Phylogenetic structure of Brazilian savannas under different fire regimes

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Abstract

Questions: Fire is a strong filter in fire-prone communities and is expected to assemble closely related species when functional traits are conserved in plant lineages. Do frequent fires assemble savannas with closely related species (phylogenetic clustering)? If so, what are the clades pruned by fire in the phylogenetic trees? Are species of semi-deciduous seasonal forests, where fires are not frequent, less related than expected by chance (phylogenetic overdispersion)? Are life forms conserved in the phylogeny of the species?

Location: Central and SE Brazilian savannas (Emas National Park, 18°18′S, 52°54′W; Brasília, 15°56′–15°57′S, 47°53′–47°56′W and Corumbataí-Itirapina, 22°13′–22°15′S, 47°37′–47°39′W); and close semi-deciduous seasonal forests (in Pirenópolis, 15°45′S, 49°04′W; Brasília, 15°33′S, 47°51′W; and São Carlos, 21°55′S, 47°48′W).

Methods: We recorded woody species in savannas under different fire regimes and in semi-deciduous seasonal forests. We obtained data from the literature and from field sampling. We compared mean phylogenetic distance of species of savanna and of nearby semi-deciduous seasonal forest sites. We obtained significance by randomizing the species among the tips of phylogenetic trees. We also assessed whether life forms were evolutionary conserved across phylogeny of the studied plants (phylogenetic signal) with tests based on the variance of phylogenetic independent contrasts.

Results: Some sites of savanna under high fire frequency were characterized by phylogenetic overdispersion of woody species whereas, in contrast, some sites of semi-deciduous seasonal forest were characterized by phylogenetic clustering. We found phylogenetic signals in the traits across the phylogeny of the 801 species investigated.

Conclusion: Fire may have different roles in assembling plant species in Brazilian savannas than in other fire-prone communities. We postulate that the absence of phylogenetic clustering in the cerrado is mainly due to the persistence of long-lived resprouting species from different plant lineages.

Keywords: Cerrado; Environmental filtering; Phylogenetic relatedness; Raunkiaer life-forms; Seasonal forest.

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Introduction

Fire is a strong evolutionary agent for plants (Bond & Midgley 1995; Schwilk & Ackerly 2001) and plays an important role in determining the distribution of savannas worldwide (Bond et al. 2005). Natural fires have occurred in savannas from the late Tertiary onwards (Bond et al. 2003). However, over the past 10 000 years, anthropogenic fires have extended areas of flammable vegetation (Bowman 1998; Brooks et al. 2004). Currently, fire-prone plant formations cover around 40% of the world's land surface (Chapin et al. 2002).

In South America, the Brazilian cerrado (Gottsberger & Silberbauer-Gottsberger 2006) is among the most extensive flammable communities on the planet (Bond & Keeley 2005). The cerrado originally covered 2 millions km^2, or approximately 23% of Brazilian territory (Gottsberger & Silberbauer-Gottsberger 2006). Like savannas in other countries, the cerrado evolved with fire (Simon et al. 2009), and the species present many adaptations, such as thick bark and underground meristems, which protect them from high temperatures and allow resprouting after fires (Gottsberger & Silberbauer-Gottsberger 2006). However, fire absence is expected to modify the vegetation structure of cerrado leading to shifts in vegetation physiognomies towards more closed forms (Moreira 2000). Even though fire may hinder plant diversity in fire-prone communities (Williams et al. 1999; Silva et al. 2001; Syphard et al. 2006; Pausas & Verdú 2008), the cerrado has one of the richest floras of the tropics (Mittermeyer et al. 1999), with up to 7000 vascular plant species (Castro et al. 1999). Thus,

understanding the maintenance of the cerrado floristic richness rests partly on understanding the effects of fire on plant species distribution under different fire regimes.

Within the cerrado biogeographic province, small, scattered patches of semi-deciduous seasonal forest emerge (Oliveira-Filho & Ratter 1995; Gottsberger & Silberbauer-Gottsberger 2006). Such forests are generally found in valleys, where the topography has cut into more mineral-rich underlying rocks, or as large extensions in more fertile areas (Oliveira-Filho & Ratter 1995). However, the forest expansion is largely constrained by the negative effects of fire on the establishment and growth of forest species, as compared to cerrado species (Hoffmann 2000; Hoffmann & Solbrig 2003; Hoffmann et al. 2003). Therefore, fire is also important in limiting the occurrence of semi-deciduous seasonal forests within the cerrado province (Silva et al. 2005; Hoffmann et al. 2009).

