



UNIVERSIDADE FEDERAL DE MATO GROSSO
INSTITUTO DE BIOCÊNCIAS
CURSO DE DOUTORADO EM ECOLOGIA E CONSERVAÇÃO DA
BIODIVERSIDADE

INTERAÇÃO ENTRE AS FORMIGAS PARABIÓTICAS *Camponotus femoratus*
(Fabricius, 1804) E *Crematogaster levior* Longino, 2003 COM SUAS EPÍFITAS
ASSOCIADAS E INFLUÊNCIA SOBRE A COMPOSIÇÃO DA ASSEMBLEIA DE
FORMIGAS DA AMAZÔNIA MERIDIONAL

RICARDO EDUARDO VICENTE

CUIABÁ – MT

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FORMIGAS DA AMAZÔNIA MERIDIONAL

RICARDO EDUARDO VICENTE

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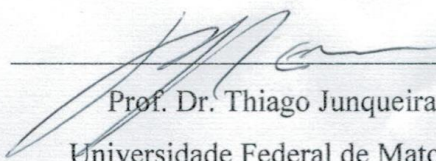
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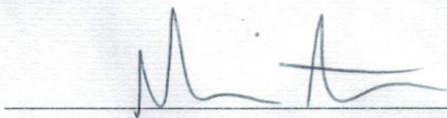
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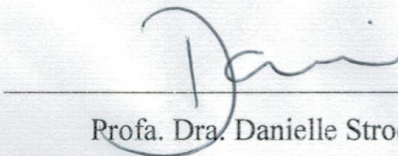
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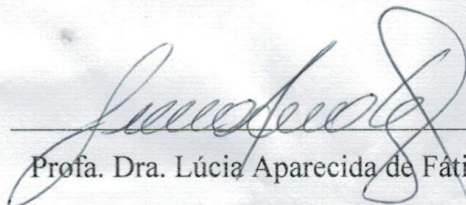
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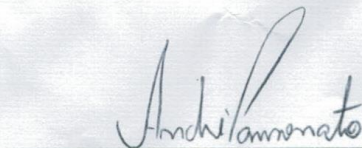
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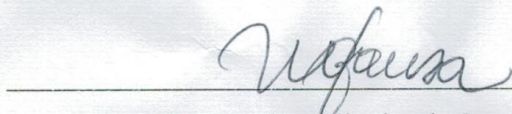
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RESUMO

Uma notável interação mutualística entre formigas e plantas encontrada em florestas tropicais é conhecida como Jardins-de-formigas (JFs). A associação entre *Camponotus femoratus* (Fabricius, 1804) (Formicinae) e *Crematogaster levior* Longino, 2003 (Myrmicinae) está entre os mais comumente encontrados na região Neotropical. Nos JFs destas duas espécies de formigas parabióticas são frequentemente encontradas algumas espécies de epífitas filogeneticamente distantes. Então, para serem parceiras mutualistas eficientes as formigas precisam reconhecer e responder a todos os compostos químicos voláteis diferentes entre todas as espécies associadas. Por outro lado, é possível que as plantas de JFs demonstrem sinais químicos semelhantes como convergência sinalizando herbivoria. Se isso fosse verdade, as formigas recrutariam igualmente a todas as espécies de JFs localmente. Considerando isso, no primeiro capítulo além de descrever a composição e a frequência das espécies de epífitas associadas aos ninhos localmente, nós testamos as hipóteses de que 1) as formigas reconhecem estímulos químicos emitidos por diferentes plantas que habitam os JFs e 2) elas podem diferenciar este estímulo químico quando comparado com os voláteis de uma planta de sub-bosque. Nós encontramos que somente *Ca. femoratus* responde a estímulos de herbivoria em suas epífitas mutualistas e que sua reação está relacionada a frequência geral das epífitas. Quando expostas às folhas das epífitas obrigatórias de JFs *Peperomia macrostachya* (Piperaceae) e *Codonanthe uleana* (Gesneriaceae) observou-se que o recrutamento de operárias de *Ca. femoratus* foi, em média, respectivamente, 556% e 246% maior do que o controle (tiras de papel). O número de formigas recrutadas por *Markea longiflora* (Solanaceae) ou pela planta de sub-bosque *Piper hispidum* (Piperaceae) não diferiu do pedaço de papel. Devido a essa forte relação das formigas parabióticas com suas epífitas mutualistas que precisam de luz para crescer, no segundo capítulo nós criamos as hipóteses de que 1) a abertura do dossel das clareiras florestais influenciam a presença de JFs, sendo que, 2) maiores clareiras terão mais ninhos e 3) tanto com o aumento na abertura do dossel quanto no tamanho da clareira haverá um aumento no tamanho das colônias em clareiras florestais. Além disso, sabe-se que apesar do ninho arborícola, as formigas parabióticas são encontradas forrageando tanto no solo como na vegetação. Então, nós também acreditamos que 4) as formigas parabióticas são mais frequentemente amostradas na vegetação e que 5) o aumento da complexidade da vegetação e do volume de serapilheira acumulada no solo aumentam o forrageio dessas formigas na vegetação e no chão, respectivamente, sendo que o aumento na abertura de dossel aumenta a atividade das duas espécies em ambos estratos. A presença, o número de Jardins-de-formigas e tamanho da colônia de formigas foi afetado pela localidade, mas não pela abertura do dossel. No entanto, não houve uma diferença da utilização de estratos verticais por *Ca. femoratus*, nem por *Cr. levior*. Por outro lado, a frequência de *Ca. femoratus* no solo diminuiu com a abertura do dossel mas não é afetada pela complexidade da vegetação. Além da frequência de *Cr. levior* no chão também diminuir com o aumento da abertura do dossel, essa espécie também demonstrou ser influenciada pela complexidade da vegetação, sendo que com o aumento da complexidade na vegetação houve uma redução na frequência de forrageamento dessa espécie no solo. Porém, nem a complexidade, bem como abertura do dossel influenciam a frequência de forrageamento dessas formigas no sub-bosque. Como essas espécies abundantes são consideradas dominantes comportamentalmente, no Capítulo 3, nós investigamos seu impacto em comunidades de formigas de solo e vegetação separadamente. Neste capítulo além de investigar o efeito das formigas parabióticas na abundância, riqueza e composição da comunidade em ambos os estratos separadamente, nós avaliamos se elas afetavam componentes diferentes da diversidade beta (substituição e aninhamento). Ainda, avaliamos quais espécies eram indicadoras de sua presença ou ausência.

Palavras-chave: Comunidade de formigas, Jardim-de-formigas, Mutualismo, Nicho

ABSTRACT

A remarkable mutualistic interactions between ants and plants found in tropical forests is known as Ants-Gardens (AGs). The association between *Camponotus femoratus* (Fabricius, 1804) (Formicinae) and *Crematogaster levior* Longino 2003 (Myrmicinae) is among the most commonly found in the Neotropics. In AGs of these two species of parabiotic ants some species of epiphytic phylogenetically distant are often found. So to be effective mutualist partner the ants need to recognize and respond to all the different volatile chemical compounds of all associated species. Moreover, it is possible that plant AGs have converged as chemical signals when attacked by herbivores. If this were true, the ants also recruit all species of AGs locally. Considering this, in addition to describing the composition and the frequency of epiphytic species associated with nests locally, in the first chapter we tested the hypotheses that 1) the ants recognize chemical stimuli issued by different plants that inhabit the AGs and 2) they can differentiate this chemical stimulus when compared to the volatiles from a abundant plant specie of the understory. We found that only *Ca. femoratus* responds to herbivory stimuli in their mutualist epiphytes and that his reaction is related to overall frequency of epiphytes. When exposed to the AG-epiphytes *Peperomia macrostachya* (Piperaceae) and *Codonanthe uleana* (Gesneriaceae) leaves it was observed that the recruitment of *Ca. femoratus* workers was, on average, respectively 556% and 246% higher than control (paper strips). The number of ants recruited by *Markea longiflora* (Solanaceae) or by the understory plant *Piper hispidum* (Piperaceae) did not differ from piece of paper. Because of this strong relationship of parabiotic ants with their mutualist epiphytes that need light to grow, in the second chapter we have created hypotheses that 1) the canopy openness of forest gaps influence the presence of AGs, and, 2) larger gaps will have more nests and 3) increase in both the canopy openness and the gap size will increase the colony size in forest gaps. Furthermore, it is known that although the arboreal nest, parabiotic ants are found foraging in the soil and in the vegetation. Then, we also believe that 4) the parabiotic ants are most frequently sampled in the vegetation and 5) increasing complexity of the vegetation and the litter accumulated volume in the soil increase the foraging of these ants in vegetation and ground, respectively, and the increase in canopy openness increases the activity of the two species in both strata. The presence and number Ants-Gardens, as colony size, was affected by the location, but not for the canopy openness. However, there was no difference in utilization of vertical strata by *Ca. femoratus* or by *Cr. levior*. On the other hand, the frequency of *Ca. femoratus* on the ground decreases with the canopy openness but is not affected by the complexity of the vegetation. In the frequency of *Cr. levior* on the ground also decrease with increasing the canopy openness. But, as opposed to *Ca. femoratus*, *Cr. levior* also shown to be influenced by the complexity of vegetation with a reduction in the frequency of workers that foraging on the ground with the increase of complexity in the vegetation. But not the complexity and canopy openness influence the foraging frequency of these ants in the understory. As these abundant species are considered dominant behaviorally, in Chapter 3, we investigated their impact on soil and vegetation ant communities separately. In this chapter in addition to investigating the effect of parabiotic ants in abundance, richness and community composition in both strata separately, we assessed whether they affected different components of beta diversity (turnover and nesting). Still, we assess which species are indicators of its presence or absence.

Keywords: Ants Community, Ants-Garden, Mutualism, Niche

INTRODUÇÃO GERAL

As formigas (Hymenoptera, Formicidae) são insetos altamente abundantes e diversificados tanto em termos de espécies quanto grupos funcionais (Fittkau & Klinge 1973; Hölldobler & Wilson 1990; Baccaro et al. 2015; Vicente et al. 2016a,b). Desempenham várias funções no ambiente, por esse motivo, as formigas são consideradas engenheiras ecossistêmicas (Folgarait 1998; Meyer et al. 2011). As formigas também favorecem a diversidade de organismos por estarem envolvidas em diversos tipos de interações com diversos outros animais (Gallego-Ropero et al. 2013; Puker et al. 2015; Dáttilo et al. 2012a), inclusive com outras formigas (Gallego-Ropero & Feitosa 2014, Sanhudo et al. 2008), microorganismos (Bekker et al. 2014, Marsh et al. 2014, Nepel et al. 2014, Sanders et al. 2014) e plantas (Vicente et al. 2014, 2012, Izzo & Benelli-Petini 2011, Izzo & Vasconcelos 2002, Dáttilo et al. 2009a,b).

Entre essas interações nas quais as formigas estão envolvidas, as interações cooperativas entre as espécies são um dos temas centrais em ecologia, e provavelmente todos os organismos na Terra estão envolvidos em pelo menos uma interação mutualística ao longo de sua história de vida (Bronstein 2001). Neste tipo de relacionamento uma espécie fornece um serviço ou um produto que seu parceiro não pode adquirir sozinho e, em troca, recebe algum tipo de pagamento ou recompensa (Hoeksema & Bruna 2000). Uma notável interação mutualística envolvendo formigas e plantas encontrada em florestas tropicais é conhecida como Jardins-de-formigas (JFs – Figura 1). Nessa interação as formigas constroem seus ninhos e plantam epífitas específicas onde incorporam matéria orgânica constantemente para o crescimento das epífitas e então, expandir os ninhos (Davison 1988; Orivel & Leroy 2011).

Em regiões neotropicais são encontradas nove espécies de formigas e 53 espécies de epífitas habitantes obrigatórias de JFs (Orivel & Leroy 2011). Dentre essas espécies de formigas que geralmente habitam solitariamente os JFs, a associação entre *Camponotus femoratus* (Fabricius, 1804) (Formicinae) e *Crematogaster levior* Longino, 2003 (Myrmicinae) está entre as mais comumente encontradas na Região Neotropical (Davidson 1988). *Ca. femoratus* e *Cr. levior* além de interagirem com algumas espécies de epífitas em uma relação mutualista, elas convivem em parabiiose, ou seja, dividem o mesmo ninho e trilhas de forrageamento (Swain 1980; Hölldobler & Wilson 1990). Nos Jardins-de-formigas destas duas espécies de formigas parabióticas são frequentemente encontradas algumas espécies de epífitas de famílias diferentes e filogeneticamente distantes (Schmit-

Neuerburg & Blüthgen 2007; Orivel & Leroy 2011). Então, para serem parceiras mutualistas eficientes as formigas precisam reconhecer e responder a todos os compostos químicos voláteis diferentes entre todas as espécies associadas. Por outro lado, é possível que as plantas de Jardins-de-formigas demonstrem sinais químicos semelhantes como convergência para um sinal generalizado ligado à herbivoria. Se isso fosse verdade, as formigas recrutariam igualmente a todas as espécies de JFs presentes localmente. Sendo assim, no primeiro capítulo (Differential recruitment of *Camponotus femoratus* (Fabricius) ants in response to Ant Garden herbivory), além de descrever a composição e a frequência das espécies de epífitas associadas aos ninhos em Cotriguaçu-MT (Figura 2), nós testamos as hipóteses de que 1) as formigas reconhecem estímulos químicos emitidos por diferentes plantas que habitam os Jardins-de-formigas e ainda 2) elas podem diferenciar este estímulo químico, quando comparado com um planta de sub-bosque.

