Phylogenetic overdispersion of plant species in southern Brazilian savannas

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(With 1 figure)

Abstract

Ecological communities are the result of not only present ecological processes, such as competition among species and environmental filtering, but also past and continuing evolutionary processes. Based on these assumptions, we may infer mechanisms of contemporary coexistence from the phylogenetic relationships of the species in a community. We studied the phylogenetic structure of plant communities in four cerrado sites, in southeastern Brazil. We calculated two raw phylogenetic distances among the species sampled. We estimated the phylogenetic structure by comparing the observed phylogenetic distances to the distribution of phylogenetic distances in null communities. We obtained null communities by randomizing the phylogenetic relationships of the regional pool of species. We found a phylogenetic overdispersion of the cerrado species. Phylogenetic overdispersion has several explanations, depending on the phylogenetic history of traits and contemporary ecological interactions. However, based on coexistence models between grasses and trees, density-dependent ecological forces, and the evolutionary history of the cerrado flora, we argue that the phylogenetic overdispersion of cerrado species is predominantly due to competitive interactions, herbivores and pathogen attacks, and ecological speciation. Future studies will need to include information on the phylogenetic history of plant traits.

Keywords: assembly rules, cerrado, competitive exclusion, phylogenetic overdispersion, phylogenetic structure.

Dispersão filogenética de espécies de plantas em savanas no Sudeste do Brasil

Resumo

Comunidades ecológicas resultam não somente de processos ecológicos atuais, como a competição e os filtros ambientais, mas também de processos evolutivos passados e contínuos. Com base nessas premissas, podemos inferir mecanismos de coexistência contemporânea a partir das relações filogenéticas das espécies em uma comunidade. Estudamos a estrutura filogenética das comunidades de plantas de quatro áreas de cerrado, no Sudeste do Brasil. Calculamos duas medidas das distâncias filogenéticas das espécies amostradas. Estimamos a estrutura filogenética comparando suas distâncias observadas com a distribuição dessas distâncias em comunidades nulas. Obtivemos comunidades nulas aleatorizando as relações filogenéticas do banco regional de espécies. Encontramos uma dispersão filogenética de espécies de cerrado. Há várias explicações para essa dispersão, dependendo da história filogenética dos traços e das interações ecológicas contemporâneas. Entretanto, com base nos modelos de coexistência entre árvores e gramíneas, nas forças ecológicas dependentes da densidade e na história evolutiva da flora do cerrado, argumentamos que a dispersão filogenética das espécies do cerrado é predominantemente devida às interações competitivas, aos ataques de herbívoros e patógenos e à especiação ecológica. Estudos futuros precisarão incluir informações sobre a história filogenética dos traços das plantas.

Palavras-chave: regras de assembleia, cerrado, exclusão competitiva, dispersão filogenética, estrutura filogenética.

1. Introduction

Ecological communities are assemblages of co-occurring species that potentially interact with one another. They are the result of not only present ecological processes, such as competition among species (Hutchinson, 1959; Leibold, 1998) and environmental filtering (Weiher and Keddy, 1995; Chase, 2003), but also past and continuing evolutionary processes (Tofts and Silvertown, 2000; Ackerly, 2003; Reich et al., 2003).

Based on these assumptions, Webb et al. (2002) proposed a logical framework to infer mechanisms of contemporary coexistence: if functional traits are conserved in the evolution of species lineages (i.e. traits are more similar between closely related species; Ackerly, 2003; Reich et al., 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). On the other hand, if 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), because of the competitive exclusion of one or more functionally similar species (Leibold, 1998). Nevertheless, if functional traits evolve convergently and closely related species tend to be functionally different, environmental filtering is expected to favour co-occurrence of more distantly related species (Webb et al., 2002). Competition, in this case, is expected to remove any systematic associations, resulting in assemblages indistinguishable from random (Webb et al., 2002).

In addition, the phylogenetic structure of a community is also expected to depend on phylogenetic and spatial scale at which the community is defined (Cavender-Bares et al., 2004; 2006; Swenson et al., 2006) and on density-dependent forces such as attacks by specialist herbivores or pathogens (Becerra, 2007; Gilbert and Webb, 2007). Studies conducted on small scales (local communities) have frequently found patterns of phylogenetic overdispersion (Cavender-Bares et al., 2004; 2006; Slingsby and Verboom, 2006). This phylogenetic overdispersion occurs because competition among species is greater on small spatial scales than large scales, limiting the co-occurrence of close relatives (Slingsby and Verboom, 2006). Likewise, herbivores and pathogens may also promote a phylogenetic overdispersion of plant communities (Becerra, 2007; Gilbert and Webb, 2007). The likelihood that a herbivore or a pathogen can infect two plant species decreases continuously with phylogenetic distance between the plants (Becerra, 2007; Gilbert and Webb, 2007). As a consequence, herbivores and pathogens acting as a density-dependent force tend to constrain the co-occurrence of close relatives.

