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Woody plant species co-occurrence in Brazilian savannas under different fire frequencies

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ABSTRACT

Fire plays an important role in determining the structure of the vegetation of savannas. Consequently, frequent fires are expected to assemble closely related plant species with very similar fire-related functional traits. We assessed the influence of different fire frequencies on patterns of co-occurrence of woody species at a fine spatial scale in Brazilian savannas. We used quantile regressions to test the relationship between co-occurrence indices and both phylogenetic distances and functional differences, calculated for every possible pair of species. Our results indicated that fire changes the pattern of co-occurrence of woody plants. Functionally different species co-occurred predominantly in a site protected from fire, whereas functionally similar species co-occurred predominantly in sites frequently burned. However, we did not find correlations between co-occurrence and phylogenetic distance of species, due probably to the random distribution of some functional traits in the phylogeny of savanna species. Thus, fire acts as an important environmental filter at fine spatial scales in Brazilian savannas, promoting functional – but not phylogenetic – clustering of plants.

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1. Introduction

Fire is one of the major forms of environmental disturbance in the world (Bond and Keeley, 2005), playing an important role in determining the occurrence of savannas (Thonicke et al., 2001; Bond et al., 2005). The occurrence of fire over the past 25 million year in savannas has allowed the evolution of fire-tolerant and fire-dependent plant species, which without fire could be potentially replaced by tropical forest species (Thonicke et al., 2001; Bond et al., 2005). In South America, the largest savanna region is the Brazilian cerrado (Gottsberger and Silberbauer-Gottsberger, 2006). Like its overseas savanna counterparts, the cerrado vegetation evolved with fire (Coutinho, 1990; Gottsberger and Silberbauer-Gottsberger, 2006). Cerrado woody species present thick corky bark and subterranean meristems that protect them from high temperatures and allow resprouting after fires (Gottsberger and Silberbauer-Gottsberger, 2006). However, annual fires tend to favour herbaceous plants at the expense of woody ones (Durigan and Ratter 2006; Hoffmann et al., 2009). Consequently, the pattern of co-occurrence of woody species is expected to change along a fire gradient.

Environmental filters, such as fire, are thought to determine the functional similarity and the phylogenetic relatedness of

co-occurring plant species (Webb et al., 2002; Cavender-Bares et al., 2006; Slingsby and Verboom, 2006). Environmental filters select those species that can persist within a community on the basis of their tolerance to the abiotic conditions (Weiher and Keddy, 1995). As a consequence, they are expected to assemble co-occurring species with similar niches, that is, species with similar morphological and physiological characteristics (i.e., functional traits, Chase, 2003; Fukami et al., 2005). In relation to phylogenetic relatedness, environmental filters are predicted to assemble closely related co-occurring species (phylogenetic clustering; Webb et al., 2002) if functional traits are conserved in the evolution of species lineages (i.e., traits are more similar among closely related species; Prinzing et al., 2001; Ackerly, 2003). Nevertheless, if functional traits evolved convergently and closely related species are functionally different, environmental filters are predicted to favor co-occurrence of more distantly related species (phylogenetic overdispersion; Webb et al., 2002).

In some cases, the evolution of traits is indistinguishable from random (Silvertown et al., 2006), and a clear pattern of phylogenetic clustering or overdispersion may not emerge (Silva and Batalha, 2009). A widespread phylogenetic signal has been observed in plant traits related to environmental tolerances (i.e., light, soil moisture, and pH, Prinzing et al., 2001). These plant traits are related to habitat requirements and, therefore, they define the 'β niche' of the species, referring to the scale at which β-diversity is determined (Silvertown et al., 2006). However, random distributions in the plant phylogeny

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of traits that determine within-habitat α -diversity (α niche) also seem to be common (Silvertown et al., 2006), because α niches define the species interactions within a community and is expected to be different for species coexistence to be possible (Silvertown et al., 2006).

