



RESEARCH ARTICLE - ANTS

Availability of Food and Nesting-sites as Regulatory Mechanisms for the Recovery of Ant Diversity After Fire Disturbance

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Abstract

Nest-site is an important resource for cavity-nesting ants, what limits colony establishment and structures ant community composition through competition. In ecosystems frequently disturbed by fire continuous establishment of new colonies is crucial to the process of natural succession. Based on this perspective, we tested the hypothesis that fire reduces the amount of cavities for nesting (e.g., hollow branches, dry leaves curled, and galls), with negative impact on ant biodiversity. We searched for natural cavities and added artificial-nests to assess the occupancy rate and its consequences for colony growth. We also evaluated the availability of food sources for ants (EFN plants, honeydew-hemipterans and preys). We found that burned areas had less diverse and structurally simple vegetation. The occupation of natural and artificial nests was the same between the areas, but the reduced availability of nesting-sites in the burned area indicates higher limitation after the fire. This effect was even stronger in foliage habitat compared to the ground. In fact, most of the 11 cavity-nesting species found were typically arboreal. Species richness was lower in burned area, possibly due to lower nesting-sites availability, but the abundance was higher, which may be explained by the greater availability of food resources, mainly EFN-bearing plants. The high food availability may also explain the bigger colony size in burned area, since nectar and honeydew boosts colony growth and low richness prevents competition. In summary, our results show that changes in the availability of nesting sites and food resources may be key mechanisms by which fire changes the ant fauna, specifically cavity-nesting ants in the Brazilian Savanna.

Introduction

Food sources and nesting-sites are important factors limiting the development of ant colonies (McGlynn, 2006; Peeters & Molet, 2010). This limitation reduces the population growth and changes the species composition of the community (McGlynn, 2006; Shik & Kaspari, 2010). The availability of nesting-sites is particularly important for species that nest in hollow twigs, the cavity-nesting ants (Ribas et al., 2003; Philpott & Foster, 2005; Houdeshell et al., 2011). On the ground, these ants use cavities in dead branches or trunks, and curled dry leaves to nest (Kaspari, 1996; Philpott & Foster, 2005; Friedrich & Philpott, 2009). While in the foliage, living and dead hollow

twigs, and domatias are the main nesting-sites (Philpott & Foster, 2005; Rico Gray & Oliveira, 2007; Friedrich & Philpott, 2009). The durability of these nesting-sites is low in both habitats, leading to constant migrations of ant colonies (Sagata et al., 2010). This dynamic colonization makes the amount, size, availability and diversity of nesting-cavities important limiting factors of ant distribution (Sagata et al., 2010).

Environmental disturbances, such as fire, increase the effect of the limiting factors of ant diversity and distribution (Philpott & Foster, 2005; Lach et al., 2010). Fire removes vegetation, destroys the litter layer (important habitat for ants), reduces the availability of prey, alters the chemical composition of the soil and enhances the effect of stressful



climatic conditions (Mistry, 1998; Lach et al., 2010; Frizzo et al., 2011). In fact, fire reduces the availability of nesting-sites leading to loss of ant diversity (Philpott & Foster, 2005; Friedrich & Philpott, 2009). This is particularly harmful for species of tree-dwelling ants, that require branches and trunks to build its nests, and ground-dwelling ants that nest in hollow cavities (i.e. leaves and twigs; Friedrich & Philpott, 2009). Thus, in recently burned areas, one can predict that the availability of nesting-sites can be a limiting factor for recovery of the ant fauna, once species that require specific locations for nests cannot colonize (Morais & Benson, 1988).

The cavity-nesting species may be the main group affected by the fire because they lose their habitat, forage areas and their nesting-site, which are often specific (Yamamoto & Del-Claro, 2008; Houdeshell et al., 2011). Nesting-sites may be a limiting factor for ant diversity when: a) ants occupy high proportion of available nesting-sites; b) ants occupy artificial-nests introduced in the environment, which reflects a saturation of natural nesting-sites; and c) when ants compete for nesting-sites and steal cavities of other ants (Byrne, 1994; Philpott & Foster, 2005; Sagata et al., 2010; Houdeshell et al., 2011). However, knowledge about nesting-site limitation remains scarce (Philpott & Foster, 2005; Houdeshell et al., 2011).

Recent studies have shown that, in general, fire reduces the ant richness and abundance (Vasconcellos et al., 2009; Lach et al., 2010; Frizzo et al., 2011). However, the mechanisms behind the effect of such disturbances on community structure have received little attention (Andersen et al., 2006; Houdeshell et al., 2011). In this study, we tested the hypothesis that fire regulate ant diversity changing food and nest-site availability. We predict that the reduction in vegetation diversity and structure (i.e. size) caused by fire leads to a reduced number of nesting-sites in burned areas. We also predicted, that new cavities will be more intensely and quickly occupied by ants in burned areas. We tested it using artificial nests as proposed by Friedrich and Philpott (2009). Moreover, we tested the hypothesis that colonies in burned areas grow less, due to reduced availability of food resources. At last, we hypothesized that nest-site occupancy may reflect in higher colonization success, thus, we predict that ant species with higher occupancy rate would present higher local abundance.

