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EFEITOS DE DIFERENTES REGIMES DE FOGO NA COMUNIDADE DE FORMIGAS DO CERRADO

JONAS MARAVALHAS

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Dissertação apresentada à Universidade Federal de Uberlândia, como parte das exigências para obtenção do título de Mestre em Ecologia e Conservação de Recursos Naturais

Orientador:
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Maravalhas, J. 2013. Efeitos de diferentes regimes de fogo na comunidade de formigas do Cerrado. Dissertação de Mestrado em Ecologia e Conservação de Recursos Naturais. UFU. Uberlândia-MG. 51 p.

Distúrbios têm recebido crescente reconhecimento como importantes fatores estruturantes da natureza. O fogo é importante em ambientes xéricos e sazonais, mantendo a estrutura do habitat e as populações locais. O Cerrado é uma savana Neotropical sujeita a queimadas freqüentes, porém mudanças no regime de fogo ameaçam a conservação deste bioma. A exclusão do fogo beneficia árvores e eventualmente transforma a vegetação numa floresta. Por outro lado, a intensificação das queimadas beneficia gramíneas e pode ser danoso a espécies adaptadas a regimes mais brandos. Portanto é fundamental desenvolver estratégias apropriadas de manejo do fogo, porém a falta de informação sobre os efeitos do fogo são um empecilho. Formigas são importantes em ambientes tropicais e respondem a mudanças no habitat, ideais para o estudo de impactos ambientais. Nós registramos mudanças na comunidade de formigas entre áreas de Cerrado submetidas a diferentes regimes de fogo. Os efeitos da freqüência de queimadas foram testados entre parcelas protegidas do fogo (C0) e parcelas queimadas no meio da estação seca a cada quatro (M4) ou dois (M2) anos. Este último foi também comparado com parcelas bianuais queimadas no início (E2) ou fim da estação seca (L2), testando os efeitos do período de queima. Nós utilizamos armadilhas de queda com isca para coletar formigas no solo (epigéicas) ou na vegetação (arbórea) em quatro blocos cada um com os cinco tratamentos de fogo. Nós testamos mudanças na riqueza e composição de espécies de formigas entre os tratamentos, com paralelos às mudanças na estrutura da vegetação. Também avaliamos o número de espécies de formigas resultantes de estratégias potenciais de manejo com grau variado de dissimilaridade de regimes de fogo. Com partição aditiva da diversidade avaliamos a contribuição da diversidade de regimes à diversidade total de formigas. Coletamos 165 espécies de formigas num total de 4.480 registros. Áreas não queimadas tiveram riqueza de espécies significativamente menor que áreas queimadas, porém nenhuma diferença foi observada entre os tratamentos de fogo, independente da freqüência ou período. Já a composição da comunidade diferiu marcadamente entre diferentes freqüências, já que tanto o estrato epigéico quanto o arbóreo mostraram separação na composição. Já entre diferentes períodos de queima, houve separação significativa somente para o estrato epigéico, com alta sobreposição de espécies arbóreas entre E2, M2 e L2. Contrastando estratégias potenciais de manejo encontramos mais espécies quando regimes mais dissimilares eram combinados, ressaltando a importância da diversidade de histórico de fogo para a diversidade biológica. Os resultados da partição reforçam esta idéia, já que a troca de espécies entre regimes de fogo contribuiu com 42% da diversidade total de formigas. Áreas protegidas do fogo continham menos espécies de formigas, porém são importantes para espécies florestais. Regimes de alta freqüência de fogo, como M2 ou L2, mantém a estrutura savânica do habitat e permitem a persistência de espécies de ambientes abertos. Assim, o uso de queimadas controladas em áreas preservadas de Cerrado deve ser estimulado, porém estratégias apropriadas de manejo devem ter algum nível de diversidade de histórico de fogo, mantendo ambientes variados e maximizando a conservação de espécies.

Palavras-chave: Distúrbios, diversidade, conservação, manejo de fogo, queimadas prescritas, savana Neotropical, assembléia de Formicidae.

ABSTRACT

Maravalhas, J. 2013. Effects of different fire regimes in the Cerrado ant community. Master of Science thesis. UFU. Uberlândia-MG. 51 p.

Disturbance has been increasingly recognized as a structuring force in nature. Fire is an important feature of many xeric and seasonal ecosystems, where it maintains habitat structure and allows the persistence of local populations. The Cerrado is a Neotropical savanna characterized by frequent burning, but changes in the fire regime threaten the conservation of this biome. Exclusion of fire causes a shift in vegetation, benefitting trees and eventually resulting in a forest. Intensification of fires benefits grasses, and can be detrimental to Cerrado organisms adapted to the natural fire regime. The development of appropriate fire management strategies is essential, but this task is hindered by the lack of scientific information on the effects of fire on Cerrado organisms. Ants are ubiquitous in tropical ecosystems and are responsive to changes in the habitat, thus ideal for studying disturbance impacts. We assessed how the ant community changed between fire regimes in a Cerrado of Central Brazil. Fire treatments were maintained for 15 years over 150 ha of typical cerrado vegetation. Fire frequency effects were tested comparing plots subjected to fire suppression (C0) or mid-season fires every four (M4) or two years (M2). The latter was also compared to early-season (E2) and late-season (L2) plots, assessing the effects of the burning period. We used baited pitfall traps to collect ants from the soil (epigaeic) and vegetation (arboreal) in four blocks containing all five regime treatments. We evaluated changes in species richness and composition of the ant community and made parallels with changes in vegetation structure. Also, we compared the number of ant species among potential management strategies with varying levels of fire regime diversity and evaluated the contribution of fire diversity in overall ant diversity with additive partitioning. We collected a total of 165 ant species from 4,480 records. There was significantly less ant species in fire-suppressed sites, but among fire-treated sites, no difference was detected irrespective of frequency or period of burning. Meanwhile, community composition changed sharply between treatments, especially at fire frequency comparison, where both arboreal and epigaeic species composition changed between C0, M4 and M2 plots. Comparing period levels, though, there was a significant separation between E2, M2 and L2 plots only for epigaeic species. Contrasting potential management strategies, we found significantly more species when dissimilar fire regimes were combined, highlighting the importance of fire regime diversity in maximizing biological diversity. The results of the additive partition reinforce this idea, as 42% of the total diversity was due to turnover between fire treatments. Fire-suppressed sites support less ant species, nevertheless they are important to forest-associated species. High frequency fires, like M2 or L2, maintain the savanna structure and allow the persistence of open-habitat species. In this sense, we advocate for the use of prescribed burning in Cerrado preserved areas. Furthermore, an appropriate fire management should have some level of regime diversity in order to maintain habitat variability and maximize conservation of species.

Key words: Disturbance, diversity, conservation, fire management, prescribed burning, Neotropical savanna, Formicidae assemblage.

INTRODUÇÃO GERAL

Introdução

Durante anos a teoria ecológica clássica considerou que os ecossistemas naturais se desenvolviam na direção de uma condição de clímax. Qualquer perturbação que afastasse o sistema do equilíbrio estável seria seguida de uma sucessão até o retorno a esse estado (Clements 1916). Essa visão do mundo natural teve conseqüências no manejo de áreas preservadas, levando à exclusão de fatores que desviem o sistema desse curso inexorável. Recentemente mais atenção tem sido dada às condições de não-equilíbrio e à natureza dinâmica dos sistemas naturais (Connell 1978; Picket e White 1985). Neste cenário, os distúrbios desempenham um importante papel no funcionamento dos ecossistemas (Chapin *et al.* 2002). Distúrbios são definidos como eventos discretos que provocam perda de biomassa de um sistema (Grime 1977). Eles provocam variabilidade espacial e temporal no habitat, garantindo a coexistência de diversas formas de vida (Parr e Brockett 1999; Cadotte 2007). Em um habitat espacialmente heterogêneo, espécies podem coexistir em uma mesma área devido à especialização de nicho, aumentando assim a diversidade (Connell 1978). De forma semelhante, a heterogeneidade temporal permite a coexistência de espécies ao longo do processo de sucessão. Espécies dominantes costumam ser limitadas pela dispersão, porém excluem outras espécies ao se estabelecerem em um habitat. A ruptura do estado clímax cria uma janela de tempo utilizada por espécies altamente dispersivas para se estabelecer e reproduzir (Grime 1977).

Mesmo com mudanças no paradigma teórico, pouco se tem avançado na aplicação de técnicas de manejo que vise, por meio do distúrbio, maximizar a diversidade de espécies e processos ecológicos (Moritz e Odion 2004). Um dos maiores desafios para a conservação da biodiversidade é compreender a dinâmica dos ambientes naturais (Chapin *et al.* 2002) e tentar prever as conseqüências das mudanças climáticas (Lawler *et al.* 2009)e transformação da terra (Fahrig 2003) na distribuição dos ecossistemas e seus organismos. Embora a distribuição potencial dos ecossistemas terrestres seja amplamente determinada por variações na temperatura e precipitação, o fogo determina a real distribuição dos biomas, consumindo grande quantidade de biomassa vegetal e provocando persistentes modificações no habitat (Bond *et al.* 2005). Esses ambientes dependem do fogo para a manutenção da estrutura e funcionamento do habitat, bem como a persistência das espécies nativas (Bond e Parr 2010).

Diversos ecossistemas entre desertos, campos, savanas tropicais, formações arbustivas mediterrâneas e florestas boreais são suscetíveis ao fogo, ocupando cerca de 40% da superfície terrestre (Chapin *et al.* 2002; Bond e Keeley 2005).

Diversos ecossistemas brasileiros são afetados por queimadas. Na Floresta Amazônica o fogo tem conseqüências severas para a estrutura florestal e é muito utilizado no avanço da fronteira agrícola (Pivello 2011). Entretanto, além do uso antrópico o fogo é um fator natural e mantenedor da estrutura dos Pampas Sulinos (Overbeck *et al.* 2007) e formações campestres e savânicas do Cerrado (Coutinho 1990).

O fogo no Cerrado data de cerca de 32.000 anos, segundo registros palinológicos (Salgado-Labouriau *et al.* 1997), indicando sua presença antes mesmo da chegada do homem na região. Queimadas naturais ocorrem exclusivamente devido a descargas elétricas, que ocorrem nas transições entre a estação chuvosa e a seca, em um intervalo de 1-9 anos (Ramos-Neto e Pivello 2000). Já queimadas antrópicas são mais freqüentes, em intervalos de 1-3 anos e a maioria ocorre na estação seca, quando a probabilidade de combustão é muito alta (Coutinho 1990; Medeiros e Fieldler 2003). A ocupação humana (Klink e Machado 2005), a invasão de gramíneas exóticas (Pivello *et al.* 1999) e a fragmentação tem alterado os regimes naturais de fogo no Cerrado. Mudanças permanentes na estrutura das formações do Cerrado ocorrem, por um lado, com a intensificação do fogo. Em um sistema sinérgico, o fogo freqüente exclui árvores e beneficia gramíneas, cujo crescimento rápido fornece biomassa e possibilita queimadas em intervalos menores (Hoffmann *et al.* 2009). Por outro lado, a ausência do fogo beneficia as espécies arbóreas e o adensamento de árvores exclui as gramíneas (Moreira 2000). Estas condições permitem a colonização de espécies florestais, acarretando numa alteração profunda do habitat.

Embora queimadas controladas estejam previstas na lei, poucas Unidades de Conservação no Cerrado utilizam essa ferramenta, em geral para a confecção de aceiros negros (IBAMA 1998). A política mais comum é da completa supressão do fogo na vegetação. Em uma paisagem altamente fragmentada, com Unidades de Conservação sofrendo pressão urbana e rural e com escassez de funcionários, a completa supressão do fogo é muito difícil. Com o acúmulo de biomassa ao longo dos anos, queimadas descontroladas são muito comuns em áreas preservadas. Elas são extensas, mais homogêneas, mais intensas e com conseqüências negativas para muitos organismos (Ramos-Neto e Pivello 2000; Pivello 2011). Conhecer os efeitos das mudanças no regime de fogo na biota nativa do Cerrado, bem como desenvolver estratégias apropriadas de manejo do fogo, é de extrema importância para a sua conservação. Este bioma é o segundo maior da região Neotropical, abrangendo aproximadamente dois milhões de km2 do território brasileiro e partes da Bolívia e Paraguai (Ratter *et al.* 1997). É considerada a savana mais biodiversa no mundo (Klink e Machado 2005), possuindo altos graus de diversidade, heterogeneidade e endemismo (Ratter *et al.* 1997), sendo considerado um hotspot da conservação global (Myers *et al.* 2000). Mesmo assim o Cerrado está ameaçado pelo crescimento das áreas urbanas e principalmente pelo rápido avanço do agronegócio no Brasil (Klink e Moreira 2002) e em 2002 por volta de 55% da área do bioma havia sido convertida (Machado *et al.* 2004).