Studies conducted at fine scales have found patterns of phylogenetic overdispersion (Cavender-Bares et al., 2004, 2006; Slingsby and Verboom, 2006). However, the functional similarity of co-occurring species still remains inconclusive (see Leibold, 1998 for references). Recently, we observed that the environmental filters might determine the co-occurrence of functionally similar tree species in cerrado (Silva and Batalha, 2009). Here, we tested whether annual fire frequencies change the pattern of local co-occurrence of cerrado woody species at a fine spatial scale, taking into account the nearest neighbours. We used quantile regressions to test the relationship between co-occurrence indices and both phylogenetic distances and functional differences, calculated for all pairs of species. We expected that the functional similarity among plants would increase with fire frequencies, whereas the phylogenetic distances among plants would either decrease, if functional traits were conserved, or show no pattern, if functional traits were randomly distributed in the phylogeny of the plants.

2. Material and methods

2.1. Study area

We surveyed three nearby cerrado sites in Emas National Park (ENP), located in the Brazilian Central Plateau (17°49'–18°28'S; 52°39'–53°10'W). The ENP comprises 132,941 ha and is one of the largest and most important reserves in the Cerrado domain (Unesco, 2001). According to Köppen's (1931) system, regional climate is classified as Aw, humid tropical, with wet summers and dry winters. Up to 1984, the ENP was exploited by farmers for cattle ranching, and burning in the dry season was used to promote forage regrowth (França et al., 2007). Afterwards, the ENP was fenced, and a fire exclusion policy was established (Ramos-Neto and Pivello, 2000). As a consequence, catastrophic fires occurred every 3–4 years, burning 80% of the park's area (Ramos-Neto and Pivello, 2000). Since 1995, around 10 km² of preventive firebreaks have been burned annually at the end of the wet season, and a fire brigade works in the park during the dry season to prevent anthropogenic fires (França et al., 2007). Thus, there are currently few occurrences of anthropogenic fires inside the ENP (less than 2.2% of the burned area from 1994 to 2003), and the largest wild-fires burn less than 30% of the total area. Fire frequency at a given site averages 6–7 years (França et al., 2007).

2.2. Data collection

In the late rainy season of 2006, we sampled the woody species occurring in three cerrado sites with similar physiognomy, similar soil type (Oxisols), and under different fire frequencies: two fire-breaks, one burned annually for the last ten years (approximately 18°18'50"S; 52°54'00"W), another burned around every two years (approximately 18°19'01"S; 52°54'10"W), and a site without fires since 1994 (approximately 18°17'28"S; 52°53'41"W). The sites were distant less than 2 km one from each other. In each site, we placed a 2500 m long transect, with 250 points, 10 m apart from each other. In each point, we used the point-quarter method (Mueller-Dombois and Ellenberg, 1974) to sample four woody plants with stem diameters at the soil level ≥ 3 cm (SMA, 1997). We identified the species by comparing collected samples to those of ENP's reference collection (Batalha and Martins, 2002) and to vouchers lodged at the University of Campinas and University of Brasília herbaria.

We measured eight soft functional traits (i.e., traits that are relatively easy and quick to quantify; Hodgson et al., 1999) that may be used as accurate surrogates of plant functional responses, such as growth coefficients and habitat requirements (Cornelissen et al., 2003). These traits were: basal area, bark thickness, canopy height, height, leaf dry matter content, specific leaf area, stem specific density, leaf nitrogen concentration, and leaf phosphorus concentration.

According to Cornelissen et al. (2003): (1) basal area is a trait positively related to space occupation, resource uptake, total biomass, and reproductive capability; (2) bark thickness is a trait related to protection of vital tissues against fire damage and may also decrease mortality by fire or accelerate post-fire recovery; (3) canopy height is related to avoidance of crown fires; (4) height is associated to competitive value, fecundity, interval between two perturbations, tolerance to stress, underground biomass, root depth, lateral ramification, and leaf size; (5) leaf dry matter contents are related to flammability and resistance to physical hazards; (6) specific leaf area is positively related to maximum photosynthetic rates, since low values of it correspond to a high leaf structure investment; (7) stem specific density is related to structural strength and resistance against physical damage; and (8) leaf nitrogen and phosphorus concentrations are related to maximum photosynthetic rate.

