

**Ecologia do fogo e diversidade funcional em comunidades vegetais de cerrado no
Parque Nacional das Emas**

Tese apresentada ao Programa de Pós-graduação em Ecologia e Recursos Naturais da Universidade Federal de São Carlos, como parte dos requisitos para a obtenção do título de Doutor em Ciências.

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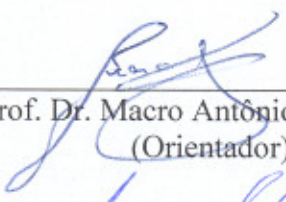
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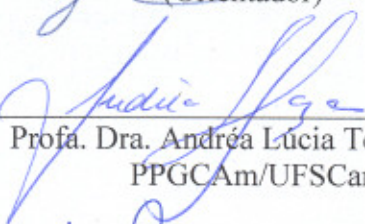
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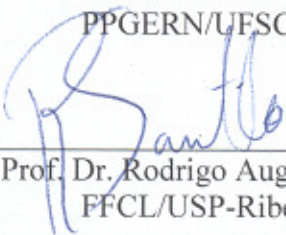
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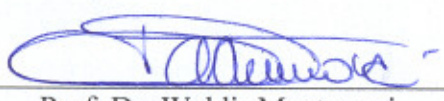
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Dedico minha tese à memória de Igor Aurélio Silva,
grande cientista, grande músico, e acima de tudo grande amigo.
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2. Resumo

O fogo é um filtro ambiental que seleciona espécies baseado nos traços e, juntamente com propriedades do solo está relacionado a diferenças na riqueza e composição de espécies. A diversidade funcional incorpora variação nos traços das espécies, permitindo avaliar os efeitos da biodiversidade sobre o funcionamento da comunidade. Ela pode ser dividida em seus componentes para elucidar relação de efeito ou resposta com o ambiente. Tanto a variação intra-específica quanto a interspecífica devem ser consideradas nas análises de efeito dos filtros ambientais sobre a estrutura da comunidade. Amostramos o componente arbóreo em uma reserva de cerrado, medimos a riqueza de espécies, traços funcionais, a abundância, variáveis ambientais e a taxa de decomposição da serapilheira. Calculamos três índices de diversidade funcional. Usamos seleção de modelos para escolher o melhor modelo preditor da biodiversidade baseado nas variáveis do solo. Nós calculamos a média ponderada pra comunidade de cada traço e usamos uma ordenação para examinar como os traços mudaram entre as frequências de fogo. Nós testamos o efeito da biodiversidade sobre o funcionamento. Além disso, usamos as variabilidades inter- e intraspecífica para testar a mudança das médias dos traços, a redução da amplitude e o aumento da diferenciação de nichos. Encontramos maiores riquezas de espécies e dispersão funcional em locais mais férteis onde o fogo era frequente, e o oposto onde o fogo era infrequente. Entretanto, o solo influenciou a equabilidade funcional somente quando a frequência de fogo era baixa, com maiores valores onde os solos eram menos férteis. Encontramos baixos valores de riqueza funcional e altos valores de equabilidade funcional e divergência funcional. Componentes funcionais estiveram relacionados às variáveis ambientais, indicando que a diversidade funcional teve relações de respostas com o ambiente: Quanto mais severas as condições ambientais menor a sobreposição fenotípica e consequentemente menos competição. Componentes funcionais não predisseram a taxa de decomposição. Entretanto, quando incluímos as variáveis ambientais, encontramos maiores taxas de decomposição relacionada a maiores inclinações, solos mais ricos, fogo mais frequente e maiores

valores de riqueza funcional. Então, as relações de efeito da diversidade funcional sobre o funcionamento foi dependente do ambiente. A inclusão da variabilidade intra-específica não aumentou a percepção dos filtros ambientais e competição para todos os traços. Nós encontramos evidência de filtros ambientais para quase todos os traços. A média mudou para cinco traços e amplitude reduziu para sete traços, comparados a expectativa nula. Além disso, cinco traços apresentaram diferenciação de nicho, indicando competição após a seleção pelo filtro. O fogo pode mudar os traços funcionais diretamente evitando o desenvolvimento das plantas ou indiretamente alterando a competição. Diferentes frequências de fogo levaram a diferentes relações planta-solo, que podem afetar o funcionamento de savanas tropicais. Tanto a diversidade funcional quanto a identidade funcional das comunidades foram afetadas pela frequência de fogo e condições de solo. O gradiente de fogo alterou os espaço de traços selecionando espécies similares com traços mais adequados.

3. Abstract

Fire is an environmental filter that selects species based on their traits and, in association with soil features are related to differences in plant species richness and composition. Functional diversity incorporates variation in species traits and allows one to evaluate the effects of biodiversity upon community functioning. It can be divided into components to elucidate response and effect links with environment. Both intra- and interspecific variation should be considered when analysing the role of environmental filters structuring communities. Sampling woody plants in a Brazilian cerrado reserve, we measured species richness, functional traits, abundance, environmental variables and litter decomposition rate. We calculate three functional diversity index. Then, we used model selection analyses to select the best model predicting functional diversity and richness based on soil variables in sites with three different fire frequencies. We calculated the community weighted mean of each trait and used an ordination to examine how traits changed across fire frequencies. We tested for effects of biodiversity upon ecological functioning. We also used an intra- and interspecific trait-based approach to test for shifts in each trait mean, reduction of trait range, and increase in niche differentiation. We found higher species richness and functional dispersion in more fertile sites where fire was frequent, and the opposite where fire was infrequent. However, soil influenced functional evenness and divergence only where fire was infrequent, with higher values where soils were poorer. We found low values of functional richness and high values of functional evenness and functional convergence. Functional components were related to environmental variables, indicating that functional diversity had response links with the environment: harsher environmental conditions lead to less phenotypic overlap and, consequently, less competition. Functional components did not predict litter decomposition rate. However, when environmental variables were also used, we found higher decomposition rate related to higher slope, richer soil, frequent fire, and higher functional richness. Therefore the effect links of functional diversity upon functioning were dependent on the cerrado environment. The inclusion of intraspecific variability

did not increase the perception of environmental filters and competition to all traits. We found evidence for environmental filter to almost all traits analysed, except basal area and leaf toughness. Mean values shifted for five traits and ranges reduced for seven traits compared to null expectation. Also five traits presented niche differentiation indicating competition after the filter selection. Fire may change functional traits directly by hindering development of plants and indirectly by changing competition. Different fire frequencies lead to different plant-soil relationships, which may affect the functioning of tropical savanna communities. Both functional diversity components and functional identity of the communities are affected by fire frequency and soil conditions. Fire gradient changed the space traits by selecting similar species with more adequate traits.

4. Introdução geral

O fogo é um dos principais fatores determinando a ocorrência e variação fisionômica do cerrado (Gottsberger & Silberbauer-Gottsberger 2006). Ele interage com o solo modificando as condições ambientais para as plantas (Silva & Batalha 2008) e remove biomassa vegetal alterando as interações biológicas (Cianciaruso et al. 2010). O fogo é um filtro ambiental importante, favorecendo à formações savânicas em detrimento das florestais (Moreira 2000; Miranda et al. 2002). Assim, as espécies nas formações savânicas do cerrado que já passaram por esse filtro ambiental devem ser adaptadas ao fogo. A frequência de fogo pode então ser considerada um filtro adicional no cerrado, pois, limita a existência das espécies selecionando aquelas que possuem características que lhes permitam lidar com um dado regime de queimadas (Silva & Batalha 2010, Silva et al. 2010). Portanto, as características funcionais das espécies são fundamentais para explicar a composição específica e variação fisionômica das comunidades de cerrado.

Os traços funcionais são características mensuráveis que correspondem a uma função para o organismo. Por exemplo, para plantas a altura, a área foliar específica e espessura da casca são traços funcionais, pois correspondem a funções relacionadas a competição, produtividade e resistência ao fogo, respectivamente (Cornelissen et al. 2003). Para sintetizar a informação contida nos traços funcionais de comunidades vegetais, utilizamos as medidas de diversidade funcional. A diversidade funcional indica quão diversos são os traços em uma comunidade, e é um indicativo das relações de complementaridade entre as espécies ou sobreposição de nichos (Petchey & Gaston 2006). A diversidade funcional pode ser medida categoricamente, na forma de grupos funcionais ou numericamente de forma contínua (Petchey & Gaston 2006). Quando trabalhamos com múltiplos traços simultaneamente, podemos considerar cada traço como uma dimensão, sendo que o conjunto de traços forma um espaço multivariado no qual as espécies e as comunidades estão posicionados segundo suas características.

Além disso é possível decompor a diversidade funcional em suas partes: riqueza (ou dispersão) funcional, equabilidade funcional e divergência funcional (Villéger et al. 2008). A riqueza e a dispersão funcionais medem o volume ocupado pelas espécies no espaço multivariado dos traços: se as espécies forem funcionalmente diferentes, então a riqueza e a dispersão funcionais apresentarão maiores valores. A equabilidade funcional mede o quão bem as abundâncias das espécies estão distribuídas no espaço de traços: se as espécies funcionalmente distintas apresentarem abundâncias parecidas, então teremos maior equabilidade funcional; por outro lado, se espécies funcionalmente parecidas concentrarem a abundância e poucos indivíduos apresentarem traços distintos das espécies dominantes, então teremos baixa equabilidade funcional. A divergência funcional mede a concentração das abundâncias no espaço de traços: se as espécies mais abundantes possuírem valores de traços próximos à média, então teremos baixa divergência funcional; se por outro lado, as espécies mais abundantes possuírem valores extremos de traços, ou seja, mais divergentes, então teremos maiores valores de divergência funcional. Para mais detalhes sobre o cálculo e propriedades dos índices veja Villéger et al. (2008) e Laliberté & Legendre (2010).

Ainda, é possível determinar a identidade funcional baseada na combinação de traços por meio da média ponderada para comunidade (Ricotta & Moretti 2011). Comunidades funcionalmente parecidas ficam próximas no espaço multivariado de traços. Por fim, a inclusão da variabilidade intra-específica, deve permitir uma melhor observação do efeito de distúrbios ou da competição sobre a estrutura das comunidades (Jung et al. 2010). O fogo, por exemplo, age sobre os indivíduos antes que nas espécies, de modo que indivíduos com características diferentes dentro da mesma espécie podem sobreviver a diferentes frequências de queimadas. Do mesmo modo, a competição deve ser menor entre indivíduos diferentes, independentemente da espécie. Quando limitamos nosso estudo às plantas arbóreas estamos perdendo informação sobre a competição com as herbáceas, que devem desempenhar um papel fundamental, principalmente nas áreas mais

abertas. Entretanto essa perda é minimizada se considerarmos que o componente herbáceo é relativamente homogêneo.

É preciso uma criteriosa escolha de quantos e quais traços serão medidos, para evitar medidas de traços redundantes ou a omissão de um traço importante (Petchey & Gaston 2006). Para espécies vegetais existe um protocolo para escolha e métodos de coleta dos traços funcionais baseados nas funções que eles exercem (Cornelissen et al. 2003). No presente estudo, por exemplo, medimos traços relacionados ao fogo, à competição e ao uso de nutrientes. Essa padronização das coletas somada a programas de computador capazes de lidar com múltiplos traços e muitas comunidades ao mesmo tempo (R Development Core Team 2010), fazem da diversidade funcional uma abordagem promissora para os estudos de ecologia (Cianciaruso et al. 2009).

No primeiro capítulo procuramos responder se o histórico de fogo e as propriedades do solo influenciavam a riqueza de espécies e a diversidade funcional em três áreas cerrado. Determinamos as variáveis do solo, medimos a riqueza, a abundância e nove traços funcionais e calculamos três componentes da diversidade funcional e a média ponderada para comunidade dos traços. Utilizamos regressões e uma ordenação para testar a influência do fogo e do solo sobre as comunidades. Encontramos que tanto os componentes da diversidade funcional quanto a identidade funcional das comunidades foram afetadas pela frequência de fogo e condições do solo.

No segundo capítulo, além de medirmos os componentes da diversidade funcional e variáveis ambientais, também utilizamos a taxa de decomposição de matéria como uma medida de funcionamento das comunidades. Amostramos estratos com diferentes frequências de fogo, medimos variáveis do solo e topográficas, e testamos os efeitos da diversidade funcional e das variáveis ambientais sobre o funcionamento. Encontramos que a diversidade funcional sozinha não explica o funcionamento, apenas quando consideramos conjuntamente as variáveis ambientais.