Traditionally, plant species from fire-prone communities are classified according to survival after fire and reproductive response to fire (Bond & Van Wilgen 1996; Pausas 1999; Pausas et al. 2004). They have been grouped into plants resistant to fire through parts of their aboveground biomass (resisters); plants dying back completely aboveground but sprouting from soil after fire (sprouters, Bond & Van Wilgen 1996; Pausas 1999); and plants germinating either from the seed bank or from newly dispersed seeds after fire (seeders, Pausas 2001; Pausas et al. 2004). However, information on germination requirements for most neotropical species is still scarce, and classification of species according to survival after fire and reproductive response to fire is hard to achieve. Hence, other disturbance-related functional traits have instead been studied in Brazilian plant communities (Overbeck & Pfadenhauer 2007). Raunkiaer life forms (Raunkiaer 1934) is a functional classification based on position and protection of regenerative buds that has been considered a good predictor of disturbance (Cornelissen et al. 2003) and has been applied to fire-prone vegetation (Chapman & Crow 1981; Batalha & Martins 2002a; Overbeck & Pfadenhauer 2007). In Brazilian fire-prone communities, frequent fires mainly favour life forms that protect their sprouting buds underground, such as hemicryptophytes and cryptophytes (Batalha & Martins 2002a; Overbeck & Pfadenhauer 2007).

Recently, analyses of the phylogenetic structure of biological communities have been increasingly used to answer questions regarding contemporary ecological forces that assemble species, such as environmental filters and competitive interactions (Vamosi et al. 2009). Most of these studies have found some phylogenetic clustering in local plant communities (Vamosi et al. 2009), i.e. a tendency of co-occurring species to be more closely related than expected by chance (Webb et al. 2002). These findings have been generally attributed to effects of local environmental filters in assembling ecologically similar species (Fukami et al. 2005). However, when a part of the diversification process happens within extant vegetation types, the species pools are likely to be biased towards closely related taxa and phylogenetic clustering in local communities might also appear (Proches et al. 2006). Although several studies have assessed the phylogenetic structure of forests (see Vamosi et al. 2009 and references therein), savannas have received less attention (Silva & Batalha 2009a).

The phylogenetic structure of fire-prone communities is expected to change along fire gradients. In Mediterranean shrub vegetation, for example, frequent fires assemble phylogenetically clustered communities (Verdú & Pausas 2007). Although changes associated with fire in savannas have been well reported throughout the world (see Miranda et al. 2002; Gottsberger & Silberbauer-Gottsberger 2006 and references therein), there is a lack of studies – to the best of our knowledge – that consider the phylogenetic relatedness of the plants and the effects of fire on them (see e.g. Silva & Batalha 2010). In this study, we investigated the phylogenetic structure of cerrado sites under different fire frequencies by comparing them to semi-deciduous seasonal forest sites. We used a framework to assess whether fire changes the phylogenetic relatedness of co-occurring plant species (Webb et al. 2002). Frequent fires are expected to assemble closely related species when functional traits are conserved in the evolution of plant lineages (i.e. traits are more similar among closely related species; Prinzing et al. 2008). Conversely, when functional traits evolved convergently and closely related species tend to be functionally different, frequent fires are expected to assemble more distantly related species (phylogenetic over-dispersion; Webb et al. 2002). Considering that plant species commonly present a high degree of evolutionary stasis (Qian & Ricklefs 2004) and conservatism of traits related to environmental tolerances (i.e. light, soil moisture and pH; Prinzing et al. 2001, 2008), cerrado sites under frequent fires are predicted to be characterized by phylogenetic clustering. In contrast, in the absence of fire as a filter, such as in semi-deciduous seasonal forests, other ecological forces, e.g. competitive

interactions, may be predominant in assembly of communities (Webb et al. 2002; Vamosi et al. 2009). Such communities are expected to be characterized by phylogenetic over-dispersion when traits are conserved in the evolution of the species so as to avoid niche overlap of plants (Webb et al. 2002; Verdú & Pausas 2007).