We measured and computed most of the traits following the procedures described in Cornelissen et al. (2003). For each species in each site, we measured stem specific density, leaf nitrogen, and leaf phosphorus for five individuals we drew at random. For the specific density, we collected a 10 cm long section of a branch of about 5 cm in diameter for each individual. For the leaf nutrient analysis, we collected 20 g of fully expanded leaves without symptoms of herbivore and pathogen attack for each individual, at the end of rainy season of 2006. We measured the other functional traits for 10 random individuals, except for rare species, for which we measured them in five individuals at least.

2.3. Phylogenetic data

We constructed a phylogenetic tree for all sampled species with the Phylomatic software, a phylogenetic toolkit for the assembly of phylogenetic trees (Fig. 1, Webb and Donoghue, 2005). Phylogenetic distances among species from different families were estimated from the dated Angiosperm super-tree of Davies et al. (2004). When a family node presented many polytomies (Fabaceae and Asteraceae, for instance), we distributed the genera into their subfamilies following the last angiosperm classification (Angiosperm Phylogeny Website; Stevens, 2001). We assigned branch lengths of these genera by spacing undated nodes evenly above family node. We drew the phylogenetic tree for the families sampled with the ADE-4 package (Analyses des Données Ecologiques; Thioulouse et al., 1996) for the R environment (R Development Core Team, 2008).

We investigated whether the functional traits tended to be phylogenetically conserved (i.e., phylogenetic signal) or convergent in the phylogeny of the sampled species, using a test based on the variance of phylogenetic independent contrasts (PIC; Blomberg et al., 2003). If related species are similar to each other, the magnitude of independent contrasts will generally be similar across the tree, resulting in a small variance of contrast values (Blomberg et al., 2003). Observed contrast variances are compared to the expectations under a null model of randomly swapping trait values across the tips of the tree. We used the mean trait values normalized by their standard deviations. We did this analysis with the Picante package (Kembel et al., 2008) for the R environment (R Development Core Team, 2008).

