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Naturais**

**PADRÕES E MECANISMOS ENVOLVIDOS NA ESTRUTURAÇÃO
DE UMA COMUNIDADE DE FORMIGAS ARBÓREAS NO
CERRADO**

FLÁVIO DE CARVALHO CAMAROTA

2016

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

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Resumo geral

Neste estudo, eu avaliei alguns dos mecanismos mais importantes na estruturação de comunidades de formigas arbóreas. Para isto, eu me aproveitei da fácil acessibilidade e da grande diversidade de formigas arbóreas das savanas do Brasil central (Cerrado). Primeiramente, eu avaliei os padrões de coocorrência das espécies de formigas arbóreas e em que extensão estes padrões podem ser explicados pela competição interespecífica ou por associação de habitat. Para isto, eu utilizei um conjunto de dados de 240 árvores e realizei análises de modelos nulos, primeiro levando em conta apenas a incidência das espécies na comunidade e depois incorporando atributos do habitat. Eu fiz as análises com todas as espécies da comunidade e então apenas com as espécies mais comuns, usando tanto uma abordagem de matrizes como par a par. Eu encontrei que a competição foi o fator mais importante por trás da distribuição destas formigas arbóreas, com uma influencia muito menor de atributos do habitat. O efeito da competição foi detectado quando eu levei em conta as 14 espécies de formigas mais comuns, tanto no nível da matriz quanto nas análises par a par. Esta importância da competição foi consistente com as diferenças observadas em algumas características biológicas importantes das espécies coexistentes. Após isto, eu foquei nos padrões de uso de recursos e em como estes padrões podem influenciar a diversidade de formigas arbóreas. Primeiro, eu avaliei como a heterogeneidade de recursos de nidificação e a presença de uma espécie dominante pode afetar os padrões de nidificação das formigas arbóreas. Para isto, eu realizei uma manipulação experimental envolvendo 80 plantas de uma mesma espécie. Em cada planta, eu coloquei 27 cavidades com diferentes buracos de entrada, divididas em dois tratamentos: ‘alta diversidade de entradas’, com nove tamanhos de entrada diferentes (0.15 a 0.55 mm²) e ‘baixa diversidade de entradas’, com três tamanhos de entrada diferentes (0.15 a 0.25 mm²). Eu considerei *Cephalotes pusillus* como a espécie dominante sobre recursos de abrigo, uma vez que foi a espécie que ocupou o maior número de cavidades e esteve presente na maior parte das plantas experimentais. Eu encontrei mais espécies de formigas nidificando no tratamento com alta diversidade de tamanhos de entrada, além de uma mudança nos tamanhos de entrada utilizadas pelas formigas com o aumento da diversidade e amplitude dos tamanhos de entrada ofertados. Eu também detectei efeitos significativos da presença da espécie dominantes nos padrões de nidificação das outras espécies, com mais espécies de formigas e mais ninhos colonizados quando esta estava ausente. Também ocorreram

mudanças no tamanho médio de entrada utilizado pelas formigas na presença de *C. pusillus*. Por último, eu avaliei os resultados da competição de formigas arbóreas sobre iscas de alimento. Eu quantifiquei as diferenças no uso destes recursos pelas diferentes espécies de formigas e perguntei se havia uma relação significativa entre a habilidade em encontrar um recurso e domina-lo. Eu ainda perguntei quais aspectos da biologia das espécies de formigas foram responsáveis pelos resultados observados. Eu fiz observações em 175 árvores de médio porte pertencentes a diferentes espécies durante o dia e em uma subamostra de 44 árvores durante a noite. Eu coloquei uma colher de isca de sardinha no ramo principal de cada árvore e observei a troca de espécies nas iscas. Eu encontrei uma relação positiva entre a habilidade de descobrir recursos e o status de dominância das espécies de formigas, apoiando a existência de efeitos de prioridade sobre recursos de alimentação. De forma geral, eu encontrei que o tamanho da colônia foi a característica mais importante determinando os resultados das interações sobre as iscas. O presente trabalho se encaixa na demanda cada vez maior de trabalhos empíricos avaliando os fatores que definem a coexistência, demonstrando a importância da competição na estruturação de uma comunidade de formigas arbóreas.

Palavras-chave: Assembleia de comunidades, Brasil, cavidades artificiais, copa das árvores, diferenças de nicho, efeitos de prioridade, especialização de recursos, espécies dominantes, exploração de recursos, tamanho da colônia.

General abstract

In this study, I evaluated some of the most important mechanisms structuring arboreal ant communities. For this I took advantage of the easy accessibility and high diversity of the arboreal ant fauna of the savannas of central Brazil (*Cerrado*). First, I assessed the co-occurrence patterns of the arboreal ant species and evaluated to which extent these patterns can be explained by interspecific competition or by habitat association. For that, I used a dataset of 240 trees and performed null model analyses, first accounting only for the species incidence in the community and later incorporating habitat attributes. I performed analyses with all the ant species in the community and then with only the most common species using both a matrix level and a pairwise approach. I found that competition is the most important factor behind the distribution of these arboreal ants, with a much smaller influence of habitat attributes. The effect of competition was detected when I accounted for the 14 most common ant species in the community, both in the matrix level and the pairwise analyses. The importance of competition is consistent with the observed differences in some important biological characteristics of the coexisting ant species. After that, I focused on the patterns of resource use and how they can influence the diversity of arboreal ants. First, I assessed how the heterogeneity of nesting resources and the presence of a dominant species can affect the nesting patterns of arboreal ants. For this, I performed an experimental manipulation in 80 trees belonging to the same species. On each tree I placed 27 cavities with different entrance holes divided in two treatments: high entrance diversity (HE), with 9 different entrance sizes (0.15 to 0.55 mm²) and low entrance diversity (LE), with only 3 different entrance sizes (0.15 to 0.25). I considered *Cephalotes pusillus* as the dominant species over shelter resources, since it was the species which occupied the highest number of cavities and was also the most common in the experimental trees. I found more nesting ant species nesting in the HE treatment trees, and also a change in the used entrance sizes with an increase in the range and diversity of entrance sizes. I also found significant effects of the presence of the dominant species in nesting patterns, with more ant species and colonized nests when it was absent. There were also changes in the mean entrance size used by the ants in the presence of *C. pusillus*. Finally, I assessed the competitive outcomes of arboreal ants at food baits. I quantified the differences in resource use by the different ant species and asked if there was a significant relationship between the ability to find resources and to dominate them. I

further asked which aspects of the ant are responsible for the observed outcomes. I performed observations in 175 medium sized trees from several species during the day and in a subset of 44 trees at night. I placed a teaspoon of sardine bait in the main branch of each tree and observed the turnover of species at the baits. I found a positive relationship between the discovery ability and the dominance of the ant species, supporting a priority effect over food resources. Overall, I found that colony size was the most important characteristic determining the outcomes at the baits. The present works fits in the growing demand for empirical studies assessing the factor defining species coexistence, showing the importance of competition for the structure of an arboreal ant community.

Key words: Artificial cavities, Brazil, canopy, colony size, community assembly, dominant species, niche differences, priority effects, resource specialization, resource exploitation.

Introdução geral

O entendimento dos mecanismos responsáveis pela coexistência entre as espécies é um dos principais objetivos da ecologia de comunidades (Agrawal et al. 2007, Sutherland et al. 2013). Em uma escala local, os processos baseados nas interações entre as espécies são considerados de grande importância, principalmente a competição (Gause 1934, Elton 1946, Hutchinson 1959, Chase & Leibold 2003). A teoria clássica afirma que a coexistência estável entre as espécies em uma comunidade requer que os competidores difiram em seus nichos (Chesson 2000, Chase & Leibold 2003, HilleRisIambers et al. 2012). A diferenciação de nicho pode se manifestar em diferentes aspectos, como na morfologia ou na utilização de recursos (Chesson 2000). Em muitos casos, a exclusão competitiva pode ser evitada simplesmente pela utilização de recursos diferentes entre as espécies (Chesson 2000). No entanto, as espécies ainda podem coexistir utilizando os mesmos recursos, desde que difiram na *forma* em que utilizam estes recursos (Chesson 2000, Amarasekare 2003). Estas diferenças de nichos fazem com que as espécies limitem mais os indivíduos da sua própria espécie do que de espécies competidoras, o que faz com estas tenham uma maior taxa de crescimento *per capita* quando são raras e seus competidores são comuns (Levine & HilleRisIambers 2009). Sendo assim, o crescimento populacional de apenas uma das espécies seria limitado, evitando a exclusão competitiva. No entanto, é importante notar que nem todas as diferenças de nicho entre as espécies promovem necessariamente a coexistência, podendo levar a dominância competitiva de algumas espécies sobre outras (Adler & Drake 2008). Portanto, para entender a importância de processos baseados no nicho das espécies muitas vezes se torna necessário não só entender as diferenças na utilização de recursos, mas também como algumas espécies dominantes influenciam na utilização destes. A influência marcante de interações interespecíficas na comunidade

pode se traduzir em ‘regras de assembléia’(Diamond 1975), onde as espécies coexistentes possuem um limite claro de similaridades entre si.

Atualmente, a ideia de que a diferenciação de nicho é essencial para a coexistência entre as espécies não é mais uma unanimidade, principalmente após o surgimento da teoria neutra da biodiversidade (Hubbell 2001), que explica a coexistência de competidores equivalentes. De fato, é possível que tanto fatores neutros quanto aqueles baseados nas interações entre as espécies são essenciais para determinar a diversidade local de espécies (Leibold & McPeeck 2006, Wenneckes et al. 2012). É possível também que a diversidade local de espécies seja determinada principalmente pelo pool regional de espécies, com as interações bióticas dentro das comunidades tendo menor importância (Ricklefs 1987, 2008). Sendo assim, as diferentes comunidades biológicas estariam em algum lugar dentro de um continuum entre aquilo previsto pela teoria clássica de nicho e pela teoria neutra da biodiversidade (Levine & HilleRisLambers 2009). No entanto, para determinar de forma mais clara quais aspectos tem maior importância dentro das comunidades são necessários estudos empíricos que comprovem modelos e teorias (Agrawal et al. 2007). Para isto, grupos de organismos diversos e abundantes e, portanto, de grande importância ecológica, seriam modelos ideais. Entre estes grupos estão o das formigas, organismos dominantes na maioria dos ecossistemas terrestres, principalmente nos trópicos (Hölldobler & Wilson 1990).

A competição interespecífica é tida como um marco das comunidades de formigas (Hölldobler & Wilson 1990), sendo assim a partição de nicho seria essencial

para promover a coexistência destes organismos. De fato, existem claras evidências da importância da partição de nicho em comunidades de formigas. Um dos exemplos está no impacto de espécies invasoras em comunidades locais de formigas, que podem eliminar totalmente aquelas espécies com nicho semelhantes ao das invasoras (Ward 1987, Hoffman 1999, Holway 1999). Outro exemplo está na distribuição de formigas arbóreas na copa das árvores de florestas tropicais. Estas comunidades podem ter uma distribuição em forma de mosaico, onde as espécies dominantes possuem territórios mutuamente exclusivos, permitindo a coexistência apenas com aquelas espécies subdominantes e dominantes (Leston 1970, Jackson 1984). Apesar de algumas evidências, a importância da partição de nichos como promotora da coexistência de formigas tem sido questionada (Anderson 2008). Em muitos casos, apenas a diferenciação de nicho entre as espécies não é suficiente para explicar os padrões de riqueza observados (Andersen 2008, 2013), levando a busca de explicações alternativas, principalmente fatores estocásticos, independentes da competição (Andersen 2008). No entanto, a importância relativa de fatores estocásticos e processos baseados no nicho ainda é pouco clara, com a necessidade de mais estudos a fim de elucidar esta questão.

Em ambientes tropicais, as formigas arbóreas são organismos de extrema importância, representando boa parte da biomassa animal (Floren 2014). Além disso, estas formigas interagem com um grande número de organismos, como plantas e outros animais (Rico-Gray & Oliveira 2007). As formigas arbóreas são de especial importância para o entendimento dos fatores de coexistência das espécies, não só pelos fatores citados acima, mas também por representarem um dos exemplos clássicos de comunidades fortemente influenciadas pela competição. No entanto, ambientes arbóreos

são geralmente de difícil acesso, dificultando determinados tipos de estudos, como manipulações experimentais. O Cerrado é uma importante exceção, uma vez que o acesso à copa das árvores é relativamente fácil, visto que estas raramente ultrapassam oito metros de altura (Oliveira-Filho & Ratter 2002). Em comum com outros ecossistemas tropicais, o Cerrado possui uma comunidade de formigas arbóreas rica e abundante (Camacho et al. 2015), que nidifica quase que exclusivamente em cavidades arbóreas preexistentes feitas por besouros escavadores de madeira (Powell et al. 2011). Além disso, a vegetação do Cerrado possui uma grande oferta de recursos alimentares em forma de exsudatos, como o néctar de nectários extraflorais, o *honeydew* de hemípteros sugadores de seiva e a secreção de larvas de lepidópteros (Oliveira & Freitas 2004, Schoereder et al. 2010).

Neste trabalho, eu busquei entender alguns dos mecanismos envolvidos na coexistência de formigas arbóreas em uma área de cerrado. Para isto utilizei abordagens diferentes, porém complementares. Primeiramente, eu relacionei os padrões observados de distribuição das espécies com expectativas baseadas em modelos nulos. Posteriormente, realizei uma manipulação experimental da oferta de recursos essenciais (locais de nidificação) para as formigas arbóreas. Por último, fiz observações diretas da utilização de recursos de alimento pelas diferentes espécies encontradas. Em todas estas três abordagens, eu relacionei os resultados encontrados com diferentes características biológicas das espécies. Mais especificamente busquei respostas para as seguintes questões: a) quais são os padrões de coocorrência das formigas arbóreas e quais são os fatores responsáveis por estes padrões? Em que medida diferenças em características biológicas destas espécies nos ajudam a entender os padrões observados? b) qual é a influência da heterogeneidade de recursos de nidificação e de uma espécie dominante na diversidade e utilização destes recursos pelas formigas arbóreas? c) quais são os padrões

de utilização de recursos de alimento das formigas arbóreas? Quais características das espécies estão relacionadas com estes diferentes padrões?

CAPÍTULO 1

**Competition, more than habitat requirements, explains co-occurrence
patterns of a diverse arboreal ant community**

Abstract

A major goal of community ecology is to identify the patterns of species associations and which are the factors promoting them. Arboreal ants are extremely diverse and abundant, being ideal organisms for tackling this issue. However, despite many works showing the co-occurrence patterns of arboreal ant communities, little has actually been showed about the processes behind these patterns. Here, I took advantage of a well structured dataset, allowing us to disentangle the different factors behind community organization. For this, I went beyond simple tests of species co-associations, incorporating habitat attributes in the co-occurrence analyses and also assessing different species traits in a way to explain the observed patterns. More specifically, I assessed the potential role of interspecific competition and habitat selection on the distribution patterns of an arboreal ant community. I ran a suite of null models, first accounting only for the species incidence in the community and later incorporating habitat attributes in the null models. I performed analyses with all the species in the community and then with only the most common species using both a matrix level and a pairwise approach. The co-occurrence patterns did not differ from randomness on the matrix level approach accounting for all ant species in the community. However, I detected a segregated pattern for the most common ant species. Moreover, with the pairwise approach, I found a significant number of negative and positive pairs of species associations. Most of the segregated associations appear to be explained mainly by competitive interactions between species. This was supported by the comparisons of the biological traits of the species that formed these pairs. These results indicates that competition is the most important factor behind the distribution patterns of these arboreal ants, with habitat attributes showing no influence on the matrix-wide results and affecting just a few number of associations. This influence of competition is consistent with the observed differences of biological characteristics (i.e. niche differences) of the coexisting ant species.

Key-words: Assembly rules, Brazil, *Cerrado*, canopy, community assembly, niche, species coexistence.

Introduction

A fundamental goal of community ecology is to identify and quantify the mechanisms allowing multispecies coexistence in biological communities (Agrawal et al. 2007, Sutherland et al. 2013). To achieve this goal, it is important to assess how species are distributed within communities, and what factors and processes generate these patterns (Chesson 2000). Niche-based processes are often offered as an explanation for species distributions within communities, with the general expectation being that species must differ in resource use to coexist (Chase & Leibold 2003, Levine & HilleRisLambers 2009). Therefore, community assembly may be shaped strongly by biotic interactions between species, particularly by interspecific competitive interactions over shared resources (Hutchinson 1959, MacArthur & Levins 1967, Schoener 1974, Chase & Leibold 2003). Nevertheless, the potential role of interspecific competition in shaping communities is a complex issue to address and remains under active investigation and debate.

In addressing the complex issue of the role of competition in community assembly, a significant body of work has focused on detecting the signature of competition in co-occurrence patterns of species within a community (Gotelli & MacCabe 2002). The central assumption of these analyses is that if competitive interactions are scaling up to an impact on community-level species distribution patterns, non-random patterns of localized species co-occurrence should be observable within a community (Diamond 1975, Connor & Simberloff 1979). These analyses are based on statistical null models (Gotelli & Graves 1996), and are particularly valuable because they facilitate the use of large biodiversity-survey datasets to address the underlying processes of community assembly (Gotelli & Graves 1996, Gotelli 2000).

However, it is important to note that non-random patterns of species co-occurrence are not necessarily the result of competitive interactions (Connor & Simberloff 1979, 1984, Peres-Neto et al. 2001). Other factors not directly related to competition, such as dispersal ability and habitat requirements, can also have great importance (Sanderson 2000, Sfenthourakis et al. 2006, Azeria et al. 2012). It is also possible that niche similarities between species can be more important in defining community assembly than niche differences, a process known as ‘niche filtering’ (Fowler et al. 2014).

A major challenge for co-occurrence analyses of community structure is therefore to be able to differentiate between the signature of competition and other factors (Connor & Simberloff 1979, Sfenthourakis et al. 2006). Often, co-occurrence analyses have been applied to large datasets that lack the sampling structure to address other influences on co-occurrence patterns, like habitat type or other environmental influences (Gotelli 2001). Additionally, most studies have assessed co-occurrence patterns only at the whole community level, and this not just ignores important interspecific interactions inside the community (Diamond & Gilpin 1982) but also weakens the potential to infer which factors are responsible for the observed patterns (Sanderson 2004, Veech 2014). This is because only with the detection of the species pairs that are negatively or positively associated one can perform a direct comparison of the biological traits and habitat affinities that promote the observed association patterns (Veech 2014). Therefore, in order to advance the understanding of species co-occurrence patterns, it is necessary to take advantage of distinct null model analyses (e.g. whole community and pairwise level) (Gotelli 2001a, Ulrich & Gotelli 2013).

Ants are abundant, highly diverse, and ecologically important in tropical systems. Moreover, ants actively engage in direct and often extremely intense competitive interactions, such that community organization has been traditionally

viewed as heavily based on direct competitive interactions between species (Hölldobler & Wilson 1990). These attributes, combined with the relative ease with which communities can be sampled, makes them especially well-suited for use in co-occurrence analyses. Not surprisingly thus, many studies have evaluated co-occurrence patterns in ant communities (Gotelli & McCabe 2002), notably in tropical arboreal ant communities (Sanders et al. 2007a, Pfeiffer et al. 2008, Dejean et al. 2010). Indeed, arboreal ant communities have been seen as one of the classic examples of non-random patterns in ant species co-occurrence (Blüthgen & Stork 2007). More specifically, these communities can have a ‘mosaic distribution’, where two or more dominant ant species maintain mutually exclusive territories, allowing coexistence only with subordinate and subdominant ant species (Leston 1970, Jackson 1984). This distribution pattern is often attributed to intense competition between dominant species (Blüthgen & Stork 2007), mainly for food and shelter resources, which can be extremely limited in tree canopies (Blüthgen & Feldhaar 2010). Nevertheless, the use of co-occurrence analyses to address the process of assembly in arboreal ant communities has been severely criticized, given the shortcomings in analytical methodologies and the lack of consideration of the role of other factors on non-random co-occurrence patterns (Gotelli 2001).

To avoid some of the criticisms it is important to analyze a suite of factors that may produce non-random co-occurrence patterns, but that are not directly related to competition, as may be the case for environmental factors. These environmental factors are often reflected in the habitat attributes of different ant species. For arboreal ants, a single tree can be seen as a distinct habitat patch, and therefore different features of individual trees, such as tree identity, size, and degree of connectivity with other trees can be considered key habitat attributes (Ribas et al. 2003). In fact different sized trees often host different numbers and species of arboreal ants (Campos et al. 2006, Powell et

al. 2011, Koch et al. 2015). Similarly, some ant species may nest in some species of host trees than in others (Sanders et al. 2007b, Klimes et al. 2012). Finally, tree canopy connectivity can also have a strong influence on the structure of arboreal communities, usually increasing the number of ant species foraging or nesting on a given tree (Powell et al. 2011). With all these aspects considered, it is possible that, in many cases, a non-random co-occurrence pattern of species association may result from distinct habitat use and not interspecific competition, as it is often claimed. Nevertheless, most arboreal ant datasets are not structured in a way that allows for co-occurrence analyses to systematically address the potential influence of environmental factors on community assembly.

In this study, I assessed the extent to which coexistence patterns of arboreal ant species can be explained by interspecific competition or by habitat associations. I further addressed whether the biological characteristics of the most common ant species in the community, such as nesting preferences and recruitment strategies, can explain the patterns we recover. I achieved this with data from a Neotropical savanna, where the natural habitat gradients and canopy accessibility allowed for an extensive biodiversity survey, structured by tree size, tree species, and canopy connectivity, and where the biological characteristics of ant species were quantifiable. I used a suite of null model to analyze these data. More specifically, I first accounted only for the species incidence in the community, and then explicitly incorporated habitat attributes in the null models. I performed all analyses first with all ant species in the community, and then with only the most frequent ant species. Moreover, since the community-wide analyses can hide relevant species interactions in the community (Veech 2014), I also searched for co-occurrence patterns of different species pairs (pairwise analyses). Following that, I assessed similarities in key biological properties of the most common ant species in

order to understand the observed pairwise analyses results. Overall, I aimed to answer three main questions: a) do arboreal ant community co-occurrence patterns in a Neotropical savanna deviate significantly from that expected under a process of random community assembly? b) to what extent do these co-occurrence patterns change when we account for potentially important habitat attributes? c) to what extent can the observed co-occurrence patterns be explained by differences or similarities in key biological characteristics of the ant species?

