

Co-occurrence of tree species at fine spatial scale in a woodland cerrado, southeastern Brazil

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Abstract Species co-occurrence at fine spatial scales is expected to be nonrandom in relation to species phylogenetic relatedness and functional similarity. On the one hand, closely related species that occur together and experience similar environmental conditions are likely to share phenotypic traits due to the process of environmental filtering. On the other hand, species that are too similar are unlikely to co-occur due to competitive exclusion. We surveyed a woodland cerrado, southeastern Brazil, to test whether co-occurrence in tree species shows functional or phylogenetic structuring at fine spatial scale. Searching for correlations between an index of species co-occurrence and both functional trait differences and phylogenetic distances, we provided evidence for a predominant role of environment filters in determining the co-occurrence of functionally similar tree species in cerrado. However, we did not find any effect of phylogenetic relatedness on tree species co-occurrence. We suggest that the phylogenetic relatedness of co-occurring cerrado tree species did not present a pattern, because the species functional traits were randomly distributed on the phylogeny. Thus, phylogenetic relatedness and functional similarity do not seem to limit the

co-occurrence at fine spatial scale of cerrado tree species.

Keywords Competitive exclusion · Environmental filter · Functional trait · Phylogenetic relatedness · Species co-occurrence

Introduction

The Brazilian cerrado is the major savanna region in America and once covered about 2 million km² (Gottsberger and Silberbauer-Gottsberger 2006). The interaction and occurrence of several environmental constraints are thought to determine the origin and richness of the cerrado flora (Sarmiento and Monasterio 1975). The cerrado is under a seasonal climate and experiences a pronounced dry season (Gottsberger and Silberbauer-Gottsberger 2006). Its soils are poor in nutrients and acidic, with low cation exchange capacities and high levels of aluminum saturation (Gottsberger and Silberbauer-Gottsberger 2006). The cerrado also undergoes frequent fires that consume mainly the grassy ground layer and limit the development of seedlings of woody species (Gottsberger and Silberbauer-Gottsberger 2006). Despite these environmental filters, the cerrado presents one of the richest floras of the tropics (Mittermeyer et al. 1999), with up to 7,000 vascular plant species (Castro

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et al. 1999). This rich flora is spatially distinct and heterogeneous, with more than half of its woody species being found in restricted floristic provinces (Bridgewater et al. 2004). Thus, understanding the origin and maintenance of the cerrado floristic richness rests partly on understanding the processes that govern local co-occurrence of species.

Two major ecological processes are thought to determine the local co-occurrence of species: competitive interactions and environmental filtering (Webb et al. 2002; Watkins and Wilson 2003; Cavender-Bares et al. 2006). Competitive interactions are expected to limit the ecological similarity of locally co-occurring species, because competition should be greater among species that share more functional traits and have consequently similar niches (Hutchinson 1959; Leibold 1998). In contrast, environmental filters, by selecting for functionally similar species on the basis of their tolerance to abiotic conditions, are expected to assemble co-occurring species with very similar functional traits (Chase 2003; Fukami et al. 2005). Weiher and Keddy (1995) postulated that limiting similarity should have greater importance at smaller spatial scales, whereas environmental filtering should predominate at larger spatial scales. Evidence in literature is sparse and inconclusive: whereas some studies show that locally co-occurring species differ more than what is expected by chance (e.g., Bowers and Brown 1982), some show the opposite (e.g., Jackson et al. 1992, Letcher et al. 1994), and others show no difference at all (e.g., Ricklefs and Travis 1980; Watkins and Wilson 2003). Consequently, the relative role that the competition and the environmental filters play in determining the functional similarity of locally co-occurring species remains unclear.