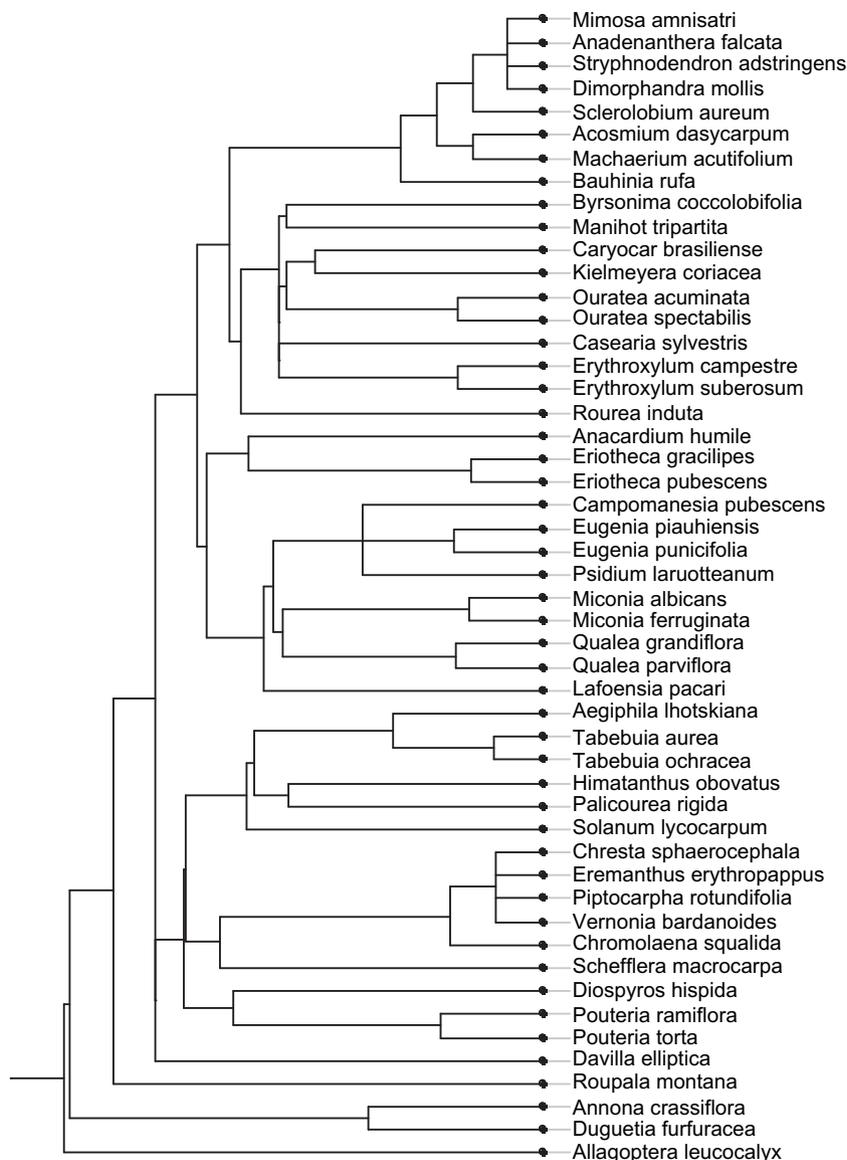


Fig. 1. Phylogenetic tree assembled for the cerrado species in all sampled sites in Emas National Park, central Brazil. The relationship among species was based on [Davies et al. \(2004\)](#).

2.4. Data analysis

We compared in each site the degree of co-occurrence of species pairs in the sampled points to the absolute value of mean pairwise differences in functional trait values. We calculated the pairwise values of co-occurrence (C) based on proportional similarity ([Schoener, 1970](#)) as follows: $C_{ih} = 1 - 0.5 \sum |p_{ij} - p_{hj}|$, where C_{ih} is the co-occurrence of species i and h , and p_{ij} is the proportion of occurrences of the i th or h th species in the j th point. Then, we tested the relationship between C values and functional differences with quantile regressions. The term 'phenotypic clustering' refers to high trait similarity among co-occurring species, whereas the term 'phenotypic overdispersion' refers to low trait similarity among co-occurring species.

If co-occurring species are phenotypically overdispersed, limited co-occurrence is expected for species with similar trait values. However, a broad range of co-occurrence levels is possible among species with different traits. Conversely, if co-occurring species are phenotypically clustered, limited co-occurrence is expected for species with different trait values. Again, a broad range

of co-occurrence levels is possible between species with similar traits. Therefore, co-occurrence may have increased or decreased variance with decreasing functional similarity, so that a triangular relationship with a positively or negatively sloping hypotenuse may arise. In these cases, quantile regression should be used ([Cade et al., 1999](#)). In this study, we were interested in the limiting effect of fire in the species co-occurrence and hence we focused on the upper bound of the variance of the relation between species co-occurrence and trait difference. We examined the nature of this upper bound with quantile regressions with data points in the 0.95 (upper 5%) quantile, using Quantreg package ([Koenker, 2008](#)) for R environment ([R Development Core Team, 2008](#)). We assessed the significance of the slopes of quantile regressions with bootstrapped standard errors ([Koenker, 2008](#)).

Then, we compared the pairwise values of co-occurrence to the phylogenetic distances among species. We calculated the phylogenetic distances from the estimated intervening branch length distances (measured in millions of years) between all species pairs with the Phylocom, using the Phylodist module ([Webb et al., 2007](#)). We also assessed the upper bound of the variance of the relation

between species co-occurrence and phylogenetic distances with quantile regressions, with data points in the 0.95 (upper 5%) quantile. We also did this analysis with Quantreg package (Koenker, 2008) for R environment (R Development Core Team, 2008). We assessed the significance of the quantile regression coefficients with bootstrapped standard errors (Koenker, 2008).

3. Results

We sampled 1000 individuals of woody plants in each site. We found 28 species in the annually burned site, 36 species in the biennially burned site, and 39 species in the protected site (Table 1). We observed significant slopes in the comparison between pairwise indices of species co-occurrence and values of mean pairwise differences in functional trait values (Table 2). We found negative slopes in the annually and biennially burned sites for basal area, stem

Table 1

Cerrado woody species sampled in Emas National Park, central Brazil. Site 1 = annually burned site (approximately, 18°18'50"S and 52°54'00"W); site 2 = biennially burned site (approximately, 18°19'01"S and 52°54'10"W); and site 3 = protected site (approximately, 18°17'28"S and 52°53'41"W).