Materials and methods

Study area

This study was conducted at the Reserva Ecológica do Panga (REP), a 404 ha reserve located 35 km south of Uberlândia, Minas Gerais, Brazil (19°10' S, 48°23' W). The region is characterized by a tropical climate with two well-defined seasons: a dry winter, from May to September, and a rainy summer, from October to April. The temperature and mean annual precipitation are of 22° C and 1650 mm, respectively. The REP has different kinds of typical Neotropical savanna (*Cerrado*) vegetation, from open grasslands to gallery forests (Cardoso et al 2009). This study was conducted in *cerrado ralo* (open savannas therein) and *cerrado sensu stricto* (closed savanna therein) areas.

Ant sampling

I collected ants on 240 trees belonging to six different species, totalling 40 trees of each of the following species: *Caryocar brasiliense* Cambess. (Caryocaraceae), *Qualea grandiflora* Mart. (Vochysiaceae), *Stryphnodendron polyphyllum* Mart. (Fabaceae), *Sclerolobium aureum* (Tul.) Benth. (Caesalpinaceae), *Machaerium opacum* Vogel (Fabaceae) and *Kielmeyera coriacea* Mart. & Zucc. (Clusiaceae). These tree species were chosen because they are common in the study area and in the Cerrado as a whole (Moreno 2005). Half of the trees were sampled in open savanna areas and the other half in closed savanna areas. Each tree species had the same number of individuals sampled in each vegetation type. The trees found in the open savanna were considered trees with lower connectivity and the trees found in the closed savanna as trees with higher connectivity. Trees from each species were classified in three size categories ('small', 'medium' and 'large') depending on their trunk diameter (measured 10 cm above the soil surface). I considered as 'small' those trees with a diameter up to 11.9 cm (60 trees), as 'medium' those between 12 and 21.9 cm (121 trees) and as large the ones with at least 22 cm of diameter (59 trees).

I used baited arboreal pitfall traps for the ant sampling, with the number of traps per tree ranging from 4 to 10, according to the size of the tree. On each tree, half of the traps contained honey diluted in water (1:7) and the other half contained human urine (diluted 1:1 in water) each with a small quantity of detergent to break the surface tension of the liquid, thus improving the killing efficiency. Each pitfall trap consisted of a small plastic cup (6 cm height and 5 cm diameter) with 80 ml of capacity. The traps were distributed throughout the trees and wired onto the stems approximately horizontally, and with the top rim touching the branch. The amount of liquids was of approximately 20 ml. The traps were left on the trees for 48 hr for the collection of both

diurnal and nocturnal ant species. The ants were sampled over a period of ten days, 24 trees on each day, with six plants of different species and different sizes on each sampling day.

Null models analyses

Co-occurrence metrics

I used the C-score (Stone & Robert 1990) to assess the co-occurrence patterns of the ant community. The C-score measures the mean number of checkerboard units between all possible pairs of species in a data matrix (Stone & Robert 1990). It can, however, also be used for analysis between a single pair of species. When compared to other indexes used to assess co-occurrence, the C-score has a smaller probability of type I and II errors (Gotelli 2000). The number of checkerboard units (CU) for each species pair is: $CU = (r_i - A)(r_j - A)$, where A is the number of shared sites (trees) and r_i and r_j are the occurrence numbers for species i and j respectively. In addition, I used a standardized version of the C-score, the St. C-score, which corrects for the differences in species incidence within the community (Azeria et al. 2009). For the standardized C-score, the number of CU is: $CU = (r_i - A)(r_j - A) / (r_i * r_j)$. Low values of CU indicate that the species have an aggregated distribution, possibly as a result of positive interactions. High values indicated that the species have a segregated distribution, probably as a result of interspecific competition or distinct habitat preferences. Finally, I used the Sorensen index (Dice 1945) to measure the mean number of shared sites (i.e. trees in our study) between the different pairs of species: The index is calculated as $SOR = 2A / (2A + B + C)$ where A represents the number of shared sites between species r and j , while B represents the number of sites where species r is present and species j is absent, and C is the converse of B .

The magnitude of the C scores and the Sorensen index depend on the frequency of occurrence of the species, thus precluding a direct interpretation of the observed values. Accordingly, observed values of these statistics can be assessed by comparing to a distribution generated by a null model. This is done by calculating a standardized effect size (SES), so that results are comparable across communities, pairs of species and even with other studies. The SES is calculated as follows: $SES = (\text{observed index value} - \text{mean of simulated index values}) / \text{standard deviation of simulated index values}$. For the C-score and St. C-score a negative SES indicates an aggregated community, which can be related to the existence of strong positive interactions (e.g. facilitation) or similar habitat preference. A positive SES indicates a segregated community, which can be related to agonistic interactions or distinct habitat preferences. For the Sorensen index, positive and negative values indicate a segregated and aggregated community, since it is a measure of species ‘togetherness’. The significance of the observed SES values was computed as the proportion of simulated values equal to or more extreme than the observed value (Gotelli 2000).

Unconstrained versus habitat-constrained null models

I used two different classes of null models: one that takes into account only aspects of the species occurrence and site species richness of the original matrix (‘unconstrained null models’), and one that incorporates the species specificity for a given habitat on the species null distribution (‘habitat-constrained null models’) (Sfenthourakis et al. 2006, Azeria et al. 2012). The unconstrained model was contrasted against three different habitat-constrained models, each using a different environmental variable. The environmental variables used in the habitat-constrained models were: tree species (*Caryocar brasiliense*, *Qualea grandiflora*, *Stryphnodendron polyphyllum*,

Sclerolobium aureum, *Machaerium opacum*, *Kielmeyera coriacea*), tree size (small, medium, large), and vegetation type (open or closed) as a proxy of tree connectivity. These three different environmental variables are related to the host plant characteristics and were chosen for their potential impact on ant species richness and composition (Djiéto-Lordon et al. 2004, Powell et al. 2011, Klimes et al. 2012).

The constrained null models differ from their unconstrained counterparts by restricting the randomization of occurrence values to the same level of the constraining factor. For instance, an ant species record found on the level '*Caryocar brasiliense*' of the factor tree species will be randomized among individuals of '*Caryocar brasiliense*'. It will not be assigned, during randomizations to generate simulated communities, to a different host plant species.

In the case where one of the indexes (e.g. C-score) is significant under both the unconstrained and habitat-constrained models, this would suggest that some interspecific interaction is indeed helping to explain the observed pattern. On the other hand, if the index is significant under the unconstrained model but not under the habitat-constrained model, it can be a sign that the habitat selection is more important for explaining the observed patterns than competition (Peres-Neto et al. 2001, Azeria et al. 2012).

Another possible outcome is that species pairs that are not significant under unconstrained analyses can be significant under habitat-constrained null models. This may indicate that there is a negative association *within* a shared habitat (for segregated pairs) or that the differences on the species affinity for a given habitat could have masked an otherwise positive interaction (for aggregated pairs) (Azeria et al. 2012).

Fixed-equiprobable (FE) and fixed-fixed (FF) null models

I used two types of constrained and unconstrained models null models: the fixed-equiprobable (FE) and the fixed-fixed (FF). In both models the frequencies of occurrence of each species are maintained (fixed columns). In the FF model, the original species richness on each tree is maintained (fixed rows), whereas in the FE mode, the species richness differences originally found among trees are eliminated, with all trees being equally probable of being colonized and host the same number of species (equiprobable rows).

Matrix level vs. pairwise approaches

Most of the methods used for co-occurrence analyses can be classified as either ‘matrix’ or ‘pairwise’ approaches. The matrix approach calculates the co-occurrence metrics as a property of the whole presence/absence species matrix (Gotelli 2000, Pitta et al. 2012). I first calculated null models for whole matrices and then performed pairwise analyses to assess the co-occurrence for each species pair separately. This was done to determine if each possible pair in the community has an aggregated, segregated or random co-occurrence pattern (Gotelli & Ulrich 2012, Pitta et al. 2012, Veech 2014). I presented data for all the indexes here considered (C-score, St. C-score and Sorensen) on the matrix level analyses. However, for the pairwise analyses I presented data for only one of the indexes (C-score), since the outcomes were quite similar between the different indexes.

For the whole matrix approach, I did analyses first including all the sampled ant species and then only the 14 most frequent ant species. For the pairwise approach, I did analyses only with the 14 most frequent ant species. Restricting the pairwise analyses to the common species avoids the loss of statistical power associated with species that

presented few occurrences (i.e., were rare). These 14 ant species were chosen because they were found in at least 5% of the sampled trees (i.e., in 20 trees or more). These 14 ant species also included the most abundant species in the community, representing 93% of the total number of ants collected in all sampled trees.

Matrix randomizations

I ran 5,000 randomizations for each null model. Randomizations according to the FF null model were done using the function ‘commsimulator’ in R environment version 3.3.3 (R Development Core Team 2014), available in the ‘vegan’ package (Oksanen et al. 2013). The FF simulated communities were obtained using the ‘quasiswap’ algorithm, where each simulation uses the original matrix and not the previous randomized matrices (Gotelli & Entsminger 2001, 2003). I wrote R routines for the pairwise analyses, the FE null model and the constrained analyses.

Species-habitat associations

I assessed whether ant species were associated to a particular tree species, to a particular tree size, or to trees with low or high degree of connectivity using the Indicator Species Analysis (Dufrêne & Legendre 1997). This analysis estimates the strength of the association of different species with distinct groups of sites (Caceres & Legendre 2009). I used the IndVal program of Dufrêne & Legendre (1997) and assessed the significance of the indicator values for each species using Monte Carlo’s permutation tests with 5,000 randomizations.

Nesting and foraging habits of the most common ant species

Ant nesting habits

To assess the nesting habits of the 14 most common species I opened and measured stems of different sizes belonging to 20 trees of each of the six plant species studied. I opened and measured at least six different branches from each tree. For each ant nest found, I measured the mean length of the cavity used as nesting site. Nests were classified as located in: ‘small live branches’, ‘small dead branches’, ‘medium live branches’, ‘medium dead branches’, ‘large live branches’, ‘large dead branches’, ‘very-large live branches’, ‘very-large dead branches’ and ‘under the tree bark’. Small sized branches were those of up to 5 cm of length, medium sized as those from 5.1 to 25 cm, large sized those from 25.1 to 50 cm and very-large sized those with more than 51 cm of length. Since I always opened at least six different stems on a single tree I was able to assess if a given ant species is polydomous (i.e. has multiple nests on a tree, with at least one non-queen) or not.

Ant activity schedule and recruitment to baits

I observed the same set of 175 plants during the day and a subset of 44 trees during the night. The ant species were classified as ‘diurnal’ if they were only or mostly seen foraging during the day, ‘nocturnal’, if they were seen only or mostly during the night and ‘both’ if they were seen foraging both during the night and day. On the same set of trees, I placed approximately 10 mg of sardine in each tree, and observed the ant activity on each of three hours of observation. On each observation, I counted the number of ants of each species present on a given sardine bait. If the same ant species remained in the bait for more than one observation, I accounted for the one with the maximum number of workers. After that, I placed the ants on four different categories of recruitment size: ‘small’, between 1 and 5 workers, ‘medium’, from 6 to 10 workers, ‘large’, from 11 to 25 workers and ‘very-large’, with more than 25 workers.

Results

Description of the community and habits of the most common species

Overall, I collected 75 ant species from 17 genera (Table S1). Most ant species had a very low frequency on the community, with only 14 species of the species occurring on at least 20 of the 240 sampled trees. The most frequent species included five species of *Camponotus*, four species of *Pseudomyrmex*, one *Azteca*, one *Cephalotes*, one *Crematogaster*, one *Solenopsis* and one *Tapinoma*. The nesting and foraging habits of these 14 species are presented in Table 2. Most species of *Pseudomyrmex* are strictly diurnal, recruit very few workers to baits, and nest exclusively in small branches. Among the *Camponotus* species, one (*Ca. melanoticus*) was only found nesting in cavities located in live branches of medium size, one (*Ca. sericeiventris*) only in cavities located in large and very-large sized live branches, whereas the remaining three species nest in branches of small, medium and large size (Table 2). Three of the *Camponotus* species are strictly nocturnal whereas the remaining two forage during the day and the night. Five of the 14 species have polidomic nests, but only three of those (*Azteca* sp. 1, *Crematogaster ampla*, and *Cephalotes pusilus*) build very large colonies whose nests are located in live and dead branches of any size.

With the exception of *Azteca* sp. 1, which was found mostly on *S. aureum* trees (Table S2), none of the remaining species presented a significant association with a given tree species (Indicator Species Analysis, Table S2). Similarly, with the exception of *Ca. sericeiventris* which was mostly found on trees located in the closed savanna habitats (high canopy connectivity), none of the remaining ant species showed a significant association with a given vegetation type. However, four of the 14 species

analyzed showed significant associations with trees of a given size (3 species with small trees and one with large trees) (Table S2).

Null models analyses

Matrix level co-occurrence analyses

The analyses with all the 75 ant species in the community showed random patterns under the unconstrained models for all the indexes here used (Table 1). Similarly, in most cases, the habitat-constrained models showed random patterns of co-occurrence. The only exception was the FE model constrained by tree size for which the SES for the C-scores (but not the Sorensen index) were significantly smaller than the values generated by the null models, thus indicating an aggregated pattern of co-occurrence (Table 1).

When I considered only the 14 most common ant species in the community, a random pattern of co-occurrence was detected in all FE models run, including the unconstrained and the constrained models (Table 1). In contrast, for all the FF models, and for two of the three indexes calculated (St. C-score and Sorensen) a significantly segregated pattern was detected (Table 1).

Pairwise level co-occurrence analyses

The pairwise analyses of the 14 most frequent species showed that 22% of the pairs analyzed (20 out of 91) have significantly non-random co-occurrence patterns under either the FE or FF unconstrained models (Table S3). The number of aggregated and segregated species pairs was similar under both null models, with 8 aggregated and 11 segregated pairs in the analyses using the FE null model and 7 aggregated and 12 segregated pairs using the FF model (Table S3). Furthermore, the identities of the

aggregated and segregated species pairs were mostly the same under the two null models (Table S3).

Only four of the 20 aggregated or segregated pairs according to the unconstrained models became non-significant under one or more of the constrained models (Table S3). Also, only three of the non-significant species pairs according to the unconstrained models became significant with the habitat constrained models (Table S3).

Looking at the 10 pairs that were segregated under both the unconstrained and constrained models it can be noticed that, in most cases, both species of the pair present similar nesting/foraging habits (Table 3). For instance, both *Azteca* sp. 1 and *Crematogaster ampla*, forage during the day and the night, nest in live and dead branches of any size, recruit massively to baits, have polidomic nests and large colonies (Table 2 and 3). Similarly *Pseudomyrmex gracilis* and *Pseudomyrmex urbanus*, which also presented a significant segregated co-occurrence pattern, are strictly diurnal species that only nest in small and medium branches. In contrast, species that formed aggregated pairs rarely shared the same nesting or foraging characteristics (Table 3).

Discussion

I assessed the potential role of interspecific competition and habitat selection on the organization of an arboreal ant community in a Neotropical savanna. I did this by taking advantage of a dataset that took into account the characteristics of the host-trees (species, size and connectivity) and of the most common ant species in the community. The matrix level co-occurrence analyses showed random pattern of species associations when all ant species were considered, but a significant segregated pattern when

accounting only the 14 most common ant species. Moreover, the pairwise analyses indicated a significant number of segregated and aggregated species associations among these most common ant species. Few of the significant segregated associations became non-significant when the species, size or the connectivity of the host-tree are taking into account. This is in agreement with the fact that few species showed significant association with a given tree species or with trees of a given size or habitat, and for most of the species that did show, the strength of the association was rather low. Overall the results suggest that these segregated associations were explained mainly by competitive interactions between species, not by habitat selection. This was further evidenced by the comparisons of the nesting and foraging habits of the species that formed segregated pairs. Species that formed these pairs almost always shared the same nesting or foraging characteristics, whereas those that formed aggregated pairs did not. Overall, I showed the extreme importance of an approach based on multiple niche aspects of the species to the understanding of the factors leading to arboreal ant community assembly.

Matrix and pairwise level analyses

The matrix level co-occurrence analyses failed to detect any pattern of species association when we accounted for all 75 ant species in the community. However, matrix level analyses represent an average of values calculated for all individual pairs of species (Gotelli 2000). Therefore, important species interactions in the studied community may be obfuscated in analyses with many species (Gotelli & Ulrich 2012), since strong interactions can be diluted by weaker ones and even cancel each other if both positive and negative interactions exist (Diamond & Gilpin 1982, Sanderson 2004). This may help to explain why contrasting results were obtained in the analyses

involving the whole community and those using only the 14 most common ant species. In the latter case, strong evidence of a segregated co-occurrence pattern was obtained.

Furthermore, with the pairwise analyses, I found a relatively large number (~21%) of non-random species associations, either segregated or aggregated, thus well above the number expected to occur by chance alone (5%). In an analysis of species pairs associations from 30 published matrices, Sfenthourakis et al. (2006) showed that only 8 matrices had a number of deviations (segregation or aggregations) higher than 5%, with just 3 matrices having more than 10%. My results and those of Sfenthourakis et al. (2006) clearly indicate the need of both matrix and pairwise level analyses to the assessment of species associations in a community. Moreover, it also calls for the possibility of novel results with the use of a pairwise approach in a reassessment of already published arboreal ant co-occurrence matrices.

Habitat attributes

The simple detection of a significant species association has been frequently used as enough evidence to infer a specific ecological process. As different processes may produce the same pattern, these inferences are usually very weak and open to criticisms (Strong et al. 1984, Gotelli & Graves 1996). However, the structured nature of the present dataset allowed me to take the next step and evaluate the relative importance of host-plant selection in explaining the observed patterns. Here, I have found that when information about the host-plants was taken into account the results of our analyses changed very little. In fact, the significance of the observed matrix-wide analyses did not change with the inclusion of host-plant attributes for the 14 most common ant species. Moreover, only a small proportion (20%) of the significant pairwise species associations became non-significant with the inclusion of host-plant

characteristics. This indicates that, for arboreal ants, species aggregations are rarely due to shared host-tree preferences. Similarly, in most cases, species segregations could not be attributed to distinct host-tree preferences between ant species. These results probably reflect the fact that none of the most common species in our community showed strong affinities for trees from a given habitat, size or species (Table S2). My results contrast with those of Azeria et al. (2012) who showed that co-occurrence patterns of saproxylic beetles are largely modulated by the species and size of the host-tree.

Species biological characteristics

Since the influence of host-plant attributes was limited, niche partition among arboreal ant species might lay on differences on the ants themselves (i.e. in their biological traits). If niche-based processes are important to control arboreal ant communities, it would be expected that a) co-occurring species would converge on certain traits because of establishment and/or survival constraints imposed by the abiotic environment (i.e. environmental filtering) (Fowler et al. 2014) or b) co-occurring species would diverge on these traits due to competition (i.e. niche differentiation) (Chesson 2000, Adler et al. 2014). I found stronger support for the latter case, since the co-occurring (aggregated) species had fewer similarities in common than the segregated species, a mechanism invoked to explain coexistence of species and avoid competitive exclusion (MacArthur & Levins 1967).

Nesting sites on trees can be very limited (Philpott & Foster 2005, Blüthgen & Feldhaar 2010), with many ant species showing some level of specialization over the use of these resources (Powell et al. 2011). Therefore, we should expect strong competition over shelter resources in arboreal ant communities. Also, competition for

this resource should be even stronger between polidomic species, which have bigger colonies and use a large proportion of the cavities available in their host trees. Concordantly, one third of the segregated pairs were formed by polidomic species.

Another important aspect to define the directions of interspecific associations was the activity period of the ant species. Almost half of the negatively associated pairs were formed by species foraging on the same time schedule. Indeed, there are a number of studies showing the importance of activity time for ant species coexistence (Cerdá et al. 1997, 1998, Stringer et al. 2007, Lessard et al. 2009). In some cases, subordinate species are better adapted than the dominant ones for foraging at extreme temperatures, avoiding direct interactions with the dominant species and the possible exclusion from a habitat patch (Bestelmeyer et al. 2000). However, this has been rarely tested in tropical habitats (Wittman et al. 2010). Also related to the ants foraging strategies were the ant recruitment rates. Between the co-occurring ant species, the recruitment rates were almost always different, which can mean that there is a trade-off between these ants on the ability to find new resource and to dominate or even monopolize them. In this trade-off, also known as ‘discovery-dominance’, ants usually differ on their recruitment ability, with superior competitors with lower recruitment rates and inferior ones investing all the energy of the colony in finding resources (Fellers 1987, Parr & Gibb 2012).

Competition on ant communities: is the mosaic theory supported?

Ant communities are often thought to be structured by interspecific competition (Hölldobler & Wilson 1990), but many assumptions allowing for such interpretation still need to be properly tested (Cerdá et al. 2013). One of these assumptions states that arboreal ant communities are spatially distributed in a mosaic formed by the mutually

exclusive territories of dominant ant species (Leston 1970, Room 1971, Majer 1972). In the classical examples of ant mosaic, the competition over territory is limited to behaviorally dominant species with large colonies (Blütgen & Stork 2007). In my study system, only two species (*Azteca* sp. 1 and *Crematogaster ampla*) fulfilled this criterion of dominance and never co-occurred on the same individual tree. It is interesting to note that these two species are ecologically very similar, using similar nesting sites, having polidomic nests, foraging during both day and night, with a massive recruitment capacity and a small body size. Moreover, these ant genera (*Azteca* and *Crematogaster*) are characterized by the presence of a modified proventriculus that enables them to harvest liquid food resources in a very effective way, reinforcing their dominance status (Davidson 1997, Davidson et al. 2004, Davidson 2005).

One of the expected patterns of the ant mosaic theory, however, is not only the mutual exclusion of the dominant ant species, but also some positive associations, especially between the subdominant and subordinate species (Blüthgen & Stork 2007). Indeed, I found a mixture of negative and positive associations between the most common ant species. Moreover, all aggregated associations formed inside the subset of the most common species did not have the presence of either *Azteca* sp. 1 or *C. ampla*, i.e. were only formed by subdominant and subordinate ant species. Overall, the observed influence of competition on community assembly, the presence of species with mutually-exclusive territories and the mixture of positive/ negative interactions between the non-dominant ants give support for the ant mosaic theory.