Os efeitos do fogo sobre os organismos podem ser diretos ou indiretos. As elevadas temperaturas da frente de fogo causam mortalidade de indivíduos e perda de investimento reprodutivo. Também de forma direta, as alterações nas condições microclimáticas do ambiente afetam a sobrevivência dos animais após queimadas (Whelan 1995). Indiretamente, mudanças no regime de fogo, como alterações na freqüência ou período de queima, causam mudanças profundas no habitat e conseqüentemente na composição de espécies. E.g. a supressão do fogo pode permitir a invasão de espécies intolerantes a queimadas, excluindo organismos adaptados ao fogo (Bond e Parr 2010). Por outro lado, uma maior freqüência de fogo aumenta a severidade do regime, podendo extinguir inclusive espécies resistentes (Hoffmann *et al.* 2009). O período de queima determina características importantes no comportamento do fogo, devido às mudanças nas condições climáticas, além de afetar diferentes fases fenológicas dos organismos (Whelan 1995).

Formigas são insetos sociais de grande importância no funcionamento dos ecossistemas terrestres. Elas ocupam diversos estratos, contribuem com grande parte da biomassa animal, são importantes herbívoros, dominam recursos e estruturam comunidades de artópodes por predação ou competição (Hölldobler e Wilson 1990). São organismos sensíveis a alterações no habitat (Andersen 2000, Ribas *et al.* 2003; Vasconcelos *et al.* 2008) inclusive ao fogo (York 2000; Parr *et al.* 2004; Hoffmann 2003; Andersen *et al.* 2006, 2009), com variadas respostas desde resistência e resiliência até alterações específicas nos grupos funcionais (Lach *et al.* 2010). No Cerrado, poucos estudos avaliaram a resposta da comunidade de formigas ao fogo e em geral abrangem somente os efeitos diretos de curto prazo. Formigas de vegetação sofrem elevada mortalidade e mesmo que a recolonização seja rápida, a recuperação das colônias é lenta (Morais e Benson 1988). Os efeitos de uma queimada em curto prazo parecem ser contrastantes entre formigas de solo e de vegetação. Enquanto a passagem do fogo reduziu a atividade de formigas no estrato arbóreo, no solo a atividade foi maior nos meses subseqüentes à queima (Frizzo *et al.* 2012). Em longo prazo, a supressão do fogo reduziu a abundância de formigas predadoras, enquanto as onívoras foram abundantes em aceiros queimados anualmente (Uehara-Prado *et al.* 2010).

Justificativa e objetivos

Até o presente momento, nenhum estudo comparou atributos das comunidades de formigas em áreas de cerrado sujeitas a diferentes regimes experimentais de fogo. O presente estudo foi realizado no maior experimento com queimadas controladas na América Latina, que inclui tratamentos com variação na freqüência e época do fogo. Essas informações são importantes para compreender as respostas dos organismos ao fogo e prever mudanças decorrentes da alteração dos regimes de queima no Cerrado. Ademais os resultados apresentados auxiliam no desenvolvimento de técnicas apropriadas de manejo do fogo neste bioma, mantendo a diversidade biológica e prevenindo incêndios descontrolados.

Mudanças na riqueza e composição de comunidades de formigas arbóreas e epigéicas foram avaliadas em áreas de cerrado com diferentes regimes de fogo. Foram testadas as hipóteses de que (i) a riqueza e composição de espécies de formigas serão afetados pelas mudanças na freqüência e período de queimadas; (ii) a comunidade do estrato arbóreo será mais sensível a essas mudanças no regime de fogo, devido à maior susceptibilidade dos ninhos e pelo efeito negativo do fogo nas árvores; (iii) regimes de alta freqüência de fogo são de forma geral danosas às populações de formigas e por isso suportarão menos espécies de formigas; (iv) de forma paralela, um aumento na severidade das queimadas com a progressão da estação seca acarretará numa menor riqueza de formigas em regimes tardios de queima, comparados com regimes precoces ou modais; (v) por fim, esperamos encontrar maior riqueza de espécies em áreas com maior dissimilaridade de regimes devido ao turnover de espécies entre áreas com diferentes históricos de fogo.

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CAPÍTULO 1. Effects of long-term fire regimes on the ant community of a Neotropical savanna

Introduction

Natural habitats have historically been regarded as stable systems where an equilibrium state is maintained over time (Clements 1916) giving rise to a still prevalent idea that conservation practices should aim to preserve these pristine refugees. More recently, nonequilibrium hypothesis highlighted the importance of historical and external factors in determining ecosystem structure and highlight the dynamic nature of natural systems (Pickett and White 1985). In this scenario, disturbance plays a crucial role in maintaining this dynamic state by allowing species coexistence in spatial and temporal scales (Parr and Brockett 1999; Cadotte 2007).

Disturbance is a discrete event in space and time that removes parts of an ecosystem´s biomass (Grime 1977). By causing changes in the physical environment and resource availability, disturbance affects populations, communities, and ecosystems, being at the same time reciprocally determined by these factors (Chapin *et al.* 2002). Spatial heterogeneity maintained trough habitat modification can support greater densities of species in areas with intermediate degree of disturbance (Connell 1978). Moreover, temporal heterogeneity created by successive habitat disturbances creates new colonization sites and disrupts the dominance of dispersal-limited species, allowing highly dispersive, subordinate species to persist over time (Grime 1977).

A global challenge in conservation biology is to understand ecosystem dynamics and its response to environmental change (Chapin *et al.* 2002), especially in the face of global climate and habitat transformations. While temperature and rainfall determine the potential distribution of ecosystems on Earth, mismatches with the realized distribution are mainly attributed to fire, a global driver of ecosystem shifts (Bond *et al.* 2005). Fire is a natural and ubiquitous phenomenon in fire-prone ecosystems, such as savannas, grasslands, Mediterranean shurblands, and boreal forests. These ecosystems occupy *ca.* 40% of the terrestrial land (Chapin *et al.* 2002), and depend on recurrent burning to maintain their habitat structure (Bond and Parr 2010).

The *Cerrado* is the second largest Neotropical biome covering 2 mi km^2 of the Brazilian central plateau and parts of Bolivia and Paraguay (Ratter *et al.* 1997). It is a fire-prone ecosystem characterized by savanic formations (*ca.* 70%) with patches of dry forests and grasslands, in a rich variety of vegetation forms (Eiten 1972; Silva and Bates 2002, Silva *et al.* 2006). It has high levels of diversity, turnover, and endemism (Ratter *et al.* 1997), and is considered to be the World's most diverse savanna (Klink and Machado 2005). The Cerrado domain has become Brazil's new agricultural frontier since the mid 1960's (Klink and Moreira 2002) and by 2002 over 54.9% of its original vegetation cover had already been converted into crop fields, pastures, or urbanized areas (Machado *et al.* 2004). It is one of the most threatened habitats in the globe and thus considered a biodiversity hotspot (Myers *et al.* 2000).

Charcoal records dating 32.4 Kya (thousand years before present), indicate the occurrence of frequent wildfires in the Cerrado region even before human establishment (Salgado-Labouriau *et al.* 1997). An even older fire presence is evidenced by the contemporary raise of flammable C4 grasses and modern plant lineages in the Cerrado around 4 Mya (Simon *et al.* 2009), suggesting that the local biota probably evolved to resist or even benefit from recurrent fires (Eiten 1972; Coutinho 1990). Cerrado vegetation naturally burns in the rainy season, mainly because of lightning strikes, with a return interval of 1-9 years (Ramos-Neto and Pivello 2000). In contrast, fires caused by humans occur every 1-3 years mainly during the dry season (Coutinho 1990; Medeiros and Fiedler 2004). Cerrado vegetation has surface-fires with behavior differing from open grasslands (*campo limpo*) to dense woodlands (*cerradão*) with regard to flame height (1.2-2.9 m), fire line intensity (557-3,693 kW m^{-1}) and patchiness (low to high) (Castro and Kauffman 1998).

Use of fire as an agricultural tool (Klink and Machado 2005), invasion of alien grasses (Pivello *et al.* 1999), and habitat fragmentation have severely altered natural fire regimes in the Cerrado. This has led to a habitat shift, with grasses acting in a positive feedback with fire (Hoffmann *et al.* 2009) to maintain an open landscape (Eiten 1972; Hoffmann 1998; Klink and Moreira 2002). Although controlled burning is allowed for ecosystem management and fire prevention, most Cerrado protected areas have a policy of complete fire suppression (IBAMA 1998), in part because public opinion and law-makers are historically hostile to burning. Fire suppression may lead to an alternative ecological state dominated by trees, with no grasses to fuel new fires, eventually converting open habitats into forests (Moreira 2000). As complete fire suppression is virtually impossible, accumulation of dry biomass over the years usually results in wildfire that severely burns large areas (Pivello 2011). The human presence in the Cerrado and consequent shifts in its fire regime reflect a global pattern of change in the use of fire in natural and cultivated areas, with consequent ecosystem alterations (Bowman *et al.* 2011).

Fire-suppression has been applied to various fire-prone ecosystems for decades, resulting in negative consequences like woody encroachment (Parr *et al.* 2012) and extinction of fire-dependent species, among others (Backer *et al.* 2004). Thus, the development of fire regimes was necessary so to maintain landscape structure, maintain populations and avoid wildfires (Bond and Parr 2010). Consequently, long-term experiments on the effects of fire have been implemented in the last two decades in fire-prone ecosystems (Driscoll *et al.* 2010). This effort aims to assess the response of organisms and ecosystem processes under different fire regimes and to develop management strategies that are able to maintain habitat stability and biotic diversity. Patch-mosaic burning has been advocated as an effective burning strategy for fire-prone ecosystems (Parr and Brockett 1999; Laris 2002; Burrows 2008). It creates patches of habitat with different fire-histories, increasing variability in abiotic conditions and resource availability, and allowing a greater array of species to coexist, as well as preventing large uncontrolled fires by fuel reduction and by creating natural firebreaks (Parr and Brockett 1999).

The effects of disturbance on biotic diversity depends on the original diversity of the habitat affected, the type and extent of the disturbance, the local climatic conditions, and the spatial and temporal disturbance scales (Bestelmeyer and Wiens 1997; Blanche *et al.* 2001; Mackey and Curie 2001; Hughes *et al.* 2007). Fire may affect populations directly through changes in mortality and reproduction rates due to fire passage and post-fire conditions, or indirectly trough habitat change (Whelan 1995). Although the most common trend is a reduction in species richness with increasing disturbance (Hughes *et al.* 2007) there may be a bias, since in most habitats the disturbance factor is not a natural phenomenon. As is also the case in most savannas throughout the World (Higgins *et al.* 2007; Parr and Andersen 2006; Wittkuhn *et al.* 2011), the Cerrado biota shows some degree of resistance and resilience both to short and long term effects of fire (Morais and Benson 1988; Hoffmann *et al.* 2009; Simon *et al.* 2009; Vasconcelos *et al.* 2009; Uehara-Prado *et al.* 2010; Frizzo *et al.* 2011).