Family	Species	Sites
Anacardiaceae	<i>Anacardium humile</i> A. St-Hil.	1
Annonaceae	<i>Annona crassiflora</i> Mart.	1,2,3
	<i>Duguetia furfuracea</i> (A. St-Hil.) Benth. & Hook.	1
Apocynaceae	<i>Himatanthus obovatus</i> (Müll. Arg.) Woods.	2
Araliaceae	<i>Schefflera macrocarpa</i> Seem.	2
Arecaceae	<i>Allagoptera leucocalyx</i> (Mart.) Kuntze	1
Asteraceae	<i>Chresta sphaerocephala</i> DC.	1
	<i>Chromolaena squallida</i> (Spr.) King & H. Rob.	1
	<i>Eremanthus erythropappus</i> Sch. Bip.	1,2,3
	<i>Piptocarpha rotundifolia</i> (Less.) Baker	1,2,3
	<i>Vernonia bardanoides</i> Less.	1
Bignoniaceae	<i>Tabebuia aurea</i> (Silva Manso) S. Moore	2,3
	<i>Tabebuia ochracea</i> (Cham.) Standl.	1,2,3
Caryocaraceae	<i>Caryocar brasiliensis</i> Cambess.	2,3
Clusiaceae	<i>Kielmeyera coriacea</i> Mart.	2,3
Connaraceae	<i>Rourea induta</i> Planch.	1,2,3
Dilleniaceae	<i>Davilla elliptica</i> A. St-Hil.	1,2,3
Ebenaceae	<i>Diospyros hispida</i> A. DC.	1,2,3
Erythroxylaceae	<i>Erythroxylum campestre</i> A. St-Hil.	1,2,3
	<i>Erythroxylum suberosum</i> A. St-Hil.	2,3
Euphorbiaceae	<i>Manihot tripartita</i> (Spreng.) Müll. Arg.	1
Fabaceae	<i>Acosmium dasyarpum</i> (Vogel) Yakovlev.	1,2,3
	<i>Anadenanthera falcata</i> (Benth.) Speg.	1,2,3
	<i>Bauhinia rufo</i> Steud.	3
	<i>Dimorphandra mollis</i> Benth.	1,2,3
	<i>Machaerium acutifolium</i> Vogel.	1,3
	<i>Mimosa amnis-atr</i> Barneby	1,2,3
	<i>Sclerolobium aureum</i> Baill.	3
	<i>Stryphnodendron adstringens</i> (Mart.) Coville	1,2,3
Lythraceae	<i>Lafoensia pacari</i> A. St-Hil.	3
Malpighiaceae	<i>Byrsonima coccolobifolia</i> A. Juss.	2,3
Malvaceae	<i>Eriotheca gracilipes</i> (K. Schum.) A. Robyns	2,3
	<i>Eriotheca pubescens</i> (Mart. & Zucc.) A. Robyns	2,3
Melastomataceae	<i>Miconia albicans</i> Triana	3
	<i>Miconia ferruginata</i> A. DC.	2,3
Myrtaceae	<i>Campomanesia pubescens</i> (A. DC.) O. Berg	3
	<i>Eugenia aff. piahuiensis</i> Mart.	1,2
	<i>Eugenia puniceifolia</i> (Kunth) A. DC.	2,3
	<i>Psidium laruotteanum</i> Cambess.	1,2,3
Ochnaceae	<i>Ouratea acuminata</i> (A. DC.) Engl.	1,2,3
	<i>Ouratea spectabilis</i> (Mart.) Engl.	2,3
Proteaceae	<i>Roupala montana</i> Aubl.	3
Rubiaceae	<i>Palicourea rigida</i> Kunth	1,2,3
Salicaceae	<i>Casearia sylvestris</i> Sw.	2,3
Sapotaceae	<i>Pouteria ramiflora</i> (Mart.) Radlk.	1,2,3
	<i>Pouteria torta</i> (Mart.) Radlk.	1,2,3
Solanaceae	<i>Solanum lycocarpum</i> A. St-Hil.	1,2,3
Verbenaceae	<i>Aegiphila lhotzkiana</i> Cham.	2
Vochysiaceae	<i>Qualea grandiflora</i> Mart.	2,3
	<i>Qualea parviflora</i> Mart.	2