Devido a essa forte relação das formigas parabióticas com suas epífitas mutualistas que precisam de luz para crescer (Leroy et al. 2016; Orivel & Leroy 2011), Jardins-de-formigas têm sido documentados em clareiras formadas por árvores caídas, margens de rios e estradas abandonadas (Dáttilo & Izzo 2012b; Davidson 1988). Além disso, clareiras maiores têm mais área disponível para construção de ninhos e para as operárias forragearem. Portanto, no segundo capítulo (Defining the niche of parabiotic ants *Camponotus femoratus* (Fabricius, 1804) and *Crematogaster levior* Longino, 2003) nós criamos as hipóteses de que 1), a abertura do dossel das clareiras florestais influencia a presença de Jardins-de-formigas, sendo que, 2) maiores clareiras terão mais ninhos e 3) tanto com o aumento na abertura do dossel quanto no tamanho da clareira haverá um aumento no tamanho das colônias em clareiras florestais. Além disso, apesar das formigas parabióticas serem encontradas forrageando tanto no solo quanto na vegetação (Ryder Wilkie et al. 2010; Dejean et al. 2007; Wilson 1987), possuem ninhos arborícolas (Davidson 1988; Paolluci et al. 2016). Então, nós também acreditamos que 4) as formigas parabióticas são mais frequentemente amostradas na vegetação e 5) o aumento da complexidade da vegetação e do volume de serapilheira acumulada no solo aumentam o forrageio dessas formigas na vegetação e no chão, respectivamente, sendo que o aumento na abertura de dossel aumenta a atividade das duas espécies em ambos estratos. As hipóteses 1 e 2 foram testadas em clareiras do município de Claudia-MT e as hipóteses 4, 5, 6 em parcelas dos municípios de Claudia-MT e Novo Mundo-MT (Figura 1).

Apesar da diversidade filogenética e comportamental das formigas que ocorrem nestas localidades da Amazônia (Vicente et al. 2016a, b), as espécies *Ca. femoratus* e *Cr.*

levior são frequentemente coletadas. Isso por que essas espécies são dominantes ocupando cerca de 95% dos Jardins-de-formigas nas áreas florestais da Amazônia (Orivel & Leroy 2011; Youngsteadt et al. 2010; Davidson 1988). Como estas formigas são encontradas frequentemente forrageando do solo até o dossel das florestas (Ryder Wilkie et al. 2010; Dejean et al. 2007; Wilson 1987) e são comportamentalmente dominantes nas comunidades de formigas onde ocorrem (Mertl et al. 2010; Vasconcelos et al. 2003), no Capítulo 3, nós investigamos seu impacto em comunidades de formigas de solo e vegetação separadamente. Neste capítulo, além de investigar o efeito das formigas parabióticas sobre a abundância, riqueza e composição da comunidade de formigas em ambos os estratos separadamente, nós avaliamos se elas afetavam componentes diferentes da diversidade beta (substituição e aninhamento). Ainda, avaliamos quais espécies e formigas eram indicadoras de sua presença ou ausência. É importante compreender esse efeito num bioma tão rico quanto a Amazônia, que possui tantas espécies de formigas tão raramente coletadas e principalmente da vegetação (Vicente et al. 2011, 2012, 2015; Santos-Silva et al. 2016; Prado et al. 2016).

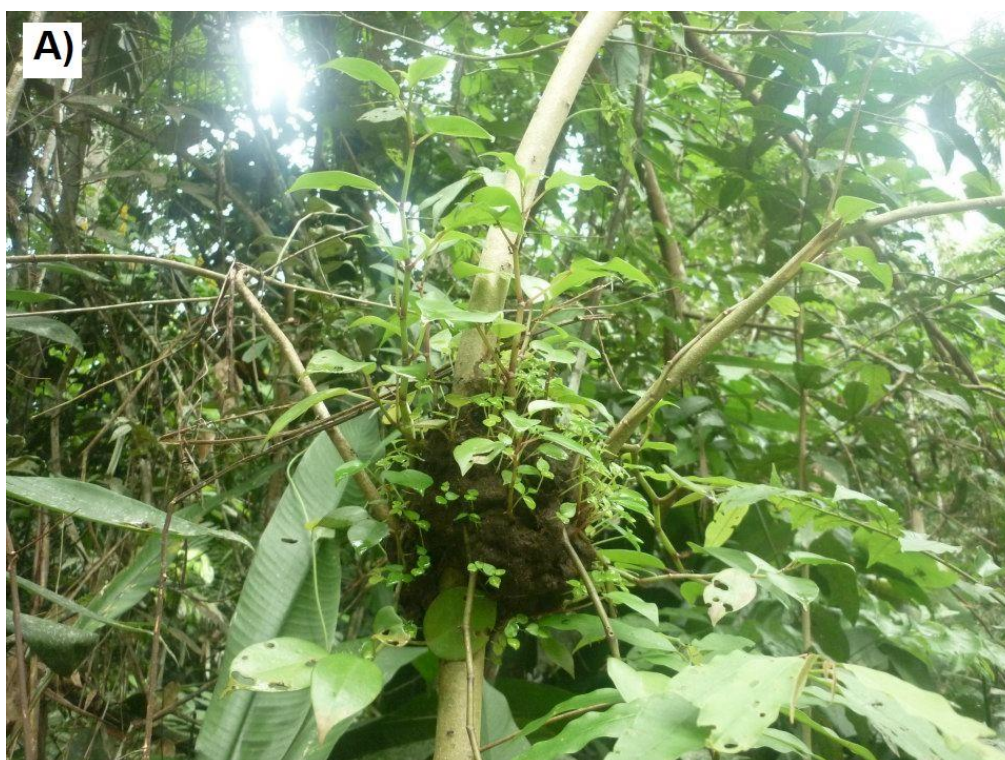




Figura 1 - Jardins de formigas de *Camponotus femoratus* (Fabricius, 1804) e *Crematogaster levior* Longino, 2003 fotografados em clareiras dos municípios de Novo Mundo (A, B) e Claudia-MT (C) durante as coletas de dados.

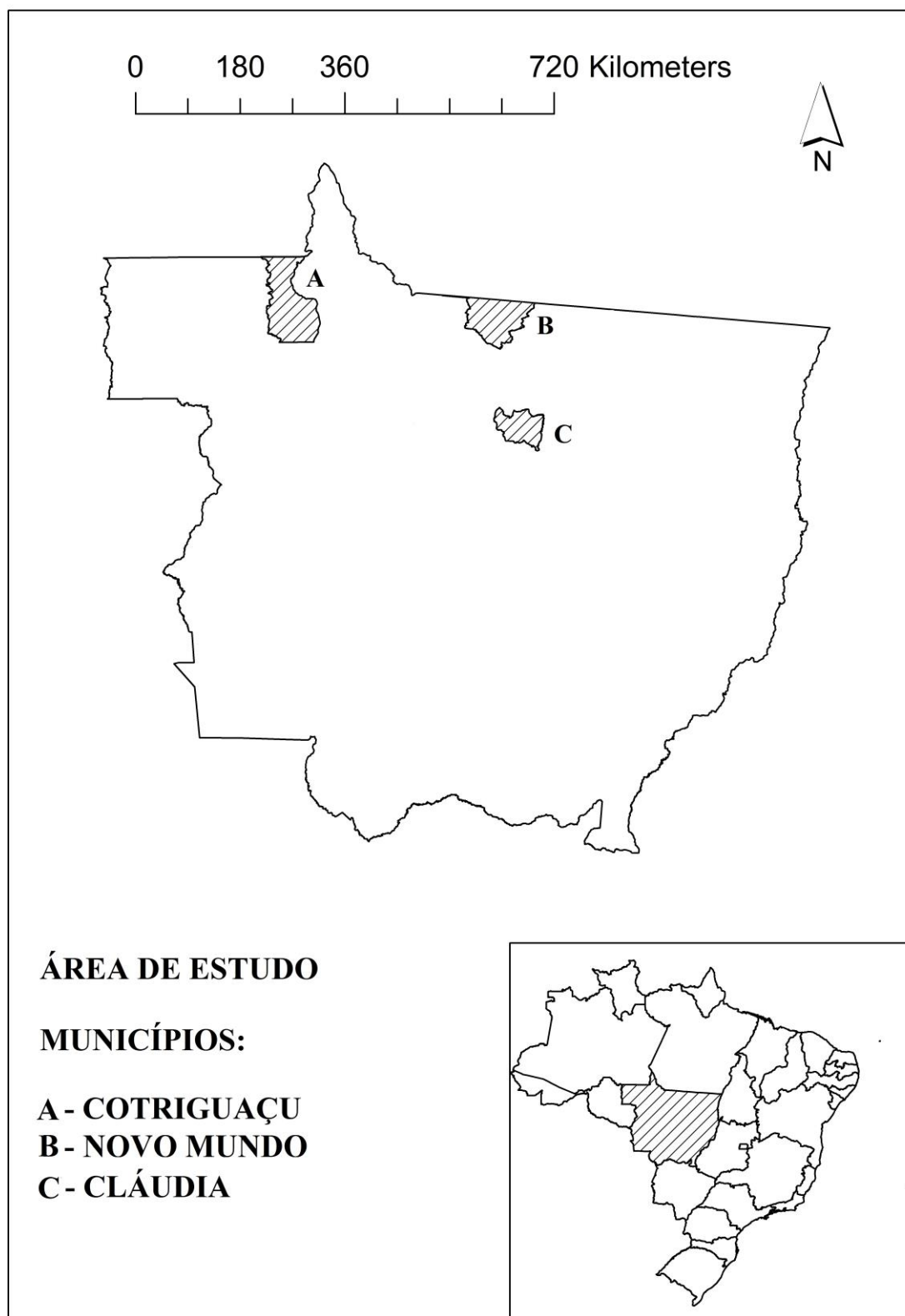


Figura 2 – Mapa ilustrando os municípios onde os dados foram coletados, sendo A) Cotriguaçu-MT, B) Novo Mundo-MT e C) Cláudia-MT. Mapa confeccionado no software ArcMap 10.1.

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CAPITULO 1 - Differential recruitment of *Camponotus femoratus* (Fabricius) ants in response to Ant Garden herbivory

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Differential recruitment of *Camponotus femoratus* (Fabricius, 1804) ants in response to Ant-Gardens herbivory

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ABSTRACT: Although several studies have shown that ants can recognize chemical cues from their host plants in ant-plant systems, it is poorly demonstrated in Ant-gardens (AGs). In this interaction, ant species constantly interact with various epiphyte species. Therefore it's possible to expect a convergence of chemical signals released by plants that could be acting to ensure that ants are able to recognize and defend epiphyte species frequently associated with AGs. In this study it was hypothesized that ants recognize and differentiate among chemical stimuli released by AGs-epiphytes and non AGs-epiphytes. With this aim, it was experimentally simulated leaf herbivore damage on three epiphytes species restricted to AGs and a locally abundant understory herb: *Piper hispidum* in order to quantify the number of recruited *Camponotus femoratus* (Fabricius, 1804) defenders. When exposed to the AG-epiphytes *Peperomia macrostachya* and *Codonanthe uleana* leaves it was observed that the recruitment of *Ca. femoratus* workers was, on average, respectively 556% and 246% higher than control. However, the number of ants recruited by the AGs-epiphyte *Markea longiflora* or by the non-AG plant did not differ from paper pieces. This indicated that ants could discern between chemicals released by different plants, suggesting that ants can select better plants. These results can be explained by evolutionary process acting on both: ants' capability in discerning plants' chemical compounds (innate attraction); or by ant's learning based on the epiphytes frequency in AGs (individual experience). To disentangle an innate behavior, a product of classical co-evolutionary process, from an ant's learned behavior is a complicated but important subject to understand in the evolution of ant-plant mutualisms.

Keywords: Ant-gardens, ant-plant system, *Peperomia macrostachya*, *Codonanthe uleana*, herbivory, mutualism.

1) Introduction

Cooperative interactions among species are one of the central issues in ecology, and probably every organism on Earth is engaged in at least one mutualistic interaction throughout its life history (Bronstein 2001). In this kind of relationship one species provides a service or a product that its partner cannot acquire alone and, in exchange, receives some kind of payment or reward (Hoeksema & Bruna 2000). Ants and plants can interact in different ways, from facultative to highly specialized mutualistic relationships (Fonseca & Ganade 1996, Rico-Gray & Oliveira 2007, Vicente *et al* 2012). Studies focusing on the mutualism between ant and plant approaches have made a notable contribution to the current understanding on mutualistic interactions (e.g. Bronstein 1998, Izzo & Vasconcelos 2002, Heil & McKey 2003).

One remarkable ant-plant mutualism found in tropical forests is known as Ant-Gardens (hereafter AGs). This interaction in Neotropical regions includes nine species of ants (obligate AGs inhabitant) and 53 epiphyte species (Orivel & Leroy 2011). However the association between *Camponotus femoratus* (Fabricius, 1804) (Formicinae) and *Crematogaster levior* Longino, 2003 (Myrmicinae) is among the most commonly found in neotropics and is categorized as parabiosis (where two species share the same nest and foraging trails - Hölldobler & Wilson 1990, see: Swain 1980, Sanhudo *et al* 2008). About 95% of AGs in the Amazon forest areas are occupied by them (Davidson 1988, Youngsteadt *et al* 2010, Orivel & Leroy 2011). Indeed, these ants are found foraging from the ground to the canopy (Wilson 1987, Dejean *et al* 2007, Ryder Wilkie *et al* 2010) and are behaviorally dominant in the ant community wherever they occur (Davidson 1988, Mertl *et al* 2010).

In AGs, ants build arboreal nests using some specific epiphyte seeds (Davidson 1988). During seed harvesting the differentiation between their mutualistic partners and other plants is made through the recognition of volatiles present in the seeds of AGs-

epiphytes (Youngsteadt *et al* 2008). When the seeds sprout and grow, the epiphyte roots increase the structural stability and complexity of the ants' nests (Yu 1994). Moreover, some AGs-epiphytes can provide food for ants through nectaries, fruits and seed arils, or indirectly, serving as a substrate to tend honeydew-producing insects (Kleinfeldt 1986, Davidson 1988, Orivel & Leroy 2011). On the other hand, epiphytes are benefited by seed dispersion, provision and maintenance of a substrate with high concentration of nutrients (Blüthgen *et al* 2001, Schmit-Neuerburg & Blüthgen 2007) and protection against herbivory (Vantaux *et al* 2007).