No terceiro capítulo incluímos a variabilidade intra-específica de cada traço e testamos a presença de filtros ambientais e de competição sobre a identidade funcional das comunidades. Para

estratos com diferentes tempo desde a última queimada, calculamos a média, a amplitude e divergência de cada traço e comparamos com aleatorizações. Encontramos que o gradiente de fogo alterou o espaço dos traços, selecionando espécies mais parecidas e com média de traços diferentes do esperado pelo acaso, e que alguns traços também indicaram a presença de competição.

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5. Capítulo 1

Influence of fire history and soil properties on plant species richness and functional diversity in a Neotropical savanna

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Influence of fire history and soil properties on plant species richness and functional diversity in a Neotropical savanna

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RESUMO: (Influência do histórico de fogo e propriedades do solo sobre a riqueza de espécies vegetais e diversidade funcional em uma savana neotropical) Propriedades do solo e distúrbios, como o fogo, estão ligados à diferenças na riqueza e composição de espécies, por isto são determinantes para a ocorrência de espécies vegetais em comunidades savânicas. Medimos a riqueza de espécies e usamos a abundância e nove atributos funcionais das plantas para calcular três índices de diversidade funcional. Então, utilizamos análises de seleção de modelos para selecionar o melhor modelo para predição da diversidade funcional e riqueza baseado em variáveis do solo em três frequências de fogo diferentes. Calculamos também a média ponderada de comunidade para cada atributo e usamos uma ordenação para examinar como os atributos mudam entre as frequências de fogo. Encontramos maior riqueza de espécies e dispersão funcional em solos mais férteis, onde o fogo era frequente, e o oposto onde o fogo era infrequente. Entretanto, as propriedades dos solos influenciaram a equabilidade e a divergência funcionais somente onde o fogo era infrequente, com maiores valores em solos pobres. O fogo deve alterar os atributos diretamente, impedindo o desenvolvimento das plantas e indiretamente, alterando a competição. Diferentes frequências de fogo levaram a diferentes relações entre solo e plantas, o que, conseqüentemente, deve afetar o funcionamento de comunidades em savanas tropicais. Tanto os componentes da diversidade funcional quanto a identidade funcional das comunidades foram afetadas pela frequência de fogo e condições do solo.

Palavras-chave: cerrado; complementaridade; efeito da fertilidade; nitrogênio no solo; atributos vegetais

ABSTRACT: (Influence of fire history and soil properties on plant species richness and functional diversity in a Neotropical savanna) Soil features, in association with disturbances such as fire, are related to differences in plant species richness and composition and, therefore, can be key determinants of species occurrence in savanna plant communities. We measured species richness and used nine plant functional traits and abundance to calculate three functional diversity indices. Then, we used model selection analyses to select the best model predicting functional diversity and richness based on soil variables in sites with three different fire frequencies. We also calculated the community weighted mean of each trait and used an ordination to examine how traits changed across fire frequencies. We found higher species richness and functional dispersion in more fertile sites where fire was frequent, and the opposite where fire was infrequent. However, soil influenced functional evenness and divergence only where fire was infrequent, with higher values where soils were poorer. Fire may change functional traits directly by hindering development of plants and

indirectly by changing competition. Different fire frequencies lead to different plant-soil relationships, which may affect the functioning of tropical savanna communities. Both functional diversity components and functional identity of the communities are affected by fire frequency and soil conditions.

Keywords: cerrado; complementarity; fertility effect; plant traits; soil nitrogen

Introduction

Plants and soil have a feedback relationship that is important to succession and competition dynamics (Kulmatiski *et al.* 2008). However, there is an unsolved debate about the relationship between plant diversity and soil features. While some studies found a negative relationship between soil fertility and plant species richness (for example, Huston 1980; Enright *et al.* 1994; Tilman 1999; Harpole & Tilman 2007), others have argued that species richness increases with fertility (for example, Stark 1970; Gentry 1988), which is in accordance with the “fertility effect” theory (Dybzinski *et al.* 2008). Also, another observed relationship predicts maximum diversity at intermediate levels of soil fertility (Tilman 1984). An alternative way to solve this issue is to take into account similarities or differences in the functional traits of species in addition to species richness *per se* (Hooper *et al.* 2005) because species turnover occurs due to suits of traits conferring different relative ecological advantages as the environment changes (Grime 2001).

Species coexistence is affected by their ability to exploit limiting resources (Tilman 1982). Since different plant species are adapted to the availability of distinct nutrients in the soil, the type and number of limiting resources may affect species composition and richness (Critchley *et al.* 2002; Venterink *et al.* 2003; Harpole & Tilman 2007). Disturbances also affect species richness and composition and change the influence of species traits on plant establishment and development (Haddad *et al.* 2008). Whereas soil properties and fire may alter the functional traits and species composition of plant communities (Müller *et al.* 2007; Silva & Batalha 2008), plants may also alter soil conditions through processes such as nitrogen fixation, nutrient cycling, and aluminium detoxification, and indirectly by litter deposition volume and quality (Göttlein *et al.* 1999; Fornara & Tilman 2008; Gessner *et al.* 2010). Thus, plants will be associated with soil in different ways depending on different levels of disturbance.

Functional diversity, or the range and value of species functional traits (Tilman *et al.* 2001; Petchey & Gaston 2006), is an important determinant of functioning (Díaz & Cabido 2001; Hooper *et al.* 2005). Usually, measures of ecosystem functioning (for example, productivity or nutrient cycling) have been found to be more consistently associated with functional diversity than with species richness (Díaz & Cabido 2001), but there are exceptions (e.g., Hector *et al.* 2000). Thus, there is growing evidence that functional diversity strongly determines ecosystem-level processes, such as resource acquisition, nutrient cycling, and productivity (e.g., Hooper & Vitousek 1997; Díaz & Cabido 2001; Hooper *et al.* 2005). Moreover, soil characteristics, in association with disturbances such as fire, may also be related with differences in plant functional groups (Higgins *et al.* 1997,

Batalha *et al.* 2011). For instance, Fornara & Tilman (2008) found that higher complementarity in plant functional traits increases soil carbon and nitrogen accumulation. Also, there is evidence that soil fertility increases with plant species richness and functional group diversity (Dybzinski *et al.* 2008). Nevertheless, the relationship between environmental factors, such as soil and fire, and functional diversity is a question rarely addressed in natural communities and, especially, to woody species.

Soil and fire are the major determinants of plant community structure and composition in Neotropical savannas (Silva 1996; Bond *et al.* 2005; Lehmann *et al.* 2011). Recurrent fires modify many soil features, such as concentration of available nutrients, amount of organic matter, toxic elements, and soil texture (Kennard & Gholz 2001; González-Pérez *et al.* 2004; Silva & Batalha 2008). Fire frequency and intensity alter savanna physiognomies and also constrain the regional species pool, selecting species that are resistant or tolerant to fire (Gottsberger & Silberbauer-Gottsberger 2006). In the cerrado (Neotropical savanna), plant growth is frequently limited by soil nitrogen availability (Bucci *et al.* 2006), and soils are usually well-drained, old Oxisols (Montgomery & Askew 1983). These soils are nutrient-poor, presenting low pH, low cation exchange capacities, and high aluminium saturation levels (Ruggiero *et al.* 2002; Bucci *et al.* 2006; Amorim & Batalha 2007). Aluminium is usually toxic to plants, reducing growth and preventing nutrient uptake (Göttlein *et al.* 1999; Heim *et al.* 2003). However, responses to aluminium toxicity depend on plant species, and some are adapted to high levels of aluminium, being restricted to this soil condition (Haridasan 2000). Therefore, species composition is related to soil texture, aluminium saturation, nitrogen, and organic matter concentration (Higgins *et al.* 1997; Dubbin *et al.* 2006; Silva & Batalha 2008).

Here we investigated the influence of fire history and soil properties on woody species richness and functional diversity in savanna sites. As long as both soil and fire are major factors structuring these plant communities, we may expect different relationships between these factors for each fire frequency. Thus, we answered the following questions: (i) Do different fire frequencies change the relationship among soil features, species richness, and functional diversity? (ii) How would fire history influence the relationships among soil features, plant species richness, and their functional diversity?

Material and methods

Study area – Our study site was the Emas National Park (ENP), located in the Brazilian Central Plateau (17°49'-18°28'S and 52°39'-53°10'W). The ENP is under a tropical warm wet climate, with at least three dry months during the winter. Annual rainfall varies from 1200 to 2000 mm, concentrated from October to March (Ramos-Neto & Pivello 2000). Soils at the ENP are mainly nutrient-poor Oxisols (Amorim & Batalha 2007; Silva & Batalha 2008). Until 1984, farmers exploited ENP for cattle ranching, and dry season burnings were used to promote forage regrowth every year. After that, the ENP was totally fenced, cattle were no longer allowed inside it and a fire exclusion policy was established (Ramos-Neto & Pivello 2000). Since 1994, annual prescribed burnings have been applied in approximately 10 km² of preventive firebreaks to remove plant dry mass and avoid the spreading of fires, which in the past resulted in catastrophic burnings every three years (Ramos-Neto & Pivello 2000). Nevertheless, in August 2010, another anthropogenic fire burned 93% of the reserve.

Community sampling - We assessed soil features and floristic composition using raw data from Silva & Batalha (2008). In the late rainy season of 2006, we sampled three nearby savanna woodlands (*campo cerrado*) subjected to different fire frequencies: one firebreak burned annually for the last ten years (hereafter “high fire frequency”, approximately 18°18'50”S and 52°54'00”W), another firebreak burned in 1996, 1999, 2001, 2002, and 2003 (hereafter “intermediate fire frequency”, approximately 18°19'01”S and 52°54'10”W), and a site protected from fire since 1994 (hereafter “low fire frequency”, approximately 18°17'28”S and 52°53'41”W). The spatial proximity of the studied sites increases the likelihood that significant differences among sites were due to the time of protection from fire and not due to prior differences among them (see Pucheta *et al.* 1998 for a similar approach). In each savanna, we delimited a 2.5 km linear transect, and in each transect we systematically marked 250 points 10 m apart from each other. At each point, we sampled four woody plants with a minimum stem diameter at soil level of 3 cm (SMA 1997), using the point-quarter sampling method (Müller-Dombois & Ellenberg 1974). We grouped vegetation data from 10 consecutive sampling points to be part of a single sampling unit. Thus, we ended up with 25 species-composition sampling units for each site. Furthermore, we collected a soil sample at a 0-5 cm depth for every point, because soil composition in this layer is the most correlated with the distribution of cerrado vegetation (Ruggiero *et al.* 2002; Amorim & Batalha 2007). We mixed soil samples collected from 10 consecutive sampling points to obtain a composite sample for every sampling unit. Thus, we ended up with 25 soil sampling units for each site.

Soil features - We selected the following soil features: total nitrogen concentration (N), organic matter (OM), exchangeable Al (Al^{3+}), clay, and sand. We used clay:sand ratio as a measure of soil texture. For more details on how soil features were determined, see Amorim & Batalha (2007) and Silva & Batalha (2008). Nitrogen concentration, organic matter, clay, and sand are the soil features most related to floristic composition, whereas Al^{3+} is related to species richness (Amorim & Batalha 2007; Silva & Batalha 2008).

Species richness and functional diversity components - Using the plant composition data, we counted the number of species (species richness) occurring in each of 25 sampling unites in each site. To estimate the functional diversity, we used nine traits (Tab. 1) that represent functional characteristics related to fire disturbance or soil conditions (Cornelissen *et al.* 2003; Pausas & Paula 2005). At the same time as the soil was sampled (Silva & Batalha 2008), we measured or determined all traits according to the protocol proposed by Cornelissen *et al.* (2003). For each species, in each site, we randomly selected 10 individuals for functional traits measurements. When, for a given species, 10 individuals were not present in the sample, we made an additional effort in searching for individuals outside the transects, trying to find at least five but preferentially 10 individuals. This procedure allowed us to include all species in subsequent analyses. An attribute is the particular value taken by the trait at any place and time (Violle *et al.* 2007). In this case, functional information was site-specific, because we considered the individuals sampled in each site separately, allowing us to include intraspecific differences among sites (Cianciaruso *et al.* 2009). We measured stem specific density, leaf nitrogen content, and leaf phosphorus content for five individuals per species.

We calculated functional diversity separated into three components that account for different aspects of functionality, that is, functional dispersion (FDis), functional evenness (FEve), and functional divergence (FDiv): FDis measures how species are dispersed in a trait multispace; FEve measures how species abundances are distributed in the given trait multispace volume; and FDiv measures how species weighted by abundance are distant from the multispace centroid (Villéger *et al.* 2008; Laliberté & Legendre 2010). Additionally, we calculated the community weighted mean (CWM, Ricotta & Moretti 2011) of each trait as a measure of functional identity of communities to examine how each trait changes in each community. We used the “FD” package of the R environment to calculate the indexes of functional diversity (R Development Core Team 2010).