The Brazilian Cerrado is the major savanna region in America and once covered about 2 million km^2, mainly in the Brazilian Central Plateau (Gottsberger and Silberbauer-Gottsberger, 2006). Disjunct areas also occur in the southern boundaries of its domain, such as in São Paulo state (Durigan et al., 2003). The cerrado has a seasonal climate and experiences a pronounced dry season (Gottsberger and Silberbauer-Gottsberger, 2006). The soils are nutrient poor 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, prejudicing seedling development of woody species (Gottsberger and Silberbauer-Gottsberger, 2006). Despite these environmental constraints, however, the cerrado presents one of the richest floras of the tropics (Mittermayer et al., 1999). This rich cerrado 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 cerrado floristic richness rests partly on understanding the phylogenetic structure of local cerrado communities.

Recent studies have investigated the phylogenetic structure of plant communities (Webb, 2000; Cavender-Bares et al., 2004; 2006). However, we did not find any study examining the phylogenetic structure of cerrado plant communities. About half of the cerrado flora is endemic and represented by many congeners (Gottsberger and Silberbauer-Gottsberger, 2006). This suggests that cerrado plant species evolved predominantly in situ (Pennington et al., 2006). In these particular areas of high endemism and with little influence of surrounding different floras, ecological speciation tends to generate a pattern of species phylogenetic overdispersion (Gillespie, 2004; Pennington et al., 2006). Here, we investigated the phylogenetic structure of local plant communities in four cerrado areas, in southeastern Brazil. We tried to answer a main question: Is the phylogenetic structure of the studied cerrado areas overdispersed relative to a regional pool of species?

2. Material and Methods

2.1. Data collection

We surveyed a cerrado site at Itirapina, São Paulo state, southeastern Brazil, approximately at 22° 13' S and 47° 51' W, 760 m above sea level. The site is a woodland cerrado, classified as cerrado *sensu stricto* following Coutinho's (1978) classification. According to Köppen's (1931) system, the climate is Cwa, that is, macrothermic temperate with rainy summer and not severely dry winter. The area belongs to the São Paulo state Forestry Institute. In this site, there is a permanent grid of 200 plots (each one with 25 m^2), of which we randomly selected 50. In these 50 plots, we sampled all plants in the reproductive period, in 12 monthly surveys, from August 2005 to July 2006. In the last survey, we also sampled the species that we did not find previously in the reproductive stage. We identified the sampled species by comparing the collected material to vouchers deposited at the Federal University of São Carlos and State University of Campinas herbaria.

We also compiled the species from floristic surveys carried out in another three cerrado areas in São Paulo state: in 1) Botucatu city (22° 50' S and 48° 29' W; Gottsberger and Silberbauer-Gottsberger, 2006), where 1 ha of cerrado woodland was sampled; 2) Moji-Guaçu city (21° 15' S and 47° 08' W; Mantovani, 1983), where about 300 ha of cerrado ranging from shrub savanna to

woodland were sampled; and 3) Santa Rita do Passa Quatro city (21° 38' S and 47° 37' W; Batalha and Mantovani, 2001), where about 1200 ha of cerrado ranging from savanna woodland to woodland were sampled. All these floristic surveys were taken under the same regional climate (Cwa; Köppen, 1931) and dystrophic soil conditions, and sampled all life-forms of cerrado species.

2.2. Regional pool of species

Species pool may be defined as 'a set of species that are potentially capable of coexisting in a certain community' (Eriksson, 1993). Consequently, a species pool is ecologically delineated and is related to a given community type, the 'target community' (Pärtel et al., 1996). Southern cerrado areas are assembled in a distinct floristic province (the southern province; Bridgewater et al., 2004). These areas present the plant species whose presence defines the vegetation type, as well as the characteristic species of the southern cerrado province (about 12% of the cerrado flora; Bridgewater et al., 2004). Considering that the studied cerrado sites (the target communities) belong to the southern province and their species are potentially capable of occurring in the entire province (Bridgewater et al., 2004), we determined the regional pool of species as the sum of species of the four sites.

According to Kraft et al. (2007), the size of the local community in relation to that of the regional pool influences the power of the phylogenetic analysis of plant community structure. In general, the greatest power is obtained for communities of intermediate size, ranging from approximately 30 to 60% of the pool. Therefore, caution should be taken in rejecting the null hypothesis in cases where the community is very species poor or rich in relation to the regional pool (Kraft et al., 2007).