Phylogenetic approaches on community structure may provide insights into the contemporary processes that govern the spatial distribution of species (Webb et al. 2002). Wherever 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) and environmental filtering is the dominant ecological process (Weiher and Keddy 1995; Webb 2000), levels of co-occurrence among closely related species are expected to be high (phylogenetic clustering, Webb et al. 2002). On the other hand, where functional traits are phylogenetically

conserved and competition for limited resources is the main ecological process, closely related species are expected to show low levels of co-occurrence (phylogenetic overdispersion, Webb et al. 2002), due to competitive exclusion of one or more functionally similar species (Leibold 1998; Watkins and Wilson 2003). Nevertheless, where functional traits evolved convergently and closely related species are functionally different, environmental filtering is expected to favor co-occurrence of more distantly related species (Webb et al. 2002). Competition, in this case, should remove any systematic associations, resulting in community assemblages indistinguishable from random (Silvertown et al. 2006).

The phylogenetic structure of communities is expected to depend on the phylogenetic and spatial scale at which the community is defined (Cavender-Bares et al. 2004, 2006; Swenson et al. 2006). Studies conducted at fine scales have found patterns of phylogenetic overdispersion (Cavender-Bares et al. 2004, 2006; Slingsby and Verboom 2006), whereas studies at broad scales have revealed patterns of phylogenetic clustering (Webb 2000; Horner-Devine and Bohannan 2006). However, we did not find any study examining patterns of phylogenetic dispersion of cerrado tree species at fine spatial scales. We searched for correlations of co-occurrence indices with phylogenetic distances and functional differences calculated for every possible pair of tree species. Here, we investigated patterns of local co-occurrence among cerrado tree species in relation to their phylogenetic relationships and functional traits. In order to test whether species co-occurrence was phylogenetically or functionally structured, we estimated levels of co-occurrence between pairs of species and compared those levels to pairwise phylogenetic distances and functional trait differences. In order to assess the relative importance of trait conservatism or convergence in generating the phylogenetic clustering or overdispersion of co-occurring species, we tested whether the plant functional traits were phylogenetically conserved. We expected that fine spatial analyses could reveal the role that competition and environmental constraints play in determining the co-occurrence of cerrado tree species. We addressed two main questions: (1) Are the levels of co-occurrence of cerrado tree species correlated with the phylogenetic distances and functional differences? (2) Are the

functional traits conserved among cerrado tree species?

Methods

Study site

We surveyed a woodland cerrado site (approximately at 22°13' S, 47°51' W), in municipality of Itirapina, São Paulo State, southeastern Brazil. The area belongs to the São Paulo State Forestry Institute. Regional climate is mesothermic, subtropical, with rainy summer and not severely dry winter (Cwa, Köppen 1931). In the site, there is a permanent grid with 200 quadrats (each one with 25 m²), from which we randomly picked 50. In March and April 2007, in the last months of the rainy season, we sampled all trees with stem diameter at soil level equal to or larger than 3 cm (SMA 1997). We identified the sampled species by comparing the collected material to vouchers lodged at the Federal University of São Carlos and State University of Campinas herbaria.

Functional trait data

We assessed whole-plant, leaf, and stem vegetative traits of all individuals sampled. These soft functional traits (i.e., traits that are relatively easy and quick to quantify, Hodgson et al. 1999) may be used as surrogates for more accurate indicators of plant functional responses, such as growth coefficients and fire or light requirements (Cornelissen et al. 2003). We first measured whole-plant traits: basal area and height. Basal area is a trait positively related to space occupation, resource uptake, total biomass (Vertessy et al. 1995), and reproducing capability (Hoffmann 1998). Height is associated to competitive value, fecundity, interval between two perturbations, tolerance to stress, underground biomass, root depth, lateral ramification, and leaf size (Cornelissen et al. 2003). We considered the height of the individuals as the least distance between the upper limit of the photosynthetic tissues and the soil (Cornelissen et al. 2003).

We measured leaf dry matter content (LDMC) and specific leaf area (SLA). Leaves with high LDMC tend to be tough and are thus assumed to be more resistant to physical hazard (Cornelissen et al. 2003).

