Universidade Federal de São Carlos

Centro de Ciências Biológicas e da Saúde

Programa de Pós-Graduação em Ecologia e Recursos Naturais

IGOR AURÉLIO SILVA

PADRÕES DE COOCORRÊNCIA DE ESPÉCIES VEGETAIS DE CERRADO EM DIFERENTES REGIMES DE FOGO

Orientador: Dr. Marco Antônio Batalha

São Carlos
Março de 2010

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Tese apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais, do Centro de Ciências Biológicas e da Saúde, da Universidade Federal de São Carlos, sob a orientação do Prof. Dr. Marco Antônio Batalha.

São Carlos

Março de 2010

Ficha catalográfica elaborada pelo DePT da
Biblioteca Comunitária/UFSCar

Silva, Igor Aurélio.
S586pc Padrões de coocorrência de espécies vegetais de cerrado em diferentes regimes de fogo / Igor Aurélio Silva. -- São Carlos : UFSCar, 2010.
146 f.

Tese (Doutorado) -- Universidade Federal de São Carlos, 2010.

1. Ecologia do cerrado. 2. Diversidade taxonômica. 3. Exclusão competitiva. 4. Facilitação. 5. Regras de montagem. 6. Similaridade funcional. I. Título.

CDD: 574.5264 (20ª)

Igor Aurélio da Silva

PADRÕES DE COOCORRÊNCIA DE ESPÉCIES VEGETAIS DE CERRADO EM DIFERENTES REGIMES DE FOGO

Tese apresentada à Universidade Federal de São Carlos, como parte dos requisitos para obtenção do título de Doutor em Ciências.

Aprovada em 09 de março de 2010

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Dedico este trabalho aos meus pais,

Neusa Maria Braga Silva e José Adejacir Silva,

que carinhosamente permitiram minha doce

aventura pelo mundo da ciência.

“O seu trabalho não é a pena que paga por ser homem,

mas um modo de amar e de ajudar o mundo a ser melhor”

Thiago de Melo

Agradecimentos

Ao Prof. Dr. Marco Antônio Batalha, pela confiança e orientação. Tua inestimável solicitude e desvelo na condução deste trabalho tornaram sua longa jornada confortável e aprazível;

Aos meus pais, por tudo que fizeram para eu chegar até aqui. Minha gratidão está para além dessa vida.

À Fundação de Amparo à Pesquisa do Estado de São Paulo, pelo apoio financeiro ao projeto no qual se insere este trabalho;

Ao Conselho Nacional de Pesquisa, pela bolsa concedida;

Ao Ibama, pela licença de coleta e pela infra-estrutura proporcionada no Parque Nacional das Emas;

Ao Programa de Pós-graduação em Ecologia e Recursos Naturais, pelo apoio na realização deste trabalho;

Aos biólogos Marcus Vinicius Cianciaruso e Priscilla de Paula Loiola, pela grande ajuda no árduo e longo trabalho de campo, pela amizade e pelo bom humor nas horas difíceis;

Aos companheiros biólogos André Vitor F. Jardim, Carlos A. Casali, Danilo M. Silva, Fernanda Q. Martins, Lígia Sims, Maira O. Maia, Mayla W. Valenti e Priscilla K. Amorim, pela inestimável ajuda no trabalho de campo;

Aos funcionários dos herbários da Universidade de Campinas e da Universidade de Brasília, em especial aos taxonomistas M.W. Ferreira, C. Proença and J. Semir, pelo auxílio na identificação das espécies.

Sumário

Resumo

O fogo tem um papel importante na determinação da estrutura do cerrado. Queimadas anuais e bienais favorecem as espécies herbáceas em detrimento das espécies arbóreas. Consequentemente, as queimadas frequentes podem modificar o padrão de coocorrência de espécies vegetais. Testamos (1) se altas frequências de fogo aumentam o número de ocorrência de pares de espécies herbáceo-subarbustivas, (2) se, em pequena escala espacial, altas frequências de fogo reúnem espécies arbustivo-arbóreas funcionalmente semelhantes e filogeneticamente aparentadas e (3) se, em escala espacial regional, altas frequências de fogo reúnem espécies arbóreas filogeneticamente aparentadas. Em 2006, amostramos as espécies vegetais de três áreas contíguas de cerrado no Parque Nacional das Emas, GO, sob diferentes frequências de fogo: um aceiro queimado anualmente desde 1994, um aceiro queimado aproximadamente a cada dois anos desde 1994 e uma área sem queimar desde 1994. Para testar o primeiro postulado, comparamos a frequência observada de pares de espécies em cada área com uma distribuição esperada de frequências gerada pelo método Monte Carlo. Para testar o segundo postulado, examinamos as relações entre índices de coocorrência de espécies e as diferenças funcionais, bem como entre esses índices e as distâncias filogenéticas, calculadas para todos os pares de espécies, com regressões de quantis. E para testarmos o terceiro postulado, comparamos distâncias filogenéticas médias de áreas com altas e baixas frequências de queimadas com um modelo nulo, usando também dados de literatura. Encontramos que a exclusão do fogo diminuiu o número de ocorrência de pares de espécies herbáceo-subarbustivas. Porém, queimadas frequentes modificaram esse padrão, gerando ocorrências estocásticas de pares de espécies. Encontramos que, em pequena escala espacial, queimadas frequentes reúnem espécies funcionalmente semelhantes. Contudo, não observamos nenhum padrão em relação às distâncias filogenéticas. Em escala regional, altas frequências de fogo também não modificaram a estrutura filogenética das áreas de cerrado.

Portanto, o fogo é um importante filtro ambiental para as plantas de cerrado em pequena escala espacial, promovendo agrupamentos fenotípicos de espécies. Quando a frequência de fogo é reduzida, a competição pode promover uma dispersão fenotípica das plantas. Contudo, nenhum padrão filogenético emergiu nas escalas espaciais investigadas. Postulamos que a ausência de agrupamentos filogenéticos em cerrados é devida à persistência de espécies rebrotantes perenes e à presença de espécies de linhagens filogeneticamente distantes.

Key words: diversidade filogenética, exclusão competitiva, facilitação, filtro ambiental, hipótese do gradiente de estresse, regras de montagem, savanas, similaridade funcional, traços regenerativos.

Abstract

Fire plays an important role in determining the structure of cerrado. Annual and biennial fires favor herbaceous species and constrain woody species. As a consequence, frequent burnings are expected to change the pattern of cooccurrence of plant species. We tested (1) whether high fire frequencies increase the number of occurrences of herbaceous and shrubby species pairs, (2) whether, at fine spatial scale, high fire frequencies assemble functionally similar and closely related woody species, and (3) whether, at regional spatial scale, high fire frequencies assemble closely related woody species. In 2006, we sampled the plant species in three nearby cerrado sites in Emas National Park, central Brazil, under different fire frequencies: two firebreaks, one burned annually since 1994, another burned around every two years since 1994, and a site without fires since 1994. To test the first postulate, we compared the observed frequency of species pairs in each site to a distribution of random frequencies generated by Monte Carlo method. To test the second postulate, we examined the relationship between co-occurrence indices and both phylogenetic distances and functional differences, calculated for all pairs of species, with quantile regressions. And to test the third postulate, we compared mean phylogenetic distances of sites with high and low fire frequencies to a null model, using also data from literature. We found that the fire exclusion decreases the number of occurrences herbaceous species pairs. However, frequent fires changed this pattern, generating stochastic occurrences of species pairs. We found that, at fine spatial scale, frequent burnings assembled functionally similar species. Nonetheless, we did not observe any pattern relative to phylogenetic distances. At regional scale, high fire frequencies did not modify the phylogenetic structure of cerrado sites. Thus, fire is an important environmental filter for cerrado plants at fine spatial scale, driving phenotypic clustering of species. When fire frequencies are reduced, competition may promote phenotypic overdispersion. However, no phylogenetic pattern emerged at studied spatial scales. We postulate that the absence of phylogenetic clustering in cerrado is due to the persistence of long-lived resprouting species and to the presence of species from phylogenetically distant lineages.

Key words: assembly rules, competitive exclusion, environmental filter, facilitation, functional similarity, phylogenetic diversity, regenerative traits, savannas, stress-gradient hypothesis.

I – Introdução Geral

Introdução geral

O fogo é um forte agente evolutivo para as plantas (Bond & Midgley 1995, Schwilk & Ackerly 2001) e tem um papel importante na determinação da distribuição de savanas no mundo (Bond *et al.* 2005). Os fogos têm ocorrido nesse tipo vegetacional há pelo menos 25 milhões de anos (Bond *et al.* 2003), associados ao surgimento e a diversificação das gramíneas C_4 em várias linhagens independentes (Christin *et al.* 2008). Isso porque as gramíneas C_4 acumulam biomassa rapidamente sob alta incidência de luz e verões úmidos, tornando-se altamente flamáveis nos invernos secos (Bond & Keeley 2005). Entretanto, evidências de assinaturas isotópicas em dentes fossilizados de mamíferos (paleodietas), partículas de carvão e altas concentrações de pólen em sítios paleobotânicos de diferentes continentes indicaram que essas linhagens de gramíneas C_4 se tornaram ecologicamente dominantes somente há 8 milhões de anos (Cerling *et al.* 1997, Latorre *et al.* 1997). Consequentemente, as queimadas tornaram-se mais frequentes, passando a ocorrer várias vezes em uma década em uma dada área (Bond & Keeley 2005). A expansão sincrônica de vegetações dominadas por gramíneas em diferentes partes do mundo é considerada como o marco do surgimento do moderno bioma savânico (Beerling & Osborne 2006). Nos últimos 10.000 anos, contudo, queimadas antrópicas geralmente associadas à agricultura têm expandido as áreas de vegetação inflamável em todo o mundo (Bowman 1998, Brooks *et al.* 2004). Atualmente, formações vegetacionais sujeitas ao fogo, como as savanas, cobrem cerca de 40% da superfície terrestre (Bond *et al.* 2005).

As savanas são formações tropicais e subtropicais, em que o componente herbáceo-subarbustivo, quase contínuo, é interrompido por arbustos e árvores em densidades variáveis; em que o fogo é frequente; e em que os principais padrões de crescimento estão fortemente associados às estações úmida e seca alternantes (Bourlière & Hadley 1983). As savanas possuem uma grande variação em sua fisionomia, na qual o balanço entre o componente arbustivo-arbóreo e o componente herbáceo-subarbustivo muda temporal e espacialmente (Bourlière & Hadley 1983), associado, dentre outros fatores, ao fogo (Moreira 2000). Na América do Sul, a maior região de savana é o cerrado, ocupando originalmente cerca de 2 milhões de quilômetros quadrados (Gottsberger & Silberbauer-Gottsberger 2006). O cerrado é o segundo maior domínio vegetacional brasileiro, cobrindo 22% do território nacional (Gottsberger & Silberbauer-Gottsberger 2006). O clima é normalmente estacional, com verão chuvoso e inverno seco (Am, Aw ou Cwa; Köppen 1931).

Como em outras savanas, as espécies de cerrado evoluíram com o fogo (Simon *et al.* 2009). A grande maioria das espécies de cerrado é capaz de rebrotar após uma queimada (Gottsberger & Silberbauer-Gottsberger 2006) e essa parece ser a estratégia ecológica mais comum entre as espécies savânicas (Bond & Midgley 2001). Além disso, as espécies arbóreas de cerrado apresentam uma casca espessa que protege os tecidos internos das altas temperaturas (Gottsberger & Silberbauer-Gottsberger 2006). No entanto, queimadas frequentes (por exemplo, anuais e bienais) tendem a favorecer as espécies herbáceas e subarbustivas devido aos seus meristemas subterrâneos (Moreira 2000, Gottsberger & Silberbauer-Gottsberger 2006). Muitas espécies herbáceas têm a produção de sementes estimulada por queimadas frequentes (Sarmiento 1992) e a persistência de algumas espécies herbáceas na comunidade depende de uma alta frequência de fogo (Canales *et al.* 1994). Consequentemente, queimadas frequentes devem modificar o padrão de coocorrência das espécies vegetais no cerrado.

Nas vegetações sujeitas a queimadas frequentes, o fogo é um filtro ambiental importante, selecionando as espécies que podem ocorrer na comunidade (Pausas & Verdú 2005, Verdú & Pausas 2007). Nesse sentido, a frequência do fogo pode determinar a similaridade funcional e o parentesco filogenético das espécies vegetais coocorrentes (Webb *et al.* 2002, Slingsby & Verboom 2006). Os filtros ambientais selecionam aquelas espécies que podem persistir dentro de uma comunidade com base na suas tolerâncias às condições abióticas (Weiher & Keddy

1995). Consequentemente, os filtros ambientais tendem a reunir espécies coocorrentes com nichos similares, ou seja, com traços funcionais similares (atração fenotípica; Chase 2003, Fukami *et al.* 2005). Em relação ao parentesco filogenético, os filtros ambientais tendem a reunir espécies mais aparentadas (atração filogenética; Webb *et al.* 2002) quando os traços funcionais são conservados na evolução das espécies e as espécies aparentadas são funcionalmente similares (sinal filogenético; Prinzing *et al.* 2001, Prinzing *et al.* 2008). Entretanto, quando os traços evoluíram convergentemente e as espécies aparentadas são funcionalmente diferentes, os filtros ambientais tendem a reunir espécies menos aparentadas (dispersão filogenética, Tabela 1; Webb *et al.* 2002).

Na ausência do fogo, ou de qualquer filtro ambiental, a competição tende a ser o processo predominante na organização de comunidades sujeitas a queimadas frequentes (Webb *et al.* 2002). Por causa da exclusão competitiva de uma ou mais espécies com nichos similares (Hutchinson 1959, Leibold 1998), a competição tende a reunir espécies coocorrentes com traços funcionais distintos (dispersão fenotípica; Webb *et al.* 2002). Em relação ao parentesco filogenético, a competição tende a reunir espécies menos aparentadas (dispersão filogenética) quando os traços funcionais são conservados na evolução das espécies (Prinzing *et al.* 2001). Contudo, a competição tende a remover qualquer associação sistemática quando os traços são filogeneticamente convergentes, resultando em comunidades que não são diferentes das esperadas ao acaso (Tabela 1; Webb *et al.* 2002).

Altas frequências de fogo podem também favorecer certo tipo de interação interespecífica – a facilitação. Segundo a hipótese do gradiente de estresse (Brooker *et al.* 2008), a facilitação aumenta com a severidade do ambiente, enquanto a competição aumenta em ambientes sem estresses abióticos e com recursos abundantes. Estudos conduzidos em gradientes altitudinais (Choler *et al.* 2001) e de humidade do solo (Holzapfel *et al.* 2006) demonstraram, por exemplo, que a frequência de interações facilitativas aumentam com a altitude e a seca. Uma maneira simples de avaliar se a competição ou a facilitação é a interação predominante em uma comunidade é considerando os padrões de coocorrência de espécies (Perry *et al.* 2009). Uma vez que espécies competitivamente inferiores são incapazes de coocorrerem com espécies competitivamente superiores, um pequeno número de espécies coocorrentes deve emergir em comunidades em que a competição é predominante (Lieberman & Lieberman 2007, Perry *et al.* 2009). Por outro lado, um grande número de espécies coocorrentes deve surgir em comunidades em que a facilitação é a interação predominante (Valiente-Banuet *et al.* 2006, Perry *et al.* 2009). Em outras palavras, quão frequente é o vizinho mais próximo da espécie *i* um indivíduo da espécie *j*? Portanto, a competição pode resultar em pares de espécies ocorrendo menos frequentemente do que esperado ao acaso, enquanto a facilitação pode resultar em pares de espécies ocorrendo mais frequentemente do que o esperado ao acaso (Lieberman & Lieberman 2007).

Esses modelos nos levaram a estudar os padrões de coocorrência de espécies herbáceas e arbóreas em três áreas com diferentes frequências de fogo no Parque Nacional das Emas, GO: (1) um aceiro queimado anualmente desde 1994 (Fig. 1); (2) um aceiro queimado aproximadamente a cada dois anos desde 1994 (Fig. 2); e uma área protegida do fogo por 12 anos (Fig. 3).

Nos dois primeiros capítulos, estudamos a coocorrência de espécies em uma escala espacial pequena, considerando os vizinhos mais próximos. No primeiro capítulo, testamos se altas frequências de fogo mudam o padrão de coocorrência de espécies herbáceas e subarbustivas em cerrado, segundo a hipótese do gradiente de estresse (*sensu* Brooker *et al.* 2008). Nesse capítulo, estávamos interessados especificamente nas frequências de ocorrência de pares de espécies, conforme Lieberman & Lieberman (2007) e Perry *et al.* (2009). Para tanto, procuramos responder (1) se um dado par de espécies ocorre mais frequentemente do que o esperado ao acaso, (2) se o número de pares de espécies em áreas com queimadas frequentes é maior do que o esperado ao acaso, e (3) se a diferença nos traços funcionais de pares heterospecíficos é menor em áreas com queimadas frequentes.

No segundo capítulo, testamos se altas frequencias de fogo mudam o padrão de coocorrência de espécies arbustivas e arbóreas, considerando o modelo proposto por Webb *et al.* (2002) sobre a atração-repulsão fenotípica e filogenética (Tabela 1). Medimos oito traços funcionais associados à resistência ou à tolerância ao fogo (Cornelissen *et al.* 2003) e calculamos as distâncias filogenéticas entre todos os pares de espécies. Esperávamos que a similaridade funcional das espécies coocorrentes aumentasse ao longo de um gradiente de queimadas, enquanto que as distâncias filogenéticas ou diminuíssem, se traços fossem conservados, ou aumentassem, se os traços fossem convergentes na filogenia das espécies.

No terceiro capítulo, estudamos as espécies coocorrentes em uma escala espacial maior, incluindo dados de literatura. Comparamos sítios com altas frequências de fogo com sítios com baixas frequências de fogo em várias áreas de cerrado e de campos. Estávamos interessados especificamente na estrutura filogenética das comunidades. Procuramos responder às seguintes perguntas: (1) as queimadas frequentes reúnem comunidades de espécies de plantas aparentadas?; caso reúnam, (2) quais clados da árvore filogenética são podados pelo fogo?; e (3) as formas de vida e os traços regenerativos são conservados na filogenia das espécies?

Escolhemos apresentar a tese em capítulos, que formatamos de acordo com as normas das revistas científicas a que foram submetidos. Como as revistas que escolhemos para publicá-los exigem a sua redação em inglês, nossos capítulos foram escritos nesse idioma. O primeiro capítulo foi submetido ao periódico *Community Ecology*, o segundo capítulo foi aceito no periódico *Acta Oecologica* e o último capítulo foi submetido ao periódico *Journal of Vegetation Science*. A divisão em capítulos se justifica, porque torna a publicação dos artigos científicos menos trabalhosa e mais rápida, ainda que repetições sejam muitas vezes inevitáveis devido à independência dos capítulos.

Tabela 1. Distribuição filogenética esperada de táxons, considerando as combinações de padrões evolutivos de traços e processos ecológicos (modificado de Webb *et al.* 2002).

	Traços ecológicos filogeneticamente	
Processo ecológico dominante:	**Conservados**	**Convergentes**
Filtros ambientais	Agregada	Dispersa
Exclusão competitiva	Dispersa	Aleatória

Figura 1. Aceiro queimado anualmente desde 1994 no Parque Nacional das Emas (GO) em março de 2006, aproximadamente 18°18’50’’S e 52°54’00’’W.

Figura 2. Aceiro queimado bienalmente desde 1994 no Parque Nacional das Emas (GO) em março de 2006, aproximadamente 18°19'01''S e 52°54'10''W.

Figura 3. Área protegida do fogo desde 1994 no Parque Nacional das Emas (GO) em março de 2006, aproximadamente 18°17’28’’S e 52°53’41’’W.

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II - Capítulo 1

Coocorrências de espécies herbáceas e arbustivas vizinhas em savanas brasileiras: o papel do fogo e do acaso[1]

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[1] Trabalho aceito para a publicação no periódico *Community Ecology* com o título "Herbaceous and shrubby species co-occurrences in Brazilian savannas: the roles of fire and chance".