Data analysis - We did a principal component analysis with CWM of each trait (see traits in Tab. 1), using data of all sites to examine how traits changed according to fire frequency.

We used separate models in each fire frequency to examine changes in the relationships between soil and diversity. First, we generated multiple ordinary least squares regression models for each of three fire frequency categories with species richness, FDis, FEve, or FDiv as the response variables and soil features (N, Al³⁺, OM, clay: sand) as the explanatory variables, resulting in 12 model sets. We also generated multiple ordinary least squares regression models for each fire frequency with the two first axes of CWM ordination as the response variables and soil features (N, Al³⁺, OM, clay: sand) as the explanatory variables, resulting in six model sets. We used a parsimonious model selection and inference strategy based on the bias-corrected Akaike's Information Criterion (AICc), according to Akaike (1973) and Burnham & Anderson (2002). AICc is an extension of likelihood theory and provides a robust and objective means for model selection that accounts for both bias and precision. The best models are those with the lowest AICc values, but a common strategy is to use the AICc of each model to calculate the Δ AICc value, which is the difference between AICc of a given model and the minimum AICc found for all models being compared. Δ AICc values higher than 7 indicate models that have poor fit relative to the best model, whereas values lower than 2 indicate models that are as suitable as the best model (Burnham & Anderson 2002). We also used Δ AICc values to compute the Akaike weight of each model, which provides additional evidence that the model is actually the best explanatory one. We examined all 15 possible regression models in each set without considering interactions between explanatory variables and selected the best model on the basis of Δ AICc, R², and AICc weight (Burnham & Anderson 2002), using the "AICcmodavg" package of the R environment (R Development Core Team 2010).

Results

Overall, we found 51 species from 28 families. The mean species richness across all samples was 12, and ranged from 6 to 14 in the high fire frequency; from 6 to 19 in the middle fire frequency; and, from 8 to 18 in the low fire frequency. We presented only the best model of each model set for clarity (Tab. 2; for the five best models for each set, see Tab. A1 in the appendix). In each fire frequency, we found different soil variables predicting species richness or functional diversity components.

Species richness and FDis best models had the same predictor variables. Under the high fire frequency, the best model included N as the predictor variable, which was positively related with

species richness and FDis ($R^2 = 0.35$, $R^2 = 0.17$, respectively; Tab. 2). Under the intermediate fire frequency, the best model included exchangeable Al^{3+} and clay:sand ratio as predictors of species richness and FDis ($R^2 = 0.24$, $R^2 = 0.31$, respectively; Tab. 2). Under the low fire frequency, the best model included only clay:sand ratio, which was negatively related with species richness and FDis ($R^2 = 0.25$, $R^2 = 0.05$, respectively; Table 2).

Functional components that consider abundance had different patterns. In the high fire frequency, the best model included N as the predictor variable, which was positively related with FEve, but presented low explanatory power ($R^2 = 0.06$; Table 2). In the intermediate fire frequency, the best model included clay:sand ratio as predictor variable, which was negatively related with FEve, but also presented low explanatory power ($R^2 = 0.01$; Table 2). The best model in the low fire frequency included N, organic matter, and clay:sand ratio as predictor variable; N was positively and OM and clay:sand was negatively related with FEve ($R^2 = 0.34$; Table 2). In the high fire frequency, the best model included Al^{3+} , which was positively related with FDiv, but presented low explanatory power ($R^2 = 0.02$; Tab. 2); in the intermediate fire frequency, the best model included OM and Al^{3+} as predictor variables; OM positively and Al^{3+} negatively related with FDiv ($R^2 = 0.23$; Tab. 2). In the low fire frequency, the best model included N and clay:sand ratio as predictor variables; N positively and clay:sand ratio negatively related with FDiv ($R^2 = 0.19$; Tab. 2). For models with coefficients lower than 0.10, we considered that explanatory variables had no effects on the response variables.

The community weighted means of traits are associated with different fire frequencies and can be used to separate the sites in the ordination diagram. The first axis of ordination separated high fire frequency from others, and the second axis separated intermediate and low fire frequencies (Fig.1). Individuals occurring in sites under high fire frequency presented higher leaf nitrogen:phosphorus ratio, wood density, leaf dry matter content, and number of resprouts and also lower plant height, bark thickness, and basal area (Fig.1). Individuals occurring in sites under intermediate fire frequency presented lower specific leaf area and leaf size, but also higher basal area (Fig.1). Individuals occurring in sites under low fire frequency presented higher specific leaf area and leaf size, but also lower leaf dry matter content and number of resprouts (Fig.1).

Discussion

Under high fire frequencies, species richness and functional dispersion were associated with higher soil nitrogen values, in accordance to the “fertility effect” theory (Dybzinski *et al.* 2008):

plant species richness and functional dispersion may increase community productivity over time by increasing the nutrient supply via both greater inputs and greater retention. Such an effect was observed in experimental grasslands, where plant species richness and functional diversity were positively related to soil nitrogen (Dybzinski *et al.* 2008). However, we found an important difference due to annual burning in the last 12 years and, therefore, the community seemed to be in constant regeneration. For the studied woody species, this regeneration is mainly through resprouting. Their persistence niche regenerates population and community structures under disturbances (Bond & Midgley 2001). In that sense, we can explain the observed “fertility effect” in two ways. First, woody encroachment in savannas increases soil organic nitrogen and nitrogen mineralization rates, suggesting that nitrogen fixation increases to accommodate nitrogen demand (Bustamante *et al.* 2006). Second, high soil nitrogen content may promote resprouting vigor in many species (Di Tommaso & Aarsen 1989; Wilson & Tilman 1993), predicting that more resprouters will be found in soil patches with high nitrogen content. In addition, despite being adapted to nutrient shortage, cerrado woody species are able to exploit fertile sites by allocating resources to maximize carbon gain and enhance growth. In a field experiment, both total leaf surface area and basal area per tree increased substantially when nitrogen limitation was alleviated (Bucci *et al.* 2006).

The probability of finding nitrogen-fixing species increases with community species richness. The presence of nitrogen fixers changes the relationship between plants and soil resources (Hector & Loreau 2005). Fire favors Fabaceae plants, and their post-fire regeneration is an important source of nitrogen, because it increases nitrogen availability in the soil (Casals *et al.* 2005). In fact, in high fire frequency sites, there is a dominance of *Mimosa amnis-atricornis* Barneby (a Fabaceae shrub), which accounts for almost 50% of all sampled individuals (Silva & Batalha 2008). Moreover, fire removes pre-existing biomass, creating open areas in which competition decreases (Hoffman 2002), and may increase facilitation among plants (Franks & Peterson 2003). At low levels of soil nitrogen, only few adapted plant species with similar traits can establish (for example, several plant species with symbiotic bacteria in their root systems; Reynolds *et al.* 2003; Fornara & Tilman 2008). In this sense, patches with higher soil nitrogen content seem to reduce niche limitation effects, and presence of nitrogen-fixing species increases the likelihood of facilitation (Fornara & Tilman 2008), resulting in an increase not only in species richness, but also in the functional dispersion of woody species.

Soil clay and sand proportions are drivers of vegetation distribution, because sandy soils have lower water retention capacity and cation exchange capability (Larcher 1995). Exchangeable

aluminium decreases nutrient availability to plants by lowering phosphorus, magnesium, and calcium absorption (Malavolta *et al.* 1977; Marschner 1989) and induces a drastic reduction in anion uptake by plant roots (Calba & Jaillard 1997). However, there is evidence of high species richness in sites where plant growth is limited by several nutrients (Braakhekke 1980; Tilman 1982; Harpole & Tilman 2007). Indeed, aluminium is positively related to species richness in some cerrado areas, a pattern that was postulated to be due to low nutrient availability (Amorim & Batalha 2008). Also, high functional diversity and complementarity under high aluminium levels and low clay content are in agreement with the idea of increasing niche dimensionality in low nutrient conditions (Harpole & Tilman 2007), which is a potential mechanism to explain the coexistence of several species in nutrient-poor as opposed to nutrient-rich patches (von Felten & Schmid 2008). In this case, coexistence in multi-specific communities is possible only due to complementary use and capture of the resources that are in short supply.

Functional diversity components that include species abundances resulted in different patterns at each fire frequency. Therefore, it is important to consider species abundance, because each species may respond differently to variation in disturbance and productivity conditions, such as soil fertility (Pakeman *et al.* 2011). Functional evenness and functional divergence were both poorly predicted by soil variables under high and intermediate fire frequencies. Fire acts as a nonselective herbivore, reducing biomass and, consequently, competition (Bond & Keeley 2005). Thus, functional complementarity is diminished under higher fire frequencies. Conversely, species abundances are more strongly influenced by soils when fire is infrequent. Following abundance patterns, functional evenness and divergence were similarly influenced by soil when the frequency of fire was low. Therefore, our findings suggest that soil fertility plays an ambiguous role in diversity: (1) organic matter- and clay-rich soil may favor dominant species (reducing functional evenness) and functionally similar species (reducing functional divergence); (2) however, nitrogen-rich soil may increase the evenness of species abundances (increasing functional evenness) and favor the occurrence of species with divergent traits (increasing functional divergence). Species coexistence is maximized by functional complementarity: the more distinct the species traits, the higher the diversity (Petchey 2003). This increase in diversity can be best explained by an optimization of resource acquisition and partition of functions (Mason *et al.* 2008). Thus, some species can become more competitively aggressive with more nutrients adsorbed in high organic matter and clay soils, although the whole community is favoured only in nitrogen-rich soils. In temperate grasslands, the community can support more species when nitrogen-fixing species co-occur with species that can

use this additional source of the nutrient to improve their growth rates (Tilman *et al.* 2001). We suggest that this could also be true for woody communities in cerrado savannas.

The functional identity of communities, here defined by species abundances and trait composition, may change due to the environment (Pakeman *et al.* 2011). Considering all areas together, functional composition responded to fire, providing ways to differentiate sites according to fire frequency. This response could be due to two mechanisms: first, fire selects plants showing resistance traits (Ojeda *et al.* 2010); alternatively, fire limits the development of resistance traits when it is too frequent, which is known as the fire trap (Hoffman *et al.* 2009). Under high fire frequency, resprouts may be the response to burning of aboveground biomass and are associated to low plant height, thin barks, and stems of new individuals. In such case, it may hinder the development of individuals to adult stages, and plants are unable to accumulate bark tissues or achieve enough height to avoid canopy burning (Medeiros & Miranda 2008; Hoffman *et al.* 2009, but see Batalha *et al.* 2011). Conversely, under lower fire frequencies, there is enough time for plants to accumulate bark to resist fire damages and, consequently, grow taller. Furthermore, leaf traits were different among sites, changing from low to intermediate fire frequency. These leaf traits are associated to competitive ability, resource exploiting, and photosynthetic rate (Cornelissen *et al.* 2003), suggesting strong resource competition under low fire frequency. The biomass of dominant species accumulates when the level of fire is low; consequently, biomass disparities enhance competition (Cianciaruso *et al.* 2010). Thus, fire acts on traits both directly, hindering the development of plants, and indirectly, changing the intensity of competitive interactions among plants.

Fire also alters plant-soil relationships in the cerrado (Silva & Batalha 2008), and soil fertility may limit trait composition. On average, soil fertility is lower under intermediate and low fire frequencies, holding about 20% less soil nitrogen, 31% less organic matter, and high aluminium and sand content values (Silva & Batalha 2008). Under short supply of nutrients, competition may become more limiting: plant species tend to become functionally distinct (von Felten & Schmid 2008). Accordingly, we found a divergent pattern under low fire frequency: species richness and functional diversity were negatively associated with clay to sand proportion; thus, for higher amounts of clay we found fewer species and lower functional dispersion. Under intermediate fire frequency, aluminium was also important, being positively associated with richness and functional dispersion. Besides, soil had effects on those functional components that incorporate abundance, but only when fire frequency was low. Changes in relative abundance of functionally similar species are

influenced by disturbance and productivity (Pakeman *et al.* 2011), although fire frequency seems to be more important than soils, at least under high fire frequencies.

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Figure 1. Principal component analysis of sites under different fire frequency according to community weighted mean of traits of woody species at a savanna in the Emas National Park, Brazil (17°49'-18°28'S and 52°39'-53°10'W). LDMC = leaf dry matter content, SLA = specific leaf area, Lsz = leaf size, BA = basal area, height = plant height, density = stem specific density, NP = nitrogen:phosphorus ratio, resp = number of resprouting at soil level, bark = bark thickness. Circles = high fire frequency, squares = intermediate fire frequency, diamonds = low fire frequency.

Figure 1.

