

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

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## ABSTRACT

Differences in plant species richness and composition are associated with soil properties and disturbances such as fire, which can therefore be key determinants of species occurrence in savanna plant communities. We measured species richness, using nine plant functional traits and abundance to calculate three functional diversity indices. We then used model selection analyses to select the best model for predicting functional diversity and richness based on soil variables at sites with three different fire frequencies. We also calculated the community-weighted mean of each trait and used ordination to examine how traits changed across fire frequencies. We found higher species richness and functional dispersion at sites that were more fertile and where fire was frequent, and the opposite at such sites where fire was infrequent. However, soil properties influenced functional evenness and divergence only where fire was infrequent, with higher values where soils were poorer. Fire can change functional traits directly by hindering development of plants and indirectly by altering competition. Different fire frequencies lead to different plant-soil relationships, which can affect the functioning of tropical savanna communities. Functional diversity components and functional identity of the communities are both 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 unresolved debate about the relationship between plant diversity and soil properties. Whereas some authors have found a negative relationship between soil fertility and plant species richness (*e.g.*, Huston 1980; Enright *et al.* 1994; Tilman 1999; Harpole & Tilman 2007), others have argued that species richness increases with fertility (*e.g.*, Stark 1970; Gentry 1988), which is in accordance with the “fertility effect” theory (Dybzinski *et al.* 2008). Another observed that this relationship predicts maximum diversity at intermediate levels of soil fertility (Tilman 1984). An alternative way to resolve 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 sets 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). Because different plant species are adapted to the availability of distinct

nutrients in the soil, the type and number of limiting resources can affect species composition and richness (Critchley *et al.* 2002; Venterink *et al.* 2003; Harpole & Tilman 2007). Disturbances also affect species richness and composition, as well as altering the influence that species traits have on plant establishment and development (Haddad *et al.* 2008). Whereas soil properties and fire can 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 aluminum detoxification, and indirectly by the volume and quality of litter deposition (Göttlein *et al.* 1999; Fornara & Tilman 2008; Gessner *et al.* 2010). Therefore, plants will be associated with soil in different ways depending on the level 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 community functioning (Díaz & Cabido 2001; Hooper *et al.* 2005). Measures of community functioning (*e.g.*, productivity and nutrient cycling) have typically been found to be more consistently associated with functional diversity than with species richness

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(Díaz & Cabido 2001), although there are exceptions (e.g., Hector *et al.* 2000). 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). In addition, soil characteristics, together with disturbances such as fire, might also be related to differences among 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. There is also evidence that soil fertility increases in parallel with plant species richness and functional group diversity (Dybziński *et al.* 2008). Nevertheless, the relationship between environmental factors, such as soil quality and fire, and functional diversity is a question rarely addressed in natural communities and especially for 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 properties, such as the 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 constrain the regional species pool, selecting species that are resistant or tolerant to fire (Gottsberger & Silberbauer-Gottsberger 2006). In the *cerrado* (neotropical savanna) of Brazil, plant growth is frequently limited by soil nitrogen availability (Bucci *et al.* 2006), and soils are typically well-drained, old oxisols (Montgomery & Askew 1983). These soils are nutrient-poor, presenting low pH, low cation exchange capacities, and high aluminum saturation levels (Ruggiero *et al.* 2002; Bucci *et al.* 2006; Amorim & Batalha 2007). Aluminum is usually toxic to plants, reducing growth and preventing nutrient uptake (Göttlein *et al.* 1999; Heim *et al.* 2003). However, responses to aluminum toxicity vary among plant species, and some are adapted to high levels of aluminum, being restricted to this soil condition (Haridasan 2000). Therefore, species composition is related to soil texture, aluminum 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 at sites in the savanna. Given that soil and fire are major factors structuring these plant communities, we would expect the relationship between these factors to differ by fire frequency. Therefore, we attempted to answer the following questions: Do different fire frequencies change the relationship among soil properties, species richness, and functional diversity? and How would fire history influence the relationships among soil properties, plant species richness, and plant functional diversity?

## Material and methods

### Study area

Our study site was Emas National Park (ENP), located on the Central Plateau of Brazil (17°49′-18°28′S; 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 is 1200-2000 mm, concentrated in the period 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 the ENP for cattle ranching, and dry season burnings were used in order to promote forage regrowth every year. After 1984, 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 km<sup>2</sup> of preventive firebreaks to remove plant dry mass and avoid the spread of fires, which in the past resulted in catastrophic burn events every three years (Ramos-Neto & Pivello 2000). Nevertheless, in August 2010, another anthropogenic fire burned 93% of the reserve.