Herbaceous and shrubby species co-occurrences in Brazilian savannas: the roles of fire and chance

Running title: Savanna plant co-occurrences

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Keywords: Cerrado, Competition, Facilitation, Phenotypic clustering, Phenotypic overdispersion, Species co-occurrence, Stress-gradient hypothesis

Abstract: Competition and facilitation are expected to leave different signatures in the pattern of species co-occurrence. Competition may result in a given species pair occurring less often than expected by chance, whereas facilitation may result in a given species pair occurring more often than expected by chance. We assessed the co-occurrence of pairs of herbaceous and shrubby species in Brazilian savannas, asking (1) whether a given species pair occurs more often than expected by chance, (2) whether the number of species pairs in sites with frequent fires is higher than expected by chance, (3) whether the difference in the functional traits of heterospecific pairs is lower in sites with frequent fires, and (4) whether small environmental variations in each site – instead of species interactions – could explain the co-occurrence of species. We used null models to answer the first two questions, analyses of variance to answer the third question, and detrended correspondence analyses to answer the fourth question. In all studied sites, approximately half of the heterospecific pairs occurred more often than expected by chance. So, facilitation seems to be important in determining the co-occurrence of some species in Brazilian savannas. However, high fire frequencies changed the pattern of occurrence of the species pairs, resulting in a spatial signature indistinguishable from random. Frequent fires also promoted phenotypic clustering of species. Nevertheless, wherever fire frequency is reduced, competition may lead to phenotypic overdispersion of plant species. Thus, less harsh environmental conditions in savannas may increase the competition among plant species.

Introduction

Competition and facilitation are important ecological interactions determining species coexistence in plant communities (Callaway and Walker 1997, Grime 2001, Bruno et al. 2003, Butterfield 2009, Lamb et al. 2009). Competition occurs when neighbouring plants share the same light, nutrient, and space requirements (Grime 1973, Grime 2001). Facilitation occurs when one plant species ameliorates the local environment for another, especially under harsh environmental conditions (Callaway 1995, Bruno et al. 2003). However, these ecological interactions are expected to be more evident within small neighbourhoods, because plants, as sessile organisms, only interact directly with nearest individuals (Stoll and Weiner 2000, Hubbell et al. 2001). Thus, competition and facilitation should leave different signatures in the pattern of co-occurrence of species at small spatial scales (Stoll and Weiner 2000, Perry et al. 2009). As competitively inferior species are unable to persist in the neighbourhood of competitively superior species, a lower number of co-occurring species than expected at random may arise from competition (Lieberman and Lieberman 2007, Perry et al. 2009). On the contrary, a higher number of co-occurring species may arise from facilitation (Cavieres et al. 2002, Arroyo et al. 2003, Cavieres and Badano 2009).

A straightforward way to evaluate whether competition or facilitation is predominant among species pairs in a community is considering the frequency of occurrence of neighbour pairs (Perry et al. 2009, Azaele et al. 2010). In other words, how often is the near neighbour of species *i* a member of species *j*? The frequency at which two species are neighbours is influenced by the kind of interaction between them (Grime 2001, Bruno et al. 2003) and their relative abundances (Perry et al. 2009). Thus, facilitation may result in a given pair of species occurring more often than expected by chance (Dullinger et al. 2007, Lieberman and Lieberman 2007, Maestre et al. 2008), whereas competition may result in a given pair of species occurring less often than expected by chance (Gotelli and Ellison 2002, Gotelli and Rohde 2002).

The outcome of competition and facilitation is frequently influenced by variation in the abiotic environment, and within a given habitat, the environmental conditions can vary through time, also influencing the outcome of biotic interactions and driving community dynamics (Butterfield 2009). Likewise, the intensity and importance of these biotic interactions vary spatially along gradients of environmental stress or resource availability (Greenlee and Callaway 1996, Goldberg and Novoplansky 1997), hereafter referred to as ‘environmental harshness’ (sensu Brooker et al. 2008). In plant communities, for instance, competition and facilitation are supposed to occur simultaneously among different species and to change as the age of the community advances. Seedlings may use larger individuals as ‘nurses’, but compete with them when they become adults (Verdú and Valiente-Banuet 2008). Notwithstanding, empirical studies have demonstrated that facilitation increases with environmental harshness, whereas competition prevails under more benign conditions (that is, the stress-gradient hypothesis; Bertness and Callaway 1994, Greenlee and Callaway 1996, Brooker et al. 2008). As a consequence, the pattern of co-occurrence of plant species at small spatial scale is also expected to change when the environmental conditions change (Collins and Klahr 1991). The number of occurrences of pairs of neighbouring plant species should be, hence, greater than expected by chance in communities that experience an increasing environmental harshness (Lieberman and Lieberman 2007, Perry et al. 2009).

The assessment of the functional traits of species is also important to infer whether competition determines the co-occurrence of heterospecific pairs of plant species. At small spatial scales, species plants compete directly for limited soil nutrients (Hubbell et al. 2001, Grime 2001, Lamb et al. 2009). Such a competition is higher among species that have similar niches and consequently share more morphological and physiological characteristics, that is, share more functional traits (Weiher et al. 1998, Grime 2001). Thus, wherever competition is predominant, neighbouring heterospecific pairs of plants are expected to differ more than expected by chance in functional trait values (Weiher and Keddy 1995, Weiher et al. 1998).

In South America, the largest savanna region is the Brazilian cerrado (Gottsberger and Silberbauer-Gottsberger 2006). Like its counterparts elsewhere, the cerrado vegetation evolved with fire and, consequently, its plant species have well-developed capabilities of regenerating, either vegetatively or by seed (Coutinho 1990, Gottsberger and Silberbauer-Gottsberger 2006). Even though most fires in cerrado occur at the surface, by consuming mainly the herbaceous layer of the vegetation (Miranda et al. 1993), frequent burnings favour the herbaceous and shrubby species, due to their underground meristems, at the expense of trees (Moreira 2000, Gottsberger and Silberbauer-Gottsberger 2006). Many herbaceous species have the reproductive output increased by recurrent fires (Sarmiento 1992), and the persistence of some species in the community depends on high fire frequency (Canales et al. 1994).

Near neighbour interactions have been recently examined in forests (Lieberman and Lieberman 2007) and shrublands (Perry et al. 2009). These studies did not corroborate the stress-gradient hypothesis. Perry et al. (2009) argued that a great number of species pairs in rich plant communities are unlikely to occur, because the species are present at low densities in samples. In this case, most of near neighbour pairs are represented by a small fraction of species and, by chance alone, the number of observed possible pairs is lower than the theoretical maximum. Nevertheless, these previous studies did not evaluate explicitly the stress-gradient hypothesis, considering the species interactions along an environmental harshness gradient. Studies conducted in altitudinal (Choler et al. 2001) and moisture (Holzapfel et al. 2006) gradients have demonstrated that the frequency of facilitative interactions increases with the environmental harshness.

Here, we tested whether an annual fire frequency changes the pattern of co-occurrence of herbaceous and shrubby species in cerrado, taking into account the near neighbours. Based on the stress-gradient hypothesis (Brooker et al. 2008), we expected that annual fires would increase the co-occurrence of pairs of herbaceous and shrubby species and assemble neighbouring species with similar functional traits. In sum, we answered (1) whether a given species pair occurs more often than expected by chance, (2) whether the number of species pairs in sites with frequent fires is higher than expected by chance, (3) whether the difference in the functional traits of the heterospecific pairs is lower in sites with frequent fires, and (4) whether small environmental variations in each site – instead of species interactions – could explain the co-occurrence of species.

Methods

Study site

We surveyed three spatially proximate cerrado sites in Emas National Park (ENP), central Brazil (17°49’-18°28’S; 52°39’-53°10’W). The ENP comprises 132,941 ha and is one of the largest and most important reserves of Cerrado (Unesco 2001). Regional climate is humid tropical, characterised by marked rainfall seasonality, with a pronounced dry season in the winter (Aw, Köppen 1931). Annual rainfall and mean temperature lie around 1,745 mm and 24.6°C, respectively. In general, the soils are poor in nutrients, well drained, and acid (Silva and Batalha 2008). Up to 1984, the ENP was annually burned in the dry season to promote forage regrowth to cattle (França et al. 2007). Afterwards, the ENP was fenced, and a fire exclusion policy was established (Ramos-Neto and Pivello 2000). As a consequence, catastrophic fires used to occur every 3-4 years, burning 80% of the park’s area (Ramos-Neto and Pivello 2000). Since 1994, around 10 km² of preventive firebreaks have been burned annually at the end of the wet season, and a fire brigade works in the park during the dry season to prevent anthropogenic fires. Thus, there are currently few occurrences of anthropogenic fires inside the ENP (less than 2.2% of the burned area from 1994 to 2003), and the largest wildfires burn less than 30% of the total area (França et al. 2007).

Data collection

In the late rainy season of 2006, we sampled the plant species of the herbaceous layer in three nearby sites with different fire frequencies, but with similar physiognomies (grassland cerrado), on the same soils (Oxisols), in the southeastern portion of the ENP. The first and second sites were firebreaks, one burned annually since 1994 (18°18’50’’S and 52°54’00’’W) and other burned approximately biennially since 1994 (18°19’01’’S and 52°54’10’’W). The third site was a protected cerrado, without fires since 1994 (18°17’28’’S and 52°53’41’’W). The sites were distant less than 2 km apart.

In each site, we placed a 1,250 m line, with 125 points, 10 m apart. In each point, we sampled four individuals in the herbaceous layer with the point-quarter method (Mueller-Dombois and Ellenberg 1974), summing up 500 individuals in each site. We defined the herbaceous layer as all herbaceous individuals and all woody individuals with stem diameter at soil level lower than 3 cm. We did not sample seedlings, defined as those individuals with cotyledons. In cerrado, most plant species present clonal growth from subterranean organs (Gottsberger and Silberbauer-Gottsberger 2006), so that it is occasionally hard to distinguish ramets and genets in field. We tried to minimise this problem counting only those individuals that did not present clear connections to other sampled individuals at soil level. We identified the individuals sampled by comparing the collected material to reference collections from

ENP (Batalha and Martins 2002) and vouchers lodged at the State University of Campinas herbarium. When identification at species level was not possible, we classified them as morphospecies.

Data analyses

First, we described the distribution of species abundances in the three sites to characterise the general structure of the plant community, considering all individuals sampled. For each site, we constructed a graph in which we plotted the relative abundance of species against species abundance rank order (Fig. 1). Then, in each sampling point, we considered that each individual could interact potentially with the other three individuals. Accordingly, we obtained six different pairs of co-occurring individuals per sampling point, summing up 750 pairs of plants in each site. First, we calculated the theoretical maximum number of species pairs for each site, computing the simple formula $S(S+1)/2$, where S was the total number of species. Then, we computed for each site the observed frequency of all possible *ij* species pairs.

To answer our first question, we generated a distribution of expected frequencies for each potential *ij* species pair in each site. We followed the null model proposed by Lieberman and Lieberman (2007), in which the combinations of species pairs in a site reflect a process of random sampling from the community: (1) we picked two plants at random, with replacement, from the complete list of individuals of the site; (2) we recorded the species identities of the pair and, if this randomly picked pair matched the *ij* species combination under consideration, we counted it; and (3) we repeated these steps until the number of pairs drawn was equal to the number of pairs in the site. We repeated this procedure 1,000 times, producing a null distribution of 1,000 expected counts for a given *ij* species combination.

To deal with a potential bias of the non-independence of the pairs at each sampling point, we also ran the previous analysis considering only two random pairs of individuals per point. So, we picked randomly two pairs of individuals without replacement at each point, summing up 250 pairs of plants in each site. In this second null model, we considered the highest number of species pairs picked by chance in each site for 1,000 randomisations. Then, we compared the frequency of these species pairs with a distribution of expected frequencies for each potential *ij* species pair in each site, as described above.

We used a Monte Carlo procedure to evaluate whether the observed number of species pairs in each site was different than expected by chance. We used the following procedure: (1) we computed the observed number of species pairs in each site; (2) we randomised the individuals in the sampling points and recorded the number of random pairs; (3) we repeated these steps 1,000 times and estimated a random mean and SD for the null communities; and (4) we calculated pseudo *P*-values for the observed number of species pairs to compare null and observed community characteristics. We also repeated this procedure considering only the conspecific pairs.

To answer our third question, we measured three functional traits: basal area, plant height, and specific leaf area. In each site, we sampled ten individuals of each species to estimate the mean of the functional traits. When there were not ten individuals of a given species, we used all individuals sampled. Basal area is a trait related to space occupation and resource acquisition (Navas and Moreau-Richard 2005). Plant height is associated to competitive ability, fecundity, and tolerance to stress (Cornelissen et al. 2003). Specific leaf area is positively related to maximum photosynthetic rates, since low values of it correspond to a high leaf structure investment (Cornelissen et al. 2003). We measured these traits according to Cornelissen et al. (2003). We calculated the leaf area with the ImageJ software (Rasband 2004). Then, we compared the absolute value of the differences in functional trait values of the heterospecific pairs of each site with an analysis of variance, followed by a Tukey test.

The term ‘phenotypic clustering’ refers to high trait similarity among neighbouring species, whereas the term ‘phenotypic overdispersion’ refers to low trait similarity among neighbouring species (Weiher et al. 1998).

Finally, to answer our last question, we constructed a detrended correspondence analysis (Jongman et al. 1995), which allowed us to observe how spread species and sites scores were in the multivariate space. With this approach, we evaluated whether theoretical environmental variables could explain patterns of co-occurrence of species within sites. We ran all analyses in the R environment (R Development Core Team 2009). The R functions we wrote are available in http://www.cerradoecology.com.

Results

We found 97 species in the three sites; 58 species in the annually burned site, 50 species in the biennially burned site, and 62 species in the unburned site (Table 1). The distribution of species abundances in the three sites was similar, with the dominance of few species, such as *Axonopus suffultus* and *Tristachya leiostachya* (Fig. 1).

With the first null model, we found 182 species pairs in the annually burned site, 168 in the biennially burned site, and 221 in the unburned site. These values were proportionally much lower than expected by the theoretical maximum number of species pairs (1,711 for the annually burned site, 1,275 for the biennially burned site, and 1,953 for the unburned site). They represented 10.63, 13.17 and 11.31% of the theoretical maxima for the three sites respectively. Moreover, in the second null model, we found 101 pairs in the annually burned site, 97 pairs in the biennially burned site and 127 pairs in the unburned site. These values accounted for 5.90, 7.60 and 6.50% of the theoretical maxima for the three sites respectively.

When we analysed each observed pair of species with the first null model, we found few pairs that occurred less often than expected by chance (two pairs in the annually burned site and three pairs in other sites (Appendix 1). However, approximately half of the observed heterospecific pairs in each site were very frequent. The observed frequencies of 50.9% of the heterospecific pairs in the annually burned site, 32.5% in the biennially burned site, and 45.5% in the unburned site were significantly higher than expected by chance ($P < 0.05$, Appendix 1). We found similar results with the second null model, given that one single pair occurred less often than expected by chance in the annually burned site, and two pairs in the biennially burned site (Appendix 2). Accordingly, 35.9, 42.8, and 41.2% of the observed heterospecific pairs in the annually burned, biennially burned, and unburned sites occurred at frequencies higher than those expected by chance ($P < 0.05$, Appendix 2).

The total number of observed pairs in the unburned site was significantly lower than expected by chance (mean of null pairs = 253.6 ± 9.7, $P < 0.001$). Nevertheless, the total numbers of observed pairs in the sites with high fire frequencies were not different from random (mean of null pairs = 195.7 ± 9.3, $P = 0.110$ for the annually burned site, mean of null pairs = 177.0 ± 8.2, $P = 0.240$ for the biennially burned site). On the other hand, the total numbers of conspecific pairs in all sites were significantly higher than expected at random ($P < 0.001$). We observed 266 conspecific species pairs in the annually burned site (mean of null pairs = 202.1 ± 12.7), 194 in the biennially burned site (mean of null pairs = 101.3 ± 9.6), and 180 in the unburned site (mean of null pairs = 103.7 ± 9.6).

We also found a significant difference in the values of specific leaf area of neighbouring heterospecific pairs ($F = 15.083$, $P < 0.001$). The neighbouring plant species in the annually burned site presented a mean difference in the values of specific leaf area (36.284 $m^2 kg^{-1}$), lower than neighbouring species in the biennially burned (70.781 $m^2 kg^{-1}$) and unburned sites (70.610 $m^2 kg^{-1}$). The mean difference between biennially burned and unburned sites was not significant. When we analysed the other functional traits, we also did not find differences among the sites (Table 2, F = 2.143 for basal area and F = 1.388 for plant height, $P > 0.100$ for all comparisons).

The site scores in the detrended correspondence analyses were somewhat spread along the first two axes (Fig. 2), indicating that the species composition in the point-quarters along transects were different. This is an indication of environmental heterogeneity within sites, which may influence the species co-occurrences differently from expected at random. However, the detrended correspondence analyses did not show any particular clustering of species scores and the overall distribution of species scores in the multivariate space was quite overlapped. Thus, species interactions, rather than local environmental variations, are likely to explain the co-occurrence of species.

Discussion

Our results supported that more benign environmental conditions in cerrado may increase the competition among species plants. Although high fire frequencies did not assemble more pairs of species as predicted by stress-gradient hypothesis (Brooker et al. 2008), they may diminish the strength of competitive exclusion among plants, resulting in co-occurrences of species indistinguishable from random. Frequent fires also promoted phenotypic clustering of herbaceous species in cerrado. So, wherever fire frequency is reduced, competition may lead to phenotypic overdispersion of plant species.

The observed number of pairs of neighbouring species was lower than the expected maximum number for the cerrado sites. In other studies, this number was also very low (Lieberman and Lieberman 2007, Perry et al. 2009). This discrepancy is primarily due to differences in the relative abundance of species plants (Table 1, Perry et al. 2009). If there are many rare and few common species in the community, chance alone would make it unlikely that rare species would occur as neighbours (Lieberman and Lieberman 2007). As long as pairs of neighbouring species are determined to a certain extent by chance (see also Hubbell 2001), the reciprocal selective pressures acting on species are dependent on community context (Perry et al. 2009). Consequently, the interactions between species may be the product of a diffuse rather than a specific pairwise selection. Diffuse evolution among plants has been also evoked to explain the tolerance of saplings to a large number of neighbouring tree species in tropical forests (Uriarte et al. 2004). Further studies should consider competition and facilitation as a network of species in the community to place the ecological interactions in an appropriate evolutionary context (Johnson and Stinchcombe 2007, Verdú and Valiente-Banuet 2008)

If chance prevents most of plant species to interact with each other, ecological interactions may not be important in structuring the co-occurrence of plant species (Perry et al. 2009). However, a certain pattern emerges from that small proportion of heterospecific pairs that occurred as neighbours at frequencies different than expected at random. In the three cerrado sites, approximately half of the heterospecific pairs occurred more often than expected by chance and few species pair occurred less often than expected by chance. In forests and shrublands, most of the observed pairs also occurred at higher frequencies than expected by chance (Lieberman and Lieberman 2007, Perry et al. 2009). These findings indicate that facilitation is important in determining the co-occurrence of some species in plant communities. In cerrado, this positive interaction seems to be more important between rare species, of which the pairs were more frequent than rare-common species pairs (see Appendix 1).

The unburned cerrado showed a number of species pairs lower than expected by chance, what is expected to occur where competition is the predominant interaction among species (Lieberman and Lieberman 2007, Perry et al. 2009), since few species could survive in the neighborhood of competitively superior species (Grime 2001, Lamb et al. 2009). In addition, a decrease in the fire frequency promoted a phenotypic overdispersion of species relative to specific leaf area. Phenotypic overdispersion is also expected when competitive exclusion structures the community. Among neighbouring plants, however, phenotypic overdispersion is thought to be even higher (Weiher and Keddy 1995), because species compete directly for limited soil nutrients (Grime 2001). Evidence of competition promoting phenotypic overdispersion among neighbours has been also found in other plant communities (prairies – Fargione et al. 2003; sand dunes – Stubbs and Wilson 2004; and tropical forests – Kraft et al. 2008). Thus, competition seems to be predominant when an environmental constraint is reduced, even though facilitation continues to occur among some species pairs.

However, for basal area and plant height, we did not find differences among the cerrado sites. Basal area and height are traits associated with the growth forms of plants (Cornelissen et al. 2003). Herbaceous and shrubby species present more restricted range in the values of basal area and height than trees, for instance. Thus, a clear pattern of phenotypic clustering or overdispersion relative to these traits may not emerge in the herbaceous layer of the savannas. On the other hand, annual fires promoted a phenotypic clustering of herbaceous plants, because frequent fires acting as an environmental filter select those species that can survive within a community on the basis of their tolerance to the abiotic conditions (Weiher and Keddy 1995). Consequently, they tend to assemble co-occurring species with similar niches, that is, species with similar functional traits (Fukami et al. 2005). Silva and Batalha (2010) have recently demonstrated that frequent fires may assemble functionally similar woody species in cerrado. In Mediterranean vegetation, high fire frequencies also promote phenotypic clustering of plants (Pausas and Verdú 2008). In other savannas (Williams et al. 1999, Silva et al. 2001), as well as in the California chaparral (see Syphard et al. 2006 for reference), frequent fires changed the plant functional types, favouring grass and shrub species. Although frequent fires favour herbaceous plants at the expense of woody ones (Moreira 2000), they reduce the range of functional traits and the number of functional types in fire-prone vegetation types, decreasing the overall functional diversity of the plant community.