SLA is positively related to maximum photosynthetic rates, since low values of SLA correspond to a high leaf structure investment (Cornelissen et al. 2003). In order to calculate these leaf traits, we collected two fully expanded leaves from each individual, with herbivory and pathogen damage as low as possible, considering the petiole as part of the leaf (Cornelissen et al. 2003). We placed the leaves in plastic bags and stored them in a cool box. Then, we took the leaves as quickly as possible to the laboratory, where we weighed and scanned them. We measured leaf area using the ImageJ 1.33 software (Rasband 2004). Afterwards, we oven-dried the leaves at 80°C for 72 h and weighed them again. Finally, we computed LDMC and SLA according to Cornelissen et al. (2003).

We also assessed leaf macro- (N, P, K, Ca, Mg, and S) and micronutrients (Cu, Fe, Mn, and Zn) concentrations. Leaf nutrient content is overall related to plant nutrient use efficiency (Larcher 1994; Cornelissen et al. 2003). Macronutrients concentrations are also associated with nutritional quality to the consumers in food webs (Cornelissen et al. 2003), which may determine pollination and dispersal success of tree species (Bawa et al. 1985; Nathan and Muller-Landau 2000). For each individual, we collected about 30 g of healthy adult leaves and oven-dried them without petioles and rachis at 80°C for 72 h. Leaf nutrient content analyses were conducted at the Soil Sciences Laboratory of the University of São Paulo.

We also measured bark thickness and stem specific density (SSD). A thick bark provides protection to vital tissues against attack by pathogens, herbivores, fire, and drought (Cornelissen et al. 2003). SSD seems to be central in a trade-off between plant relative growth rates (high rate at low SSD) and stem defenses (high defense at high SSD). In combination with plant size traits, it also plays an important global role in the aboveground storage of carbon (Cornelissen et al. 2003). In order to calculate these stem traits, we took, for each individual, four measures of bark thickness at 0.5 m individual high. The bark was defined here as everything external to the wood (i.e., any vascular cambium, secondary phloem, secondary cortex, cork, Cornelissen et al. 2003). We then cut out a 10 cm-long section of a healthy stem and placed them in plastic bags. We stored the stems in a cool box and weighed them as quick as possible in the laboratory. We obtained the volume of the stem

sections by the replacement volume method (see Cornelissen et al. 2003 for details). Lastly, we also computed the SSD according to Cornelissen et al. (2003).

The trait values of each species were expressed as averages considering all individuals sampled in each species. We conducted the subsequent analyses in two ways: (1) excluding the rare species with fewer than five individuals in the sample, as recommended by Cornelissen et al. (2003), and (2) including them. Even at the risk of losing accuracy and precision, the inclusion of the rare species increases the generalization power of our predictions (Westoby 1999; Vepsäläinen and Spence 2000). In this approach, overall differences among species are more important than exact magnitudes of species traits (Vepsäläinen and Spence 2000).

Phylogenetic data

We constructed a phylogenetic tree for all species by using the Phylomatic software, a phylogenetic database and toolkit for the assembly of phylogenetic trees (Webb and Donoghue 2005). The tree generated was based on information from numerous published molecular phylogenies (Fig. 1, Phylomatic reference tree R20050610) with the APG II (Angiosperm Phylogeny Group 2003). We assigned branch lengths to the phylogenetic tree using the BLADJ (Branch Length Adjustment) averaging algorithm of the Phylocom version 3.41 software package (Webb et al. 2007). The branch length was based on minimum ages of nodes determined for genera, families, and higher orders from fossil data (Wikström et al. 2001), by spacing undated nodes evenly between dated nodes in the tree.

We investigated whether the functional traits tended to be phylogenetically conserved or convergent in the phylogeny of local tree assemblage, using the analysis of traits module implemented in Phylocom (Webb et al. 2007). This method assesses trait evolution by comparing the standard deviations of the descendent trait means against a null hypothesis generated by randomizing the trait values across the tips of the local phylogenetic tree. The analysis of traits is used in tests to search for a phylogenetic signal, which is defined as the tendency for close relatives to resemble each other (Blomberg and Garland 2002). If trait evolution is conserved, then