### Community sampling

We assessed soil properties and floristic composition using raw data from Silva & Batalha (2008). In the late rainy season of 2006, we sampled three nearby savanna woodlands subjected to different fire frequencies: one firebreak burned annually for the last ten years (hereafter “high fire frequency” site, at approximately 18°18′50″S; 52°54′00″W), another firebreak burned in 1996, 1999, 2001, 2002, and 2003 (hereafter “intermediate fire frequency” site, at approximately 18°19′01″S; 52°54′10″W), and a site protected from fire since 1994 (hereafter “low fire frequency” site, at approximately 18°17′28″S; 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 rather than to prior differences among them (see Pucheta *et al.* 1998 for a similar approach). In each savanna, we delineated a 2.5-km linear transect, and in each transect we systematically marked 250 points 10 m apart. 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 into a single sampling unit. Thus, we ended up with 25 species-composition sampling units for each site. In addition, from every point, we collected a soil sample at a depth of 0-5 cm, because soil composition in this layer is the most strongly 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 properties

We selected the following soil properties: total nitrogen concentration (N), organic matter, exchangeable aluminum ( $Al^{3+}$ ), clay, and sand. We used the clay/sand ratio as a measure of soil texture. For more details on how soil properties were determined, see Amorim & Batalha (2007) and Silva & Batalha (2008). The N, organic matter, clay, and sand are the soil properties most closely 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 (*i.e.*, determined species richness) in each of 25 sampling units in each site. To estimate 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 time of soil sampling (Silva & Batalha 2008), we measured or determined all traits according to the protocol proposed by Cornelissen *et al.* (2003). For each species, at each site, we randomly selected 10 individuals for functional trait 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 at each site separately, which allowed 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 function-

ality—functional dispersion (FDis), functional evenness (FEve), and functional divergence (FDiv): FDis is a measure of how species are dispersed in a trait multispace; FEve is a measure of how species abundances are distributed in the given trait multispace volume; and FDiv is a measure of how distant species weighted by abundance are from the multispace centroid (Villéger *et al.* 2008; Laliberté & Legendre 2010). In addition, we calculated the community-weighted mean (Ricotta & Moretti 2011) of each trait as a measure of functional identity of communities to examine how each trait changes in each community. To calculate the indices of functional diversity, we used the “FD” package of the R environment software (R Development Core Team 2010).

### Data analysis

We did a principal component analysis with the community-weighted mean of each trait (see traits in Tab. 1), using data from 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 the three fire frequency categories with species richness, FDis, FEve, and FDiv as the response variables and soil properties (N,  $Al^{3+}$ , organic matter, and clay/sand ratio) as the explanatory variables, resulting in 12 model sets. We also generated multiple ordinary least squares regression models for each fire frequency with the first two axes of the community-weighted mean ordination as the response variables and soil properties (N,  $Al^{3+}$ , organic matter, and clay/sand ratio) as the explanatory variables, resulting in six model sets. We used a parsimonious model selection and inference strategy based on the bias-corrected Akaike Information Criterion (AICc), according to Akaike (1973) and Burnham & Anderson (2002). The AICc is an extension of likelihood theory and provides a robust and objective means for model selection that accounts for both bias and precision. Although the best models are those with

**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 <sup>2</sup>	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 <sup>2</sup> mg <sup>-1</sup>	highly correlated with several physiological traits related to resource uptake and use efficiency and plant growth strategies
5. Leaf size	mm <sup>2</sup>	ecological strategy, with respect to environmental nutrient stress and disturbances
6. Leaf dry matter content	mg g <sup>-1</sup>	related to flammability, resistance to physical hazard, disturbed environments
7. Stem specific density	mg mm <sup>-3</sup>	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

the lowest AICc values, a common strategy is to use the AICc of each model to calculate the  $\Delta$ AICc value, which is the difference between the AICc of a given model and the minimum AICc found for all models being compared. A  $\Delta$ AICc value higher than 7 indicates a model that has a poor fit relative to the best model, whereas a  $\Delta$ AICc value lower than 2 indicates a model that is as suitable as the best model (Burnham & Anderson 2002). We also used  $\Delta$ AICc values to compute the Akaike weight of each model, which provides additional evidence that a model is actually the best explanatory model. 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  $\Delta$ AICc,  $R^2$ , and AICc weight (Burnham & Anderson 2002), using the “AICcmodavg” package of the R environment software (R Development Core Team 2010).