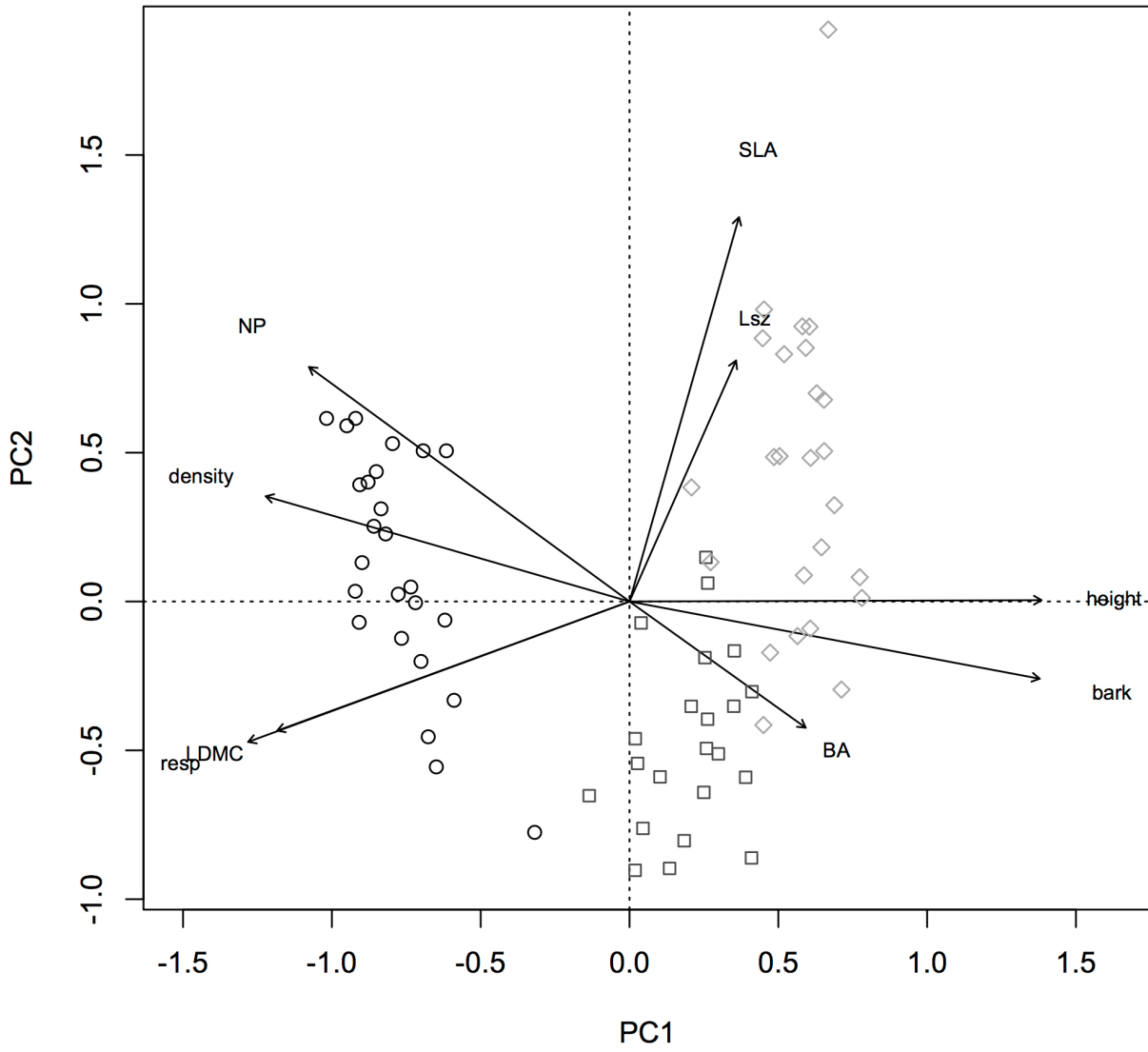


Table 1. Functional traits used to measure functional diversity in savanna woody species at Emas National Park, Brazil (17°49'-18°28'S and 52°39'-53°10'W).

Trait	Unit	Functional significance
1. Plant height	m	associated with competitive vigor, whole plant fecundity, tolerance or avoidance of disturbances
2. Basal area	m ²	competitive vigor, survival ability after fire
3. Bark thickness	mm	protection of vital tissues against damage, thick barks can decrease mortality by fire or accelerate post-fire recovery
4. Specific leaf area	mm ² mg ⁻¹	highly correlated with several physiological traits related to resource uptake and use efficiency and plant growth strategies
5. Leaf size	mm ²	ecological strategy, with respect to environmental nutrient stress and disturbances
6. Leaf dry matter content	mg g ⁻¹	related to flammability, resistance to physical hazard, disturbed environments
7. Stem specific density	mg mm ⁻³	structural strength, resistance against physical damage
8. Leaf N:P ratio		maximum photosynthetic rate, LNC: LPC ratio related to carbon cycling processes
9. Resprouting at soil level	number	competitive vigor, persistence after environmental disturbance

Table 2. Selected models of the relationships between different aspects of plant assemblage diversity with soil texture and nutrients in a savanna at Emas National Park, Brazil (17°49'-18°28'S and 52°39'-53°10'W). The best models for each selection are presented (for the five best models for each selection, see Table A1 in the appendix). R^2 = coefficient of determination, AICc = Akaike Information Criterion bias-corrected, Δ AICc = difference between each model AICc and the minimum AICc found, and AICc w_i = Akaike's weighting of each model. S-rich = Species richness, FDis = functional dispersion, FEve = functional evenness, FDiv = functional divergence.

Fire Frequency	Response variable	Explanatory Model	R^2	AICc	Δ AICc	AICc w_i
High	S-rich	N	0.353	103.841	0	0.430
Intermediate	S-rich	Al + clay:sand	0.246	126.288	0.452	0.233
Low	S-rich	clay:sand	0.253	118.733	0	0.495
High	FDis	N	0.174	23.164	0	0.314
Intermediate	FDis	Al + clay:sand	0.311	8.097	0	0.395
Low	FDis	clay:sand	0.05	3.391	0	0.196
High	FEve	N	0.058	-24.218	0	0.215
Intermediate	FEve	clay:sand	0.013	-46.806	0	0.173
Low	FEve	N + OM + clay:sand	0.342	-61.657	0.394	0.172
High	FDiv	Al	0.019	-41.272	0	0.187
Intermediate	FDiv	OM + Al	0.228	-66.540	1.02	0.198
Low	FDiv	N + clay:sand	0.194	-61.603	0.207	0.187

Table A1. Model selection results to the different fire frequency, predicting diversity indices with soil texture and nutrients. The five best models are presented for each selection. The selected model are in bold, R^2 = coefficient of determination, R^2_{adj} = adjusted coefficient of determination, AICc = Akaike Information Criterion bias-corrected, $\Delta AICc$ = difference between each model AICc and the minimum AICc found, and AICc wi = Akaike's weighting of each model. S rich = Species richness, FDis = functional dispersion, FEve = functional evenness, FDiv = functional divergence.

Fire frequency	Model	Variables	R^2	R^2_{adj}	AICc	$\Delta AICc$	AICc wi
High	S rich	N	0.353	0.325	103.841	0	0.430
High	S rich	N + clay: sand	0.384	0.328	105.478	1.637	0.190
High	S rich	N + OM	0.364	0.306	106.284	2.443	0.127
High	S rich	N + Al	0.353	0.294	106.697	2.856	0.103
High	S rich	N + OM + clay: sand	0.388	0.300	108.470	4.629	0.043
Intermediate	S rich	clay: sand	0.170	0.134	125.836	0	0.292
Intermediate	S rich	Al + clay: sand	0.246	0.178	126.288	0.452	0.233
Intermediate	S rich	N + clay: sand	0.183	0.109	128.282	2.446	0.086
Intermediate	S rich	OM + clay: sand	0.173	0.098	128.590	2.754	0.074
Intermediate	S rich	OM	0.066	0.025	128.798	2.962	0.066
Low	S rich	clay: sand	0.253	0.221	118.733	0	0.495
Low	S rich	OM + clay: sand	0.256	0.189	121.487	2.754	0.125
Low	S rich	Al + clay: sand	0.255	0.188	121.520	2.787	0.123
Low	S rich	N + clay: sand	0.253	0.186	121.588	2.855	0.119
Low	S rich	OM + Al + clay: sand	0.258	0.152	124.583	5.850	0.027
High	FDis	N	0.174	0.139	23.164	0	0.314
High	FDis	N + OM	0.215	0.144	24.757	1.593	0.142
High	FDis	N + Al	0.192	0.119	25.478	2.314	0.099
High	FDis	OM	0.087	0.047	25.694	2.529	0.089
High	FDis	N + clay: sand	0.18	0.105	25.853	2.689	0.082
Intermediate	FDis	Al + clay: sand	0.311	0.249	8.097	0	0.395
Intermediate	FDis	clay: sand	0.16	0.123	10.209	2.112	0.138
Intermediate	FDis	N + Al + clay: sand	0.326	0.23	10.695	2.598	0.108
Intermediate	FDis	OM + Al + clay: sand	0.316	0.218	11.084	2.987	0.089
Intermediate	FDis	N	0.084	0.044	12.37	4.273	0.047
Low	FDis	clay: sand	0.05	0.009	3.391	0	0.196

Low	FDis	Al	0.04	-0.002	3.658	0.267	0.172
Low	FDis	OM	0.009	-0.034	4.441	1.051	0.116
Low	FDis	Al + clay: sand	0.11	0.029	4.616	1.225	0.106
Low	FDis	N	0.001	-0.042	4.644	1.254	0.105
High	FEve	N	0.058	0.017	-24.218	0	0.215
High	FEve	clay: sand	0.041	-0.001	-23.762	0.456	0.171
High	FEve	Al	0.032	-0.01	-23.532	0.686	0.152
High	FEve	OM	0.003	-0.041	-22.787	1.431	0.105
High	FEve	N + Al	0.072	-0.012	-21.728	2.49	0.062
Intermediate	FEve	clay: sand	0.013	-0.03	-46.806	0	0.173
Intermediate	FEve	OM	0.011	-0.032	-46.758	0.048	0.169
Intermediate	FEve	N	0.002	-0.042	-46.537	0.269	0.151
Intermediate	FEve	Al	0.001	-0.043	-46.513	0.293	0.149
Intermediate	FEve	N + OM	0.049	-0.038	-44.877	1.928	0.066
Low	FEve	clay: sand	0.176	0.14	-62.052	0	0.21
Low	FEve	N + OM + clay: sand	0.342	0.248	-61.657	0.394	0.172
Low	FEve	N + clay: sand	0.232	0.162	-60.947	1.105	0.121
Low	FEve	N + OM + Al + clay:	0.41	0.292	-60.866	1.186	0.116
Low	FEve	sand					
Low	FEve	Al + clay: sand	0.212	0.14	-60.311	1.741	0.088
High	FDiv	Al	0.019	-0.024	-41.272	0	0.187
High	FDiv	OM	0.009	-0.034	-41.025	0.247	0.166
High	FDiv	N	0.005	-0.038	-40.918	0.354	0.157
High	FDiv	clay: sand	0.005	-0.038	-40.918	0.355	0.157
High	FDiv	OM + Al	0.035	-0.052	-38.838	2.434	0.055
Intermediate	FDiv	Al	0.169	0.133	-67.56	0	0.33
Intermediate	FDiv	OM + Al	0.228	0.158	-66.54	1.02	0.198
Intermediate	FDiv	N + Al	0.187	0.113	-65.222	2.338	0.103
Intermediate	FDiv	Al + clay: sand	0.182	0.107	-65.07	2.489	0.095
Intermediate	FDiv	clay: sand	0.031	-0.011	-63.717	3.842	0.048
Low	FDiv	N	0.104	0.065	-61.81	0	0.207
Low	FDiv	N + clay: sand	0.194	0.121	-61.603	0.207	0.187
Low	FDiv	clay: sand	0.056	0.015	-60.51	1.3	0.108
Low	FDiv	N + Al + clay: sand	0.24	0.132	-59.926	1.884	0.081
Low	FDiv	N + Al	0.125	0.045	-59.548	2.263	0.067

6. Capítulo 2

Functional diversity components and functioning in cerrado communities with different environmental conditions

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Functional diversity components and functioning in cerrado communities with different environmental conditions

Running title: Diversity components and functioning

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Abstract

Functional diversity incorporates variation in species traits and allows one to evaluate the effects of biodiversity upon community functioning. Functional diversity can be divided into components to elucidate response and effect links with environment. Sampling woody plants in a Brazilian cerrado reserve, we used functional components (functional richness, functional evenness, and functional divergence), environmental variables (topography, soil conditions, and fire regimes) and a measure of functioning (litter decomposition rate) to answer questions about effects of biodiversity upon ecological functioning through a trait-based approach. Overall, we found low values of functional richness and high values of functional evenness and functional convergence. Functional components were related to environmental variables, indicating that functional diversity had response links with the environment: harsher environmental conditions lead to less phenotypic overlap and, consequently, less competition. Functional components did not predict litter decomposition rate. However, when environmental variables were also used, we found higher decomposition rate related to higher slope, richer soil, frequent fire, and higher functional richness. Therefore the effect links of functional diversity upon functioning were dependent on the cerrado environment.