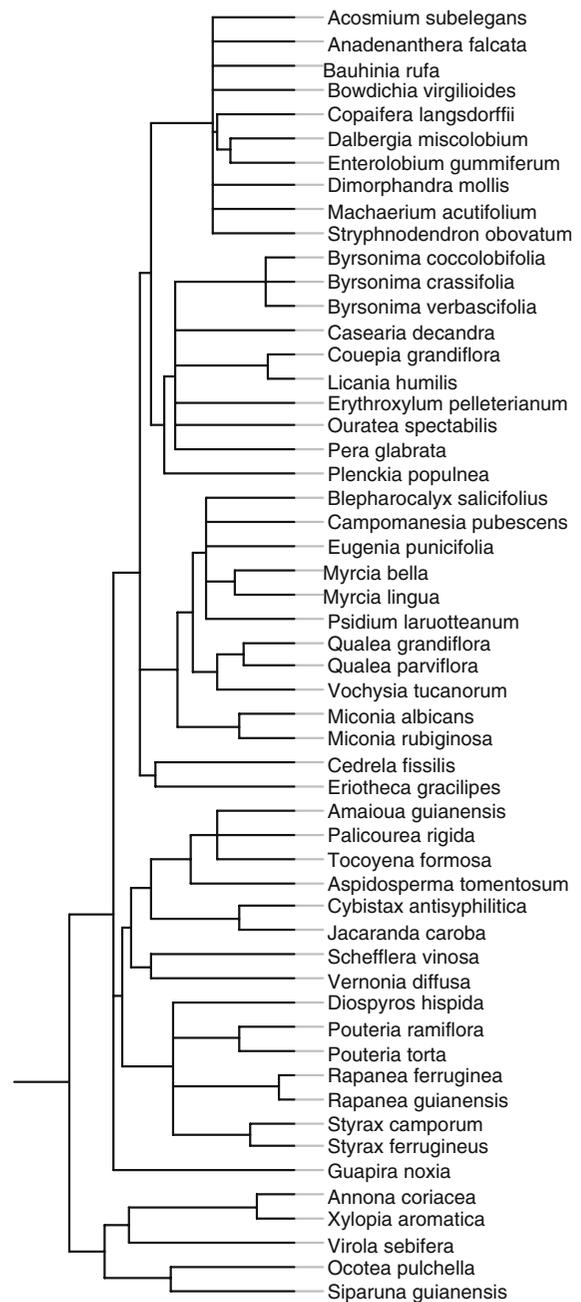


Fig. 1 Phylogenetic tree assembled for the cerrado tree species sampled in Itirapina, southeastern Brazil

divergences will be small and related species will be similar to each other, so that the average divergence deviation will be small relative to the null hypothesis (Webb et al. 2007). We used the trait values normalized by the standard deviation of the traits.

Tests of spatial phylogenetic structure and functional divergence

We examined the spatial phylogenetic structure of co-occurring cerrado trees by comparing the degree of co-occurrence of species pairs in the quadrats to the phylogenetic distance between them. 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 quadrat. We calculated the phylogenetic distances from the estimated intervening branch length distances (measured in millions of years) between all species pairs using the Phylocom 3.41 software package (Webb et al. 2007). Then, we compared the correlation coefficient between C values and phylogenetic distances of all species pairs to a null model, in which the phylogenetic relationships among species were randomized (Mantel test, Manly 2000). The Mantel test of associations was conducted on similarity pairwise species matrices, with 1,000 randomizations.

In order to investigate the potential influence of the competitive interactions on co-occurring species, we used a similar test by comparing the absolute value of mean pairwise differences in functional trait values to the degree of co-occurrence between species pairs. The observed correlation coefficients were tested against a null model, in which the values of species trait differences were randomized (Mantel test, Manly 2000). The Mantel test of associations was also conducted on similarity pairwise species matrices, with 1,000 randomizations. 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.