## Results

Overall, we found 51 species within 28 families. The mean species richness across all samples was 12, ranging from 6 to 14 at the high fire frequency site; from 6 to 19 at the middle fire frequency site; and from 8 to 18 at the low fire frequency site. For clarity, we presented only the best model of each model set (Tab. 2; for the five best models for each set, see Tab. 3). For 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 condition, the best model included N as the predictor variable, which

was positively correlated with species richness and FDis ( $R^2 = 0.35$  and  $R^2 = 0.17$ , respectively; Tab. 2). Under the intermediate fire frequency condition, the best model included Al<sup>3+</sup> and the clay/sand ratio as predictors of species richness and FDis ( $R^2 = 0.24$  and  $R^2 = 0.31$ , respectively; Tab. 2). Under the low fire frequency condition, the best model included only the clay/sand ratio, which was negatively correlated with species richness and FDis ( $R^2 = 0.25$  and  $R^2 = 0.05$ , respectively; Table 2).

Functional components that consider abundance had different patterns. In the high fire frequency condition, the best model included N as the predictor variable, which was positively correlated with FEve but presented low explanatory power ( $R^2 = 0.06$ ; Table 2). In the intermediate fire frequency condition, the best model included the clay/sand ratio as the predictor variable, which was negatively correlated with FEve but also presented low explanatory power ( $R^2 = 0.01$ ; Table 2). The best model in the low fire frequency condition included N, organic matter, and clay/sand ratio as predictor variables, FEve correlating positively with N, whereas it correlated negatively with organic matter and the clay/sand ratio ( $R^2 = 0.34$ ; Tab. 2). In the high fire frequency condition, the best model included Al<sup>3+</sup>, which was positively correlated with FDiv but presented low explanatory power ( $R^2 = 0.02$ ; Tab. 2); in the intermediate fire frequency condition, the best model included organic matter and Al<sup>3+</sup> as predictor variables, FDiv correlating positively with organic matter and negatively with Al<sup>3+</sup> ( $R^2 = 0.23$ ; Tab. 2). In the low fire frequency condition, the best model included N and the clay/sand ratio as predictor variables, FDiv correlating positively with N and negatively with the clay/sand ratio ( $R^2 = 0.19$ ; Tab. 2). For models with coeffi-

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,  $\Delta$ 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	Response variable	Explanatory Model	$R^2$	AICc	$\Delta$ AICc	AICc wi
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



coefficients lower than 0.10, we considered that the explanatory variables had no effect 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 the high fire frequency condition from the others, and the second axis separated the intermediate and low fire frequencies (Fig. 1). Individuals occurring at sites under the high fire frequency condition 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 at sites under the intermediate fire frequency condition presented lower specific leaf area and leaf size but also higher basal area (Fig. 1). Individuals occurring at sites under the low fire frequency condition presented higher specific leaf area and leaf size but also lower leaf dry matter content and number of resprouts (Fig. 1).

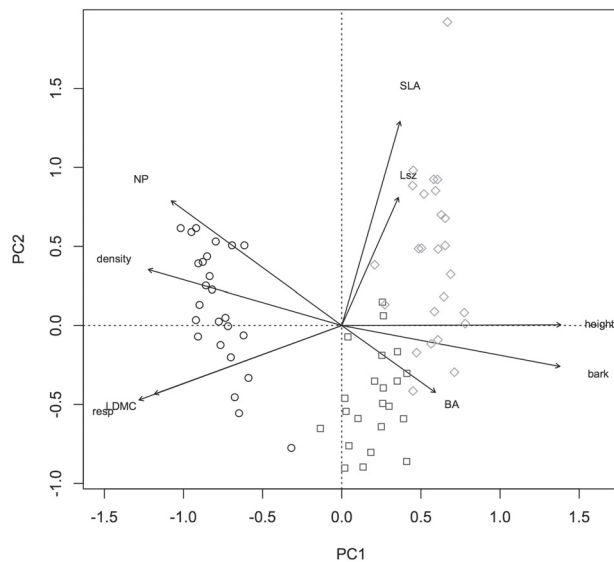
## Discussion

Under the high fire frequency condition, species richness and FDis were associated with higher soil nitrogen values, in accordance with the “fertility effect” theory (Dybzinski *et al.* 2008): plant species richness and FDis can increase community productivity over time by increasing the nutrient supply via greater inputs and greater retention. Such an effect was observed in experimental grasslands, where plant species