Conclusion

I provided evidence that assembly of the studied arboreal ant community is, at least in part, determined by niche-based mechanistic processes. When accounting for

the most common ant species I detected a strong segregation of the ant community. Moreover, despite the majority of the species pairs not forming significant associations and the lack of strong signs of habitat choices, I could find strong associations between biological characteristics and the significantly segregated or aggregated species pairs. These findings showed the importance of niche differentiation in determining the coexistence in our arboreal ant community. I am aware that other factors not detected here can also be important to explain the community organization and therefore encourage future works exploring novel approaches and different datasets than the ones used here. To my knowledge, this is one of the few works to integrate a suite of ecological features that allowed the inference of processes generating co-occurrence patterns on arboreal ant communities.

Tables

Table1: Co-occurrence patterns at the community level of arboreal ant under unconstrained and habitat constrained analyses and under two null models (FE = Fixed species frequency and Equiprobable frequency of occurrence on tree sites; FF = Fixed species frequency and Fixed frequency of occurrence on tree sites). Negative values of Standardized Effect Size (SES) indicate aggregation between species pairs while positive values indicate segregation between species pairs. (SES in bold and with * indicates values of $p < 0.05$).

Species Matrix	Unconstrained		Habitat constrained					
			plant species		plant size		plant connectivity	
	FE	FF	FE	FF	FE	FF	FE	FF
a) All 75 ant species								
SES of C-score	-1.55	0.69	-1.86	0.21	-2.05*	0.22	-1.57	0.78
SES of St. C-score	-1.73	-0.93	-1.81	-1.11	-2.03*	-1.06	-1.79	-1.03
SES of Sorensen	1.39	0.61	1.08	0.32	1.12	0.34	1.43	0.79
b) The 14 most frequent ant species								
SES of C-score	-1.42	-1.7	-1.51	-1.62	-1.47	-1.62	-1.48	-1.59
SES of St. C-score	1.41	4.27*	1.35	4.21*	1.43	4.28*	1.38	4.2*
SES of Sorensen	-0.84	-3.87*	-0.78	-3.65*	-0.86	-3.75*	-0.8	-3.67*

Table 2: Biological characteristics of the 14 most common ant species in the study area.

Ant species	Species biological properties											
	Nesting habits								Other			
	Live small branches	Dead small branches	Live medium branches	Dead medium branches	Live large branches	Dead large branches	Live very-large branches	Dead very-large branches	Under bark	Polidomic nests	Activity period	Recruitment
<i>Azteca</i> sp. 1	X	X	X	X	X	X	X	X		yes	both	XL
<i>Ca. melanoticus</i>					X					no	nocturnal	M
<i>Ca. sericeiventris</i>					X	X	X	X		no	both	M
<i>Ca. atriceps</i>			X	X	X	X	X	X		no	nocturnal	L
<i>Ca. bonariensis</i>			X	X	X	X				no	nocturnal	L
<i>Ca.senex</i>	X	X	X	X	X	X				no	diurnal	M
<i>Ce. pusilus</i>	X	X	X	X	X	X	X	X		yes	both	L
<i>Cr. ampla</i>	X	X	X	X	X	X	X	X		yes	both	XL
<i>P. curacaensis</i>	X	X	X	X						no	diurnal	S
<i>P. elongatus</i>	X	X	X	X						no	both	S
<i>P. gracilis</i>	X	X	X	X						no	diurnal	S
<i>P. urbanus</i>	X	X	X	X						no	diurnal	S
<i>Solenopsis</i> sp. 1	X	X	X	X					X	yes	Both	XL
<i>Tapinoma</i> sp. 1	X	X	X	X					X	yes	Both	XL

Table 3: Species characteristics in common inside each significant species pair on a) segregated pairs and b) aggregated pairs:

Species pairs	Species biological characteristics			
	Nesting habits		Other	
	Both have same nest structure?	Both have polidomic nests?	Both have same activity period?	Both have same recruiting strategy?
a) Segregated pairs				
<i>Azteca</i> sp. 1 X <i>Ce. pusillus</i>	yes	yes	yes	
<i>Azteca</i> sp. 1 X <i>Cr. ampla</i>	yes	yes	yes	yes
<i>Azteca</i> sp. 1 X <i>Solenopsis</i> sp. 1		yes	yes	yes
<i>Azteca</i> sp. 1 X <i>Tapinoma</i> sp. 1		yes	yes	yes
<i>Ca. bonariensis</i> X <i>Ca. atriceps</i>			yes	yes
<i>Ca. bonariensis</i> X <i>Ca. sericeiventris</i>				
<i>Ca. senex</i> X <i>Ce. pusillus</i>				
<i>Ce. pusillus</i> X <i>Cr. ampla</i>	yes	yes	yes	
<i>P. curacauensis</i> X <i>P. urbanus</i>	yes		yes	yes
<i>P. gracilis</i> X <i>P. urbanus</i>	yes		yes	yes
b) Aggregated pairs				
<i>Ca. atriceps</i> X <i>Ca. sericeiventris</i>				
<i>Ca. bonariensis</i> X <i>P. urbanus</i>				
<i>Ce. pusillus</i> X <i>P. curacauensis</i>				
<i>P. gracilis</i> X <i>Ce. pusillus</i>				
<i>P. gracilis</i> X <i>Tapinoma</i> sp. 1				
<i>Tapinoma</i> sp. 1 X <i>Ca. sericeiventris</i>			yes	

Supporting Information

Table S 1: List of ant species/ morphospecies, divided by the genera and the subfamily they belong to, together with number of trees where these ant species were collected in this study. (Species with an * are those amongst the 14 most common).

Ant species	Number of trees
DOLICHODERINAE	
<i>Azteca</i> sp. 1*	55
<i>Azteca</i> sp. 3	2
<i>Dolichoderus bispinosus</i>	4
<i>Dolichoderus lamellosus</i>	12
<i>Dolichoderus lutosus</i>	15
<i>Dorymyrmex</i> sp. 1	5
<i>Dorymyrmex</i> sp. 2	2
<i>Tapinoma</i> sp. 1*	62
ECTATOMMINAE	
<i>Ectatomma tuberculatum</i>	1
<i>Gnamptogenys</i> sp. 1	1
FORMICINAE	
<i>Brachymyrmex</i> sp. 1	3
<i>Camponotus arboreus</i>	6
<i>Camponotus atriceps</i> *	81
<i>Camponotus balzani</i>	3
<i>Camponotus blandus</i>	9
<i>Camponotus bonariensis</i> *	123
<i>Camponotus cingulatus</i>	14
<i>Camponotus fastigatus</i>	3
<i>Camponotus innocens</i>	1
<i>Camponotus lespesii</i>	3
<i>Camponotus melanoticus</i> *	28
<i>Camponotus senex</i> *	164
<i>Camponotus sericeiventris</i> *	34
<i>Camponotus</i> sp. 15	13
<i>Camponotus</i> sp. 20	2
<i>Camponotus</i> sp. 37	10
<i>Camponotus</i> sp. 58	11
<i>Camponotus</i> sp. 6	14
<i>Camponotus</i> sp. 65	2
<i>Myrmelachista</i> sp. 1	4

Myrmelachista sp. 2 1

MYRMICINAE

Atta laevigatta 3

Cephalotes adolphi 1

Cephalotes angustus 2

Cephalotes atratus 3

Cephalotes clypeatus 1

Cephalotes cordatus 2

Cephalotes depressus 1

Cephalotes eduarduli 1

Cephalotes grandinosus 9

Cephalotes liepini 2

Cephalotes maculatus 4

Cephalotes minutus 2

Cephalotes pallidoides 4

Cephalotes pellans 5

Cephalotes persimilis 7

*Cephalotes pusillus** 131

Cephalotes specularis 2

*Crematogaster ampla** 20

Crematogaster sp. 2 2

Crematogaster sp. 4 1

Nesomyrmex asper 1

Nesomyrmex sp. 2 3

Pheidole sp. 1 5

Pheidole sp. 3 5

Pheidole sp. 6 5

Pheidole sp. 7 2

Solenopsis sp. 1* 21

Solenopsis sp. 2 3

Wasmania sp. 1 7

PONERINAE

Hypoponera sp. 1 1

Neoponera villosa 13

PSEUDOMYRMICINAE

*Pseudomyrmex curacaensis** 44

*Pseudomyrmex elongatus** 28

*Pseudomyrmex gracilis** 149

Pseudomyrmex kuenckeli 4

Pseudomyrmex maculatus 2

Pseudomyrmex lizeri 2

Pseudomyrmex sericeus 3

Pseudomyrmex simplex 7

<i>Pseudomyrmex</i> sp. 10	2
<i>Pseudomyrmex</i> sp. 11	2
<i>Pseudomyrmex tenuissimus</i>	10
<i>Pseudomyrmex unicolor</i>	3
<i>Pseudomyrmex urbanus</i> *	20

Table S 2: Species-habitat association, with the IndVal results of the 14 most common arboreal ants on our study area. Between brackets are the habitat characteristics most associated with a given ant species (Numbers with * indicates values of $p < 0,05$, with ** $p < 0,01$ and with *** $p < 0,005$).

Ant species	Tree species	Tree size	Vegetation type
<i>Camponotus senex</i>			
<i>Pseudomyrmex gracilis</i>			
<i>Cephalotes pusilus</i>		26.24* (small)	
<i>Camponotus bonariensis</i>		26.27* (small)	
<i>Camponotus atriceps</i>		21.86** (Large)	
<i>Tapinoma</i> sp. 1			
<i>Azteca</i> sp. 1	13.14* (SA)		
<i>Camponotus melanoticus</i>			
<i>Pseudomyrmex curacaensis</i>			
<i>Camponotus sericeiventris</i>			12.97* (closed)
<i>Pseudomyrmex elongatus</i>			
<i>Solenopsis</i> sp. 1			
<i>Crematogasters ampla</i>			
<i>Pseudomyrmex urbanus</i>		11.83*** (small)	

Table S 3: Pairwise co-occurrence patterns of the 14 most common ant species in our study. S= segregated associations, A= aggregated associations.

Species pairs	Unconstrained		Habitat constrained					
			plant species		plant size		tree conectivity	
	FE	FF	FE	FF	FE	FF	FE	FF
<i>Ca. senex</i> X <i>Ce. Pusillus</i>	S	S						
<i>Ce. pusillus</i> X <i>Cr. Ampla</i>	S	S						
<i>Ca. bonariensis</i> X <i>Ca. atriceps</i>	S	S						
<i>Ca. bonariensis</i> X <i>Ca. sericeiventris</i>	S	S						
<i>Azteca</i> sp. 1 X <i>Solenopsis</i> sp. 1	S	S						
<i>Tapinoma</i> sp. 1 X <i>Azteca</i> sp. 1	S	S						
<i>Azteca</i> sp. 1 X <i>Cr. Ampla</i>	S	S						
<i>P. gracilis</i> X <i>P. urbanus</i>	S	S						
<i>Ce. pusillus</i> X <i>Azteca</i> sp. 1	S	S						
<i>Ca. atriceps</i> X <i>Ca. melanoticus</i>	S	S	R		R			
<i>P. curacauensis</i> X <i>P. urbanus</i>	S	S						
<i>P. gracilis</i> X <i>Azteca</i> sp. 1	R	S		R		R		R
<i>Ca. atriceps</i> X <i>Tapinoma</i> sp. 1	R	R	A					
<i>Ce. pusillus</i> X <i>Ca. Atriceps</i>	R	R					A	
<i>P. gracilis</i> X <i>Tapinoma</i> sp. 1	A	R		A		A		
<i>Tapinoma</i> sp. 1 X <i>Ca. sericeiventris</i>	A	A						
<i>Ca. bonariensis</i> X <i>P. urbanus</i>	A	A						
<i>Ca. atriceps</i> X <i>Ca. sericeiventris</i>	A	A						
<i>Ca. senex</i> X <i>Ca. sericeiventris</i>	A	A		R				
<i>P. gracilis</i> X <i>Ce. pusillus</i>	A	A						
<i>Ce. pusillus</i> X <i>Ca. bonariensis</i>	A	A		R				
<i>Ce. pusillus</i> X <i>P. curacaensis</i>	A	A						

CAPÍTULO 2

**Nesting patterns of arboreal ants are affected by heterogeneity in nest
entrance sizes and the presence of a dominant species**

Abstract

Niche based processes, like interspecific competition, are considered as extremely important to determine the diversity of ant communities. Competition should be even stronger over resources that are limited, like shelter. Arboreal ant species rely on the existence of empty cavities produced by wood boring beetles as nesting sites. There is a strong variation in the sizes of the exit holes of these cavities, and it is suggested that well defined nest site preferences have evolved in the majority of arboreal ant species. Being so, it is expected that the greater the diversity of nesting sites the greater the diversity of ants using them. However, some ant species can be extremely abundant and generalists, using a large number of available cavities, being capable to exclude many other ant species from these resources. These species can be considered as dominants over shelter resources, and may, therefore, have a strong influence on the species assembly of nesting ants. Here, I aimed to understand the importance of the diversity of shelter resources for canopy ants in nest site occupation patterns. I also assessed how the presence of a dominant species influenced the use of these essential resources, either reinforcing or interacting with the effects of shelter diversity on arboreal ant community assembly. For this, I set up an experiment in 80 trees of the same species, where we placed 27 cavities of different entrance holes sizes divided in two treatments: high entrance diversity, with 9 different entrance sizes (0.15 to 0.55 mm) and low entrance diversity, with only 3 different entrance sizes (0.15 to 0.25). I considered *Cephalotes pusillus* as the dominant species over nesting resources, since it occupied 37% of the artificial cavities and was present in ~ 47% of the experimental trees. I found no differences in the number of colonized nests per tree between the treatments, but found significantly more nesting ant species in the high entrance diversity treatment. Furthermore, I found a strong relationship between the mean head width of the 12 most common ant species and the entrance sizes they used for both treatments. All ant species considered used larger diameter cavities in the high than in the low entrance diversity. I found significant effects of the presence of the dominant species, with less species richness and mean number of nests colonized by other ant species per tree in the presence of *C. pusillus*. I also detected changes in the mean entrance size used by other ant species in the presence of *C. pusillus*. Overall, I showed that both the diversity of nesting resources and the presence of a dominant species can have a significant

influence on arboreal ant assemblages, influencing the diversity of nesting ants and their cavity use patterns.

Key words: Artificial cavities, Brazil, canopy, *Cerrado*, niche differences, resource specialization, species coexistence.

INTRODUCTION

Niche differences between organisms may be essential to promote species coexistence and therefore the diversity patterns observed in biological communities (Chesson 2000, Chase & Leibold 2003, Levine & HilleRisLambers 2009). These niche differences can often reflect in resource use specialization by many species, and a high heterogeneity of these resources can lead to a high level of species diversity (Armbrecht et al. 2004). In many cases, however, other factors not directly related to niche aspects may also influence the coexistence of different species in a community (Andersen 2008). One example is the presence of dominant species (Andersen 2008), which can be extremely frequent and abundant, usually showing low levels of resource specialization. These dominant species can directly interact with most other species and may use a large proportion of the essential, and sometimes limited, resources (Andersen 1992). Therefore, to better understand the processes underlying community diversity patterns it is important to assess not only differences in resources use between the organisms, but also the possible influence of ecologically dominant species.

Arboreal ants are diverse and abundant, particularly in tropical regions (Floren et al. 2014), being ideal for studies of the processes affecting the structure of biological communities. Moreover, the presence of dominant species is a common characteristic of many tropical arboreal ant communities (Blüthgen & Stork 2007). Several studies have evaluated the importance of resources diversity (Armbrecht et al. 2004, Philpott & Foster 2005, Powell et al. 2011) or the presence of dominant species (Philpott 2010) in shaping arboreal ant assemblages. However, except for the case of obligate ant-plant mutualisms (Stanton et al. 2002, Palmer et al. 2002, Palmer et al. 2003), these two aspects were rarely considered together, and whether their effects interact with or reinforce each other remains an open venue of investigation.

Nesting resources can be extremely limited on the tree canopy (Blüthgen & Feldhaar 2010) and therefore, we should expect some interspecific differentiation over their use in order to avoid competitive exclusion. As nesting sites, ants use mostly empty cavities produced by wood boring beetles (including many species of Buprestidae, Cerambycidae and Curculionidae, among others (Calderon-Cortés et al. 2011, Satoh et al. 2015)). These cavities are produced as the beetles lay their eggs on the trees and their larvae burrow into the wood for feeding, creating a tunnel system by the end of the larval stage (Linsley 1959). After enclosing, adults chew an exit hole and disperse (Linsley 1959, Lieutier et al. 2004). The exit holes are typically just large enough to allow the adults to pass through, and thus have taxon-specific shapes. Consequently, the differences in exit holes size and shape can lead to different ant species using different sets of cavities according to their morphology (Satoh et al. 2015). In fact it is suggested that well defined nest site preferences have evolved in the majority of arboreal ant species. This ecological specialization is particularly high in some ant genera, like *Cephalotes* (Powell 2008, 2009), but can also be true for the community as a whole (Powell et al. 2011). Furthermore, it should be expected a relationship between the diversity of beetle engineered cavities and the diversity of arboreal ant species.

Another important feature of most arboreal ant communities, especially in the tropics, is the relatively high frequency of ecologically dominant species (Blüthgen & Stork 2007). Although the definition of dominant ant species can vary a lot, a common ground is that these species usually have a strong impact on other members of the community (Andersen 1992, Cerdá et al. 2013). However, so far, studies on dominant arboreal ants have focused almost only on competition over food resources (Andersen 1992, Cerdá et al. 1997, Blüthgen et al. 2004b), even though nesting resources are of

equal or even greater importance for arboreal ants (Philpott & Foster 2005, Davidson et al. 2006, Powell et al. 2011). Their limited nature implies the possibility of strong competition over their use (Blüthgen & Feldhaar 2010). In fact, many studies of arboreal communities show that some ant species are not just more frequent and abundant on the top of the trees, but also uses most of the available shelter resources (Powell et al. 2011, Camarota et al. 2015). Despite being reasonable to recognize these species as dominants over shelter resources, there still a need of studies showing properly if their presence have an impact on resources use by the other members of the community.

To effectively assess the influence of the diversity of nesting resources on arboreal ants' diversity patterns and the impact of dominant species over it, it is essential to perform experiments involving the manipulation of these resources. However, given the inherent difficulties in reaching the canopy of tropical forests, these types of experiments are rarely done (but see Klimes et al. 2012). Assess to tree crowns is comparatively much easier in savanna trees, as is the case in the savannas of central Brazil, known locally as *Cerrado*. These savannas are characterized by a loosely interconnected tree canopy of approximately 2-8 m in height (Oliveira-Filho & Ratter 2002). In common with other tropical systems, the *Cerrado* have an abundant and diverse arboreal ant community that nests almost exclusively in preexisting arboreal cavities made by wood boring beetles (Oliveira et al. 2004), making it ideal for experiments concerning the diversity of arboreal ants.

In this study I aimed to understand not just the importance of the diversity of shelter resources to promote the diversity of canopy ants, but also how the presence of a dominant species influences the use of these essential resources by other members of the community. For this, I performed an experiment in which I supplied artificial nests

with varying entrance sizes to ant-defaunated trees. Firstly, I assessed the levels of specialization of the different ant species to their nesting resources. If there was a significant specialization, then IT should be expected that a wider range of nesting entrance sizes would increase the diversity of nesting ants and the number of colonized nests. Then, after defining the dominant species over shelter resources, I assessed whether its presence would have a significant impact on the patterns of use of artificial nests by non-dominant species. Since dominant ants can control a significant proportion of the available nests, I predicted that their presence would decrease the occupation rate and species richness of non-dominant ants. Furthermore, I also expected that, in the presence of dominant ants, the non-dominant species would change their nesting site preferences to avoid competitive exclusion from the trees. More specifically, I gathered information to answer the following questions: a) Is there an influence of nest entrance diversity on ant species diversity and the number of occupied nests?; b) Does the preferences for different entrance sizes change accordingly to the different entrance diversity treatments?; c) Does the dominant species influence the diversity of nesting ants and the number of occupied nests by the other ant species?; d) Does that dominant species influence on the entrance sizes usage by the other ant species?

METHODS

Study area

This study was conducted at the '*Reserva Ecológica do Panga*' (REP) (19°10' S, 48°23' W), a 409 ha reserve located 35 km south of Uberlândia, Minas Gerais, Brazil. The region is characterized by a tropical climate with two well defined seasons: a dry winter, from May to September, and a rainy summer, from October to April. The temperature and mean annual precipitation are of 22° C and 1650 mm, respectively. The

REP has different kinds of typical Cerrado vegetation, from open grasslands to gallery forests (Cardoso et al 2009). The experiment was conducted in one type of savanna vegetation (*cerrado strictu senso*).

Nest diversity experiment

The experiment was set in the field in July of 2011 and it lasted for 18 months. I used 80 medium sized trees (diameters 15 cm above soil ranging from 13.9 to 27.1 cm) of *Caryocar brasiliense* (Caryocaraceae) a very common tree species in the studied area and in the Cerrado as a whole (Moreno 2009). Using only one species for the experiment controlled for potential differences in resource availability between different tree species. Before the beginning of the experiment all the ants were removed from the trees. I removed the ants from the trees in a way to control for the prior presence of other ant species, making all the trees equally probable sites of colonization by new species. For the ant removal, I exposed the ant colonies to the poison Fipronil in early June of 2011 (using a mixture of urine diluted in water (1:1) and the poison (12:1) in plastic cups fixed onto the trees), and subsequently baited twice to confirm that the colonies were actually killed. All woody vegetation that contacted experimental trees was cut at the initial experimental setup. After that, a rope was placed at each of four points to connect experimental trees to provide uniform connection with surrounding vegetation (cf. Powell et al., 2011).