In summary, we addressed the following questions: (1) Do frequent fires assemble cerrado communities with closely related species?; (2) If so, what are the clades pruned by fire in the phylogenetic trees?; (3) Are semi-deciduous seasonal forests characterized by phylogenetic over-dispersion?; and (4) Are life forms conserved in the phylogeny of the species?

Methods

Study area and data

We surveyed two nearby cerrado sites in Emas National Park (ENP), in the Brazilian Central Plateau ($17°49' - 18°28'$S; $52°39' - 53°10'$W). The ENP is one of the largest reserves in the cerrado province, with 132 941 ha (Unesco 2001). Regional climate is humid tropical, with a wet summer and a dry winter (Köppen 1931). The dry season is from June to August and the wet season from September to May. Annual rainfall and mean temperature lie around 1745 mm and 24.6°C, respectively. In the ENP, there is a gradient from open (68.1% of its area) to closed (25.1%) savannas, as well as wet grasslands (4.9%) and riparian and semi-deciduous forests (1.2%; Ramos-Neto & Pivello 2000). There are currently few occurrences of anthropogenic fires inside the ENP, and the largest wildfires burn less than 30% of the total area. Fire frequency at a given point is around 6-7 years on average (França et al. 2007).

In the late rainy season of 2006, we sampled the woody species occurring in two cerrado sites with similar physiognomy, similar soil types and under different fire frequencies: a firebreak burned annually for the last 10 years (approximately, $18°18'50''$S; $52°54'00''$W) and a site that had not been burned since 1994 (approximately, $18°17'28''$S; $52°53'41''$W). The sites were less than 2 km from each other. In each site, we placed a 2500-m transect, with 250 points, 10-m apart . In each point, we used the point-quarter method (Mueller-Dombois & Ellenberg 1974) to sample four woody plants having a stem diameter at soil level ≥ 3 cm. We identified the species by comparing collected sample to those of the ENP (Batalha & Martins 2002b) and to vouchers lodged at the herbaria of the State University of Campinas and the University of Brasília.

In addition, we carried out a broad survey of published articles and theses with floristic data on cerrado under different fire regimes and on semi-deciduous seasonal forests (Table 1). We recorded the woody plant species and their relative abundances of cerrados in SE (César et al. 1988; Durigan et al. 1994) and central Brazil (Sato 2003; Fiedler et al. 2004; Castro-Neves 2007) as well as of

Table 1. Summary of the sampling sites in cerrado and seasonal semi-deciduous forest from the articles used for this study. Number of sites, fire frequencies and location of sites are shown. The references of the sources are provided in the reference list of this study.

Source	Number of sites and fire frequencies	Location	Vegetation type
This study	One site annually burned and another protected from fire for 12 years	Emas National Park, central Brazil (18°18′S, 52°54′W)	Cerrado
César et al. (1988)	One site protected from fire for 25 years	Corumbataí municipality, SE Brazil (22°13′S, 47°37′W)	Cerrado
Durigan et al. (1994)	One site burned annually for several years	Itirapina municipality, SE Brazil (22°15′S, 47°49′W)	Cerrado
Silva & Soares (2002)	One site of semi-deciduous seasonal forest protect from fire	São Carlos municipality, SE Brazil (21°55′S, 47°48′W)	Forest
Sato (2003)	Three sites protected from fire for 18 years were burned biennially from 1992 to 2000 in the late dry season	Brasília municipality, central Brazil (15°56′S, 47°53′W)	Cerrado
Fiedler et al. (2004)	One site sampled 1 month and 3 years after the fire	Brasília municipality, central Brazil (15°57′S, 47°56′W)	Cerrado
Castro-Neves (2007)	Two sites protected from fire for 18 years were burned biennially and quadrennially from 1992 to 2004	Brasília municipality, central Brazil (15°56′S, 47°53′W)	Cerrado
Haidar (2008)	One site of semi-deciduous seasonal forest protect from fire	Brasília municipality, central Brazil (15°33′S, 47°51′W)	Forest
Imaña-Encinas et al. (2008)	One site of semi-deciduous seasonal forest protect from fire	Pirenópolis municipality, central Brazil, (15°45′S, 49°04′W)	Forest

semi-deciduous seasonal forest sites protected from fire in close proximity to these cerrado sites (Silva & Soares 2002; Haidar 2008; Imaña-Encinas et al. 2008) (Table 1). The woody species correspond to one component of the cerrado flora (Gottsberger & Silberbauer-Gottsberger 2006) and this may introduce a bias in our generalization. Nonetheless, we did not find any published article or thesis with floristic data on herbaceous species in cerrados under different fire regimes.