Different fire regimes can have different frequencies of occurrence and such variation determines how many disturbance events a population will face and how much time it will have to recover until the next event. Another component of a fire regime is the period of fire, *i.e.* exactly when along the year the fire is set (Whelan 1995). In the Cerrado, dry flammable biomass increases as humidity decreases along the dry season, so probability of ignition, intensity and homogeneity of the fire is greater at the end of the dry season than at the end of the wet season (Miranda *et al.* 1993; Castro and Kauffman 1998; Ramos-Neto and Pivello 2000). Also of importance, it determines the phenological phase in which organisms are affected. Milder fires remove flammable biomass such as dead grasses, twigs and leaves and thus reduce the probability of new fires, so early-season burning can even favor trees, because fire adaptations such as thick bark and underground reserve organs prevent mortality (Coutinho 1990). At the end of the dry season, trees begin the production of new leaves, so late-season fires destroys this investment and are a heavy burden for the woody vegetation as repeated fires can kill trees, in contrast, grasses benefit because they quickly resprout from underground meristems (Miranda *et al.* 2002).

Ants play an essential role on the functioning of tropical terrestrial ecosystems at multiple strata. They account for a significant amount of animal biomass, are important herbivores, structure arthropod communities trough intense predation and competition (Hölldobler and Wilson 1990), and are involved in many ecosystem services (Del Toro *et al.* 2012). Ant communities are affected by changes in habitat structure (Andersen 2000, Ribas *et al.* 2003; Vasconcelos *et al.* 2008) and can be sensitive to fire (York 1994; Parr *et al.* 2002; Hoffmann 2003; Andersen *et al.* 2006, 2009; Vasconcelos *et al.* 2009), with a variety of responses from resistance and resilience to specific chances in functional groups (Lach *et al.* 2010). The few existing studies on the response of Cerrado ants to fire are based on BACIP designs (Before-After-Control-Impacted-Pairs, Oaten *et al.* 1992) that only evaluate the short-term effects of a single fire event. One of these studies indicate that arboreal-nesting ants can suffer high mortality after a fire event, and that recolonization is fast even though nests were still relatively small 1.5 year after the fire (Morais and Benson 1988). There is also evidence that ants from distinct strata show opposite short-term responses to fire, as while the number of arboreal species foraging in individual trees decreased, that of epigaeic species foraging on ground below trees increased within the first few months after a fire (Frizzo *et al.* 2012). Finally there is evidence that predatory ants are less frequent in unburned sites while omnivores become more abundant in sites burned annually (Uehara-Prado *et al.* 2010).

To our knowledge no study has compared the attributes of ant communities from different Cerrado areas subject to various long-term experimental fire regimes. This information is crucial for understanding how ant diversity responds to the most common burning practices applied in the Cerrado and can contribute to the development of fire management strategies in this diverse and threatened biome. Here we evaluated the differences in richness and composition of the arboreal and epigaeic ant communities in areas with fire regimes of varying frequency and/or period of burning.

We hypothesized that (i) ant species richness and composition will respond to changes in the frequency and period of burning; (ii) we believe arboreal ants will be more susceptible to changes in the fire regime, due to the greater exposure of aerial nests and the negative effect of fire on trees; (iii) high frequency fire regimes are more severe to overall ant populations due to habitat changes and increased nest mortality, and thus will support less ant species. In addition, we expect a major change in the composition of the ant community; (iv) in parallel, increased fire severity along the dry season will be reflected by less ant species at late-season regimes, compared to early or mid-season fires. Again we expect that changes in the burning season will have a pronounced effect on the composition of ant species; and finally, (v) we expect to find more ant species in potential management strategies that encompass more dissimilar fire treatments, and this is due to turnover of species between sites with different fire histories.

Material and methods

Study site

The study was conducted at the *Reserva Ecológica do IBGE*, a 1,300 ha reserve located 16 km south of Brasilia, DF, Brazil (15° 56' 40.9 S, 47° 53' 7.0 W). It is part of a 25,000 ha area of preserved vegetation encompassing the Paranoá Basin, at the core of the Cerrado distribution. Elevation at the site averages 1,100 m a.s.l and soils are well drained red latossols (Miranda *et al.* 2011).

The region has an Aw (Köppen 1948) climate characterized by relatively uniform temperatures (mean temperature for 2011 at the reserve was 22.1 ºC), moderate levels of rainfall (1.387 mm annually, IBGE records for 2011), and a marked dry season from June to September, when humidity reaches very low levels and fire risk is greater. The reserve harbors characteristic Cerrado physiognomies ranging from open grasslands to closed forests. The *campo limpo* and *campo sujo* are grasslands with few scattered trees, while the *cerrado sensu stricto* is a savanna characterized by a continuous herbaceous layer and a discontinuous woody canopy. The cerrado sensu stricto is the most common formation both at the reserve and in the Cerrado biome (Eiten 1972).

Experimental design

The “Fire Project” (*Efeitos de diferentes regimes de queima sobre a estrutura das comunidades de Cerrado, Projeto Fogo*) was established in two adjacent areas of cerrado sensu stricto (totaling about 100 ha) that were protected from fire since 1974. Each area was divided into five sections of 200 x 500 m each. Different fire treatments were assigned to each group of five sections (Figure 1) in 1991 and these treatments were maintained until 2008 (i.e. for 17 consecutive years). Treatments were variable with regard to either fire frequency or time of burning (fire period). Two sections of 200 x 500 m remained unburned (hereafter C0 treatment), two were burned every four years in mid August (middle of the dry season) (hereafter M4), and six were burned every two years, of which two were burned at the end of June (early dry season) (hereafter E2), two in mid August (hereafter M2), and two at the end of September (late dry-season) (hereafter L2).

For the purpose of our study we established, within each 200 x 500 m section, two sampling plots near and along the narrowest borders of each section (Fig. 1). We treated each of these two plots as true replicates because the distance between them (420m) was greater than the average distance between the four other adjacent plots subject to different fire treatments (400m on average) (Fig. 1). A standardized protocol for sampling leaf-litter ants recommends a minimum distance of 10 meters between samples along a transect (Agosti and Alonso 2000). Furthermore, 20 meters-spaced leaf-litter samples have been considered as independent for ants (Mezger and Pfeiffer 2011), as most ant species forage only few meters away from the nest entrance. This reduces the probability of overestimating the frequency of occurrences by collecting workers from one single colony in more than one sample. Besides, topographic variations along the study area (which has a mean declivity of 3.5%; N-S oriented) resulted in some differences in vegetation structure among the original sections of the Fire Project (e.g., towards the east there was a more open vegetation than towards the west; J.Maravalhas, pers. obs.). We justify treating the extremes of each section as two independent plots due to habitat differences and the great between-plot distance – considering the small reach of ant territories.

In this way, four groups of five plots (each subject to a different treatment) were formed and these groups were treated as independent samples in all of our statistical analyses. The replicates are shown in Figure 1 as dark gray areas and they encompass four fire treatment plots plus a control plot, with the latter not necessarily established in the original 200 x 500 m control section because of the occurrence of accidental fires. Our controls plots were then re-alocated to adjacent area that effectively have not been burned since1974.

Our study took place in July 2011, four years after the last fire in the M4 plots, three years after the last fire in the E2, M2, and L2 plots and at least 37 years after the last known fire in the C0 plots. Detailed images and characteristics of representative plots from each treatment are presented in Figure 2. For further information about the study area and the experimental design see Miranda *et al.* (2011).

Ant sampling

In each plot we established 16 sampling points arranged in a 160 x 20 m grid, keeping a minimum distant of 20 m between sampling points. We installed four pitfall traps in each point; two were placed in the branches (between 0.5 and 2 m in height) of the nearest tree, and two were placed on the ground (2 m from each other). Traps consisted of 250 ml plastic cups. In each sampling point one trap was filled (to about half of its volume) with a 2% solution of sugar dissolved in water and the other with a 33% solution of human urine dissolved in water. A few drops of liquid soap were added to each trap in order to increase the killing efficiency of the traps. Traps remained in operation for 48h. The contents obtained in different traps located within the same sampling point were combined to form a single sample, thus generating 16 arboreal and 16 epigaeic samples per plot. A total of 640 samples preserved in ethanol 96% was then sorted under a stereomicroscope and all ants collected were identified to genus (following the nomenclature of Bolton *et al.* 2005) and then to species. Specimens whose identification to species level was not possible were assigned a morphospecies code.

Woody plant structure

To assess the effects of different fire regimes on the structural attributes of the woody vegetation we estimated tree density and average tree size in the 20 plots studied. These features were measured because they could be of importance in shaping ant communities (Ribas *et al.* 2003; Powell *et al.* 2011). We established three 4 x 50 m transects within each plot, and counted and measured the trunk diameter (30 cm above the ground) of all trees with a diameter ≥ 5 cm.

Statistical analyses

Because the experiment was not fully factorial we analyzed the effects of fire frequency and fire period separately in all analyses described below. The effect of fire frequency was tested comparing unburned plots (C0) versus those burned every two or four years during the middle of the dry season (M2 and M4). The effect of fire period was assessed by contrasting the three biennial treatments, E2, M2 and L2. i.e., burned early, in the middle, or latter during the dry season.

We evaluated differences in woody plant structure among the different fire treatments using a MANOVA, with tree density ($\log_{10}$ number of trees) and tree size (median trunk diameter) as dependent variables. Differences in ant species richness were assessed with a one-way ANOVA (followed by Bonferroni's *post hoc* tests). Because traps from one or two sampling points were lost in some plots, analyses were based in the rarified species richness for a sample of $N = 14$ sampling points in all plots.

Sample-based accumulation curves were built using the Mao Tau index to evaluate the sampling completeness and to compare species richness at the treatment level, *i.e.*, combining all four plots from each treatment. Species accumulation curves were built using the default configurations of EstimateS 7.5 (Colwell 2005).

For the analyses of ant community composition we built matrices of the relative frequencies of each species in each plot and tested for differences in species composition between fire treatments using Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson 2001). This analysis does not require homoscedasticity and normality of data, because statistical significance is obtained through comparisons with a null-model (999 permutations of the original matrix). To visualize eventual differences in composition across treatments we built Non-Metric Multi-Dimensional Scaling (nMDS) plots using as dissimilarity measure, the Bray-Curtis index.

Indicator species of different fire treatments were identified using the Indicator Species Analysis (Ind Val) (Dufrene & Legendre 1997). We considered as indicator species all species with an IndVal score of at least 60% and/or $p<0.05$. Indicator values were calculated using the PCORD 5 software (McCune and Grace 2002). For this analysis we used the relative frequency of each species in each plot in order to equalize between-plot differences in ant activity.

To evaluate the possible influence of fire regime diversity (pyrodiversity) on overall ant diversity we produced species lists based on the combination of information derived from the four plots of the same treatment or from information derived by a combination of four plots from two different treatments (2 plots of each from the same replicate). We determined how dissimilar (in terms of ant species composition) each fire treatment was from the other through visual examination of the nMDS plots (figure 6.C). We then gave a score of "0" when all four plots belonged to the same treatment, and a score ranging from 1 to 4 based on how dissimilar any two treatments combinations were. In this way the two most dissimilar treatments combinations (C0 with M2, and C0 with L2) received a score of "4" to (C which comprised), whereas the combination M2 and L2 received a score of "1". Different treatments were always combined using plots located within the same block, which resulted in a total of six possible combinations per "combination of treatments". Because the premises of the ANOVA were violated with the multiple comparisons of samples, the statistical significance was assessed by contrasting the observed results with a null-model obtained through 999 permutations of the dataset. Differences between the dissimilarity scores were evaluated graphically.

To assess the relative contributions of alpha and beta diversities to overall ant species richness (γ diversity) we used additive diversity partitioning (Veech *et al.* 2002). Diversity partitioning is a method of decomposing total species richness into the components of mean diversity within samples (alpha diversity, or α) and diversity among samples (beta diversities, or β). In additive partitioning α and β have the same units and are expressed as means (Veech *et al.* 2002). Thus, in our study α1 represented the within sampling points diversity, β1 the diversity due to species turnover among sampling points within the same sampling plot, (between sampling points within each plot), β2 the diversity due to turnover of species between plots of the same fire regime, and β3 the diversity due to turnover of species among the five different fire treatments. The analyses were performed using the software Partition 3.0 (Crist and Veech 2006). This program calculates α and β and uses a randomization method for evaluating the statistical significance of each diversity component. The randomization procedure produces diversity values that would be expected from randomized data (i.e., a null model) and then compare these expected values to the actual (observed) diversity values. We used individual-based randomizations (999 iterations) which reassign each individual of the dataset to any sample (Crist *et al.* 2003; Crist and Veech 2006).

