respective abundance and mean leaf damage for each species, utilized in the analyzes in Emas National Park, Brazil. Abundance is presented in log (for original values see Table 2S). The relationship among species was based on dated phylogeny constructed by Zanne *et al*. (2014). The scale is in million years and the values of abundance are logarithmic.

Table 1. Results of the global mixed effects model relating the predictors and relative herbivory. Standardized coefficients and standard errors are shown for the fixed effects conspecific abundance, phylogenetic isolation, relative specific leaf area, relative leaf toughness, and relative height. The conditional R^2 was of 0.42 and marginal R^2 was of 0.07. P values computed using the Satterthwaite's approximation (815 observations; 27 species). Ma: millions of years before of present; n: number of individuals.

	Groups	Variance	Std.Dev.		
Random effects	Plot	0.74	0.86		
	Species Identity	5.10	2.26		
	Residual	9.78	3.13		
	Variables	*Std. Coeff.*	*Std. Error*	*t-value*	*p*
Fixed effects	SLA (cm^2 g^{-1})	0.040	0.039	1.023	0.313
	Relative SLA (cm^2)	-0.066	0.039	-1.715	0.094
	Leaf toughness (mm)	1.321	0.385	3.432	0.002
	Relative leaf toughness (mm)	-1.070	0.441	-2.425	0.018
	Phylogenetic isolation (Ma)	$-2.57x10^{-4}$	$2.53x10^{-4}$	-1.018	0.315
	Conspecific abundance (n)	-0.072	0.065	-1.105	0.272
	Height (cm)	$-1.44x10^{-3}$	$5.11x10^{-3}$	-0.282	0.780
	Relative height (cm)	$-1.67x10^{-3}$	$5.28x10^{-3}$	0.317	0.753