Materials and Methods

Study area

We performed this study in an area of rocky montane Savanna, known as Rupestrian Fields (*Campos rupestres*, Alves et al., 2014) between October 2012 and February 2013. The area belongs to the Parque Estadual do Itacolomi (PEIT) (20°22'30" S and 43°32'30" W), located in Ouro Preto city, in the state of Minas Gerais, Brazil. Rupestrian Fields are a type of Cerrado ecosystem, the Brazilian Tropical Savanna, composed of wet grass fields with patches of shrubs;

the vegetation grows in quartzite or iron rock outcrops in elevation higher than 1000m (Giulletti et al., 1997; Alves et al., 2014). The climate in PEIT is temperate humid with 1700 mm of mean annual rainfall and mean annual temperature of 18.5° (Giulletti et al., 1997). To perform the study, we used two sites within a Rupestrian Field area (proximately 10 ha), one area burned eighteen months prior the experiments (hereafter burned area) and one unburned area (hereafter control area). Fire events are very common in the Brazilian Savanna directly interfering in biodiversity and interactions (Alves-Silva & Del-Claro, 2014). Rupestrian Fields, as well as the Brazilian Cerrado, is often disturbed by fire (Kolbek & Alves, 2008; Alves et al., 2014). In fact, it is an ecosystem with many plant species adapted to resist fire (Rapini et al., 2008). Therefore, a suitable environment for studying the impacts of fire on biodiversity both due to recurrence of fire (increased by human activity) but also because of the urgency of conservation (Jacobi & Carmo, 2008; Alves et al., 2014).

Effects of fire in the environment

We started by evaluating the effect of fire in the environment in October of 2012. We drew one 300x1m transect in the burned area and one in the control area to evaluate differences in the vegetation. We identified all shrubs inside the transect line. Additionally, we used one at each 10m in the transect line to evaluate differences in plant morphology (30 shrubs total). We measured plant height, crown diameter and number of branches. We also evaluated differences in the food availability. Thus so, using the same transects, we quantified the number of plants with extrafloral nectaries (EFNs) and honeydew-producer hemipterans, since nectar and honeydew are important items in ant diet in the Brazilian Tropical Savanna (Del-Claro & Torezan-Silingardi, 2009; Lach et al., 2010; Byk & Del-Claro, 2011; Lange & Del-Claro, 2014). Additionally, we used pitfall traps to evaluate the number of preys available for ants. We draw four 20x1m transects separated by 5m. In each transect we installed a pitfall trap every 5 m, one in the ground and one in the foliage (1m height). The pitfall consists of a 20 mL cup with 3 cm diameter filled with a solution of water, salt (5%) and a few drops of detergent to break the water tension. The pitfalls remained on the field for 96 hours. After that, the arthropods collected were separated in ants and non-ants specimens. From the last group, we quantified potential ant preys by counting all Coleoptera, Hemiptera, Diptera, Collembola and larvae sampled. We used the ants sampled to quantify ant diversity by abundance and richness.

Natural-nests sampling

We searched in the field for cavity-nests and identified the ant species found in these nests. We searched the nests in three 100x1m transects in each area by scouring the litter on

the ground and searching for hollow twigs and curled leaves; we also assessed the foliage to search for live or dead hollow twigs, domatias and abandoned galls. All twigs were broken and considered as occupied by a colony when we found brood, workers or queens. Sometimes we could not assure the presence of a queen, but we considered as a colony whenever at least brood was present (Friedrich & Philpott, 2009). Then, we quantified the number of nesting-sites occupied and collected some individuals for taxonomic identification. We used this information to separate the ants collected by the pitfalls in cavity-nesting ants and other ants (those not found nesting in cavities).

Artificial-nests sampling

We evaluated the limitation of nesting-sites using artificial nests to quantify the number of occupied artificial-nests (new nests formed) as well as the size of the established colony (number of individuals, *sensu* Friedrich & Philpott, 2009). In each area, we draw two transects of 100m separated by 500m. We installed one artificial nest in the soil and one in the vegetation 10m apart (1.5 m height; total of 40 nests per area). The artificial nest constituted of Falcon® test tubes of 30mL, with 10cm length and 2cm diameter, to mimic a cavity, lined inside with a 10x10cm paper cardboard to keep dark, and a cotton ball in the tube bottom to keep moisture. The height and diameter of the tube were chosen to maximize the efficiency of the trap, reducing the sampling effort by dismissing inefficient types of artificial-nests (Philpott & Foster, 2005; Cobb et al., 2006; Friedrich & Philpott, 2009). There is no difference in results compared to artificial-nests made with bamboo (natural materials) or test tubes (artificial material), considering the pipe size used in this study (Friedrich & Philpott, 2009). Since we are not testing preferences for types of nests, in fact we wanted to reduce this effect, we preferred to use plastic tube for standardization of artificial-nests.

Artificial nests remained in the field for four months (Philpott & Foster, 2005; Friedrich & Philpott, 2009) during the rainy season (October-January 2012/2013) to coincide with the period of ant's reproduction, when the establishment of new colonies is higher. The artificial-nests were placed declined (10°) so that rainwater does not accumulate inside the artificial-nests. However, this has proven to be unnecessary because the ants closed the openings of the tubes using carton material, a mixture of crushed dried plant material and saliva commonly used in building nests by arboreal ants (Hölldobler & Wilson, 1990), avoiding water entrance. At the end of the sample period, we collected the artificial-nests and then quantified the ant colonization. We also quantified the number of workers, immatures (larvae and pupae) and eggs found inside each artificial nest. For the analysis, these numbers were divided by the number of days the artificial-nest was occupied by the colony (from the queen arrival to the collection day) to remove time effect.

Data analyses

We compared the plant diversity using Diversity t-test based on Shannon index. We used multiple analysis of variance (MANOVA) to compare the size of the plants. We considered height, crown diameter and number of branches as dependent variables and the areas (burned and control) as fixed factor. We compared the number of preys between the areas and the habitats (ground and foliage) using two-way analysis of variance (ANOVA). We compared the number of EFN-bearing plants and hemipteran-host plants in the flora between the areas using Chi-square test. We compared the percentage of cavity-nesting ants (transformed by square-root arcsin), over the total ant abundance and richness per plant between the areas and habitats using two-way ANOVA. We compared the percentage of occupied natural and artificial-nests between areas and habitats using General Linear Model (GLM), accepting Binomial distribution of error and logit link function. We compared the size of the colony between the areas and the habitats using GLM with Poisson distribution and log-linear link function. We used this approach to compare the number of eggs, immature and workers per colony between the areas and habitats. We evaluated the relation between the number of nests and the local ant abundance (continuous factor) in both areas (fixed factor) using GLM, accepting Poisson distribution and log link function. All statistical tests were performed in PAST statistical software version 2.16.