Results

Woody plant structure

We found substantial differences in woody plant structure between treatments (Figure 3). With regard to the effects of fire frequency, tree density was significantly greater in the control, unburned plots compared to the M4 and M2 fire treatments ($F_{2,6}$=19.67, p=0.002), while median trunk diameter showed the opposite trend – although differences were only close to significance ($F_{2,6}$=4.58, p=0.062) (Figure 3). Results of the multivariate statistic (Pillai Trace=0.93, $F_{4,12}$=2.61, p=0.089) were also only close to significance.

With regard to differences in vegetation structure due to the influence of fire period we found that tree density was significantly higher in E2 than in M2, and significantly higher in M2 than in L2 ($F_{2,6}$=34.32, p=0.001). Differences in median trunk diameter were only close to significance ($F_{2,6}$=3.96, p=0.08), with a trend towards finding bigger trees in M2 than in E2 and L2 (Figure 3).In spite of this, results of the multivariate statistic were highly significant (Pillai Trace=1.399, $F_{4,12}$= 6.98, p=0.004).

Ant species richness

We collected 165 ant species from 41 genera and eight subfamilies, in a total of 4.480 species records. A total of 83 species were collected in the arboreal pitfall traps (representing 29.5% of all species records) and 148 epigaeic species were collected in traps placed on ground (representing 70.5% of all species records) (see Appendix 1 for a detailed list of species).

Fire frequency did not significantly affect the richness of arboreal ants ($F_{2,9}$=0.41, p=0.675). However, fire frequency did affect the species richness of epigaeic ants ($F_{2,9}$=7.74, p=0.011), as well as the overall ant species richness (arboreal and epigaeic combined) ($F_{2,9}$=6.15, p=0.021). On average more species were recorded in the M4 and M2 than in the control (C0) plots (Figure 4a). Similarly, species accumulation curves showed that the number of species recorded in the M2 and M4 plots was slightly greater than the one recorded in the C0 plots (Figure 5a). Differences in species richness of plots burned (biannually) in different periods (i.e., fire period effect) were not significant (Arboreal: $F_{2,9}$=1.68, p=0.239; Epigaeic: $F_{2,9}$ = 0.06, p = 0.943; All: $F_{2,9}$ = 0.078, p = 0.925). However, there was a trend towards finding less arboreal species in the L2 compared to the M2 and E2 treatments (Figure 4b), with the same trend being observed in the species accumulation curves (Figure 5b).

Community composition

Fire frequency did significantly affect the species composition of the arboreal (PERMANOVA: $F_{2,9}$=1.67, p=0.036), epigaeic ($F_{2,9}$=2.07, p=0.001), and overall ant communities ($F_{2,9}$=2.07, p=0.003). In general, the M2 plots were more dissimilar to the C0 plots than were the M4 plots (Figure 6a). Seventeen ant species were considered indicators of different fire frequency regimes: *Hylomyrma* sp.1, *Brachymyrmex patagonicus*, *Cephalotes pusillus Gnamptogenys* sp.1, and three *Camponotus* species were indicators of the control (fire suppression) regime; *Camponotus* sp.26 of the M4 regime, whereas *Pheidole oxyops, Pheidole* sp. 13., *Camponotus* sp.5, *Crematogaster* sp.2, and *Ectatomma planidens* were indicators of the M2 regime (Table 1).

Fire period did not influence the species composition of arboreal ant community (PERMANOVA: $F_{2,9}$= 1.23, p = 0.185) and had a marginal effect on the composition of epigaeic and overall ant communities ($F_{2,9}$=1.38, p=0.071; $F_{2,9}$=1.37 , p=0.095). The L2 and E2 treatments were more dissimilar to each other than to the M2 treatment (Figure 6b). A total of 10 indicator species were identified (Table 1). *Br. patagonicus*, *Ce. pusillus* and *Crematogaster* sp.2 were indicators of the early season (E2) burning regime, *Camponotus crassus* two other *Camponotus* species were indicators of M2, whereas *Apterostigma* sp.1, *Atta laevigata*, *Ce. Depressus* and *Pheidole* sp.21 were indicators of the L2 regime.

Fire management

There was a trend towards finding more ant species overall as the dissimilarity between the fire treatments that were combined increased (Figure 7). In particular significantly more species were recorded in the combinations C0 with M2 or C0 with L2 than in the remaining fire treatment combinations ($F_{4,60}$=2.7035, p=0.035) (Figure 7).

Partitioning of overall ant diversity showed that the turnover of ant species generated by different fire regimes (β3) was significantly greater than expected by chance (p<0.001). In contrast, the turnover of species among plots of the same fire regime (β2) was not different from expected (p = 0.492), whereas the turnover of species among sampling points within plots (β1) was smaller than expected (p<0.001). The contribution of the point diversity (α) was also significantly higher than expected (p<0.001). (The turnover of ant species generated by different fire regimes contributed with nearly half (42%) of the total observed species richness (γ diversity) (Figure 8). The remaining diversity components, α1, β1 and β2, contributed respectively with 7.4%, 24.1% and 26.5% of the total observed species richness.

Discussion

Effects of fire frequency

Ants from a wide variety of ecosystems often exhibit a global pattern of resistance and/or resilience to fire, showing no or only little changes in species richness, abundance and composition (reviewed in Lach *et al.* 2010). Here, in contrast, ant species richness and composition showed a clear response to changes in the frequency of burning. In particular, there was a significant reduction in ant species richness in unburned sites when compared to the M2 and M4 treatments and a clear separation of community composition between all fire frequency treatments. However, plots burned bi-annually or quadri-annually presented comparable levels of species richness for all ants and for each foraging/nesting stratum. Lach and coauthors (2010) argued that in flammable ecosystems, changes in species richness and community composition are marked when unburned areas are compared to frequently burned ones (Andersen *et al.* 2006) with little changes between different fire treatments (Parr *et al.* 2004). We found similar results, as fire suppression clearly affected both species richness and composition of the ant community.

Contrary to the expected (hypothesis iii) the major change in species richness occurred not with an intensification of the regime, but rather with the suppression of the disturbance factor. Unburned plots presented the highest density of woody plants and the lowest average tree size. In addition, unburned plots had lower temperatures, a much smaller grass cover, and a greater accumulation of leaf-litter than the burned plots (J. Maravalhas, pers. obs.), *i.e.* the unburned plots were showing signs of an ecosystem shift from savanna to forest. Animal diversity generally increases with habitat complexity (Tews *et al.* 2004) and the same seems true for ants (Ribas *et al.* 2003; Sarty *et al.* 2006; Klimes *et al.* 2011). However, in spite of the higher habitat complexity in the unburned plots, we found less ant species there than in the structurally simpler burned plots. Ant diversity may be negatively correlated to habitat structure, e.g. in Australian woodland where sites with higher complexity were also highly homogeneous in a larger scale, while simpler sites exhibited higher variation in structure among them (Lassau and Hochuli 2004). It may be the case that highly complex and undisturbed habitats in the Cerrado are more homogeneous at a broader spatial scale and thus supports less ant species. Alternatively or in addition, the low richness of ants found in the unburned plots may be related to the fact that fire suppression is a form of habitat change of the cerrado, transforming a savanna into a forest (Moreira 2000; Geiger *et al.* 2011). Ants are thermophilic organisms (Hölldobler and Wilson 1990; Lach *et al.*2010) so cooler temperatures are probably stressful for most ants in the species pool of the Cerrado, a sunny, fire-prone landscape for several million years (Simon *et al.* 2009).

Nevertheless, the reduced species richness in control plots should be viewed with caution, since only one sampling method was used. The leaf-litter is an ideal stratum for many ant species (Hölldobler and Wilson 1990) which are appropriately collected with leaf-litter extractors (Andersen *et al.* 2002). In an African savanna undergoing woody encroachment, for instance, there was a decline in open-habitat ant species, with no effect on richness (Parr *et al.* 2012). The same study, though, found a significant reduction in richness in encroached areas when only pitfall samples were considered, meaning that reduction in epigaeic species were compensated by increase in litter-dwelling species. This may be the case in this study, but we are confident with the results, as pitfall traps are widely used in studies of ant communities (Agosti *et al.* 2000) and even simplified protocols can be used to assess the impact of disturbance on these organisms (Andersen *et al.* 2002) . Moreover, Cerrado fires remove most part of the leaf-litter (Kauffman *et al.* 1994) and accumulation of this material was negligible at frequently burned plots, justifying the choice not to use this method in this study. Our findings reflect the results for other comparisons of burned vs. unburned sites. The overall abundance of arthropods was positively correlated to fire frequency in a cerrado area, though ant response depended on the feeding guild (Uehara-Prado 2010). Also, savanic formations usually harbors more ant species than forest patches in the Cerrado (Lopes and Vasconcelos 2008), the same being true in an Australian savanna (Andersen 1991; Andersen *et al.* 2006).

Both the arboreal and the epigaeic ant community composition showed clear differences between the M4 and M2 treatments. Again, tree structure did not assist in the interpretation of the differences in the ant community between fire treatments. Vertical structure is important in shaping arthropod diversity (Gardner 1995) and so is tree size and connectivity for ant species composition in the Cerrado (Powell *et al.* 2011). It is possible that subtle differences in habitat structure were influential in the composition of the ant community. Nevertheless, cerrado vegetation subjected to different frequencies of fires did not show changes in functional diversity of herbaceous plants (Loiola *et al.* 2010).

Fire frequency also determines the extent of the impact of the regime, *i.e.*, the number of fire events and the time available to recover after them. Variation in the fire-return interval had minimal effects on many taxa in an Australian savanna, including ants (Whittkuhn *et al.* 2011). Moreover, many studies on the ant community responses to different frequencies of fire did not detect changes in species richness. Community composition, though, can differ between burned and unburned plots (Andrew *et al.* 2000; York 2000) but not between burned areas with different frequencies (Parr *et al.* 2004; Vasconcelos *et al.* 2008). As was the case in our study, ant species richness in unburned savannas is lower than burned areas, irrespective of the frequency of fires. Community composition, on the other hand, showed great turnover of species both between unburned and burned sites, but also between sites burned every two or four years. This indicates that Cerrado ants may be more sensitive to changes in the fire regime compared to other fire-prone savannas.

Effects of burning period

Contrary to the expected, we did not find any differences in species richness between plots burned at the same frequency but at different periods of the year. Studies examining the effects of changes on the period of burning are much less common than the ones comparing burning frequencies. In *Pinus* forests of the USA, dormant-season fires (after leaf fall) are more intense than growing-season fires (during leaf expansion), but in spite of that no differences in tree structure or species composition were detected (Sparks *et al.* 1999). In the present study tree density was significantly lower in the L2 and M2 than in the E2 plots, but ant species richness did not followed this trend. Late-season fires caused a decline in richness and abundance of ground-dwelling beetles in an Australian savanna, but this was only detected at the wet season, when activity was higher than in the dry season (Blanche *et al.* 2001). Effects of fire on termites in savannas in Australia were also more marked in the wet than in the dry season (Davies *et al.* 2012). It is possible we could have detected differences in species richness in response to differences in the burning period if our sampling had been undertaken at both the wet and dry season. But we are confident with the completeness of our samples, evidenced by the smoothing of the accumulation curves. Besides, pitfall traps are known to be highly efficient in capturing ants in extreme dry conditions (Delsinne *et al.* 2008).