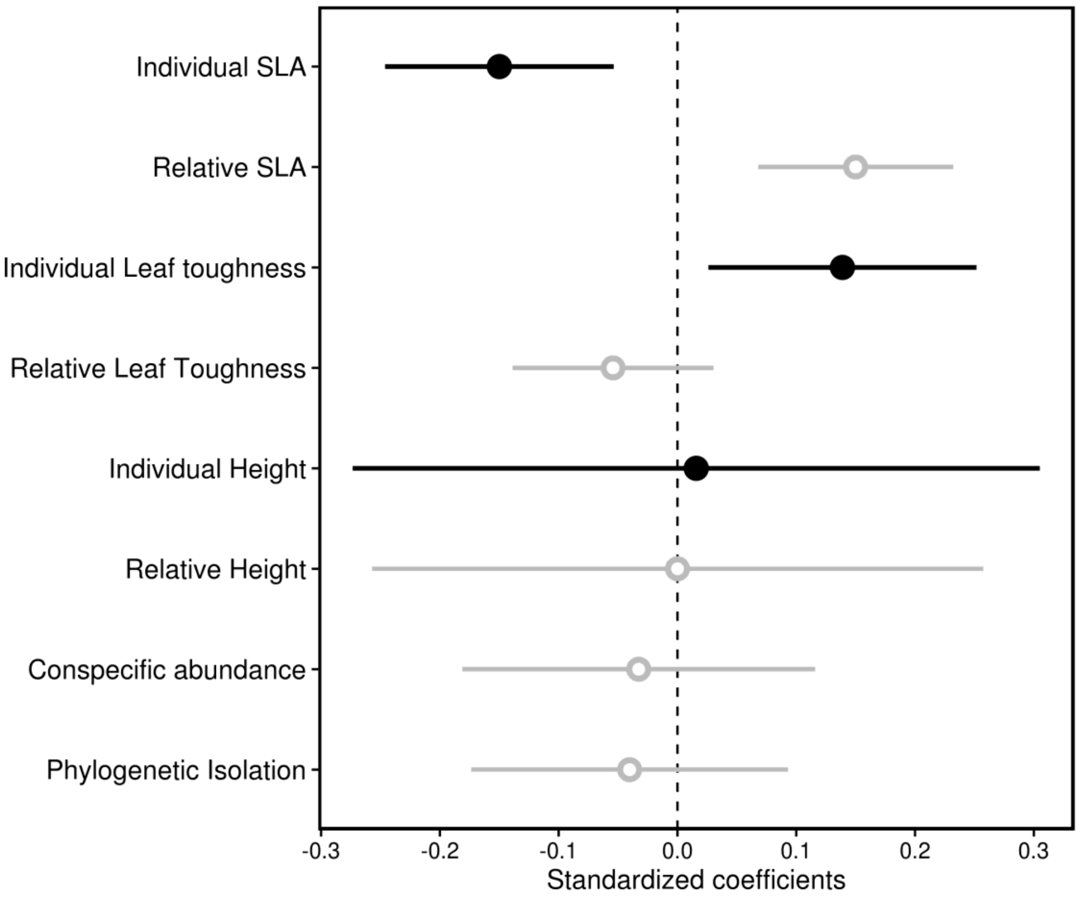

Fig. 2. Standardized effect size (mean ± 95% confidence intervals) computed under a global mixed effects model relating the predictors and relative herbivory for 27 cerrado species in Emas National Park, Brazil. Black line represents predictors related to effects at the level of individual, while white line indicates effects at the level of plots. Confidence intervals when do not overlap zero indicates significant relationship (positive or negative), but the marginal R^2 of the model was very low (0.07).

Discussion

Neighboring plants can affect the herbivore damage levels, attracting, retaining or repulsing herbivores (Root 1973; Hambäck & Englund 2005; Hakes & Cronin 2011). We hypothesized that focal plants more similar to neighboring plants will show higher herbivory damage than focal plants less similar to neighbouring plants. However, our results did not corroborate this expectation, because we found that the herbivory level of focal plants were not affected by traits of neighboring plants. This result can be explained by three principal factors: (1) dominance of generalist herbivores in savannas, (2) coevolution of plants and specialist herbivores, and (3) preferential consume of immature leaves by herbivores.

The herbivorous fauna in Neotropical savannas is composed predominantly by generalist insects, such as leaf-cutter ants, grasshoppers and caterpillars (Diniz & Morais 1997; Ribeiro, Carneiro & Fernandes 1998; Mundim, Costa & Vasconcelos 2009). These generalist herbivores can consume indiscriminately different plant types (Meijden 1996; Diniz & Morais 1997; Ali & Agrawal 2012), and range seasonally in the their diet breadth (Scherrer *et al.* 2016). The indiscriminate consume of savanna plants by generalist herbivores can explain the lack of effect of neighbor plants on leaf damage of focal plants.

Several herbivores insects coevolved with their host plants (Coley & Barone 1996) and this represent evolutionary and ecological consequences for plant-herbivore interactions (Becerra 2003, 2007; Futuyma & Agrawal 2009). These species of herbivores usually are specialized in their host plants, consuming their leaves independently of the traits from neighbor individuals. Another potential explanation may be related to the preferential consume of young leaves by herbivore insects. When young, savanna species leaves have high nutritional quality and are vulnerable to herbivores, contrary to mature leaves that have low nutrient concentrations and high protection against herbivores (Coley & Barone 1996; Awmack & Leather 2002; Lewinsohn, Freitas & Prado 2005; Mundim *et al.* 2009). Mature leaves of savanna plant species have strategy of protection against herbivores, such as thick leaves with trichomes and high leaf carbon-nitrogen ratio (Dantas & Batalha 2012; Dantas, Batalha & Pausas 2013). Moreover, savanna plants synchronize the leaf production at the end of dry season (Marquis, Diniz & Morais 2001; Mundim *et al.* 2009), which can affect the seasonal supply of resources for herbivores (Scherrer *et al.* 2016). Thus, insect herbivores in Neotropical savannas tend to consume indiscriminately immature leaves independent of neighbouring context, mainly in stage of high leaf production.

Our results also showed that phylogenetic isolation, leaf toughness, plant height and conspecific abundance do not influence the herbivore damage on the plants of this Neotropical savanna. The non-effect of phylogenetic isolation on the herbivory can be explained that, even for important traits in the determination of leaf damage by herbivore, the leaf damage level did not have relationship with the kinship between species (Agrawal 2007; Pearse & Hipp 2009; Uriarte *et al.* 2010; Gilbert *et al.* 2012), because same species phylogenetically more related or distant are consumed by herbivores. Pearse and Hipp (2009) argument that leaf volatile chemicals can be more phylogenetically informative than structural defence traits.