Results

Effects of fire in the environment

The burned area presented less plant diversity (20 species, $H' = 2.15$) than the control area (31 species, $H' = 2.62$; Diversity t-test: $t = 2.75$; d.f. = 203.86; $p = 0.007$) even after 18 months of recovery. Moreover, the plants in the control area were higher (mean \pm standard deviation: 1.25 ± 0.37 m, $N = 30$), had more branches (77.07 ± 61.63 , $N = 30$) and wider crowns (0.7 ± 0.21 m, $N = 30$) than in burned area (0.57 ± 0.22 m, 24.07 ± 15.17 , 0.55 ± 0.15 m, $N = 30$; MANOVA: $F_{3,56} = 27.24$, $p < 0.001$). Thus, fire reduced the potential cavities to ant nests by simplification of vegetation structure.

Burned areas also had less prey for ants (0.65 ± 0.15 , $N = 20$) than control area (1.85 ± 0.31 , $N = 20$) (ANOVA: $F_{1,76} = 13.25$, $p < 0.001$). No difference in prey availability was found between ground and vegetation in any area ($F_{1,76} = 2.91$, $p = 0.09$). On the other hand, the number of extrafloral nectar sources was higher in the burned area (32 EFN-bearing plants, 30%) than in the control area (10%) ($\chi^2 = 11.28$, d.f.=1, $p < 0.001$). We found no difference between burned (29 plants with hemipterans, 30%) and control area (34, 35%) in the number of honeydew sources ($\chi^2 = 0.33$, d.f.= 1, $p = 0.57$). We do not found EFN-bearing plants hosting hemipterans.

Natural-nests sampling

We found 11 ants species nesting in cavities (Table 1). The burned area had less species (6) than control area (9), with two exclusives species against four in the control area. Moreover, we observed two-fold more species nesting on foliage (burned: 6, control: 7) compare to the ground (3, 4) in both areas. *Camponotus rufipes* and *C. crassus* were the most common species nesting in the ground, while *Cephalotes pusillus* was the most common nesting in the foliage. According to the pitfall samples, cavity-nesting ants represented 49% of 140 sampled ants and 29% of the 38 species collected in both areas.

Table 1. Ant species nesting in cavities found in burned and unburned areas in a Brazilian Savanna area. Columns show nest quantity assessed with trap-nests and active search and local abundance assessed using pitfall traps.

	Nests	Abundance
Formicidae		
Subfamily Dolichoderinae		
<i>Linepithema micans</i> Forel 1908	2	7
Subfamily Formicinae		
<i>Brachymyrmex</i> sp.1	2	2
<i>Camponotus alboannulatus</i> Mayr 1887	1	3
<i>Camponotus crassus</i> Mayr 1962	16	14
<i>Camponotus rufipes</i> Fabricius 1775	7	10
<i>Camponotus senex</i> Smith 1858	1	1
Subfamily Myrmicinae		
<i>Cephalotes pusillus</i> Klug 1824	19	14
<i>Crematogaster goeldii</i> Forel 1903	3	1
<i>Crematogaster</i> sp.1	1	1
<i>Crematogaster</i> sp.2	5	5
<i>Solenopsis</i> sp.1	3	1

The ant fauna in the burned area presented higher ant abundance per pitfall ($F_{1,76} = 6.78$, $p = 0.01$) but lower percentage of cavity-nesting ants ($F_{1,76} = 11.63$, $p = 0.01$) (Figure 1a). We also found higher richness in burned area ($F_{1,76} = 9.88$, $p = 0.002$), but lower richness of cavity-nesting species ($F_{1,76} = 10.36$, $p = 0.002$) (Fig 1b). Foliage showed higher percentage of cavity-nesting ants regarding the total abundance ($F_{1,76} = 6.25$, $p = 0.01$) and richness ($F_{1,76} = 5.86$, $p = 0.02$) of ants, in both areas ($F_{1,76} = 1.45$, $p = 0.23$; $F_{1,76} = 0.93$, $p = 0.34$) (Fig 1).

We found 66 nesting-sites in the burned area (19 colonized) and 82 in the control area (26 colonized). However, there was no difference in the occupancy ($\chi^2 = 0.15$, d.f. = 1, $p = 0.7$). Apparently, the number of nesting-sites found in the ground (burned: 42; control: 32) was similar to that found in the foliage (40; 34) in both areas. However, the nesting rate in the foliage (burned: 44%, control: 43%) was higher than in the ground (13%, 21%) in both areas (GLM: $\chi^2 = 8.04$, d.f. = 1, $p = 0.001$; $\chi^2 = 4.2$, d.f. = 1, $p = 0.04$; Fig 1).