Introduction

The functional diversity approach is a growing area of interest in community ecology that allows one to infer about the functionality of the biodiversity. The functional diversity can be partitioned into components that are complementary measures of differences among species traits and abundances (Villéger et al. 2008): (1) functional richness measures the volume of trait multispace and represents the functional space filled by the community (Villéger et al. 2008); (2) functional evenness comprises the evenness of abundance distribution into the trait multispace and the functional differences among species (Mason et al. 2005, Villéger et al. 2008); and (3) functional divergence represents the degree of trait differentiation and consequent resource competition (Mason et al. 2005, Villéger et al. 2008). When considered separately, none of these indices fits all criteria for a good index (Ricotta et al. 2005, Mason et al. 2003), but, when considered together, they fit all of them (Villéger et al. 2008). Partitioning functional diversity results in a more detailed comprehension of the mechanisms linking biodiversity to community functioning (Villéger et al. 2008).

Changes in functional space filled by species imply pressure by environmental filters, whereas changes in distribution of species abundances in that space imply alteration of competitive interactions (Villéger et al. 2008). As each component of functional diversity measures an aspect of trait space, searching for relations into the set of indices allows one to infer whether there is specialisation or change in trait volume (Villéger et al. 2008). Lower functional richness indicates less use of available resources, less resistance to invasion, and less buffering against environmental fluctuations (Mason et al. 2005). Lower functional evenness represents a misbalance on occupancy of trait multispace, that is, portions of occupied functional volume are underused (Mason et al. 2005). Higher functional divergence implies trait differentiation and lower competition (Mason et al. 2005). Thus, negative relationship between functional richness and functional evenness indicates

specialisation at lower functional richness, whereas positive relationship between functional richness and functional divergence indicates coexistence of complementary species with low competition. However, it is also necessary to evaluate environmental conditions, because these interactions depend on resource availability (Mason et al. 2008).

Functional traits can allow species both to respond to environmental conditions, such as resprouting capacity and tolerance to drought, or to influence the environment, such as nitrogen fixation and leaf nutrient concentration (Cornelissen et al. 2003). Accordingly, the functional diversity can have both response and effect links (Villéger et al. 2008). Response links are changes in functional diversity driven by environmental factors (Villéger et al. 2008). In the Brazilian savanna known as “cerrado”, there are many environmental factors that act over the communities, such as fire, soil, and water availability (Gottsberger and Silberbauer-Gottsberger 2006). For example, different fire regimes and soil conditions support different species (Silva and Batalha 2008) and plant available water affects species richness and evenness in cerrado (Ferreira et al. 2009).

Effect links are changes in environment driven by functional diversity: differences in species traits result in different functions and, consequently, in alteration of functioning (Villéger et al. 2008). For example, plant community affects decomposition either directly, by changing litter quality, or indirectly, by creating favourable conditions to faunal decomposers (Madritch and Cardinale 2007, Vivanco and Austin 2008). Decomposition rate could be used as a surrogate for community functioning, since it represents a dynamic part of functioning, is linked to several trophic levels, and affects nutritional conditions of soils (Hättenschwiler et al. 2005). Environmental conditions could also affect the functioning. For example, water availability, soil composition, and fire regime are abiotic factors that could explain the variation in decomposition rate (Neary et al. 1999, Vivanco and Austin 2008). Thus, we expected that environmental variables could predict

functional diversity and that both functional diversity and environmental variables could predict litter decomposition.

Relationship between biodiversity and functioning are certainly affected by environmental differences and disturbance regimes. Thus communities that present environmental constraints and presence of disturbance are ideal to test these effects. Cerrado includes the major savanna area in south-america and presents several environmental filters (Gottsberger and Silberbauer-Gottsberger 2006). Soil are poor and acid, climate is seasonal with a dry season and fire are the main disturbance that occur naturally in cerrado. Many aspects of cerrado plants allow species coexistence due to complementarity (Silva et al. 2010). Some environmental filters of cerrado are known to limit species traits range and competition (Cianciaruso et al. 2010). Cerrado is an adequate environment to test the role of biodiversity on community functioning.

Here, we used an approach that partitions functional diversity into three components – functional richness, functional evenness, and functional divergence (Villéger et al. 2008) –, relating them to environmental variables (topography, soil conditions, and fire regime) and to a measure of functioning (litter decomposition rate) to answer questions about the effects of biodiversity upon community functioning. We addressed the following questions: (1) Are the functional components correlated with each other, indicating trait differentiation? If the species coexistence related to resource use is dependent of trait multispace (Mason et al. 2008) and if the relationships among the functional diversity components are not mathematical artifacts (Villéger et al. 2008), then if we find such relationships among them we can infer about trait differentiation and functional amplitude; (2) Which environmental variables (topography, soil characteristics, or fire regime) are predictors of the functional diversity components? If traits can both be responsive to or have effects on the environment (Cornelissen et al. 2003) and if there are many environmental factors acting together in cerrado (Gottsberger and Silberbauer-Gottsberger 2006), then we expect the functional diversity to present response links with the environment; (3) Are the functional components related to

decomposition rate? If higher functional diversity represents better resource use and more complementary functions (Villéger et al. 2008) and if plants may affect the decomposition process (Madritch and Cardinale 2007, Vivanco and Austin 2008), then we expect the functional diversity to present effect links with the functioning; and (4) Are environmental variables related to decomposition rate? If there are abiotic factors that could explain the variation in decomposition rate (Neary et al. 1999, Vivanco and Austin 2008) and if environmental factors alter community composition and species interactions (Fraterrigo and Rusak 2008), then we expect environmental factors to predict community functioning.

Materials and methods

Study area

We carried out this study in Emas National Park (ENP), located in the Brazilian Central Plateau (17°49'-18°28'S and 52°39'-53°10'W), during the raining season of 2009. Regional climate is tropical and humid (Aw, Köppen 1931), with dry winter from May to September and rainy summer from October to April. Annual rainfall vary from 1,200 to 2,000 mm, and mean annual temperature is around 24.6°C (Ramos-Neto and Pivello 2000). Soils in ENP are mainly acid, poor with high content of aluminum, being classified as Oxisols (França et al. 2007). Across its total extension (131,800 ha), there are predominantly open cerrado physiognomies covering 68.1% of the reserve (104,359 ha), followed by closed cerrado physiognomies that cover 25.1% of the reserve (18,408 ha, Ramos-Neto and Pivello 2000).

Before 1994, a policy of total suppression of fires in ENP resulted in great accumulation of dry mass and, consequently, in catastrophic fires approximately each three years (Ramos-Neto and Pivello 2000, França et al. 2007). After 1994, fire management has changed: natural fires were no

longer suppressed and a system of firebreaks was created (Ramos-Neto and Pivello 2000, França et al. 2007). Currently, there is a mosaic of areas with different history of fires, ranging from annually burned areas to areas burned only once in the last 14 years (França et al. 2007).

Sampling

We divided the study site into 10 strata according to time since last burning, using satellite images from 1973 to 2009. Then, we randomly placed 10 plots of 5 m x 5 m in each stratum. In each plot, we sampled all woody plants – individuals with stem diameter at soil level equal to or greater than 3 cm (Secretaria de Estado do Meio Ambiente 1997) –, identified them to species level, classified them into families according to APG III (Angiosperm Phylogeny Group 2009), and measured 14 functional traits (*sensu* Díaz and Cabido 2001): topkilling, basal area, height, tortuosity, bark thickness, stem specific density, leaf toughness, leaf size, leaf specific area, leaf nitrogen concentration, leaf phosphorus concentration, leaf potassium concentration, pollination system, and dispersal syndrome (Cornelissen et al. 2003, Agrawal and Fishbein 2006). These trait can be considered functional traits because they affect or are responsive to the environment (Díaz and Cabido 2001, Appendix 1)

We considered an individual as topkilled when terminal bud was dead and the individual was resprouting from lateral buds. We calculated basal area by measuring stem perimeter at soil level. Using a telescopic ruler, we measured height, the shortest distance between the upper boundary of the main photosynthetic tissues and soil level. We considered tortuosity as one minus the stem length until first bifurcation divided by height of first bifurcation. We removed a portion of the stem at 30 cm high with a knife and measured bark thickness with a digital caliper. We cut 10 cm long sections of the stems and removed the bark. Then, we calculated stem specific density as oven-dried weight divided by volume. We measured leaf toughness with a dynamometer (dynamometer DFE

010, Chatillon) with a cone tip. We recorded the force required to penetrate the leaf, considering the mean of a measure at each side of the mid rib. We scanned the leaf surface and calculated the area using the ImageJ software (Rasband 2004) to find leaf size. We divided the leaf size by oven-dried leaf mass to calculate specific leaf area. We used leaves without rachis or petiole to measure nitrogen, phosphorus, and potassium concentration. We classified each species into pollination systems and dispersal syndromes according to literature (Gottsberger and Silberbauer-Gottsberger 2006).

In each plot, we also measured environmental variables related to topography, soil, and fire regime. We measured altitude with an altimeter and slope with a clinometer. We used these topographic measures as a surrogate for water availability: in Emas National Park, the higher the altitude and the lower the slope, the lower the water availability. We collected composite soil samples at 0-5 cm. We analysed soil samples for pH, organic matter, total nitrogen, available phosphorus, exchangeable potassium, exchangeable calcium, exchangeable magnesium, exchangeable aluminum, sand proportion, silt proportion, and clay proportion (Silva and Batalha 2008). We also calculated the sum of bases, cation exchange capacity, base saturation, aluminum saturation. We determined occurrence of fire from 1984 to 2009, using satellite images. We calculated fire interval as the average period between two consecutive fires and assigned the time since last fire. Interval of fire represents an ecological time with which plant species must cope, particularly for reproductive strategies (Vilà-Cabrera et al. 2008). Time since last fire represents the successional stage of plant community in ecotones, because some species can reestablish quickly after fire by germinating or resprouting and others need to be dispersed from nearby sites (Müller et al. 2007, Fidelis et al. 2010).

Functional diversity components

We created a matrix of functional traits by species with average values for quantitative traits (topkilling, basal area, height, tortuosity, bark thickness, stem specific density, leaf toughness, leaf size, leaf specific area, leaf nitrogen concentration, leaf phosphorus concentration, and leaf potassium concentration) and categories for nominal traits (pollination system and dispersal syndrome) as entries. We also counted the number of individuals of each species in each plot as a measure of species abundance. Then, using the “FD” package (Laliberté and Legendre 2010, Laliberté and Shipley 2010) for R, we calculated three components of functional diversity according to Villéger et al. (2008): functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv). FRic measures the hull volume of the trait multispace, FEve measures the evenness of the distribution of abundances in the trait multispace, and FDiv measures how abundance is distributed within this volume (see Villéger et al. 2008 for details on how these indices are calculated and their mathematical properties). These indices can be calculated only for plots with three species at least (Villéger et al. 2008).

Functioning

Decomposition rate can be used as a good measure of functioning, because the decomposition process is related to energy flux and nutrient cycles (Srivastava and Vellend 2005) and is one of the key functions to the maintenance of a community (Sulkava and Huhta 1998). To estimate litter decomposition rate, we collected leaves recently shed by trees and oven-dried them at 80°C for 24 h. We then homogenised the leaves to avoid differences in litter quality and distributed 5 g of the material into 20 cm x 20 cm litterbags of 1 mm² nylon mesh. We placed a group of 3 litterbags at each corner of each plot. After one, three, and six months, we collected one litterbag per group, oven-dried (80°C for 24 h) it, and weighted the remaining litter. We calculated average proportion of remaining mass for each plot. Then, we used an exponential regression to fit the mass proportion

to the time of decomposition and the exponential coefficient as a measure of decomposition rate (Wieder and Lang 1982, Valenti et al. 2008).

Statistical analyses

We used Spearman correlation to test whether the functional components were related with each other. We used multiple regressions to test which environmental variables predicted each component of functional diversity. We used only the environmental variables that were not highly correlated with others ($R < 0.7$): altitude, slope, pH, organic matter, nitrogen, phosphorus, potassium, aluminum, sum of bases, cation exchange capacity, base saturation, silt, clay, fire interval, and time since last fire. We tested all assumptions of linear regression and fit the linearity (Zar 1999). We selected the best models, using backward elimination and Akaike Information Criterion (Akaike 1973, Burnham and Anderson 2002). To test whether each component of functional diversity predicted litter decomposition rate, we used simple linear models. To test whether environmental variables and functional diversity could predict decomposition rate, we used a multiple regression with environmental variables and functional diversity components as explanatory variables. We carried out all analyses in R (R Development Core Team 2009).