A negative effect of conspecific abundance via shared enemies is the main mechanism behind the well-tested Janzen-Connell hypothesis (Janzen 1970; Comita *et al.* 2014; Kim & Underwood 2015). However, we did not find effects of conspecific abundance at the plot on the levels of herbivory. The relationship between plant patch size and insect abundance is highly variable and dependent on the group specificities (Bukovinszky *et al.* 2005; Hambäck & Englund 2005). Therefore, this lack of effect may be a reflection of the response pattern of visual and olfactory searchers of the most important chewing groups in our study system, that can be able to reduce differences between small and large patches, such as orthopteran and larval lepidopteran (Hambäck & Englund 2005).

This is the first study that investigate the leaf damage caused by insect herbivores in a neighboring context in Neotropical savannas. In conclusion, we highlight that the phylogenetic isolation, specific leaf area, leaf toughness, plant height and plant abundance not influenced the herbivore damage on the woody plants of Neotropical savannas, both in the individual context as at neighboring plants. Overall, our results suggest that dominance of herbivore generalists, coevolution between plant and specialist herbivores and preferential consume of young leaves can be more important than the neighboring context for determine the leaf damage by herbivores in savanna woody species studied. As savanna plant species have leaves with low quality nutritional, herbivores compensate increasing the consumption rates to obtain more nitrogen from leaves. Furthermore, generalist herbivores consume immature leaves because they are vulnerable and present high-quality nutrients (Marquis *et al.* 2001). Future studies may improve these investigations, adding more species and develop this approach with other plant groups, including herbaceous and grasses, and species from other Neotropical vegetation types adjacent to savannas, such as forests and grassland environments.

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Supporting information

Table S1. List of families, species and number of individuals recorded in this study. The species were identified and organized following the last Angiosperm Phylogeny Group classification (APG-IV 2016). Bold type indicates the 27 cerrado most abundant and frequent species utilized in the analyzes

Family	**Species**	**Individuals**
Annonaceae	*Annona crassifolia* Mart.	4
	Annona coriacea Mart.	1
	Bocageopsis mattogrossensis (R.E.Fr.) R.R.Fr.	1
Apocynaceae	*Aspidosperma macrocarpon* Mart.	1
	Aspidosperma nobile Müll.Arg	1
	Hancornia speciosa Gomes	1
Araliaceae	*Schefflera macrocarpa* (Cham. & Schltdl.) Frodin	11
	***Schefflera vinosa* (Cham. & Schltdl.) Frodin & Fiaschi**	**13**
	***Eremanthus erythropappus* (DC.) MacLeish**	**24**
	***Piptocarpha rotundifolia* (Less.) Baker**	**25**
Bignoniaceae	***Handroanthus ochraceus* (Cham.) Mattos**	**16**
	Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex S.Moore	2
Calophyllaceae	*Kielmeyera coriacea* Mart. & Zucc.	6
	Kielmeyera grandiflora (Wawra) Saddi	7
	Kielmeyera rubriflora Cambess.	3
Caryocaraceae	***Caryocar brasiliense* Cambess.**	**14**
Celastraceae	*Plenckia populnea* Reissek	1
Chrysobalanaceae	*Licania humilis* Cham. & Schltdl.	5
Connaraceae	***Connarus suberosus* Planch.**	**22**
	Rourea induta Planch.	5
Dilleniaceae	***Davilla elliptica* A.St.-Hil.**	**13**
Ebenaceae	***Diospyros hispida* A.DC.**	**35**
Erythroxylaceae	***Erythroxylum engleri* O.E.Schulz**	**23**
	***Erythroxylum suberosum* A.St.-Hil.**	**27**
Fabaceae	*Anadenanthera peregrina* (L.) Spe.g.,	10
	Andira cujabensis Benth.	6
	Bowdichia virgilioides Kunth	7