The richness patterns of the whole ant community were highly influenced by the epigaeic strata. Arboreal ants accounted for less than 30% of the species records, with about 10% of all species being unique to this stratum. Meanwhile, soil-dwelling ants had almost 50% of unique species and harbored nearly 90% of all species found in this study. This was probably due to the fact that many ant species nest on the soil but forage at both the epigaeic and arboreal strata, as observed in other cerrado ant studies (Campos *et al.* 2008; Lopes and Vasconcelos 2008). Contrary to the expected (hypothesis ii), there was little variation of arboreal richness between biennial and quadrennial mid-season treatments, Nevertheless, by contrasting different periods of burning we found a clear – though not significant – tendency of reduced richness at the late-season plots (L2). Tree density at these sites was extremely low and average tree size was medium. Sparse trees in these plots may explain the low diversity of arboreal ants, as greater canopy connectivity can increase the number of species foraging on individual trees (Powell *et al.* 2011). The lower density of trees in the L2 plots frequently forced us to sample at small trees, so reduced tree size (Powell *et al.* 2011) may also explain the tendency of less arboreal species in this treatment. Arboreal ants suffered high mortality after a single fire event in a Brazilian cerrado area, and colonies were still recovering after more than one year (Morais and Benson 1988). At the time of sampling, the L2 plots had not experienced fires for almost three years, and this suggest that the tendency of finding less arboreal species in these plots did not result from direct fire effects (on colony survival), but to fire-mediated changes in habitat structure. Late-season fires occurred in September, period when many ant species are nursing alates to fly with the onset of the rainy season (Hölldobler and Wilson 1990). Therefore even if colony survival was not affected, late-season fires may have negatively affected the reproductive investment of the colonies. If late-season burning somewhat impoverished the arboreal ant fauna, at the same time it seems to have improved the diversity of epigaeic species, given that one our L2 plots was the richest of all our 20 sampling plots. Although not very abundant, sixteen species were exclusive of the L2 treatment, including some genera not collected elsewhere, *e.g. Prionopelta, Ochetomyrmex, Pyramica* and *Nesomyrmex*. As discussed previously, hot and sunny habitats are suitable for a many ant species. Dominants, on the other hand, tend to prefer cooler, shadier conditions (Andersen 1995), where they extend the period of dominance of resources and can exclude subordinate species (Retana and Cedrá 1999; Andrew *et al.* 2000; Bestelmeyer 2000).

No significant differences were found with regard to the species composition of arboreal ants in different burning periods, also evidenced by the great overlap of plots in the nMDS ordination. Epigaeic and overall species were somewhat sensitive to changes in the period of burning, though not statistically significant. There was some separation of the plots from different treatments in the nMDS, in a similar fashion as seen in fire frequency comparisons, where the species composition changes progressively with the intensification of the regime. In this sense, the changes in the frequency and period of burning of cerrado vegetation may have a parallel effect on the ant community, though the latter seems weaker than the former. To our knowledge, no study with ant communities successfully detected responses due to differences in the period of fire. The epigaeic ant community of an African savanna was only distinguished between burned and unburned sites, no differences being detected between burning treatments (Parr *et al.* 2004). Also, there is evidence of dominance shifts with changes in the period of burning in Australian savannas (Andersen *et al.* 2007). In the Cerrado, although the burning regime is usually highlighted as an important factor in determining the fire behavior and shaping communities (Coutinho 1990; Miranda *et al.* 2002; Pivello *et al.* 2011), few studies actually tested differences between burning periods in this biome. Late-season fires seem to benefit graminoids, while forbs increased in biomass in quadrennial mid-season fire treatment (Oliveiras *et al.* 2012). Caterpillars, a common tree-dwelling organisms in the Cerrado, showed reduced species richness in areas subjected to late-season fires, being intermediate at unburned and greater in mid-season burning areas (Diniz *et al.* 2011), a somewhat opposite response than the one found presently. This brings new insights to the knowledge of long-term responses of cerrado organisms to fire and can help in the development of fire management strategies.

In contrast to what was expected (hypothesis iv), we did not find significant variation in ant species richness between burning periods. We found a greater effect of fire frequency in determining the richness and composition of ant species in the Cerrado. This indicates that the two components of the fire regime are not equally influential in shaping ant communities. Consistently across both comparisons, though, there was a more clear response of the epigaeic fauna compared to the arboreal one. Although it was expected that arboreal species would be more sensitive to changes in fire regime (hypothesis ii), our findings do not support this. It is possible that the short-term effects of fire are important mainly for arboreal species, while epigaeic species are responsive to long-term changes in the habitat structure. An appropriate comparison should test both effects simultaneously. Sessile organisms that cannot escape from the impacts of the heat from the fire front, or move to a more suitable site usually show adaptations to survive frequent burning. Cerrado plants bare thick barks, underground meristems or reserve organs and vegetative reproduction prevent individual mortality even after frequent fires (Hoffmann 1998). Survival of ground-nesting ant species is high after a single fire event, due to little changes in soil temperatures at depths under 5 cm (Miranda *et al.* 1993) and many species can even increase their activity in the post-fire habitat conditions (Farji-Brenner *et al.* 2002; Frizzo *et al.* 2012). Aerial-nesting colonies, on the contrary, can suffer high mortality after a single fire event. Recovery is fast, though, not affecting much of the community composition (Morais and Benson 1988). In the Cerrado, leaf-litter ants suffered some reduction in abundance, no changes in richness or composition, and recovery was fast following a single fire event (Vasconcelos *et al.* 2009). Thus, the perceived severity of a fire event will depend on the nesting habits of the species. Also, the response to the long term changes in the fire regime is contingent upon the habits of the species considered.

Contributions to fire management in the Cerrado

The results presented here bring new insights to the development of appropriate fire management strategies for the Cerrado. It is important to balance the costs and benefits while implementing fire policies in any Protected Area. Prescribed burning suffers high prejudice from the general public and also requires financial investments and human resources to be maintained. Moreover, it is a risky strategy, as fires can become uncontrollable and affect sites intended not to be burned, like forest patches, infrastructure of the unit or adjacent lands (Ramos-Neto and Pivello 2000). On the other hand, suppression may also result in uncontrolled fires, because of high accumulation of flammable biomass (Pivello 2011). The absence of the fire factor furthermore affects the original cerrado vegetation, transforming an open savanna into a closed forest, with negative impacts on open-habitat species (Pivello and Coutinho 1996; Moreira 2000). Before generally applying certain fire regimes in Cerrado reserves, much information is needed on the response of organisms to fire. Moreover, decisions should always be made on a regional context, considering variations in habitat type, distribution of species, climatic conditions and anthropic pressure (Pivello and Norton 1996).

Our findings indicate that fire suppression is not the best management strategy to be applied to Cerrado protected areas. Ant richness was reduced in unburned sites, both at the plot level and at the landscape level. This was especially true for epigaeic species, which had low diversity in C0 plots, probably due to the shadier conditions of these tree-dominated habitats. Conversely, in more open areas like M2 and L2 plots, epigaeic ants showed high species richness. Seven ant genera were collected uniquely in these two treatments, while C0 treatment had no unique genera. In this sense, maintaining grassy habitats in preserved cerrado areas is of crucial importance for biodiversity conservation. Implementing mid or late-season fires is an effective way of maintaining grass-dominated landscape and assuring the persistence of open-habitat species. Changes in abiotic and biotic conditions increase the probability of fires with the progression of the dry season (Pivello and Coutinho 1996; Miranda *et al.* 2002), so adopting a late-season regime is a risky choice, as fires can get out of control. The usual burning regime in the Cerrado is characterized by high-frequency mid-season fires, mainly because of optimal burning conditions and traditional land-management strategies (Coutinho 1990). Biennial mid-season fires, in this sense, may be a good management choice, as it can reduce fire risk by consuming flammable biomass and at the same time maintain a more open habitat with a high richness of ants. Early-season burning is usually used to produce firebreaks (Ramos-Neto and Pivello 2000), due to the mild and homogenous nature of these fires and the ease to control it (Coutinho 1990). In the present study, E2 plots were highly variable between themselves (both in terms of tree density and in ant species composition), indicating that this regime does not homogenize the vegetation structure as much as the mid or the late-season fires. This is an interesting result, as we would expect more species richness in more heterogeneous sites. Nevertheless, the ant community in this burning regime resembled that of unburned sites and although species richness was also high, many open-habitat species were absent in this treatment. The conservation of many epigaeic ant species would be threatened if this regime was to be solely implemented in cerrado areas.

As discussed above, ant richness was largely influenced by epigaeic species, so these treatment recommendations may not apply to species in other strata. In fact, the arboreal ant richness showed a somewhat opposed trend than that found for epigaeic species. Although ants belong to a single insect family, they are highly variable in terms of nesting sites, feeding guilds, thermal tolerance, dominance hierarchy, etc., so we expected that responses would vary between strata. Thus it is important to assess the effects of contrasting fire regimes on other organisms, so to develop management strategies that conserve the maximum diversity of various life forms (Parr *et al.* 2003; Driscoll *et al.* 2010). Besides the scarcity of studies on fire effects, the presence of this factor has been widely recognized as essential in the management of Cerrado protected areas (Ramos-Neto and Pivello 2000; Uehara-Prado *et al.* 2010; Frizzo *et al.* 2012). This is a global trend, since prescribed burning has been increasingly used in the management of protected areas on various fire-prone ecosystems (Andersen 1991; Parr *et al.* 1999; Odion and Sarr 2007; Bond *et al.* 2010). Patch mosaic burning (PMB) is a fire management system that aims to conserve maximum biodiversity in fire-prone ecosystems (Brockett *et al.* 2001). It is based on the assumption that increased spatial and temporal variability in fire regimes (pyrodiversity) will increase habitat variability and sustain more species. Although PMB was largely implemented in African and Australian savannas, Parr and Andersen (2006) argue that the costs in implementing and maintaining a mosaic of fire histories are not justifiable, since recent studies showed little variation in species richness or composition between sites of varying fire histories. We found a greater number of ant species when plots with dissimilar fire regimes were combined into potential management strategies, compared to more homogeneous combinations. The more contrasting situations, obtained by combining C0 plots with M2 or L2, yielded significantly more species than in a scenario of no dissimilarity: combining plots from the same treatment. These results suggests that – at least for the Cerrado ant community – maintaining only two highly dissimilar fire regimes may be enough to maximize species conservation in a certain area.

So is it worth it to invest in PMB practices in the Cerrado? High ant diversity was obtained with just two contrasting regimes, a more feasible strategy to be applied in Cerrado reserves compared to the large costs associated to the maintenance of small grain mosaics of vegetation with different fire histories. Unburned areas could create habitat variability by maintaining patches of closed habitats and allowing the persistence of forest-associated species. Mid-season fires could maintain habitat openness and at the same time remove biomass and prevent uncontrolled fires, buffering zones of fire protection. Similarly to other savannas (Parr and Andersen 2006) the costs of PMB may not be justifiable in the Cerrado, as simpler strategies may obtain similar richness values, but further research must be done before any conclusion is made. In the present study, nevertheless, fire treatments maintained for 15 years produced a great variability in habitats, ranging from unburned woody sites to frequently burned grasslands. This fire-maintained mosaic of habitats was responsible for a major species turnover that accounted for nearly half of the 165 ant species collected. Even though information about the effects of long-term fire regimes in the Cerrado biota is scarce, the results for the ant community highlight the importance of fire for the persistence of the high diversity in this ecosystem. We recommend that fire policies should maintain habitat variability and that fire regime diversity is important to maximize overall diversity or organisms. An appropriate fire policy for the Cerrado must be developed with the integration of knowledge from various sources (Pivello and Norton 1996). The millenary knowledge of traditional populations on the use of different fire regimes should not be neglected (Mistry *et al.* 2005, Pivello 2011). Experience from managers of protected areas is also crucial for developing a realistic fire management strategy (Parr and Andersen 2006). Finally, we urge the need for more observational and experimental information on the short and long-term effects of burning in cerrado ecosystems and its organisms (revised by Frizzo *et al.* 2011).