Frequent fires, however, did not assemble species pairs at frequencies higher than expected by chance, favouring facilitation among plant species (Perry et al. 2009). Facilitation has been documented in alpine, arid, and Mediterranean-type plant communities (Brooker et al. 2008), that is, in environments that experience harsh abiotic conditions, as the savannas. In these vegetation types, facilitation takes the form of ‘nurse plants’, in which larger plants act as favoured recruitment sites for seedlings and for herbs by modifying microclimate, or reducing herbivory or both (Callaway 1995, Brooker et al. 2008). Here, we tested the stress gradient hypothesis with herbaceous and shrubby species, which are affected directly by fires in cerrado (Miranda et al. 1993). Consequently, possible nurse effects of large woody species were not captured by our analysis. Despite this bias, our results showed that frequent fires may decrease the strength of competitive exclusion among herbaceous plants, resulting in co-occurrences of species indistinguishable from random. Further studies in savannas should also assess the pairwise co-occurrence between herbs and trees when testing the stress gradient hypothesis.

The number of conspecific pairs of species was higher than expected at random in the three cerrado sites. In other vegetation types, the number of conspecific pairs was also higher than expected by chance (Perry et al. 2009, but see Lieberman and Lieberman 2007). This general pattern is a direct consequence of the spatial distribution of plant populations. In rich communities, most plant species present an aggregated spatial distribution (Condit et al. 2000, Perry et al. 2008). In cerrado, the spatial pattern of the populations is not different (San Jose et al. 1991, Silva et al. 2009). Aggregation of individuals of the same species is a response to patchiness of favourable soil conditions or to dispersal limitation (Condit et al. 2000). In cerrado, the conspecific aggregation is increased by the clonal growth of the large majority of their plant species (Gottsberger and Silberbauer-Gottsberger 2006). So, frequent fires do not seem to change the clumped pattern of spatial distribution of herbaceous species and, consequently, the co-occurrence of conspecific pairs in cerrado.

Moreover, it is worth noticing that the large dominance of some grasses in the studied sites, such as *Axonopus suffultus* and *Tristachya leiostachya* (Fig. 1), contributed largely to the significance of the results. Nevertheless, dominance of graminoid species are common features in other savannas (San Jose et al. 1991, Sarmiento 1992, Canales et al. 1994), so that the pattern in the co-occurrence of conspecific pairs we found was consistent in other savannas as well.

Our results also supported that the species interactions, rather than environmental heterogeneity, explain the co-occurrence of species pairs in cerrado. Other studies in temperate forests (Cavender-Bares et al. 2006) and sclerophyllous shrublands (Slingsby and Verboom 2006) also demonstrated similar trends at fine spatial scales. Thus, even thought small variations in the environment might also influence the outcome of competition and facilitation (Butterfield 2009), species interactions seem to be the predominant ecological process in the assembly of neighbour species pairs.

It is also important to notice that we could not include genuine replications (sensu Hurlbert 1984) in our experimental design. In cerrado, where fire frequency is high, very few sites protected from fire during a decade can be found (França et al. 2007), so that replicated treatments may be hard to obtain. Hence, other non-controlled variables differing between the cerrado sites may also account for a fraction of the observed results.

In conclusion, the frequencies of neighbour species pairs in cerrado, as in other vegetation types, follow mostly a distribution expected by chance. However, competition and facilitation may also influence the co-occurrence of herbaceous and shrubby species. Among the heterospecific pairs that departed from the frequency expected at random, facilitation seems to be the predominant ecological interaction in cerrado. Competition, on the other hand, seems to take place in the absence of an environmental constraint. Frequent fires may hence decrease the strength of competitive exclusion among plants, resulting in random co-occurrences of neighbouring species.

Acknowledgments: We are grateful to Fapesp, for financial support; to CNPq, for the scholarship granted to I.A.S. and M.A.B.; to Ibama, for research permission; to Emas National Park staff, for logistical assistance; to R. Moreira, M.B. Ramos-Neto, and Oreades Núcleo de Geoprocessamento for the ENP’s satellite images; to A.T. Fushita for help in ENP’s fire history map; to UnB and Unicamp herbarium staffs; to the taxonomists M.W. Ferreira, C. Proença and J. Semir, for their assistance in species identification; to P.K. Amorim, S.P. Campos, C.A. Casali, A.V.F. Jardim, M.O. Maia, L.T. Manica, F.Q. Martins, D.M. Silva, and L. Sims, for helping us in field work.

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Appendix 1. Observed herbaceous species pairs for which the null hypothesis was rejected ($\alpha = 0.05$) with the first null model. The names of the species *i* and *j* for each pair are shown, followed by the number of individuals of each species in the three cerrado sites, n(i) and n(j); f(obs) = observed number of times species *i* and *j* occurred as a near neighbour pair; f(exp) = expected number based on the null model. Site 1: annually burned; site 2: biennially burned; and site 3: unburned since 1994.

Species *i*	Species *j*	n (i)	n (j)	f (obs)	f (exp)	*P*
Annually burned site						
Eremanthus erythropappus	*Bulbostylis junciformis*	2	9	2	0.10	0
Erythroxylum campestre	*Erythroxylum campestre*	11	11	3	0.33	0
Eugenia angustissima	*Campomanesia adamantium*	9	4	2	0.20	0
Gomphrena macrocephala	*Anacardium humile*	1	15	2	0.08	0
Gymnopogon foliosus	*Andropogon leucostachys*	1	1	1	0.01	0
Jacaranda rufa	*Diplusodon virgatus*	3	3	1	0.04	0
Kielmeyera rubriflora	*Axonopus barbigerus*	1	2	1	0.02	0
Mimosa gracilis	*Chromolaena squalida*	3	8	2	0.15	0
Mimosa xanthocentra	*Chromolaena squalida*	3	8	2	0.15	0
Myrciaria delicatula	*Axonopus barbigerus*	15	2	2	0.19	0
Myrciaria delicatula	*Kielmeyera rubriflora*	15	1	2	0.08	0
Myrtaceae sp.1	*Byrsonima guilleminiana*	1	4	1	0.03	0
Myrtaceae sp.4	*Declieuxia fruticosa*	7	1	1	0.04	0
Ouratea humilis	*Myrciaria delicatula*	2	15	3	0.18	0
Panicum sp.	*Erythroxylum campestre*	2	11	2	0.12	0
Paspalum sp.	*Campomanesia adamantium*	1	4	1	0.02	0
Paspalum sp.	*Coelorachis* sp.	1	2	1	0.01	0
Pavonia rosa-campestris	*Eugenia* sp.1	4	3	2	0.09	0
Poaceae sp.1	*Campomanesia pubescens*	1	4	1	0.03	0
Poaceae sp.1	*Ipomoea* sp.	1	3	1	0.03	0
Polycarpaea corymbosa	*Palicourea coriaceae*	1	4	1	0.02	0
Pradosia brevipes	*Anacardium humile*	4	15	3	0.35	0
Pradosia brevipes	Myrtaceae sp.1	4	1	1	0.02	0

Riencourtia tenuifolia	*Casearia* sp.	6	1	1	0.03	0
Rourea induta	*Byrsonima guilleminiana*	1	4	1	0.03	0
Coelorachis sp.	*Annona warmingiana*	2	6	1	0.07	0
Loudetiopsis chrysothryx	*Allagoptera campestris*	5	1	1	0.03	0
Paspalum sp.	*Annona warmingiana*	1	6	1	0.04	0
Polycarpaea corymbosa	*Bulbostylis junciformis*	1	9	1	0.04	0
Psidium rufum	*Psidium rufum*	5	5	1	0.08	0
Coelorachis sp.	*Campomanesia adamantium*	2	4	1	0.05	0
Galactia decumbens	*Bulbostylis junciformis*	1	9	1	0.06	0
Melastomataceae sp.	*Annona warmingiana*	3	6	1	0.09	0
Myrtaceae sp.3	*Chromolaena squalida*	1	8	1	0.05	0
Pradosia brevipes	*Jacaranda rufa*	4	3	1	0.08	0
Ipomoea sp.	*Eugenia* sp.1	3	3	1	0.05	0.01
Jacaranda rufa	*Campomanesia adamantium*	3	4	1	0.07	0.01
Jacaranda rufa	*Campomanesia pubescens*	3	4	1	0.08	0.01
Palicourea coriaceae	*Campomanesia adamantium*	4	4	1	0.10	0.01
Palicourea coriaceae	*Campomanesia pubescens*	4	4	1	0.08	0.01
Palicourea coriaceae	*Jacaranda rufa*	4	3	1	0.07	0.01
Myrtaceae sp.3	*Aspilia leucoglossa*	1	13	1	0.08	0.01
Myrtaceae sp.4	*Chromolaena squalida*	7	8	2	0.37	0.01
Pavonia rosa-campestris	*Ipomoea* sp.	4	3	1	0.08	0.01
Sida cordifolia	Myrtaceae sp.4	2	7	1	0.10	0.01
Myrtaceae sp.4	*Myrciaria delicatula*	7	15	3	0.66	0.01
Pradosia brevipes	*Byrsonima guilleminiana*	4	4	1	0.10	0.01
Pradosia brevipes	*Diplusodon virgatus*	4	3	1	0.08	0.01
Campomanesia pubescens	*Campomanesia adamantium*	4	4	1	0.10	0.01
Ipomoea sp.	*Campomanesia pubescens*	3	4	1	0.07	0.01
Campomanesia adamantium	*Annona warmingiana*	4	6	1	0.16	0.02
Erythroxylum campestre	*Aspilia leucoglossa*	11	13	3	0.84	0.02
Mimosa gracilis	*Eugenia angustissima*	3	9	1	0.19	0.02
Riencourtia tenuifolia	Melastomataceae sp.	6	3	1	0.12	0.02
Eugenia angustissima	*Chromolaena squalida*	9	8	2	0.46	0.02
Myrtaceae sp.4	Melastomataceae sp.	7	3	1	0.14	0.02
Eugenia angustissima	*Diplusodon virgatus*	9	3	1	0.16	0.02
Sida cordifolia	*Anacardium humile*	2	15	1	0.19	0.02
Ouratea humilis	*Erythroxylum*	2	11	1	0.11	0.02

	campestre					
Tristachya leiostachya	*Campomanesia adamantium*	254	4	2	6.14	0.02
Byrsonima guilleminiana	*Axonopus suffultus*	2	40	2	0.45	0.02
Tristachya leiostachya	*Myrciaria delicatula*	254	15	14	22.99	0.03
Psidium rufum	*Annona warmingiana*	5	6	1	0.17	0.03
Riencourtia tenuifolia	*Palicourea coriaceae*	6	4	1	0.16	0.03
Eugenia sp.1	*Erythroxylum campestre*	3	11	1	0.20	0.03
Myrciaria delicatula	*Diospyros híspida*	15	2	1	0.18	0.03
Eugenia angustissima	*Eugenia angustissima*	9	9	1	0.23	0.03
Jacaranda rufa	*Eugenia angustissima*	3	9	1	0.16	0.03
Loudetiopsis chrysothryx	*Axonopus suffultus*	5	40	4	1.22	0.03
Palicourea coriaceae	*Bulbostylis junciformis*	4	9	1	0.20	0.03
Riencourtia tenuifolia	*Annona warmingiana*	6	6	1	0.20	0.03
Melastomataceae sp.	*Eugenia angustissima*	3	9	1	0.19	0.04
Myrciaria delicatula	*Annona warmingiana*	15	6	2	0.54	0.04
Ipomoea sp.	*Erythroxylum campestre*	3	11	1	0.20	0.04
Axonopus suffultus	*Axonopus derbyanus*	40	7	4	1.66	0.04
Pradosia brevipes	*Eugenia angustissima*	4	9	1	0.23	0.04
Sida cordifolia	*Myrciaria delicatula*	2	15	1	0.20	0.04
Eriosema crinitum	*Axonopus suffultus*	1	40	1	0.25	0.05
Mimosa xanthocentra	*Aspilia leucoglossa*	3	13	1	0.22	0.05
Myrtaceae sp.1	*Axonopus suffultus*	1	40	1	0.24	0.05
Parinari excelsa	*Myrciaria delicatula*	3	15	1	0.26	0.05
Myrtaceae sp.4	*Axonopus suffultus*	7	40	4	1.72	0.05
Biennially burned site						
Declieuxia fruticosa	*Alibertia sessilis*	2	1	1	0.01	0
Eugenia sp.2	*Alibertia sessilis*	1	1	1	0.01	0
Eugenia sp.2	*Declieuxia fruticosa*	1	2	1	0.01	0
Manihot tripartita	*Anemopaegma arvense*	2	1	1	0.02	0
Myrcia uberavensis	*Gomphrena macrocephala*	2	1	1	0.01	0
Myrcia uberavensis	*Anemopaegma acutifólia*	2	1	1	0.01	0
Ouratea acuminata	*Myrcia* sp.	1	2	1	0.01	0
Parinari excelsa	*Anemopaegma acutifólia*	6	1	1	0.04	0
Parinari excelsa	*Axonopus barbigerus*	6	2	3	0.07	0
Peltodon pusillus	*Anacardium humile*	1	11	2	0.06	0
Panicum sp.	Myrtaceae sp.5	7	1	1	0.03	0
Protium ovatum	Myrtaceae sp.4	1	6	1	0.04	0
Tristachya leiostachya	*Axonopus derbyanus*	98	102	22	60.03	0
Myrtaceae sp.4	*Manihot tripartita*	6	2	1	0.08	0
Myrtaceae sp.5	Myrtaceae sp.4	1	6	1	0.03	0
Pradosia brevipes	*Croton sp.*	9	2	1	0.10	0

Syagrus flexuosa	*Pradosia brevipes*	3	9	2	0.17	0
Myrtaceae sp.4	*Anemopaegma arvense*	6	1	1	0.04	0
Parinari excelsa	*Myrcia uberavensis*	6	2	1	0.07	0.01
Psidium rufum	*Eugenia angustissima*	3	17	2	0.33	0.01
Eugenia angustissima	*Campomanesia pubescens*	17	3	2	0.30	0.01
Poaceae sp.1	*Eugenia angustissima*	1	17	1	0.10	0.01
Mimosa polycephala	*Axonopus derbyanus*	1	102	3	0.61	0.01
Myrciaria delicatula	*Gomphrena macrocephala*	73	1	2	0.44	0.01
Eugenia angustissima	*Anacardium humile*	17	11	4	1.14	0.01
Manihot tripartita	*Anacardium humile*	2	11	1	0.13	0.01
Mimosa amnis-atri	*Erythroxylum campestre*	1	15	1	0.11	0.01
Syagrus flexuosa	Myrtaceae sp.4	3	6	1	0.11	0.01
Tristachya leiostachya	*Erythroxylum campestre*	98	15	16	8.73	0.01
Myrtaceae sp.6	*Anacardium humile*	5	11	2	0.37	0.02
Eugenia sp.1	*Erythroxylum campestre*	2	15	1	0.15	0.02
Panicum sp.	*Campomanesia pubescens*	7	3	1	0.13	0.02
Pradosia brevipes	*Declieuxia fruticosa*	9	2	1	0.10	0.02
Myrciaria delicatula	*Axonopus derbyanus*	73	102	30	45.03	0.02
Sida cordifolia	*Axonopus suffultus*	1	88	2	0.53	0.02
Tontelea micrantha	Myrtaceae sp.6	5	5	1	0.14	0.02
Eugenia sp.1	*Eugenia angustissima*	2	17	1	0.19	0.02
Myrciaria delicatula	*Hyptis sp.*	73	1	2	0.45	0.03
Tristachya leiostachya	*Palicourea coriacea*	98	1	2	0.56	0.03
Campomanesia adamantium	*Anacardium humile*	3	11	1	0.19	0.03
Tristachya leiostachya	*Panicum* sp.	98	7	1	4.07	0.03
Myrciaria delicatula	*Croton SP.*	73	2	3	0.95	0.03
Bulbostylis junciformis	*Axonopus suffultus*	1	88	2	0.54	0.03
Psidium rufum	*Axonopus suffultus*	3	88	4	1.59	0.04
Erythroxylum campestre	*Annona warmingiana*	15	3	1	0.23	0.04
Diodia teres	*Axonopus derbyanus*	1	102	2	0.57	0.05
Myrcia sp.	*Axonopus suffultus*	2	88	3	1.05	0.05
Tristachya leiostachya	*Trachypogon* sp.	98	1	2	0.63	0.05
Protium ovatum	*Axonopus derbyanus*	1	102	2	0.62	0.05
Tristachya leiostachya	Myrtaceae sp.6	98	5	6	2.91	0.05
Unburned since 1994						
Campomanesia adamantium	*Axonopus derbyanus*	5	37	5	1.13	0
Campomanesia pubescens	*Campomanesia pubescens*	2	2	1	0.02	0
Chromolaena squalida	*Annona warmingiana*	2	5	2	0.05	0
Croton pohlianus	*Casearia* sp.	1	2	1	0.01	0

Eugenia calycina	*Coelorachis* sp.	4	2	1	0.04	0
Galactia decumbens	*Anacardium humile*	1	11	1	0.08	0
Galactia decumbens	*Campomanesia adamantium*	1	5	1	0.03	0
Galactia martii	*Eugenia angustissima*	1	14	1	0.09	0
Mimosa gracilis	*Andira laurifólia*	1	1	1	0.01	0
Myrcia uberavensis	*Loudetiopsis chrysothryx*	3	10	3	0.18	0
Myrtaceae sp.6	*Andiralaurifólia*	7	1	1	0.05	0
Myrtaceae sp.6	*Byrsonima guilleminiana*	7	1	1	0.04	0
Myrtaceae sp.6	*Mimosa gracilis*	7	1	1	0.03	0
Ouratea acuminata	*Duguetia furfuracea*	3	10	2	0.17	0
Ouratea humilis	*Alibertia sessilis*	1	3	2	0.03	0
Palicourea coriácea	*Mimosa amnis-atri*	6	1	1	0.03	0
Panicum sp.	*Andira laurifólia*	1	1	1	0.01	0
Panicum sp.	*Mimosa gracilis*	1	1	1	0.00	0
Poaceae sp.1	*Allagoptera campestris*	4	1	1	0.02	0
Poaceae sp.1	*Diodia teres*	4	2	2	0.05	0
Protium ovatum	*Croton glandulosus*	6	1	2	0.04	0
Psidium rufum	*Paspalum carinatum*	4	1	1	0.02	0
Senna rugosa	*Casearia silvestris*	4	1	1	0.03	0
Senna rugosa	*Rauvolfia weddelliana*	4	1	1	0.04	0
Talisia angustifólia	*Pradosia brevipes*	3	6	3	0.10	0
Trachypogon sp.	*Axonopus suffultus*	19	27	9	3.03	0
Campomanesia pubescens	*Anacardium humile*	2	11	2	0.14	0
Duguetia furfuracea	*Byrsonima guilleminiana*	10	1	1	0.08	0
Eugenia angustissima	*Campomanesia pubescens*	14	2	2	0.19	0
Ouratea acuminata	*Coelorachis* sp.	3	2	1	0.04	0
Palicourea coriácea	*Croton glandulosus*	6	1	1	0.03	0
Parinari excelsa	*Erythroxylum campestre*	4	9	2	0.23	0
Parinari excelsa	Myrtaceae sp.6	4	1	1	0.03	0
Protium ovatum	*Palicourea coriacea*	6	6	2	0.21	0
Tristachya leiostachya	*Myrciaria delicatula*	163	67	43	65.00	0
Myrtaceae sp.6	*Jacaranda decurrens*	7	2	1	0.07	0
Panicum sp.	Myrtaceae sp.6	1	7	1	0.04	0
Parinari excelsa	*Parinari excelsa*	4	4	1	0.06	0
Poaceae sp.1	*Erythroxylum campestre*	4	9	2	0.21	0
Psidium australe	*Myrcia* sp.	2	4	1	0.05	0
Senna rugosa	*Coelorachis* sp.	4	2	1	0.06	0
Syagrus flexuosa	*Bulbostylis junciformis*	7	5	2	0.22	0
Casearia sp.	*Annona warmingiana*	2	5	1	0.07	0.01
Erythroxylum campestre	*Croton pohlianus*	9	1	1	0.05	0.01
Psidium australe	*Axonopus suffultus*	2	27	2	0.30	0.01