Family	Species	Individuals
	***Dimorphandra mollis* Benth.**	**10**
	Hymenaea stigonocarpa Mart. ex Hayne	9
	***Leptolobium dasycarpum* Vogel**	**11**
	Mimosa amnis-atri Barneby	1
	Tachigali aurea Tul.	2
	Tachigali vulgaris L.G.Silva & H.C.Lima	2
	***Stryphnodendron adstringens* (Mart.) Coville**	**22**
	Stryphnodendron rotundifolium Mart.	3
Malpighiaceae	*Byrsonima basiloba* A.Juss.	3
	***Byrsonima coccolobifolia* Kunth**	**26**
	Byrsonima pachyphylla A.Juss.	4
	Byrsonima verbascifolia (L.) DC.	4
Malvaceae	*Eriotheca gracilipes* (K.Schum.) A.Robyns	6
	***Eriotheca pubescens* (Mart. & Zucc.) Schott & Endl.**	**13**
Melastomataceae	***Miconia albicans* (Sw.) Triana**	**91**
	Miconia ferruginata DC.	2
	Miconia ligustroides (DC.) Naudin	4
	Mouriri elliptica Mart.	1
Myrtaceae	*Campomanesia adamantium* (Cambess.) O.Berg	2
	Eugenia aurata O.Berg	2
	Eugenia punicifolia (Kunth) DC.	7
	Eugenia ternatifolia Cambess.	2
	Eugenia sp.	1
	***Myrcia bella* Cambess.**	**73**
	***Myrcia camapuanensis* N.Silveira**	**11**
	***Myrcia guianensis* (Aubl.) DC.**	**15**
	Myrcia multiflora (Lam.) DC.	1
	Myrcia variabilis DC.	1
	Myrcia vestita DC.	3
	Myrcia sp.	2
	***Psidium laruotteanum* Cambess.**	**54**
Nyctaginaceae	*Guapira noxia* (Netto) Lundell	6
Ochnaceae	***Ouratea hexasperma* (A.St.-Hil.) Baill.**	**65**
	***Ouratea spectabilis* (Mart.) Engl.**	**21**
Proteceae	***Roupala montana* Aubl.**	**24**

Family	Species	Individuals
Rubiaceae	*Palicourea rigida* Kunth	7
Salicaceae	*Casearia sylvestris* Sw.	9
Sapotaceae	***Pouteria ramiflora*** **(Mart.) Radlk.**	**91**
	Pouteria torta **(Mart.) Radlk.**	**51**
Styracaceae	*Styrax ferrugineus* Nees & Mart.	4
Vochysiaceae	***Qualea grandiflora*** **Mart.**	**12**
	Qualea multiflora Mart.	1
	Qualea parviflora **Mart.**	**12**
	Vochysia cinnamomea Pohl	5

Table S2. Predictor variables used in the model and their definition.

Predictor variables	Definition
Conspecific abundance (AB)	The number of individuals of the same species in the same plot.
Phylogenetic isolation (PI)	The total sum of branches separating each individual and all other heterospecific individuals in the same plot.
Relative SLA (SLA)	The difference between the specific leaf area (SLA) of the individual and the mean SLA of the other individuals in the plot.
Relative height	The difference between the plant height of the individual and the mean height of the other individuals in the plot.
Relative leaf toughness (LT)	The difference between the leaf toughness (TO) of the individual and the mean TO of the other individuals in the plot.