richness and functional diversity were positively correlated with soil nitrogen (Dybzinski *et al.* 2008). However, we found a significant difference due to annual burning in the last 12 years, and, therefore, the community seemed to be in constant regeneration. For the woody species studied, this regeneration occurs 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 might 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, woody *cerrado* species are able to exploit fertile sites by allocating resources to maximize carbon gain and enhance growth. In a field experiment, total leaf surface area and basal area per tree both 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, at high fire frequency sites, there is a reported dominance of *Mimosa amnis-atri* Barneby (a Fabaceae shrub), which accounts for almost 50% of all sampled individuals (Silva & Batalha 2008). In addition, fire removes pre-existing biomass, creating open areas in which competition decreases (Hoffman 2002), and can increase facilitation among plants (Franks & Peterson 2003). At low levels of soil nitrogen, only a few adapted plant species with symbiotic bacteria in their root systems) can establish themselves (Reynolds *et al.* 2003; Fornara & Tilman 2008). In this sense, patches with higher soil nitrogen content seem to reduce niche limitation effects, and the 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 FDis of woody species.

The proportions of clay and sand in soil are drivers of vegetation distribution, because sandy soils have lower water retention capacity and cation exchange capability (Larcher 1995). Exchangeable aluminum decreases nutrient availability to plants by lowering phosphorus, magnesium, and calcium absorption (Malavolta *et al.* 1977; Marschner 1989), as well as inducing 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 &



**Figure 1.** Principal component analysis of sites under different fire frequency conditions, according to community-weighted means of woody species traits, in areas of savanna within the Emas National Park, Brazil (17°49'–18°28'S; 52°39'–53°10'W).

PC1 – axis 1; PC2 – axis 2; 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 resprouts at soil level; bark – bark thickness. Circles – high fire frequency; squares – intermediate fire frequency; diamonds – low fire frequency.

Tilman 2007). In fact, aluminum has been positively correlated with species richness in some areas of *cerrado*, a pattern that was postulated to be due to low nutrient availability (Amorim & Batalha 2008). In addition, high functional diversity and complementarity in the presence of high aluminum levels and low clay content are in agreement with the idea of increasing niche dimensionality under 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 that 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 variations in disturbance and productivity conditions, such as soil fertility (Pakeman *et al.* 2011). Functional evenness and FDiv were both poorly predicted by soil variables under high and intermediate fire frequency conditions. Fire acts as a nonselective herbivore, reducing biomass and, consequently, competition (Bond & Keeley 2005). Therefore, functional complementarity is diminished under higher fire frequency conditions. Conversely, species abundances are more strongly influenced by soils when fire is infrequent. Following abundance patterns, FEve and divergence were similarly influenced by soil when the frequency of fire was low. Our findings suggest that soil fertility plays an ambiguous role in diversity. Organic matter- and clay-rich soil can favor dominant species (reducing FEve) and functionally similar species (reducing FDiv). However, nitrogen-rich soil can increase the evenness of species abundances (increasing FEve) and favor the occurrence of species with divergent traits (increasing FDiv). 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 favored only on 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 the *cerrado*.

The functional identity of communities, here defined by species abundances and trait composition, may change depending on the environment (Pakeman *et al.* 2011). Considering all areas together, functional composition responded to fire, providing ways to differentiate sites by 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 with low plant height, thin barks, and thin stems of new individuals. In that case, it might hinder the development of individuals to adult stages, and plants might be 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 frequency conditions, there is enough time for plants to accumulate bark to resist fire damage and, consequently, grow taller. In the present study, leaf traits differed among sites, specifically between the low and intermediate fire frequency sites. These leaf traits are associated with competitive ability, resource exploitation, and photosynthesis rate (Cornelissen *et al.* 2003), suggesting strong resource competition under low fire frequency conditions. The biomass of dominant species accumulates when fire frequency is low; consequently, biomass disparities enhance competition (Cianciaruso *et al.* 2010). Thus, fire acts on traits 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 can limit trait composition. In general, soil fertility is lower under intermediate and low fire frequency conditions, holding approximately 20% less soil nitrogen and 31% less organic matter, with high aluminum and sand contents (Silva & Batalha 2008). Under conditions of nutrient shortages, competition can become more limiting: plant species tend to become functionally distinct (von Felten & Schmid 2008). Accordingly, we found a divergent pattern under the low fire frequency condition: species richness and functional diversity were negatively associated with the clay/sand ratio; thus, for higher proportions of clay, we found fewer species and lower FDis values. Under the intermediate fire frequency condition, aluminum was also important, being positively associated with richness and FDis. In addition, soil properties affected the functional components that incorporate abundance, although 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 are soil properties, at least under high fire frequency conditions.

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