Results

We sampled 298 individuals comprising 54 tree species in the woodland cerrado site, of which only 30 were common, with more than five individuals sampled (Table 1, Fig. 1). In all analyses, we obtained the same overall result either with all species or with only the common ones. We did not find a

phylogenetic signal in the phylogeny of the species sampled. Change in the trait values across the phylogenetic tree was not different from random (Table 2). The mean value of the standard deviations at daughter nodes (divergences) across the phylogenetic tree for all traits was 0.386 (mean of the P values = 0.638) when considering all species and 0.488 (mean of the P values = 0.551) when considering the common ones. Consequently, phylogenetically close tree species were not functionally similar in cerrado.

The comparison between pairwise indices of species co-occurrence and phylogenetic distances showed non-significant levels of co-occurrence values among phylogenetically related species (Table 3), indicating that phylogenetic relatedness did not influence the co-occurrence of tree cerrado species. Alternatively, the comparison between pairwise indices of species co-occurrence and values of mean pairwise differences in functional trait values showed some significant levels of co-occurrence values among functionally similar species (Table 3). We found significant negative correlations between species co-occurrence and differences in leaf functional traits and some leaf nutrient contents, which imply that co-occurring cerrado tree species were in some aspects more functionally similar than would be expected by chance. However, we observed no significant correlations between levels of co-occurrence and whole-plant and stem functional traits. Thus, phylogenetic relatedness and functional similarity did not limit, in general, the co-occurrence at fine spatial scale of cerrado tree species.

Discussion

We explored the influence of phylogeny and functional traits on patterns of co-occurrence among cerrado tree species at fine spatial scale. We postulated that, when environmental filters are more important than competitive exclusion at fine spatial scale, functionally similar tree species will co-occur in local cerrado communities. We also postulated that, when the species functional traits are randomly distributed on the phylogeny, the phylogenetic relatedness of co-occurring cerrado tree species will not present a pattern. Nevertheless, since our expectations were based on local species frequencies, the

Table 1 Cerrado tree species sampled in Itirapina, southeastern Brazil

Family	Species
Annonaceae	<i>Annona coriacea</i> Mart.* <i>Xylopia aromatica</i> (Lam.) Mart.*
Apocynaceae	<i>Aspidosperma tomentosum</i> Mart.*
Araliaceae	<i>Schefflera vinosa</i> (Cham. and Schltld.) Frodin*
Asteraceae	<i>Vernonia diffusa</i> Less.
Bignoniaceae	<i>Cybistax antisiphilitica</i> Mart.* <i>Jacaranda caroba</i> (Vell.) DC.
Celastraceae	<i>Plenckia populnea</i> (Reiss.) Lund.
Chrysobalanaceae	<i>Couepia grandiflora</i> (Mart. and Zucc.) Benth and Hook. <i>Licania humilis</i> Cham. and Schl
Ebenaceae	<i>Diospyros hispida</i> A. DC.*
Erythroxylaceae	<i>Erythroxylum pelleterianum</i> A. St.-Hil.*
Euphorbiaceae	<i>Pera glabrata</i> (Schott.) Baill.
Fabaceae	<i>Acosmium subelegans</i> (Mohl.) Yakovlev* <i>Anadenanthera falcata</i> (Benth.) Speg.* <i>Bauhinia rufa</i> Steud.* <i>Bowdichia virgilioides</i> Kunth.* <i>Copaifera langsdorffii</i> Desf. <i>Dalbergia miscolobium</i> Benth.* <i>Dimorphandra mollis</i> Benth. <i>Enterolobium gummiferum</i> (Mart.) Macb. <i>Machaerium acutifolium</i> Vogel <i>Stryphnodendron obovatum</i> Mart.
Lauraceae	<i>Ocotea pulchella</i> Mart.*
Malpighiaceae	<i>Byrsonima coccolobifolia</i> Kunth* <i>Byrsonima crassifolia</i> (L.) Kunth <i>Byrsonima verbascifolia</i> Rich.
Malvaceae	<i>Eriotheca gracilipes</i> (K. Schum.) A. Robyns*
Melastomataceae	<i>Miconia albicans</i> (Sw.) Triana* <i>Miconia rubiginosa</i> (Bonpl.) DC.*
Meliaceae	<i>Cedrela fissilis</i> Vell.
Monimiaceae	<i>Siparuna guianensis</i> Aubl.
Myristicaceae	<i>Virola sebifera</i> Aubl.
Myrsinaceae	<i>Rapanea ferruginea</i> (Ruiz and Pav.) Mez <i>Rapanea guianensis</i> Aubl.*
Myrtaceae	<i>Blepharocalyx salicifolius</i> (Camb.) Burr.* <i>Campomanesia pubescens</i> (DC.) O. Berg. <i>Eugenia puniceifolia</i> (Humb., Bonpl. and Kunth) DC.* <i>Myrcia bella</i> Cambess. <i>Myrcia lingua</i> (O. Berg.) Mattos* <i>Psidium laruotteanum</i> Cambess.