Psidium bergianum	*Anacardium humile*	1	11	1	0.05	0.01
Senna rugosa	*Myrcia uberavensis*	4	3	1	0.07	0.01
Syagrus flexuosa	*Cayaponia espelina*	7	1	1	0.05	0.01
Tontelea micrantha	*Eugenia angustissima*	3	14	2	0.26	0.01
Tristachya leiostachya	*Axonopus derbyanus*	163	37	23	36.49	0.01
Eugenia calycina	*Bulbostylis junciformis*	4	5	1	0.13	0.01
Hyptis SP.	*Erythroxylum campestre*	2	9	1	0.12	0.01
Loudetiopsis chrysothryx	*Axonopus derbyanus*	10	37	6	2.25	0.01
Paspalum carinatum	*Myrciaria delicatula*	1	67	2	0.39	0.01
Panicum sp.	Poaceae sp.1	3	4	1	0.07	0.01
Panicum sp.	*Eugenia angustissima*	3	14	2	0.27	0.01
Tontelea micrantha	*Protium ovatum*	3	6	1	0.11	0.01
Erythroxylum campestre	*Diodia teres*	9	2	1	0.11	0.01
Syagrus flexuosa	*Axonopus suffultus*	7	27	4	1.16	0.01
Miconia albicans	*Duguetia furfuracea*	2	10	1	0.12	0.01
Psidium rufum	*Pradosia brevipes*	4	6	1	0.15	0.02
Campomanesia adamantium	*Anacardium humile*	5	11	2	0.35	0.02
Duguetia furfuracea	*Axonopus derbyanus*	10	37	6	2.28	0.02
Psidium australe	*Myrciaria delicatula*	2	67	3	0.81	0.02
Senna rugosa	*Eugenia calycina*	4	4	1	0.09	0.02
Tristachya leiostachya	*Diplusodon virgatus*	163	3	7	2.97	0.02
Erythroxylum campestre	*Casearia* sp.	9	2	1	0.11	0.02
Loudetiopsis chrysothryx	*Coelorachis* sp.	10	2	1	0.11	0.02
Myrciaria delicatula	*Jacaranda decurrens*	67	2	3	0.81	0.02
Panicum sp.	*Erythroxylum campestre*	3	9	1	0.15	0.02
Myrciaria delicatula	*Miconia albicans*	67	2	3	0.84	0.02
Parinari excelsa	Myrtaceae sp.6	4	7	1	0.16	0.02
Trachypogon sp.	*Eugenia calycina*	19	4	2	0.45	0.02
Byrsonima guilleminiana	*Axonopus derbyanus*	1	37	1	0.21	0.02
Chromolaena squalida	*Axonopus derbyanus*	2	37	2	0.44	0.02
Diospyros híspida	*Axonopus suffultus*	1	27	1	0.18	0.02
Miconia albicans	*Eugenia angustissima*	2	14	1	0.16	0.02
Myrciaria delicatula	*Allagoptera campestris*	67	1	2	0.42	0.02
Syagrus flexuosa	*Syagrus flexuosa*	7	7	1	0.12	0.02
Ouratea acuminata	*Erythroxylum campestre*	3	9	1	0.17	0.03
Tristachya leiostachya	*Trachypogon* sp.	163	19	10	18.54	0.03
Pradosia brevipes	*Bulbostylis junciformis*	6	5	1	0.18	0.03
Diodia teres	*Axonopus derbyanus*	2	37	2	0.44	0.03
Duguetia furfuracea	*Diplusodon virgatus*	10	3	1	0.19	0.03
Palicourea coriácea	*Axonopus derbyanus*	6	37	4	1.34	0.03
Palicourea coriácea	*Annona warmingiana*	6	5	1	0.19	0.03

Protium ovatum	*Campomanesia adamantium*	6	5	1	0.17	0.03
Trachypogon sp.	*Bulbostylis junciformis*	19	5	2	0.55	0.03
Tristachya leiostachya	*Ctenium chapadenses*	163	1	3	0.95	0.04
Tristachya leiostachya	*Eriosema crinitum*	163	1	3	0.93	0.04
Bauhinia rufa	*Axonopus derbyanus*	1	37	1	0.23	0.04
Ouratea acuminata	*Loudetiopsis chrysothryx*	3	10	1	0.20	0.04
Myrtaceae sp.2	*Axonopus derbyanus*	1	37	1	0.24	0.05
Poaceae sp.1	*Myrciaria delicatula*	4	67	4	1.59	0.05
Galactia decumbens	*Axonopus derbyanus*	1	37	1	0.23	0.05
Senna rugosa	*Loudetiopsis chrysothryx*	4	10	1	0.23	0.05

Appendix 2. Observed herbaceous species pairs for which the null hypothesis was rejected (α = 0.05) with the second null model. The names of the species *i* and *j* for each pair are shown, followed by the number of individuals of each species in the three cerrado sites, n(i) and n(j); f(obs) = observed number of times species *i* and *j* occurred as a near neighbour pair; f(exp) = expected number based on the null model.

Species *i*	Species *j*	n (i)	n (j)	f (obs)	f (exp)	*P*
Annually burned site						
Sida cordifolia	*Anacardium humile*	2	15	1	0.057	0
Paspalum SP.	*Annona warmingiana*	1	6	1	0.013	0
Myrtaceae sp.3	*Aspilia leucoglossa*	1	13	1	0.021	0
Kielmeyera variabilis	*Axonopus barbigerus*	1	2	1	0.002	0
Polycarpaea corymbosa	*Bulbostylis junciformis*	1	9	1	0.018	0
Campomanesia pubescens	*Campomanesia adamantium*	4	4	1	0.029	0
Coelorachys sp.	*Campomanesia adamantium*	2	4	1	0.013	0
Ipomoea sp.	*Campomanesia pubescens*	3	4	1	0.028	0
Panicum sp.	*Erythroxylum campestre*	2	11	1	0.046	0
Pavonia rosa-campestris	*Ipomoea* sp.	4	3	1	0.022	0
Palicourea coriaceae	*Jacaranda rufa*	4	3	1	0.017	0
Pradosia brevipes	Myrtaceae sp.1	4	1	1	0.011	0
Loudetiopsis chrysothryx	*Allagoptera campestris*	5	1	1	0.014	0.01
Melastomataceae SP.	*Annona warmingiana*	3	6	1	0.035	0.01
Banisteriopsis campestris	*Aspilia leucoglossa*	1	13	1	0.023	0.01
Mimosa xanthocentra	*Chromolaena squalida*	3	8	1	0.044	0.01
Eugenia sp.1	*Erythroxylum campestre*	3	11	1	0.054	0.01
Pradosia brevipes	*Jacaranda rufa*	4	3	1	0.023	0.01
Ouratea humilis	*Myrciaria delicatula*	2	15	1	0.058	0.01
Eugenia angustissima	*Diplusodon* sp.	9	3	1	0.06	0.01
Myrtaceae sp.4	*Myrciaria delicatula*	7	15	2	0.217	0.01
Eugenia angustissima	*Campomanesia adamantium*	9	4	1	0.075	0.01
Pavonia rosa-campestris	*Aspilia leucoglossa*	4	13	1	0.095	0.01
Pradosia brevipes	*Anacardium humile*	4	15	1	0.122	0.02
Eugenia angustissima	*Chromolaena squalida*	9	8	1	0.151	0.02

Sida cordifolia	*Axonopus suffultus*	2	40	1	0.179	0.02
Tristachya leiostachya	*Anacardium humile*	254	15	3	7.655	0.03
Myrciaria delicatula	*Annona warmingiana*	15	6	1	0.177	0.03
Ouratea humilis	*Axonopus suffultus*	2	40	1	0.154	0.03
Eugenia sp.1	*Axonopus suffultus*	3	40	1	0.228	0.04
Mimosa gracilis	*Axonopus suffultus*	3	40	1	0.264	0.04
Byrsonima guilleminiana	*Axonopus suffultus*	7	40	2	0.582	0.04
Biennially burned site						
Declieuxia fruticosa	*Alibertia sessilis*	2	1	1	0.004	0
Campomanesia adamantium	*Anacardium humile*	3	11	1	0.052	0
Peltodon pusillus	*Anacardium humile*	1	11	1	0.028	0
Parinari excelsa	*Axonopus barbigerus*	6	2	1	0.024	0
Tristachya leiostachya	*Axonopus derbyanus*	98	102	5	19.984	0
Pradosia brevipes	*Declieuxia fruticosa*	9	2	1	0.038	0
Psidium rufum	*Eugenia angustissima*	3	17	2	0.092	0
Myrtaceae sp.4	*Manihot tripartita*	6	2	1	0.02	0
Ouratea acuminata	*Myrcia sp.*	1	2	1	0.005	0
Protium ovatum	Myrtaceae sp.4	1	6	1	0.018	0
Syagrus flexuosa	Myrtaceae sp.4	3	6	1	0.035	0
Poaceae sp.1	*Eugenia angustissima*	1	17	1	0.033	0.01
Parinari excelsa	*Myrcia uberavensis*	6	2	1	0.023	0.01
Syagrus flexuosa	*Pradosia brevipes*	3	9	1	0.061	0.01
Eugenia angustissima	*Anacardium humile*	17	11	2	0.383	0.01
Eugenia sp.1	*Erythroxylum campestre*	2	15	1	0.073	0.01
Eugenia angustissima	*Campomanesia adamantium*	17	3	1	0.117	0.01
Eugenia angustissima	*Campomanesia pubescens*	17	3	1	0.11	0.01
Panicum sp.1	Myrtaceae SP.4	7	6	1	0.08	0.01
Myrtaceae sp.6	*Anacardium humile*	5	11	1	0.106	0.02
Myrciaria delicatula	*Anemopaegma arvense*	73	1	1	0.14	0.02
Myrciaria delicatula	*Axonopus suffultus*	73	88	6	12.985	0.02
Myrciaria delicatula	*Hyptis sp.*	73	1	1	0.153	0.02
Peltodon tomentosus	*Myrciaria delicatula*	1	73	1	0.151	0.02
Mimosa gracilis	*Axonopus suffultus*	1	88	1	0.192	0.02
Paspalum carinatum	*Myrciaria delicatula*	1	73	1	0.13	0.02
Diodia teres	*Axonopus derbyanus*	1	102	1	0.176	0.02
Myrciaria delicatula	*Gomphrena macrocephala*	73	1	1	0.155	0.02
Sida cordifolia	*Axonopus suffultus*	1	88	1	0.16	0.02
Mimosa amnis-atri	*Axonopus suffultus*	1	88	1	0.174	0.03
Tontelea micrantha	*Axonopus suffultus*	5	88	3	0.887	0.03
Eugenia sp.2	*Axonopus suffultus*	1	88	1	0.181	0.03
Tristachya leiostachya	*Trachypogon* SP.	98	1	1	0.208	0.03
Mimosa polycephala	*Axonopus derbyanus*	1	102	1	0.201	0.03
Casearia SP.	*Axonopus suffultus*	1	88	1	0.182	0.03

Myrtaceae sp.5	*Axonopus derbyanus*	1	102	1	0.188	0.03
Tristachya leiostachya	*Palicourea coriacea*	98	1	1	0.198	0.04
Tristachya leiostachya	*Bulbostylis junciformis*	98	1	1	0.221	0.04
Galactia decumbens	*Axonopus derbyanus*	1	102	1	0.233	0.04
Unburned since 1994						
Ouratea humilis	*Alibertia sessilis*	1	3	1	0.005	0
Campomanesia pubescens	*Anacardium humile*	2	11	1	0.034	0
Galactia decumbens	*Anacardium humile*	1	11	1	0.019	0
Myrtaceae sp.7	*Andira laurifolia*	7	1	1	0.012	0
Chromolaena sp.1	*Annona warmingiana*	2	5	1	0.023	0
Campomanesia adamantium	*Axonopus derbyanus*	5	37	3	0.384	0
Duguetia furfuracea	*Byrsonima guilleminiana*	10	1	1	0.028	0
Senna rugosa	*Coelorachys* SP.	4	2	1	0.016	0
Palicourea coriácea	*Croton glandulosus*	6	1	1	0.012	0
Erythroxylum campestre	*Croton pohlianus*	9	1	1	0.017	0
Miconia albicans	*Duguetia furfuracea*	2	10	1	0.049	0
Galactia martii	*Eugenia angustissima*	1	14	1	0.03	0
Panicum sp.	*Mimosa gracilis*	1	1	1	0.002	0
Senna rugosa	*Rauvolfia weddelliana*	4	1	1	0.005	0
Bauhinia rufa	*Axonopus derbyanus*	1	37	1	0.064	0.01
Eugenia angustissima	*Campomanesia pubescens*	14	2	1	0.068	0.01
Hyptis sp.	*Erythroxylum campestre*	2	9	1	0.034	0.01
Miconia albicans	*Eugenia angustissima*	2	14	1	0.047	0.01
Myrciaria delicatula	*Jacaranda decurrens*	67	2	2	0.256	0.01
Ouratea acuminata	*Loudetiopsis chrysothryx*	3	10	1	0.054	0.01
Pradosia brevipes	*Bulbostylis junciformis*	6	5	1	0.063	0.01
Erythroxylum campestre	*Diodia teres*	9	2	1	0.036	0.01
Talisia angustifólia	*Pradosia brevipes*	3	6	1	0.05	0.01
Erythroxylum campestre	*Annona warmingiana*	9	5	1	0.101	0.01
Poaceae sp.4	*Axonopus derbyanus*	4	37	2	0.309	0.01
Casearia sp.	*Axonopus suffultus*	2	27	1	0.11	0.01
Psidium australe	*Axonopus suffultus*	2	27	1	0.116	0.01
Myrcia uberavensis	*Loudetiopsis chrysothryx*	3	10	1	0.061	0.01
Psidium rufum	*Eugenia angustissima*	4	14	1	0.115	0.01
Protium ovatum	Myrtaceae SP.7	6	7	1	0.078	0.01
Eugenia calycina	*Eugenia angustissima*	4	14	1	0.119	0.01
Senna rugosa	*Loudetiopsis chrysothryx*	4	10	1	0.092	0.01
Paspalum carinatum	*Myrciaria delicatula*	1	67	1	0.119	0.01

Myrtaceae sp.6	*Myrciaria delicatula*	1	67	1	0.126	0.02
Poaceae sp.4	*Erythroxylum campestre*	4	9	1	0.094	0.02
Myrciaria delicatula	*Allagoptera campestris*	67	1	1	0.147	0.02
Chromolaena sp.1	*Axonopus derbyanus*	2	37	1	0.143	0.02
Duguetia furfuracea	*Bulbostylis junciformis*	10	5	1	0.127	0.02
Tristachya leiostachya	*Diplusodon* sp.	163	3	3	0.984	0.02
Tontelea micrantha	*Axonopus suffultus*	3	27	1	0.153	0.02
Coelorachys sp.	*Axonopus derbyanus*	2	37	1	0.159	0.02
Syagrus flexuosa	*Myrciaria delicatula*	7	67	3	0.926	0.02
Trachypogon sp.	*Eugenia calycina*	19	4	1	0.165	0.03
Trachypogon sp.	*Bulbostylis junciformis*	19	5	1	0.183	0.03
Ouratea acuminata	*Axonopus derbyanus*	3	37	1	0.219	0.03
Myrcia sp.	*Axonopus suffultus*	4	27	1	0.207	0.04
Psidium australe	*Myrciaria delicatula*	2	67	1	0.255	0.05

Table 1. Number of individuals of the species sampled in Emas National Park, central Brazil. Annually burned site (18°18’50’’S and 52°54’00’’W), biennially burned site (18°19’01’’S and 52°54’10’’W), and unburned since 1994 site (18°17’28’’S and 52°53’41’’W).

Family	Species	Annually	Biennially	Unburned
Amaranthaceae	*Gomphrena macrocephala* A. St-Hil.	1	1	-
Anacardiaceae	*Anacardium humile* A. St-Hil.	15	11	11
Annonaceae	*Annona warmingiana* Mello-Silva & Pirani	6	3	5
Annonaceae	*Duguetia furfuracea* (A. St.-Hil.) Saff.	-	-	10
Apocynaceae	*Rauvolfia weddelliana* Müll. Arg.	-	-	1
Arecaceae	*Allagoptera campestris* (Mart.) Kuntze	1	-	1
	Syagrus flexuosa (Mart.) Becc.	-	3	7
Asteraceae	*Aspilia leucoglossa* Malme	13	-	-
	Chromolaena squalida (A. DC.) King & H.Rob.	8	-	2
	Eremanthus erythropappus (DC.) MacLeish	2	-	-
	Riencourtia tenuifolia Gardner	6	-	-
	Vernonia bardanoides Less.	1	-	-
Bignoniaceae	*Anemopaegma acutifolium* DC.	-	1	-
	Anemopaegma arvense (Vell.) Stellfeld	-	1	-
	Jacaranda decurrens Cham.	-	-	2
	Jacaranda rufa Silva Manso	3	-	-
Burseraceae	*Protium ovatum* Engl.	-	1	6
Caryophyllaceae	*Polycarpaea corymbosa* (L.) Lam.	1	-	-
Celastraceae	*Tontelea micrantha* (Mart. ex Schult.) A.C. Sm.	-	5	3
Chrysobalanacecae	*Parinari excelsa* Sabine	3	6	4
Clusiaceae	*Kielmeyera rubriflora* Cambess.	1	-	-
Connaraceae	*Rourea induta* Planch.	1	-	-
Convolvulaceae	*Ipomoea* sp.	3	-	-
Cucurbitaceae	*Cayaponia espelina* Cogn.	-	-	1
Cyperaceae	*Bulbostylis junciformis* (Kunth) C.B.Clarke	9	1	5
	Scleria scabra Willd.	-	-	1
Ebenaceae	*Diospyros hispida* A.DC.	2	1	1
Erythroxylaceae	*Erythroxylum campestre* A. St-Hil.	11	15	9
Euphorbiaceae	*Croton glandulosus* L.	-	-	1
	Croton pohlianus Müll. Arg.	-	-	1
	Croton sp.	-	2	-
	Manihot tripartita (Spreng.) Müll. Arg.	-	2	-
Fabaceae	*Andira laurifólia* Benth.	-	-	1
	Bauhinia rufa (Bong.) Steud.	-	-	1
	Chaemecrista setosa (Vogel) Irwin & Barneby	2	-	-
	Eriosema crinitum (Kunth) Gardner	1	-	1
	Galactia decumbens (Benth.) Chodat & Hassl.	1	1	1
	Galactia martii DC.	-	-	1

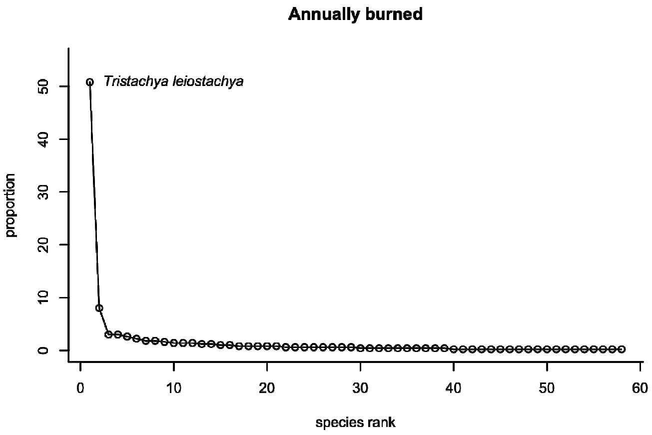
	Mimosa amnis-atri Barneby	2	1	1
	Mimosa gracilis Benth.	3	1	1
	Mimosa polycephala Benth.	-	1	-
	Mimosa xanthocentra Mart.	3	-	-
	Senna rugosa (G. Don) H.S. Irwin & Barneby	-	-	4
Lamiaceae	*Hyptis* sp.	-	1	2
	Peltodon pusillus Pohl	-	1	-
	Peltodon tomentosus Pohl	-	1	-
Lythraceae	*Diplusodon virgatus* Gardn. ex Koehne	3	-	3
Malpighiacecae	*Banisteriopsis campestris* (A. Juss.) Little	1	-	-
	Byrsonima guilleminiana A.Juss.	7	-	1
Malvaceae	*Pavonia rosa-campestris* A. St-Hil.	4	-	-
	Peltaea edouardii (Hochr.) Krapov. & Cristóbal	2	-	-
	Sida cordifolia A. St-Hil.	2	1	-
Melastomataceae	Melastomataceae sp.	3	-	-
	Miconia albicans (Sw.) Triana	-	-	2
Myrtaceae	*Campomanesia adamantium* (Cambess.) O.Berg	4	3	5
	Campomanesia pubescens (A. DC.) O.Berg	4	3	2
	Eugenia angustissima O.Berg	9	17	14
	Eugenia calycina Cambess.	-	-	4
	Eugenia sp.1	3	1	-
	Eugenia sp.2	-	2	-
	Myrcia bella Cambess.	-	2	-
	Myrcia sp.	-	2	4
	Myrcia uberavensis O. Berg	-	2	3
	Myrciaria delicatula (A. DC.) O.Berg	15	73	67
	Myrtaceae sp.1	1	-	-
	Myrtaceae sp.2	1	-	1
	Myrtaceae sp.3	1	-	-
	Myrtaceae sp.4	7	6	-
	Myrtaceae sp.5	-	1	1
	Myrtaceae sp.6	-	5	7
	Psidium australe Cambess.	-	3	2
	Psidium bergianum (Nied.) Burret	1	-	1
	Psidium rufum Mart. Ex A.DC.	5	3	4
Ochnaceae	*Ouratea acuminata* (DC.) Engl.	-	1	3
	Ouratea humilis Engl.	2	-	1
Poaceae	*Andropogon leucostachys* Kunth	1	-	-
	Axonopus barbigerus Hitchc.	2	2	-
	Axonopus derbyanus Black	7	102	37
	Axonopus suffultus (J.C.Mikan) Parodi	40	88	27
	Coelorachis sp.	2	-	2
	Ctenium chapadense Döll	-	-	1
	Gymnopogon foliosus (Willd.) Nees.	1	-	-

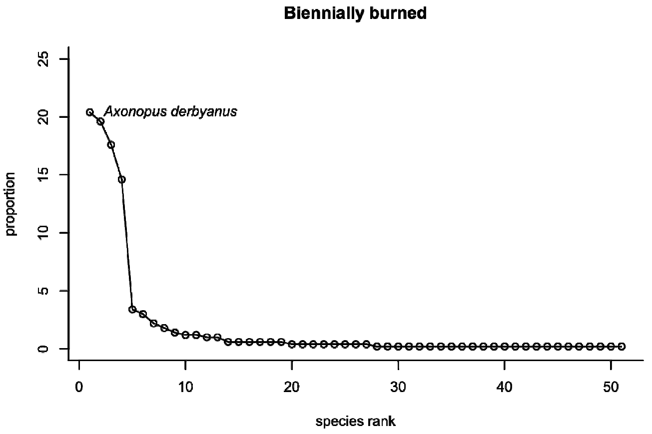
	Loudetiopsis chrysothryx (Ness) Conert	5	-	10
	Panicum sp.	2	7	1
	Paspalum carinatum Humb. & Bonpl. ex Flüggé	-	1	1
	Paspalum sp.	1	-	-
	Poaceae sp.	1	1	7
	Trachypogon sp.	-	1	19
	Tristachya leiostachya Nees	254	98	163
Rubiaceae	*Alibertia sessilis* Schum.	-	1	3
	Declieuxia fruticosa Kuntze	1	2	-
	Diodia teres Walter	-	1	2
	Palicourea coriacea Schum.	4	1	6
Salicaceae	*Casearia sp.*	1	1	2
	Casearia sylvestris Eichler	-	-	1
Sapindaceae	*Talisia angustifolia* Radlk.	-	-	3
Sapotaceae	*Pradosia brevipes* (Pierre) Penn	4	9	6

Table 2. Mean differences ± standard deviations in basal area (cm^2), height (cm), and specific leaf area (m^2 kg^{-1}) between neighbouring species of herbaceous plants in cerrado, Emas National Park, central Brazil. Different letters indicate significant differences between means (α = 0.05) in the annually burned site, the biennially burned site, and in the site unburned since 1994.