Results

Of the 100 plots, 55 presented three or more species. For these 55 plots, we could calculate the three components of functional diversity (Table 1). These plots still represented the whole study area because they were distributed along all strata. Plots presented low density of woody individuals, with some plots presenting only two individuals and the denser plot presenting 19 individuals (Table 1). Although we found 55 species across the communities, the highest species

richness in a single plot was 10 species (Table 1). Decomposition rate was low (mean = 0.02 g month⁻¹, sd = 0.01) and varied moderately across plots (Table 1). We found low values of functional richness, but intermediate to high values of functional evenness and divergence (Table 1). Functional richness was positively related to functional divergence ($\rho = 0.47$, $P < 0.001$) and not related with functional evenness ($\rho = -0.06$, $P=0.67$). Functional evenness and functional divergence were not related ($\rho = -0.24$, $P = 0.08$).

Environmental variables predicted functional richness and functional divergence, but not functional evenness (Table 2). Higher functional richness was related to soils with higher aluminum concentration and lower clay content ($R^2_{\text{adj}} = 0.32$, $P < 0.001$). The best model to predict functional evenness included altitude, pH, organic matter, aluminum concentration, and time since last fire, but it was not significant ($R^2_{\text{adj}} = 0.02$, $P = 0.31$). Higher functional divergence was related to soils with lower nitrogen and potassium concentration, higher cation exchange capacity, higher slope, and shorter fire interval ($R^2_{\text{adj}} = 0.15$, $P = 0.02$).

The functional components did not predict community functioning when considered separately ($R^2_{\text{adj}} < 0.02$, $P > 0.14$ for all tests), but they predicted it when environmental variables were also used as explanatory variables. In this case, decomposition rate was positively related to slope, phosphorus, cation exchange capacity, base saturation, clay, and functional richness and negatively related to potassium, aluminum, and fire interval ($R^2_{\text{adj}} = 0.17$, $P = 0.04$).

Discussion

Functionally richer communities were also functionally more divergent. In this case, species at the edge of the trait multispace might be performing exclusive or rare functions. Thus, we may infer that partitioning allowed species coexistence. The negative interference of neighbouring trees in cerrado is considered low when compared to other savannas, probably due to the high richness of

cerrado that provides a more complementary use of resources (Gonçalves and Batalha 2011). Communities with large expansion and divergence of species can support more individuals and species, because it decreases interspecific interference (Mason et al. 2008). Abundant species might be complementary to each other, occupying different portions of space and performing distinct functions.

The abundance of species are primarily determined by their traits, which respond to variation in abundance of different resources (Cornwell and Ackerly 2010). Since abiotic conditions allow species with specific traits to become common at a given site (Cornwell and Ackerly 2010), environmental conditions changes the interaction of species and the amount of resource available. Functional diversity presented response links with the environment in cerrado, where slope, soil fertility, and fire regime predict diversity. Fertility of soil represents resource to be used: more fertile soils implies larger amplitude of available niche (Dybzinski et al. 2008). Conversely, fire frequency represents a disturbance that decreases plant biomass, acts as a environmental filter (Cianciaruso et al. 2010), and interacts with soil changing the conditions to species recruitment (Silva and Batalha 2008).

Each component of biodiversity responded differently to environmental conditions. Functional richness increased in sites with unfavourable soil conditions. Harsh environments favour positive relations among species (Tielbörger and Kadmon 2000), because complementary species can make better use of resource and resist negative environmental effects (Petchey 2003). In plots with harsher conditions, species with complementary traits facilitated the co-existence of others. Functional divergence was higher in plots with higher slope, poorer soils, and more frequent fires. At Emas National Park higher slope are related to more available water. In the cerrado, more water availability is related to more individuals (Ferreira et al. 2007), which may compete less for water but more for other resources, such as soil nutrients. Besides, frequent fires decrease the importance of competition among species in cerrado plant communities (Silva et al. 2010). Fire may remove

potential competitors and functionally divergent species may become more abundant. Thus, harsher environmental conditions lead to less overlap of traits and consequently less competition (Fig. 1).

Initially, we expected that the components of functional diversity would predict the community functioning. Species traits should correspond to functions and, consequently, be good predictors of functioning (Petchey and Gaston 2002, 2006). In other communities, functional diversity and other aspects of biodiversity influence the decomposition process (Scherer-Lorenzen 2008, Gessner et al. 2010). However, the functional components did not predict litter decomposition rate in cerrado. Functional plant traits affect decomposition rate (Cornelissen and Thompson 1997, Cornwell et al. 2008), and one of the main factors of this relation is litter quality (Coûteaux et al. 1995, Gessner et al. 2010). Nevertheless, diversity of litter quality has multiple confounding effects on the decomposition rate, with positive, negative, or neutral outcomes, and depends on the identity of species that are present in the mixture of leaves (Gessner et al. 2010). We homogenised the litter in bags across the plots to avoid these confounding effects, but other plant functions could affect decomposition independently of litter quality, such as the intensity of light reaching the ground or an indirect influence on the soil biota (Paul and Gwynn-Jones 2003, Negrete-Yankelevich et al. 2008).

We only found effects links when we also considered the environmental variables. In cerrado, higher decomposition rate was related to lower slope, richer soils, more frequent fire, and higher functional richness. Soil features and fire regimes are abiotic factors that affect the decomposition rate (Neary et al. 1999, Vivanco and Austin 2008). Soil composition affects soil biota and so could influence decomposition (Gessner et al. 2010). Fire regime affects soil cover and temperature and, consequently, is related to decomposition (Neary et al. 1999). In communities with higher functional richness, complementary traits might interact with the environment, creating favourable conditions to faunal decomposers. For example, plant and soil interaction creates microsites and alters microbial and invertebrate communities affecting decomposition (Hobbie et al. 2006, Vivanco

and Austin 2008). Since functional richness only predicted the functioning when environmental variables were also used, the effect links of functional diversity upon functioning were dependent on the cerrado environment. We argue that functional approach testing response and effects links should also consider interactions between traits and environment in predicting the functioning.

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Table 1. Mean, standard deviation, range, coefficient of variation, and number of samples (n) of density of individuals, species richness, decomposition rate, three functional components and 19 environmental variables in cerrado plant communities at Emas National Park, Brazil.

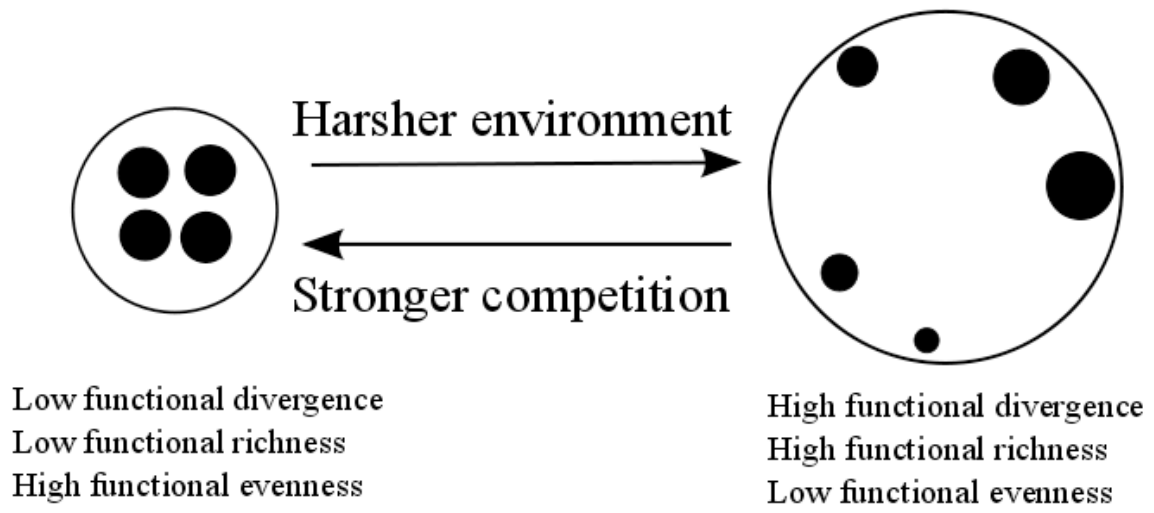
	Mean (sd)	Range (CV)	n
Density of individuals	5.31 (3.70)	2.00 - 19.00 (69.63)	100
Species richness	3.27 (1.85)	2.00 - 10.00 (56.65)	100
Decomposition rate (g month ⁻¹)	0.02 (0.01)	0.01 - 0.05 (33.83)	100
<i>Functional component</i>			
Functional richness	0.17 (0.17)	< 0.01 - 0.61 (100.01)	55
Functional evenness	0.81 (0.14)	0.39 - 0.99 (17.07)	55
Functional divergence	0.80 (0.10)	0.49 - 0.98 (12.36)	55
<i>Environmental variable</i>			
Altitude (m)	797.60 (40.08)	709.00 - 884.00 (5.03)	100
Slope (degrees)	2.07 (1.36)	0.30 - 8.70 (65.90)	100
pH	3.83 (0.18)	3.40 - 4.40 (4.59)	100
Organic matter (g kg ⁻¹)	56.61 (16.61)	11.00 - 100.00 (29.34)	100
Nitrogen (mg kg ⁻¹)	2013.05 (329.64)	1019.00 - 2746.00 (16.37)	100
Phosphorus (mg kg ⁻¹)	6.55 (1.74)	1.00 - 13.00 (26.34)	100
Potassium (mmol kg ⁻¹)	1.13 (0.36)	0.20 - 3.10 (31.56)	100
Calcium (mmol kg ⁻¹)	1.51 (1.03)	1.00 - 10.00 (68.20)	100
Magnesium (mmol kg ⁻¹)	1.36 (0.92)	1.00 - 9.00 (67.34)	100
Aluminum (mmol kg ⁻¹)	18.43 (4.56)	5.00 - 38.00 (24.74)	100
Sum of bases (mmol kg ⁻¹)	4.00 (2.14)	2.20 - 22.10 (53.50)	100
Cation exchange capacity (mmol kg ⁻¹)	108.58 (34.53)	33.00 - 387.80 (31.80)	100
Base saturation (%)	3.92 (2.28)	1.00 - 23.00 (58.20)	100
Aluminum saturation (%)	81.99 (8.11)	18.00 - 92.00 (9.90)	100
Sand (%)	29.30 (17.88)	9.00 - 85.00 (61.02)	100
Silt (%)	4.40 (3.46)	1.00 - 13.00 (78.73)	100
Clay (%)	66.30 (16.96)	13.00 - 88.00 (25.58)	100
Fire interval (year)	2.99 (1.10)	1.18 - 8.00 (36.79)	100
Time since last fire (year)	5.14 (4.07)	0.00 - 15.00 (79.19)	100

Table 2. Selected linear models of environmental variables predicting functional diversity components in cerrado plant communities at Emas National Park, Brazil. FRic: Functional richness; FEve: Functional evenness; FDiv: Functional divergence; Al: Aluminum; alt: Altitude; OM: Soil organic matter; lastfire: Time since last fire; slo: Slope; N: Soil nitrogen; K: Soil potassium; CEC: Cation exchange capacity; interval: Mean fire interval. *p < 0.05; **p < 0.01; ***p < 0.001

response variable	linear model	AIC	R²_{adj}
FRic	0.28 + 0.013(Al**) - 0.006(clay***)	-211.3	0.32***
FEve	0.75 - 0.001(alt) + 0.23(pH) - 0.003(OM) + 0.01(Al) - 0.07(lastfire)	-213.3	0.02
FDiv	0.92 + 0.02(slo) - 0.0001(N) - 0.122(K*) + 0.002(CEC*) - 0.028(interval*)	-258.3	0.15*

Figure 1. Schematic relationships among functional components, environmental conditions, and species interactions in cerrado plant communities at Emas National Park, Brazil. Open circles represent community trait space and solid circles represent species whose abundances are proportional to diameter.

Figure 1



7. Capítulo 3

Intraspecific variability and trait-based community assembly in a cerrado meta-community: does fire gradient affect trait space?