Table 1 continued

Family	Species
Nyctaginaceae	<i>Guapira noxia</i> (Netto) Lundell*
Ochnaceae	<i>Ouratea spectabilis</i> (Mart.) Engl.*
Rubiaceae	<i>Amaioua guianensis</i> Aubl.* <i>Palicourea rigida</i> Kunth <i>Tocoyena formosa</i> (Cham. and Schltld.) K. Shum.*
Salicaceae	<i>Casearia decandra</i> Jacq.*
Sapotaceae	<i>Pouteria ramiflora</i> (Mart.) Radlk.* <i>Pouteria torta</i> (Mart.) Radlk.*
Styracaceae	<i>Styrax camporum</i> Pohl <i>Styrax ferrugineus</i> Nees and Mart.
Vochysiaceae	<i>Qualea grandiflora</i> Mart.* <i>Qualea parviflora</i> Mart. <i>Vochysia tucanorum</i> Mart.*

* Common species

patterns we found cannot predict processes operating at a regional scale, such as the allopatric distributions of species.

Functional similarity

Although competitive interactions are expected to limit the ecological similarity of locally co-occurring species (Hutchinson 1959; Leibold 1998; Watkins and Wilson 2003), species with similar functional traits are expected to co-occur where environmental filters are predominant (Chase 2003; Fukami et al. 2005). Based on these expectations, Weiher and Keddy (1995) postulated that limiting similarity should have greater importance at smaller spatial scales, whereas environmental filtering should predominate at larger spatial scales. However, our analyses indicated that functional similarity did not limit the co-occurrence at fine spatial scale of cerrado tree species. Consequently, environmental filters in the cerrado (e.g., drought, nutrient-poor soil, or fire, Gottsberger and Silberbauer-Gottsberger 2006) should define the co-occurrence of tree species at small scale.

In most of the leaf traits investigated, we observed a higher co-occurrence of similar tree species than expected by chance. Leaf functional traits may be used as surrogates of many important ecological processes (Westoby et al. 2002; Cornelissen et al.

Table 2 Analyses of functional trait evolution on the phylogeny of all cerrado tree species, in Itirapina (approximately 22°13' S, 47°51' W), Southeastern Brazil

Trait	Mean D	Low	High	<i>P</i>
Basal area	0.829	653	346	0.654
Height	0.928	686	313	0.687
Leaf dry matter content	0.663	664	335	0.665
Specific leaf area	0.889	791	208	0.792
Bark thickness	0.704	663	336	0.664
Stem specific density	0.464	343	656	0.343
Leaf N concentration	0.661	687	312	0.688
Leaf P concentration	0.634	676	323	0.677
Leaf K concentration	0.779	671	328	0.672
Leaf Ca concentration	0.693	683	316	0.684
Leaf Mg concentration	0.831	651	348	0.652
Leaf S concentration	0.893	661	338	0.662
Leaf Cu concentration	0.925	668	331	0.669
Leaf Mn concentration	0.432	359	640	0.359
Leaf Fe concentration	0.886	672	327	0.673
Leaf Zn concentration	0.933	675	324	0.676

Mean *D* = mean value of divergence deviations across phylogenetic tree; Low = number of means of random standard deviations lower than the means of observed standard deviations; High = number of means of random standard deviations higher than the means of observed standard deviations