Functional trait	Annually	Biennially	Unburned	F	*P*
Basal area	3.562^a ± 6.446	2.248^a ± 6.120	3.22^a ± 5.048	2.143	0.118
Height	19.782^a ± 14.281	19.677^a ± 12.831	22.042^a ± 17.657	1.388	0.25
Specific leaf area	36.284^a ± 32.909	70.781^b ± 81.244	70.610^b ± 71.063	15.083	0.001

Figure 1. Rank-abundance curves of the herbaceous species found in three cerrado sites under different fire frequencies in Emas National Park, central Brazil.


Annually burned
Tristachya leiostachya
proportion
0
10
20
30
40
50
species rank
0
10
20
30
40
50
60


Biennially burned
Axonopus derbyanus
proportion
0
5
10
15
20
25
species rank
0
10
20
30
40
50

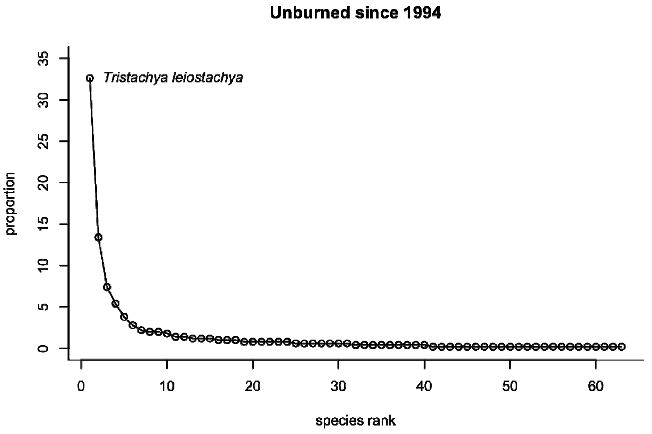
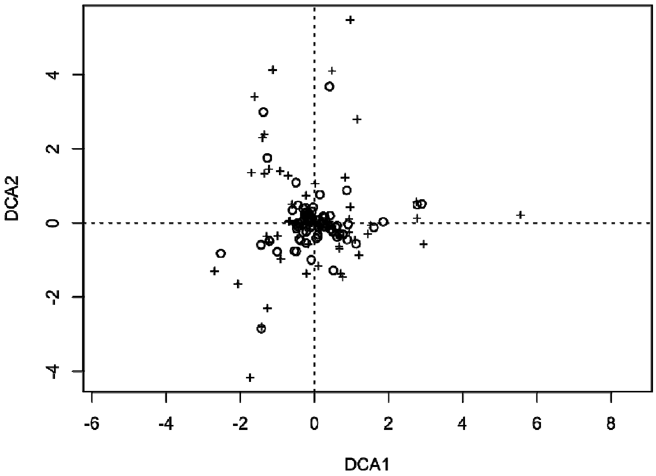
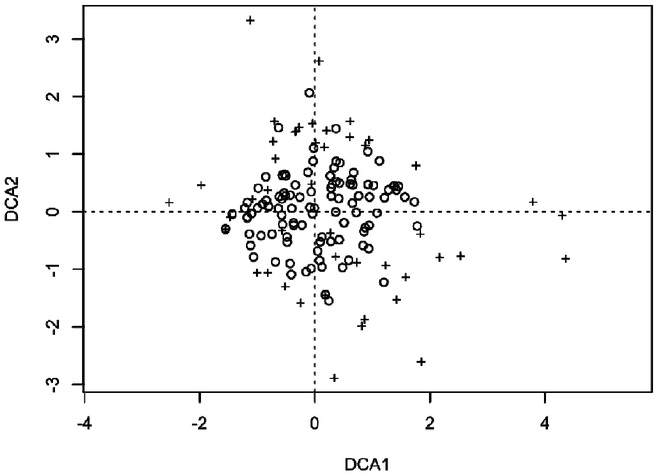
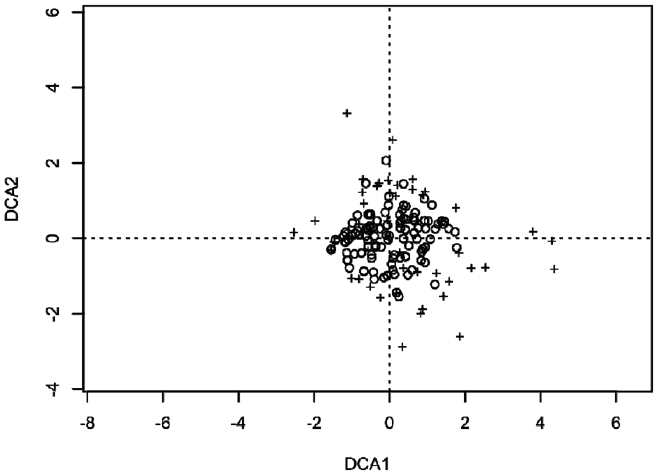

Unburned since 1994
Tristachya leiostachya
proportion
0
5
10
15
20
25
30
35
species rank
0
10
20
30
40
50
60

Figure 2. Detrended correspondence analysis of herbaceous species abundances in three cerrado sites under different fire frequencies at Emas National Park, central Brazil. Open black circles are species scores, and crosses are sites scores.


Annually burned


Biennially burned


Unburned since 1994

III - Capítulo 2

Coocorrência de espécies arbóreas em savanas brasileiras sob diferente frequências de fogo[2]

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[2] Trabalho aceito no periódico *Acta Oecologia* com o título “Woody plant species co-occurrence in Brazilian savannas under different fire frequencies”.

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

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ABSTRACT

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

Keywords: cerrado, competitive exclusion, environmental filter, phenotypic clustering, phylogenetic relatedness

1. Introduction

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

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

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

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

2. Material and Methods

2.1. Study area

We surveyed three nearby cerrado sites in Emas National Park (ENP), located in the Brazilian Central Plateau (17°49’-18°28’S; 52°39’-53°10’W). The ENP comprises 132,941 ha and is one of the largest and most important reserves in the Cerrado domain (Unesco, 2001). According to Köppen’s (1931) system, regional climate is classified as Aw, humid tropical, with wet summers and dry winters. Up to 1984, the ENP was exploited by farmers for cattle ranching, and burning in the dry season was used to promote forage regrowth (França et al., 2007). Afterwards, the ENP was fenced, and a fire exclusion policy was established (Ramos-Neto and Pivello, 2000). As a consequence, catastrophic fires occurred every 3-4 years, burning 80% of the park’s area (Ramos-Neto and Pivello, 2000). Since 1995, around 10 km^2 of preventive firebreaks have been burned annually at the end of the wet season, and a fire brigade works in the park during the dry season to prevent anthropogenic fires (França et al., 2007). Thus, there are currently few occurrences of anthropogenic fires inside the ENP (less than 2.2% of the burned area from 1994 to 2003), and the largest wildfires burn less than 30% of the total area. Fire frequency at a given site averages 6-7 years (França et al., 2007).

2.2. Data collection

In the late rainy season of 2006, we sampled the woody species occurring in three cerrado sites with similar physiognomy, similar soil type (Oxisols), and under different fire frequencies: two firebreaks, one burned annually for the last ten years (approximately 18°18’50’’S; 52°54’00’’W), another burned around every two years (approximately 18°19’01’’S; 52°54’10’’W), and a site without fires since 1994 (approximately 18°17’28’’S; 52°53’41’’W). The sites were distant less than 2 km one from each other. In each site, we placed a 2,500 m long transect, with 250 points, 10 m apart from each other. In each point, we used the point-quarter method (Mueller-Dombois and Ellenberg, 1974) to sample four woody plants with stem diameters at the soil level ≥ 3 cm (SMA, 1997). We identified the species by comparing collected samples to those of ENP’s reference collection (Batalha and Martins, 2002) and to vouchers lodged at the University of Campinas and University of Brasília herbaria.

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

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

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

2.3. Phylogenetic data

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

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

2.4. Data analysis

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

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

Then, we compared the pairwise values of co-occurrence to the phylogenetic distances among species. We calculated the phylogenetic distances from the estimated intervening branch length distances (measured in millions of years) between all species pairs with the Phylocom, using the Phydist module (Webb et al., 2007). We also assessed the upper bound of the variance of the relation between species co-occurrence and phylogenetic distances with quantile regressions, with data points in the 0.95 (upper 5%) quantile. We also did this analysis with Quantreg package (Koenker, 2008) for R environment (R Development Core Team, 2008). We assessed the significance of the quantile regression coefficients with bootstrapped standard errors (Koenker, 2008).

3. Results

We sampled 1,000 individuals of woody plants in each site. We found 28 species in the annually burned site, 36 species in the biennially burned site, and 39 species in the protected site (Table 1). We observed significant slopes in the comparison between pairwise indices of species co-occurrence and values of mean pairwise differences in functional trait values

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

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

4. Discussion

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

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

Competitive interactions are expected to limit the functional similarity of locally co-occurring species, because competition should be greater among species that have similar niches (Hutchinson, 1959; Leibold 1998). Based on these expectations, Weiher and Keddy (1995) postulated that phenotypic overdispersion of plants is greater at smaller spatial scales, where species compete directly for limited soil nutrients. Evidence of competitive exclusion determining phenotypic overdispersion at fine spatial scale has been found in different plant communities (e.g., prairies – Fargione et al., 2003; oak forests – Cavender-Bares et al., 2004; sand dunes – Stubbs and Wilson 2004; and tropical forests – Kraft et al. 2008). However, Valiente-Banuet et al. (2006) demonstrated recently that facilitation is also expected to promote phenotypic overdispersion in fire-prone communities. Nurse species may favour species with different traits to establish in the community (Valiente-Banuet et al., 2006). We found a phenotypic overdispersion in the site protected from fire. So, competitive interactions and facilitation may limit the co-occurrence of functionally similar plants in cerrado, but only insofar as fire is excluded.

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

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

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

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

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

Acknowledgments

We are grateful to Fapesp, for financial support; to CNPq, for the scholarship granted to both authors; to Ibama, for research permission; to Emas National Park staff, for logistical assistance; to R. Moreira, M.B. Ramos-Neto, and Oreades Núcleo de Geoprocessamento for the ENP’s satellite images; to A.T. Fushita for help in ENP’s fire history map; to UnB and Unicamp herbarium staffs; to the taxonomists C. Proença and J. Semir, for their assistance in species identification; to P.K. Amorim, S.P. Campos, C.A. Casali, M.V. Cianciaruso, A.V.F.

Jardim, P.P. Loiola, M.O. Maia, L.T. Manica, F.Q. Martins, D.M. Silva, and L. Sims, for helping us in field work, and to M.A.R. Mello for useful comments on a draft of this manuscript.

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

Family	Species	Sites
Anacardiaceae	*Anacardium humile* A. St-Hil.	1
Annonaceae	*Annona crassiflora* Mart.	1,2,3
	Duguetia furfuracea (A. St-Hil.) Benth. & Hook.	1
Apocynaceae	*Himatanthus obovatus* (Müll. Arg.) Woods.	2
Araliacae	*Schefflera macrocarpa* Seem.	2
Arecaceae	*Allagoptera leucocalyx* (Mart.) Kuntze	1
Asteraceae	*Chresta sphaerocephala* DC.	1
	Chromolaena squalida (Spr.) King & H. Rob.	1
	Eremanthus erythropappus Sch. Bip.	1,2,3
	Piptocarpha rotundifolia (Less.) Baker	1,2,3
	Vernonia bardanoides Less.	1
Bignoniaceae	*Tabebuia aurea* (Silva Manso) S. Moore	2,3
	Tabebuia ochracea (Cham.) Standl.	1,2,3
Caryocaraceae	*Caryocar brasiliensis* Cambess.	2,3
Clusiaceae	*Kielmeyera coriacea* Mart.	2,3
Connaraceae	*Rourea induta* Planch.	1,2,3
Dilleniaceae	*Davilla eliptica* A. St-Hil.	1,2,3
Ebenaceae	*Diospyros hispida* A. DC.	1,2,3
Erythroxylaceae	*Erythroxylum campestre* A. St-Hil.	1,2,3
	Erythroxylum suberosum A. St-Hil.	2,3
Euphorbiaceae	*Manihot tripartita* (Spreng.) Müll. Arg.	1
Fabaceae	*Acosmium dasycarpum* (Vogel)Yakovlev.	1,2,3
	Anadenanthera falcata (Benth.) Speg.	1,2,3
	Bauhinia rufa Steud.	3
	Dimorphandra mollis Benth.	1,2,3
	Machaerium acutifolium Vogel.	1,3
	Mimosa amnis-atri Barneby	1,2,3
	Sclerolobium aureum Baill.	3
	Stryphnodendron adstringens (Mart.) Coville	1,2,3
Lythraceae	*Lafoensia pacari* A. St-Hil.	3
Malpighiaceae	*Byrsonima coccolobifolia* A. Juss.	2,3
Malvaceae	*Eriotheca gracilipes* (K. Schum.) A. Robyns	2,3
	Eriotheca pubescens (Mart. & Zucc.) A. Robyns	2,3
Melastomataceae	*Miconia albicans* Triana	3
	Miconia ferruginata A. DC.	2,3
Myrtaceae	*Campomanesia pubescens* (A. DC.) O. Berg	3

	Eugenia aff. *piahuiensis* Mart.	1,2
	Eugenia punicifolia (Kunth) A. DC.	2,3
	Psidium laruotteanum Cambess.	1,2,3
Ochnaceae	*Ouratea acuminata* (A. DC.) Engl.	1,2,3
	Ouratea spectabilis (Mart.) Engl.	2,3
Proteaceae	*Roupala montana* Aubl.	3
Rubiaceae	*Palicourea rigida* Kunth	1,2,3
Salicaceae	*Casearia sylvestris* Sw.	2,3
Sapotaceae	*Pouteria ramiflora* (Mart.) Radlk.	1,2,3
	Pouteria torta (Mart.) Radlk.	1,2,3
Solanaceae	*Solanum lycocarpum* A. St-Hil.	1,2,3
Verbenaceae	*Aegiphila lhotzkiana* Cham.	2
Vochysiaceae	*Qualea grandiflora* Mart.	2,3
	Qualea parviflora Mart.	2

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

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

Table 3 - Tests for phylogenetic signal of the functional traits of cerrado woody species, in Emas National Park, central Brazil. The observed variance and the mean of random variances of the phylogenetic independent contrasts are given. Significant values at α = 0.05 are presented in bold face.

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

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

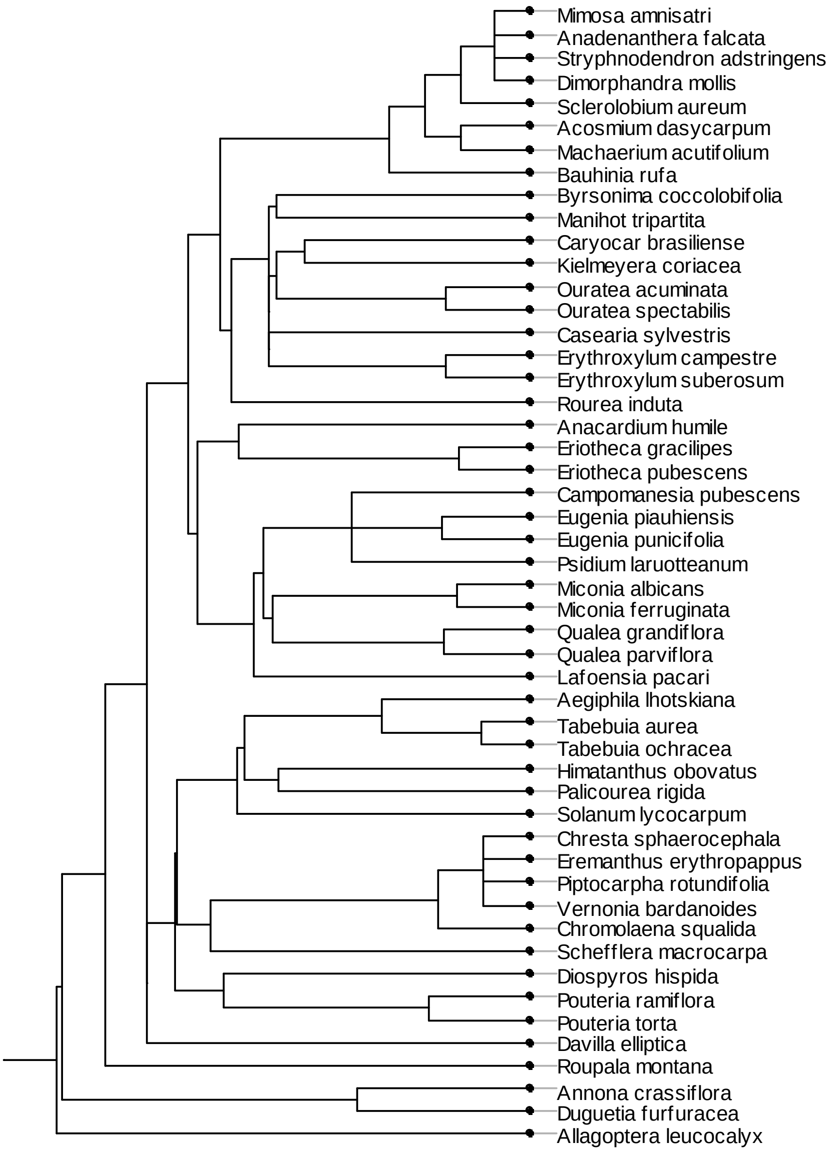
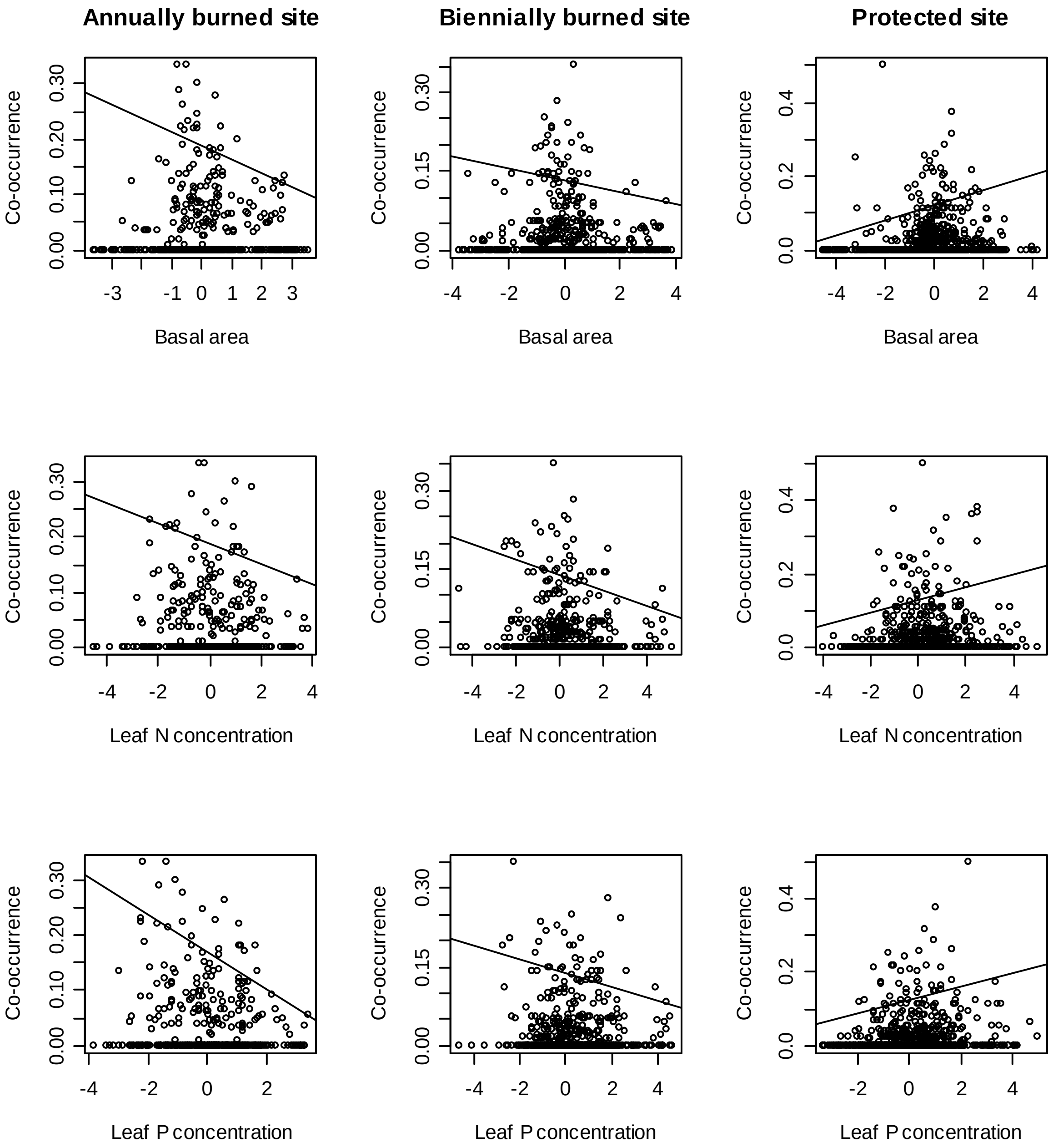