I used two experimental treatments of entrance sizes diversity, with 40 trees per treatment (80 in total). I placed 27 artificial wooden nests on each individual tree. The two experimental treatments were the following: a) 'Low entrance diversity and lower range of entrance sizes (LE)' (three sizes- 0.15, 0.20, 0.25 cm²); b) 'High entrance diversity and wider range of entrance sizes (HE)' (nine sizes- 0.15, 0.20, 0.25, 0.30,

0.35, 0.40, 0.45, 0.50, 0.55 cm²). The choice of the entrance sizes of both LE and HE treatments was based on a prior study where 20 stems of each of six different tree species (20 trees of each species in total) including *C. brasiliense*, were opened and their cavities and entrance holes were quantified (Galen Priest et al. unpublished data). The LE treatment focused on the most commonly found entrance sizes (from 0.15 to 0.25 cm²) on the cavities of these sampled trees. The HE treatment represented an addition of less commonly found entrance sizes, representing a much broader entrance size range that can be used for the ants.

Nest collection and processing

After 18 months the nests were carefully collected, in a way to avoid the ants to escape from the cavities. On each nest I measured the diameter of entrance hole and searched for any modification on it. After that, I opened the cavity in a way to assess their inhabitants, counting the number of ants and sorting them inside each nest according to their castes (worker, soldier, gyne, male or queen) and stage of development (adult, incipient and brood). A nest was considered occupied if it had either: a) at least one queen; b) one or more workers and brood; c) or at least ten workers but no brood. This is the same criterion used in previous experiments (Camarota et al., 2015). In each nest, at least one ant specimen was collected and mounted for posterior identification to the level of species or morphospecies in the laboratory. In some cases the inhabitants were not ants, and were identified to the level of order.

Definition of dominant species

One species (*Cephalotes pusillus*) was considered as numerically dominant in our system since it was found in over one-third of the occupied nests, which is more than twice the number of nests occupied by the second most frequent ant species (see Results section).

Head width measurements

I performed head-width measurements of the nesting species in a way to assess the strength of the relationship between the mean entrance sizes used by each species and their mean head widths. I measured a minimum of 20 workers of each ant species that was present on at least five trees and occupied more than 10 nests ($n = 12$ species). Since there can be variations on the size between workers of different colonies, I always measured a maximum number of five workers on each colony, being at least four different colonies for each ant species measured.

Statistical analyses

Entrance diversity experiment

One tree was excluded prior to the statistical analyses, since it did not have any colonized nest. To compare the overall number of ant species nesting on trees from different treatments I built species accumulation curves (Gotelli & Colwell 2001) using the software EstimateS version 9.1.0 (Colwell 2015). I built sample based curves, first assessing for the observed number of species (using the Mao-tau statistics) and then the estimated number of species (using the Chao 2 statistics). For comparisons of the number of ant species per individual tree I used a t-test, with entrance diversity

treatment (LE or HE) as the predictor variable. The number of species was square-root transformed prior to the analysis, to suit the premises of the statistical test. I also did a t-test to compare the number of occupied cavities per tree between the two entrance treatments (LE or HE). Differences in community composition in trees according to their entrance treatments (LE or HE) were evaluated using a permutational multivariate analysis of variance (Permanova, formerly known as nonparametric Manova; Anderson 2001). The presence/ absence of each ant species on each tree was the response variable, whereas the predictor variable was the entrance treatment (LE or HE). Statistical significance was assessed through comparison with a null model (999 permutations of the original matrix).

To examine the level of specialization of the entrance size used by different species of ants, I performed a quadratic regression. I performed two regressions, one for the LE treatment and one for the HE treatment. The quadratic regression has the following equation: $y = ax^2 + bx + c$, with “y” being the mean entrance size used by different ant species and “x” their head widths. For all regressions, I considered only those species that occurred on a minimum of five trees and occupied more than 10 nests (n= 12 species).

Presence of a dominant species

To compare the differences in total ant species richness between trees with or without the dominant species I built species accumulation curves, with the software EstimateS version 9.1.0 (Colwell 2015). As before, I did both a observed species (Mao Tau) and an estimated species numbers (Chao 2) curve, but now I performed one of each curve inside a given entrance diversity treatment (LE or HE). To evaluate the effect of the dominant species on ant species richness (except the dominant) per tree I

used a two-way Anova, with entrance treatments and presence/ absence of the dominant species as main factors. The number of other ant species per tree was square-root transformed prior to the analysis to suit the premises of the test. I also used a two-way Anova to assess for differences in the number of occupied cavities of other ant species (except the dominant), with the entrance treatments and the presence of the dominant species as main factors. I evaluated if there were differences on ant species composition in relation to the presence of the dominant species with a Permanova. The presence/ absence of each ant species was our response variable and the entrance treatments (LE or HE) and the presence of the dominant species were the response variables. To examine if there were differences on the mean entrance size used by the other ant species with the presence of the dominant species I performed a non parametric paired t-test (Friedman test). I did a separate test for each treatment (LE or HE), based on differences on the mean entrance size used by each ant species with or without the dominant species.

RESULTS

Entrance diversity experiment

Originally 2160 nests were placed on the trees, but 157 (7.27 %) were lost during the experiment, either by falling on the ground, destruction by termites or occupation by other organisms. A total of 76 artificial nests were occupied by other organisms, with the occupants being mostly termites (33 nests), spiders (20 nests), bee larvae (13 nests) and cockroaches (nine nests). Of the 2003 nests that were collected, 831 (41.5%) were considered occupied according to the occupation criteria (see methods). Of the 831 nests recovered, 661 (79%) had brood on it and only 46 (0.55% of 831) had queens. There was a mean of 10.52 ± 0.49 occupied nests per tree. Of all 2003

nests, 217 (84.7%) were actively modified by ants, but not all of these nests were occupied when we collected them, with 82 (32%) empty ones. This indicates that these nests were occupied in the past but not anymore. Some nest entrance holes ($n=135$, 6.7%) were also actively modified by the ants, usually by diminishing ($n=65$) or augmenting it ($n=70$). I did not find any significant difference in the number of occupied nests between the HE and LE treatments with 9.8 ± 0.76 nests being occupied per tree on LE and 11.2 ± 0.61 on HE ($t=1.52$, $df=77$, $p=0.132$).

The different entrance sizes were used by a different numbers of species (Fig. 3). Moreover, I detected a significant relationship between the mean head size of the 12 most common nesting ant species and the entrance size they were using in both the LE treatments ($F_{3,9} = 326$, $R^2=0.746$, $p<0.001$) and the HE treatments ($F_{3,9} = 205$, $R^2=0.732$, $p<0.001$) (Fig. 4). I found 25 species ant species nesting in the artificial nests, with 2.88 ± 0.12 (Mean \pm SE) ant species per tree, with a maximum number of six species nesting in a single tree. The most diverse ant genus was *Camponotus*, with seven species, followed by *Cephalotes* (six species) and *Pseudomyrmex* (five species). There was a significant effect of the entrance size diversity treatments on ant species richness ($t=9.36$, $df=77$, $p=0.003$), with more species per tree in the HE (mean \pm SE: 3.28 ± 0.18) than in the LE (2.5 ± 0.15) treatment (Fig. 1). The cumulative number of ant species was also higher in the HE than in the LE trees (23 species and 17 species, respectively) (Fig. 2a). This was also true for the estimated number of species, with a mean of $24.8 (\pm 0.52)$ ant species on HE and $18.4 (\pm 0.51)$ on LE (Fig. 2b). Despite finding a different number of species between treatments, I did not find significant differences on ant species composition ($F_{1,74}=1.45$, $p=0.203$) (Table 1). The species with the highest number of occupied nests was *Cephalotes pusillus*, with 307 nests (37% of the 831 occupied nests), followed by *Camponotus senex* (144 nests) and *Pseudomyrmex gracilis*

(113 nests). *C. pusillus* was also the ant with more nests occupied per tree (8.3), followed again by *C. senex* (3.89) and *P. gracilis* (3.23). The mean number of ants (workers + soldiers) per occupied nest was of 31.3, with *Tapinoma* sp. 1 and *C. pusillus* being the species with the greatest mean number of ants per nest (55.3 and 46 respectively).

Presence of the dominant species

I found significant differences in the number of ant species per tree (excluding the dominant) between trees with or without *C. pusillus* ($F_{1,75}=7.78$, $p=0.007$), and this effect was independent of type of nest treatment (HE or LE) ($F_{1,75}=1.16$, $p=0.28$) (Fig. 5). The cumulative observed number of species was higher in the absence of *C. pusillus* than in its presence; 22 species versus 16 species (Fig. 6a). The same was true with regard to for the estimated number of ant species; 24.98 (± 0.58) species in trees without and 17.66 (± 0.50) species with *C. pusillus* (Fig. 6b). I did not find a significant effect of the presence or absence of *C. pusillus* on the composition of species occupying the artificial nests ($F_{1,74}=1.07$, $p=0.384$), nor an effect of the nest entrance treatment ($F_{1,74}=1.45$, $p=0.212$) or an interaction between these two factors ($F_{1,74}=0.96$, $p=0.455$) (Table 2). I found differences in the number of occupied nests per tree by other ant species in relation to the different entrance treatments ($F_{1,75}=7.09$, $p=0.009$) and the presence of *C. pusillus* ($F_{1,75}=19.45$, $p< 0.001$), with no interaction between these two factors ($F_{1,75}=0.07$, $p=0.78$). There were more occupied nests per tree when *C. pusillus* was absent, and this effect was independent of the treatment (Fig. 7). Comparing the mean entrance sizes used by different ant species in the presence or absence of *C. pusillus* we found that in the HE treatment these species used larger entrance sizes in the presence of the dominant species (Friedman-test=5.44, $p=0.002$) whereas in the LE

treatment there was no difference in mean entrance sizes between trees with or without *C. pusillus* (Friedman-test=0.2, $p=0.655$) (Fig.8).

DISCUSSION

Here, I presented data showing how nest entrance size heterogeneity and the presence of a dominant species affected the occupation of artificial nests by arboreal ant species. To effectively assess these effects, I manipulated the diversity of nesting resources in 80 trees belonging to the same tree species (*C. brasiliense*). The dominant species was present at very similar frequencies in the two different nest entrance treatments considered (HE and LE), allowing me to examine the influence of this species on the nesting patterns of the remaining species of the ant community. Overall, I detected a reasonable level of specialization of the ant species with regard to nest entrance size and an increase in the number of species colonizing the artificial nests with an increase in the range and diversity of entrance sizes. The presence of *C. pusillus* reduced not just the number of ant species but also the number of colonized nests. This effect was true for both kinds of nest entrance treatments but its magnitude was greater for the LE than for the HE treatment. The influence of *C. pusillus* on nesting patterns by the other ant species is further confirmed by the observed change of their preferred nest entrance sizes in trees where *C. pusillus* was present. These ant species used larger entrance sizes than when *C. pusillus* was present than when it was not. To my knowledge, this is the first study to analyze together the influence of a dominant ant species and of the heterogeneity in nesting resources on nesting patterns by arboreal ants. Furthermore, this study suggests that the concept of dominance should be extended not only to those species that are aggressive but also to those that efficiently use essential resources.

Nest site specialization

I found a total 25 ant species in our experimental nests, with up to six different ant species nesting on a single tree. Moreover, there was an occupation rate of 41.5%, which is very similar to the ones found in much more specialized ant-plant systems (i.e. myrmecophytes) (ranging from 37% to 64%, but mostly for one ant species) (Campbell et al. 2015). The high number of species using the experimental nests as well as the relatively high occupation rates suggest that tree cavities are a limited resource for these arboreal ants. As expected, an increase in the range and diversity of nest entrance sizes led to an increase in the number of species using the artificial nests (total and on a per tree basis). The importance of nest entrance size diversity was showed before (Powell et al. 2011, Jiménez-Soto & Philpott 2015), but in these other studies the range of entrance sizes was much higher than in our experiment. Thus, this study was the first to show that even subtle differences in nest entrance sizes can affect the number of arboreal nesting ant species. Overall, these results and those of others (Powell et al. 2011, Jiménez-Soto & Philpott 2015) give support to the idea that a higher diversity of resources also increases the diversity of species using those resources (Armbrecht et al. 2004).

Different species tended to prefer different nest entrance sizes, suggesting an ecological specialization of the ant species for nesting resources (Powell et al. 2011). Indeed, at both the HE and LE treatments, I detected a strong relationship between mean head widths and the mean entrance sizes used by the most common species in the study site. Interestingly, the greater the range of sizes available the greater the magnitude of the differences in preferred entrance sizes used by each ant species. This was in part explained by the fact that some ant species remained using small entrance sizes (e.g. *P. elongatus* and *P. curacaensis*) in the HE treatment even though the trend of the rest of

the ant community was the use of larger entrance sizes than those used in the LE treatment. This indicates that some ant species are more specialized than others using a narrow range of entrance sizes.

Impact of the dominant ant species

Usually, dominant ant species in tree canopies are those that show an extremely aggressive behavior towards other species, especially when competing for food resources (Blüthgen & Stork 2007, Parr & Gibb 2010). However, there is growing evidence that shelter resources are also very important for arboreal ants (Byrne 1994, Kaspari 1996, Ambrecht et al. 2004, Davidson et al. 2006, Philpott & Foster 2005, Ambrecht et al. 2006, Powell et al. 2011). Thus, there may be a strong competition over these resources, and the presence of competitively dominant species may be a key factor in defining the number and identities of species nesting in a given tree. The outcomes of this competition may be related not just to the aggressiveness of the interacting species but also to the differences in the ability to find and defend these resources (Palmer et al. 2003). This may be especially true for perennial resources, like beetle made cavities, which presumably have lower species turnover rates than ephemeral resources, like twigs (Philpott 2010).

In the study area, *Cephalotes pusillus* is a very common arboreal species (Camacho et al. 2015), being found in a large number of trees and usually occupying most of the available nesting sites, with relatively large polydomous colonies (Powell et al. 2011, Camarota et al. 2015). Being common and abundant can be helpful in finding new nesting sites, especially because arboreal ants can also forage on trees other than the ones they are nesting, which give them good opportunities to identify any newly available resources. Besides that, previous works showed that *C. pusillus* tends to

occupy cavities with a wide range of entrance sizes, being much more less limited by specific entrance sizes than most other *Cephalotes* species (Powell 2008). This is mainly due to the less specialized head morphology of the soldiers ('domed head'), which does not allow a perfect match between their head and the entrance holes, unlike the case of other *Cephalotes* species with a complete head disc (Powell 2008). Moreover, *C. pusillus* is one the few species in the study area that can actively modify the tree cavities where they nest, including the nest entrance (F. Camarota, pers. obs.). After finding new nests, *C. pusillus* is presumably good in keeping them, since like other *Cephalotes* species they have a specialized defense, with the soldiers blocking their nest entrances with their heads (De Andrade & Baroni-Urbani 1999, Powell 2008, 2009). Moreover, *C. pusillus* soldiers can also actively attack possible nest usurpers (Powell 2008). In addition to their abundance, polydomy, and generalist nesting habits, the dominance of *C. pusillus* can also be related to the action of a 'priority effect', since they are good in finding new nests and after that, they usually keep them. In many cases of priority effects, early arrivers prevent colonization by late-arrivers (Fukami 2015), which can help to explain the lower species richness in the presence of *C. pusillus*. Priority effects over shelter resources have been documented before for ants (e.g. Stanton et al. 2002, Palmer et al. 2002, 2003), but never in such a species rich community like the one here studied.

The preference of the ant species for different entrance sizes changed in the presence of *C. pusillus*. This shows a certain level of plasticity of these species, which can be fundamental to their persistence in a given tree. If this is true, maybe the species absent in the presence of *C. pusillus* were just those who could not adjust their nesting site requirements, probably due to mechanical limitations (i.e. their head sizes and the available entrances). However, this plasticity was only detected in the HE treatments,

with a general increase on entrance size usage of the other ant species in the presence of *C. pusillus*. The explanation for this may be quite simple: in the HE treatment the ant species had more options for ‘escaping’ competition, using different entrance sizes than the ones preferred by *C. pusillus*. With less possibility of using different entrance sizes, some of the most frequent ant species did not occur in the presence of *C. pusillus* on trees of the LE treatment. This is particularly true for two of the most abundant and frequent species in the studied community (*Azteca* sp. 1 and *Crematogaster ampla*) which did not establish a single nest in the LE trees with *C. pusillus*. Nevertheless, it is not clear why there were fewer rare species with *C. pusillus* on these same trees. Maybe these rarer species could have even more specialized nesting requirements than the common ant species. Therefore, the shift of the entrance sizes use by the other ant species towards sizes less used by *C. pusillus* could have lowered the probabilities of finding proper nesting sites by these species.

This study is not the first showing the influence of a dominant ant species over the number of species occupying artificial nests (e.g. Philpott 2010). However, it is the first one to show the influence of a species that it is actually dominant in *using* these resources over other species. Therefore, this study is new by changing the focus of dominance from species with an aggressive territorial behavior to species that are actually *using* nesting resources more successfully than others. This approach over dominance was supported by the strong impact of *C. pusillus* not just over the presence of other ant species but also on their nesting patterns. Despite the usual focus on dominance over food resources, it is possible that, in some systems, shelter resources are even more limited than food, thus having a stronger influence on ant community structure (Powell et al. 2011, Camarota et al. 2015). Future works are needed to elucidate more aspects of the competition over shelter resources among arboreal ants.

For example, we need a better understanding of the succession in nest site occupation through time, as well as on how long some species can keep their nests on the trees. Nest expansion rates also need to be verified more closely. If a priority effect happens also for other ant species than *C. pusillus*, then the turnover in nest site occupation may be very low and nest site expansion may be essential to define the dominance over shelter resources.

Figures:

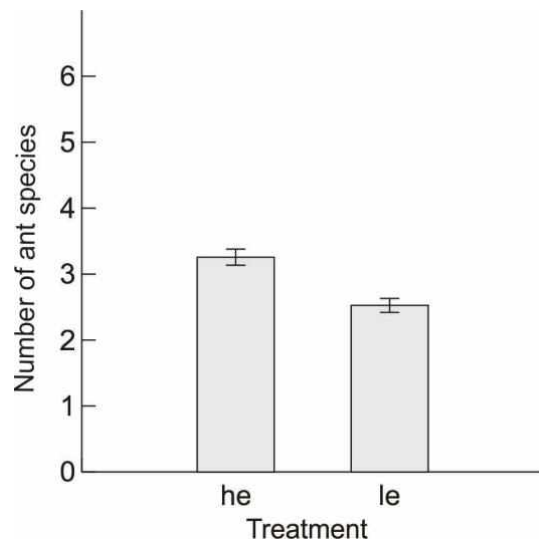


Fig. 1: Mean number (\pm SE) of ant species per tree on trees which either received artificial wooden nests with a low diversity and small range of entrance sizes (LE treatment) or nests with a high diversity and wider range of entrance sizes (HE)

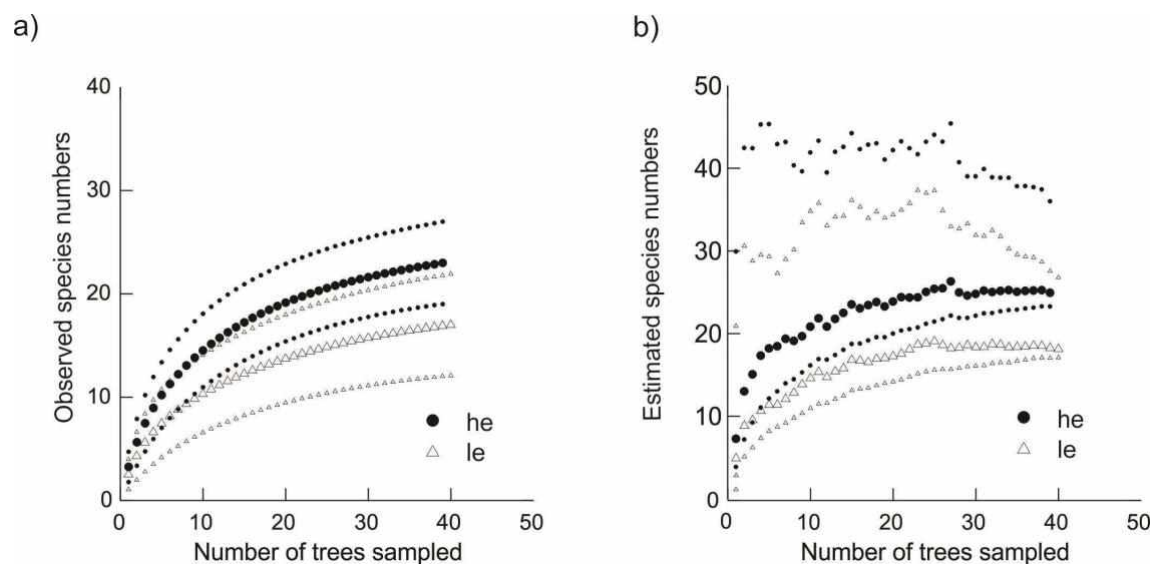


Fig. 2: Sample based rarefaction curves showing the (a) observed and (b) estimated (Chao 2) number of ant species. Circles represent the numbers of species (\pm 95% CI) that were found in the HE treatment and triangles the number of species (\pm 95% CI) found in LE

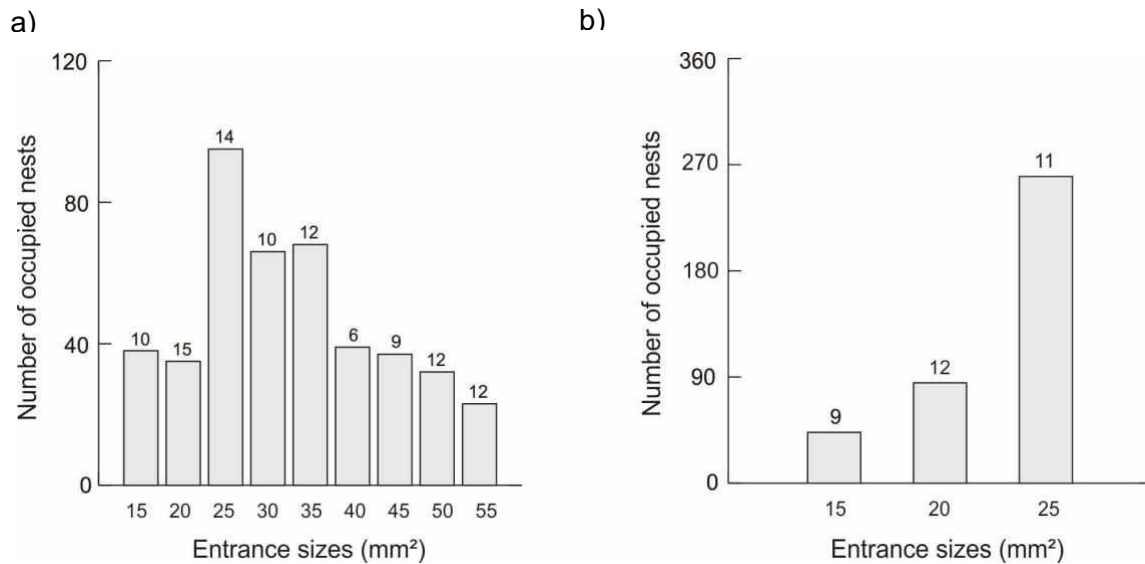


Fig. 3: Number of occupied nests in relation to nest entrance size, for trees of the a) HE and b) LE treatments. The numbers above each bar represent the number of species using each nest entrance size