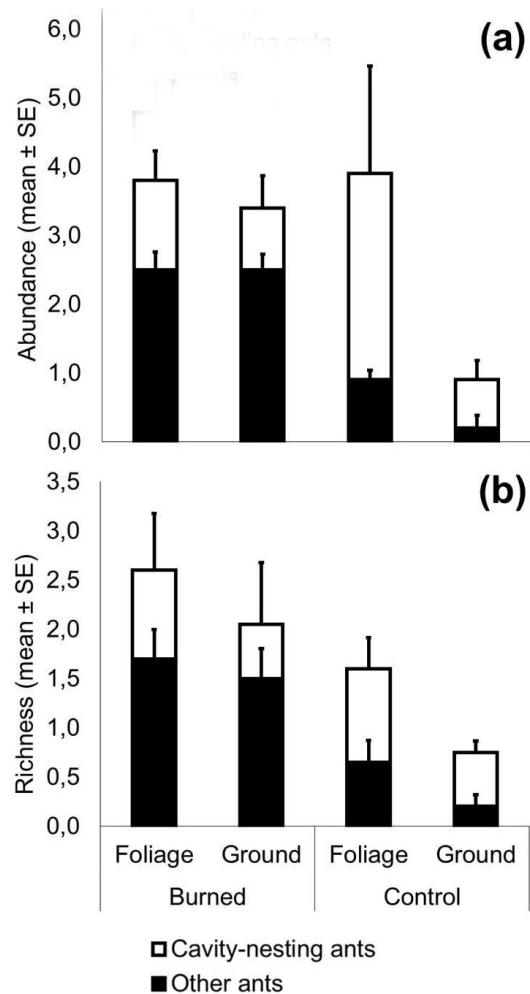


Fig 1. Contrasts between burned and unburned areas of Cerrado for ant diversity. Ants presents higher abundance ($p = 0,01$) in the burned area but lower percentage ($p = 0,01$) of cavity-nesting ants (a). The same is true for ant richness ($p = 0,002$) and percentage of cavity-nesting species ($p = 0,002$; b).

Artificial-nests sampling

We found 15 colonies occupying artificial-nests with the presence of queens, workers, soldiers, eggs and pupae. Only two of the 11 cavity-nesting species occupied the artificial-nests: *C. crassus* and *C. pusillus* (Table 1). The general nesting rate was 18.8%. The burned area had 22.5% occupied nests, while the control area had 15%. We found no difference between the rate of nesting in burned and control areas (GLM $\chi^2 = 0.83$, d.f. = 1, $p = 0.36$). However, nesting was higher in the vegetation (30% occupancy) than in the soil (7%) (GLM $\chi^2 = 6.88$; d. f. = 1; $p = 0.01$) (Fig 2).

We found differences between colonies of burned and control areas. The number of queens was always one per colony, but colonies had more individuals in burned than control areas (GLM: eggs: $\chi^2 = 33.7$, d.f. = 1, $p < 0.001$; immatures: $\chi^2 = 47.13$, d.f. = 1, $p < 0.001$, workers: $\chi^2 = 10.11$, d.f. = 1, $p < 0.001$; Figure 2). However, this difference was greater for colonies in soil, which hardly grew in the control area, as in initial

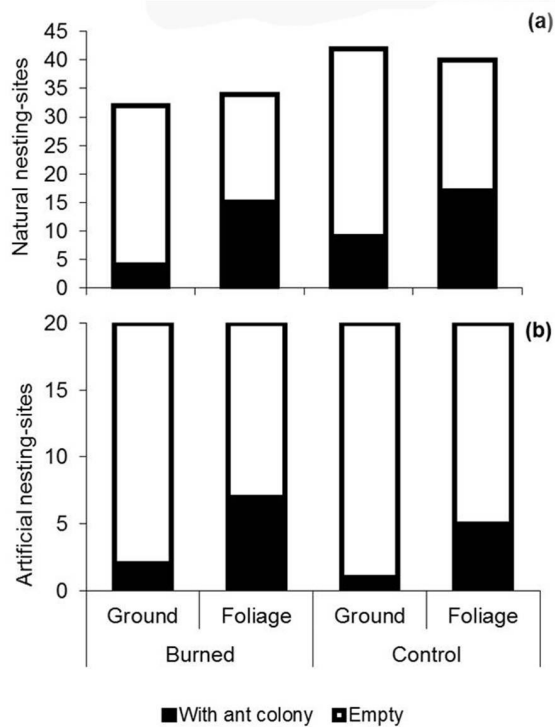


Fig 2. Number of natural (a) and artificial (b) nesting-cavities placed on the ground and foliage, occupied by ant colonies in burned and recovered areas of Cerrado. The burned area presents lesser availability of nest-sites, but the proportion of occupied nests was not different between burned and non-burned habitats for natural ($p = 0.04$) and artificial ($p = 0.36$) cavities. The proportion of occupied nests was higher in vegetation for natural ($p = 0.04$) and artificial ($p = 0.01$) cavities.

state had few workers and immature (GLM: eggs: $\chi^2 = 42.8$, d.f. = 2, $p < 0.001$; immature: $\chi^2 = 262.5$, d.f. = 2; $p = 0.0001$; workers: $\chi^2 = 116.8$, d.f. = 2; $p < 0.001$; Fig 2). Regarding vegetation nests, the size of the colonies was almost the same between the areas (Fig 3). At last, we found a positive relation between the number of occupied nests and the local abundance (GLM: $\chi^2 = 11.6$, d.f. = 1, $p = 0.006$) consistent in burned and unburned area (GLM interaction: $\chi^2 = 0.13$, d.f. = 1, $p = 0.72$).