2003). For example, species with high SLA can have strategies associated with rapid production of new leaves during early life, and the consequent faster turnover of plant leaves allows a more flexible response to the spatial patchiness of light and soil resources (Westoby et al. 2002). Conversely, species with low SLA can accumulate a greater mass of leaf and capture a great amount of light, and their long mean residence time of nutrients allows a larger share of the nitrogen pool to be sequestered (Westoby et al. 2002). For leaf nutrient concentration, the observed patterns could be due to local variation in nutrient distribution in the soil (Larcher 1994). However, considering that the nutrient distribution in the soil at fine-scale tends to be uniform (Cross and Schlesinger 1999), leaf nutrient content should be mainly related to plant nutrient use efficiency (Larcher 1994; Cornelissen et al. 2003). Thus, functionally similar tree species may be expected to co-occur at fine spatial scale in cerrado areas.

Table 3 Tests for spatial phylogenetic and functional structure of all co-occurring cerrado tree species sampled in Itirapina, southeastern Brazil. For each data set, the observed correlation coefficients (*r*) of the correlation matrices between co-occurrence indices and phylogenetic distances and functional differences are given

Data type	<i>r</i>	Low	High	<i>P</i>
Phylogenetic distance	0.014	466	434	0.434
Basal area	-0.043	377	623	0.337
Height	0.043	667	333	0.333
Leaf dry matter content	-0.171	14	986	0.014
Specific leaf area	-0.147	28	972	0.028*
Leaf N concentration	-0.099	112	888	0.112
Leaf P concentration	0.001	578	422	0.422
Leaf K concentration	-0.097	82	918	0.082
Leaf Ca concentration	-0.144	21	979	0.021*
Leaf Mg concentration	-0.220	1	999	0.001
Leaf S concentration	0.015	579	421	0.421
Leaf Cu concentration	-0.131	35	965	0.035*
Leaf Mn concentration	-0.267	1	999	0.001
Leaf Fe concentration	-0.144	1	999	0.001
Leaf Zn concentration	-0.180	1	999	0.001
Bark thickness	0.127	812	188	0.188
Stem specific density	0.128	825	175	0.175

The *P* values of Mantel statistical test are also given. Significant values at $\alpha = 0.05$ are in bold. * = non-significant values when we considered only the common species. Low = number of random correlation coefficients lower than the observed coefficients; High = number of random correlation coefficients higher than the observed coefficients

However, we did not find a significant departure from a null model when we took into account whole-plant and stem functional traits. The whole-plant and stem traits we measured are of functional significance for trees, mainly in terms of light capture, which must be an important aspect of survival in woodland cerrado sites (Cornelissen et al. 2003; Gottsberger and Silberbauer-Gottsberger 2006). We also examined a situation in which evidence for community structuring is most likely to be found, that is, at fine spatial scale within a relatively uniform habitat (Cavender-Bares et al. 2004, 2006, Slingsby and Verboom 2006). Finding evidence for whole-plant and stem functional similarity of co-occurring tree species at fine spatial scale would indicate evidence for a prevailing role of environmental filters in cerrado relative to competitive interactions. Nevertheless, the

absence of significant results in analyses of these traits is not an evidence for absence of environmental filtering in these functional traits. On the contrary, it may be a consequence of the complex interactions between these traits and environmental filters along the phylogenetic history of cerrado tree species.

Phylogenetic relatedness

The pattern of phylogenetic relatedness of co-occurring species depends mainly on the evolutionary history of species functional traits and the influence of these traits on the environmental filtering and species interactions (Webb et al. 2002). However, our analysis indicated no clear pattern of phylogenetic clustering or overdispersion at fine spatial scale. The non-significant correlation between co-occurrence and phylogenetic distance might be attributed either to the functional trait distribution indistinguishable from random on the investigated phylogeny (Webb et al. 2002; Kembel and Hubbell 2006) or to species interactions and environmental filtering operating in opposite directions with similar strength (Cavender-Bares et al. 2006). Environmental filtering in the cerrado seems to be predominant in tree assemblage structuring at fine spatial scale, since species sharing similar leaf functional traits co-occurred more than expected by chance. Thus, species phylogenetic relatedness may not limit tree co-occurrence in woodland cerrado sites mainly because of the random distribution of functional traits in the phylogeny of cerrado trees.