Table 2

Tests for spatial phylogenetic and functional structure of all co-occurring cerrado woody plant species sampled in Emas National Park, central Brazil. For each data set, the slope of the regression with data points in the 0.95 (upper 5%) quantile between co-occurrence indices and phylogenetic distances and functional differences are given. The *P* values for bootstrapped standard errors are also given. Significant values at $\alpha = 0.05$ are presented in bold face. Site 1 = annually burned site; site 2 = biennially burned site; and site 3 = protected site.

Data type	Site 1		Site 2		Site 3	
	slope	<i>P</i>	slope	<i>P</i>	slope	<i>P</i>
Phylogenetic distance	0.001	0.769	0.001	0.189	0.001	0.767
Basal area	-0.025	0.041	-0.019	0.045	0.020	0.002
Bark thickness	-0.011	0.357	-0.006	0.560	0.015	0.010
Canopy height	0.003	0.804	-0.036	0.001	-0.002	0.884
Leaf dry matter content	-0.006	0.599	-0.005	0.559	0.001	0.901
Plant height	0.005	0.688	0.006	0.496	-0.002	0.884
Specific leaf area	0.006	0.582	-0.006	0.491	-0.004	0.714
Stem specific density	-0.027	0.021	-0.024	0.019	-0.003	0.765
Leaf N concentration	-0.018	0.017	-0.015	0.041	0.017	0.045
Leaf P concentration	-0.031	0.014	-0.012	0.047	0.018	0.026

specific density, and leaf N and P concentration indicating that co-occurring species were more similar than expected by chance. However, we found positive slopes in the protected site for basal area, bark thickness, and leaf N and P concentration indicating that co-occurring species were less similar than expected by chance (Fig. 2, Table 2). On the other hand, the comparison between pairwise indices of species co-occurrence and phylogenetic distances showed non-significant levels with the quantile regressions (Table 2).

We found phylogenetic signals in some functional traits (Table 3). The mean value of the variances and of the random variance means of the phylogenetic independent contrasts were 0.020 and 0.034 respectively (mean of the *P* values = 0.101). Consequently, phylogenetically related woody species showed some degree of functional similarity in the cerrado.

4. Discussion

Our results supported the postulate that fire changes the pattern of co-occurrence of plants at fine spatial scales. The functional similarity among co-occurring species was higher in sites with higher fire frequency. Thus, fire acts as an important environmental filter at fine spatial scale in cerrado, driving phenotypic clustering of plants.

Our results indicated that a high fire frequency may assemble functionally similar plant species in cerrado areas. In Mediterranean vegetation, high fire frequencies also promote phenotypic clustering of plants (Pausas and Verdú, 2008). However, evidence in other fire-prone vegetations is only indirect. In other savannas (Williams et al., 1999; Silva et al., 2001) as well as in the California chaparral (see Syphard et al., 2006 for reference), frequent fires promote changes in plant functional types, favouring grass and shrub species. Thus, frequent fires may reduce the range of functional traits and the number of functional types in fire-prone vegetation types, decreasing the overall functional diversity of the plant community as a result.

Competitive interactions are expected to limit the functional similarity of locally co-occurring species, because competition should be greater among species that have similar niches (Hutchinson, 1959; Leibold, 1998). Based on these expectations, Weiher and Keddy (1995) postulated that phenotypic overdispersion of plants is greater at smaller spatial scales, where species compete directly for limited soil nutrients. Evidence of competitive exclusion determining phenotypic overdispersion at fine spatial scale has been found in different plant communities (e.g., prairies – Fargione et al., 2003; oak forests – Cavender-Bares et al., 2004; sand dunes – Stubbs