Fig.2 - Quantile Regression for significant (α = 0.05) upper 5% quantiles between functional trait differences and co-occurrence indices of co-occurring cerrado woody plant species, central Brazil. The slopes of quantile regressions for basal area, leaf N and leaf P concentrations in the annually burned,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



IV - Capítulo 3

Estrutura filogenética de campos e savanas brasileiras sob diferentes regimes de fogo[3]

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[3] Trabalho submetido ao periódico *Journal of Vegetation Science* com o título “Phylogenetic structure of Brazilian grasslands and savannas under different fire regimes”.

Phylogenetic structure of Brazilian grasslands and savannas under different fire regimes

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Abstract

Question: Do frequent fires assemble grasslands and savannas with closely related species (phylogenetic clustering)? If so, what are the clades pruned by fire in the phylogenetic trees? Are life forms and regenerative traits conserved on the phylogeny of the species?

Location: Central and southeastern Brazilian savannas (in Emas National park, 18°18’S, 52°54’W; in Brasília sites, 15º56’-15º57’S, 47º53’-47º56’W; and in Corumbataí-Itirapina sites, 22°13'-22°15'S, 47°37'-47°39'W) and Southern Brazilian grasslands (in Porto Alegre, 30°03’S, 51°07’W)

Methods: We recorded woody species in several savanna sites and herbaceous species in grassland sites under different fire regimes. We obtained data from literature and field sampling. We compared the mean phylogenetic distance of the species between sites with different fire regimes. We obtained significance by randomising the species among the tips of phylogenetic trees. We also assessed whether life-forms and regenerative traits were evolutionary conserved across phylogeny of all plants (phylogenetic signal) with tests based on the variance of phylogenetic independent contrasts.

Results: No marked pattern emerged from sites with different fire regimes. We observed a phylogenetic overdispersion as well as a phylogenetic clustering in savannas sites protected from fire. In grasslands, nonetheless, recent fires led to a phylogenetic clustering of the plant community. We found phylogenetic signals in the traits across the phylogeny of the 325 species investigated.

Conclusion: Fire may have different roles in assembling plant species in Brazilian grasslands and savannas. We postulate that the absence of phylogenetic clustering in savannas is mainly due to the persistence of long-lived resprouting species.

Key words: Campos; Cerrado; Environmental filtering; Phylogenetic diversity; Regenerative traits.

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 grasslands and savannas in the world (Bond et al. 2005). Natural fires have occurred in these vegetation types 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, southern Brazilian grasslands (campos, Overbeck et al. 2007) and central Brazilian savannas (cerrado, Gottsberger & Silberbauer-Gottsberger 2006) are amongst the most widespread flammable communities (Bond & Keeley 2005). Together, they covered originally 2.2 million km^2, or approximately 25% of the Brazilian territory (IBGE 2004). Like their overseas fire-prone vegetation counterparts, Brazilian grasslands and savannas evolved with fire (Overbeck et al. 2007), and their species present many adaptations to it (Gottsberger & Silberbauer-Gottsberger 2006; Overbeck & Pfadenhauer 2007). Fire absence is expected to modify the structure of these vegetation types: protection from fire leads to woody encroachment and forest expansion in campos (Oliveira & Pillar 2004; Müller et al. 2006) and to shifts in vegetation physiognomies to more closed forms in cerrado (Moreira 2000). Although changes in the structure of grasslands and savannas have been well reported throughout the world (see Gottsberger & Silberbauer-Gottsberger 2006; Overbeck et al. 2007 and references therein), there is a lack of studies – to the best of our knowledge – considering the phylogenetic relatedness of the plants and the effects of fire on it.

Traditionally, plant species from fire-prone communities are classified according to survival of fire and reproductive response to fire (Bond & Van Wilgen 1996). They have been grouped into plants resisting fire with part of their aboveground biomass (resisters), plants dying back completely aboveground, but sprouting from soil after fires (sprouters, Bond & Van Wilgen 1996), and plants germinating either from the seed bank or from newly dispersed seeds (seeders, Verdú & Pausas 2007). However, information on germination requirements for most of the Neotropical species is still scarce, and other disturbance-related functional traits have been studied in Brazilian plant communities (Overbeck & Pfadenhauer 2007). Raunkiaer's life forms (Raunkiaer 1934), on the other hand, 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 applied to fire-prone vegetation (Chapman & Crow 1981; Batalha & Martins 2002a; Overbeck & Pfadenhauer 2007).

Recently, analyses of the phylogenetic structure of biological communities have been increasingly used to answer questions on contemporary ecological forces assembling species (Vamosi et al. 2009). Most of the these studies have found a phylogenetic clustering (Vamosi et al. 2009), that is, the tendency of co-occurring species to be more closely related than expected by chance (Webb et al. 2002). These findings have been attributed to effects of local environmental filters assembling ecologically similar species (Fukami et al. 2005). Since species present commonly a high degree of evolutionary stasis (Qian & Ricklefs 2004) and niche conservatism (Prinzing et al. 2001; Prinzing et al. 2008), closely related species tend to present similar niches, being preferentially selected by local environmental filters (Webb et al. 2002). Although several studies assessed the phylogenetic structure of forests (see Vamosi et al. 2009 and references therein), grasslands and savannas still remain poorly studied (Proches et al. 2006; Silva & Batalha 2009).

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). In this study, we investigated the phylogenetic structure of Brazilian grasslands (campos) and savannas (cerrado) under different fire frequencies. We used a logical 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 (that is, 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 overdispersion; Webb et al. 2002). Accordingly, if fire acts as a strong environmental filter in fire-prone vegetation types (Verdú & Pausas 2007), campos and cerrados under frequent fires should present phylogenetic clustering. We addressed the following questions: (1) Do frequent fires assemble plant communities with closely related species?; (2) If so, what are the clades pruned by fire in the phylogenetic trees?; and (3) Are life forms and regenerative traits conserved on 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 domain with 132,941 ha (Unesco 2001). Regional climate is humid tropical, with a wet summer and a dry winter (Aw, 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 1,745 mm and 24.6°C, respectively. In the ENP, there is a gradient from open (68.1% of its area) to closed savannas (25.1%), as well as wet grasslands (4.9%) and riparian and semideciduous 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, with similar soil types, and under different fire frequencies: a firebreak burned annually for the last ten years (approximately, 18°18’50’’S; 52°54’00’’W) and a site without burnings since 1994 (approximately, 18°17’28’’S; 52°53’41’’W). The sites were distant less than 2 km one from the other. In each site, we placed a 2,500 m transect, with 250 points, 10 m apart one from the other. In each point, we used the point-quarter method (Müller-Dombois & Ellenberg 1974) to sample four woody plants with stem diameters at the 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 of the University of Brasília.

In addition, we carried out a broad survey of published articles and theses with data on Brazilian plant communities under different fire frequencies (Table 1). We recorded the plant species and their abundances or relative densities in campos (Overbeck & Pfadenhauer 2007) and cerrados (Cesar et al. 1988; Durigan et al. 1994; Sato 2003; Fiedler et al. 2004; Castro-Neves 2007).

We assigned the life form of the cerrado species considering the following Raunkiaer’s (1934) classes: phanerophytes, chamaephytes, hemicryptophytes, geophytes, and therophytes (see Electronic appendix 1). For a detailed description of the life forms and their functional significance, see Cornelissen et al. (2003). We also established the main regenerative strategy of the cerrado species (Electronic appendix 1). We grouped them into: (1) non-sprouter, when the species dies after fire; (2) sprouter, when the species loses its aboveground biomass but can recover from belowground organs; or (3) resister, when the species manages to keep at least some aboveground biomass during a fire. Most of cerrado species present belowground organs which allow them to sprout after fires that remove completely the aboveground parts of the plant (Gottsberger & Silberbauer-Gottsberger 2006). As a consequence, a clear distinction between sprouters and resisters is hard to achieve. Thus, we classified the species according to the most common regenerative strategy under surface fires. We obtained the life forms and the regenerative traits of the grassland species from Overbeck & Pfadenhauer (2007).

Phylogenetic data

We constructed a phylogenetic tree for the species in each plant community with the Phylomatic software, a phylogenetic toolkit for the assembly of phylogenetic trees (Webb & Donoghue 2005). Phylogenetic distances among species from different families were estimated from the dated Angiosperm super-tree of Davies et al. (2004). We assigned branch lengths to the phylogenetic tree by using the BLADJ (Branch Length Adjustment) averaging algorithm of the Phylocom version 4.0.1 software package (Webb et al. 2008). The BLADJ spaces undated nodes evenly between dated nodes in the tree (Webb et al. 2008). When a family (Asteraceae, Fabaceae, and Poaceae) node presented many polytomies, we distributed the genera into their subfamilies following the last angiosperm classification (Angiosperm Phylogeny Website, Stevens 2001). We assigned branch lengths of these genera by spacing undated nodes evenly above the family node.

We investigated whether the life forms and regenerative traits tended to be phylogenetically conserved (that is, to present a phylogenetic signal) or convergent in the phylogeny of the sampled species with a test based on the variance of phylogenetic independent contrasts (PIC, Blomberg et al. 2003). If related species are similar to each other, the magnitude of independent contrasts will generally be similar across the tree, resulting in a small variance of contrast values (Blomberg et al. 2003). Observed contrast variances are compared to the expectations under a null model of randomly swapping trait values across the tips of the tree. For a detailed description of comparative analyses using phylogenetically independent contrast, see Garland et al. (1992). As recommended by Webb et al. (2008), we considered life form as a trait with ordered states in the analysis, from therophytes to phanerophytes, according to the increasing degree of bud protection. The regenerative traits, nevertheless, were coded as a set of s - 1 binary dummy variables, where s was the number of states. We did this analysis with a phylogenetic tree for all species, with the Picante package (Kembel et al. 2008) for the R environment (R Development Core Team 2008).

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 we sampled in ENP; (2) between the two sites with bi- and quadrennial fires studied by Castro-Neves (2007); (3) between the two nearby southeastern sites studied by Cesar et al. (1988) and Durigan et al. (1994); (4) between the two samples in a site studied by Fiedler et al. (2004); (5) between the two sites with different periods after fire studied by Overbeck & Pfadenhauer (2007); and (6) between the two samples in a site studied by Sato (2003) - one sample before fire and other after five biennially fires in the late dry season (Table 1).

To answer whether fire constrains the phylogenetic structure of Brazilian fire-prone communities, we compared the mean phylogenetic distance (MPD) between sites with different fire regimes (Webb et al. 2008). We calculated the MPD as the mean phylogenetic distance among all pairwise combinations of species (Webb et al. 2008). The MPD is a measure of the phylogenetic diversity of communities that is computed in millions of years. To determine whether the phylogenetic structure of the sites with high fire frequency or recently burned sites (hereafter, HiFi) differed from the phylogenetic community structure of low fire frequency or unburned sites (hereafter, LowFi), we compared observed MPD values to the distribution of MPD values for randomly generated null communities (Gotelli & Graves 1996). We generated null communities by randomising the phylogenetic relationships among species of both HiFi and LowFi sites. This null model assumes that species of the LowFi sites are equally able to colonise HiFi sites. This procedure is implemented in Phylocom (COMSTRUCT algorithm), which shuffles species labels across the entire phylogeny (Webb et al. 2008). We also tested other null models, as implemented in this software,, but the results were the same.

Then, we calculated the net relatedness index (NRI), which was defined as [–(MPD – MPDnull)/sd.MPDnull], where MPDnull was the mean MPD for the cerrado species from 999 null communities and sd.MPDnull was the standard deviation of MPD for the cerrado species from these 999 null communities (Webb et al. 2008). NRI has been proposed as a measure of tree-wide phylogenetic distance of species (Webb et al. 2008). 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.

Finally, we also compared the architecture of the phylogenetic trees of LowFi and HiFi sites. We assembled the phylogenetic trees for the genera sampled in the cerrado sites with the highest fire frequencies (the annually burned sites we and Durigan et al. 1994 sampled) and cerrado sites with the lowest fire frequencies (the protected sites we and Cesar et al. 1988 sampled), as well as in the campos without fire for one and three years (Overbeck & Pfadenhauer 2007). Then, we computed the proportion of shared nodes in the campos and cerrado trees, by using the COMNODE algorithm in the Phylocom to idendify common nodes between trees (Webb et al. 2008). We also assessed the similarity of families and genera with Sørensen indexes (Magurran 2004) between LowFi and HiFi sites. We drew and determined the number of nodes and paths of the phylogenetic trees with the ADE-4 package (Analyses des Données Ecologiques; Thioulouse et al. 1996) for the R environment (R Development Core Team 2008).

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). We found phylogenetic signals in life forms and regenerative traits across the phylogeny of the 325 species investigated ($P < 0.05$). The values of the variance and of the mean of the random variances of the phylogenetic independent contrasts were respectively 0.024 and 0.033 for life forms and 0.004 and 0.008 for regenerative traits.

The mean of MPDs of LowFi sites were 215.6 ± 7.6 and of HiFi sites were 215.3 ± 6.6 million years, respectively. In general, no marked pattern emerged from sites with different fire regimes (Table 2). We observed a phylogenetic overdispersion as well as a phylogenetic clustering in cerrado sites protected from fire (Table 2). In campos, nonetheless, recent fires led to a phylogenetic clustering of the plant community (Table 2).

The phylogenetic trees of the LowFi and HiFi cerrado sites, as well as of the recently burned and unburned sites in campos, were similar. The phylogenetic trees of the cerrado sites shared 42 nodes, which comprised all nodes of the tree of the HiFi sites and 71% of the nodes of the tree of LowFi sites (see Electronic appendix 2). The phylogenetic trees of the campos shared 45 nodes, which comprised 98% of the nodes of the tree of recently burned campos and 85% of the nodes of the tree of unburned campos (see Electronic appendix 3). We found

50 genera and 29 families in HiFi cerrado sites and 78 genera and 39 families in LowFi cerrado sites, and 80 genera and 25 families in recently burned campos and 92 genera and 31 families in unburned campos. The genus and family similarities were high in the cerrados (0.634 and 0.677, respectively) and in the campos (0.821 and 0.744, respectively). Accordingly, frequent fires excluded some genera and families, but without pruning entire older clades.

Discussion

Fire did not promote the phylogenetic clustering in cerrados. On the contrary, the fire exclusion led to opposite patterns of phylogenetic structuring of plant communities in cerrados. In campos, however, recent fires assembled closely related plants. Consequently, fire may have different roles in assembling plant species in cerrados and in campos. We postulate that the absence of phylogenetic clustering in the cerrado is mainly due to the persistence of long-lived resprouting species.

The studies in frequently burned communities found a short-term enrichment of the plant communities in campos (Overbeck et al. 2005) and a long-term impoverishment in cerrados (Durigan et al. 1994). These findings suggest a different role of frequent fires on these communities, favouring a greater number of species in campos than in cerrado. In fact, fire exclusion changes the specific composition of campos, leading to the dominance of tall tussock grasses, which are better competitors for light (Rodríguez et al. 2003; Overbeck et al. 2007). In cerrados, alternatively, fire exclusion allows the growth of fire-sensitive species, increasing the richness of woody plants (Cesar et al. 1988; Moreira 2000). In other grasslands and savannas, however, this is not always the case, and frequent fires may lead to opposite patterns of diversity and richness (see Uys et al. 2004 for references). Thus, high fire frequency may assemble closely related species in campos; but, in cerrados, only the absence of fire seems to modify the phylogenetic structure of the plant community. Similarly to the patterns of species diversity in savannas (see Uys et al. 2004), the absence of fire in cerrados may lead to opposite patterns of phylogenetic diversity.

The absence of phylogenetic clustering in cerrado may be due to the persistence of many plant species after frequent fires. The 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 60% of the species in campos (Overbeck & Pfadenhauer 2007), in cerrados, they may represent more than 90% of the species (Gottsberger & Silberbauer-Gottsberger 2006). Thus, the presence of a great number of resprouting species in cerrado may prevent fire to assemble closely related plants.

Savannas have experienced fire for 30 million years (Bond et al. 2003). However, fire becomes more frequent in this vegetation type only with the predominance of C_4 grasses, at 8 million years (Beerling and Osborne 2006). Thus, there was sufficient time for multiple colonisations in flammable environments by phylogenetically distant lineages. In the Mediterranean vegetation, conversely, fire appeared only in the Quaternary, and some important adaptations (for example, seeders) that appeared concomitantly to fire are also recent (Pausas & Verdú 2005). These adaptations are concentrated in few lineages (such as Cistaceae and Fabaceae) and are specific adaptive answers to fire (Verdú & Pausas 2007). However, fire-related traits in cerrados are not related to specific families or older clades (Simon et al. 2009). Fabaceae, for example, has species with all regenerative traits and presents vicariant species from tropical rainforest (Simon et al. 2009). In general, vicariant rainforest species, with long and different phylogenetic histories, constitute an important element of the component of the cerrado flora (Gottsberger & Silberbauer-Gottsberger 2006). These vicariant species present functional traits, such as the strong suberization of trunks and branches, which are vital to survive in flammable environments (Simon et al. 2009). They could colonise the cerrado environment because they evolve in situ such characteristics, in a scenario of successive colonisations from late Tertiary (Simon et al. 2009). In cerrado, for example, the great number of species without congeners belonging to distant related clades (for example, Bowdichia virgilioides Kunth, Fabaceae, and Hancornia speciosa Gomes, Apocynaceae; see Electronic appendix 3) indicates that fires have occurred long enough to allow a differentiation at the generic level (Gottsberger & Silberbauer-Gottsberger 2006). In campos, fires also became very frequent only in the Quaternary (Overbeck et al. 2007). Thus, the long history of fire occurrence in cerrado may also justify the absence of phylogenetic clustering in their plant communities.