Several studies have shown that in other protective ant-plant interactions, as myrmecophyte systems, ants can recognize the herbivores presence on their host plants using cues. Some myrmecophyte-ants can detect physical stimuli of the herbivore on plants as Volatile Organic Compounds (VOCs) released by plants when the leaf tissue is ruptured at the moment of herbivory and immediately recruit nest mates (Romero & Izzo 2004, Christianini & Machado 2004, Dejean *et al* 2007). Just one study demonstrated such response in AGs-epiphytes, but the authors described the response of ants to herbivory simulated in only one host plant (Vantaux *et al* 2007). In AGs, the ant chemical recognition of leaf volatiles comes up against a more complex picture because more than one ant species constantly interacts with various epiphyte species that compose the same nest. In such scenario, as in AG-seeds (Youngsteadt 2010), AG-ants face several plants belonging to different families (Orivel & Leroy 2011) and, consequently, distinct phylogenetic histories. This diversity of partners can be associated to a diversity of chemical compounds released when the leaf is damaged by herbivores. Thus to be an efficient partner, the ants needs to recognize and respond to all different chemicals. In other hand, it is possible that the AGs plants show similar chemical signals by convergence to a generalized signal linked to herbivory. So, the ants would to recruit equally to all AG species in a given site. Therefore we hypothesize that: 1) ants recognize chemical stimuli emitted by different

AGs-plants and 2) they can differentiate this stimulus when compared with a plant understory. To test these hypotheses, we used as a study model a colony of *Ca. femoratus*, their sympatric epiphytes in a secondary forest located in the southern Brazilian Amazon.

2. Material and Methods

2.1) Study area

This study was conducted on the São Nicolau Farm (9°48'S and 58°15'W, elev. 254m), located in the municipality of Cotriguaçu, north of Mato Grosso State, Brazil. According to the Köppen classification, the climate is tropical humid (Am) with annual average: 24-26 °C and precipitation of 3,000 mm year⁻¹ (Alvares *et al* 2013). There are two well-defined seasons, a rainy season between November and April and a dry season between May and October (pers. obs). The local vegetation is classified as Open Ombrophylous Forest and Dense Ombrophylous Forest contrasting with large areas of Teak (*Tectona grandis*) plantations and 28 native arboreal tree species (Vicente *et al* 2011). The experiments were conducted on a native forest edge with approximately 7.250m² bordering a reforestation site of *Ficus* spp. (Moraceae). Canopy in this area was composed by young trees (about 3 meters high), mainly *Vismia* sp. (Hypericaceae) a typical plant of open areas and forest edges (Santos & Machado 1998).

2.2 Experimental design

Previously, to determine the composition of epiphytes in this study site, the frequency epiphytes found in 17 AGs of one *Ca. femoratus* colony were recorded. Only the species with established roots inside ant colonies (Kaufmann & Maschwitz 2006) were considered as epiphytic plants. Based on this ratio, three AGs-restricted epiphytes were selected so as to conduct the recruitment of ants experiment, two common plant species *Peperomia macrostachya* (Piperaceae) and *Codonanthe uleana* (Gesneriaceae) and the

least common, *Markea longiflora* (Solanaceae).

For recognition experiments 20 AGs were chosen in this same *Ca. femoratus* colony. We selected nests with at least two of the three species found in the region. These nests were found at least 10 meters one to another. Twenty-four hours before the beginning of the experiments a circular transparent plastic platform 15cm in diameter was fixed with wire to the arboreal phorophyte trunk, at a distance of 30cm from the each selected nest, in order to allow easy access by the ants. This time period (24 hours) was required to reduce the disturbance caused by the installation of the experiment.

We simulated leaf herbivore damage by placing gently leaf pieces of 5cm² in center of each platform. Leaf pieces were obtained immediately before we start the experiment and collected in others AGs at least 10 meters apart the one we conduct the experiment. As the ants could recruit when exposed to any leaf volatile, a herb that occurs abundantly in understory of the study site but is not present in the AGs: *Piper hispidum* (Piperaceae) was used. Furthermore, in order to control the effect of the manipulative disturbance when inserting new material near the colony, pieces of paper (5cm²) were used. All five treatments (three epiphytes, one non-epiphyte and one control) were carried out in each of the 20 AGs. At the beginning of all experiments (time zero) there was no ant worker in any platforms. The order of administration of each treatment was randomized at the moment of the experiment. Thereafter, before the administration of each, the number of ants patrolling on these platforms was quantified in 1, 3, 7 and 10 minutes. In order to reduce any other external interference, at the end of each experimental trial any residue was removed and the platforms were washed using ethanol. Additionally, there was a interval of 24 hours among each experiment. Despite the variety linked to activity time of ants of the genus *Camponotus* (for examples see: Yamamoto & Del-Claro 2008) *Ca. femoratus* patrol equally during the whole day (Vantaux *et al* 2007). However, the period of the experiment was always the same, between 13 and 15 pm. order to avoid climatic variations that come

interfere in volatilization of the compounds or the effect of temperature on ant's behavior.

2.3) Data analysis

To test the hypothesis that ants' recruitment is stimulated by volatile to AGs-epiphytes over time, a randomized block repeated measures ANOVA was used. In this analysis the number of recruited worker ants was the dependent variable. Each species of plant and control was the independent factor. Each ant-garden where five treatments were carried out was the blocking factor and the time factor (0, 1, 3, 7 or 10 minutes) was the repetition factor. Later, each leaf strip was tested against control (paper strip) in *a posteriori* analysis in order to determine to which plant the ants were effectively recruiting. In this case, the Bonferroni correction for multiple comparisons was employed. All analyzes were performed using the SYSTAT v.13.0 software (Wilkinson 1998) and the figure prepared using GraphPad Prism version 5.0 (Motulsky 1999).

3) Results

3.1 Ant-gardens composition

In the AGs survey (n=17) four epiphyte species were observed. Seven AGs harbored more than one epiphyte species. *Peperomia macrostachya* (Piperaceae) was the most frequent, present in 88% of the observed AGs. The second most frequent was *Codonanthe uleana* (Gesneriaceae) (41%), followed by *Philodendron* sp. (Araceae) (18%) and *Markea longiflora* (Solanaceae) (6%). Combinations of species varied among nests but *P. macrostachya* was the only one to be associated with all other epiphyte species. *Co. uleana* was recorded with *P. macrostachya* or *Philodendron* sp., sometimes the three species being present together. *M. longiflora* occurred only once, in a large nest sharing substrate only with *P. macrostachya*. Only *Co. uleana* and *P. macrostachya* were found alone in the AGs, usually in nests at early development stages. In not-sampled nearby AGs other epiphyte

species such as *Anthurium* sp. (Araceae) and an unidentified Bromeliad (Bromeliaceae) occurring in extremely low frequencies were found. The ant species *Ca. femoratus* and its parabioc partner *Cr. levior* were recorded in all studied AGs. Except for them, only two species of ants were seen foraging near the nest: *Cephalotes* sp. and *Cephalotes clypeatus*. However neither of them occurred on experimental platforms during the experiment.

3.2 AGs' Ant recruitment

Camponotus femoratus account for almost 100% of the ants recruited in the experiment. *Crematogaster levior* was observed only on a few occasions represented by solitary workers, almost always occurring when *Codonanthe uleana* strips were exposed, but as they did not perform massive recruitments, this fact was not consider as biologically significant. Thus, all following statistical analyzes were performed for *Ca. femoratus*.

Different recruitment among treatments ($F_{4,100} = 20.92$, $P < 0.001$) were observed, with no variation among AGs (block effect - $F_{18,100} = 0.78$, $P > 0.5$) or different response patterns among different AGs (block effect*treatments - $F_{72,100} = 1.74$, $P = 0.36$). During 10 minutes of experiment the recruitment of *Ca. femoratus* workers increased 556% in *Pe. macrostachya* (Mean of ants workers \pm SD: 3.89 ± 2.37) and 246% in *Co. uleana* (1.72 ± 1.89) than paper strip (0.7 ± 1.07) ($F_{1,37} = 50.412$, $P < 0.001$ and $F_{1,38} = 6.633$, Bonferroni $P = 0.014$, Table 1).

The higher ant recruitment occurred after three minutes of experiment in *Pe. macrostachya* (6.21 ± 3.14) ($F_{3,111} = 17.234$, $P < 0.001$). In *Co. uleana* the recruitment was more intense in the seventh (2.15 ± 2.25) and tenth (2.15 ± 2.41) minute of the experiment ($F_{3,111} = 17.234$, $P < 0.001$). The average number of worker ants in other treatments did not exceed 1.2 recruited at any time (Figure 1). Additionally, the number of ants recruited by *M. longiflora* or the non-AGs *Piper hispidum* did not differ from those found when paper pieces were placed on platforms (respectively, $F_{1,37} = 0.004$ and $F_{1,38} = 1.282$, Bonferroni P

> 0.5). Although the *Camponotus femoratus* recruitment increased only when ants faced volatiles from the two most abundant epiphytes (*Pe. macrostachya* and *Co. uleana*), differences were found between them ($F_{1,37} = 15.496$, $P < 0.001$). In addition, the recruitment strength was different between these two epiphytes over time ($F_{3,111} = 10.586$, Bonferroni $P < 0.001$).

4) Discussion

The epiphytic species found in this study are reported constantly associated with Ant-gardens (AGs) in a wide geographic range throughout Amazon (Yu 1994, Orivel & Dejean 1999, Dejean *et al* 2000, Orivel & Leroy 2011) often associated with *Ca. femoratus* and its parabiotic partner *Cr. levior* (Orivel & Dejean 1999). These results indicate a high specificity of this relationship over the whole geographic range. Indeed, this partner stability in such large geographic area is a scenario that may result from the development of local co-evolutionary mechanisms of recognition among mutualistic partners (Thompson 2005). Moreover, we note that only *Ca. femoratus* workers recruit to AGs leaf pieces drumming, and becoming agitated and walking randomly around the nest, a behavior that may be linked to the recruitment of other workers (Santos *et al* 2005). It's not surprising, since *Cr. levior* lost their chemical defense relying on the protection of *Ca. femoratus* (Longino 2003) and, additionally, *Cr. levior* is mainly nocturnal, unlike *Ca. femoratus* that patrols throughout the day (Vantaux *et al* 2007). Indeed, *Cr. femoratus* recruiting workers at different intensities and only to more common AGs epiphytes.

Plants defense by ants has been related to the specificity of the interaction (Bruna *et al* 2008, Dáttilo *et al* 2009) probably because the quantity and quality of food resources offered by different plants species can vary (Bronstein 1998, Ness *et al* 2009, Heil & Mckey 2003) and resource intake is intrinsically connected to ant fitness (Byk & Del-Claro 2011). In fact, part of the difference observed in plant attractivity to ants can be supported

by the food reward provided by the plants. *Markea longiflora* and *Codonanthe uleana* provide extrafloral nectar to *Ca. femoratus* ants, and *P. macrostachya* have oil glands on their leaves, inflorescence and fruits (Madison 1979, Benzing 1990, Carvalho-Silva 2008). AGs usually occur in areas with high-light incidence and productivity, as treefall gaps and riverbanks (Davidson 1988). In such habitats, *Ca. femoratus* can use a plethora from other plants with extrafloral nectar and cultivate honeydew-producing insects in other plants nearby AGs (Davidson 1988, Schupp & Feener 1991, TJI pers. obs.). This suggests that the demand for extrafloral nectar (sugar) could not be the key factor for the AGs ants. On the other hand, the oil provided by *Pe. macrostachya* is a rare reward among plants and can be more valuable in such environments when compared to extrafloral nectar. In fact, *Ca. femoratus* were observed several times feeding on *Pe. macrostachya* oil glands, but no ant was observed foraging on the extrafloral nectaries of either *M. longiflora* or *Co. uleana*. Indeed, *Co. uleana* is more frequently found than *M. longiflora* and bear fruits throughout the year from the early stages of the plant life cycle. Nevertheless, *M. longiflora* invests more in growth and reproduce late (Davidson 1988). Despite these environments being apparently Nitrogen rich resources, *Co. uleana* can be considered as a predictable resource over the year.

Experiments on seed harvesting by *Ca. femoratus* claim no direct relationship between the choice of the seed and the resource offer (Orivel and Dejean 1999, Davidson 1988). In such cases the seed dispersal is linked mainly to the chemical composition of volatiles released by seeds (Youngstead *et al* 2008). However, there is probably a link among the plant defense by *Ca. femoratus* and the plant frequency and the quality of the existence of food resource. So, the high frequency of *P. macrostachya* can be a product of an evolutionary pattern, once plants should emit specific volatile compounds, imposing a possibility of selection of *Ca. femoratus* to discern between resource-rich, resource-poor or cheater plants. However, better plants, with the denser root system and/or that produce

better food resources could be positively selected and more vigorously defended. Therefore, it is possible to expect a coevolutionary scenario, in which the better-defended plants would produce more seeds and become more frequent and the better defender ant, with the better VOCs detection capability, will receive more food and nest and, consequently, produce more alates (reproductive ants).

On the other hand, VOCs released by plants during herbivory play other roles in the plant life cycle and are present in a large number of plant species (Heil 2008, Kessler & Heil 2011). Other studies show no evidence of adaptation traits of VOCs to the alarm of herbivores, suggesting that communication among plants and a third trophic level may not be a coevolutionary trait (reviewed on Kessler & Heil 2011). In this present study, the coevolutionary hypothesis fits as a reasonable explanation, but one cannot expel an alternative hypothesis that it is not necessarily a product of a direct evolutionary pressure: the VOCs recognition can be a product of imprinting (Djeto-Lordon & Dejean 1999a,b) or also a product of the ant's learning capacity. There are several examples in which some ant species have the ability to learn from past experiences (Langridge *et al* 2004, Blatrix & Sermage 2005, Ravary *et al* 2007, Langridge *et al* 2008, Van-Wilgenburg *et al* 2010) and also when it comes to discrimination of chemical cues (Dupuy *et al* 2006, Errard *et al* 2008, Bos *et al* 2010). The learning process demands a certain frequency of similar repeated experiences (Takabayashi *et al.* 2006). Indeed, *P. macrostachya* is the most common plant on AGs of the study area. It suggests that the higher *Camponotus femoratus* recruitment to the most frequent plant volatiles may be a product of learning. *Camponotus femoratus* could have learned that frequent VOCs release is associated to the presence of a herbivore (a possible food resource). Distinguish an innate behavior, a product of a classical co-evolutionary process, from an ant's learned behavior is complicated but an important subject in understanding the evolution of ant-plant mutualisms (see for example: Djeto-Lordon & Dejean 1999a,b). Future experiments manipulating plant frequency in

AGs along its ontogeny should be made in order to determine if the chemical recognition of plants is due to a coevolutive process or learning from multiple experiences.