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List of figures and tables

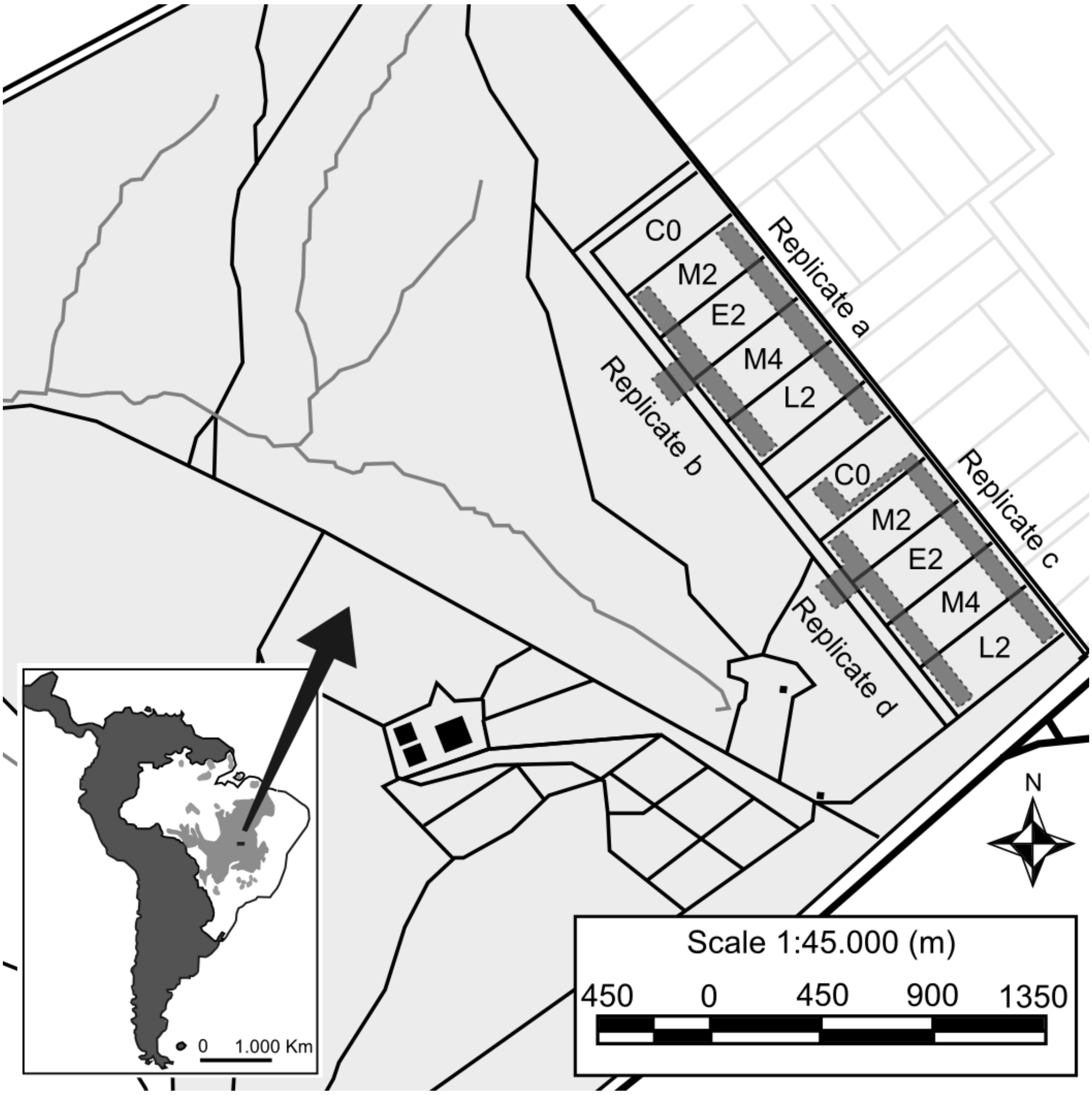


Figure 1. Map showing the 10 original experimental sections of the “Fire Project” (*Efeitos de diferentes regimes de queima sobre a estrutura das comunidades de Cerrado, Projeto Fogo*) at the *Reserva Ecológica do IBGE* (light gray), in Brasilia, Brazil. Ant sampling took place within the dark gray areas, which were arranged in four replicates (a - d) each containing five fire treatments: control, unburned (C0), burned every four years during the middle of the dry season (M4), and burned every two years early (E2), in the middle (M2), or late (L2) during the dry season. One of the original control plots (C0) was not sampled because it was accidentally burned in 2005. Two new control sampling plots were then established in adjacent, unburned sites. The South America map shows the distribution of the Cerrado biome in Brazil (light gray; adapted from Ratter *et al.* 1997), with Brasilia highlighted as a dark spot in the center.

Control (C0)

Burning period: none
Frequency (prescribed fires): none (0)
Note: complete fire suppression, is applied to most Cerrado Conservation Units; may onset woody encroachment, with loss of grassy species and complete ecosystem shift;
Time since last fire: ~37 years.

Mid-quadrennial (M4)

Burning period: middle of August (mid-season);
Frequency (prescribed fires): four years (5);
Note: although mid-season fires are harsh, this treatment can benefit trees because the long fire-return interval prevents mortality;
Time since last fire: four years.

Early-biennial (E2)

Burning period: end of June (early-season);
Frequency (prescribed fires): two years (9);
Note: hazard-reducing treatment, remove flammable biomass and promotes plant resprouting, increasing resource availability for animals during the dry season;
Time since last fire: three years.

Mid-biennial (M2)

Burning period: middle of August (mid-season);
Frequency (prescribed fires): two years (9);
Note: mimics anthropogenic fires, the most common regime in the Cerrado; tree mortality is moderate, but fires may be difficult to control due to extreme dry conditions;
Time since last fire: three years.

Late-biennial (L2)

Burning period: end of September (late-season);
Frequency (prescribed fires): two years (9);
Note: probably the harshest regime, destroys the investment of trees in vegetative growth, favoring grasses; fires are intense, homogeneous and spatially extent;
Time since last fire: three years.

Figure 2. Image and description of the different fire treatments. Prescribed fires were set at the *Reserva Ecológica do IBGE,* in Brasilia, Brazil, between 1992 and 2009.

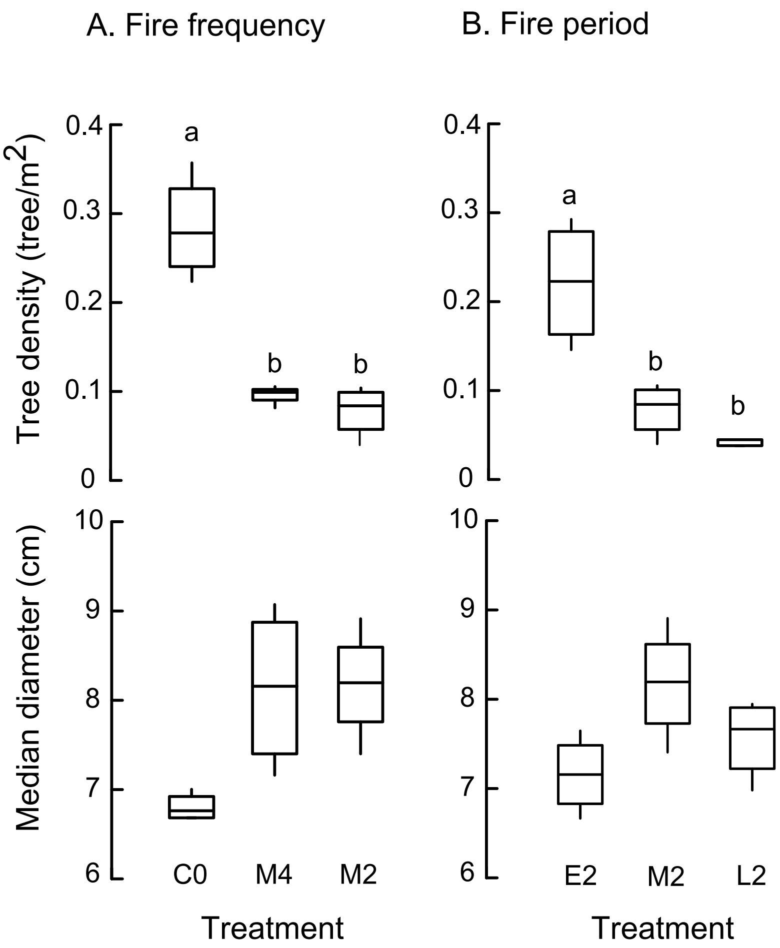


Figure 3. Effects of (A) fire frequency and (B) fire period on the structure of the arboreal vegetation. Box-plots show the density of trees and the median trunk diameter (30 cm above soil level) of all trees ≥ 5 cm found in 200 m^2 plots (n =3 per treatment). Fire frequency treatments were: unburned (C0), or burned during the middle of the dry season at two (M2) or four (M4) year intervals. Fire period treatments included biennial fires set early (E2), in the middle (M2), or late (L2) during the dry season.

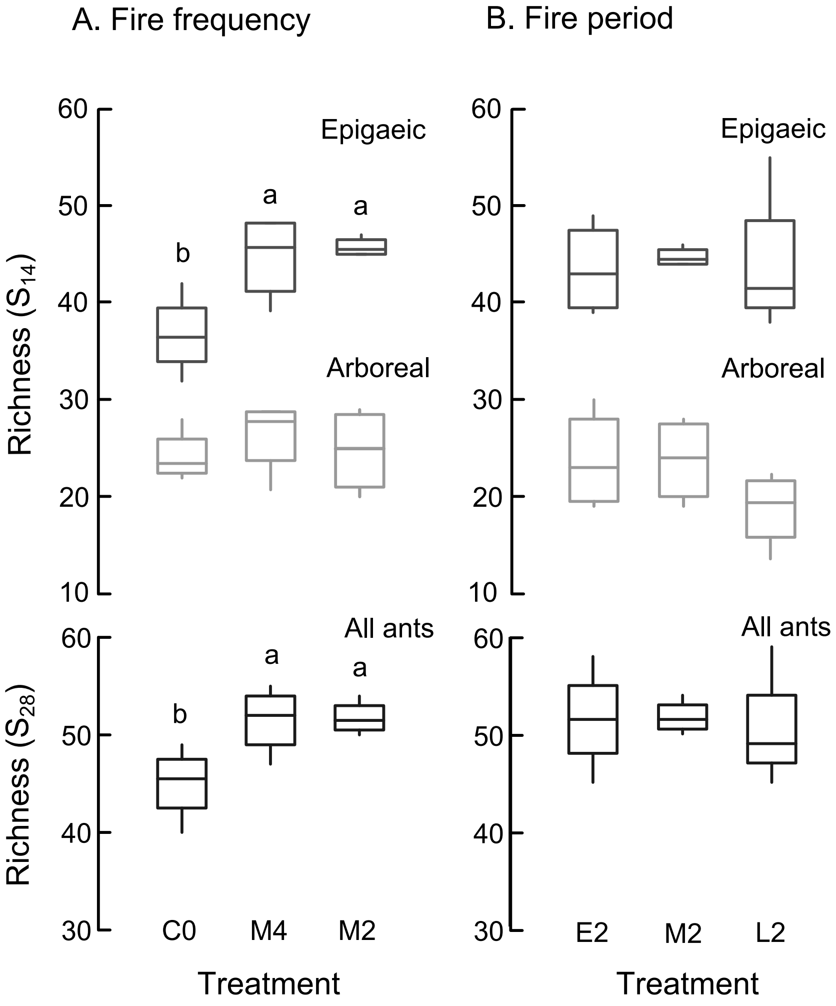
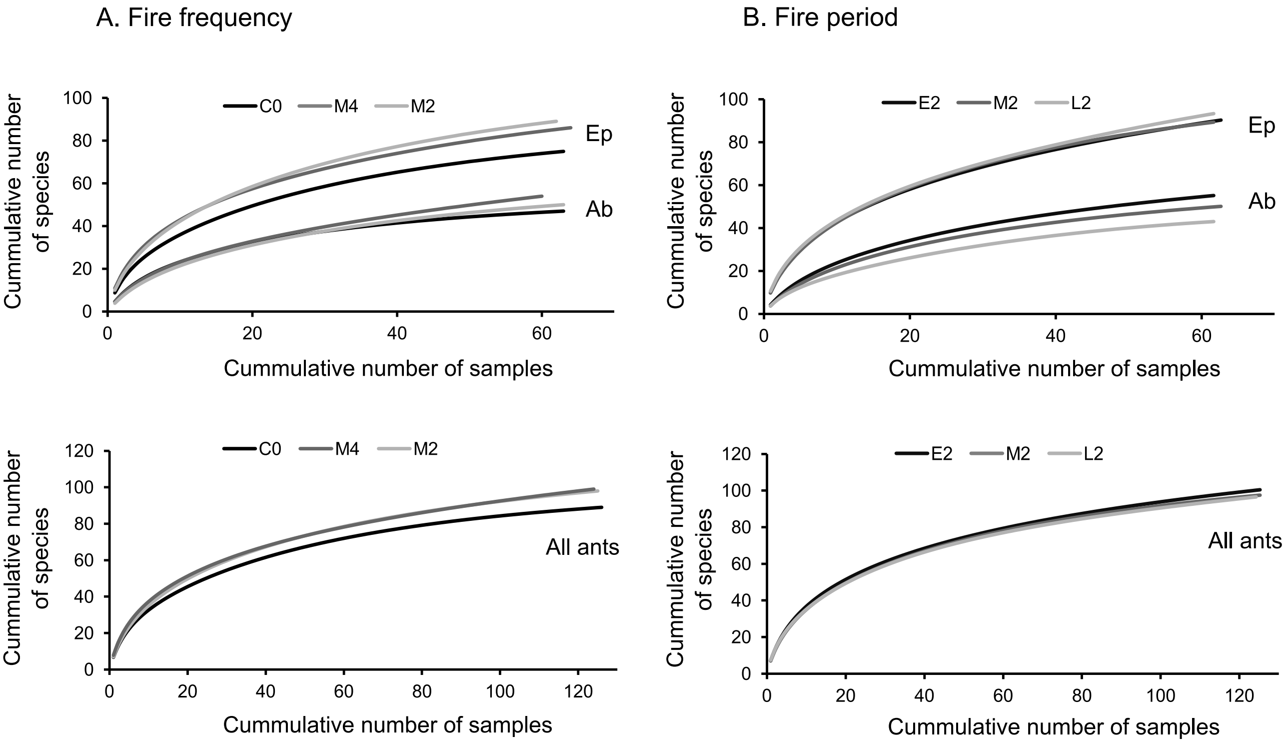