The similar design of the phylogenetic trees of LowFi and HiFi sites also indicated that species of campos and cerrados experience a long evolutionary history of fire. Species from different lineages share traits that allow them to tolerate frequent fires (Electronic appendix 1). Notwithstanding, in campos, frequent fires tend to assemble closely related species. The herbaceous component of the campos flora includes a higher number of C_3 grass species that cannot withstand high fire frequencies (Overbeck et al. 2007). In addition, the fire exclusion in campos allows the colonisation of forest pioneer species of distinct families (for example, Anarcadiaceae and Sapindaceae) that cannot also tolerate frequent fires (Overbeck & Pfadenhauer 2007). As a result, campos with high fire frequencies may present a low phylogenetic diversity.

Life forms and regenerative traits were evolutionary conserved on the phylogeny of plant species of Brazilian grasslands and savannas. In general, these traits are broadly conserved across phylogeny of European plants (Verdú & Pausas 2007; 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 regenerative traits, however, this taxonomic pattern is less evident (Electronic appendix 1), because sprouting ability is widely distributed in plant lineages, being especially common among species of harsh environments (Bond & Midgley 2001). Nevertheless, in some fire-prone vegetation types, such as in Mediterranean woody communities, germination is stimulated by fire-derived factors (heat, smoke, and charred wood). Consequently, sprouting, although also widespread, is not predominantly favoured by frequent fires (Verdú & Pausas 2007). In campos and cerrados, alternatively, sprouting is the prevalent regenerative strategy after fires.

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

Fire has been viewed as a force that triggers diversification in fire-prone communities (Ojeda 1998, Verdú & Pausas 2007). Nonetheless, frequent fires should play different roles in the structuring of Brazilian fire-prone communities, promoting phylogenetic clustering in campos, but not constraining the phylogenetic structure of cerrados. The presence of many resprouting species 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 relation between fire frequency and plant relatedness in African and Australian savannas and grasslands to validate our generalisations.

Acknowledgments. We are grateful to Fapesp, for financial support; to CNPq, for the scholarship granted to both authors; to Ibama, for research permission; to Emas National Park staff, for logistical assistance; to R. Moreira, M.B. Ramos-Neto, and Oreades, for the ENP's satellite images; to A.T. Fushita, for helping in the ENP's fire history map; to UnB and Unicamp herbarium staffs; to the taxonomists C. Proença and J. Semir, for their assistance in the species identification; to P.K. Amorim, S.P. Campos, C.A. Casali, M.V. Cianciaruso, A.V.F. Jardim, P.P. Loiola, M.O. Maia, L.T. Manica, F.Q. Martins, D.M. Silva, L. Sims, and M.W. Valenti, for helping us in the field.

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Table 1. Number of sites, fire frequencies, and location of the fire-prone communities.

Source	Number of sites and fire frequencies	Location	Vegetation type
This study	One site annually burned and other protected from fire during 12 years	Emas National Park, central Brazil (18°18’S, 52°54’W)	savanna
Cesar et al. (1988)	One site protected from fire during 25 years	Corumbataí, southeastern Brazil (22°13'S, 47°37'W)	savanna
Durigan et al. (1994)	One site burned annually for several years	Itirapina, southeastern Brazil (22°15'S, 47°49'W)	savanna
Sato (2003)	Three sites protected from fire during 18 years were burned biennially from 1992 to 2000 in the late dry season.	Brasília, central Brazil (15º56’S, 47º53’W)	savanna
Fiedler et al. (2004)	One site sampled one month and three years after the fire	Brasília, central Brazil (15°57’S, 47°56’W)	savanna
Castro-Neves (2007)	Two sites protected from fire during 18 years were burned biennially and quadrennially from 1992 to 2004	Brasília, central Brazil (15º56’S, 47º53’W)	savanna
Overbeck & Pfadenhauer (2007)	Two similar sites without fire for one and three years	Porto Alegre, Southern Brazil (30°03’S, 51°07’W)	grassland

Table 2. Number of taxa (N), observed (MPD) and randomised (rndMPD) mean phylogenetic distances, and net relatedness indexes (NRI, Webb et al. 2008). LowFi = sites with low frequency of fire, HiFi = sites with high frequency of fire. The values of MPD and rndMPD are in million years. The *P*-value of the sites reflects the departure of the observed MPD and MNTD values from the null model. Significant values at α = 0.05 are in bold.

Source	Sites	N	MPD	rndMPD	NRI	*P*
This study	LowFi	39	**210.3**	215.3	**1.865**	0.046
	HiFi	28	216.5	213.3	-0.617	0.288
Cesar et al. (1988) and Durigan et al. (1994)	LowFi	95	**219.9**	218.1	**-1.143**	0.046
	HiFi	44	209.0	216.5	1.491	0.108
Sato (2003)	LowFi	58	219.3	219.0	-0.405	0.422
	HiFi	55	218.8	218.8	0.031	0.419
Fiedler et al. (2004)	LowFi	40	206.5	206.1	-0.215	0.461
	HiFi	34	207.3	205.7	-0.509	0.327
Castro-Neves (2007)	LowFi	31	211.1	213.1	0.486	0.300
	HiFi	36	214.9	212.3	-1.095	0.133
Overbeck and Pfadenhauer (2007)	LowFi	130	226.7	227.6	0.692	0.223
	HiFi	120	**225.3**	227.9	**1.578**	0.043

Appendix 1. Species, life forms (LF), and regenerative traits (RT) of Brazilian grasslands and savannas. We classified life forms into therophyte (t), geophyte (g), hemicryptophyte (h), chamaephytes (c), phanerophytes, (p), and liana (l) and regenerative traits in resister (r), sprouter (s), and non-sprouter (n).

Family	Species	LF	RT
Amaranthaceae	*Pfaffia tuberosa* Hicken	g	s
Amaryllidaceae	*Habranthus gracilifolius* Herb.	g	s
Anacardiaceae	*Anacardium humile* A. St.-Hil.	c	s
	Schinus weinmanniaefolius Engl.	c	s
Annonaceae	*Annona coriacea* Mart.	p	r
	Annona crassiflora Mart.	p	r
	Duguetia furfuracea (A. St.-Hil.) Saff.	c	s
	Xylopia aromatica (Lam.) Mart.	p	r
Apiaceae	*Eryngium ciliatum* Cham. & Schltdl.	g	s
	Eryngium elegans Cham. & Schltdl.	g	s
	Eryngium horridum Malme	g	s
	Eryngium pristis Cham. & Schltdl.	g	s
	Eryngium sanguisorba Cham. & Schltdl.	g	s
	Hydrocotyle exigua Malme	h	n
Apocynaceae	*Aspidosperma macrocarpon* Mart.	p	r
	Aspidosperma tomentosum Mart.	p	r
	Hancornia speciosa Gomes	p	r
	Himatanthus obovatus (Müll.Arg.) Woodson	p	r
Aquifoliaceae	*Ilex cerasifolia* Reissek	p	n
Araliaceae	*Schefflera macrocarpa* (Cham. & Schltdl.) Frodin	p	r
	Schefflera vinosa (Cham. & Schltdl.) Frodin & Fiaschi	p	s
Arecaceae	*Allagoptera leucocalyx* (Drude) Kuntze	g	s
	Butia capitata (Mart.) Becc.	p	r
	Syagrus comosa (Mart.) Mart.	c	r
	Syagrus flexuosa (Mart.) Becc.	g	s
Asteraceae	*Achyrocline satureioides* (Lam.) DC.	h	s
	Acmella bellidioides (Smith in Rees) R.K. Jansen	h	s
	Aspilia montevidensis (Spreng.) Kuntze	h	s
	Baccharis articulata (Lam.) Pers.	c	s
	Baccharis cognata DC.	c	s
	Baccharis dracunculifolia DC.	c	n
	Baccharis intermixta Gardner	c	n
	Baccharis leucopappa DC.	c	s
	Baccharis ochracea Spreng.	c	s
	Baccharis patens Baker	c	s
	Baccharis rufescens Spreng.	c	s

	Baccharis sessiliflora Vahl	c	s
	Baccharis trimera DC.	c	s
	Calea uniflora Less.	g	s
	Chaptalia integerrima (Vell.) Burkart	h	s
	Chaptalia runcinata Kunth	h	s
	Chaptalia sinuata (DC.) Baker	h	s
	Chresta sphaerocephala DC.	h	r
	Conyza bonariensis (L.) Cronquist	h	s
	Conyza chilensis Spreng.	h	s
	Eremanthus eriopus Baker	c	r
	Eremanthus glomerulatus Less.	c	r
	Eremanthus goyazensis (Lam.) Cuatrec. & Lourteig	c	r
	Eremanthus mollis Sch. Bip.	c	r
	Chromolaena squalida (DC.) R.M. King & H. Rob.	c	n
	Eupatorium ascendens Sch. Bip. ex Baker	h	s
	Eupatorium intermedium DC.	c	s
	Eupatorium ivaefolium Hook. & Arn.	h	s
	Eupatorium lanigerum Hook. & Arn.	h	s
	Eupatorium ligulaefolium Hook. & Arn.	h	s
	Eupatorium tweedianum Hook. & Arn.	c	s
	Eupatorium vauthierianum DC.	c	n
	Gochnatia pulchra Cabrera	c	r
	Heterothalamus psiadioides Less.	c	n
	Hieracium commersonii Monnier	g	s
	Hypochoeris sp. L.	h	s
	Lucilia acutifolia (Poir.) Cass.	g	s
	Lucilia nitens Less.	g	s
	Noticastrum gnaphalioides (Baker) Cuatrec.	h	s
	Otopappus angustifolius Gleason	h	s
	Piptocarpha rotundifolia (Less.) Baker	p	r
	Porophyllum lanceolatum DC.	c	s
	Pterocaulon rugosum (Vahl) Malme	h	s
	Senecio heterotrichius DC.	c	n
	Stenachaenium riedelii Baker	g	s
	Stevia aristata D. Don ex Hook. & Arn.	h	s
	Stevia cinerascens Sch. Bip. ex Baker	h	s
	Verbesina subcordata DC.	h	s
	Vernonia bardanoides Less.	h	s
	Vernonia diffusa Less.	p	r
	Vernonia flexuosa Sims	h	s
	Vernonia nudiflora Less.	c	s
	Viguiera anchusaefolia (DC.) Baker	h	s
Bignoniaceae	*Cybistax antisyphilitica* (Vell.) J.F. Macbr.	p	r
	Jacaranda caroba (Vell.) A. DC.	c	s

	Tabebuia aurea (Silva Manso) Benth. & Hook. f. ex S. Moore	p	r
	Tabebuia caraiba (Mart.) Bureau	p	r
	Tabebuia ochracea (Cham.) Standl.	p	r
Campanulaceae	*Wahlenbergia linarioides* (Lam.) A. DC.	t	n
Caryocaraceae	*Caryocar brasiliense* A.St.-Hil.	p	r
Celastraceae	*Maytenus communis* Reissek	p	n
	Plenckia polpunea Reissek in Mart. & Eichler	p	r
	Salacia crassifolia G.Don	p	r
	Salacia elliptica G.Don	p	n
Chrysobalanaceae	*Couepia grandiflora* (Mart. & Zucc.) Benth. ex Hook. f.	p	r
	Licania humilis Cham. & Schltdl.	p	r
Cistaceae	*Halimium brasiliense* (Lam.) Grosser	h	s
Clusiaceae	*Kielmeyera coriacea* Mart. & Zucc.	p	r
	Kielmeyera rubriflora Cambess.	p	r
	Kielmeyera speciosa A. St.-Hil.	p	r
	Kielmeyera variabilis Mart. & Zucc.	c	s
Combretaceae	*Terminalia argentea* Mart.	p	n
	Terminalia brasiliensis (Cambess. ex A. St.-Hil.) Eichler	p	n
Commelinaceae	*Commelina erecta* L.	h	s
Connaraceae	*Connarus suberosus* Planch.	p	r
	Rourea induta Planch.	c	s
Convolvulaceae	*Convolvulus crenatus* Vahl	l	s
	Dichondra sericea Sw.	h	n
	Evolvulus sericeus Sw.	h	n
Cyperaceae	*Bulbostylis closii* Barros	h	r
	Bulbostylis juncoides (Vahl) Kük. ex Osten	h	r
	Bulbostylis sp	h	r
	Bulbostylis sphaerocephalus C.B.Clarke	h	r
	Carex phalaroides Kunth	g	s
	Cyperus aggregatus (Willd.) Endl.	g	s
	Cyperus lanceolatus Poir.	g	s
	Rhynchospora globularis (Chapm.) Small	h	r
	Rhynchospora setigera (Kunth) Boeckeler	h	r
	Scleria sellowiana Kunth	g	s
	Scleria sp.	g	s
Dilleniaceae	*Davilla elliptica* A. St.-Hil.	c	s
Ebenaceae	*Diospyros burchellii* Hiern	p	r
	Diospyros hispida A. DC.	p	r
	Diospyros inconstans Jacq.	p	n
Erythroxylaceae	*Erythroxylum ambiguum* A. St.-Hil.	c	s
	Erythroxylum argentinum O.E. Schulz	p	n
	Erythroxylum campestre A. St.-Hil.	c	s
	Erythroxylum deciduum A. St.-Hil.	c	r
	Erythroxylum suberosum A. St.-Hil.	p	r

	Erythroxylum tortuosum Mart.	p	r
Euphorbiaceae	*Croton nitrariifolium* Baill.	c	n
	Croton thermarum Müll.Arg.	c	n
	Euphorbia selloi (Klotzsch & Garcke) Boiss.	h	s
	Manihot tripartita (Spreng.) Müll.Arg.	h	s
	Pera glabrata (Schott) Poepp. ex Baill.	p	n
Fabaceae	*Acosmium dasycarpum* (Vogel) Yakovlev	p	r
	Acosmium subelegans (Mohlenbr.) Yakovlev	p	r
	Aeschynomene elegans Cham. & Schltdl.	h	s
	Anadenanthera falcata (Benth.) Speg.	p	r
	Andira humilis Mart.	h	s
	Andira inermis (W. Wright) Kunth ex DC.	p	r
	Bauhinia rufa (Bong.) Steud.	p	r
	Bowdichia virgilioides Kunth	p	r
	Centrosema virginianum (L.) Benth.	h	s
	Chamaecrista nictitans Moench	c	s
	Clitoria nana Benth.	g	s
	Collaea stenophylla (Hook. & Arn.) Benth.	c	s
	Copaifera langsdorffii (Desf.) Kuntze	p	r
	Crotalaria tweediana Benth.	h	s
	Dalbergia miscolobium Benth.	p	r
	Desmanthus tatuhyensis Hoehne	c	s
	Desmodium incanum DC.	h	s
	Dimorphandra mollis Benth.	p	r
	Enterolobium gummiferum (Mart.) J.F. Macbr.	p	r
	Galactia marginalis Benth.	g	s
	Hymenaea stigonocarpa Mart. ex Hayne	p	r
	Machaerium acutifolium Vogel	p	r
	Machaerium opacum Vogel	p	r
	Machaerium stipitatum Vogel	p	n
	Machaerium villosum Vogel	p	n
	Macroptilium prostratum (Benth.) Urb.	h	s
	Mimosa amnis-atri Barneby	c	r
	Mimosa claussenii Benth.	p	r
	Mimosa parvipinna Benth.	c	s
	Plathymenia reticulata Benth.	p	r
	Platypodium elegans Vogel	p	r
	Pterodon pubescens Benth.	p	r
	Rhynchosia diversifolia Micheli	h	s
	Sclerolobium aureum (Tul.) Baill.	p	r
	Stryphnodendron adstringens (Mart.) Coville	p	r
	Stryphnodendron obovatum Benth.	p	r
	Stylosanthes montevidensis Vogel	g	s
	Sweetia dasycarpa (Vogel) Benth.	p	n

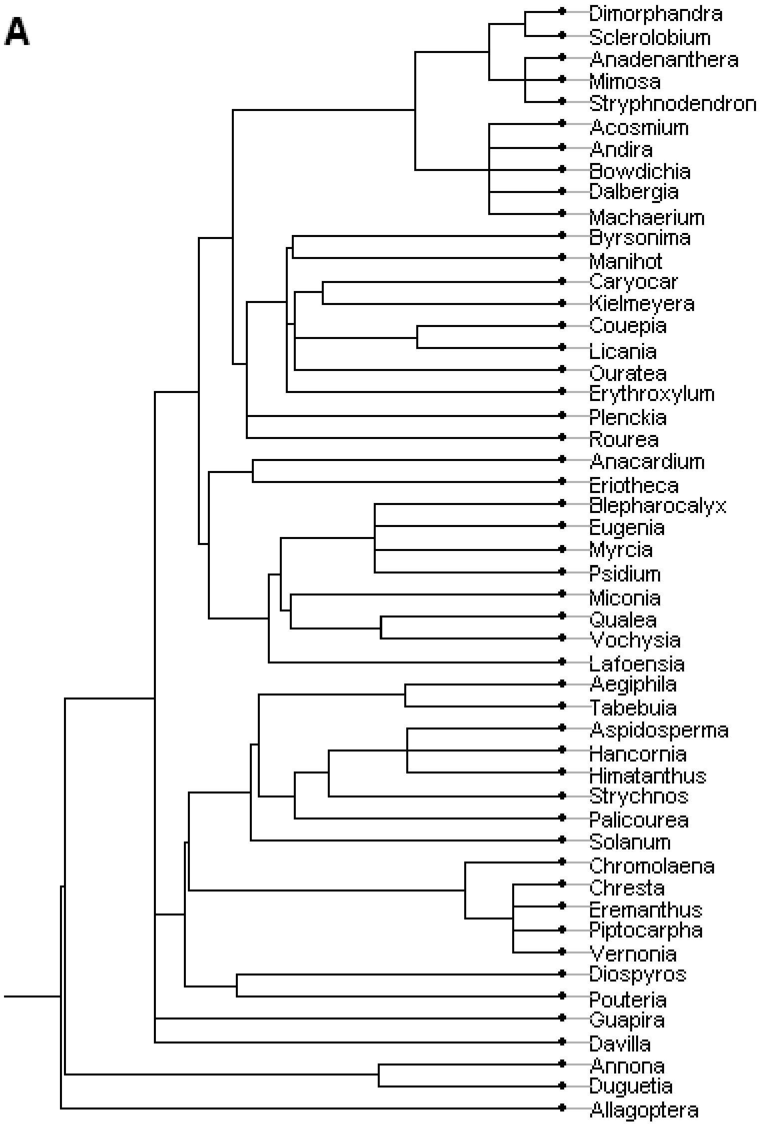
	Vatairea macrocarpa (Benth.) Ducke	p	r
	Zornia sericea Moric.	h	s
Iridaceae	*Cypella coelestis* (Lehm.) Diels	g	s
	Sisyrinchium macrocephalum Graham	h	s
	Sisyrinchium scariosum I.M.Johnst.	h	s
	Sisyrinchium vaginatum Spreng.	h	s
Lacistemataceae	*Lacistema floribundum* Miq.	p	n
Lamiaceae	*Glechon squarrosa* Benth.	c	s
	Salvia procurrens Benth.	h	n
Lauraceae	*Ocotea acutifolia* (Nees) Mez	p	n
	Ocotea pulchella (Nees) Mez	p	r
Linaceae	*Cliococca selaginoides* (Lam.) C.M. Rogers & Mildner	h	s
Loganiaceae	*Strychnos brasiliensis* (Spreng.) Mart.	c	n
	Strychnos pseudoquina A. St.-Hil.	p	r
Lythraceae	*Cuphea glutinosa* Cham. & Schltdl.	h	s
	Lafoensia pacari A. St.-Hil.	p	r
Malpighiaceae	*Byrsonima coccolobifolia* Kunth	p	r
	Byrsonima crassa Nied.	p	r
	Byrsonima crassifolia Lunan ex Griseb.	p	r
	Byrsonima intermedia A. Juss.	p	r
	Byrsonima pachyphylla A. Juss.	p	r
	Byrsonima verbascifolia (L.) DC.	p	r
	Heteropterys byrsonimifolia A. Juss.	p	r
	Heteropterys escalloniifolia A. Juss.	p	r
Malvaceae	*Eriotheca gracilipes* (K. Schum.) A. Robyns	p	r
	Eriotheca pubescens (Mart. & Zucc.) Schott & Endl.	p	r
	Krapovickasia urticifolia (A. St.-Hil.) Fryxell	c	s
	Pavonia hastata Cav.	c	s
	Sida rhombifolia L.	c	s
	Waltheria douradinha A. St.-Hil.	c	s
	Wissadula glechomatifolia R.E.Fr.	c	s
Melastomataceae	*Leandra involucrata* DC.	p	r
	Leandra lacunosa Cogn.	p	r
	Miconia albicans (Sw.) Triana	p	r
	Miconia ferruginata DC.	p	r
	Miconia langsdorffii Cogn.	p	n
	Miconia ligustroides (DC.) Naudin	p	r
	Miconia pohliana Cogn.	p	r
	Miconia rubiginosa (Bonpl.) DC.	p	r
	Miconia sellowiana Naudin	p	n
	Miconia stenostachya DC.	p	n
	Tibouchina clidemioides Cogn.	p	n
	Tibouchina gracilis (Bonpl.) Cogn.	c	s
Monimiaceae	*Siparuna guianensis* Aubl.	p	n