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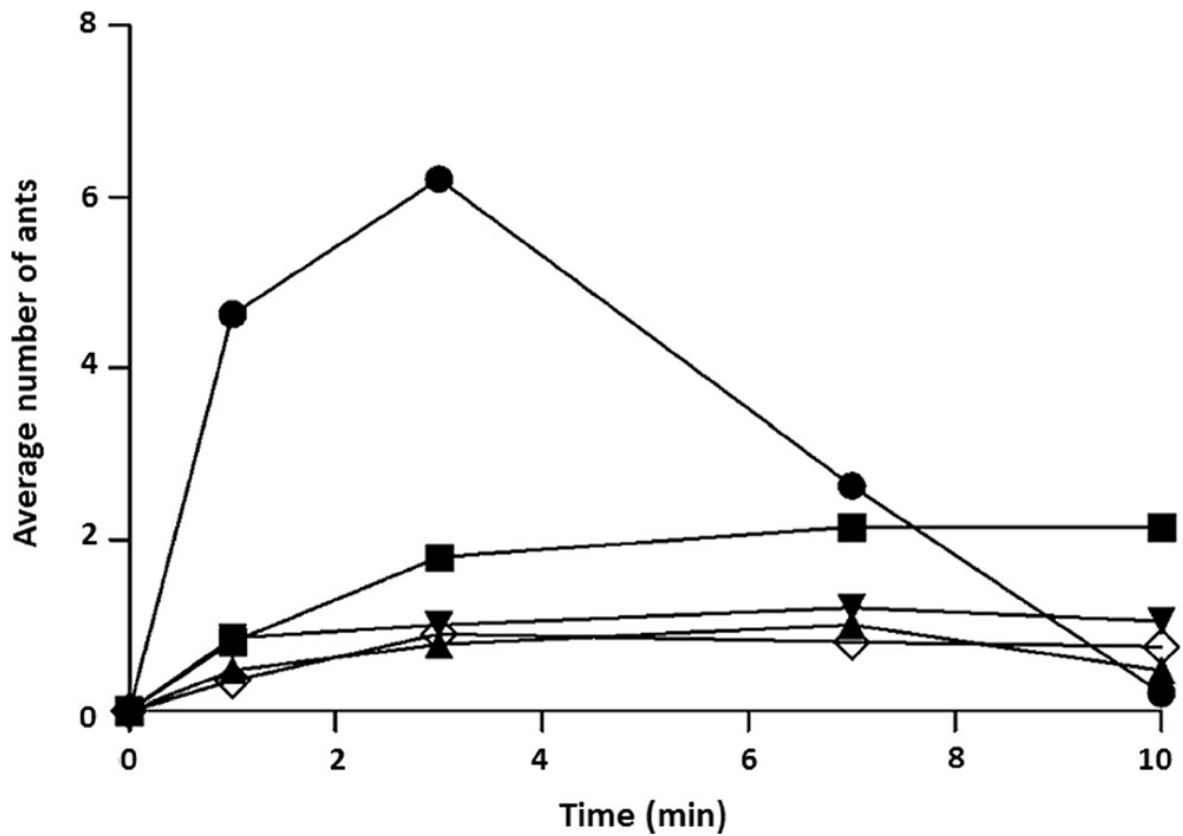
Table 1. Repeated measures ANOVA for the effect of chemicals cues released by plants in recruitment of *Camponotus femoratus* workers

Experiment	Source of variation	d.f.	MS	F
<i>Peperomia macrostachya</i> versus Control	Plant	1	397,786	50,412***
	Error	37	7,891	
	Time	3	35,264	17,234***
	Time × Plant	3	35,401	17,300***
	Error	111	2,046	
<i>Codonanthe uleana</i> versus Control	Plant	1	42,025	6,633 **
	Error	38	6,336	
	Time	3	7,342	5,810***
	Time × Plant	3	1,975	1,563
	Error	114	1,264	
<i>Markea longiflora</i> versus Control	Plant	1	0,010	0,004
	Error	37	2,344	
	Time	3	1,968	2,758*
	Time × Plant	3	0,464	0,650
	Error	111	0,714	
<i>Piper hispidum</i> versus Control	Plant	1	4,225	1,282
	Error	38	3,296	
	Time	3	1,292	1,462
	Time × Plant	3	0,292	0,330
	Error	114	0,884	
<i>Peperomia macrostachya</i> versus <i>Codonanthe uleana</i>	Plant	1	183,482	15,496***
	Error	37	11,841	
	Time	3	27,008	10,586***
	Time × Plant	3	50,461	19,779***
	Error	111	2,551	

Significance values: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

FIGURE LEGEND

Fig 1 - Mean number of *Camponotus femoratus* workers recruited along time after administration of five experimental treatments: *Peperomia macrostachya* (circle symbol), *Codonanthe uleana* (squared), *Markea longiflora* (triangle), understory plant *Piper hispidum* (inverted-triangle) and control paper strips (lozenge). There are no difference between treatments in the beginning of experiment (Time 0).



CAPÍTULO 2 - Defining the niche of parabiotic ants *Camponotus femoratus* (Fabricius, 1804) and *Crematogaster levior* Longino, 2003

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1 *Running title: Niche of Ant-garden ants*

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3

4 Defining the niche of parabiotic ants *Camponotus femoratus* (Fabricius, 1804) and
5 *Crematogaster levior* Longino, 2003

6

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15

16 Key-words: Canopy openness, Complexity, Gap size, Habitat use, Niche partitioning,
17 Vertical habitat

18

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26 ABSTRACT - Ant-garden ants have a strong relationship with epiphytes that need light
27 to grow, for these reason, it has been previously documented in forest gaps. Moreover, larger
28 gaps have more available area for nesting and habitats for use as forage. Thus we hypothesize
29 that 1) openness canopy influence the presence of ant´s gardens in gaps, and 2) greater gaps
30 will have more nests, and 3) both openness canopy and area determine the colony size in
31 forest gaps. Furthermore, it is known that parabiotic ants foraging on the ground and in
32 vegetation, the nests are arboreal. So, we also hypothesize that 4) parabiotic ants are more
33 often sampled in arboreal strata and 5) increasing complexity of vegetation and the volume of
34 accumulated litter in the soil increase the foraging of the ants in vegetation and ground,
35 respectively, with the increase in canopy openness increasing the activity of the two species in
36 both strata. Presence, number of Ant-gardens, as colony size, was affected by area and
37 locality, but not by canopy openness. Nevertheless, there was not overall difference in the use
38 of strata by *Camponotus femoratus*, neither by *Crematogaster levior*. On the other hand,
39 frequency of *Ca. femoratus* on the ground decreases with canopy openness but is not affected
40 by the complexity of vegetation. Also, *Cr. levior* frequency on the ground also decreases with
41 the increase of complexity of vegetation and canopy openness. In addition, neither
42 complexity, or canopy openness influence the frequency of foraging of these ants in
43 understory.

44 Key-words: Canopy openness, Complexity, Gap size, Habitat use, Niche partitioning,
45 Vertical habitat

46

47 INTRODUCTION

48 Niche is the interaction between tolerances and requirements of conditions and
49 resources of a species (Hutchinson, 1957) and has been employed to describe various
50 biological and evolutionary aspects of species and to test functional ecology hypotheses
51 (Blonder et al., 2014). The niche concept was historically important due to its application in
52 the understanding of several practical issues such as management of economic species
53 (Milstein et al., 2000; Almeida & Valle, 2007; Penha & Mateus, 2007), policies of public
54 health (Medeiros et al., 2006; Dicko et al., 2014; Guichard et al., 2014) and conservation
55 (Leite-Rezende et al., 2014; Dorado-Rodrigues et al., 2015; Nekaris et al., 2015). However,
56 little is known about the niche characteristics of ant species at various scales (Dáttilo et al.,
57 2012a,b; Nakano et al., 2013, Gallego-Ropero et al., 2013, Gallego-Ropero & Feitosa, 2014;
58 Pape, 2016). Especially because the distribution of many ant species still has many gaps
59 (Brandão et al., 2008; Vicente et al., 2015; Schmidt et al., 2014; Camacho & Feitosa, 2016;
60 Prado et al., 2016; Santos-Silva et al., 2016). Works such as these are scarce, but important to
61 disassemble old concepts about the species and help to understand patterns in ant
62 communities (Feitosa et al., 2008, 2016; Delabie et al., 2010).

63 The ecological role, and as a consequence, the niche of two Neotropical ants
64 *Camponotus femoratus* (Fabricius, 1804) (Formicinae) and *Crematogaster levior* Longino,
65 2003 (Myrmicinae) is virtually unknown. These ants share the same foraging trails and their
66 arboreal nests in a mutualism relationship known as parabiosis (Swain, 1980). In the nests,
67 they actively plant one or several epiphyte species, forming a complex nest, known as Ant-
68 Gardens (hereafter AGs) (Davidson, 1988; Longino, 2003; Youngsteadt et al., 2009). This
69 interaction includes nine species of ants (obligate AGs inhabitant) however, AGs with
70 parabioc association between *Ca. femoratus* and *Cr. levior* are among the most commonly
71 found in the Amazon (Davidson, 1988; Orivel & Leroy, 2011). In exchange for support and
72 humidity control for the nest and, in some cases, extrafloral nectar (Davidson, 1988; Schmit-

73 Neuerburg & Blüthgen, 2007), the ants offer dispersion and protection to their mutualistic
74 epiphyte (Vantaux et al., 2007; Youngsteadt et al., 2008, 2009; Vicente et al., 2014). However,
75 it is important to know the aspects of the niche of these parabiotic ant species whose one
76 species extinction can harm the survival of their partner and can lead to a cascade effect of the
77 loss of other species (Guimarães et al., 2007; Dáttilo, 2012).

78 Ant-garden ants have a strong relationship with epiphytes that need light to grow (Leroy
79 et al. 2016; Orivel & Leroy 2011), for this reason, they have been previously documented in
80 tree-fall gaps, river banks and abandoned roads (Dáttilo & Izzo, 2012; Vicente et al., 2014).
81 Moreover, larger gaps have more available area for the building of nests and habitats for use
82 as forage. Thus we hypothesize that 1) the openness canopy influences the presence of ant´s
83 gardens in gaps, and 2) greater gaps will have more nests, and 3) both openness canopy and
84 area determine the colony size in forest gaps. Furthermore, even though the nests are
85 essentially arboreal, it is known that parabiotic ants forage on the ground and in vegetation.
86 So, we also hypothesize that 4) parabiotic ants are more often sampled in arboreal strata and
87 5) increasing complexity of vegetation and the volume of accumulated litter on the soil
88 increase the foraging of the ants in vegetation and ground, respectively, with the increase in
89 canopy openness increasing the activity of the two species in both strata.

90

91 **MATERIAL AND METHODS**

92 **Study area**

93 The study was carried out on two municipalities of the southern Amazonia as part of the
94 Research Program in Biodiversity (PPBio). The standard sampling protocol used in PPBio is
95 the RAPELD methodology (see Costa & Magnusson 2010). In each of the two municipality a
96 set of trails of 250m in length are installed at a minimum distance of 1 km each other, linked
97 by access trails (henceforward Module). In Claudia municipality, three modules are installed
98 close to each other (less than 20km), in a large fragment surrounded by plantations. The

99 Claudia modules are Module I (11°34'S, 55°17'W) and Module II (11°35'S, 55°17'W) that
100 are broadly connected, and Module III (11°39'S, 55°04'W) that is an area with about 900ha
101 almost completely surrounded by plantations and narrowly connected to the rest of the
102 fragment. The area of these three modules had selective logging more than eight years ago.
103 Because of this, they have older gaps caused by the management of selective logging as wood
104 storage yards and trails used for the dragging of cut trees (abandoned roads). One other area is
105 the Parque Estadual do Cristalino Reserve, a continuous pristine forest in the municipality of
106 Novo Mundo municipality, Mato Grosso States (9°28'S, 55°50'W).

107 According to the Köppen classification, the climate is tropical humid (Am) with annual
108 average of 25°C. Precipitation is about 2.500 to 2.800 mm year in forest remnants of the
109 municipality of Claudia and 2.800 to 3.100 mm year in Parque Estadual do Cristalino
110 (Alvares et al., 2013). In both, there are two well-defined seasons, a rainy season between
111 November and April and a dry season between May and October (Vicente et al., 2014). The
112 local vegetation in Claudia is classified as area of ecological tension between Open
113 Ombrophyllous Forest and Savanna. For the Parque Estadual do Cristalino local vegetation is
114 classified as Open Ombrophyllous Forest and ecological tension areas between Ombrophyllous
115 Forest and Savanna, Savanna and Seasonal Forest, Seasonal Forest and Ombrophyllous Forest
116 (Instituto Brasileiro de Geografia e Estatística, 2004).

117 **Data collection**

118 **Gap-occupation**

119 We carried out the experiment about occupation of forest-gaps only in forest remnants
120 in the municipality of Claudia. In these areas, we surveyed all access trails that link plots,
121 totaling approximately 32km. In these trails, all forest-gaps, including the gaps caused by
122 selective logging, within the range of 10 meters of each side of the trails (20 m wide) were
123 selected and we recorded the presence or absence of AGs, number of nests and colony size.
124 Furthermore, we measured the canopy openness and the length of the two central

125 perpendicular axes of the forest gap.