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(Artigo submetido a revista Plant Ecology)

**Intraspecific variability and trait-based community assembly in a cerrado meta-community:
does fire gradient affect trait space?**

Running title: fire effects on trait space

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Abstract

Fire is an environmental filter that selects species based on their traits. We expected that both intra- and interspecific variation contribute to explain the role of environmental filters structuring communities. We used an intra- and interspecific trait-based approach to test whether fire affects community traits in cerrado. At Emas National Park, central Brazil, we measured 10 functional traits of cerrado woody species in communities under seven different fire regimes. We tested for shifts in each trait mean, reduction of trait range, and increase in niche differentiation. Contrary to our expectation, the inclusion of intraspecific variability did not increase the perception of environmental filters and competition for most of the traits. We found evidence for environmental filtering to almost all traits analysed. Mean values shifted for five traits. Ranges were reduced for seven traits compared to null expectation. Also five traits presented niche differentiation indicating competition after the filter selection. Due to low contribution of intraspecific variability, we can consider species mean trait values as good predictors of community functional traits. Fire gradient changed the space traits by selecting similar species with more adequate traits, and posterior competition lead to divergence of traits in cerrado.

Keywords

Disturbance, environmental filter, interspecific variability, niche differentiation, savanna

Introduction

The occurrence of species relies on their ability to survive the disturbances and the negative biotical interactions in the area (Kraft et al. 2008; Venn et al. 2011). Due to the intraspecific variation of traits, some individuals can handle elevated degree of a given disturbance, whereas other individuals of the same species cannot survive even to low levels of the same disturbance (Whitlock et al. 2007). Fire is an environmental filter that selects species based on their traits and may change species composition, replacing, for example forest species by savanna species (Silva et al. 2010; Staver et al. 2011). Therefore, fire changes intra- and interspecific trait values (Cianciaruso et al. 2009; Dantas et al. 2013). Moreover, different fire frequencies are also associated to intraspecific differences in plant traits, since fire selects individuals rather than the whole species (Cianciaruso et al. 2009; Dantas et al. 2013). In meta-community, both intra- and interspecific variations in functional traits influence species composition of each community (Whitlock et al. 2007; Jung et al. 2010). Thus, fire may be shaping meta-communities, selecting different trait values among populations.

Environmental filters and competition are two opposite forces determining species coexistence into the communities (Webb et al. 2002). Predictions on the presence of a given species change when we consider that individuals of the same species are not equal (Cianciaruso et al. 2009), because abiotic and biotic filters and competition will act on the individual rather than on the species. Filters favour individuals within a range of trait values, whereas competition tend to exclude individuals with similar traits (Webb et al. 2002). Even though intraspecific variability is usually lower than interspecific variability, it accounts for a large part of the trait-gradient relationship, and it is expected to enhance the detection of environmental filters and competition assembling communities (Jung et al. 2010). We expect environmental filters to decrease variation and competition to increase it (Jung et al. 2010). However, not all traits are affected in the same way: some traits may be under selection pressure and others may be neutral in relation to the

environmental filter or competition (Silva et al. 2010). Thus, it is important to search for the effects of fire and competition on each trait instead of using a single measure of functional diversity.

The cerrado vegetation is under pressure of many environmental filters, such as fire, herbivory, oligotrophism, and drought (Gottsberger and Silberbauer-Gottsberger 2006; Silva et al. 2010). Although fire have been occurring in cerrado for thousands of years caused by natural lightning, its frequency and intensity have greatly increased in the last centuries due to human activities (Ledru 2002; Miranda et al. 2002). That increase is a question of concern for the conservation and management of natural areas, which demands elucidation of fire effects on species distribution and community diversity (Silva et al. 2011). Emas National Park is a protected natural reserve, which contains a large area of connected cerrado vegetation and presents areas with different fire frequencies (Batalha et al. 2011). Thus, it is a suitable site to study the effects of different fire frequencies on the change of species traits among communities.

Increasing the level of a disturbance may shift the population mean of a given trait towards a value more compatible with that disturbance, either above or below the null expectation; also, it may reduce the trait population range due to the exclusion of individuals with inadequate traits (Jung et al. 2010). After this filter selection, competition is expected to increase niche differentiation, that is, similar species will compete, leading to more divergent trait values (Jung et al. 2010). We used an intra- and interspecific trait-based approach to detect the presence of community assembling processes as environmental filter and competition. We answered the following questions: (1) inclusion of intraspecific variability enhance the relationship between fire and community weighted mean trait? (2) does fire shift mean population trait values?, (3) does fire reduce the range of population trait values?, and (4) does competition increase niche differentiation? (5) including intraspecific variability increase the perception of environmental filters and competition?

Material and Methods

Study area

We carried out this study in Emas National Park (ENP), located in the Brazilian Central Plateau (17°49'-18°28'S and 52°39'-53°10'W). Regional climate is tropical and humid (Aw, Köppen 1931), with dry winter from May to September and rainy summer from October to April. Annual rainfall vary from 1,200 to 2,000 mm, and the mean annual temperature is 24.6°C (Ramos-Neto and Pivello 2000). Soils in ENP are mainly acid, poor, with high content of aluminum, classified as Oxisols (França et al. 2007). In 1994, fire management has changed from total suppression of fires to a system of firebreaks, where natural fires were no longer suppressed (Ramos-Neto and Pivello 2000; França et al. 2007). Currently, there is a mosaic of areas with different history of fires, ranging from annually burned areas to areas burned once in the last 14 years (França et al. 2007).

Sampling

We divided the study sites into seven strata according to time since last fire, using satellite images from 1994 to 2009. The strata experienced 1, 3, 5, 7, 9, 11, and 15 years as median time since the last fire. We randomly placed five square plots of 25 m² in each stratum. In each plot, we sampled all woody plants with stem diameter at soil level equal to or greater than 3 cm (Secretaria de Estado do Meio Ambiente 1997), identified them to species level, classified them into families according to APG III (Angiosperm Phylogeny Group 2009), and measured 10 functional traits (sensu Díaz and Cabido 2001): basal area, height, bark thickness, stem specific density, leaf toughness, leaf size, leaf specific area, leaf nitrogen concentration, leaf phosphorus concentration

and leaf potassium concentration (Cornelissen et al. 2003; Agrawal and Fishbein 2006). These traits are related to disturbance and are expected to be related to environmental filters and competition among plants. We measured the traits according to Cornelissen et al. (2003).

Analysis

We used the procedures proposed by Jung et al. (2010) to test the effects of fire acting as an environmental filter and later niche differentiation due to competition among trees on both intra- and interspecific trait variation. First, we calculated the population mean trait value, which is the mean of each trait for each species inside the stratum, including intraspecific variability (Jung et al. 2010). Second, we calculated the species mean trait value, which is the mean of each trait for each species over all the strata, not accounting for intraspecific variability (Jung et al. 2010). We assume that inside the stratum there is a single population and along all strata there is a meta-population, and the differences among populations of the same species account for the intraspecific variability. We calculated the intraspecific variability as the coefficient of variation of the population mean trait value across all populations and the interspecific variability as the coefficient of variation of species mean trait value across all species for each trait (Jung et al. 2010).

We calculated the community mean trait value as the mean trait value of all species in the same stratum using either population mean or species mean. We calculated the slope of the linear regression between community mean trait and the mean time since last fire of strata and quantified the contribution of intraspecific variability as a percentage reduction of this slope for each trait (Cornwell and Ackerly 2009; Jung et al. 2010).

To test for habitat filtering and niche differentiation, we created one thousand null communities for each level of species richness, randomly selecting species from the species pool and randomly allocating to each selected species one of its population means (Jung et al. 2010). We

used the mean, the range, and the coefficient of variation of nearest-neighbour distance to compare our data to the null models with Wilcoxon signed-rank tests (Jung et al. 2010). Shifts in the mean and reduction of range indicate the effect of environmental filters selecting similar traits, whereas reduction of the coefficient of variation of nearest-neighbour distance indicates niche differentiation, as the trait values are more evenly spaced (Kraft et al. 2008; Jung et al 2010). For a given plot, we calculated the three metrics with population mean or species mean to account for intra- and interspecific variability. We carried out all analyses in R (R Development Core Team 2009). We used principal component analyses to reduce dimensionality of traits and to visualize directions of trait changes among fire strata, for both interspecific variability and joint inter- and intraspecific variability.

Results

We found 47 species across all strata, and the richness found in each strata of fire frequency varied from 12 to 19 species. Community mean trait value varied among the strata showing different patterns for each trait (Appendix 1). Species mean trait value presented the following mean (and standard deviation) values of all species: basal area was 52.24 (72.49) cm², height was 1.84 (1.04) m, bark thickness was 9.53 (3.48) mm, stem specific density was 0.40 (0.11) mg mm⁻³, leaf toughness was 1.29 (0.76) N, leaf size was 121.36 (137.81) cm², leaf specific area was 7.55 (2.79) mm² mg⁻¹, leaf nitrogen concentration was 18.81 (5.77) mg g⁻¹, leaf phosphorus concentration was 1.09 (0.34) mg g⁻¹, and leaf potassium concentration was 6.71 (3.11) mg g⁻¹.

Intraspecific trait variability (as the coefficient of variation of the population mean trait values) varied from 0.02 to 114.18, being lower for stem density and specific leaf area and higher for basal area, leaf potassium concentration, and leaf size (Appendix 2). Interspecific variability (as the coefficient of variation of the species mean trait values) was: 138.75 for basal area; 56.79 for

height; 36.51 for bark thickness; 24.61 for stem specific density; 59.55 for leaf toughness; 113.55 for leaf size; 36.11 for specific leaf area; 30.70 for leaf nitrogen concentration; 31.67 for leaf phosphorus concentration; and 46.33 for leaf potassium concentration.

The contribution of intraspecific variability to the trait-gradient relationship, as a percentage reduction of regression slope, was lower than 10% for all traits, except for bark thickness (97%), leaf toughness (12%), and leaf potassium concentration (64%, Fig. 1, Table 2). Moreover, in the ordination diagram the addition of intraspecific variability produced very similar results (comparing Fig. 2A and B): the stratum with one year since last fire was related to higher values of basal area, height, and specific leaf area; the strata with three, five, and nine years since last fire were related to higher values of stem specific density and lower values of leaf toughness; the strata with seven and 11 years since last fire were related to higher values of leaf size and lower values of stem specific density; and the stratum with 15 years since last fire was related to average values of traits (Fig. 2). When we considered intraspecific variability the first axis of ordination explained 40% of the variation and the second axis explained 29%; when we considered only interspecific variability the first axis explained 42% and the second axis explained 25%.

When we considered only interspecific variability, we observed significant deviation from null models for: the means of bark thickness and specific leaf area; the range of leaf nitrogen content, height, stem density, leaf size, specific leaf area, and leaf phosphorus concentration; and the coefficient of variation of nearest-neighbour distance on height, leaf phosphorus, and basal area (Table 1). When we included intraspecific variation, we still observed significant deviation from null models for the the means of bark thickness and specific leaf area, and revealed differences in the means of leaf nitrogen concentration, and leaf potassium concentration (Table 1). However, for range, only the deviation of leaf nitrogen concentration remained significant (Table 1). The coefficient of variation of nearest-neighbour distance of height, bark thickness, leaf toughness, and

leaf phosphorus concentration were below the null expectation, but deviation of basal area were no longer significant (Table 1).

Discussion

Intraspecific variability is supposed to describe trait variation in environmental gradients better than interspecific variability alone (Cianciaruso et al. 2009; Jung et al. 2010, Dantas et al. 2013). However, the contribution of intraspecific variability to the trait-gradient relationship was very low, except for three traits (bark thickness, leaf toughness, and leaf potassium concentration). For most of the traits, species composition explained more the changes in functional traits across fire gradient than trait variation within the same species. Accordingly, the inclusion of intraspecific variability increased the observation of community assembly processes only in three out of ten functional traits. Nonetheless, the mean values of leaf nitrogen and potassium were reduced only with the inclusion of intraspecific variability. Also, bark thickness and leaf toughness showed niche differentiation only when intraspecific variability was taken into account. However, five traits revealed filtering, with their range reduced, only when we did not include intraspecific variability. In these cases, selection was weaker than expected for species mean, allowing plastic species to assume wider trait values. Also, basal area showed niche differentiation when we excluded intraspecific variability. Plant traits are not individually selected, they are rather selected in the context of other traits (Agrawal 2006). Thus, the importance of intraspecific variability for plant response to fire gradient were different for each trait. Overall, including intraspecific variability did not change the multivariate patterns of fire-trait relationships, that is, fire effects over traits were diminished after fifteen years and communities reached the average values of traits. Therefore, interspecific variability seems to explain the larger part of trait-gradient relationship, with low extra contribution of intraspecific variability.