Discussion

In this study, we found that the availability of nesting-sites might be an important limiting factor for the diversity of cavity-nesting ants in a Brazilian Savanna, mainly for tree-dwelling species. Although nesting rate was similar between burned and control areas, burned areas presented plants with small size, less number of stems and reduced crown, then with a reduced number of potential cavities to be used by ants. Thus, we confirmed our hypothesis that nesting-sites would be a more limiting resource in burned areas. This effect was stronger on foliage because the nesting rate was higher than in the ground, but the number of nesting-sites available was similar. Moreover, the abundance of cavity-nesting ants was higher in burned areas, but the number of colonies and richness of species

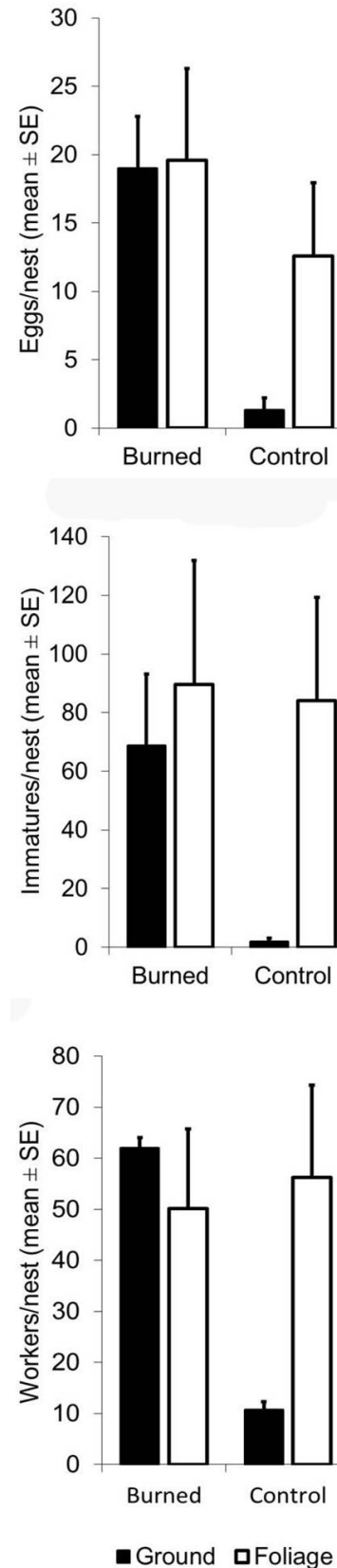


Fig 3. Differences in size (number of eggs [a], immature [b] and workers [c]) of colonies established in artificial cavities placed on the ground and foliage of burned and recovered areas of Cerrado. Colonies established in cavities placed on the ground grew less in control areas ($p = 0.001$ for all variables), but no difference occur for nests in cavities on the foliage. In general, colonies of burned areas present higher number of individuals ($p = 0.0001$ for all variables).

was lower. This scenario may reflect higher competition for nesting-sites leading to low coexistence between species, but lower competition for food, leading to higher abundance. Burned areas presented higher number of EFN-bearing plants, and nectar is a primary food resource for cavity-nesting ants, leading to intense colony growth and higher abundance (e.g. Byk & Del-Claro, 2011).

Our results surpassed the expected in the literature for ants nesting in natural or artificial cavities (Philpott & Foster, 2005; Ambrecht et al., 2006; Cobb et al., 2006; Davidson et al., 2006; Fagundes et al., 2010; Houdeshell et al., 2011). We found 43% occupancy rate of natural-nests, and 19% occupancy of artificial-nests. In Rupestrian Fields the vegetation is short (Giuletti et al., 1997; Alves et al., 2014), which may prevent the construction of nests in the canopy, and the soil is shallow and sandy (Giuletti et al., 1997; Alves et al., 2014), which could hindering the formation of large terrestrial nests, so we supposed that ants may rely mostly in natural cavities to build nests. In addition, many ants possess nest territories that avoid other ants to colonize nesting-sites near the established colonies (Lach et al., 2010). So, even when a nesting-site is empty, it cannot be occupied due to territorial interference. We believed that, even with less than 50% of the available nesting-sites occupied, nesting-sites are a scarce resource and the artificial nest occupancy reflects the limiting effect of this resource.

We found that burning alters the vegetation structure and then reflects in the nesting-sites availability. First, the burned area had fewer plant species than control areas and most are grasses and herbs, which provides no cavities for nesting (Friedrich & Philpott, 2009). Second, the vegetation structure is simpler in burned areas with smaller and lesser branched plants, which provides few suitable twigs for nesting, since ants prefer twigs thicker than 10mm (Philpott & Foster, 2005; Friedrich & Philpott, 2009). The cavities used for nesting come from parts of living or dead plant, thus the availability of this resource is directly related to the vegetation structure (Armbrecht et al., 2004). Low availability of nesting-sites and then high nesting-site limitation is associated with areas with less complex vegetation structures (Armbrecht et al., 2004; Philpott & Foster, 2005; Marquis & Lill, 2010). Moreover, vegetation diversity is positively related to the occupancy of nesting-sites and composition of cavity-nesting species (Armbrecht et al., 2004; Philpott & Foster, 2005).

The availability of nesting-sites is naturally less for arboreal ants, since space is limited to hollow cavities of dead branches or cavities created by beetles and gall, which is scarce and unpredictable (McGlynn, 2006; Houdeshell et al., 2011). Small shrubs mostly compose the vegetation of Rupestrian fields, which prevents the construction of nests with soil or carton in the foliage (Yamamoto & Del-Claro, 2008). Thus, natural cavities are essential for the establishment of tree-dwelling ant species (Philpott & Foster, 2005; Yamamoto & Del-Claro, 2008). This becomes even stronger in burned areas, because vegetation is small and dominated by grasses and herbaceous plants, providing

little structure for nesting and preventing colonization (Morais & Benson, 1988; Mistry, 1998). In burned areas, the arboreal ant species that also nest on the ground need to compete for space with the ground ant species, which increases the limiting effect of nesting-sites (Frizzo et al., 2011).