126 Canopy openness was measured with Concave Spherical Densiometer. It is considered
127 a practical and cheap device that provides a reliable proxy as to the relative availability of
128 light (Baudry et al., 2014). In the center of each forest-gap, we recorded four measurements in
129 the cardinal directions to calculate an average availability of light (Dáttilo et al., 2013, 2014;
130 Baudry et al., 2014). The first two major perpendicular measures of gaps were used as length
131 and width to calculate the gap area, using the formula of the ellipse area (Runkle, 1981;
132 Arihafa & Mack, 2013). In forest-gaps formed by abandoned roads, because of the difficulty
133 in measuring their main axes, we considered a continuous habitat and we assigned an
134 arbitrary value area, the double of our largest forest gap.

135 Vertical habitat use

136 To access the information about the use of the vertical habitat by parabiotic ants thirty
137 four (34) plots allocate in the four areas previously mentioned were investigated. In each plot,
138 every 25 meters a collection of *Ca. femoratus* and *Cr. levior* ants on the ground and in
139 vegetation was performed, totaling 680 samples (340 on ground and 340 in vegetation). For
140 the collection of ground-dwelling ants, we installed pitfall-traps buried at ground level
141 containing water and detergent. Pitfalls were on field for 48 hours. For sampling arboreal ants
142 was used beating-tray. At four points on the North, South, East and West, 2 meters away from
143 each pitfall all vegetation within 1m² between 1 to 3 meters tall was sampled (more details:
144 Vicente et al., 2016). Posteriorly we made comparisons with specimens deposited at the
145 Laboratório de Ecologia de Comunidades from the Centro de Biodiversidade da Universidade
146 Federal de Mato Grosso (UFMT) and the ant collection from the Laboratório de Sistemática,
147 Evolução e Biologia de Hymenoptera from the Museu de Zoologia da Universidade de São
148 Paulo (MZSP). Vouchers were deposited in the collections mentioned above and in Setor de
149 Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso, Departamento
150 de Biologia e Zoologia, Cuiabá, Mato Grosso, Brazil (CEMT).

151 In these points, measurements of vegetation complexity and litter height were taken.
152 Vegetation complexity was accessed with a number of touches in the understory of a stem of 2
153 meters positioned one meter high, perpendicular to the ground. Litter height was accessed
154 with a rule and canopy openness with Concave Spherical Densiometer as explained earlier in
155 the section gap-occupation.

156 **Data analysis**

157 **Gap-occupation**

158 To test which characteristics determine the colonization and abundance of Ant-gardens
159 in gaps, presence of AG and number of nests were the dependent variables and forest-gap area
160 and canopy openness average were the independent variables. We tested the correlation
161 between independent variables with Pearson correlation (Pearson: 0.026). Among the three
162 sampled areas, Module III is almost totally isolated area and which has the least amount of
163 gaps colonized by parabiotic ants (only 10.3%) while Module I and Module II showed more
164 than twice the number of colonized gaps (24.2% and 25.5% respectively). This is an
165 indication of the intrinsic characteristics of this locality, as area and edge effects, affecting the
166 population dynamics of this ant species. Consequently, the location was inserted into the
167 GLM analyses using Orthogonal Contrast established a priori, considering the principles
168 described by Gotelli & Ellison (2011), being set up as Contrast: Module I (+1), Module II
169 (+1) and Module III (-2). We used the R software to perform all analyzes (R Core Team,
170 2014).

171 To test whether the colony size, which indirectly is represented by the volume of the
172 nests, was related to independent variables a GLM was performed. The variable colony size
173 was calculated using the formula of the volume of spheres (V), where r is the radius of the
174 sphere and π is the constant pi:

$$175 \quad V = \frac{4 * \pi * r^3}{3}$$

$$176 \quad 3$$

177 Finally, to test whether the colony size was related to the amount of nests one Pearson
178 correlation was made.

179 Vertical habitat use

180 To confirm the hypothesis that *Ca. femoratus* and *Cr. levior* have different preferences
181 about the use of vertical habitat a Test-t was performed for each species. In this analysis the
182 frequency of each species per plot was the dependent variable and stratum was the
183 independent factor. To access the information about what structural environmental variable
184 affects the strata use of *Ca. femoratus* and *Cr. levior* a GLM with Negative binomial
185 distribution was used. This error distribution is indicated when Poisson error distribution
186 shows overdispersion (Hilbe, 2007; Lindén & Mäntyniemi, 2011). Because a correlation
187 between independent variables was detected with Pearson correlation with Bonferroni
188 correction, we excluded litter height variable of analyses.

189

190 RESULTS

191 Gap-occupation

192 We recorded 27 colonies of ant-garden ants in all 142 forest-gaps (125 in tree-fall gaps
193 and 17 in abandoned roads). Regarding environmental variables of forest gaps, they had an
194 average size of 215.125 m² (SD: 130.947 - values excluding the 880.44m² value established
195 for abandoned roads). The canopy openness had an average of 32.94% (SD: 14.61).

196 Presence of Ant-gardens colony was affected by area ($Z_{1,138}$: 2.470, p : < 0.05 – Table 1)
197 and locality ($Z_{1,138}$: 2.269, p : < 0.05), but not by canopy openness ($Z_{1,138}$: -1.849, p : < 0.05).
198 Abundance of Ant-gardens nests was also affected by area ($Z_{1,138}$: 2.090, p : < 0.05) and
199 locality ($Z_{1,138}$: 2.570, p : 0.010) and also not by canopy openness ($Z_{1,138}$: -1.583, p : 0.113 –
200 Table 1). Ants colony size was also influenced by the gap area ($Z_{1,138}$: 3.494, p : < 0.05), the
201 locality ($Z_{1,138}$: 2.422, p : < 0.05) and not the canopy opening ($Z_{1,138}$: -1.230, p : 0.221 – Table
202 1). Therefore, the abundance of Ant-gardens and the colony size present a strong correlation

203 (Pearson: 0.883).

204 Vertical habitat use

205 *Camponotus femoratus* and *Crematogaster levior* were sampled in 21 of the 34 plots
 206 studied. At least one of the two species was collected in 69 samples (30 on the ground and 39
 207 on vegetation) of the 420 samples (210 on the ground and 210 on vegetation) corresponding
 208 to 21 plots where these ants were found. *Ca. femoratus* was collected in 49 samples of 18
 209 plots (30 samples in soil and 19 on vegetation) and *Cr. levior* on 30 samples (15 times in each
 210 stratum). We assumed that in all cases both species are co-occurring in the same area, but with
 211 differences in abundance and, thus, in the probably of being collected. Therefore, these
 212 species were collected in the same sample in 13 cases (8 on the ground and 5 on vegetation).
 213 Regarding the environmental variables evaluated, they had an average of vegetation
 214 complexity of 1.417 (SD: 0.645). The canopy openness had an average of 32.94% (SD:
 215 14.61).

216 Nevertheless, there was no an overall difference in the use of vegetation and ground
 217 strata by *Camponotus femoratus* ($Z_{1,66}$: -1.519, p : 0.129 – Figure 1), nor by *Crematogaster*
 218 *levior* ($Z_{1,66}$: 0.908, p : 0.364 – Figure 1). *Ca. femoratus* occurs in average 1.67 (SD: 1.63)
 219 samples per plot in ground and 1.06 (SD: 1.47) on vegetation. *Cr. levior* occurs in average
 220 1.25 (SD: 1.16) samples per plot in ground and 1.25 (SD: 1.23) on vegetation. On the other
 221 hand, the frequency of *Ca. femoratus* on the ground decreases with canopy openness ($Z_{1,31}$: -
 222 2.435, p : < 0.05 – Table 2) but is not affected neither by the complexity of vegetation ($Z_{1,31}$: -
 223 1.407, p : 0.159) nor for interaction of two factor ($Z_{1,31}$: 1.771, p : < 0.05). Also, *Cr. levior*
 224 frequency on the ground also decreases with complexity of vegetation ($Z_{1,31}$: -2.243, p : < 0.05
 225 – Table 2), but, in this case, a decrease was also noted in the frequency associated with canopy
 226 openness ($Z_{1,31}$: -1.977, p : < 0.05) and an interaction between these factors ($Z_{1,31}$: 2.265, p : <
 227 0.05). In addition, neither complexity (*Ca. femoratus*: $Z_{1,32}$: 0.200, p : 0.841; *Cr. levior* $Z_{1,31}$: -
 228 1.225, p : 0.221 – Table 2), nor canopy openness (*Ca. femoratus*: $Z_{1,32}$: 0.580, p : 0.562; *Cr.*

229 *levior* $Z_{1,32}$: 0.804, p : 0.421) influence the frequency of foraging of these ants in understory.

230

231 **DISCUSSION**

232 Our results demonstrate that the size and local intrinsic characteristics of the forest gaps
233 are determinant to the occupation by the parabiotic ants *Camponotus femoratus* and
234 *Crematogaster levior*. These factors influence the presence as well as the quantity of Ant-
235 Gardens and the ants colony size. Also, larger gaps host more and larger AGs than smaller
236 forest gaps. This can be explained because large forest gaps remains available for longer once
237 the time of full restoration of a large forest gap, from its formation till the canopy closure is
238 probably much longer than in small gaps. In fact, larger patches implies in a higher probability
239 of colonization and a lower risk of extinction (MacArthur & Wilson, 1967; Donner et al.,
240 2010; McCarthy & Lindenmayer, 1999). Thus, a colony of parabiotic ants has more time to
241 colonize, grow and cultivate its mutualistic epiphytes in large gaps. As a consequence, larger
242 gaps are probably a much more profitable resource to maintain *Ca. femoratus* and *Cr. levior*
243 populations.

244 As in gaps the incident light in the lower vegetation is higher, there is an associated
245 increase in the total primary productivity, including a major production by extrafloral nectar
246 (Radhika et al. 2010; Bixenmann et al., 2011; Brenes-Arguedas et al., 2011). Several studies
247 also demonstrate that this increase in primary production attracts more herbivores (Harrison,
248 1987; Coley & Barony, 1996; Louda & Rodman 1996; Sipura & Tahvanainen, 2000). The
249 increase in both extrafloral nectar and herbivores means an increase in food resources for ants
250 (Swain, 1980; Davidson, 1988; Vantaux et al., 2007). However, canopy openness of forest
251 gaps has not influenced on AGs presence, neither quantity of AGs or colony size. Probably
252 the lack of a relationship in the occupation of forest gaps and canopy openness can be
253 explained by the low variation among the sampled gaps. Furthermore, the size of the forest
254 gaps induces changes that go beyond the light intensity, changing moisture and biological

255 properties of soil are characteristics responsible for the forest recovery (Muscolo et al., 2014).

256 Parabiotic ants do not show any preference for foraging in the understory plants or on
257 the ground. In fact, these ants are widespread and found in the soil and in vegetation in the
258 Amazon (Davidson, 1988; Dejean et al., 2000; Ryder Wilkie et al., 2010; Vicente et al., 2014,
259 2016). Nevertheless, canopy openness was a determining factor on the habitat use by *Ca.*
260 *femoratus* and *Cr. levior*. With the increase of canopy openness, and consequently an increase
261 in food resources in vegetation (as discussed above) inducing a preferential foraging by ants,
262 there was a reduction in the parabiotic ants frequency foraging on the ground. However, the
263 decrease of ants on soil is not associated to an increase in the frequency of this ant species on
264 vegetation.

265 Although the increased complexity of vegetation does not influence the use of the
266 arboreal strata by *Cr. levior*, there was a decrease in soil use. The increase of the vegetation
267 complexity means a more connected understory, forming bridges among plants. Thus,
268 valuable resources for *Cr. levior* as extrafloral nectary (Davidson, 1988) are easier to access,
269 and run away from ant predators and competitors, with a complexity increase. This reduction
270 in the need of the ground use minimizes possible confrontations with other ant species, once
271 the ground strata is naturally richer in ant species (Vasconcelos & Vilhena, 2006; Vicente et
272 al., 2016; Neves et al., 2013). On the other hand, *Ca. femoratus* did not show influence of
273 complexity in use of strata, showing a partition in the niche between the two ant species. This
274 niche partitioning should go beyond the influence of plant complexity in resource exploration
275 demonstrated in this work. Davidson (1988) showed that *Cr. levior* accumulates more workers
276 in sugary baits than *Ca. femoratus*. Also, while workers of *Cr. levior* did not show any
277 preference among plants with extrafloral nectaries, *Ca. femoratus* actively choose plant
278 species with larger nectaries and with greater concentration of nectar (Davidson, 1988).
279 Therefore, plant traits are probably not associated to the complexity of the habitat.

280 Our results demonstrate that although these parabiotic ants occupy the same sites

281 sharing their nests and maintenance activities of the colonies, they have divergences in their
282 niche with regards to the exploitation of habitat. The use of habitat by *Ca. femoratus* and *Cr.*
283 *levior* differ among each other depending on the stratum and environmental characteristics. It
284 also shows that these dominant ants, with different biological characteristics, can influence
285 both soil and vegetation communities differently. Therefore, the influence of both *Ca.*
286 *femoratus* and *Cr. levior* on soil and vegetation ant communities should be investigated in
287 order to understand whether these parabiotic ants alter the ant communities, where they occur
288 and what the mechanisms involved in this alteration are.