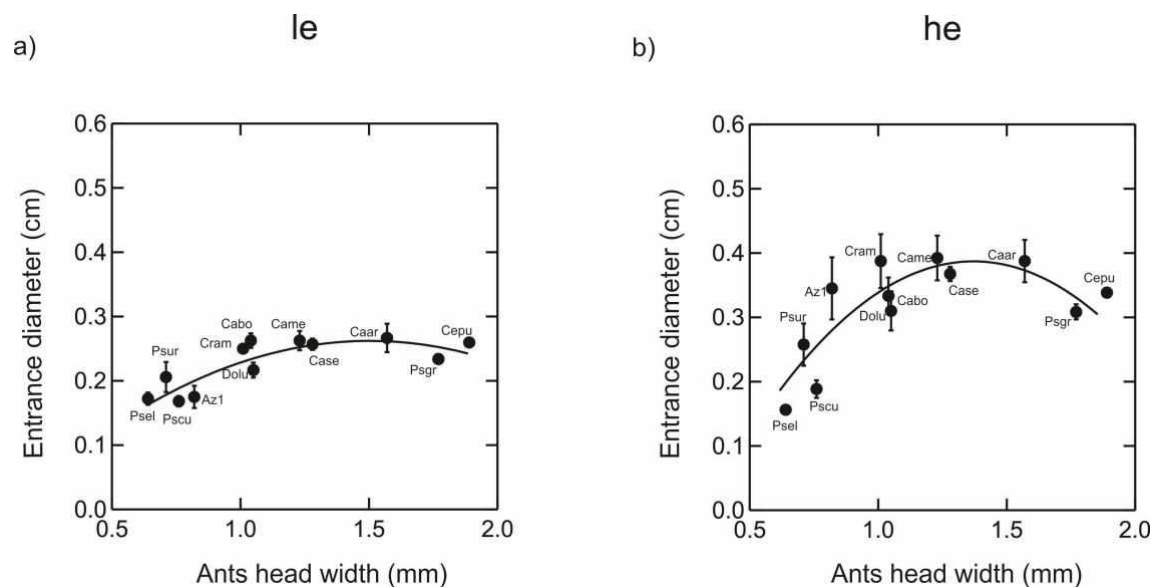


Fig. 4: Relationship between mean ant species head width and the mean entrance size they used on LE and HE treatments (\pm CL). Abbreviations are as follows: Psel= *Pseudomyrmex elongatus*, Psur= *Pseudomyrmex urbanus*, Pscu= *Pseudomyrmex curacaensis*, Azt= *Azteca* sp. 1, Cram= *Crematogaster ampla*, Cabo= *Camponotus bonariensis*, Dolu= *Dolichoderus lutosus*, Came= *Camponotus melanoticus*, Case= *Camponotus senex*, Caar= *Camponotus arboreus*, Psgr= *Pseudomyrmex gracilis*, Cepu= *Cephalotes pusillus*

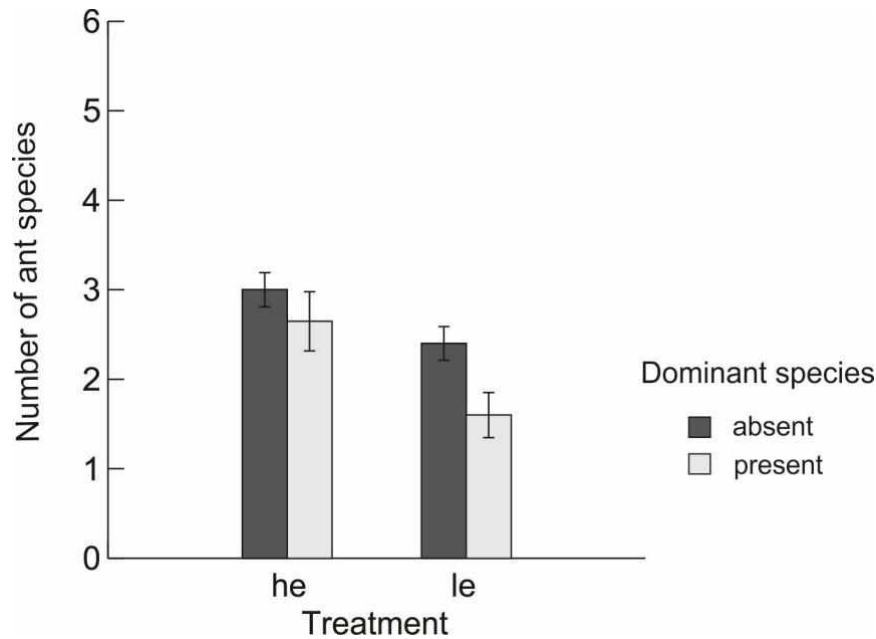


Fig. 5: Mean number (\pm SE) of ant species per tree (excluding *C. pusillus*) in HE and LE treatments and with the absence or presence of the dominant species (*C. pusillus*)

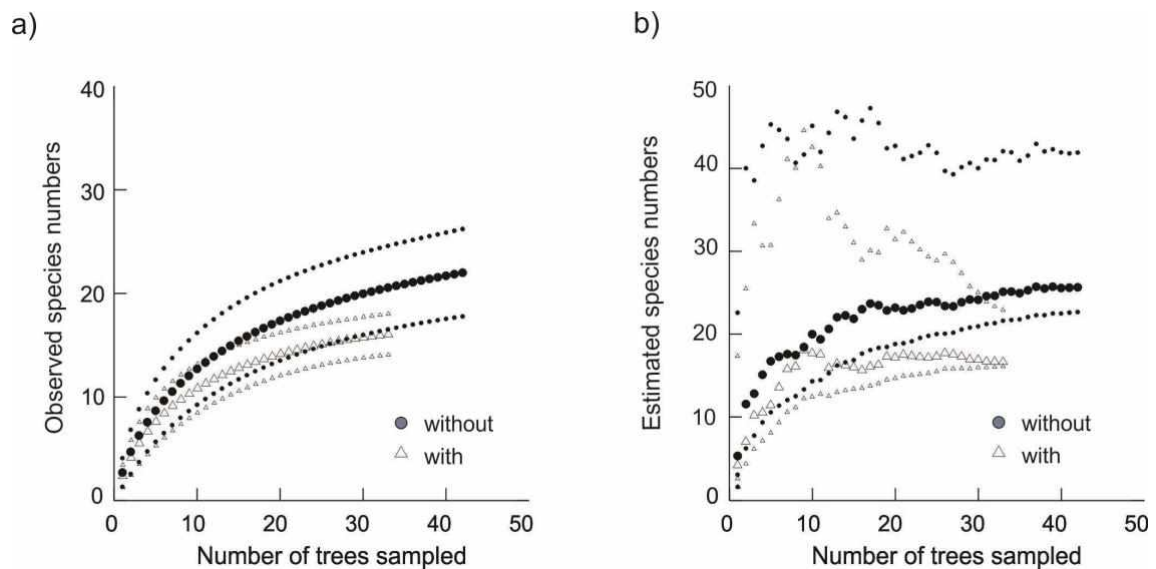


Fig. 6: Sample based rarefaction curves showing the (a) observed and (b) estimated number of non-dominant ant species in the presence or absence of the dominant ant *Cephalotes pusillus*. Circles represent the numbers of species (\pm 95% CI) that are found in the absence of *C. pusillus* and triangles the number of species (\pm 95% CI) found in its presence

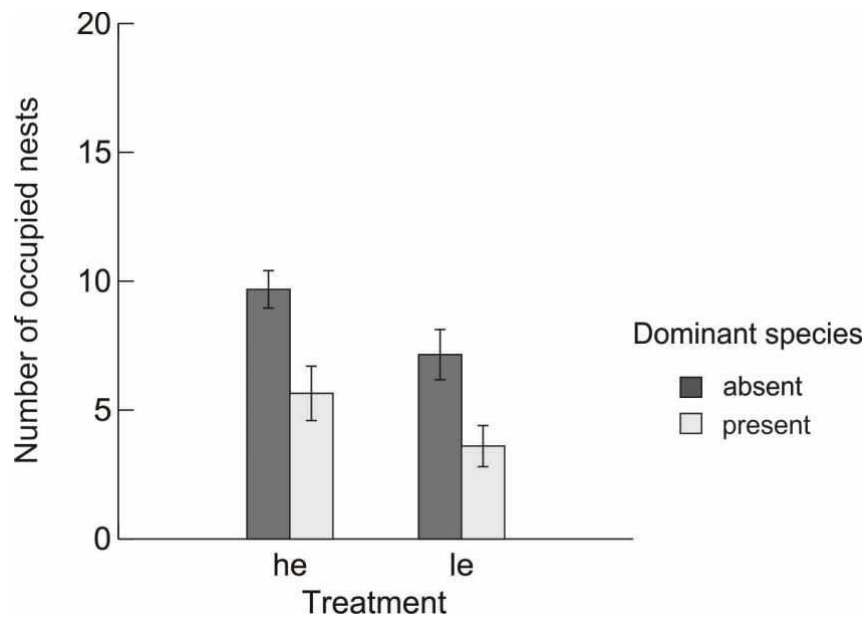


Fig. 7: Mean number (\pm SE) of occupied nests per tree (excluding the ones occupied by *C. pusillus*) in HE and LE treatments and with the absence or presence of the dominant species *C. pusillus*

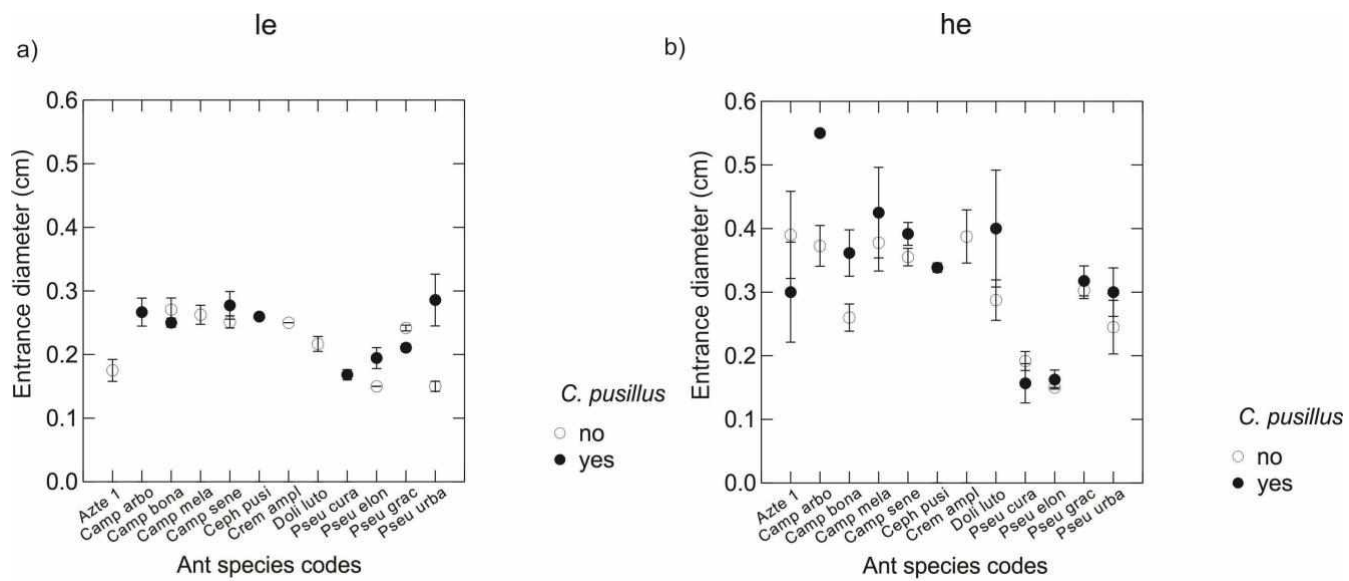


Fig. 8: Differences in mean (\pm SE) nest entrance size used by non-dominant ant species in the presence or absence of *C. pusillus* on a) LE and b) HE treatments

Tables

Table 1: List of the number of trees with nests and number of occupied nests for each ant species on the HE and LE treatment plants.

Ant species	entrance diversity treatments			
	he		le	
	n trees	n nests	n trees	n nests
<i>Azteca</i> sp. 1	6	10	2	4
<i>Camponotus</i> sp. 15	2	5	0	0
<i>Camponotus arboreus</i>	4	12	1	3
<i>Camponotus atriceps</i>	4	4	0	0
<i>Camponotus bonariensis</i>	9	19	13	28
<i>Camponotus melanoticus</i>	10	13	3	4
<i>Camponotus</i> sp. 65	3	7	0	0
<i>Camponotus senex</i>	21	92	16	52
<i>Cephalotes specularis</i>	1	2	0	0
<i>Cephalotes adolphi</i>	1	1	0	0
<i>Cephalotes angustus</i>	0	0	1	2
<i>Cephalotes grandinosus</i>	1	1	0	0
<i>Cephalotes pellans</i>	2	2	0	0
<i>Cephalotes pusillus</i>	17	130	20	177
<i>Crematogaster ampla</i>	3	13	2	2
<i>Dolichoderus lutosus</i>	5	10	2	6
<i>Nesomyrmex</i> sp. 2	2	2	2	2
<i>Pseudomyrmex curacaensis</i>	8	33	3	11
<i>Pseudomyrmex elongatus</i>	3	8	6	18
<i>Pseudomyrmex gracilis</i>	17	56	18	57
<i>Pseudomyrmex sericeus</i>	0	0	1	2
<i>Pseudomyrmex urbanus</i>	5	13	5	17
<i>Solenopsis</i> sp. 1	1	1	1	2
<i>Solenopsis</i> sp. 2	2	3	0	0
<i>Tapinoma</i> sp. 4	1	2	4	5

Table 2: List of the number of trees with nests and number of occupied nests for each ant species (excluding *C. pusillus*) on trees without or with *C. pusillus*.

Ant species	<i>Cephalotes pusillus</i>			
	without		with	
	n trees	n nests	n trees	n nests
<i>Azteca</i> sp. 1	5	9	3	5
<i>Camponotus</i> sp. 15	2	5	0	0
<i>Camponotus arboreus</i>	3	11	2	4
<i>Camponotus atriceps</i>	2	2	2	2
<i>Camponotus bonariensis</i>	12	22	10	25
<i>Camponotus melanoticus</i>	10	13	3	4
<i>Camponotus</i> sp. 65	3	7	0	0
<i>Camponotus senex</i>	22	100	15	44
<i>Cephalotes specularis</i>	1	2	0	0
<i>Cephalotes adolphi</i>	1	1	0	0
<i>Cephalotes angustus</i>	0	0	1	2
<i>Cephalotes grandinosus</i>	1	1	0	0
<i>Cephalotes pellans</i>	1	1	1	1
<i>Crematogaster ampla</i>	5	15	0	0
<i>Dolichoderus lutosus</i>	5	14	2	2
<i>Nesomyrmex</i> sp. 2	0	0	4	4
<i>Pseudomyrmex curacaensis</i>	5	30	6	14
<i>Pseudomyrmex elongatus</i>	3	13	6	13
<i>Pseudomyrmex gracilis</i>	21	78	14	35
<i>Pseudomyrmex sericeus</i>	1	2	0	0
<i>Pseudomyrmex urbanus</i>	5	20	5	10
<i>Solenopsis</i> sp. 1	2	3	0	0
<i>Solenopsis</i> sp. 2	1	2	1	1
<i>Tapinoma</i> sp. 4	3	5	2	2

CAPÍTULO 3

Ant species at food resources: testing the discovery-dominance trade-off and assessing differences in species abilities to find and defend resources

Abstract

In this work, I assessed the competitive outcomes of arboreal ants at food baits and further asked which aspects of the ants' biology are responsible for the observed outcomes. First of all, I searched for a significant correlation between the ant's ability to find resources and to dominate these resources. After that, I searched for the relationship of the differential competitive abilities of the ants with the following characteristics: two morphological traits (leg and body size), the mean number of recruits (a proxy of colony size) and the mean $\delta^{15}\text{N}$ isotopic ratios (a proxy for trophic position). I performed observations in 175 medium sized trees belonging to several species. Observations were also performed in a subset of 44 trees to ensure data collection of exclusively nocturnal ant species. Approximately a teaspoon of sardine bait was placed on the main branch of each tree. A total of four observations were performed in each tree. During each observation I recorded the identity and number of ants present on each bait. I detected a positive correlation for the ants that forage during the day, which supports the existence of priority effects at the baits, instead of the discovery-dominance trade-off. There was a lack of evidences of any apparent benefit of having particular morphological features (i.e., longer legs and larger body sizes). However, there was a positive correlation between the mean number of foragers at the baits and the discovery ability of the ants. I also found a positive correlation between the species abundance and dominance index, with more abundant species being superior in both repelling and taking over the baits. Despite being related to ant abundance on this study, diets heavily based on carbohydrates did not guarantee that the ant species would be superior in finding and keeping the baits. However, it was a good indication that a given ant species would succeed in taking over baits from other species. All the significant relationships described above were only for the subset of ant species that forage during the day, without any correlation with a species characteristic and its competitive ability for nocturnal ants. Overall, I found evidences that colony size was the most important determinant of foraging success for these arboreal ants.

Key words Brazil, canopy, *Cerrado*, colony size, resources exploitation, dominant ants.

INTRODUCTION

Competitive interactions are often thought as an important factor promoting the coexistence of different species in ecological communities (Elton 1946, Connell 1983, Schoener 1983). To avoid competitive exclusion, the species must differ in one or more aspects of their niche, like food preferences and time of activity (Hutchinson 1959, Schoener 1974, Chesson 2000). However, even when different species are using the same resources, they can still coexist by changing the way they use these resources (MacArthur 1972, Chase & Leibold 2003). Moreover, a species adaptation to one circumstance (e.g. resource usage patterns) can compromise the performance on other circumstances, a phenomenon also known as ecological trade-off (Stearns 1989). At a local scale, different species can display trade-offs in many aspects, like competitive ability, tolerance to predators, environment use, and resistance to disturbances (Tilman 1982, Kneitel & Chase 2004). Therefore, interspecific trade-offs can be essential for the maintenance of a high diversity of species in many biological communities (Tilman 2000, Amarasekare 2003, Kneitel & Chase 2004).

Similarly to what happens with other highly diverse organisms, trade-offs are usually invoked to explain the observed diversity patterns of ants (Cerdá et al. 2013). This is especially true for food resources, since most ant species seem to overlap in their diets at least in some degree (Carroll & Janzen 1973, Bernstein 1979, Davidson et al. 2003, Blüthgen et al. 2003). Competition over food can be asymmetrical, leading to strong dominance hierarchies in some ant communities (Vepsäläinen & Pisarski 1982, Savolainen & Vepsäläinen 1988). For ants, there is some evidence of the existence of a trade-off between the ability to discover and the ability to dominate a food resource (the discovery-dominance trade-off; Fellers 1987). The classical view of this trade-off is that good discoverers are subordinate species that invest in increasing their resource finding

rates before being displaced by dominant ant species, which are superior in harvesting and controlling the food resources (Vepsäläinen & Pisarski 1982, Fellers 1987, Savolainen & Vepsäläinen 1988). Thus, being a good discoverer can be one way by which competitively inferior species would have access to resources and successfully persist in the community (Adler et al. 2007).

Under the discovery-dominance trade-off, some species would evolve to improve their competitive ability to find a resource (i.e. exploitative competition) while others would improve their ability to defend a resource (i.e. interference competition) (Savolainen & Vepsäläinen 1988). This would imply in differential biological traits investments by the different ant species within a community. Usually, there are two ways in which an ant species can enhance its probability of successfully finding or defending a food resource: investing on foragers' individual traits or in the number of foragers employed (i.e. colony size) (Pearce-Duvet et al. 2011b). The level of advantages obtained by investing in one of these strategies can vary due to many factors, including resource size and distribution (Bernstein 1975, Traniello 1989, Stringer et al. 2007, Lester et al. 2010). Since both strategies can be costly, in the cases where there is a clear advantage in taking one of these two strategies (e.g. large number of foragers), we should not expect a selective pressure to refine the other (e.g. workers individual traits) (Case & Gilpin 1974, Pearce-Duvet et al. 2011b).

Important individual traits related to an ant species competitive success at food resources can be related to their morphology, more specifically their legs and body sizes (Traniello 1989, Pearce-Duvet et al. 2011a). For example, species with relatively longer legs are usually faster than species with shorter legs, obtaining advantage at successfully arriving at newly available resources (Oster & Wilson 1978, Kaspari & Weiser 1999, Hurlbert et al. 2008). On the other hand, species with large body sizes can be better at

taking over and defending the resources from other smaller species, as long as there are a minimal number of workers of that larger species (Fellers 1987, Johnson et al. 1987). Another possibility for a given ant species to be successful at exploring food resources is to invest in an increase in colony size, therefore having a larger worker force to explore an area and subsequently find the resources (Johnson et al. 1987, Savolainen & Vepsäläinen 1988, Traniello 1989, Davidson 1998). Moreover, a larger number of workers can compensate the small body size of some ant species, making them able to defend resources from larger species, with no damage to the overall colony population (Holway 1999, Pearce-Duvet & Feener 2010).