We found low richness of ants in artificial-nest than natural nests, and this was unexpected (Phillpot & Foster, 2005; Houdeshell et al., 2011). Of the 11 species nesting on natural cavities, *C. pusillus* (on the foliage) and *C. crassus* (on the ground) occupied most of the artificial nesting-sites. These species are very common and abundant in Rupestrian Fields, mainly in the tree layer (Fagundes et al., 2012; Lopes et al., 2012; Viana-Silva & Jacobi, 2012). *Camponotus* species are commonly found nesting in artificial-nests (Armbrecht, 2004, Cobb et al., 2006, Sagata et al., 2010). *Camponotus crassus* nests in soil chambers in the ground having satellite nests in dead hollow branches and collect food more intensely in trees, especially extrafloral nectar of plants and exudates of Hemiptera (Silvestre et al., 2003; Marques & Del-Claro, 2006; Fagundes et al., 2012). *Cephalotes pusillus* build nests on live branches and trunks in the foliage where it forages for the same food of *Camponotus*, besides pollen and animal excrements (Byk & Del-Claro, 2010). *Camponotus* species are fire resistant and have increased in abundance in recently burned areas (Frizzo et al., 2011; Alves-Silva & Del-Claro, 2013), but *Cephalotes* is considered to be vulnerable to fire (Morais & Benson, 1988), although we do not found less abundance of *C. pusillus* in the burned area.

Reduced availability of nesting-sites in burned area reflected in lower richness of cavity-nesting ants compared to control area. On the other hand, the overall abundance of cavity-nesting ants was higher in the burned area particularly in the foliage. This can be explained in part by the availability of food, once the cavity-nesting ants are adapted to feed on sugary secretions of animals and plants (Davidson et al., 2004), which in turn tend to be higher in burned areas (Alves-Silva & Del-Claro, 2013). The consumption of extrafloral nectar increases the growth of the colony compared to a predatory diet (Byk & Del-Claro, 2011), and provides energy for intensively forage (Davidson et al. 2004), which concentrates on the foliage (Blüthgen et al., 2000). Dominant ants are commonly associated with the consumption of extrafloral nectar and exudates of hemipteran (Bluthgen et al., 2000; Davidson et al., 2004). In the study area, *C. crassus* and *C. pusillus* are the main species collecting extrafloral nectar (Dáttilo et al., 2014). This dominance of highly energetic food sources can provide the energy needed for the dominance of the nesting-sites and explain why those two were the main species occupying the artificial-nests.

We did not found difference in the size of colonies grown in burned areas compared to the control areas. Colonies in burned areas grew more than in control area, but only for colonies founded on the ground. Two hypotheses may explain this scenario. First, as we have shown, the burned area possesses

higher quantity of food resources for arboreal cavity-nesting ants (i.e. nectar and honeydew), especially on the foliage leading to higher colony growth (Byk & Del-Claro, 2011), since food is not limited. Second, the competition for preys and space may be lower in burned areas, because predatory ground ant species are few and may not completely have recovered yet. Indeed, most of the species occupying natural ground-nesting-sites in burned area consisted of tree-dwelling species, while ground-dwelling Myrmicinae species occupy cavities in the control area. Additionally, ground-nesting species were more abundant in the control area. In short, we believed that competition for nesting-sites between ground-dwelling and tree-dwelling species may have suppressed the growth of colonies founded on the ground of the control area, along with the competition for food resource, since control area had few EFN-bearing plants and more preys, favoring predatory ants. More importantly, ants need to found new nest-sites to expand population size and even though with plenty of food resources in burned areas and proper colony growth, the population growth and distribution remain limited by nesting-site availability.

The mechanisms of how fire alters the ant fauna are poorly known, and increased competition for resources between species of the same guild such as cavity-nesting ants may be a key mechanism (Frizzo et al., 2011; Houdeshell et al., 2011; Powell et al., 2011). The reduced nesting-site availability helps to explain the low richness in burned areas (Powell et al., 2011), while the higher amount of sugary resources help to explain the higher abundance of cavity-nesting ants (Blüthgen et al., 2000; Fagundes et al., 2012; Alves-Silva & Del-Claro, 2013, 2014). However, further studies may focus in how species interacts to determinate which species will dominate the nesting-site, or even if the occupation is opportunistic, and the temporal dynamic of these occupation. Including different types of nesting-sites must be also important to reduce effect of ant selective nesting behavior (Mallon et al., 2001). Cavity-nesting ants may be key species to understanding community structure by competitive mechanisms and the effect of disturbances (Fonseca, 1999; Del-Claro & Torezan-Silingardi, 2009; Houdeshell et al., 2011), especially for species that nest in plants (Fonseca, 1999; Philpott & Foster, 2005; Philpott, 2009; Powell et al., 2011). Some studies show that the effect of fire can be specie-specific, and even though the overall ant fauna may not change after fire (Vasconcellos et al., 2009), some species may be damaged (Bess et al., 2002; Underwood & Christian, 2009; Houdeshell et al., 2011). The study of disturbance effects in specific taxa may provide quick answers about disturbance mechanisms. This is even more important in high endemic ecosystems such as Rupestrian Fields, which are threatened by mining activity and urge for conservation politics (Jacobi & Carmo, 2008). Studies that transcend simple comparisons between areas with different impacts and focus in ecological mechanisms of disturbances should be priority in environmental conservation (Lewinsohn et al., 2005; Jacobi & Carmo, 2008; Del-Claro & Torezan-Silingardi, 2009).