289

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300 **Author Contributions**

301 REV collected data, REV and TJI analysed data and wrote the text.

302

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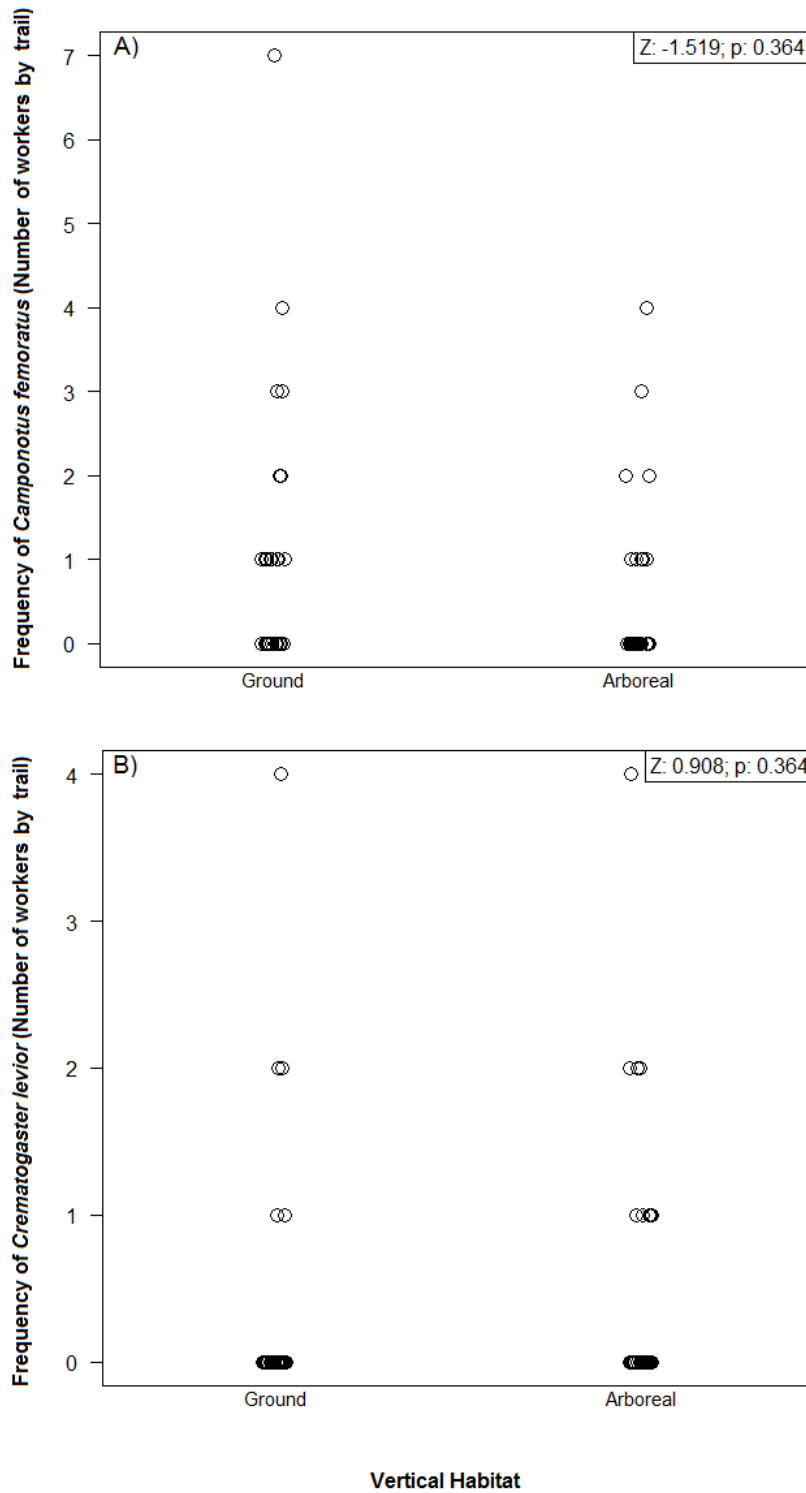
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496 Fig 1 – Works frequency by trail of ant species *Camponotus femoratus* and497 *Crematogaster levior* on the ground (A) ou arboreal (B) vertical stratum.

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503 Table 1. Influence of factors in gap occupation by Ant-Gardens nests of parabiotic ants *Camponotus femoratus*
 504 and *Crematogaster levior*.

		Z	p-value
Presence of AGs	Area	2.470	< 0.05*
	Locality	2.269	< 0.05*
	Canopy openness	-1.849	0.064
Abundance of AGs	Area	2.090	< 0.05*
	Locality	2.570	< 0.05*
	Canopy openness	-1.583	0.113
Colony size of AGs ants	Area	3.494	< 0.05*
	Locality	2.422	< 0.05 *
	Canopy openness	-1.230	0.221

505 * Significant

506

507

508 Table 2. Factors that influence the frequency of use of each stratum by *Camponotus femoratus* and
 509 *Crematogaster levior*.

	<i>Camponotus femoratus</i>		<i>Crematogaster levior</i>	
	Z	p-value	Z	p-value
GROUND				
Canopy openness	-2.572	< 0.05*	-1.977	< 0.05*
Complexity of vegetation	-1.407	0.159	-2.243	< 0.05*
Interaction	1.771	0.077	2,265	< 0.05*
VEGETATION				
Canopy openness	-0.700	0.484	-1.034	0.301
Complexity of vegetation	-1.006	0.315	-1.474	0.141
Interaction	1.022	0.307	1.396	0.163

510 * Significant

511

512

513

CAPÍTULO 3 - Effect of dominant parabiotic ants *Camponotus femoratus* (Fabricius) and *Crematogaster levior* Longino on the arboreal and ground-dwelling ant community in amazon rainforest

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Effect of dominant parabiotic ants *Camponotus femoratus* (Fabricius) and *Crematogaster levior* Longino on the arboreal and ground-dwelling ant community in Amazon rainforest

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Key-words – Beta-diversity, Community, Dominance, Neotropical, Nested, Parabiosis, Partition of diversity, Turnover.

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Effect of dominant parabiotic ants *Camponotus femoratus* (Fabricius) and *Crematogaster levior* Longino on the arboreal and ground-dwelling ant community in Amazon rainforest

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ABSTRACT. *Camponotus femoratus* (Fabricius, 1804) and *Crematogaster levior* Longino, 2003 are ants that live together in a parabiotic association nesting arboreally. They are locally abundant and aggressive, occupying the ground and vegetation. In this paper we evaluated the effect of these abundant and aggressive parabiotic ants on the ants in the southern Amazon. We found that *Ca. femoratus* and *Cr. levior* decrease both the abundance and richness of ground ants and change the community composition causing a nested pattern. However, we find that they do not cause changes in the community of arboreal ants.

Key-words – Beta-diversity, Community, Dominance, Neotropical, Nested, Parabiosis, Partition of diversity, Turnover.

INTRODUCTION

Camponotus femoratus (FABRICIUS, 1809) (Formicinae) and *Crematogaster levior* LONGINO, 2003 (Myrmicinae) are ants that live together in a parabiotic association (DAVIDSON 1988). In this mutualistic interaction, most often found in the tropics, two or more species share the same nest keeping their brood separate, and share the trails of foraging (HÖLLDOBLER & WILSON 1990; see: SWAIN 1980; SANHUDO & al. 2008). These ants build their nests by planting seeds of some specific epiphyt plants known as Ant Gardens (hereafter called AGs) (ORIVEL & LEROY 2011). These epiphytes provide stability and moisture to the nest and a food supply for the ants (SCHMIT-NEUERBURG & BLÜTHGEN 2007, DAVIDSON 1988). *Ca. femoratus* and *Cr. levior* are widely distributed species in the Amazon, being often collected in all vertical strata of vegetation and on the ground (RYDER-WILKIE & al. 2010, DÁTTILO & IZZO 2012, DEJEAN & al. 2015a, SOUZA & al. 2015).

Both ant species in the association differ in behavior. *Ca. femoratus* defends the AGs nest, showing massive recruitment after any kind of perturbation, becoming agitated and walking randomly around the nest (VICENTE & al. 2014). Several studies so far demonstrated the local abundance and aggressiveness of this parabiotic ant species (WHEELER 1921, WILSON 1987, VICENTE & al. 2014), mainly in and around the AG (VASCONCELOS & al. 2003, VICENTE & al. 2014). On the other hand, *Cr. levior* seems to take advantage of the defensive behavior of their mutualistic partner *Ca. femoratus*. This ant species does not show massive recruitment and supposedly has lost the chemical defense common to the *Cr.* genus (DAVIDSON 1988, LONGINO 2003, VICENTE & al. 2014).

Studies have demonstrated that there are two distinct types of ants assembly occupying the soil and vegetation of the forest and they can share few species (BRUHL & al. 1998, FRIZZO & al. 2012, CAMPBELL & al. 2015), with the parabiotic ants being

among them (VICENTE & al. 2016). Agonistic interspecific interactions are considered one of the main factors structuring ant communities, in both soil and vegetation (CERDÁ & al. 2013, STUBLE & al. 2012). However, most part of studies about the factors that structure ant communities is focused on ground dwelling communities (SOLAR & al. 2016, BACCARO al. 2013, DÁTTILO & al. 2012). Little is known about the factors that structure the arboreal communities (CAMAROTA & al. 2015, KLIMES & al. 2015, RIBAS & SCHOEREDER 2002).

One parameter commonly evaluated in ant communities is dissimilarity (DÁTTILO & IZZO 2012, VASCONCELOS & al. 2003, SOUZA & al. 2012, PAOLLUCI & al. 2016). The dissimilarity between samples is an ancient measure that was called diversity-beta by WHITTAKER 1960. There were many discussions aiming at proposing a measure of beta-diversity independent of alpha-diversity, ie, regardless of the richness of the species (BASELGA 2010a,b, BASELGA 2012, BASELGA & LEPRIRUR 2015). From these discussions, it was shown that diversity-beta is formed by two antithetical components: Turnover (species substitution) and nesting-resultant (poorest sites as sub-samples of the richest sites) (BASELGA 2007, BASELGA 2012). Understanding these components can help understand the patterns that structure the biological communities (BASELGA 2012, SI & al. 2015, BASELGA & al. 2015, MATEO & al. 2015).

AGs ants are locally abundant and aggressive and are sampled foraging on the vegetation and on the soil (WHEELER 1921, WILSON 1987, VASCONCELOS & al. 2003, VICENTE & al. 2014). They are so aggressive that are observed driving out other species of ants (REV. pers. obs.). Therefore, these species can be a strong competitor, structuring the ant community. In this study, we determined if the presence of parabiotic ants, *Ca. femoratus* and *Cr. levior*, could be a factor structuring the ant community of a southern Amazon forest hypothesizing that the frequency of parabiotic ants from AGs 1) decrease the abundance and 2) the number of species of ground and vegetation ants

communities. Furthermore, we believe that the frequency of parabiotic ants from AGs 3) alter the composition of the ground and arboreal communities, making the communities where they are in a poorer set than where they are not present (nested-resultant component) and not causing a replacement of species (turnover component). Finally, we check which species were being influenced by the presence of parabiotic ants from AGs. All questions are made for both the ground and arboreal ant communities separately.

MATERIAL AND METHODS

Study area

This study was carried out on two municipalities in the southern Brazilian Amazon, north of Mato Grosso state, as part of the Research Program in Biodiversity (PPBio). The standard sampling protocol used in PPBio is the RAPELD methodology (see: COSTA & MAGNUSSON 2010). Each municipality has a set of trails of 250m in length installed at a minimum distance of 1 km from each other, hereinafter called modules. Three modules are located in Claudia municipality (MCLA), installed close to each other (less than 20km), in a fragment connected by forest corridors and surrounded by plantations: Module I (11°34'S, 55°17'W – ten trails sampled), Module II (11°25'S, 55°18'W – six trails sampled), and Module III (11°39'S, 55°16'W – eight trails sampled). Nonetheless, the other modules are installed in the Parque Estadual do Cristalino (henceforward PEC), a continuous pristine forest in Novo Mundo municipality (9°28'S, 55°50'W – 10 trails sampled) that are about 220 km distant far from the first three.

Ant sampling

The ant inventory was conducted in 34 trails (24 in MCLA and 10 in PEC). In each trail, ants were collected every 25m on the ground and vegetation, resulting in 20 samples per trail (10 on the ground and 10 in low vegetation) and totaling 680 samples (340 on the

ground and 340 in the understory). The collection of the ground ant community was done using a single pitfall trap installed in each sample point. The pitfalls consisted of plastic containers of 500ml with 14cm radius and 9.5cm high, installed at ground level, with water and detergent. We sampled ants foraging on vegetation at 4 points around each pitfall using the beating-tray method. At each point herein, all vegetation within 1m² which was between 1 to 3 meters high was shaken totaling 4m² of inspected vegetation per sample. Invertebrates that fell on the entomological umbrella were collected (for more details: VICENTE & al. 2016).

The ants collected were carried out the laboratory where they were processed and identified using dichotomous key for subfamilies and genera available in BACCARO & al. (2015). Posteriorly, to separate into morphospecies and identify to a specific level we used several taxonomic keys (BRANDÃO 1990, FERNÁNDEZ 2003, LONGINO 2003, MACKAY & MACKAY 2010, FERNANDES & al. 2014). Finally, we compare with specimens deposited at the Laboratório de Ecologia de Comunidades from the Centro de Biodiversidade da Universidade Federal de Mato Grosso (UFMT) and the ant collection from the Laboratório de Sistemática, Evolução e Biologia de Hymenoptera from the Museu de Zoologia da Universidade de São Paulo (MZSP), where vouchers were deposited. The morphotypes not identified at the species level received the epithet of the collection (TJI) of the Laboratório de Ecologia de Comunidades from the Centro de Biodiversidade da Universidade Federal de Mato Grosso (UFMT) that also has epithets of morphotypes of myrmecology collection Instituto Nacional de Pesquisas da Amazônia (INPA). We also consulted specialists to confirm species identification (see acknowledgments).

Data analysis

Ant abundance of each trail was accessed with the sum of frequencies of each

species per sample in trail (0 to 10). We opted for this sample-based measure because real ant abundance is not an independent information on biodiversity estimates, since they are social insects (GOTELLI & al. 2011). So, the sampled abundance of workers in pitfalls may be strongly related to the proximity to the nest (GOTELLI & al. 2011) and the workers' number in a colony varies greatly between species (BACCARO al. 2015). Due to the aforementioned reasons, sample-based measurement is commonly used in studies with ants (BACCARO al. 2013; DÁTTILO & IZZO 2012; DEJEAN & al. 2015a; RYDER WILKIE & al. 2010). The variable “*frequency of parabiotic ants*” was created with the same principle. Since both, *Ca. femoratus* and *Cr. levior*, they were seen always together in areas, the collection of any of them in a single sample implies in the existence of an AG nearby. The frequency of AGs per trail was independent of the stratum where they were collected.