Despite a relatively large numbers of studies focusing on the discovery-dominance trade-off, the debate over its existence is still open, as there is only limited evidence supporting the trade-off (revision in Parr & Gibb 2012, Cerdá et al. 2013). Other factors can interact with the competitive abilities of the ant species, including the environmental context (Wiescher et al. 2011), the presence of natural enemies (Holway 1999, LeBrun & Feener 2007, Feener et al. 2008) and the local temperature (Cerdá et al. 1997, Bestelmeyer 2000, Lessard et al. 2009). Instead of a trade-off, in many cases it is observed a priority effect, on which the first species to arrive at a food resource is the one to keep control of it (Parr & Gibb 2012). Like any ecological trade-off, priority effects can be important in maintaining the diversity of ant communities, since it allows the persistence of competitively inferior species, weakening the advantage of the dominant ant species (Stanton et al. 2002, Palmer et al. 2002, Andersen 2008).

Most tropical arboreal ant species rely extensively on liquid food resources (i.e. exudates) (Davidson et al. 2003, Blüthgen et al. 2003), available mostly in the form of extrafloral nectar, secretion from caterpillars, or honeydew from sap-sucking hemipterans (Beattie 1985, Rico-Gray & Oliveira 2007). Despite being very rich in

carbohydrates, these exudates usually have a poor protein content (Baker et al. 1978, Blüthgen et al. 2004a). This may cause a nutrient imbalance, leading the ant species that feed mainly on exudates to use huge amounts of carbohydrates in order to enhance protein gain (Davidson 1997, Kay 2004). The high carbohydrate intake is usually reflected in colonies with large number of individuals and also with an increase in the activity of these ants ('high tempo activity') (Davidson 1997, 1998, Grover et al. 2007). These two factors combined can lead the same ant species to have high rates of resource discovery and also make it capable of successfully defending them, thus breaking a possible trade-off (Davidson 1998). Under this scenario, priority effects are expected to be more frequent than discovery-dominance trade-offs among arboreal ant species. However, this assumption has been not formally tested, since there is a lack of studies focusing on ant competitive interactions governing food resource partitioning on trees.

Here, I assessed the existence (or not) of a discovery-dominance trade-off among the members of an arboreal ant community. I did this by measuring the relationship between the discovery ability of the most common ant species in this community and their dominance status. For the trade-off to operate there must be a turnover of the ant species at a food source, with the species with better discovery abilities arriving first but being displaced by dominant species, which arrives latter but takes control of the food. If this is not the case and the same species are usually good in both finding and dominating the resources, than a priority effect may be operating in this community. I also evaluated the possible influence of body size and recruitment rates (a proxy of colony size) in affecting species discovery and dominance abilities. Finally, I evaluated if the discovery and dominance abilities of a given species is related to its trophic position. It is expected that since a carbohydrate based diet may fuel the ants to acquire protein, ant species with higher trophic levels would discovery resources

faster and/ or successfully defend or takeover these resources from other ant species. I specifically asked the following questions: 1) is there a relationship between the ant's discovery ability and their dominance status? 2) is there a relationship between the ant body size and discovery ability and dominance status? 3) is there an influence of colony size on the ant species discovery ability and dominance status? 4) is the trophic position of the ants related with their discovery ability and dominance status?

METHODS

Study area

This study was conducted at Reserva Ecológica do Panga (REP) (19°10' S, 48°23' W), a 404 ha reserve located 35 km south of Uberlândia, Minas Gerais, Brazil. The region is characterized by a tropical climate with two well-defined seasons: a dry winter, from May to September, and a rainy summer, from October to April. The mean annual temperature and the mean annual precipitation are 22° C and 1650 mm, respectively. The REP is composed of a mosaic of vegetation types, including savannas (the dominant vegetation), dry forests, gallery forests and palm swamps (Cardoso et al 2009). This study was conducted in the dominant savanna physiognomy (*cerrado sensu stricto*) of the reserve, characterized by a woody layer of trees and large shrubs 3–8 m tall, and a ground layer composed of grasses, herbs, and small shrubs (Cardoso et al 2009).

Ant baiting

To assess the foraging behavior of ants (recruitment and dial activity) I conducted observations in 175 medium sized trees (12-22 cm of trunk diameter,

measured 10 cm above the soil) belonging to several plant species, between 8:00 and 12:00 h. These 175 trees were divided in 19 groups (with 8-10 trees per group). A subset of 44 trees (divided in 5 groups of 8-10 trees) were also sampled during the night (between 19:00 and 23:00 h) to ensure the data collection of exclusively nocturnal species. These nocturnal observations were always performed at least one week after the diurnal ones, to avoid any effect of the prior presence of the bait on the ant's recruitment patterns. Each tree was distant at least 20 meters from one another, thus assuring independence of the observational data. Approximately a tea spoon of canned sardine was placed in a main branch on each tree. Meat baits, such as tuna and sardine, are widely used to assess the foraging behavior of ants and are attractive to most of the ant community (Fellers 1987, Savolainen & Vepsäläinen 1988, Andersen 1992). A total of four observations were performed in each tree. The first observation was right after the placement of all the baits in a group of trees (around 15-20 minutes after the first bait placement). After one hour of the bait placement a second observation was performed. The other observations took place in the two subsequent hours. For example, during the morning (starting at 8:00) the first observation at a bait started at ~8:20h, the second one at 9:00h, the third at 10:00h, and the fourth at 11:00h. During each observation I recorded the identity and number of ants present on each bait. Ant species were counted only if they were seen touching the bait. Since some ants were difficult to identify in the field, a voucher specimen was collected for posterior identification in the laboratory. To avoid disrupting the normal foraging behavior of the ants at the baits, these specimens were usually collected only after the end of the baiting trials.

Ant species morphology

As morphological characteristics I used the head length (HL) and tibia length (TL) of the 14 most frequent ant species at the baits, based on measurements performed on at least 20 workers of each species. In order to embrace the natural body size variance between workers of different colonies, only five workers of the same colony were measured, in a way that each ant species had representatives of at least four different colonies. Head length measurements were used as a proxy of body size (Kaspari & Weiser 1999) and tibia length as a proxy of leg size (Pearce-Duvet et al. 2011a). In ants, it is common the existence of a positive allometry between leg size and body size (Kaspari & Weiser 1999). The existence of this allometry was checked by performing a Standardized Major Axis line-fitting (SMA) in the ‘smatr’ package in R 3.0.1 (R Development Core Team 2015). The SMA analyzes if the slope of the relation between the two morphological variables (head length and tibia length) is different from a predicted isometry (slope=1) (Warton et al. 2006). The residuals of the relationship of the two morphological variables were used as the ‘relative leg length’ of the ant species.

Ant recruitment size

Since the number workers found on food sources is often related to the size of the colony (Dornhaus & Powell 2010, Dornhaus et al. 2012), the mean recruitment size of each species at the baits was used as a proxy of colony size. If the same ant species remained in the bait for more than one observation, only the observation with the maximum number of workers was considered.

Measuring outcomes at interactions

Since baits on 8-10 trees were simultaneously monitored during each baiting trial, it was not always possible to record direct interactions among the species recruited to baits. Because of that, the replacement of species through time (turnover) was taken as a proxy of the outcome of interspecific interactions at the baits. Four outcomes of interactions were quantified at the baits. If the species that was the first to reach bait kept control of it after the presence of another species it was scored a ‘repel’ (R). If the ant species lost control of the bait for a different species it was scored as ‘failure to repel’ (FR). On the other hand, if one species reached the bait after another one and successfully kept it, a ‘takeover’ (T) was scored, while if the species did not remain on the bait, it was scored as ‘failure to takeover’ (FT).

Discovery ability and behavioral dominance measurements

The discovery ability index (DAI) of each species was calculated as the number of times a species arrived first at the bait divided by the total number of baits visited by this species. For calculating the dominance index (DI), an overall proportion of wins was used, which is the number of repels (R) plus takeovers (T) (i.e. both kinds of winning interactions) divided by the total number of interactions $((R + T) / (R + T + FR + FT))$. The DI was further divided in two kinds of behavioral dominance indexes: the proportion of successful repels or the “repel fraction” $(R / (R + FR))$, and the proportion of successful takeovers or the “takeover fraction” $(T / (T + FT))$. In many cases, it was observed a monopolization event, where a given species was the only one present at the bait from the beginning to the end of the observations. Because of that, the DI and the proportion of successful repels were calculated twice: without any monopoly and with monopolies accounted. Since there was a very strong correlation between the DI

indexes with and without monopolizations ($r=0.97$, $p<0.0001$ for DI, $r=0.95$, $p<0.0001$ for repel fraction) I further used only the measurements of dominance including the monopolizations.

Ant trophic position

The diets of the different ant species were assessed by nitrogen stable isotopes analysis. Nitrogen isotopes analyses are particularly useful to understand nutritional aspects of organisms whose feeding habits are mostly cryptic, like ants (Tillberg et al. 2006, Feldhaar & Blüthgen 2010). The ratios between heavy and light nitrogen isotopes (^{15}N to ^{14}N) of an ant body mass are used as an indicator of its trophic position and nitrogen source (Feldhaar & Blüthgen 2010).

Sample preparation

After the ants were collected in the field, they were stored in 95% ethanol and subsequently dried in an oven at 60°C for 48 hours. After drying, all samples were homogenized and weighted in tin capsules using a microbalance. Only the alitrunk and legs of ant workers were used, to minimize the risk that undigested food in the head, gut or crop would influence the results (Blüthgen et al. 2003, Tillberg et al. 2006). The samples were analyzed at the UC Davis Stable Isotope Facility, in Davis, California. Data was obtained for 11 out of the 14 most common ant species at the baits.

Statistical analyses

For all statistical analyses, only those species that occurred in at least five different baits were included ($n=14$), in a way to avoid artifacts due to small sample sizes. Moreover, separated analyses were performed for the ant species foraging during

the day (n=12) and for the ones foraging at night (n=8). The Pearson correlation analysis was used to test for correlation between the DAI and the DI, and the DAI and the ants repel fraction and takeover fraction. Pearson correlation analyses were also used to assess the importance of morphological aspects in the ant's discovery ability and dominance status. First, it was searched a correlation between the ant's relative leg length and their DAI. After that, a correlation was assessed between the ant's body size (i.e. head length) and their DI. Finally I did a separate analysis for each of the two different kinds of dominance: the repel fraction and the takeover fraction. Before the correlations were done, the head length measurements were log transformed to suit the assumptions of normality. I further assessed the relationship of the recruitment size of the ant species and their DAI and DI. As before, separate analyses were made for the repel fraction and takeover fraction of the ants. To suit normality, the recruitment size was log transformed prior to the tests. Finally, I performed Pearson correlations to assess the influence of the ant's trophic position (based on their mean $\delta^{15}\text{N}$) on their DAI and DI (and also repel fraction and takeover fractions). There was information for the isotope ratios of 11 ant species, being nine foraging during the day and six foraging at night. All analyses above were performed in Systat 10.2 (Systat Software Inc. 2002).

RESULTS

Community description

Of the 219 baits placed on the trees, two were never visited, 121 were used by at least two ant species and 97 were used by a single species, i.e. were monopolized. The proportion of monopolized baits was much higher at night than during the day (70.45% vs. 32%). A total of 33 ant species (13 genera, 6 subfamilies) were found using the baits; however, 58 % of these species were observed on less than five different baits

(Table 1). Of the 33 ant species observed at the baits, 29 were found during the day and 12 at night (Table 1). There was also, on average, fewer ant species per bait at the night than during the day (2 vs. 2.36 ants per bait respectively). There was a shift in the community in relation to the foraging period, with 18 species found on baits exclusively during the day and five species found exclusively at night (Table 1). The most common species during the day were *Camponotus senex* (38.8 % of the baits), *Cephalotes pusillus* (28 %) and *Azteca* sp. 1 (25.7 %) (Table 1). The most common species foraging during the night were *Camponotus bonariensis* (27.3% of the baits), *Ca. atriceps* (20.45%) and *Azteca* sp. 1 (18.2%) (Table 1).

Discovery-dominance trade-off or priority effect

For the ant species that forage during the day, there was a significant positive correlation between the discovery ability index (DAI) and the dominance index (DI) ($r=0.637$, $n=12$, $p=0.026$) (Fig. 1a). The relationship between the DAI and the repel fraction was not significant for either diurnal and nocturnal species (diurnal species: $r=0.359$, $n=12$, $p=0.25$; nocturnal: $r=-0.03$, $n=8$, $p=0.87$) (Fig. 2a,b), and the relationship between the DAI and the takeover fraction was only significant for diurnal species (diurnal species: $r=0.611$, $n=12$, $p=0.035$; nocturnal: $r=-0.39$, $n=8$, $p=0.34$) (Fig. 3a,b). The respective indexes of discovery ability and dominance, together with repel and takeover fractions of the most common species are shown on table 2.

Species morphology, dominance and discovery abilities

The morphological traits of the most common ant species are summarized in table 3. The two morphological variables were highly correlated ($R^2=0.94$, $p<0.000001$), showing a negative allometry ($r=-0.84$, $n=14$, $p<0.001$). Because of that, the relative tibia length was used instead of the actual tibia length. No correlation was

found between the relative tibia length and the discovery ability index for the diurnal species ($r=-0.25$, $n=12$, $p=0.44$) (Fig. S1a), and only a marginally significant correlation was found for the nocturnal ant species ($r=0.70$, $n=8$, $p=0.051$) (Fig. S1b). There was also no correlation between the mean body size (i.e. head length) and the dominance index of the ant species that forage during the day ($r=-0.27$, $n=12$, $p=0.40$) or during the night ($r=0.18$, $n=8$, $p=0.68$) (Fig. S2a,b).

Recruitment rates, dominance and discovery abilities

The frequency of the 14 most common ant species (i.e. the total number of baits in which the species was found) and their mean number of ants recruited at the baits are shown in table 3. There was a marginally significant correlation between frequency of occurrence and the discovery ability index (diurnal species: $r=0.53$, $n=12$, $p=0.08$; nocturnal: $r=0.65$, $n=8$, $p=0.08$), and no correlation with the dominance index (diurnal species: $r=-0.21$, $n=12$, $p=0.61$; nocturnal: $r=-0.48$, $n=8$, $p=0.22$).

For the diurnal species, there was a positive correlation between the number of ants recruited to baits and the discovery ability ($r=0.63$, $n=12$, $p<0.05$) or the dominance index ($r=0.86$, $n=12$, $p<0.001$) (Fig. 4a, 5a). The same happened when we consider the species repel fraction ($r=0.60$, $n=12$, $p<0.05$) (Fig. S3a) and take over fraction ($r=0.82$, $n=12$, $p<0.01$) (Fig. S4a). The mean number of ants recruited to baits was not related with the discovery or dominance abilities of the nocturnal species (discovery ability: $r=-0.21$, $n=8$, $p=0.61$; dominance index: $r=0.38$, $n=8$, $p=0.36$) (Fig. 4b, 5b).

Relationship between trophic position and competitive ability

For the diurnal species, there was a significant relationship between the number of ants recruited to baits and the isotope ratio of the ant species (mean $\delta^{15}\text{N}$) ($r=0.71$, $n=9$, $p=0.03$) (Fig. 6a). There was no correlation between mean $\delta^{15}\text{N}$ with the ant's DAI

($r=0.43$, $n=9$, $p=0.25$) (Fig. 7a), DI ($r=0.55$, $n=9$, $p=0.13$) (Fig. 8a) or repel fraction ($r=0.24$, $n=9$, $p=0.53$) (Fig. S5a). However, there was a strong relationship between the species mean $\delta^{15}\text{N}$ and its takeover fraction during the day ($r=0.79$, $n=9$, $p=0.01$) (Fig. 9a). For the nocturnal species, no significant relationship with mean $\delta^{15}\text{N}$ values was detected (Fig. 6b, 7b, 8b, 9b, S5b).

DISCUSSION

In this work, I assessed the competitive outcomes of arboreal ants at food baits and further asked which aspects of the ants' biology are responsible for the observed outcomes. Since a different set of ant species foraged during the day and night, I performed separate analyses for each period of the day. First of all, I searched for a significant correlation between the ant's ability to find resources and to dominate these resources. I detected a positive correlation for the ants that forage during the day, which supports the existence of priority effects at the baits, instead of the discovery-dominance trade-off. After that, I searched for the relationship of the differential competitive abilities of the ants with the following characteristics: two morphological traits (leg and body size), the mean number of recruits (a proxy of colony size) and the mean $\delta^{15}\text{N}$ isotopic ratios (a proxy for trophic position). There was a lack of evidence of any apparent benefit of having particular morphological features (i.e., longer legs and larger body sizes). However, there was a positive correlation between the mean number of foragers at the baits and the discovery ability of the ants. I also found a positive correlation between the species abundance and dominance index, with more abundant species being superior in both repelling and taking over the baits. Despite being related to ant abundance in this study, diets heavily based on carbohydrates did not guarantee that the ant species would be superior in finding and keeping the baits. However, it was

a good indication that a given ant species would succeed in taking over baits from other species. All the significant relationships described above were only detected for the subset of ant species that forage during the day, without any correlation with a species characteristic and its competitive ability for nocturnal ants.

Discovery-dominance trade-off or priority effect

Despite being credited as an important mechanism allowing multispecies coexistence, the discovery-dominance trade-off has been detected in only a few studies so far (revision in Parr & Gibb 2012). Trade-offs only makes sense in a highly competitive environment, and maybe competition over food is not strong in arboreal ant assemblages (Schoereder et al. 2011, Camarota et al. 2015). What are the main reasons for that? First, competition should be expected only for those species that are highly dependable of the same food resources. However, while most arboreal ants are omnivores and feed on carbohydrate-rich exudates, their diets can be highly variable (Cook & Davidson 2006). While some ant species have morphological specialization to maximize the nutrient intake of an exudates based diet (Davidson 1997, Davidson et al. 2004, Cook & Davidson 2006), others may use exudates in just a complementary way (Kay 2002), feeding mainly as predators or scavengers (Davidson et al. 2003, Blüthgen et al. 2003). Second, even amongst the subset of ants that are highly dependable of the same food resources, there should be other niche axes by which these species avoid direct competition. For example, they can forage in different periods of the day (Cerdá et al. 1997, Bestelmeyer 2000, Stuble et al. 2012). Indeed, I found different sets of species foraging during the day and night, which may have some importance in food partition (e.g. Houadria et al. 2014).

The positive relationship between the discovery ability and dominance revealed the existence of a priority effect for most members of the ant community I studied. Consistently, with the exception of the two *Pseudomyrmex* species (*P. gracilis* and *P. urbanus*), all ant species kept control of at least 50% of the baits they discovered. In many cases, priority effects are important to maintain high levels of diversity in a community, allowing competitively inferior species to persist (Andersen 2008, Fukami 2015). In this case, however, the ant species that showed a priority effect were competitively superior, with very high takeover rates. In situations like that, it is possible that the priority effect would act to reduce the diversity of species instead of promoting it (see chapter 2). However, the lack of a strong signal of competition over food resources on the trees may buffer this apparent deleterious effect of priority effects on ant species richness. Furthermore, despite the two contrasting possibilities (enhancing or lowering the local diversity) being possible, there is still a need of proper tests on the effects of priority effects over food resources in arboreal ant communities.

Species morphology, dominance and discovery abilities

I failed to find any influence of the ant species morphology in either their discovery and dominance abilities. Having longer legs, and presumably being faster, did not assure that a species would be the first to arrive at the resources, unlike what was expected by Oster & Wilson (1978) and observed in a prior study (Pearce-Duvet et al. 2011a). The bark surface can be too much variable across different species of trees, even in a small area, making it less advantageous to choose for a given morphological strategy. However, even if there was a clear benefit in investing in a given leg size to forage on the trees, it would probably be smaller legs, which are presumably better to walk in wood crevices (Kaspari & Weiser 1999). The fact that I found a negative allometry between body size and leg size support this idea, since the ants in this study

tended to have shorter legs relatively to their body size. Furthermore, this negative allometry gives support to the size-grain hypothesis (SGH) of Kaspari and Weiser (1999). The SGH, states that longer legs would be more advantageous in planar environments, like bare soils, while shorter legs would confer benefit to the ants in interstitial environments, like the leaf litter (Kaspari & Weiser 1999).

I did not find any correlation of the ant body size and its dominance status, i.e. having a large body was not a guarantee of neither defending nor taking over the resources from other species. Having a large body can improve the defense strategies of some ant species; however, its relative importance can vary according to the type of combat displayed. For example, it will be beneficial in battles involving just a few individual ants, but of no importance in battles involving a large number of ants, when smaller species often have much more workers and soldiers (Franks & Partridge 1993, Adams & Mesterton-Gibbons 2006). Moreover, other individual defense strategies can be of greater importance than body size, like heavy armours, shields and spines (Dornhaus & Powell 2010). These are common features of some arboreal ant taxa (e.g. *Cephalotes*) (Powell 2008, Dornhaus & Powell 2010) and might explain why *C. pusillus* was so successful at retaining their food from other species. When quantifying dominance, I not assessed just the defensive ‘capacity’ of the different ant species (i.e. repel fraction), but also they success in attacking and taking over resources. In general, larger bodies did not affect the ability of the different species to takeover resources from other ant species. However, the two biggest ant species found on the baits, *Cephalotes atratus* and *Camponotus sericeiventris*, had high takeover rates (67% and 86% respectively). Probably, in these cases, the balance of very large body sizes and a certain number of workers assured the ants the potential to obtain food found by other species first.

Recruitment rates, dominance and discovery abilities

Foraging is a very costly activity performed by an ant colony, thus an ant species must optimize its benefits by lowering the time spent, as well as the chances of being killed while searching for resources (Dornhaus & Powell 2010). Having a large number of workers can increase the possibility of a species to successfully find resources (Dornhaus et al. 2012), which was confirmed by the present data: in general, resources were found first by species with more ants per bait. This can happen mainly due to random processes, with ants gathering at resources mediated by their abundance (Pearce-Duvet & Feener 2010, Pearce-Duvet et al. 2011b). If the number of foragers is limited by colony size as it is suggested (Holldobler & Wilson 1990, Dornhaus et al. 2012), thus having large colonies can be the key to successfully explore newly available resources (Palmer 2004). However, when we take a closer inspection of species by species indexes, we observe that this relationship is not so clear-cut. For example, *Solenopsis* sp. 1, a species that showed a massive number of recruits per bait was just slightly more successful in finding resources than *P. urbanus* (DAIs of 0.67 and 0.6 respectively), which forage in small groups. Perhaps, other factors are as important as group size to define the discovery ability of each ant species, like the number of nests in a given tree. Having a polydomous colony can be of great importance, since ants usually forage near their nests (Carroll & Janzen 1973, Traniello 1989) and nesting all over a tree would expand considerably the foraging territory of a given ant species (Lanan et al. 2011). For example, *C. pusillus*, with its polydomic colony, was the ant species with the highest discovery ability rates, even though their recruitment rates were only intermediate (~20 workers per bait).