Figure 4. Effects of (A) fire frequency and (B) fire period on the species richness of arboreal and epigaeic ants. Species richness represent the number of species found in 14 arboreal samples, in 14 ground samples, or in the 28 samples combined (*n* = 4 set of samples per treatment). Fire frequency treatments were: unburned (C0), or burned during the middle of the dry season at two (M2) or four (M4) year intervals. Fire period treatments included biennial fires set early (E2), in the middle (M2), or late (L2) during the dry season.



A. Fire frequency

B. Fire period

Figure 5. Sample-based species accumulation curves (Mao Tau function) of the number of arboreal and epigaeic ants found in plots subject to different (A) fire frequency or (B) fire period treatments. Fire treatment abbreviations as in Figure 3 and 4.

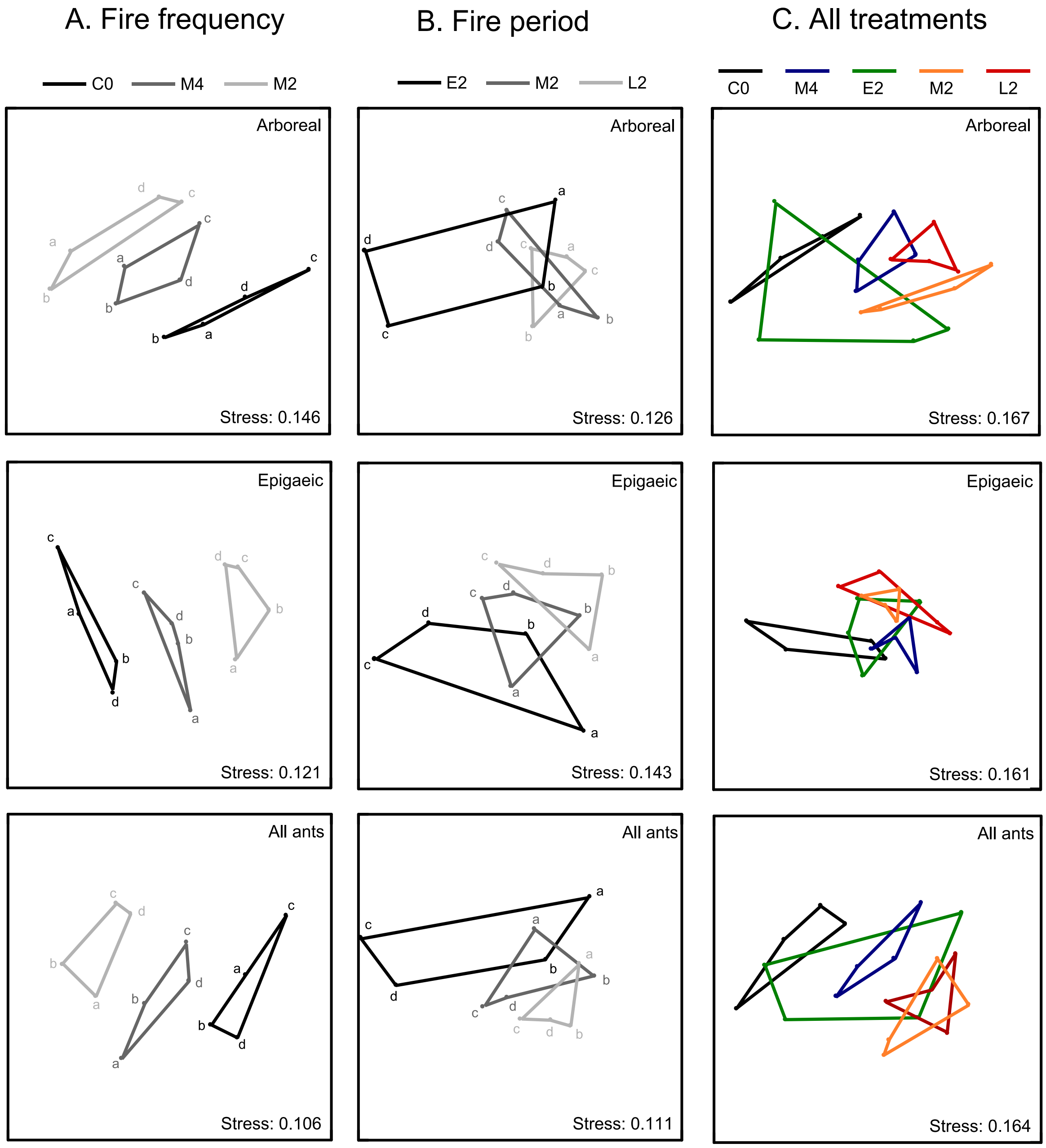


Figure 6. Non-metric Multi-Dimensional Scaling (nMDS) ordination plots showing the effects of (A) fire frequency and (B) fire period on the species composition of arboreal and epigaeic ants, as well as the ordination of (C) all regime treatments together. Letters represent plots within different blocks, except in C, where they were suppressed for better visualization. Stress of the final nMDS configuration is shown at the lower right side of the plots. Fire treatment abbreviations as in Figure 3 and 4.

Table 1. Indicator species of different fire-frequency or fire-period treatments. The Indicator Values (IndVal) and the fire treatment to which the species was associated are shown. P values < 0.05 indicate a significant association of a species to a fire treatment Fire frequency treatments were: unburned (C0), or burned during the middle of the dry season at two (M2) or four (M4) year intervals. Fire period treatments included biennial fires set early (E2), in the middle (M2), or late (L2) during the dry season.

Species	Fire treatment	IndVal (%)	p
Fire frequency			
Brachymyrmex patagonicus	C0	58.9	0.0458
Camponotus arboreus	C0	70.2	0.0252
Camponotus renggeri	C0	73.6	0.024
Camponotus sp.13	C0	92	0.0062
Cephalotes pusillus	C0	50.2	0.046
Hylomyrma sp.1	C0	90.7	0.0062
Camponotus sp.26	M4	63.6	0.0278
Camponotus sp.5	M2	49.2	0.0262
Crematogaster sp.2	M2	65.4	0.041
Ectatomma planidens	M2	83.4	0.0228
Pheidole oxyops	M2	43.5	0.0008
Pheidole sp.13	M2	63.5	0.0182
Fire period			
Brachymyrmex patagonicus	E2	72.9	0.0116
Cephalotes pusillus	E2	54.8	0.0426
Crematogaster sp.1	E2	74.3	0.0718
Camponotus crassus	M2	37.3	0.0654
Camponotus sp.15	M2	66.9	0.0178
Camponotus sp.23	M2	74.9	0.0248
Apterostigma sp.1	L2	73.4	0.0074
Atta laevigata	L2	78.1	0.0128
Cephalotes depressus	L2	46.9	0.02
Pheidole sp.21	L2	64.3	0.0306

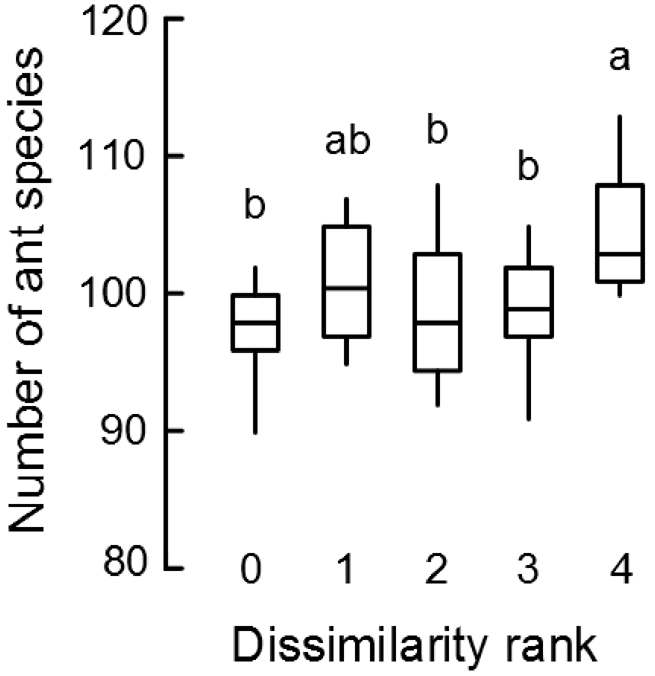


Figure 7. Number of ant species recorded using a combination of fire treatments in groups of four plots, each representing a potential fire management strategy. Different letters above the bars represent a significant difference in number of ant species. There was an increasing level of dissimilarity between plots within strategies, 0 being the lowest, as treatments were combined within themselves (C0, M4, M2, E2 or L2). Levels 1 - 4 represent groups of two treatments combined, and dissimilarity scores were determined by visual examination of the dissimilarity in species composition between the combined treatments.

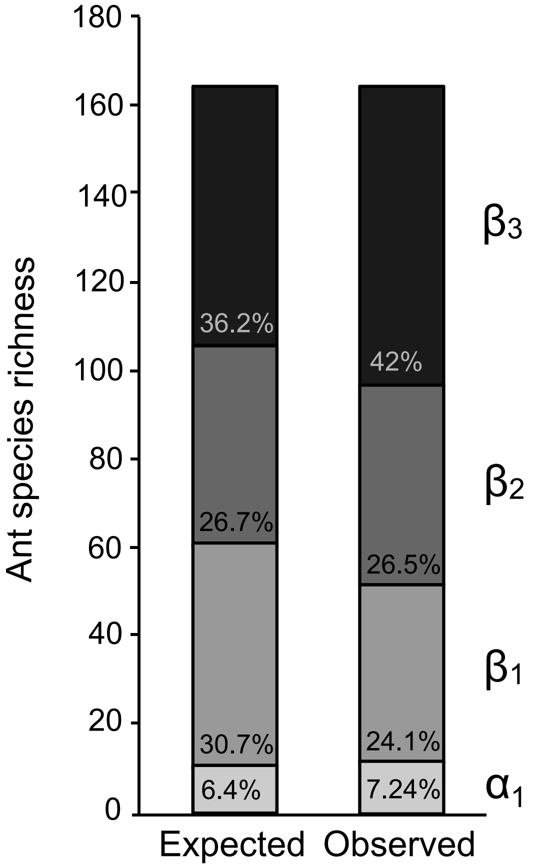


Figure 8. Additive partitioning of total ant species richness into their alpha and beta components. α1 is the species richness at the sampling points, β1 represents beta diversity due to species turnover among sampling points within the same plot, β2 represents the turnover of species among plots of the same fire treatment, whereas β3 reflects the turnover of species among different fire treatments. Shown are observed values and expected values generated through 1,000 randomizations of the dataset

Table 2. Mean richness (standard deviation) of arboreal, epigaeic and total ant species and results from the ANOVA (species richness) and PERMANOVA (community composition) comparisons between treatments of varying (A) frequency and (B) period of burning. P values < 0.05 (in bold) were considered significant.