In order to evaluate the effect of parabiotic ants in abundance and richness of ground and arboreal ant species along of Amazon forest, we performed a generalized linear mixed-effects models (GLMM) with frequency of parabiotic ants as factor and geographical region (PEC or MCLA) as random factor. The total beta diversity, turnover and nestedness components of ant community was calculated between pair of trails based in a binary matrix with presence and absence data with Sorensen and Simpson index. The proposed framework is a partition of true diversity independent of richness difference (BASELGA & LEPRIRUR 2015, BASELGA 2010a, b). Then the dissimilarity matrices were used in Multiple Regression on distance Matrices (MRM) with frequency of parabiotic ants as a discrete factor and geographical region as categorical factor, in order to evaluate the effect of *Ca. femoratus* and *Cr. levior* on composition of ant community. The MRM was used because it is a flexible method in terms of the types of data that may be analyzed, whether data of presence-absence, discrete, continuous or categorical (LICHSTEIN 2007)

Furthermore, an analysis of indicator species (IndVal) was performed to determine

which species of ants were being affected by the presence of parabiotic ants (occurring in more than one point) or its absence indicator (not occurring at any point). We know previously that abundance, richness and composition of community are different between vertical strata (VICENTE & al. 2016). Therefore, we decided to conduct all the analysis separately by vertical strata.

All graphs and analysis are performed with R-software (R CORE TEAM 2015) using packages: betapart (partition of beta diversity - BASELGA & ORME 2012), ecodist (MRM – LICHSTEIN 2007), effects (graphics - FOX & HONG 2009), indicpecies (IndVal - DE CÁCERES & JANSEN 2010), lme4 (GLMM - BATES & al. 2016), vegan (OKSANEN & al. 2015).

RESULTS

We registered a total of 4.408 occurrences and 328 species of ants in all sample plots with 85 species collected in both strata. The most frequent species, independent of strata, was *Pheidole transversostriata* Mayr, 1887 (210 samples, 30.88% of both strata samples), *Crematogaster tenuicula* Forel, 1904 (177 samples, 26.03%), *Ectatomma lugens* Emery, 1894 (157 samples, 23.09%), *Pachycondyla crassinoda* (Latreille, 1802) (129 samples, 18.97%) and *Ochetomyrmex semipolitus* Mayr, 1878 (106 samples, 15.59%).

The ground was the most diverse stratum with 3.121 occurrence of 251 species, including 168 species collected only in this stratum. The most frequent species on the ground were *Pheidole transversostriata* (205 samples, 60.29% of ground samples), *Ectatomma lugens* (157 samples, 46.18%), *Pachycondyla crassinoda* (129 samples, 37.94%), *Trachymyrmex* TJI01 (92 samples, 27.06%), *Crematogaster tenuicula* (90 samples, 26.47%). In vegetation, the abundance was of 1.287 records of 158 species with 75 species collected exclusively in this stratum. The most frequent species in vegetation were *Ochetomyrmex semipolitus* (93 samples, 27.35% of arboreal samples), *Crematogaster*

tenuicula (87 samples, 25.59%), *Crematogaster brasiliensis* Mayr, 1878 (67 samples, 19.71%), *Ectatomma tuberculatum* (Olivier, 1792) (59 samples, 17.35%) and *Solenopsis* TJI01 (44 samples, 12.94%). Parabiotic ants, *Ca. femoratus* and *Cr. levior*, were collected in 20 of the 34 trails in both vertical strata.

The abundance of ground ants was negatively influenced by frequency of parabiotic ants ($Z_{2,34} = -4.64$, $p < 0.05$ – Fig. 1). The mean abundance of ants in plots where the AGs is found is 85.9 (SD: 20.60) and 94.1 (SD: 17.16) in plots where the AGs are absent. The number of ground ant species per plot also was influenced by frequency of parabiotic ants ($Z_{2,34} = 2.76$, $p < 0.05$ – Fig. 2). The mean number of richness of species in plots where AGs are found is 45.57 (SD: 8.58) and 48 (SD: 8.199) where the AGs were not present.

In vegetation, ant abundance was not influenced by frequency of parabiotic ants ($Z_{2,34} = -0.984$, $p > 0.05$). The mean abundance was of 85.9 (SD: 20.62) where parabiotic ants are present and 94.07 (SD: 17.16) where AGs were absent. Richness of arboreal ants already was not influenced by frequency of parabiotic ants ($Z_{2,34} = -0.673$, $p > 0.05$). The mean number of species was 22.35 (SD: 7.46) where parabiotic ants are present and 22.35 (SD: 7.46) where the AGs were not present.

The analysis of the composition of the ground ant community demonstrates that the beta diversity is related to frequency of parabiotic ants in the site ($r = 0.688$, $p < 0.05$). This dissimilarity related to the frequency of AG ants was also related as a nested-resultant component ($r = 0.132$, $p < 0.05$). However, the dissimilarities are not resultant of turnover component ($r = 0.609$, $p > 0.05$) not being related to the frequency of parabiotic ants. Beta diversity of arboreal ant communities shows no difference related to frequency of parabiotic ants ($r = 0.419$, $p > 0.05$). The frequency of parabiotic ants also does not cause influence of nested-resultant component ($r = 0.002$, $p > 0.05$) or turnover component ($r = 0.286$, $p > 0.05$).

Alteration in composition of ground ants can be observed by changes in the abundance

of 26 species that indicated the absence (19 species) and presence (7 species) of AGs ants (Table I). The indicator species of AGs absence that were more frequent in soil samples were *Pheidole transversostriata* (202 samples, 59.41% of ground samples), *Pachycondyla crassinoda* (125 samples, 36.76%), *Solenopsis* TJI06, *Pheidole nitella* Wilson 2003 and *Nylanderia* TJI02 (70 samples each, 20.59% each). Also, the more frequent indicator ground species of AGs presence were *Megalomyrmex* pr. *wallacei* (48 samples, 14.12% of ground samples), *Pheidole* INPA14 (34 samples, 10%), *Pheidole bufo* Wilson 2003 (25 samples, 7.35%) and *Gnamptogenys moelleri* (Forel, 1912) (23 samples, 6.76%). Only three arboreal ant species were related to the occurrence of AGs. *Ochetomyrmex semipolitus* (92 samples, 27.06% of arboreal samples) and *Neoponera unidentata* (Mayr, 1862) (32 samples, 9.41%) indicated the presence of AGs ants whereas only *Crematogaster wardi* Longino, 2003 (16 samples, 2.77%) indicate the absence of AGs (Table 1).

DISCUSSION

Although there are several studies on Ant-Gardens (DAVIDSON 1988, ORIVEL & LEROY 2011, VICENTE & al. 2014), this is the first to investigate the influence of the AGs ants on ant community of ground and vegetation habitats. It has been suggested so far that *Camponotus femoratus* and *Crematogaster levior* ants can be considered as dominant species in the community (VASCONCELOS & al. 2003). Dominant ants are locally abundant and have aggressive behavior (PARR & GIBB 2010). Parabiatic ants occur in large numbers of workers' on the ground and in the canopy (RYDER WILKIE & al. 2010, VASCONCELOS & al. 2003) and are aggressive in the defense of their nests (VICENTE & al. 2014) and territory (VANTAUX & al. 2008), often being seen driving out other species (REV. obs. pers.). This aggressive behavior of parabiatic ants can prevent access to resources by other species, leading to a decrease in the number of nests (abundance) and

even to exclusion of some competitor species (richness) as seen in our results. In this way, AGs ants promote the decrease of both, the abundance and the species richness of ground ants. A similar pattern can be seen in French Guiana, in which the richness and abundance of ants decreases with the abundance of the dominant ant *Solenopsis saevissima* (DEJEAN & al. 2015b). Also, in three habitats in South African savanna, the richness of ants' community decreases in presence of other dominant species (PARR 2008).

The frequency of parabiotic ants in a given site also affects the dissimilarity of the ground ant community by a non-random removal of ant species, causing nested patterns. Whereas allowing for the permanence of some ant species, the AG-ants drive out others, probably species that compete for resources. Consequently, the AGs promote a modification in the ant community by decreasing the local number of species by forming poorer sites that are subsets of the richest sites (nesting-resultant component). Hence, some species may be favored by the presence or being eliminated by parabiotic ants. In fact, our data show that there are 19 species that indicate (and thus are favored by) the AG-ants absence, but just 7 are identified as indicators of AG-ants presence. Among the 19 species favored by the absence of AG ants in the soil samples were *Pheidole transversostriata* and *Pheidole nitella*. Both species are very small and their biology are partially unknown (WILSON 2003). *P. nitella* inhabit the soil or leaf litter of humid forests and also nest in small cavities in dead wood or, less frequently, in low vegetation (LONGINO 2005, ANTWEB 2016). Despite the lack of biological information, the phylogenetic relationship and since both are often collected in the soil when parabiotic ants are absent, can represent that both *Pheidole* species have narrow niches that overlap with parabiotic ants.

Pheidole bufo and *Gnamptogenys moelleri* are Neotropical ant species that indicate the presence of parabiotic ants in samples collected in the soil. *P. bufo* is a recently described specie and occurs from the western Amazonia to the northeast of the Brazilian Atlantic forest (WILSON 2003, SALAZAR & al. 2015, SANTOS & al. 2006, VICENTE

& al. 2016). Workers of *P. bufo* were observed eating beetle larvae but no biological information is available for this species and neither for conspecific species (WILSON 2003). *G. moelleri* a widely collected species (SOUZA & al. 2007, 2015, RYDER WILKIE & al. 2010, ULYSSÉA & al. 2011, ULYSSÉA & BRANDÃO 2013) is an arboreal ant with a very wide food niche that varies between seasons and items from live or dead invertebrates, extrafloral nectaries and fleshy seeds and fruits (COGNI & OLIVEIRA 2004). Even parabiotic ants feed on nectaries and dead matter or hunt invertebrates (SWAIN 1980), these species take advantage of the niche width to occupy the ground where other species are driven out by parabiotic ants.

Despite the observed effect on the ground-dwelling ant fauna, the parabiotic ants have not changed either in abundance, richness, nor the composition of the vegetation ants. Many times we have seen in field *Ca. femoratus* driving out other species of ants, mainly in the vicinities of extrafloral nectaries (REV pers. obs.). Extrafloral nectaries are predictable resources (RICO-GRAY & OLIVEIRA 2007) and parabiotic ants can potentially be only defending the plants with nectaries, driving out other ant species from these plants. However, even considering that nectary bearing plants are abundant in Amazonia, the major part of the understory plants do not have nectaries (DÁTTILO & al. 2013). These plants can be seen by the parabiotic ants as foraging sites for prey or even as arboreal bridges linking resource rich locations to the nest. It has been seen that these access bridges (complexity) comprise a very important factor that has been considered as being responsible for myrmecophilous ants pruning neighboring plants (WEIR & al. 2012, DÁTTILO & DYER 2014).

The major part of the understory plants are connected among each other by branches, vines and other plants forming a very complex environment. This complexity provides important routes of resource access or ways to flee from dominant species (POWELL & al. 2011, YANOVIK & SCHNITZER 2013, YANOVIK 2015). Thus, the understory can

be seen as a complex three dimensional environment where the resource (e.g. nectary bearing plants) is path distributed. Indeed, in other environments, the connectivity of the vegetation has proven to be an important factor influencing the community of arboreal ants (RIBAS & al. 2003, POWELL & al. 2011, YANOVIK & SCHNITZER 2013). We suggest that, if a dominant ant specie has any effect on the diversity of their competitors, this effect should be on and in the vicinities of the resource path, (so nectaries or by analogy, baits in some studies). Once there was no difference in the composition of vegetation ants, a very low number (3) of species could be named as indicators of the presence of ant gardens. Of these, two species have a broad niche, *Ochetomyrmex semipolitus* and *Neoponera unidentata*, and both occur most frequently and can be found in sites where AGs also occurs. The Neotropical species *O. semipolitus* was mainly observed at ground level feeding of animal protein and also in the vegetation feeding in nectaries (RYDER WILKIE & al. 2007, 2010, SOUZA & al. 2012, 2015, DÁTTILO & DYER 2014). *Neoponera unidentata* is a relatively common species, observed nesting mainly in hollow branches both in vegetation and in the soil of the forest, but also in rotten logs, stumps and epiphytes (MACKAY & MACKAY 2010, LONGINO 2010). Only *Crematogaster wardi* indicated the absence of parabiotic ants in understory. In fact, *C. wardi* workers were collected foraging in extrafloral nectaries of low vegetation (LONGINO 2003). This specie was recently described, with little known distribution only to Nicaragua, Costa Rica, French Guiana and in Brazil only for the state of Pará, resulting in several distribution gaps. But probably this specie has a wider distribution, occurring in habitat patches where AGs are not present.

The parabiotic ants *Ca. femoratus* and *Cr. levior* usually inhabit areas with high light intensity such as forest gaps (DAVIDSON 1988, DEJEAN & al. 2000, VICENTE & al. 2014). Natural gaps are formed by fallen trees, being a very common and predictable habitat in natural environments (MUSCOLO & al. 2014). This habitat, however, is

ephemeral and along the succession a temporal change in the composition of plants and animals is observed. Whereas some species inhabit more frequently open environments (in the beginning of succession), others species replace them in more advanced stages of gap regeneration (VAN TEEFFELEN & al. 2012, VAN BREUGEL & al. 2013, MUSCOLO & al. 2014). The time of the replacement and the final composition of the area is determined by a myriad of factors (MUSCOLO & al. 2014) and by random (HUBBEL 2001) but these processes are in part responsible for the maintenance of diversity in a regional and biome scale (DÁTTILO & IZZO 2012, NEVES & al. 2010, BICKNELL & al. 2014, MUSCOLO & al. 2014, ALTMAN & al. 2016, VÉLE & al. 2016). Therefore, as demonstrated here, the presence of parabiotic ants in a given forest gap changes the ground ant community by eliminating several ant species. As ants are ecological engineers and interact with several other organisms in tropical habitats (DEL TORO & al. 2012), the effect of the parabiotic ants can be extended to other organisms inhabiting gaps along succession. Also, the parabiotic ants can have a direct effect on succession in these gaps by modifying for example, the quality of the protection of nectary-bearing plants, the herbivory or other processes in the gaps that occur. So, more than modifying ant composition, the effect of these dominant species can influence the final stage of the forest succession. However, future studies should address these questions in order to measure the influence of the direct and indirect effect of dominant ants on biodiversity.