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References

- Alves, R.J.V., Silva, N.G., Oliveira, J.A. & Medeiros, D. (2014). Circumscribing Campo rupestre – megadiverse Brazilian rocky montane savanas. *Brazilian Journal of Biology*, 74: 355-362.
- Alves-Silva, E. & Del-Claro, K. (2013). Effect of post-fire resprouting on leaf fluctuating asymmetry, extrafloral nectar quality, and ant–plant–herbivore interactions. *Naturwissenschaften*, 100: 525-532.
- Alves-Silva, E. & Del-Claro, K. (2014). Fire triggers the activity of extrafloral nectaries, but ant fail to protect the plant against herbivores in a Neotropical Savanna. *Arthropod-Plant Interactions*, 8: 233-240.
- Andersen, A.N., Hertog, T. & Woinarski, J.C.Z. (2006). Long-term fire exclusion and ant community structure in an Australian tropical Savanna: congruence with vegetation succession. *Journal of Biogeography*, 33: 823-832.
- Ambrecht, I., Perfecto, I. & Vandermeer, J. (2004). Enigmatic biodiversity correlations: ant diversity responds to diverse resources. *Science*, 304: 284-286.
- Ambrecht, I., Perfecto, I. & Silverman, E. (2006). Limitation of nesting resources for ants in Colombian forests and coffee plantations. *Ecological Entomology*, 31: 403-410.
- Bess, E.C., Parmenter, R.R., McCoy, S. & Molles, M.C. (2002). Responses of a riparian forest-floor arthropod community to wildfire in the Middle Rio Grande Valley, New Mexico. *Environmental Entomology*, 31: 774-784.
- Blüthgen, N., Verhaagh, M., Goitia, W., Jaffé, K., Morawetz, W. & Barthlott, W. (2000). How plants shape the ant community in the Amazonian rainforest canopy: the key role of extrafloral nectaries and homopteran honeydew. *Oecologia*, 125: 229-240.
- Byk, J. & Del-Claro, K. (2010). Nectar and pollen gathering *Cephalotes* ants provide no protection against herbivore: a new manipulative experiment to test ant protective capabilities. *Acta Ethologica*, 13: 33-38.
- Byk, J. & Del-Claro, K. (2011). Ant-plant interaction in the Neotropical Savanna: direct beneficial effects of extrafloral nectar on ant colony fitness. *Population Ecology*, 53: 327-332.

- Byrne, M.M. (1994). Ecology of twig-dwelling ants in a wet lowland tropical forest. *Biotropica* 26: 61-72.
- Cobb, M., Watkins, K., Silva, E.N., Nascimento, I.C. & Delabie, J.H.C. (2006). An exploratory study on the use of bamboo pieces for trapping entire colonies of arboreal ants (Hymenoptera: Formicidae). *Sociobiology*, 47: 215-223.
- Davidson, D.W., Cook, S.C. & Snelling, R.R. (2004). Liquid-feeding performances of ants (Formicidae): ecological and evolutionary implications. *Oecologia*, 139: 255-266.
- Davidson, D.W., Arias, J.A. & Mann, J. (2006). An experimental study of bamboo ants in western Amazonia. *Insectes Sociaux*, 53: 108-114.
- Dáttilo, W., Fagundes, R., Gurka, C.A.Q., Silva, M.S.A., Vieira, M.C.L., Izzo, T.J., Díaz-Castelazo, C., Del-Claro, K. & Rico-Gray, V. (2014). Individual-based ant-plant networks: diurnal-nocturnal structure and species-area relationship. *PLoS One*, 9(6): e99838, doi:10.1371/journal.pone.0099838
- Del-Claro, K. & Torezan-Silingardi, H.M. (2009). Insect-plant interactions: new pathways to a better comprehension of ecological communities in Neotropical Savannas. *Neotropical Entomology*, 38: 159-164.
- Fagundes, R., Terra, G., Ribeiro, S.P. & Majer, J.D. (2010). O bambu *Merostachys fischeriana* (Bambusoideae: Bambuseae) como habitat para formigas de Floresta Tropical Montana. *Neotropical Entomology*, 39: 906-911.
- Fagundes, R., Del-Claro, K. & Ribeiro, S.P. (2012). Effects of the trophobiont herbivore *Calloconophora pugionata* (Hemiptera) on ant fauna associated with *Myrciaobovata* (Myrtaceae) in a montane tropical forest. *Psyche*, 2012: 1-8. doi:10.1155/2012/783945
- Fonseca, C.R. (1999). Amazonian ant plant interactions and the nesting space limitation hypothesis. *Journal of Tropical Ecology*, 15: 807-825.
- Friedrich, R. & Philpott, S. (2009). Nest-site limitation and nesting resources of ants (Hymenoptera: Formicidae) in urban green spaces. *Environmental Entomology*, 38: 600-607.
- Frizzo, T.L.M., Bonizário, C., Borges, M.P. & Vasconcelos, H.L. (2011) Revisão dos efeitos do fogo sobre a fauna de formações savânicas do Brasil. *Oecologia Australis*, 15: 365-379.
- Giuletti, A.M., Pirani, J.R. & Harley, R.M. (1997) Espinhaço range region, eastern Brazil. In: S.D. Davis, V.H. Heywood, O.J. Herrera-MacBride, O. Villa-Lobos, A.C. Hamilton (Eds.), *Centers of plant diversity: a guide and strategy for their conservation* (pp: 397-404). Oxford: Oxford University Press.
- Kolbek, J.I.R.I. & Alves, R.J.V. (2008). Impacts of cattle, fire and wind in Rocky Savannas, Southeastern Brazil. *Acta Universitatis Carolinae Environmentalica*, 22: 111-130.
- Lopes, J.F.S., Hallack, N.M.D., Sales, T.A.D., Brugger, M.S., Ribeiro, L.F., Hastenreiter, I.N. & Camargo, R.D.S. (2012). Comparison of the Ant Assemblages in Three Phytophysionomies: Rocky Field, Secondary Forest, and Riparian Forest - A Case Study in the State Park of Ibitipoca, Brazil. *Psyche*, 2012: 1-7. doi:10.1155/2012/928371
- Hölldobler, B. (1976). Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. *Behavioral Ecology and Sociobiology*, 1: 3-44.
- Hölldobler, B., & Wilson, E.O. (1990). *The Ants*. Cambridge: Harvard University Press, 732 p
- Houdeshell, H., Friedrich, R.L. & Philpott, S.M. (2011). Effects of Prescribed Burning on Ant Nesting Ecology in Oak Savannas. *The American Midland Naturalist*, 166: 98-111.
- Jacobi, C.M. & Carmo, F.F. (2008). The contribution of ironstone outcrops to plant diversity in the Iron Quadrangle, a threatened Brazilian landscape. *AMBIO*, 37: 324-326.
- Kaspari, M. (1996). Litter ant patchiness at the 1-m² scale: disturbance dynamics in three Neotropical forests. *Oecologia*, 107: 265-273.
- Lach, L., Parr, C.L. & Abbott, K.L. (2010). *Ant Ecology*. Oxford: Oxford University Press, 424 p
- Lange, D. & Del-Claro, K. (2014). Ant-Plant Interaction in a Tropical Savanna: May the Network Structure Vary over Time and Influence on the Outcomes of Associations? *Plos One*, 9(8): 1-10.
- Lewinsohn, T.M., Freitas, A.V.L. & Prado, P.I. (2005). Conservation of terrestrial invertebrates and their habitats in Brazil. *Conservation Biology*, 19: 640-645.
- Mallon, E.B., Pratt, E.C. & Franks, N.R. (2001). Individual and collective decision making during nesting site selection by the ant *Leptothorax albipennis*. *Behavioral Ecology and Sociobiology*, 50: 352-359.
- Marques, G.V.D. & Del-Claro, K. (2006). The ant fauna in a Cerrado area: the influence of vegetation structure and seasonality (Hymenoptera: Formicidae). *Sociobiology*, 47: 1-18.
- Marquis, R.J. & Lill, J.T. (2010). Impact of plant architecture versus leaf quality on attack by leaf-tying caterpillars on five oak species. *Oecologia*, 163: 203-213.
- McGlynn, T.P. (2006). Ants on the move: Resource limitation of a litter-nesting ant community in Costa Rica. *Biotropica*, 38: 419-427
- Morais, H.C. & Bemson, W.W. (1988). Recolonização de vegetação de Cerrado após queimada por formigas arbóricolas. *Revista Brasileira de Biologia*, 48: 459-466
- Mistry, J. (1998). Fire in the Cerrado (Savannas) of Brazil: an ecological review. *Progress in Physical Geography*, 224: 425-448.
- Parr, C.L. & Gibb, H. (2010). Competition and the role of dominant ants. In L. Lach, C. Parr & K.L. Abbott (Eds.), *Ant Ecology* (pp: 77-96). Oxford: Oxford University Press.