2.3. Phylogenetic data

We constructed a phylogenetic tree for the all species by using 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 (Figure 1; Phylomatic reference tree R20050610). 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 in the tree evenly between dated nodes. This was done using an averaging algorithm in Phylocom (Webb et al., 2007) called BLADJ (Branch Length Adjustment).

2.4. Community phylogenetic structure

We conducted all analyses of community phylogenetic structure by using the Phylocom 3.41 software package (Webb et al., 2007). We calculated two raw phylogenetic distances among the species of each site. Each phylogenetic distance captures a different aspect of the species phylogenetic relatedness (Webb, 2000).

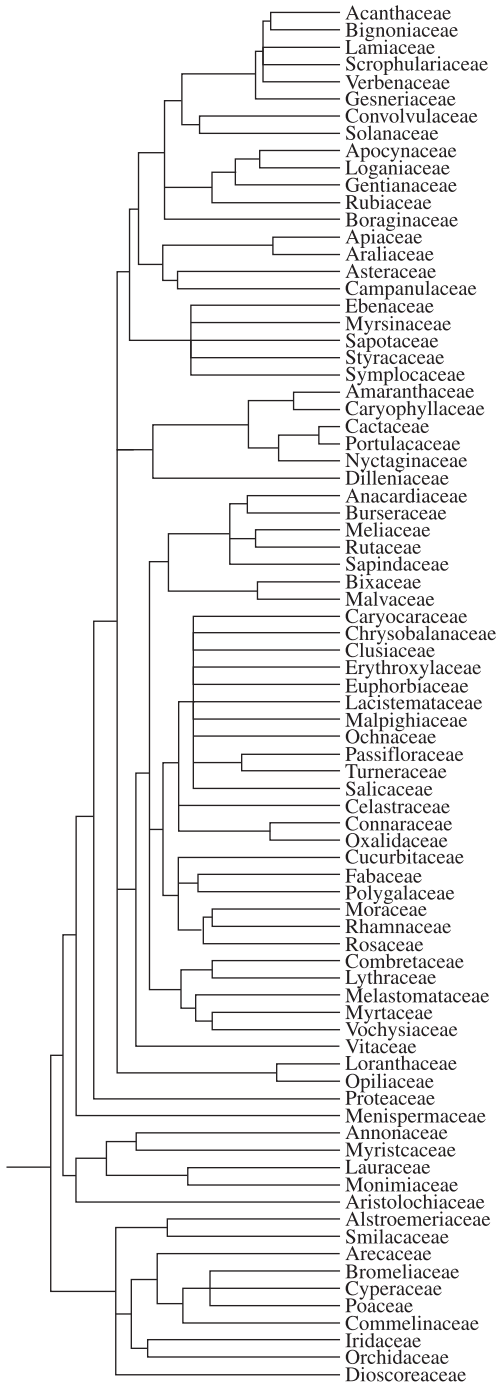

Figure 1. Summary of the phylogenetic tree assembled for the cerrado species, southeastern Brazil. The relationship among families was based on Phylomatic reference tree R20050610 (Webb and Donoghue, 2005).

The mean pairwise distance (MPD) was calculated as the mean phylogenetic distance among all pairwise combinations of species, and the mean nearest neighbor distance (MNND) was calculated as the mean phy-

logenetic distance to the nearest relative for all species (Webb, 2000). Both MPD and MNND were reported in terms of millions of years (million year).

To determine whether the phylogenetic structure of the cerrado sites differed from the phylogenetic community structure expected by chance, we compared observed phylogenetic distances among species to the distribution of phylogenetic distances for randomly generated null communities (Gotelli and Graves, 1996). We generated null communities by randomizing the phylogenetic relationships among species. This procedure is implemented in Phylocom, which shuffles species labels across the entire phylogeny (Webb et al., 2007). This null model assumes that all species of the regional pool are equally able to colonize any plot within the region, whether in cerrado or not.