A larger colony implies in a stronger defensive force, with numerous aggressive workers and soldiers being often recruited. More than just using a significant physical

workforce, collectively defending resources may optimize other defensive strategies, like the use of chemical weaponry (Buschinger & Maschwitz 1984). Large foraging groups can be essential for the maintenance of more stable resources, like honeydew producing hemipterans, which need a constant flux of workers to assure their defense (Hölldobler & Wilson 1990, Blüthgen et al. 2000, Palmer 2004). Concordantly, in this study I found that the ants with bigger colonies were often the best holders of the baits, even though, again, the number of nests in a tree may have had some importance (see above). Since overall the ants with larger colonies usually discovered a considerable amount of resources, they concentrated their efforts more in repelling other species from the baits than in stealing the baits, with the exception of *Solenopsis* sp. 1.

Relationship between trophic position and competitive ability

Most arboreal ants feed extensively on sugar rich exudates, obtained mainly from extrafloral nectaries and honeydew producing hemipterans (Beattie 1985, Rico-Gray & Oliveira 2007). This fact led to the assumption that these ants have an essentially plant-based diet, acting like ‘cryptic herbivores’ (Tobin 1991, Davidson & Patrell-Kim 1996, Davidson 1997). Stable isotopes analyses supported the idea that exudates are an important part of arboreal ant diets, but also showed a more complex scenario, with the different species diet displaying a continuum from extreme herbivores to specialist predators (Davidson et al. 2003, Blüthgen et al. 2003). Indeed, Blüthgen et al. (2003) and Davidson et al. (2003) found that the most dominant species have intermediate trophic positions, while the subordinate species were primarily herbivores. However, in their works, they compared the trophic position not just amongst arboreal ants but also with some strictly predatorial ground dwelling species (e.g. army ants) (Davidson et al. 2003, Blüthgen et al. 2003). Thus, at least on the top of the trees, the dominant, and therefore, most abundant ant species were the ones with the highest

trophic levels. Concordantly, in this work, we detected a positive correlation between the number of ants per bait and the ants' trophic level, with the most abundant ants occupying the highest position in the food web. As expected, these ants had a mixed diet of exudates and prey, like *Azteca* sp. 1 and *Crematogaster ampla*, which were observed feeding on extrafloral nectar but also often seen carrying dead prey to their colony (F. Camarota, p. obs.).

High loads of CHO in the diet can increase the ant's activity and aggressiveness (Davidson 1997, Grover et al. 2007), making them efficient at both finding and dominating the food resources, thus breaking the possibility of a discovery-dominance trade-off (Davidson 1998). Some prior studies provided some evidence that dominant superior ants have high rates of protein: carbohydrates (Palmer 2003, Ottoneti et al. 2008, but see Wiescher 2010). Despite the two ants with the highest trophic levels (*Azteca* sp. 1 and *C. ampla*) also showing high activity rates, being good finders and repelling other ants, I did not observe a general pattern in the community. For example, *P. gracilis* had a relatively high trophic level, but a small discovery ability index and an even smaller dominance index. This particular case (*Pseudomyrmex*) is an example of ants that use exudates in a complementary way, also actively preying on other arthropods (Wheeler 1920, Carroll & Janzen 1973). The only detected relationship of a species competitive ability with its trophic position was in the takeover rates, since we found that species with higher $\delta^{15}\text{N}$ mean usually were effective at taking over baits from other species, which may be directly related to their aggressive behavior.

Conclusions

In this study I found the existence of priority effects over food resources rather than a discovery-dominance trade-off. This indicates the importance of the discovery phase, since the ants that found the bait usually kept control of them. I also found

indications that the most important characteristic related to the successful use of food sources was the colony size. Thus, having larger colonies often implies in a high number of workers available to find and subsequently defend these resources. This is one of the few works to effectively test for the discovery-dominance in tropical arboreal ant communities. Moreover, is one of the few to relate different characteristics of the ant species and their competitive ability at food sources. However, this works presents just a glimpse on the subject as there are still much to be explored in this field. For example, it would be of great interest to experimentally test how the observed priority effects can influence aspects of the diversity of these arboreal ants. It also would be interesting to manipulate different kinds of resources (e.g. liquid foods and dead insects) and in different amounts which was done before (e.g. Pearce-Duvet et al. 2010, Houadria et al. 2014), but never on the tree canopy.

Figures:

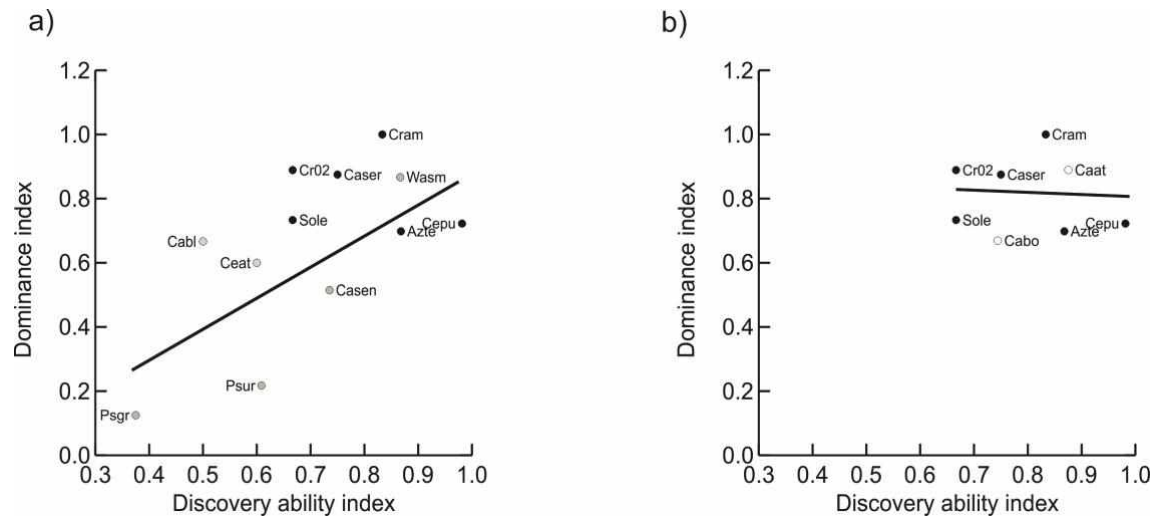


Fig. 1: Relationship between the discovery ability index and the dominance index of the most common ant species found on baits a) for diurnal species and b) for species that forage at night. Black dots represent species that forage both during the day and night, gray dots species that forage only during the day and white dots species that forage only at night. Abbreviations are as follows: Azt= *Azteca* sp. 1, Caat= *Camponotus atriceps*, Cabl= *Camponotus blandus*, Cabo= *Camponotus bonariensis*, Case= *Camponotus senex*, Caser= *Camponotus sericeiventris*, Ceat= *Cephalotes atratus*, Cepu= *Cephalotes pusillus*, Cram= *Crematogaster ampla*, Cr2= *Crematogaster* sp. 2, Psgr= *Pseudomyrmex gracilis*, Psur= *Pseudomyrmex urbanus*, Sole= *Solenopsis* sp. 1, Wasm= *Wasmmannia* sp. 1.

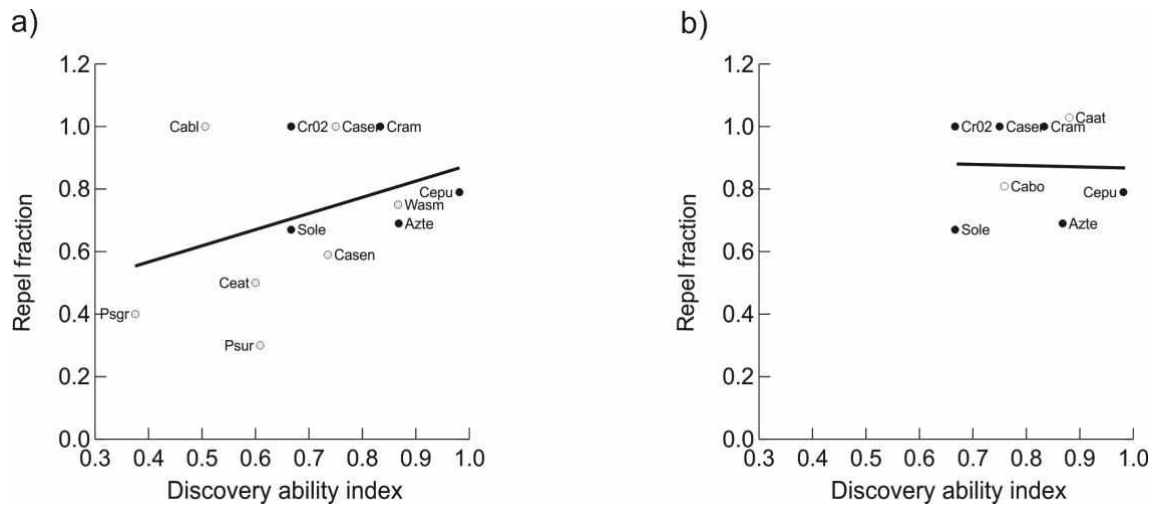


Fig. 2: Relationship between the discovery ability index and the repel fraction for a) species foraging at the day and b) species foraging at night. Symbols and abbreviations are as in fig. 1.

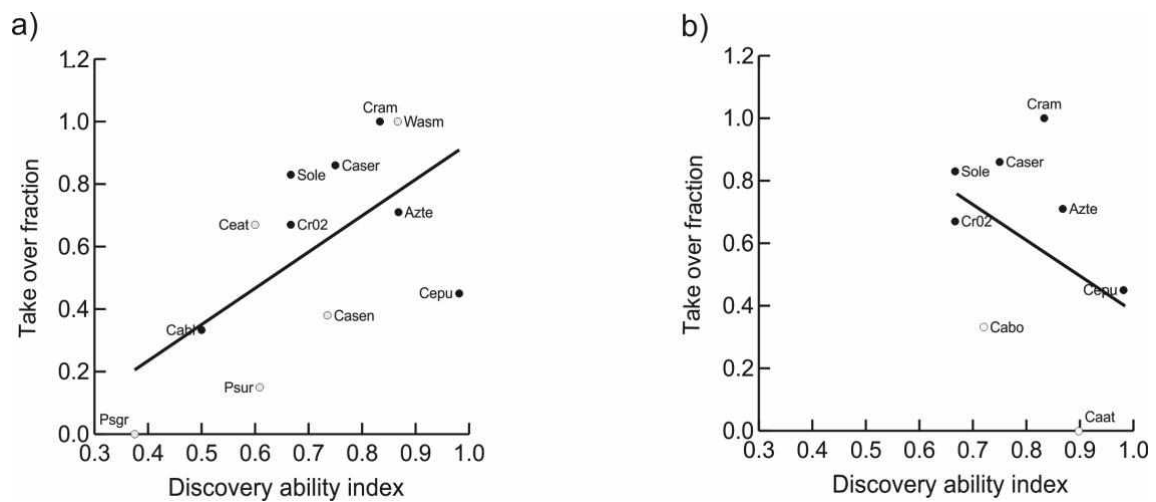


Fig. 3: Relationship between the discovery ability index and the takeover fraction for a) species foraging at the day and b) species foraging at night. Symbols and abbreviations are as in fig. 1.

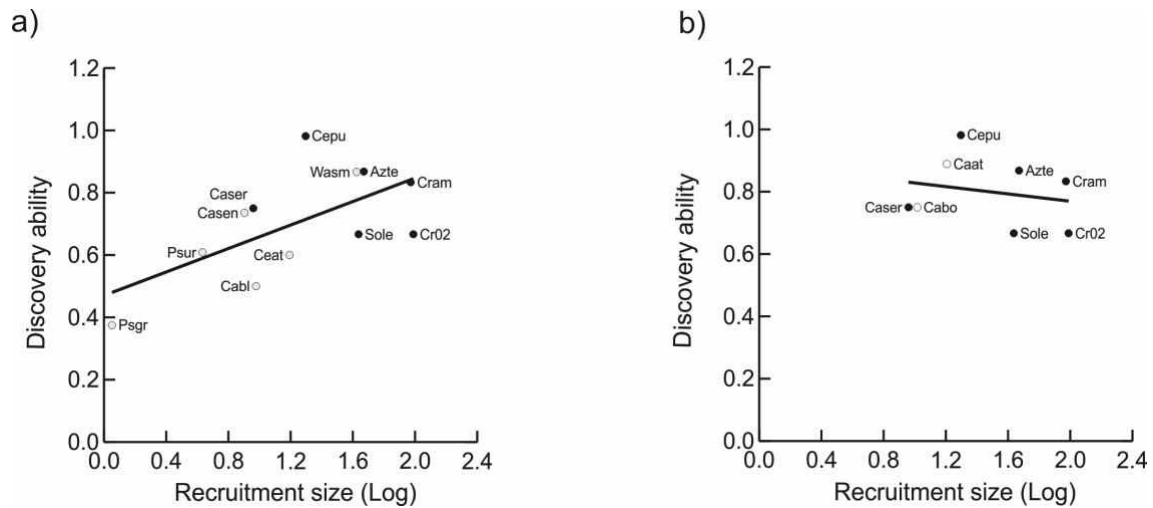


Fig. 4: Relationship between the mean number of ants recruited to baits (log) and the discovery ability index for a) species foraging at the day and b) species foraging at night. Symbols and abbreviations are as in fig.1.

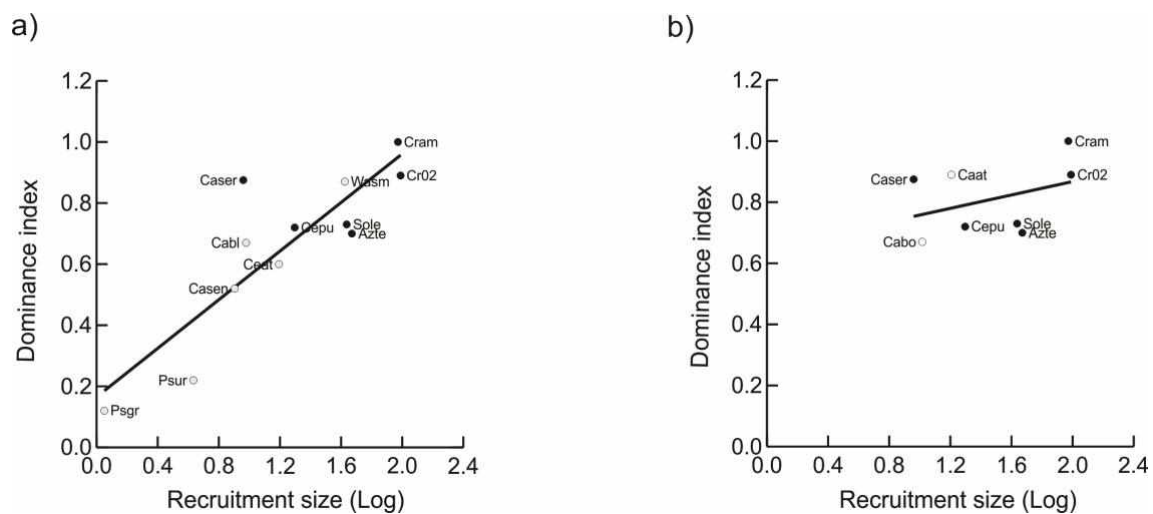


Fig. 5: Relationship between the mean number of ants recruited to baits (log) and the dominance index for a) species foraging at the day and b) species foraging at night. Symbols and abbreviations are as in fig.1.

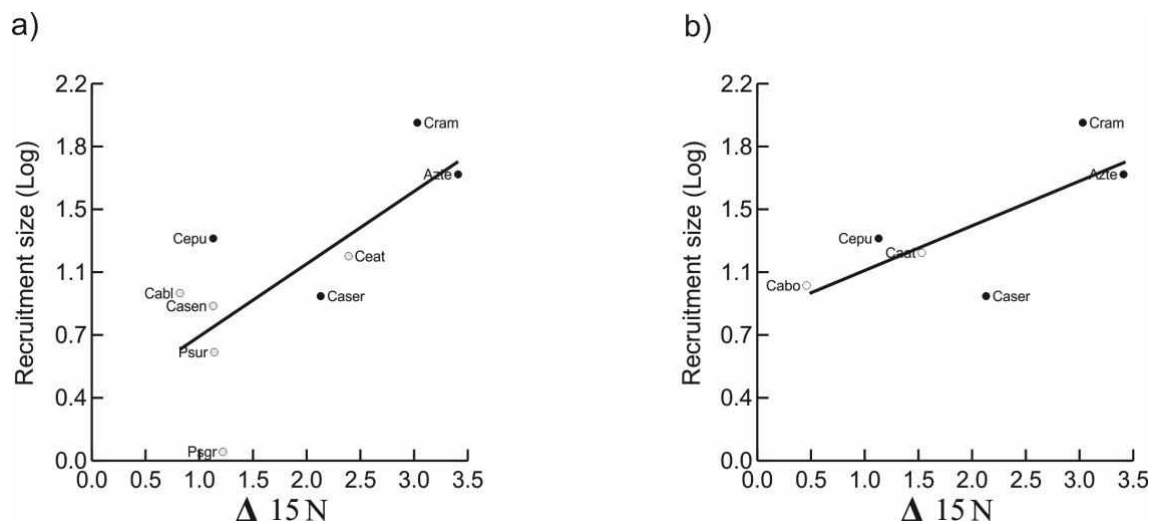


Fig. 6: Relationship between the recruitment size (log) and $\delta^{15}\text{N}$ isotope ratios for a) species foraging at the day and b) species foraging at night. Symbols and abbreviations are as in fig.1.

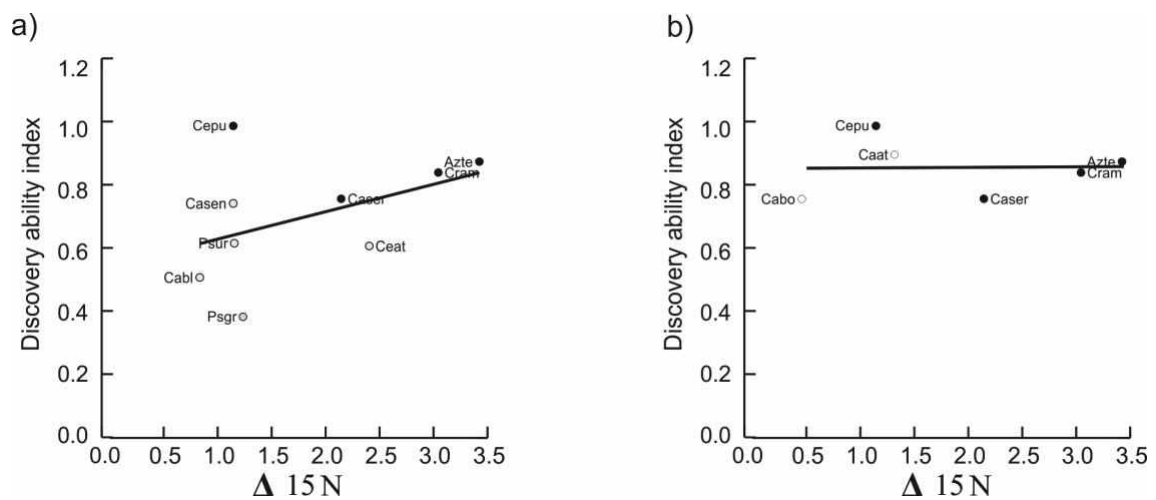


Fig. 7: Relationship between the $\delta^{15}\text{N}$ isotope ratios and the discovery ability index for a) species foraging at the day and b) species foraging at night. Symbols and abbreviations are as in fig.1.

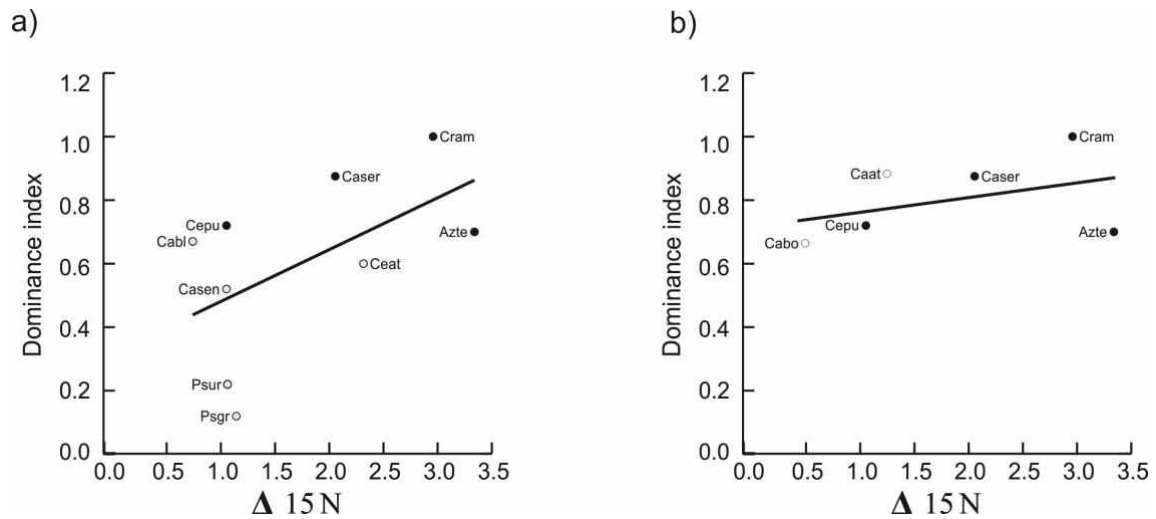


Fig. 8: Relationship between the $\delta^{15}\text{N}$ isotope ratios and the dominance index for a) species foraging at the day and b) species foraging at night. Symbols and abbreviations are as in fig.1.