- Peeters, C. & Molet, M. (2010). Colonial reproduction and life histories. In L. Lach, C. Parr & K.L. Abbott (Eds.), *Ant Ecology* (pp: 159-176). Oxford: Oxford University Press.
- Philpott, S.M. & Foster, P.F. (2005). Nest-site limitation in coffee agroecosystems: artificial-nests promote maintenance of arboreal ant diversity. *Ecological Applications*, 15: 1478-1485.
- Powell, S., Costa, A.N., Lopes, C.T. & Vasconcellos, H.L. (2011). Canopy connectivity and the availability of diverse nesting resources affect species coexistence in arboreal ants. *Journal of Animal Ecology*, 80: 352-360.
- Rapini, A., Ribeiro, P.L., Lambert, S. & Pirani, J.R. (2008). A flora dos campos rupestres da Cadeia do Espinhaço. *Megadiversidade*, 4: 15-23.
- Ribas, C.R., Schroeder, J.H., Pie, M. & Soares, S.M. (2003). Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. *Austral Ecology*, 28: 305-314.
- Rico-Gray, V. & Oliveira, P.S. (2007). *The ecology and evolution of ant-plant interactions*. Chicago: University of Chicago Press, 320 p
- Sagata, K., Mack, A.L., Wright, D.D. & Lester, P.J. (2010). The influence of nest availability on the abundance and diversity of twig-dwelling ants in a Papua New Guinea forest. *Insectes Sociaux*, 57: 333-341.
- Shik, J.Z. & Kaspari, M. (2010). More food, less habitat: how necromass and leaf litter decomposition combine to regulate a litter ant community. *Ecological Entomology*, 35: 158-165.
- Silvestre, R., Brandão, C.R.F. & Silva, R.R. (2003). Grupos funcionales de Hormigas: El caso de los gremios del Cerrado. In: F. Fernández (Eds.), *Introducción a las Hormigas de la Región Neotropical* (pp: 113-148), Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.
- Underwood, E.C. & Christian, C.E. (2009) Consequences of prescribed fire and grazing on grassland ant communities. *Environmental Entomology*, 38: 325–332.
- Vasconcellos, H.L., Pacheco, R., Silva, R.C., Vasconcelos, P.B., Lopes, C.T., Costa, N.A. & Bruna, E.M. (2009). Dynamics of the leaf-litter arthropod fauna following fire in a Neotropical woodland Savanna. *Plos One*, 4: 1-9.
- Viana-Silva, F.E.C. & Jacobi, C.M. (2012). Myrmecofauna of ironstone outcrops: composition and diversity. *Neotropical Entomology*, 41: 263-271.
- Yamamoto, M. & Del-Claro, K. (2008). Natural history and foraging behavior of the carpenter ant *Camponotus sericeiventris* Guérin, 1838 (Formicinae, Camponotini) in the Brazilian tropical Savanna. *Acta Ethologica*, 11: 55-65.