Most of the cerrado species have below-ground organs that allow them to sprout after fires that have completely removed the aboveground plant parts (Gottsberger & Silberbauer-Gottsberger 2006). As a consequence, it is difficult to make a clear distinction between sprouters and resisters, and a traditional classification of cerrado species according to survival after fire (sensu Bond & Van Wilgen 1996) becomes impracticable. For that reason, we used the life forms of species as a proxy for regenerative strategies of cerrado plants. Life forms are functional traits associated with plant responses to environmental filters, such as fire (Cornelissen et al. 2003). The classification of life forms proposed by Raunkiaer (1934) is based on the position and degree of protection of renewing buds. In his system, the more pronounced the environmental constraints, the more protected the renewing buds. We assigned life forms of the cerrado species considering the following Raunkiaer's (1934) classes: phanerophytes, chamaephytes, hemicryptophytes, geophytes and therophytes (see supporting information Appendix S1). We also used published data to assign the life forms of cerrado and forest species (Batalha & Mantovani 2001; Gottsberger & Silberbauer-Gottsberger 2006).

Phylogenetic data

We constructed phylogenetic trees for the species with the Phylomatic software, a phylogenetic toolkit for the assembly of phylogenetic trees (Webb & Donoghue 2005). The node ages of families were estimated from the dated angiosperm super-tree of Davies et al. (2004). We assigned branch lengths to genera and species of the phylogenetic tree using the BLADJ (Branch Length Adjustment) averaging algorithm of the Phylocom software package (version 4.0.1, http://www.phylodiversity.net/phylocom/). The BLADJ spaces undated nodes evenly between dated nodes in the tree. When a family node presented more than three polytomies (e.g. Asteraceae and Fabaceae), we distributed the genera into their subfamilies following the latest angiosperm phylo-

genetic relationship (Angiosperm Phylogeny Website, Version 9, http://www.mobot.org/MO-BOT/research/APweb/). We assigned branch lengths of these genera by spacing undated nodes evenly above the family node.

We investigated whether the life forms tended to be phylogenetically conserved (i.e. present a 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 were compared to the expectations under a null model of randomly swapping trait values across the tips of the tree, with 999 randomizations. For a detailed description of comparative analyses using phylogenetically independent contrast, see Garland et al. (1992). As recommended by Webb and collaborators (in the Phylocom User's Manual, Version 4.0.1, http://www.phylodiversity.net/phylocom/), we considered life form as a trait with ordered states, from therophytes to phanerophytes, according to the increasing degree of bud protection. We added the plants sampled by Batalha & Mantovani (2001) and Gottsberger & Silberbauer-Gottsberger (2006) to include the life forms for herbaceous and shrub species. We did this analysis with a phylogenetic tree for all species using the Picante package (version 0.2-0, http://picante.r-forge.r-project.org) for the R environment (http://www.R-project.org).

Data analyses

Since the plant communities were sampled with different methods and efforts, we first established a design for comparisons among sites based on their locations and fire frequencies. We made the following comparisons: (1) between the two sites sampled in ENP; (2) between the two sites with bi- and quadrennial fires studied by Castro-Neves (2007); (3) between the two samples in a site studied by Fiedler et al. (2004); (4) between the two samples (three sites) studied by Sato (2003) – one sample before fire and the other after five biennially fires in the late dry season; and (5) between the two nearby SE sites studied by César et al. (1988) and Durigan et al. (1994) (Table 1).

We then compared (1) the species found in the cerrado sites in ENP in central Brazil, with the species found in a semi-deciduous seasonal forest site in Pirenópolis, a nearby municipality (Imaña-Encinas

et al. 2008); (2) the species found in cerrado sites in Brasília, in central Brazil (studies 2, 3, and 4 above) with the species found in a semi-deciduous seasonal forest in Brasília (Haidar 2008); and (3) the species found in SE cerrado sites with the species found in a semi-deciduous seasonal forest site in São Carlos, a nearby municipality (Silva & Soares 2002) (Table 1).