Then, we calculated the net relatedness index (NRI) and the nearest taxon index (NTI; Webb, 2000). The NRI was defined as $[-(MPD - MPD_{null})/sd.MPD_{null}]$, where MPD_{null} was the mean MPD for the cerrado species from 999 null communities and $sd.MPD_{null}$ was the standard deviation of MPD for the cerrado species from these 999 null communities (Webb et al., 2007). NRI has been proposed as a measure of tree-wide phylogenetic distance of species (Webb, 2000). Positive NRI scores indicate that species occurring together are more phylogenetically related than expected by chance. Negative NRI scores indicate that co-occurring species are less phylogenetically related than expected by chance. The NTI was defined as $[-(MNND - MNND_{null})/ sd.MNND_{null}]$, where $MNND_{null}$ was the mean MNND for the cerrado species from 999 null communities and $sd.MNND_{null}$ was the standard deviation of MNND for the cerrado species from these 999 null communities (Webb et al., 2007). NTI has been proposed as a measure of terminal (branch tip) phylogenetic clustering of species on a phylogeny (Webb, 2000). NTI scores tend to be positive due to this terminal phylogenetic clustering of species when species occur together with other closely related species (e.g., with congeners or confamilials). When species do not occur together with other closely related species, NTI scores tend to be negative.

3. Results

We sampled 103 plant species belonging to 38 families in Itirapina, southeastern Brazil. We included in the regional pool 764 plant species belonging to 80 families (Figure 1), following the Angiosperm Phylogeny Group's (2003) classification. The percentage of sampled species in Itirapina, Botucatu, Moji-Guaçu, and Sta Rita do Passa Quatro relative to that of the regional pool were respectively 13.5, 36.6, 67.3, and 46.3%.

We found an overall phylogenetic overdispersion in the cerrado sites. The MPDs of the plant species in the cerrado sites were larger than expected by chance (Table 1, $p < 0.05$). The mean value of the MPDs was 254.153 ± 2.546 million year. The mean value of the NRIs was smaller than zero (-3.784 ± 1.087). Thus, the cerrado species seem to be separated by more nodes than expected by chance. However, only the MNNDs of the species in Itirapina and Sta Rita do Passa Quatro were larger than expected by chance ($p < 0.05$). In the other sites, the MNNDs were not different from random (Table 2). The mean value of the MNNDs was 65.163 ± 14.055 million year. The mean value of the NTIs was smaller than zero (-1.186 ± 1.274). As a consequence, there was a tendency of the species to not occur together with congeners.

4. Discussion

We assessed the phylogenetic relationship of cerrado species and found a phylogenetic overdispersion. Considering that plant species show commonly a high degree of evolutionary stasis (Qian and Ricklefs, 2004) and niche conservatism (Ackerly, 2003; Reich et al., 2003), we suggest three explanations for this pattern of phylogenetic structure: 1) competitive exclusion of close relatives (Cavender-Bares et al., 2004, 2006); 2) attacks by specialist herbivores or pathogens (Becerra, 2007; Gilbert and Webb, 2007); and 3) ecological speciation of populations that evolved in situ (Pennington et al., 2006).

The cerrado plant community might be predominantly assembled by competitive interactions. In this case, competitive exclusion between co-occurring species may limit the coexistence of closely related plants within a cerrado site (Webb et al., 2002; Cavender-Bares et al., 2006). The knowledge of cerrado plant interactions is far from reasonable and much of our comprehension comes from studies of other savannas (Gottsberger and Silberbauer-Gottsberger, 2006). The theory of species coexistence in these savannas has been based on competition models between two functional groups, grasses and trees (Sankaran et al., 2004). According to these models, water and nutrients are the main resources for which they compete: grasses and trees coexist because of their differential ability to acquire and partition these resources (Sankaran et al., 2004). For instance, grasses and trees have a root niche separation because they explore different soil profiles (Langevelde et al., 2003) and a phenological niche separation because they bloom, crop, and shoot in different periods of the year (House et al., 2003). Nevertheless, if the niche separation reduces the competitive interactions between grasses and trees (Sankaran et al., 2004), it is expected that, within these two functional groups, the competition is larger and causes exclusion of close relatives (Leibold, 1998). We analysed the phylogenetic structure of grass and trees species of cerrado and the phylogenetic overdispersion we found supports this expectation.

In addition, we observed a small tendency of the species to not occur together with congeners. Competition for limited resources may lead to exclusion of closely related species when the functional traits are conserved in the plant lineages (Webb et al., 2002), resulting in a pattern of terminal phylogenetic overdispersion in the phylogenetic trees of local communities (Webb, 2000).

Table 1. Number of species, observed mean pairwise phylogenetic distance (MPD), mean MPD for the cerrado species from 999 null communities (MPDnull), standard deviation of the MPDnull (sd.MPDnull), and the net relatedness index (NRI; Webb, 2000). Values of MPD, MPDnull, and sd.MPDnull are in millions of years. The p-value and the suggested pattern of phylogenetic structure for each cerrado site reflect the departure of the observed MPD value from the null model.