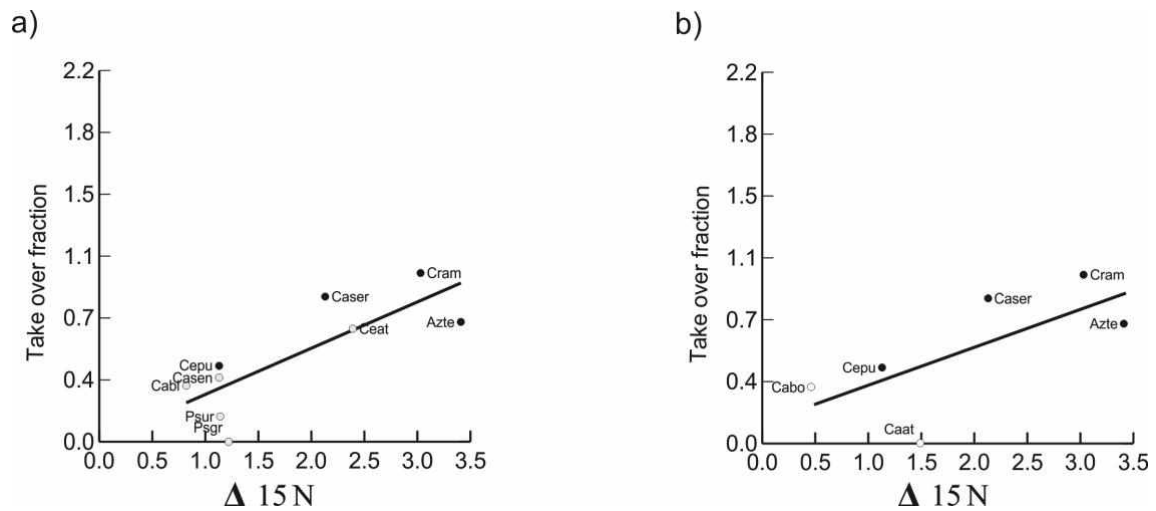


Fig. 9: Relationship between the $\delta^{15}\text{N}$ isotope ratios and takeover fraction for a) species foraging at the day and b) species foraging at night. Symbols and abbreviations are as in fig.1.

Tables:

Table 1: Number of baits that each of the 33 ant species divided by diurnal and nocturnal observations. Ant species are in order of frequency at baits.

Ant species	n of baits	Period of the day	
		day	night
<i>Camponotus senex</i>	68	68	0
<i>Cephalotes pusillus</i>	54	49	5
<i>Azteca</i> sp. 1	53	45	8
<i>Pseudomyrmex urbanus</i> group	23	23	0
<i>Camponotus bonariensis</i>	12	0	12
<i>Pseudomyrmex gracilis</i>	16	16	0
<i>Solenopsis</i> sp. 1	15	12	3
<i>Wasmmania lutzi</i>	15	15	0
<i>Crematogaster ampla</i>	18	14	4
<i>Camponotus atriceps</i>	9	0	9
<i>Camponotus sericeiventris</i>	8	7	1
<i>Crematogaster</i> sp. 2	9	7	2
<i>Camponotus blandus</i>	6	6	0
<i>Cephalotes atrattus</i>	5	5	0
<i>Neoponera villosa</i>	4	4	0
<i>Brachymyrmex</i> sp. 1	4	1	3
<i>Dorymyrmex</i> sp. 1	2	2	0
<i>Dorymyrmex</i> sp. 2	1	1	0
<i>Ectatomma tuberculatum</i>	3	3	0
<i>Camponotus arboreus</i>	2	2	0
<i>Cephalotes persimilis</i>	2	2	0
<i>Pseudomyrmex elongatus</i>	2	2	0
<i>Tapinoma</i> sp. 1	2	1	1
<i>Camponotus melanoticus</i>	1	0	1
<i>Camponotus</i> sp. 65	1	1	0
<i>Camponotus</i> sp. 15	1	1	0
<i>Camponotus rufipes</i>	1	0	1
<i>Cephalotes clypeatus</i>	1	1	0
<i>Cephalotes grandinosus</i>	1	1	0
<i>Nesomyrmex</i> sp. 1	1	1	0
<i>Pseudomyrmex sericeus</i>	1	1	0
<i>Pseudomyrmex simplex</i>	1	1	0
<i>Pseudomyrmex unicolor</i>	1	1	0

Table 2: Competitive outcomes of the 14 most common ants found foraging at the baits in our study. Ant species are in order of frequency at baits.

Ant species	Discovery ability index	Dominance index	Repel fraction	Takeover fraction
<i>Camponotus senex</i>	0.74	0.52	0.37	0.38
<i>Cephalotes pusillus</i>	0.98	0.73	0.68	0.45
<i>Azteca</i> sp. 1	0.87	0.67	0.33	0.71
<i>Pseudomyrmex urbanus</i> group	0.61	0.29	0.125	0.15
<i>Crematogaster ampla</i>	0.375	0	0.25	0
<i>Solenopsis</i> sp. 1	0.87	0.85	0.67	1
<i>Pseudomyrmex gracilis</i>	0.83	1	1	1
<i>Wasmmania lutzii</i>	0.67	0.81	0.57	0.83
<i>Camponotus bonariensis</i>	0.75	1	1	0.86
<i>Crematogaster</i> sp. 2	0.67	0.86	1	0.67
<i>Camponotus atriceps</i>	0.75	0.66	0.333	0.333
<i>Camponotus sericeiventris</i>	0.89	0.88	0	0
<i>Camponotus blandus</i>	0.5	0.67	1	0.333
<i>Cephalotes atratus</i>	0.6	0.6	0.5	0.67

Table 3: Summary of characteristics of the 14 most common ant species found at the baits. Ant species are in order of frequency at baits.

Species names	Species attributes					
	Frequency	Activity period	Relative tibia length (mm)	Head length (mm)	Recruitment size	Stable isotope ratios (N15)
<i>Camponotus senex</i>	68	diurnal	-0.52	1.73	8.01	1.13
<i>Cephalotes pusillus</i>	54	both	0.84	1.69	19.8	1.13
<i>Azteca</i> sp. 1	53	both	0.007	1.5	46.84	3.41
<i>Pseudomyrmex urbanus</i> group	23	diurnal	0.004	1.72	4.3	1.14
<i>Crematogaster ampla</i>	16	both	0.21	1.75	93.75	3.03
<i>Solenopsis</i> sp. 1	15	both	0.26	1.26	43.33	–
<i>Pseudomyrmex gracilis</i>	18	diurnal	0.038	1.58	1.125	1.22
<i>Wasmmania lutzii</i>	15	diurnal	-0.002	1.32	42.07	–
<i>Camponotus bonariensis</i>	8	nocturnal	-0.45	1.96	10.38	0.47
<i>Crematogaster</i> sp. 2	9	both	0.038	1.5	97.54	–
<i>Camponotus atriceps</i>	12	nocturnal	-0.75	1.68	16.11	1.47
<i>Camponotus sericeiventris</i>	9	both	0.67	1.91	9.12	2.13
<i>Camponotus blandus</i>	6	diurnal	-0.08	1.36	9.5	0.82
<i>Cephalotes atratus</i>	5	diurnal	0.67	3.57	15.6	2.39

Supplementary information

Figures:

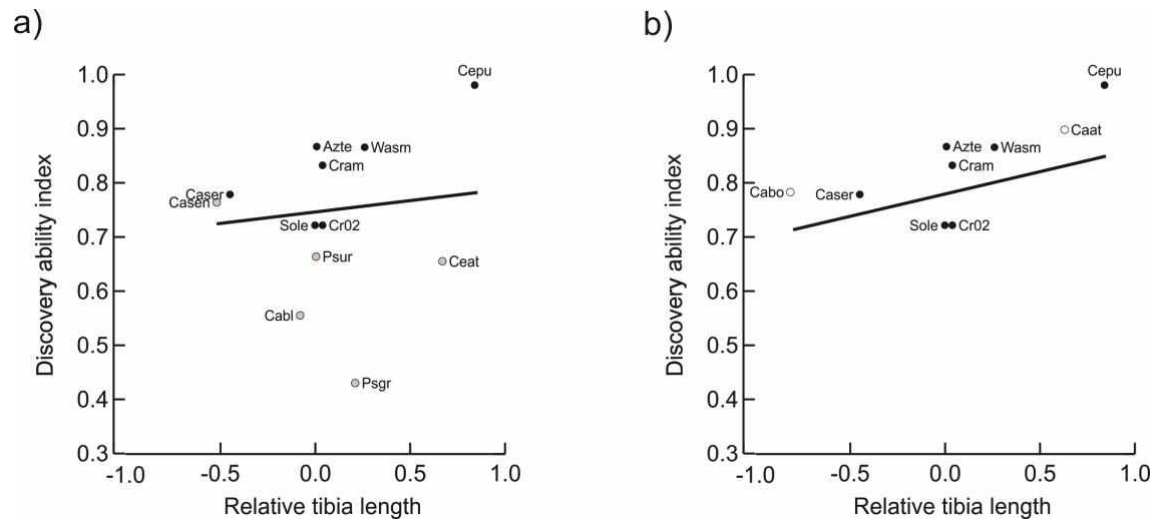


Fig. S1: Relationship between the discovery ability index and the relative tibia length for a) species foraging at the day and b) species foraging at night. Black dots represent species that forage both during the day and night, gray dots species that forage only during the day and white dots species that forage only at night. Abbreviations are as follows: Azt= *Azteca* sp. 1, Caat= *Camponotus atriceps*, Cabl= *Camponotus blandus*, Cabo= *Camponotus bonariensis*, Case= *Camponotus senex*, Caser= *Camponotus sericeiventris*, Ceat= *Cephalotes atratus*, Cepu= *Cephalotes pusillus*, Cram= *Crematogaster ampla*, Cr2= *Crematogaster* sp. 2, Psgr= *Pseudomyrmex gracilis*, Psur= *Pseudomyrmex urbanus*, Sole= *Solenopsis* sp. 1, Wasm= *Wasmania* sp. 1.

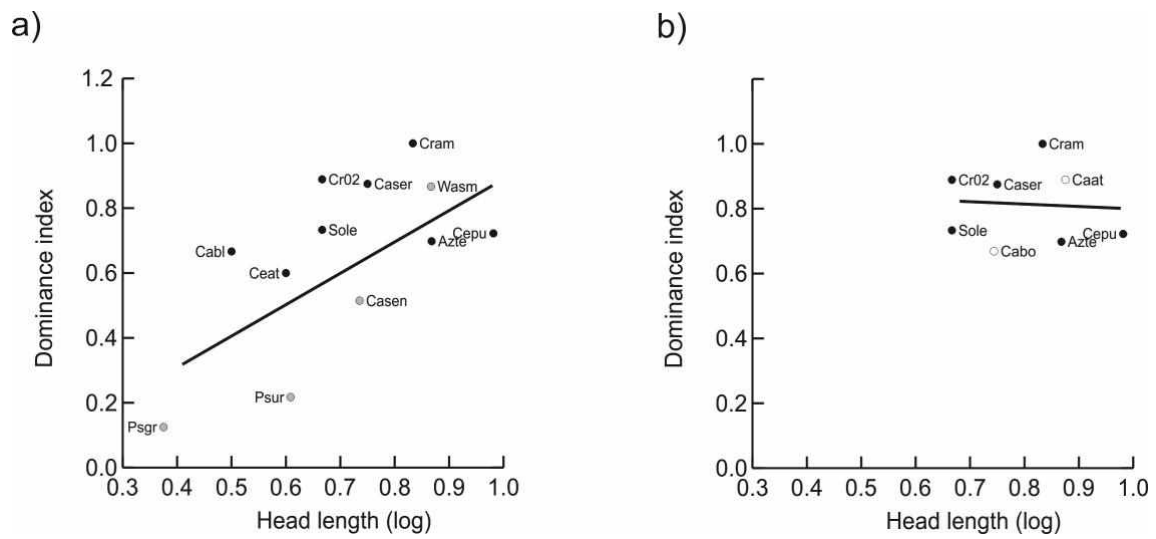


Fig. S2: Relationship between the dominance index and the mean head length (log) for a) species foraging at the day and b) species foraging at night. Symbols and abbreviations are as in fig.S1.

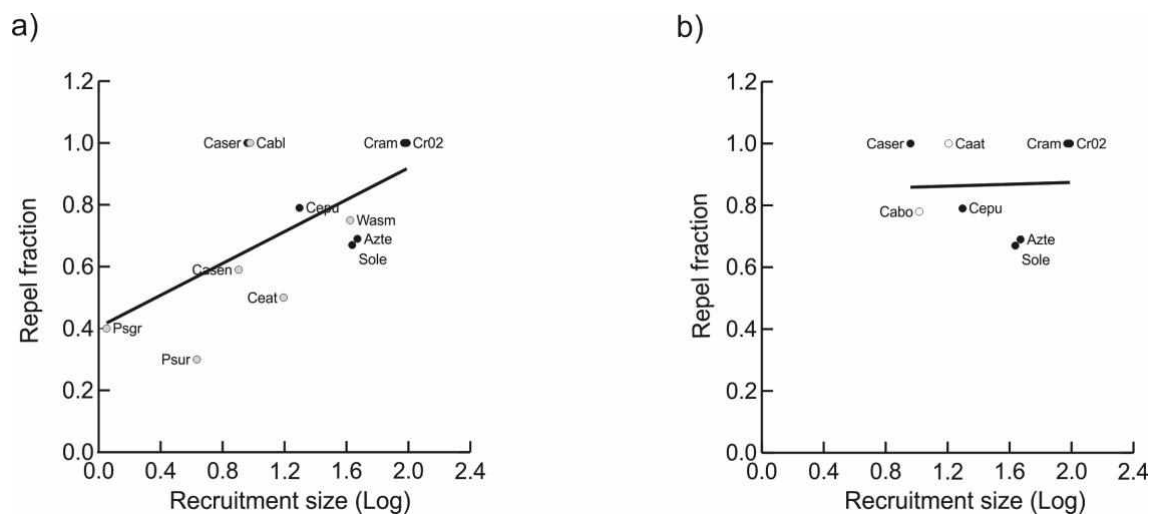


Fig. S3: Relationship between the mean number of ants per bait and the repel fraction for a) species foraging at the day and b) species foraging at night. Symbols and abbreviations are as in fig.S1.

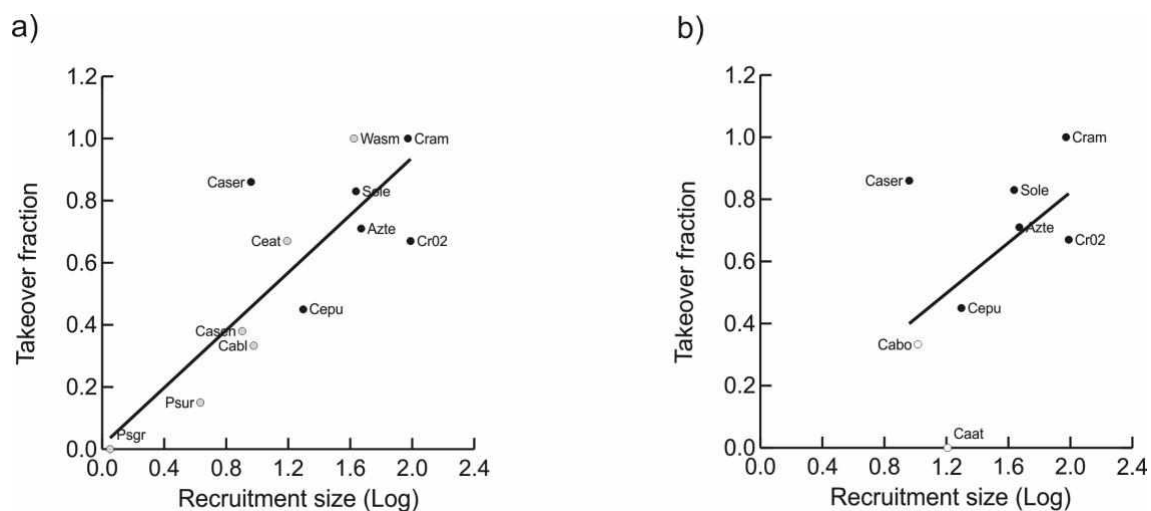


Fig. S4: Relationship between the mean number of ants per bait and the takeover fraction for a) species foraging at the day and b) species foraging at night. Symbols and abbreviations are as in fig.S1.

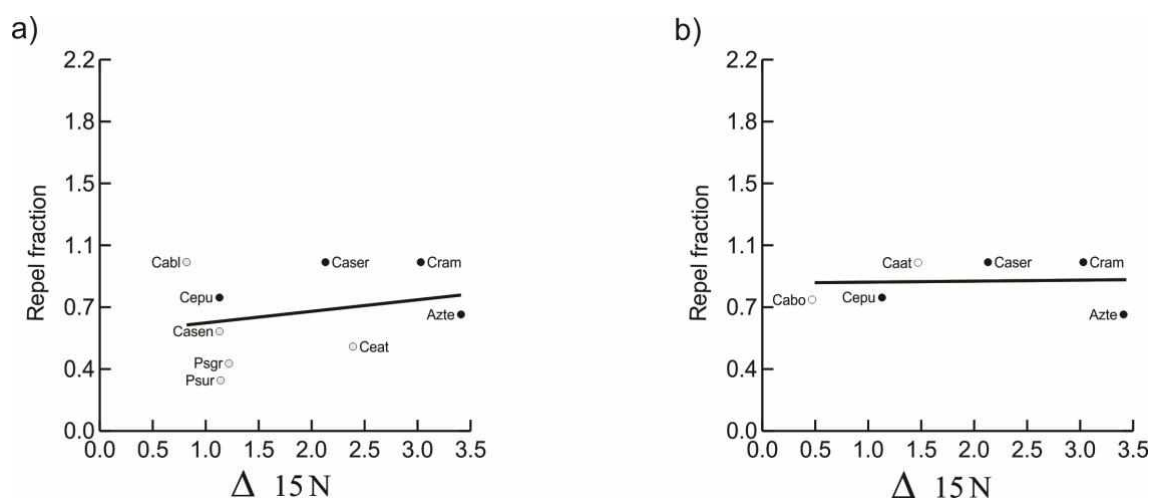


Fig. S5: Relationship between the $\delta^{15}N$ isotope ratios and repel fraction for a) species foraging at the day and b) species foraging at night. Symbols and abbreviations are as in fig.S1.

Discussão geral

Neste trabalho obtive evidências de que a competição é um fator importante na organização da comunidade de formigas arbóreas estudada. Entre estas evidências está o padrão de distribuição não aleatório das espécies mais comuns na comunidade. Além disso, foi encontrado um número relativamente grande de pares de espécies que tendem a coexistir com menor frequência do que o esperado pelo acaso. Em geral estes pares tinham maior similaridade em seus hábitos de nidificação ou horário de atividade do que os pares que co-ocorreram com maior frequência do que o esperado ao acaso (ver capítulo 1). Também foi observada uma utilização diferencial de recursos de nidificação, com evidências de certo grau de especialização das espécies por determinados tamanhos de entrada dos ninhos. A presença de uma espécie dominante sobre os recursos de nidificação evidenciou ainda mais a limitação destes, com a exclusão competitiva daquelas espécies competitivamente inferiores (ver capítulo 2). Por último, foram observadas diferenças marcadas entre algumas espécies (porém não todas) na habilidade de explorar recursos de alimento (ver capítulo 3).

Recursos de abrigo e alimento são considerados extremamente limitados na copa das árvores (Blüthgen & Feldhaar 2010), sendo que a utilização diferencial destes recursos pode ser essencial para a promoção da coexistência. De fato, os resultados aqui apresentados sugerem que recursos de abrigo são os mais importantes para definir a coexistência das espécies de formigas arbóreas (ver capítulo 2). Por exemplo, dentre as características avaliadas, os hábitos de nidificação (localização do ninho e ninhos polidômicos) foram de maior importância para definir os pares de espécies coexistentes (ver capítulo 1). Além disso, o tamanho da colônia foi o fator mais importante para definir o resultado das interações por recursos de alimento (ver capítulo 3). Ao contrário do que acontece com recursos de nidificação, não foi observada uma competição

pronunciada por recursos de alimento. Isto pode ser confirmado pela ausência de uma clara hierarquia de dominância entre as espécies e pela ausência de um *trade-off* na utilização de recursos de alimento (ver capítulo 3).

A teoria acerca da ecologia de comunidades vem se desenvolvendo tão rapidamente que dados empíricos baseados em observação e experimentação se tornaram extremamente necessários para testar as teorias propostas (Agrawall et al. 2007, Sutherland et al. 2013). Uma das questões principais está em entender o que determina o número de espécies coexistentes em uma comunidade e quais fatores podem prevenir a exclusão competitiva (Agrawall et al. 2007). Sendo assim, o presente trabalho dá uma importante contribuição neste entendimento, ao demonstrar através de diferentes abordagens a importância diferenciação de nichos em promover a coexistência das espécies de formigas arbóreas. No entanto, comunidades biológicas podem ser bastante idiossincráticas e contingentes (Lawton 1999), se tornando necessário o acúmulo de vários estudos de caso para o melhor entendimento e possíveis generalizações acerca das propriedades destas (Simberloff 2004, Agrawall et al. 2007).

Apesar de ter abordado a utilização de recursos essenciais, este trabalho está longe de oferecer uma lista exaustiva do efeito diferencial de cada fator que potencialmente pode influenciar na coexistência das formigas arbóreas do cerrado. As diferenças de nicho podem depender também das condições ambientais únicas de uma dada comunidade, e a coexistência entre as espécies pode ser sensível a perturbações neste ambiente (HilleRisLambers et al. 2012). Dentre as perturbações mais comuns e importantes no cerrado está o fogo, que já foi estudado em trabalhos anteriores (e.g. Frizzo et al. 2012, Maravalhas & Vasconcelos 2014). Talvez o aspecto mais importante não abordado diretamente aqui seja o das diferenças na habilidade de dispersão das espécies de formigas arbóreas. É possível que importantes aspectos da coexistência das

espécies sejam determinados por processos operando na fase de recrutamento das espécies e não depois que estas já estão estabelecidas na comunidade (Gaines & RoughGarden 1985, Andersen 2008, Sutherland et al. 2013). Aliás, está é uma das grandes lacunas da ecologia de formigas em geral, com pouquíssimos estudos avaliando as diferenças na habilidade de dispersão entre as espécies coexistentes (Andersen 2008).

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