A. Fire frequency

	Mean richness (sd)			ANOVA		PERMANOVA	
	C0	M4	M2	$F_{2,9}$	p	$F_{2,9}$	p
Ab	24.25 (2.63)	26.5 (3.79)	24.74 (4.42)	0.41	0.675	1.67	**0.036**
Ep	36.75 (4.11)	44.5 (4.36)	45.75 (0.96)	7.74	**0.011**	2.07	**0.001**
All	45 (3.74)	51.5 (3.40)	51.75 (1.71)	6.15	**0.021**	2.07	**0.003**

B. Fire period

	Mean richness (sd)			ANOVA		PERMANOVA	
	E2	M2	L2	$F_{2,9}$	p	$F_{2,9}$	p
Ab	24.75 (5.19)	24.74 (4.42)	19.75 (3.59)	1.68	0.239	1.23	0.185
Ep	44.5 (4.79)	45.75 (0.96)	45 (7.53)	0.06	0.943	1.38	0.071
All	51.5 (5.32)	51.75 (1.71)	50.5 (5.97)	0.078	0.925	1.37	0.095

Ab: arboreal ants
Ep: epigaeic ants
All: both strata combined

E2: early-season biennial
M2: mid-season biennial
L2: late-season biennial

C0: control
M4: mid-season quadrennial

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Appendix

SUBFAMILY Species	Total occurences	Occurence in each stratum (%)	
		Arboreal	Epigaiec
AMBLYOPONINAE			
Prionopelta sp.1	2	-	100.0
DOLICHODERINAE			
Azteca sp.1	32	62.5	37.5
Azteca sp.2	19	57.9	42.1
Dolichoderus sp.1	10	80.0	20.0
Dorymyrmex sp.1	3	-	100.0
Forelius sp.1	1	-	100.0
Linepithema aztecoides	4	-	100.0
Linepithema micans	115	7.8	92.2
Linepithema sp.04	7	-	100.0
Tapinoma sp.1	1	100.0	-
Tapinoma sp.2	3	100.0	-
ECITONINAE			
Labidus sp.1	20	20.0	80.0
Labidus sp.2	10	-	100.0
Nomamyrmex sp.1	1	-	100.0
Nomamyrmex sp.2	2	-	100.0
ECTATOMMINAE			
Ectatomma bruneus	2	-	100.0
Ectatomma edentatum	103	-	100.0
Ectatomma lugens	13	-	100.0
Ectatomma permagnum	27	-	100.0
Ectatomma planidens	17	-	100.0
Gnamptogenys sp.1	7	-	100.0
FORMICINAE			
Brachymyrmex sp.1	78	12.8	87.2
Brachymyrmex sp.2	5	20.0	80.0
Brachymyrmex sp.3	3	33.3	66.7
Brachymyrmex sp.4	13	-	100.0
Brachymyrmex sp.5	8	-	100.0
Brachymyrmex sp.6	2	-	100.0
Brachymyrmex sp.7	3	-	100.0
Camponotus crassus	328	28.0	72.0
Camponotus sp.1	34	50.0	50.0
Camponotus sp.2	77	35.1	64.9
Camponotus sp.3	45	15.6	84.4
Camponotus sp.4	158	23.4	76.6
Camponotus sp.5	196	43.9	56.1
Camponotus sp.6	165	60.0	40.0

appendix 1. continued

Camponotus sp.7	40	57.5	42.5
Camponotus sp.8	2	100.0	-
Camponotus sp.9	17	23.5	76.5
Camponotus sp.10	44	9.1	90.9
Camponotus sp.11	19	47.4	52.6
Camponotus sp.12	23	17.4	82.6
Camponotus sp.13	36	30.6	69.4
Camponotus sp.14	8	62.5	37.5
Camponotus sp.15	16	37.5	62.5
Camponotus sp.16	10	90.0	10.0
Camponotus sp.17	2	50.0	50.0
Camponotus sp.18	3	100.0	-
Camponotus sp.19	2	50.0	50.0
Camponotus sp.20	2	50.0	50.0
Camponotus sp.21	22	45.5	54.5
Camponotus sp.22	1	-	100.0
Camponotus sp.23	2	-	100.0
Camponotus sp.24	45	33.3	66.7
Camponotus sp.25	1	-	100.0
Camponotus sp.26	3	66.7	33.3
Camponotus sp.27	2	50.0	50.0
Myrmelachista sp.1	15	73.3	26.7
Nylanderia sp.1	2	100.0	-
Nylanderia sp.2	28	-	100.0
Nylanderia sp.3	2	-	100.0
Nylanderia sp.4	4	-	100.0
MYRMICINAE			
Attini			
Acromyrmex sp.1	1	-	100.0
Apterostigma sp.1	21	4.8	95.2
Apterostigma sp.2	1	-	100.0
Atta laevigata	51	5.9	94.1
Cyphomyrmex sp.1	1	-	100.0
Cyphomyrmex sp.2	9	-	100.0
Cyphomyrmex sp.3	6	-	100.0
Cyphomyrmex sp.4	1	-	100.0
Mycocepurus sp.1	101	-	100.0
Mycocepurus sp.2	22	4.5	95.5
Nov. gen	1	-	100.0
Trachymyrmex sp.1	2	-	100.0
Trachymyrmex sp.2	5	-	100.0
Trachymyrmex sp.3	7	-	100.0
Trachymyrmex sp.4	3	-	100.0
Trachymyrmex sp.5	1	-	100.0
Carebara sp.1	1	-	100.0

appendix 1. continued

Cephalotes atrattus	63	61.9	38.1
Cephalotes grandinosus	7	85.7	14.3
Cephalotes persimilis	26	57.7	42.3
Cephalotes sp.1	245	55.1	44.9
Cephalotes sp.2	214	43.9	56.1
Cephalotes sp.3	1	100.0	-
Cephalotes sp.4	3	100.0	-
Cephalotes sp.5	4	100.0	-
Cephalotes sp.6	6	66.7	33.3
Cephalotes sp.7	33	54.5	45.5
Cephalotes sp.8	2	100.0	-
Crematogaster sp.1	81	54.3	45.7
Crematogaster sp.2	46	8.7	91.3
Crematogaster sp.3	6	66.7	33.3
Crematogaster sp.4	1	100.0	-
Crematogaster sp.5	1	-	100.0
Crematogaster sp.6	3	-	100.0
Hylomyrma sp.1	7	85.7	14.3
Megalomyrmex sp.1	1	-	100.0
Nesomyrmex sp.1	3	100.0	-
Nesomyrmex sp.2	10	-	100.0
Ochetomyrmex sp.1	1	-	100.0
Oxypoecus sp.1	1	-	100.0
Pheidole sp.1	183	12.6	87.4
Pheidole sp.2	302	17.5	82.5
Pheidole sp.3	133	5.3	94.7
Pheidole sp.4	216	23.1	76.9
Pheidole sp.5	27	29.6	70.4
Pheidole sp.6	15	20.0	80.0
Pheidole sp.7	8	37.5	62.5
Pheidole sp.8	91	17.6	82.4
Pheidole sp.9	30	3.3	96.7
Pheidole sp.10	76	11.8	88.2
Pheidole sp.11	2	-	100.0
Pheidole sp.12	3	-	100.0
Pheidole sp.13	16	-	100.0
Pheidole sp.14	14	-	100.0
Pheidole sp.15	1	-	100.0
Pheidole sp.16	1	-	100.0
Pheidole sp.17	12	-	100.0
Pheidole sp.18	1	-	100.0
Pheidole sp.19	3	-	100.0
Pheidole sp.20	3	-	100.0
Pheidole sp.21	4	-	100.0
Pogonomyrmex sp.1	2	-	100.0

appendix 1. continued

Pyramyca sp.1	1	-	100.0
*Solenopsis*sp.1	81	13.6	86.4
*Solenopsis*sp.2	29	41.4	58.6
*Solenopsis*sp.3	7	28.6	71.4
*Solenopsis*sp.4	3	-	100.0
*Solenopsis*sp.5	1	-	100.0
*Solenopsis*sp.6	1	-	100.0
*Solenopsis*sp.7	2	-	100.0
*Solenopsis*sp.8	1	-	100.0
*Solenopsis*sp.9	16	6.3	93.8
*Solenopsis*sp.10	1	-	100.0
Wasmannia sp.1	11	45.5	54.5
Wasmannia sp.2	17	-	100.0
Wasmannia sp.3	1	-	100.0
Xenomyrmex sp.1	1	100.0	-
PONERINAE			
Dinoponera australis	10	-	100.0
Hypoponera sp.1	1	-	100.0
Hypoponera sp.2	1	-	100.0
*Odontomachus*sp.1	20	-	100.0
*Odontomachus*sp.2	1	-	100.0
*Odontomachus*sp.3	1	-	100.0
Pacycondyla verenae	19	-	100.0
Pachycondyla sp.1	19	63.2	36.8
Pachycondyla sp.2	17	-	100.0
Pachycondyla sp.3	10	-	100.0
Pachycondyla sp.4	1	-	100.0
Pachycondyla sp.5	1	-	100.0
PSEUDOMYRMECINAE			
Pseudomyrmex sp.1	129	98.4	1.6
Pseudomyrmex sp.2	3	100.0	-
Pseudomyrmex sp.3	12	33.3	66.7
Pseudomyrmex sp.4	15	93.3	6.7
Pseudomyrmex sp.5	2	100.0	-
Pseudomyrmex sp.6	4	100.0	-
Pseudomyrmex sp.7	3	100.0	-
Pseudomyrmex sp.8	7	57.1	42.9
Pseudomyrmex sp.9	1	100.0	-
Pseudomyrmex sp.10	7	-	100.0
Pseudomyrmex sp.11	7	-	100.0

Appendix 1. List of ant species collected in plots of the “Fire Project” (*Efeitos de diferentes regimes de queima sobre a estrutura das comunidades de Cerrado, Projeto Fogo*) at the *Reserva Ecológica do IBGE*, Brasilia, Brazil.

CONCLUSÃO

Mudanças em longo prazo no regime de fogo do Cerrado claramente afetaram a comunidade de formigas tanto no solo quanto na vegetação. Embora em geral as mudanças na riqueza de espécies fossem sutis entre os tratamentos, a supressão do fogo teve efeito considerável na riqueza de formigas epigéicas. Em parcelas controle a riqueza de espécies foi sempre menor quando comparada a parcelas queimadas, independente do tratamento de fogo. A composição da comunidade de formigas, por outro lado, diferiu marcadamente não só entre áreas queimadas e não queimadas, como também entre os diferentes tratamentos. Essas diferenças foram mais expressivas quando comparando os níveis de freqüência de fogo, já que esta influenciou tanto a fauna de solo quanto a de vegetação. A variação no período de queima influenciou somente a composição de formigas epigéicas, embora houvesse uma tendência para menos espécies arbóreas em áreas de queima bianual tardia. Nós encontramos um maior número de espécies de formigas quando a estratégia de manejo em potencial incluía tratamentos altamente dissimilares, em especial quando áreas controle eram combinadas com áreas bianuais queimadas no meio ou fim da estação seca. Adicionalmente, quase metade das espécies de formigas coletadas no presente estudo é decorrente da troca de espécies entre os tratamentos de fogo. Isso ressalta a importância de se manter pelo menos algum nível de dissimilaridade no regime de fogo na escala da paisagem. Estes resultados são de grande importância para compreender as respostas da comunidade de formigas a diferentes regimes de queima no Cerrado, além de contribuir para o desenvolvimento de estratégias de manejo do fogo em áreas preservadas do bioma Cerrado.