To find out whether fire constrains the phylogenetic structure of cerrado plant communities, we compared the mean phylogenetic distance (MPD) among sites (Webb 2000). We calculated the MPD as the mean phylogenetic distance among all pairwise combinations of species (Webb 2000). MPD is a measure of the phylogenetic diversity of communities and is computed in millions of years. To determine whether the phylogenetic structure of the cerrado sites with high fire frequency or recently burned sites (hereafter, HiFi) differed from the phylogenetic community structure of low fire frequency or unburned cerrado sites (hereafter, LowFi), as well as from the forest sites protected from fire, we compared observed MPD values for each site to the distribution of MPD values for randomly generated null communities (Gotelli & Graves 1996), with the significance adjusted ($\alpha = 0.025$). We constructed a phylogenetic tree with the species of the three sites; then generated null communities by randomizing the phylogenetic relationships among species and resampling 999 pseudo-HiFi, LowFi and forest communities with the same number of species. This null model assumes that species of the LowFi and forest sites are equally able to colonize the HiFi site, and vice versa. This procedure was implemented in Phylocom (COMSTRUCT algorithm, version 4.0.1, http://www.phylodiversity.net/phylocom/), which shuffles species labels across the entire phylogeny. We repeated this analysis with phylogenetic trees constructed for the species of HiFi, LowFi and forest sites of each comparative design explained above. We also tested other null models, as implemented in this software, using the relative density of species, but the results were the same.

We then calculated the net relatedness index (NRI), defined as [–(MPD – MPDnull)/sd.MPD null], where MPDnull is the mean MPD for the cerrado species from 999 null communities and sd.MPDnull is the standard deviation of MPD for the cerrado species from these 999 null communities (Webb 2000). NRI has been proposed as a measure of tree-wide phylogenetic distance of species (Webb 2000). Positive NRI scores indicate that species are more phylogenetically related than expected by chance, whereas negative NRI scores indicate that

species are less phylogenetically related than expected by chance. We compared the mean of NRIs of HiFi, LowFi and forest sites with an analysis of variance and posterior Tukey test (Zar 1999).

Finally, we compared the architecture of the phylogenetic trees of LowFi, HiFi and forest sites. We assessed the similarity of species and families between LowFi, HiFi and forest sites using the Sørensen index (Magurran 2004), with the software EstimateS (version 7.5, http://purl.oclc.org/estimates). We drew the phylogenetic trees with the ADE-4 package (Analyses des Données Ecologiques; Thioulouse et al. 1996) for the R environment (http://www.R-project.org).

Results

In the ENP, we found 28 species in the annually burned site and 39 species in the protected site. The species number was among the expected values for frequently burned sites (Table 2). Overall, we found 104 species in HiFi cerrado sites, 149 species in LowFi cerrado sites and 191 species in forest sites. We also found phylogenetic signals in life forms across the phylogeny of the 801 species investigated ($P = 0.001$). The values for the variance and the mean of random variances of the PICs were, respectively, 0.020 and 0.050 for life forms (see supporting information Appendix S1). The observed variance of the PICs was significantly lower than expected by chance and, hence, the life forms were conserved in the phylogeny of species.

The mean of MPDs of LowFi, HiFi and forest sites were, respectively, 214.6 ± 6.9, 213.3 ± 6.6 and 212.2 ± 8.4 million years. In general, no straightforward pattern emerged from the sites (Table 2). We observed a significant phylogenetic over-dispersion in cerrado sites and a phylogenetic clustering in a semi-deciduous seasonal forest site (Table 2). However, we found that most cerrado sites had negative NRI values, whereas all seasonal forest sites had positive NRI values (Table 2). The mean of NRIs for LowFi, HiFi and forest sites were, respectively, -1.041, -0.723 and 1.362 (for analysis of variance, $F = 4.831$, $P = 0.028$). The mean of NRIs of HiFi sites was significantly different from that of forest sites ($t = 2.404$, $P < 0.05$). Other pair-wise comparisons were not significantly different ($t < 2.086$, $P > 0.05$). Thus, the woody species of seasonal forest sites tend to be more closely related than those of cerrado sites under high fire frequency.