Although trait conservatism is widespread on plant lineages (Prinzing et al. 2001; Ackerly 2003; Reich et al. 2003), random trait distributions are expected in large plant communities, where trait evolution is a complex mix of conservatism and convergence (Webb et al. 2002). This may also be expected in cerrado communities. It is recognized, for example, that vicariants rainforest species, with long and different phylogenetic histories, constitute an important element of the woody component of the cerrado flora (Gottsberger and Silberbauer-Gottsberger 2006). Some of these vicariants species belong to genera sampled were: *Annona*, *Aspidosperma*, *Bauhinia*, *Blepharocalyx*, *Diospyros*, *Jacaranda*, *Licania*, *Ouratea*, *Palicourea*, *Qualea*, and *Xylopia*. Overall, these vicariants rainforest species converged functional traits similar to typical cerrado species, such as the strong suberization of trunks and branches

(Gottsberger and Silberbauer-Gottsberger 2006). As a consequence, a clear pattern of trait conservatism or convergence on the tree cerrado phylogeny may be hard to detect. In cases of random trait distributions on phylogeny, the effects of competitive interactions and environmental filters on phylogenetic relatedness of species assemblages cannot be clearly assessed, and the community structuring may be attributed to stochastic evolution of community traits (Hubbell 2001, Kembel and Hubbell 2006).

On the contrary, some recent studies have found a phylogenetic overdispersion at fine spatial scales (Cavender-Bares et al. 2004, 2006, Slingsby and Verboom 2006), suggesting that the observed spatial patterns were generated by past competitive exclusion among close relatives. However, these studies focused on phylogenetic analyses of many congener species (e.g., 17 *Quercus* species, Cavender-Bares et al. 2004; 22 *Tetradlea* species, Slingsby and Verboom 2006). Here, we investigated few congener species and found a random pattern of phylogenetic structuring. We included in our phylogenetic analysis tree species from distinct clades, with no clear trait conservatism. The pattern of phylogenetic structure of the plant communities depends on the phylogenetic scale at which the community is defined (Cavender-Bares et al. 2006). Thus, the pattern of phylogenetic dispersion at fine spatial scale may also depend on phylogenetic scale at which the community is defined.

In communities subjected to intense abiotic conditions, with high species richness, such as the cerrado, distantly related clades with similar traits may be common. For example, in the California chaparral, many plant species from distantly related clades co-occur and share many similar trait values related to drought and disturbance (Ackerly 2004). This common convergence of traits in distantly related species generates frequently random phylogenetic structures in species-rich assemblages (Kraft et al. 2007). With a simulation framework to model trait evolution, Kraft et al. (2007) suggested that a greater number of clades will evolve similar trait values solely by chance in rich-species communities. Therefore, the random pattern of phylogenetic relatedness of the co-occurring tree species may be also a consequence of the high richness in the cerrado flora.

Finally, because communities may be structured by a combination of several community assembly

processes acting simultaneously or in sequence (Silvertown et al. 2006; Kraft et al. 2007), it is useful to include as many different kinds of functional traits and species as possible that might contribute to ecological filtering and interactions among species. The cerrado presents a rich tropical flora, with twice the number of herbaceous species than woody ones (Castro et al. 1999). The cerrado species present many pollination and dispersal traits (Oliveira and Gibbs 2000, Gottsberger and Silberbauer-Gottsberger 2006), which are also expected to influence the co-occurrence of species (Bawa et al. 1985, Nathan and Muller-Landau 2000). Thus, to allow more accurate predictions about the processes determining the spatial species distribution and trait evolution, future studies in cerrado should include both herbaceous and woody species, as well as reproductive traits in phylogenetic analysis.

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