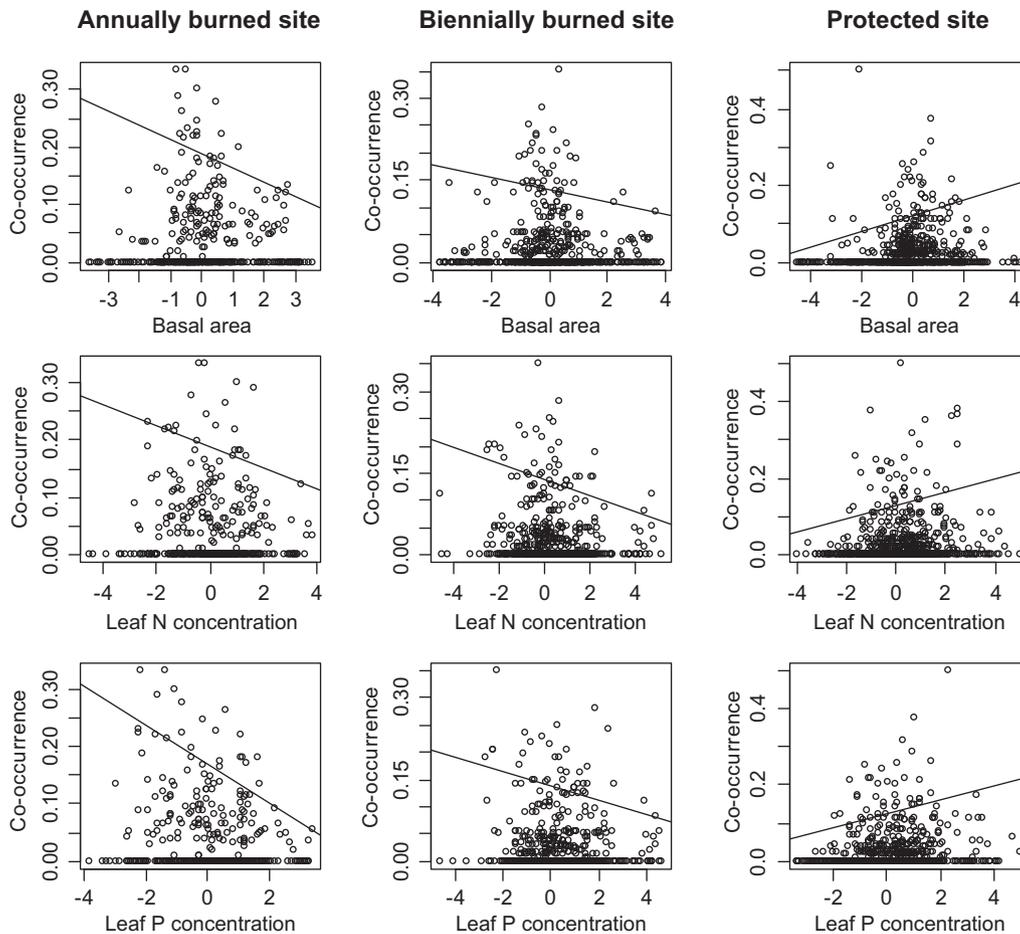


Fig. 2. Quantile Regression for significant ($\alpha = 0.05$) upper 5% quantiles between functional trait differences and co-occurrence indices of co-occurring cerrado woody plant species, central Brazil. The slopes of quantile regressions for basal area, leaf N and leaf P concentrations in the annually burned, biennially burned and protected sites were respectively -0.025 , -0.018 , -0.031 , -0.019 , -0.015 , -0.012 , 0.020 , 0.017 , 0.018 .

and Wilson, 2004; and tropical forests – Kraft et al., 2008). However, Valiente-Banuet et al. (2006) demonstrated recently that facilitation is also expected to promote phenotypic overdispersion in fire-prone communities. Nurse species may favour species with different traits to establish in the community (Valiente-Banuet et al., 2006). We found a phenotypic overdispersion in the site protected from fire. So, competitive interactions and facilitation may limit the co-occurrence of functionally similar plants in cerrado, but only insofar as fire is excluded.