The phylogenetic trees of cerrado and seasonal forest were somewhat different, with 44 and 50 fa-

Table 2. Number of taxa (N), observed (MPD) and randomized (rndMPD) mean phylogenetic distances and net relatedness index (NRI, Webb 2000) of cerrado and semi-deciduous seasonal forest sites in SE and central Brazil. HiFi = cerrado sites with high frequency of fire, LowFi = cerrado sites with low frequency of fire, Forest = sites of semi-deciduous seasonal forest protected from fire, ENP = Emas National Park sites. The values of MPD and rndMPD are in million years. Positive NRI scores indicate that species are more phylogenetically related than expected by chance, whereas negative NRI scores indicate that species are less phylogenetically related than expected by chance. The *P*-value of the sites reflects departure of the observed MPD values from the null model. Significant values at $\alpha = 0.025$ are in bold.

Source	Sites	N	MPD	rndMPD	NRI	*P*
ENP and Imaña-Encinas et al. (2008)	HiFi	28	223.2	215.1	− 1.114	0.122
	LowFi	39	211.3	215.4	0.772	0.223
	Forest	82	214.8	215.4	0.231	0.403
César et al. (1988), Durigan et al. (1994),	HiFi	44	209.0	215.7	1.070	0.144
and Silva & Soares (2002)	LowFi	95	219.9	218.4	− 0.453	0.327
	Forest	72	219.0	220.1	1.006	0.165
Sato (2003) and Haidar (2008)	HiFi	55	**219.3**	207.2	**− 2.965**	0.001
	LowFi	58	**218.8**	207.1	**− 2.760**	0.001
	Forest	79	**202.8**	211.5	**3.330**	0.001
Fiedler et al. (2004) and Haidar (2008)	HiFi	34	206.5	204.5	− 0.430	0.346
	LowFi	40	205.7	204.5	− 0.323	0.401
	Forest	79	202.8	204.5	0.909	0.186
Castro-Neves (2007) and Haidar (2008)	HiFi	36	**214.9**	205.7	**− 1.767**	0.024
	LowFi	31	211.1	206.0	− 0.853	0.194
	Forest	79	202.8	206.0	1.338	0.086

milies, respectively (supporting information Appendix S2). Differences between the phylogenetic trees are mainly due to the presence of typical forest families, such as Dichapetalaceae, Lecythidaceae, Meliaceae and Rutaceae, which rarely appear in cerrado sites. The species and family similarities were higher between HiFi and LowFi cerrado sites (mean of species and family similarity was 0.723 and 0.765, respectively) than between those and forest sites (mean of species and family similarity between HiFi and forest sites was 0.047 and 0.449, and between LowFi and forest sites was 0.058 and 0.504, respectively) (Table 3). Accordingly, the cerrado flora, which may withstand fire, is very different from that of the semi-deciduous seasonal forest.

Discussion

Contrary to our expectations, fire did not promote phylogenetic clustering in cerrado communities, and we did not find phylogenetic overdispersion in semi-deciduous seasonal forests. On the contrary, plant species in cerrado sites under high fire frequencies were less phylogenetically related than those in semi-deciduous seasonal forests. Consequently, fires in cerrados might have different roles in assembling plant species when compared with roles in other fire-prone communities. We postulate that the absence of phylogenetic clustering in the cerrado is mainly due to the persistence of long-lived resprouting species from different plant lineages.

Table 3. Similarity of species and families of woody species among cerrado sites having different fire regimes and in semi-deciduous seasonal forest sites. Values of similarity were obtained using the Sørensen index. HiFi = sites with high frequency of fire, LowFi = sites with low frequency of fire, Forest = sites of semi-deciduous seasonal forest protected from fire, ENP = Emas National Park sites. The references of sources are described in the reference list in this study.

Source	Similarity	Species	Family
ENP and Imaña-Encinas et al. (2008)	HiFi versus LowFi	0.626	0.684
	HiFi versus Forest	0.054	0.500
	LowFi versus Forest	0.083	0.551
César et al. (1988), Durigan et al. (1994), and Silva & Soares (2002)	HiFi versus LowFi	0.434	0.655
	HiFi versus Forest	0	0.304
	LowFi versus Forest	0.049	0.419
Sato (2003) and Haidar (2008)	HiFi versus LowFi	0.955	0.983
	HiFi versus Forest	0.059	0.474
	LowFi versus Forest	0.058	0.500
Fiedler et al. (2004) and Haidar (2008)	HiFi versus LowFi	0.746	0.820
	HiFi versus Forest	0.090	0.468
	LowFi versus Forest	0.067	0.500
Castro-Neves (2007) and Haidar (2008)	HiFi versus LowFi	0.848	0.684
	HiFi versus Forest	0.034	0.500
	LowFi versus Forest	0.035	0.550