We found evidence in support of the effects of environmental filters for almost all traits, except basal area and leaf toughness. Some traits presented shift in mean value and some traits reduced range. Specific environmental filters cause shifts in traits, selecting individuals in the community with specific requirements to survive those filters (Jung et al. 2010; Venm et al. 2011). In cerrado, bark thickness, specific leaf area, leaf nitrogen, and leaf potassium shifted from the null expectation. Thicker barks provide protection for internal tissues from the elevated temperature, higher specific leaf area provide tolerance by increasing growth and photosynthetic rates, and leaf nutrients respond to fire changes in soil conditions (Pivello-Pompéia and Coutinho 1992; Cornelissen et al. 2003, Silva and Batalha 2008, Lawes et al. 2011). Moreover, fire reduced the range of height, stem specific density, leaf size, specific leaf area, leaf nitrogen, and leaf phosphorus. All these traits are related to fire resistance, escape, or tolerance (Cornelissen et al. 2003; Anacker et al. 2011), indicating that environmental filter is selecting species with more similar traits that allow them to survive under specific conditions, as predicted (Jung et al. 2010). Shift in mean and range reduction of these traits supported the idea that fire acts as an environmental filter in cerrado communities.

Species functional traits must cope simultaneously with environmental filters and biological interactions (Diaz and Cabido 2001; Violle et al. 2007). If two or more species were too similar, competition would lead either to competitive exclusion or niche differentiation (Szabó and Meszéna 2006). Then, after fire selection, competition lead species to diverge their traits from each other. In cerrado, we found niche differentiation for five traits. Basal area and plant height represent space occupation, being highly associated with competition capacity (Cornelissen et al. 2003; Lawes et al. 2011). In cerrado savannas, high species richness seems to lessen structural competition trough species complementarity (Gonçalves and Batalha 2011). Bark growth has a trade-off with vertical growth, indicating coexistence of two different strategies: some plants invest in vertical growth to escape from fire flames and other plants invest in bark growth to resist and resprout after fire

(Higgins et al. 2000, 2007; Midgley et al. 2010). Leaf toughness is related to herbivory resistance and change right after fire due to regrowth of young leaves (Agrawal 2006; Lopes and Vasconcelos 2011). Plant competition by soil nutrients may have led to divergence in leaf phosphorus concentration, because phosphorus shortage and competition limit plant acquisition of nutrients in post-fire vegetations (Yelenik et al. 2013). Thus, competition were acting over species traits leading to niche differentiation.

Considering that the contribution of intraspecific variation related to fire gradient was low, except for three traits, we can consider species mean trait values as good predictors of community functional traits. In sum, some traits indicated presence of environmental filter and others also presence of competition. Fire gradient changed the space traits by selecting similar species with more adequate traits, and posterior competition lead to divergence of traits in cerrado.

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Table 1. P values of Wilcoxon signed-rank tests comparing null models and observed data in cerrado plant communities at Emas National Park (Brazil), for trait mean, range and coefficient of variation of nearest-neighbour distance (CVNND). Intra- and interspecific based on population means. Interspecific variability based on species means. P values < 0.05 are in bold.

Trait	Intraspecific + Interspecific			Interspecific		
	Mean	Range	CVNND	Mean	Range	CVNND
Basal area	0.5781	0.8906	0.5313	0.375	0.1094	0.0391
Plant height	0.5781	0.1094	0.0078	0.1094	0.0156	0.0078
Bark thickness	0.0156	0.1874	0.0391	0.0312	0.0546	1.0000
Specific stem density	1.0000	0.2891	0.1094	0.8125	0.0078	0.0781
Leaf toughness	0.2188	0.1875	0.0234	0.9375	0.0781	0.0781
Leaf size	0.0781	0.7656	0.6562	0.5781	0.0391	0.9219
Specific leaf area	0.0156	0.1094	0.8125	0.0468	0.0234	0.1875
leaf N concentration	0.0156	0.0078	0.4688	0.1563	0.0391	0.7656
Leaf P concentration	0.2188	0.2891	0.0391	0.0781	0.0156	0.0156
Leaf K concentration	0.0468	0.9453	1.0000	0.1094	0.2891	0.9922

Table 2. Coefficient of regression (b) and R² of linear models with species traits as response variable and median of time since last time for inter + intraspecific variability based on population mean trait and interspecific variability based on species mean trait, contribution of intraspecific variability to explanation of trait-gradient relationship.

Trait	Inter + intraspecific		Interspecific		Contribution intraspecific (%)
	b	R ²	b	R ²	
Basal area	-0.01	0.07	-0.02	0.08	-79
Plant height	-0.02	0.10	-0.02	0.13	-4
Bark thickness	0.01	0.09	<0.01	0.04	97
Specific stem density	-0.01	0.09	-0.01	0.09	-2
Leaf toughness	0.01	0.09	0.01	0.10	12
Leaf size	0.01	0.05	0.02	0.15	-102
Specific leaf area	-0.01	0.14	-0.01	0.64	-49
leaf N concentration	-0.01	0.08	-0.01	0.60	-48
Leaf P concentration	>-0.01	0.02	-0.01	0.54	-54
Leaf K concentration	>-0.01	<0.01	>-0.01	0.01	64

Fig. 1 Regression analyses between time since last fire and community mean trait considering interspecific variability (dashed lines, crosses) and inter- and intraspecific variability (solid lines, circles), in cerrado plant communities at Emas National Park (Brazil). Data were log-transformed.

Fig. 2 Ordination diagram of principal component analysis of community mean traits, in seven strata with different times since last fire. A: considering inter- and intraspecific variability; B: considering only interspecific variability. ba = basal area; h = height; brk = bark thickness; woo = stem specific density; tgh = leaf toughness; lsz = leaf size; sla = specific leaf area; N = leaf nitrogen concentration; P = leaf phosphorus concentration; K = leaf potassium concentration; Numbers in strata s1-s15 correspond to median of time since last fire.

Appendix 1 Median of time since last fire and community mean (and standard deviation) trait based on population mean trait of plant species of cerrado communities at Emas National Park (Brazil)

Appendix 2 Intraspecific trait variability of plant species in cerrado communities at Emas National Park (Brazil) estimated as the coefficient of variation of the population mean trait

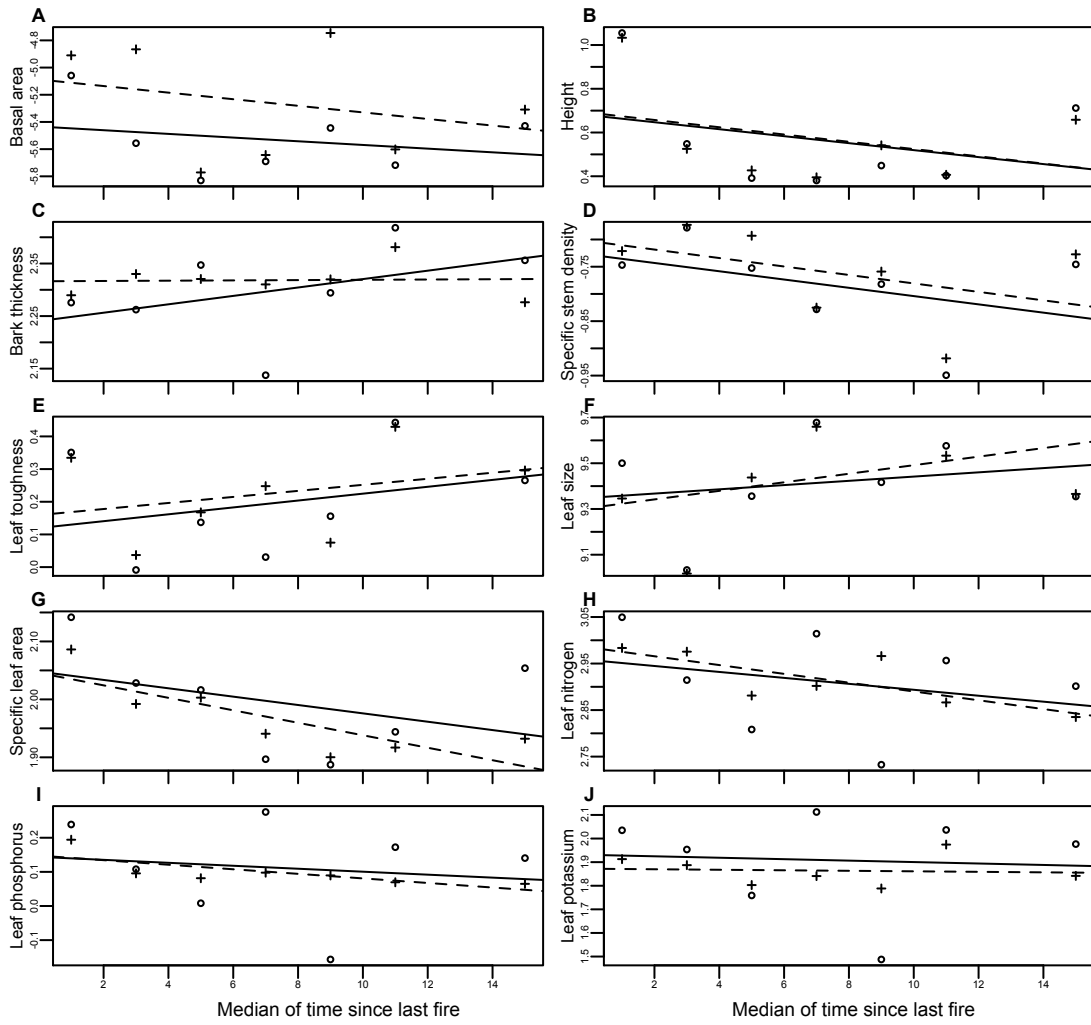


Figure 1

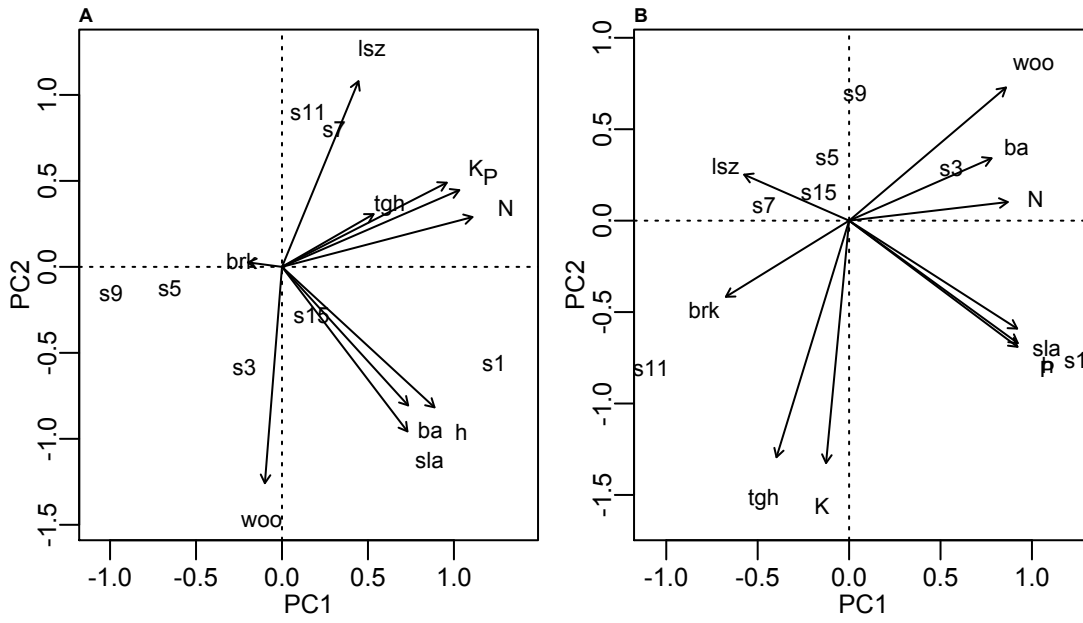


Figure 2

8. Considerações finais

Como esperado, o fogo foi um filtro ambiental para comunidades vegetais de cerrado. O fogo ocorre no cerrado há milhares de anos, portanto as espécies de cerrado já devem estar adaptas a sua presença. Mesmo assim, a frequência de fogo e o tempo desde a última queimada apresentaram características de filtros ambientais adicionais. No primeiro capítulo a frequência de fogo alterou tanto os componentes da diversidade funcional, quanto a identidade funcional das comunidades. Além disso, o regime de fogo alterou a relação entre solo e vegetação, provavelmente por uma ação indireta sobre a competição. No segundo capítulo, a diversidade funcional só pode prever o funcionamento quando acompanhada pelas variáveis ambientais. Mostrando a importância de se considerar o meio abiótico para as relações de efeito da biodiversidade. Por fim no terceiro capítulo, o gradiente de fogo alterou as características das plantas, selecionando espécies mais parecidas e com médias para os traços diferentes das esperadas pelo acaso. Os resultados dos três capítulos corroboraram que o fogo é um importante fator ambiental nas comunidades de cerrado, apresentando efeitos diretos e indiretos sobre a diversidade e sobre o funcionamento, alterando tanto as composições específicas quanto os traços das espécies vegetais.