For some functional traits, we did not find significant correlations with the species co-occurrence, which may be due to high

similarity among the values of functional traits among species. For instance, the most important morphological modification associated to burnings in cerrado woody plants is thick corky bark (Gottsberger and Silberbauer-Gottsberger, 2006). This attribute is widespread in tree and larger shrub species (Gottsberger and Silberbauer-Gottsberger, 2006), so that a clear phenotypic clustering of plants relative to bark thickness may not emerge in frequently burned cerrados. Frequent fires also reduce the height of woody species and, as a result, the range of height values (Moreira, 2000). Thus, the small range of some traits among cerrado plant species may prevent overall correlations between trait differences and species co-occurrences.

Our analysis indicated no clear pattern of phylogenetic clustering or overdispersion of the cerrado woody species. For a woodland cerrado in southeastern Brazil, we also did not find any pattern of species co-occurrence in relation to species phylogenetic relatedness (Silva and Batalha, 2009). The absence of a phylogenetic pattern, in these cases, may be due to random distributions of some functional traits in the phylogeny of species (Webb et al., 2002; Silvertown et al., 2006). Most of the functional traits we analysed are surrogates of habitat requirements in fire-prone vegetations (that is, bark thickness, leaf nutrient concentration, stem specific density; Cornelissen et al., 2003), which are expected to be conserved in the phylogeny of plant species (Prinzing et al., 2001). However, others, such as plant height and leaf specific area, are surrogates of growing coefficients (Cornelissen et al., 2003), which are not expected to present phylogenetic signal (Silvertown et al., 2006). Differences in

Table 3

Tests for phylogenetic signal of the functional traits of cerrado woody species, in Emas National Park, central Brazil. The observed variance and the mean of random variances of the phylogenetic independent contrasts are given. Significant values at $\alpha = 0.05$ are presented in bold face.

Trait	Observed variance	Random mean	P
Bark thickness	0.024	0.026	0.307
Basal area	0.018	0.027	0.054
Canopy height	0.019	0.026	0.107
Leaf dry matter content	0.020	0.026	0.180
Leaf N concentration	0.021	0.027	0.158
Leaf P concentration	0.017	0.026	0.023
Plant height	0.017	0.026	0.029
Specific leaf area	0.026	0.098	0.048
Stem specific density	0.015	0.026	0.007

the values of these traits are important for species coexistence to be possible, mainly at fine spatial scales, where the species interactions are stronger (Silvertown et al., 2006). As a consequence, a clear phylogenetic pattern in the co-occurrence of plant species may not emerge at fine spatial scales.

Moreover, other factors may also account for the low phylogenetic signal of functional traits compared to morphological or physiological ones (Freckleton et al., 2002), which present a wide-spread conservatism on plant lineages (Ackerly, 2003). The temporal and geographical variation, as well as poor estimates taken from few populations, may introduce error in analysis of trait evolution (Losos, 2008). Further studies on evolution of functional traits in cerrado plants should consider a higher number of species and of traits, analysing traits of species from distinct places to confirm our findings.

It is worth noticing that environmental filters are more commonly observed at large spatial scales (Chase, 2003; Pausas and Verdú, 2008). At fine spatial scales, competition and facilitation are thought to be the most important ecological processes (Cavender-Bares et al., 2006; Slingsby and Verboom, 2006). However, the effects of environmental filtering at fine spatial scale have been recently investigated (Silva and Batalha, 2009). For example, Fukami et al. (2005) demonstrated that experimental plant communities in small plots converged similar functional traits under similar environmental constraints irrespective of the initial specific composition. Here, we also observed phenotypic attraction under a severe environmental constraint, that is, under high fire frequencies. Thus, environmental filters are also important at fine spatial scales.

Finally, fire is a strong environmental filter in savannas and also determines the species co-occurrence at fine spatial scales. High fire frequencies tend to assemble plant species with similar niches. Under low fire frequencies, plant species with different niches tend to co-occur. However, fire may not drive phylogenetic clustering of species, as expected for larger spatial scale (Verdú and Pausas, 2007). Thus, the pattern of species co-occurrence at fine spatial scale was independent, to a certain extent, of the evolutionary history of the functional traits in the cerrado.

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