The previous studies in frequently burned cerrados found a long-term impoverishment of species (Durigan et al. 1994; Miranda et al. 2002). Fire exclusion allows the growth of fire-sensitive species generally emanating from seasonal forests (Hoffmann et al. 2003), increasing the richness of woody plants (San José & Fariñas 1991; Moreira 2000; Miranda et al. 2002). However, we observed that fire did not assemble closely related species, as in other

fire-prone communities (see Verdú & Pausas 2007 for Mediterranean vegetation), which might be related to the persistence of many plant species after frequent fires. Resprouting ability is recognized as an important dimension of the "persistence niche" of plants and may explain the survival of plants under several environmental constraints (Bond & Midgley 2001). Most cerrado species of distant plant lineages can resprout after complete removal of the aboveground parts (Gottsberger & Silberbauer-Gottsberger 2006); whereas sprouters comprise around 50% of species in other Brazilian fire-prone communities, such as in southern grasslands (Overbeck & Pfadenhauer 2007), in the cerrado, they may represent more than 90% of species (Gottsberger & Silberbauer-Gottsberger 2006). Thus, the presence of a large number of resprouting species from different plant lineages in the cerrado flora may prevent fire from assembling closely related plants.

Savannas have experienced fire for 30 million years (Bond et al. 2003). However, fire became more frequent in this vegetation type only about 8 million years ago, with the predominance of C_4 grasses (Beerling & Osborne 2006) that can take advantage of high light and warm wet summers to rapidly accumulate biomass, which becomes flammable in the long dry winters, promoting fires (Bond & Keeley 2005). Thus, there was sufficient time for multiple colonizations in flammable environments of phylogenetically distant lineages. Conversely, in the Mediterranean vegetation frequent fires appeared only in the Quaternary (Verdú et al. 2003), and some important adaptations (e.g. seeders) that appeared concomitantly with fire are also recent (Pausas & Verdú 2005; Verdú et al. 2007). These adaptations are concentrated in a few lineages (e.g. Cistaceae and Fabaceae) and are specific adaptations to fire (Verdú & Pausas 2007). However, fire-related traits in the cerrado are not related to specific families or older clades (Simon et al. 2009). Fabaceae, for example, has species with several regenerative traits (sprouters and resisters) and life forms (see supporting information Appendix S1). In addition, many families in cerrado present vicariant species from tropical forests (Simon et al. 2009). In general, vicariant rain forest species, with long and different phylogenetic histories, constitute an important element within the components of the cerrado flora (Gottsberger & Silberbauer-Gottsberger 2006). These vicariant species have functional traits, such as the strong suberization of trunks and branches, which are vital to survival in flammable environments (Simon et al. 2009). Such species could

colonize the cerrado environment because they evolved in situ the necessary characteristics in a scenario of successive colonizations from the late Tertiary (Simon et al. 2009). In cerrado, for example, the large number of species without congeners belonging to distantly related clades (e.g. *Bowdichia virgilioides* Kunth, Fabaceae, and *Hancornia speciosa* Gomes, Apocynaceae, supporting information Appendix S1) indicate that fires have occurred for sufficiently long periods to allow differentiation at the generic level (Gottsberger & Silberbauer-Gottsberger 2006). Thus, the long history of fire occurrence in the cerrado may also justify the absence of phylogenetic clustering in cerrado plant communities.

Moreover, phylogenetic over-dispersion seems to be a common characteristic in the cerrado, in spite of fire (Silva & Batalha 2009b). Hence, frequent fires did not prune entire specific clades; instead, fire evenly excluded species from all branches of the phylogenetic tree. Conversely, the phylogenetic clustering in semi-deciduous seasonal forest may be explained by a large number of species from related and typical forest families. Most exclusive forest families are closely phylogenetically related (supporting information Appendix S2), e.g. Meliaceae, Rutaceae and Sapindaceae (Sapindales, Eurosids II), of which we found six, six and five species respectively. Other closely related families are not exclusive to seasonal forest, but contain a greater number of tree forest species than cerrado species, e.g. Apocynaceae and Rubiaceae (Gentianales, Euasterids I), of which we found, respectively, eight and 11 species in semi-deciduous seasonal forests, against only four and five species in cerrados.