Site	n. species	MPD	MPDnull	sd.MPDnull	NRI	p	Pattern
Itirapina	103	254.684	245.669	4.504	–2.002	0.012	overdispersion
Botucatu	280	257.578	245.538	2.454	–4.905	0.001	overdispersion
Moji-Guaçu	514	250.709	245.602	1.301	–3.924	0.001	overdispersion
Sta Rita P. Quatro	356	253.640	245.619	1.863	–4.305	0.001	overdispersion

Table 2. Number of species, observed mean nearest neighbour distance (MNND), mean MNND for the cerrado species from 999 null communities (MNNDnull), standard deviation of the MNNDnull (sd.MNNDnull), and the nearest taxon index (NTI; Webb, 2000). Values of MNND, MNNDnull, and sd.MNNDnull are in millions of years. The p-value and the suggested pattern of terminal structure of the phylogenetic tree for each cerrado site reflect the departure of the observed MNND value from the null model.

Site	n. species	MNND	MNNDnull	sd.MNNDnull	NTI	p	Pattern
Itirapina	103	88.687	74.805	5.217	–2.661	0.006	overdispersion
Botucatu	280	60.631	59.900	2.105	–0.347	0.366	-
Moji-Guaçu	514	51.433	51.900	1.066	0.438	0.330	-
Sta Rita P. Quatro	356	59.900	56.289	1.660	–2.174	0.018	overdispersion

For that reason, the role of the environmental constraints in determining the phylogenetic structure of local cerrado communities may be secondary in some sites and the competitive exclusion may predominantly lead to a phylogenetic overdispersion of cerrado species.

Specialist herbivores or pathogens might limit the number of closely related species that can co-occur within a cerrado site. Due to a high degree of evolutionary stasis and niche conservatism in plants (Reich et al., 2003; Qian and Ricklefs, 2004), close relatives tend to share similar defence traits. Consequently, closely related species are more likely to be susceptible to the same herbivores and pathogens (Gilbert and Webb, 2007). Thus, herbivores and pathogens fed on several closely related congeneric plants, by acting as a density-dependent force, tend to assemble distantly related species. In cerrado, herbivores present a high degree of specificity (Marquis et al., 2002) and they may promote the assembly of distantly related plants in local communities as well.

The ecological speciation of the cerrado plants might also generate a species phylogenetic overdispersion. The high level of endemism and number of congeners in cerrado (Gottsberger and Silberbauer-Gottsberger, 2006) suggests that most of the evolutionary events of plants occurred in situ (Pennington et al., 2006). In these particular areas, ecological speciation tends to generate similar functional types in different lineages (Gillespie, 2004). When local environmental conditions constrain a community to a few functional types, they tend to assemble species with similar phylogenetic history of adaptation, but from different lineages (Gillespie, 2004), generating a pattern of species phylogenetic overdispersion. In oak forests in Florida, for instance, the ecological speciation of oak species has lead to phylogenetic overdispersion in oak lineages (Cavender-Bares et al., 2004). Taking into account that the cerrado-type climate has been around for 25 million years (Gottsberger and Silberbauer-Gottsberger, 2006), it seems to be a sufficient time for multiple colonizations in the cerrado environment by phylogenetically-divergent lineages. Furthermore, selection for traits that confer advantages in the cerrado habitat probably came at a cost, making it disadvantageous for plants to survive in other habitats. This increases the probability of ecological speciation in cerrado.

However, it is recognized that vicariant rainforest species constitute an important element of the woody component of the cerrado flora, which converges to similar niches of typical cerrado species (Gottsberger and Silberbauer-Gottsberger, 2006). Of 261 genera reported for the cerrado, 205 genera also have species in the Atlantic forest and 200 in the Amazon forests (Gottsberger and Silberbauer-Gottsberger, 2006). If cerrado congeners are more closely related to each other than to rainforest species, ecological speciation in situ must account for the observed pattern of phylogenetic overdispersion (Pennington et al., 2006). Alternatively, if rainforest and cerrado species are resolved as pairs of species, habitat switching must have played the predominant role in generating the woody cerrado species (Pennington et al., 2006). This issue deserves more attention in future investigations of phylogenetic history of cerrado plants.

Finally, competitive interactions among closely related plants, density-dependent forces, and ecological speciation may concomitantly generate the phylogenetic overdispersion of cerrado plants. However, species interactions with environmental filtering could give rise to this pattern of phylogenetic overdispersion, if functional traits evolve convergently and closely related species are functionally different (Webb et al., 2002). Further studies will need to include information on the functional traits of plant species as well as on the evolutionary history of these traits in cerrado to determine the relative importance of environmental filtering in structuring local cerrado communities.

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