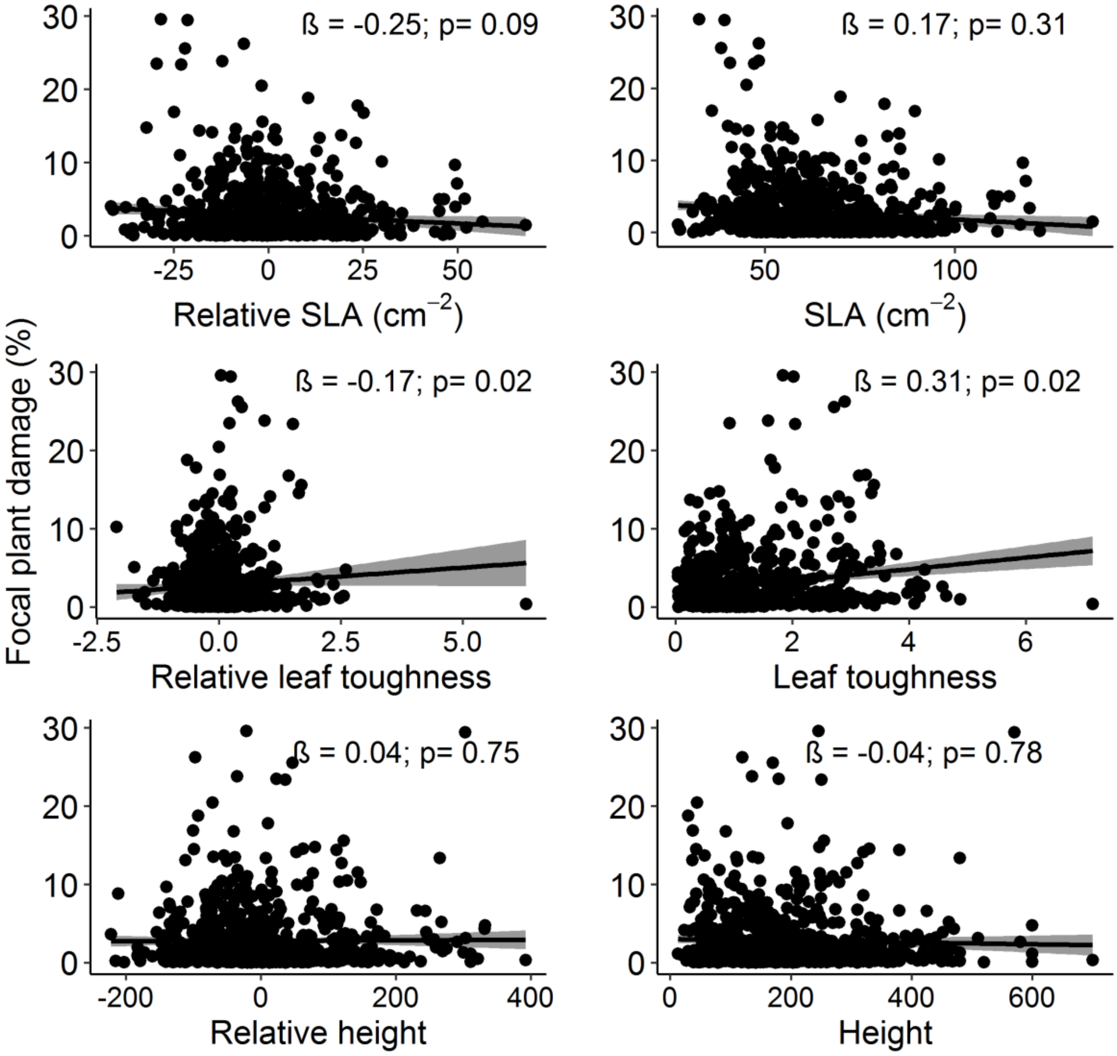

Figure S1. Relationship between the relative traits and absolute trait values focal plant and the herbivore leaf damage on 27 cerrado species in Emas National Park, Brazil. The shaded bands indicate the 95% confidence interval of the response.

Conclusão Geral

Neste trabalho demonstramos que:

- Para ambientes contrastantes que ocorrem lado a lado como florestas estacionais e cerrado sentido restrito, as estratégias ecológicas das espécies estão de acordo com os fatores limitantes para a ocorrência de espécies em cada um destes habitats. Atributos aquisitivos que representam habilidade competitiva e rápida aquisição de recursos foram relacionados para espécies especialistas de floresta, enquanto atributos conservativos que promove resistência contra o fogo e estresse ambiental foram associados a espécies especialistas de savanas. Além disso, a plasticidade fenotípica pode determinar a habilidade das espécies em habitats contrastantes como florestas estacionais e cerrado sentido restrito.
- Espécies de comunidades de florestas estacionais e cerrado sentido restrito de fato adotam diferentes estratégias relacionada ao uso de recursos. Nós demostramos uma forte relação negativa de densidade de indivíduos com o gradiente de fertilidade e toxicidade do solo. Para os valores médios dos atributos, nós registramos que em solos mais férteis e menos tóxicos tem espécies com atributos relacionados à estratégias de aquisição de recursos, enquanto solos com baixa fertilidade e mais tóxicos tem espécies com atributos associados à estratégias de conservação de recursos.
- Em ambientes savânicos, a distância ecológica e evolutiva de uma espécie focal para a sua vizinhança não é fundamental para determinar o nível de dano foliar por herbívoros. Sugerimos que outros fatores, tais como dominância de herbívoros

generalistas, co-evolução de plantas e herbívoros e consumo de folhas jovens são mais importantes para determinar o dano foliar do que o contexto da vizinhança.