Frequent fires are predicted to decrease the number of woody species in the cerrado (San José & Fariñas 1991; Moreira 2000; Miranda et al. 2002). The lower number of species observed in HiFi than in LowFi sites supports this prediction. Alternatively, the overall high similarity among cerrado sites might suggest that woody species are also very resilient to different fire frequencies. This resilience may also be explained by the long evolution of cerrado plants in an environment with high fire frequencies (since 8 million years ago, Beerling & Osborne 2006; Simon et al. 2009). Again, it seems that there was sufficient time for the selection of plant species capable of tolerating high fire frequencies.

Life forms were evolutionarily conserved in the phylogeny of plant species of cerrado and semi-deciduous seasonal forest. In general, these traits are broadly conserved across the phylogeny of

European plants (Prinzing et al. 2008). It is well know that some life forms are concentrated in a few families, such as the therophytes in Poaceae. When considering the hemicryptophytes, however, this taxonomic pattern is less evident, because hemicryptophytes, and the sprouting ability associated with this life form, are widely distributed in plant lineages of the cerrado, being especially common among angiosperms of harsh environments (Bond & Midgley 2001). Nevertheless, in some fire-prone vegetation types, such as in Mediterranean communities, germination is also stimulated by fire-derived factors (heat, smoke and charred wood). Consequently, sprouting, although also widespread, is not the predominantly favoured form in areas of frequent fires (Pausas 2001; Pausas & Verdú 2005; Verdú et al. 2007). In contrast, in cerrados sprouting is the prevalent regenerative strategy after fires.

On the other hand, most semi-deciduous seasonal forest species cannot sprout after fires (Hoffmann 2000; Hoffmann & Solbrig 2003; Hoffmann et al. 2003), even though sprouting is a widespread characteristic of many woody plants (Bond & Midgley 2001). As a consequence, fire seems to contribute to the evolution of a different woody flora in the cerrado, when compared with the seasonal forest flora. However, the absence of forest families in cerrado sites protected from fire (supporting information Appendix S2) reinforces the idea that not only fire is an important environmental filter for seasonal forest species, but also nutrient-poor soils, which are an important feature of the cerrado environment (Oliveira-Filho & Ratter 1995; Gottsberger & Silberbauer-Gottsberger 2006).

As more information on dated phylogenetic trees becomes available, analyses of phylogenetic structure of communities will become increasingly possible and more reliable. The node ages of the trees used here were taken from one of the fully dated angiosperm trees (Davies et al. 2004); however, a single calibration point was used to date this tree (Davies et al. 2004). Multiple calibration points, as well as the use of different data and methods in constructing trees, will bring new insights into the phylogenetic structuring of savannas and forests.

Fire has been viewed as a force that triggers diversification in fire-prone communities (Ojeda 1998; Verdú et al. 2007) and assembles closely related plants (Verdú & Pausas 2007). Nonetheless, frequent fires seem to play different roles in the structuring of the cerrado, promoting phylogenetic over-dispersion. The presence of many resprouting species from different plant lineages in cerrados may blur the link between fire frequency and phylogenetic structure of plant communities, contrary to what has been observed in other fire-prone vegetation types (Verdú & Pausas 2007). Further studies should assess the relationship between fire frequency and plant relatedness in African and Australian savannas to validate our generalizations.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Species and life forms of cerrados (C) and semi-deciduous seasonal forests (F) in central and SE Brazil. Life forms were classified into therophyte (T), cryptophyte (Cr), hemicryptophyte (H), chamaephyte (Ch) and phanerophyte (Ph), according to the major Raunkiaer (1934) classes. The herbaceous and shrub species sampled by Batalha & Mantovani (2001) and Gottsberger & Silberbauer-Gottsberger (2006) were included.

Appendix S2. Summary of the phylogenetic tree assembled for woody species in cerrado sites (A) and in semi-deciduous seasonal forest sites (B) in central and SE Brazil. The relationship among families was based on the angiosperm super-tree of Davies et al. (2004).

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