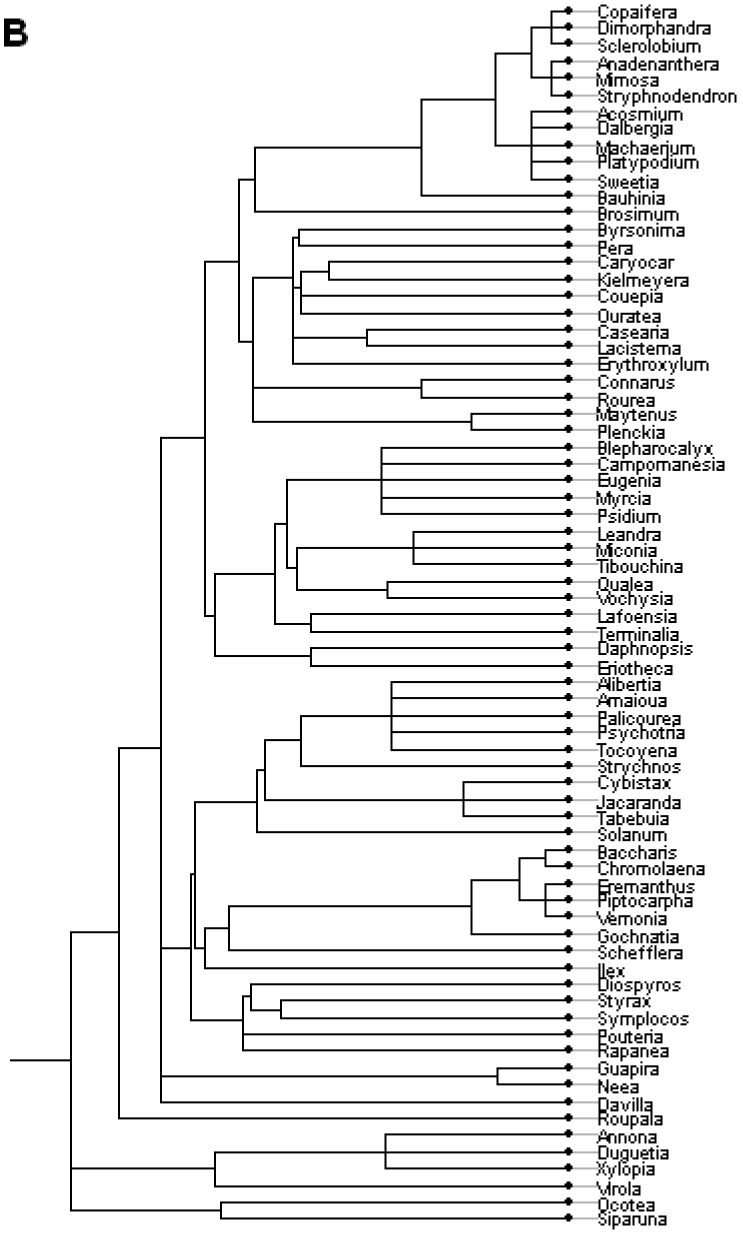
Moraceae	*Brosimum gaudichaudii* Trécul	p	n
Myristicaceae	*Virola sebifera* Aubl.	p	r
Myrsinaceae	*Myrsine ferruginea* (Sw.) R. Br. ex Roem. & Schult.	p	n
	Myrsine guianensis (Aubl.) Kuntze	p	r
	Myrsine lancifolia Mart.	p	n
	Myrsine umbellata (Mart.) Mez	p	n
Myrtaceae	*Blepharocalyx salicifolius* (Kunth) O.Berg	p	r
	Campomanesia aurea O.Berg	c	s
	Campomanesia cambessedeana O.Berg	p	n
	Campomanesia pubescens (Mart. ex DC.) O.Berg	c	r
	Eugenia aurata O.Berg	c	r
	Eugenia bimarginata O.Berg	c	r
	Eugenia livida O.Berg	p	r
	Eugenia piauhiensis O.Berg	p	r
	Eugenia punicifolia (Kunth) DC.	p	r
	Myrcia albotomentosa DC.	p	r
	Myrcia castrensis (O.Berg) D.Legrand	p	n
	Myrcia lingua (O.Berg) Mattos	p	r
	Myrcia multiflora (Lam.) DC.	p	n
	Myrcia rostrata DC.	p	n
	Myrcia tomentosa (Aubl.) DC.	p	n
	Psidium laruotteanum Cambess.	p	r
	Psidium myrsinoides O.Berg	p	r
	Psidium pohlianum O.Berg	p	r
Nyctaginaceae	*Guapira graciliflora* (Mart. ex J.A.Schmidt) Lundell	p	n
	Guapira noxia (Netto) Lundell	p	r
	Neea theifera Oerst.	p	r
Ochnaceae	*Ouratea hexasperma* (A. St.-Hil.) Baill.	p	r
	Ouratea spectabilis (Mart. ex Engl.) Engl.	p	r
Oxalidaceae	*Oxalis brasiliensis* G. Lodd.	g	s
	Oxalis conorrhiza Jacq.	g	s
Poaceae	*Andropogon lateralis* Nees	h	r
	Andropogon leucostachyus Kunth	h	r
	Andropogon selloanus (Hack.) Hack.	h	r
	Andropogon ternatus Nees.	h	r
	Aristida circinalis Lindm.	h	r
	Aristida filifolia (Arechav.) Herter	h	r
	Aristida flaccida Trin. & Rupr.	h	r
	Aristida laevis (Nees) Kunth	h	r
	Axonopus suffultus (Mikan ex Trin.) Parodi	h	r
	Briza calotheca (Trin.) Hack.	h	r
	Briza sp.	h	r
	Briza subaristata Lam.	h	r
	Briza uniolae (Nees) Steud.	h	r

	Danthonia montevidensis Hack. & Arechav.	h	r
	Danthonia secundiflora J.Presl & C.Presl	h	r
	Dichanthelium sabulorum (Lam.) Gould & C.A.Clark	g	s
	Elionurus muticus (Spreng.) Kuntze	h	r
	Eragrostis polytricha Nees	h	r
	Leptocoryphium lanatum (Kunth) Nees	h	r
	Melica brasiliana Ard.	g	s
	Panicum peladoense Henrard	h	r
	Paspalum plicatulum Michx.	h	r
	Piptochaetium montevidense (Spreng.) Parodi	h	r
	Saccharum asperum Steud.	h	r
	Schizachyrium microstachyum (Ham.) Roseng., B.R.Arrill. & Izag.	h	r
	Schizachyrium spicatum (Spreng.) Herter	h	r
	Schizachyrium tenerum Nees	h	r
	Setaria parviflora (Poir.) Kerguélen	h	r
	Setaria vaginata Spreng.	h	r
	Sporobolus multinodis Hack.	h	r
	Stipa filiculmis Delile	h	r
	Stipa filifolia Nees	h	r
	Stipa tenuiculmis Hack.	h	r
	Trachypogon montufari Nees	h	r
Polygalaceea	*Monnina oblongifolia* Arechav.	c	s
Proteaceae	*Roupala montana* Aubl.	p	r
Rubiaceae	*Alibertia macrophylla* K.Schum.	p	n
	Amaioua guianensis Aubl.	p	r
	Borreria capitata DC.	h	s
	Borreria fastigiata K.Schum.	h	s
	Borreria verticillata G.Mey.	h	s
	Chiococca alba (L.) Hitchc.	l	s
	Diodia apiculata (Willd. ex Roem. & Schult.) K.Schum.	h	s
	Galium uruguayense Bacigalupo	h	s
	Palicourea rigida Kunth	p	r
	Psychotria sessilis Vell.	p	n
	Relbunium hirtum K.Schum.	h	s
	Richardia grandiflora (Cham. & Schltdl.) Steud.	h	s
	Richardia humistrata (Cham. & Schltdl.) Steud.	h	s
	Tocoyena formosa (Cham. & Schltdl.) K.Schum.	p	r
Salicaceae	*Casearia sylvestris* Sw.	p	r
Sapotaceae	*Pouteria ramiflora* (Mart.) Radlk.	p	r
	Pouteria torta (Mart.) Radlk.	p	r
Scrophulariaceae	*Angelonia integerrima* Spreng.	c	s
	Gerardia communis Cham. & Schltdl.	t	n
	Mecardonia herniarioides (Cham.) Pennell	h	s

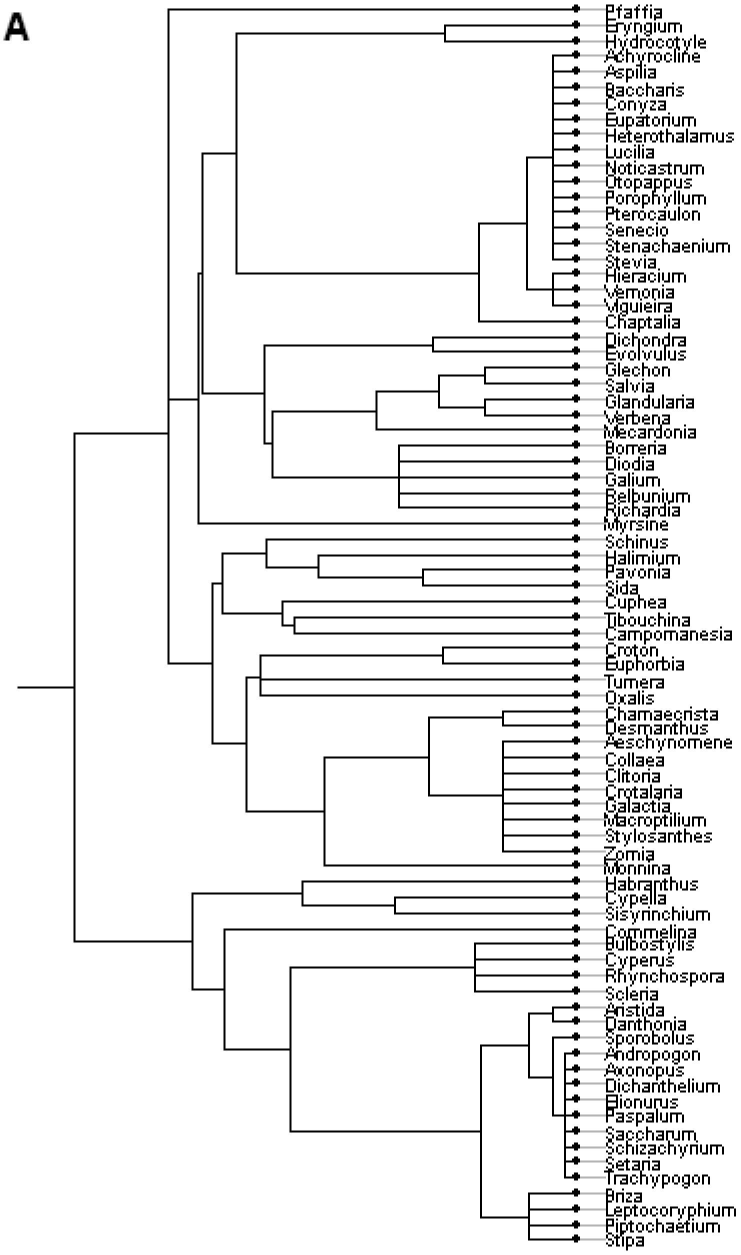
Smilacaceae	*Smilax campestris* Griseb.	l	s
Solanaceae	*Petunia integrifolia* (Hook.) Schinz & Thell.	h	s
	Solanum lycocarpum A. St.-Hil.	c	r
Styracaceae	*Styrax camporum* Pohl	p	n
	Styrax ferrugineus Nees & Mart.	p	r
Symplocaceae	*Symplocos rhamnifolia* A. DC.	p	r
	Symplocos tenuifolia Brand	p	n
	Symplocos uniflora (Pohl) Benth.	p	n
Thymelaeaceae	*Daphnopsis fasciculata* (Meisn.) Nevling	p	n
Turneraceae	*Turnera selloi* Arechav.	c	s
	Turnera sidoides L.	c	s
Velloziaceae	*Vellozia squamata* Pohl	p	r
Verbenaceae	*Aegiphila lhotzkiana* Cham.	p	r
	Glandularia megapotamica (Spreng.) Cabrera & G.Dawson	h	s
	Lantana montevidensis (Spreng.) Briq.	h	s
	Verbena ephedroides Cham.	h	s
	Verbena pseudojuncea (Gay) Moldenke	h	s
Vitaceae	*Cissus striata* Ruiz & Pav.	l	s
Vochysiaceae	*Qualea dichotoma* (Mart.) Warm.	p	r
	Qualea grandiflora Mart.	p	r
	Qualea multiflora Mart.	p	r
	Qualea parviflora Mart.	p	r
	Vochysia cinnamomea Pohl	p	r
	Vochysia elliptica Mart.	p	r
	Vochysia thyrsoidea Pohl	p	r
	Vochysia tucanorum Mart.	p	r

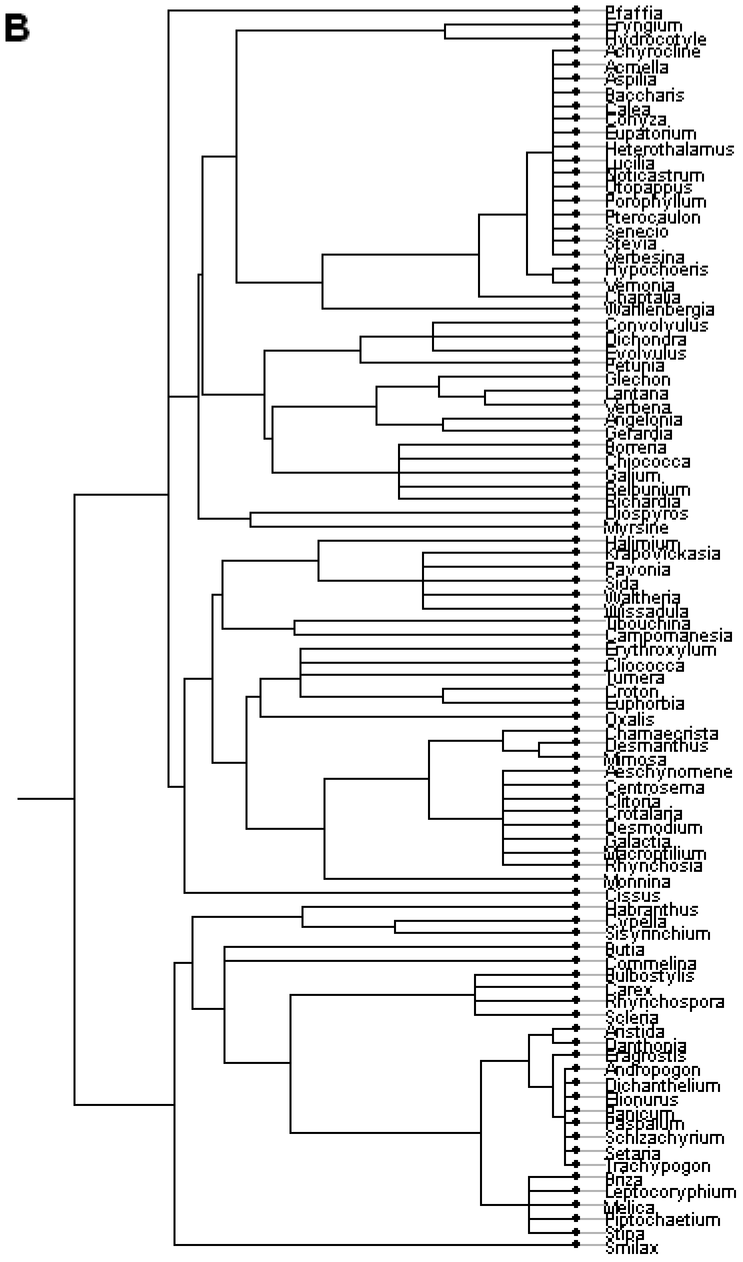
Appendix 2. Summary of the phylogenetic tree assembled for Brazilian savanna species under (A) annual fire frequency and (B) fire exclusion. The tree A presents 41 nodes and 91 branches, and the tree B presents 58 nodes and 131 branches. We based the relationship among families on the Angiosperm super-tree of Davies et al. (2004).




B
Copaifera
Dimorphandra
Sclerolobium
Anadenanthera
Mimosa
Stryphnodendron
Acosmium
Dalbergia
Machaerium
Platypodium
Sweetia
Bauhinia
Brosimum
Byrsonima
Pera
Caryocar
Kielmeyera
Couepia
Ouratea
Casearia
Lacistema
Erythroxylum
Connarus
Rourea
Maytenus
Plenckia
Blepharocalyx
Campomanesia
Eugenia
Myrcia
Psidium
Leandra
Miconia
Tibouchina
Qualea
Vochysia
Lafoensia
Terminalia
Daphnopsis
Eriotheca
Alibertia
Amaioua
Palicourea
Psychotria
Tocoyena
Strychnos
Cybistax
Jacaranda
Tabebuia
Solanum
Baccharis
Chromolaena
Eremanthus
Piptocarpha
Vernonia
Gochnatia
Schefflera
Ilex
Diospyros
Styrax
Symplocos
Pouteria
Rapanea
Guapira
Neea
Davilla
Roupala
Annona
Duguetia
Xylopia
Virola
Ocotea
Siparuna

Appendix 3. Summary of the phylogenetic tree assembled for Brazilian grassland species (A) one year and (B) three years after fire. The tree A presents 46 nodes and 126 branches and the tree B presents 53 nodes and 143 branches. We based the relationship among families on the Angiosperm super-tree of Davies et al. (2004).




B
Pfaffia
Eryngium
Hydrocotyle
Achyrocline
Acmella
Aspilia
Baccharis
Calea
Conyza
Eupatorium
Heterothalamus
Lucilia
Noticastrum
Otopappus
Porophyllum
Pterocaulon
Senecio
Stevia
Verbesina
Hypochoeris
Vernonia
Chaptalia
Wahlenbergia
Convolvulus
Dichondra
Evolvulus
Petunia
Glechon
Lantana
Verbena
Angelonia
Gerardia
Borreria
Chiococca
Galium
Relbunium
Richardia
Diospyros
Myrsine
Halimium
Krapovickasia
Pavonia
Sida
Waltheria
Wissadula
Tibouchina
Campomanesia
Erythroxylum
Cliococca
Turnera
Croton
Euphorbia
Oxalis
Chamaecrista
Desmanthus
Mimosa
Aeschynomene
Centrosema
Clitoria
Crotalaria
Desmodium
Galactia
Macroptilium
Rhynchosia
Monnina
Cissus
Habranthus
Cypella
Sisyrinchium
Butia
Commelina
Bulbostylis
Carex
Rhynchospora
Scleria
Aristida
Danthonia
Eragrostis
Andropogon
Dichanthelium
Elionurus
Panicum
Paspalum
Schizachyrium
Setaria
Trachypogon
Briza
Leptocoryphium
Melica
Piptochaetium
Stipa
Smilax

V - Conclusão geral

Conclusão geral

O fogo é um importante filtro ambiental para as plantas de cerrado em uma pequena escala espacial, promovendo agrupamentos fenotípicos tanto de espécies do componente herbáceo-subarbustivo quanto do componente arbustivo arbóreo. Quando a frequência de fogo é reduzida, a competição pode promover uma dispersão fenotípica das plantas. Contudo, elevadas frequências de fogo parecem não afetar a estrutura filogenética da comunidade e nenhum padrão parece emergir em nas escalas espaciais investigadas. Postulamos que a ausência de agrupamentos filogenéticos em cerrados é devido à persistência de espécies rebrotantes de longa vida e a presença de espécies de linhagens filogeneticamente distantes. Por outro lado, em escala espacial regional, a ausência do fogo pode modificar a estrutura filogenética em cerrados, levando a padrões opostos de estruturação, ou seja, a atração e dispersão filogenética. Isso porque a exclusão do fogo permite que espécies tanto de linhagens distantes quanto aparentadas colonizem o ambiente.

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