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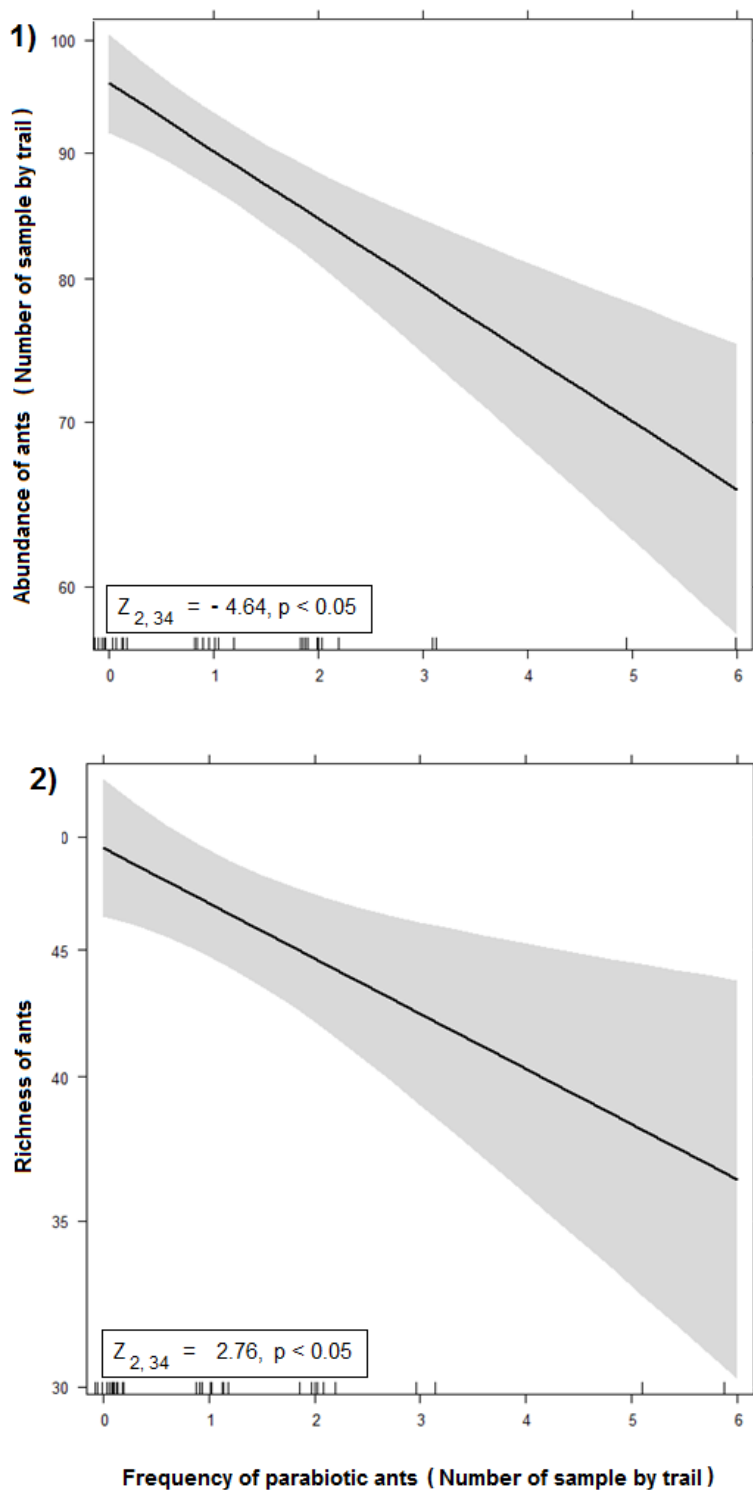
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Table 1 – Indicator species of parabiocotic ants in ground and arboreal ant community.

Taxa	Fidelity (A)	Specificity (B)	Stat	Vertical Strata	<i>Ca. femoratus</i> and <i>Cr. levior</i>	
					Absence	Presence
<i>Trachymyrmex</i> cf. <i>bughioni</i>	0.5861	0.7857	0.679	Ground	X	
<i>Pachycondyla crassinoda</i> Latreille, 1802)	0.4670	0.9286	0.659	Ground	X	
<i>Pheidole nitella</i> Wilson 2003	0.4196	1.0000	0.648	Ground	X	
<i>Pheidole</i> TJI41	0.6022	0.6429	0.622	Ground	X	
<i>Pheidole transversostriata</i> Mayr, 1887	0.3633	1.0000	0.603	Ground	X	
<i>Pheidole</i> TJI49	0.7200	0.5000	0.600	Ground	X	
<i>Solenopsis</i> TJI06	0.3878	0.8571	0.577	Ground	X	
<i>Pheidole</i> TJI21	0.3453	0.9286	0.566	Ground	X	
<i>Odontomachus</i> cf. <i>meinerti</i>	0.6316	0.5000	0.562	Ground	X	
<i>Apterostigma urichii</i> Forel, 1893	0.4400	0.7143	0.561	Ground	X	
<i>Atta cephalotes</i> (Linnaeus, 1758)	0.4818	0.6429	0.557	Ground	X	
<i>Pheidole</i> TJI22	0.6067	0.5000	0.551	Ground	X	
<i>Neoponera apicalis</i> (Latreille, 1802)	0.4235	0.7143	0.550	Ground	X	
<i>Nylanderia</i> TJI02	0.3667	0.7857	0.537	Ground	X	
<i>Pheidole</i> INPA019	0.7552	0.3571	0.519	Ground	X	
<i>Pheidole</i> TJI35	0.4465	0.5714	0.505	Ground	X	
<i>Trachymyrmex</i> INPA03	0.5243	0.4286	0.474	Ground	X	
<i>Acromyrmex hystrix</i> (Latreille, 1802)	1.0000	0.2143	0.463	Ground	X	
<i>Myrmicocrypta</i> sp02	0.6316	0.2857	0.425	Ground	X	
<i>Gnamptogenys moelleri</i> (Forel, 1912)	0.5385	0.7500	0.635	Ground		X
<i>Pheidole</i> INPA014	0.4619	0.6667	0.555	Ground		X
<i>Megalomyrmex</i> pr. <i>wallacei</i>	0.4570	0.6667	0.552	Ground		X
<i>Pheidole bufo</i> Wilson 2003	0.4413	0.6667	0.542	Ground		X
<i>Camponotus ager</i> (Smith, 1858)	0.7000	0.4167	0.540	Ground		X
<i>Pheidole</i> TJI17	0.5746	0.5000	0.536	Ground		X
<i>Mycocepurus smithii</i> (Forel, 1893)	1.0000	0.2500	0.500	Ground		X
<i>Ochetomyrmex semipolitus</i> Mayr, 1878	0.6372	0.4286	0.4286	Arboreal	X	
<i>Neoponera unidentata</i> (Mayr, 1862)	0.5161	0.8333	0.656	Arboreal	X	
<i>Crematogaster wardi</i> Longino, 2003	0.3772	0.8333	0.561	Arboreal		X



Figures: Abundance (1) and richness (2) of ground ants.

ANEXO 1 – Fauna de formigas (Insecta, Hymenoptera, Formicidae)

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FAUNA DE FORMIGAS (INSECTA, HYMENOPTERA, FORMICIDAE) DO
PARQUE ESTADUAL DO CRISTALINO, MT, BRASIL

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Resumo: Este trabalho lista os gêneros de formigas coletados tanto no solo quanto na vegetação do Parque Estadual do Cristalino, MT, Brasil. Também traz o número de morfoespécies para cada um dos gêneros identificados, o local de ocorrência e informações complementares quanto à distribuição e biologia.

Palavras-chaves: Amazônia, Formicidae, Inventário faunístico, Mirmecologia, Unidades de Conservação.

Abstract: This work lists the genera of ants collected both on the ground and in the vegetation of Parque Estadual do Cristalino (9 ° 32'47 "S, 55 ° 47'38" W), MT, Brazil. Also, we provided information on the number of species by genus, occurrence and information about the distribution and biology. **Keywords:** Amazon, Formicidae, Myrmecology, Protected area, Wildlife survey.

INTRODUÇÃO

As formigas são insetos eussociais altamente abundantes e diversificados tanto em termos de espécies quanto comportamentalmente (Kaspari 2005; Brandão et al. 2009). Até o momento, a família Formicidae Latreille (1809) reúne 16 subfamílias e cerca de 15.000 espécies descritas (Bolton 2015), mas estimativas sugerem que haja o dobro de espécies (Hölldobler & Wilson 1990; Fernández 2003a). Os formicídeos são ecologicamente dominantes, desempenham diversas funções no ambiente sendo consideradas engenheiras ecossistêmicas (Folgarait 1998; Meyer et al. 2011) e influenciam profundamente as comunidades terrestres devido sua abundância e relações estabelecidas com diversos grupos como microrganismos (Nepel et al. 2014; Sanders et al. 2014), plantas (Izzo & Vasconcelos 2002; Dáttilo et al. 2009; Izzo & Petini-Benelli 2011; Vicente et al. 2012, 2014) e animais (Dáttilo et al. 2012; Gallego-Roperó et al. 2013; Puker et al. 2015), inclusive com outras formigas (Sanhudo et al. 2008; Gallego-Roperó & Feitosa 2014). Além disso, formigas são modelos para mimetismo para mais de 2.000 espécies de artrópodes (Grimaldi & Engel 2005). Logo, dada sua alta diversidade, fácil amostragem e taxonomia relativamente bem resolvida formigas são modelos para avaliações de biodiversidade (Agosti et al. 2000) e confiáveis indicadores biológicos (Andersen et al. 2002).

Apesar das listagens disponíveis de espécies de formigas que ocorrem na região Neotropical (Kempf 1972; Fernández & Sendoya 2004), os trabalhos envolvendo a fauna brasileira se concentram em biomas como o Cerrado (Silva & Silvestre 2004, Silva & Brandão 2014; Schoereder et al. 2010; Brandão et al. 2011), Mata Atlântica (Feitosa & Ribeiro 2005; Silva et al. 2007; Figueiredo et al. 2013), Pantanal (Battirola et al. 2005; Ribas et al. 2007; Silva et al. 2013) e Caatinga (Neves et al. 2013; Ulysséa & Brandão 2013). Na Amazônia estes estudos se concentram principalmente nas regiões Central e Oriental (Vasconcelos et al. 2006, 2010; Santos et al. 2007; Oliveira et al. 2009; Bastos &

Harada 2011; Baccaro et al. 2012; Souza et al. 2012; Harada et al. 2013) e são extremamente restritos a algumas localidades na Amazônia Meridional (Dáttilo et al. 2013, Falcão et al. 2015). Dessa forma, este trabalho tem como objetivo 1) listar os gêneros de formigas que ocorrem no Parque Estadual do Cristalino, Mato Grosso, localizado na Amazônia Meridional, uma área de alta, porém pouco conhecida, diversidade de diversos taxa (Peres 2005) e 2) apresentar resumidamente informações sobre a distribuição geográfica e biologia desses gêneros.

METODOLOGIA

As coletas foram realizadas entre novembro de 2012 e maio de 2013, em 11 parcelas que possuem 250 m de comprimento, instaladas a uma distância mínima de 1 km (ver Capítulo 1 deste livro). Em cada parcela, a cada 25 metros foram realizadas coletas de formigas no solo e na vegetação, totalizando 220 amostras. Para coleta de formigas no solo, foram utilizadas armadilhas de queda do tipo *Pitfall*. Para amostragem de formigas que forrageiam na vegetação foi utilizado Guarda-chuva Entomológico sendo que em quatro pontos a dois metros de distância de cada *Pitfall* foram feitas batidas na vegetação. Em cada ponto deste, toda vegetação dentro de 1m² que possuísse entre 1 a 3 metros foi agitada. Os invertebrados que caíram sobre o guarda-chuva entomológico foram coletados, armazenados em álcool e posteriormente separados em subfamílias e gêneros seguindo a classificação de Bolton (2015) e os *vouchers* foram depositados no Laboratório de Ecologia de Comunidades do Instituto de Biologia da Universidade Federal de Mato Grosso e na coleção de formigas do Laboratório de Sistemática, Evolução e Biologia de Hymenoptera do Museu de Zoologia da Universidade de São Paulo.

RESULTADOS E DISCUSSÃO

A fauna do Parque Estadual do Cristalino conta com 1.566 ocorrências de formigas

divididas em 202 morfoespécies, 47 gêneros e oito subfamílias. Quanto aos gêneros, quatro foram coletados somente na vegetação, 22 somente no solo, e 21 em ambos os estratos. Abaixo a lista dos gêneros de formigas amostrados no Parque Estadual do Cristalino:

SUBFAMÍLIA AMBLYOPONINAE

Prionopelta Mayr, 1866: Distribuição cosmopolita. Dentre as 15 espécies descritas (Bolton 2015), uma foi amostrada no solo do Parque Estadual do Cristalino. São predadoras especializadas que nidificam no solo, sob a casca de árvores ou em troncos podres caídos (Hölldobler *et al.* 1992; Jiménez *et al.* 2008).

SUBFAMÍLIA DOLICHODERINAE

Azteca Forel, 1878: Distribuição Neotropical (Fernández 2003a). Possui 84 espécies descritas (Bolton 2015) sendo nove amostradas na vegetação do P. E. Cristalino. São territorialistas (Dejean *et al.* 2009) e constroem seus ninhos de cartão na vegetação, em alguns casos associados a epífitas, ou ocupam galhos vivos ou mortos de plantas (Longino 2007). As que habitam plantas vivas, muitas vezes se alimentam de herbívoros (Dejean *et al.* 2009) ou possuem relações mutualísticas com hemípteros (Longino 2007).

Dolichoderus Lund, 1831 (fig. A): Distribuição cosmopolita. Possui 132 espécies descritas (Bolton 2015) sendo oito amostradas (cinco no solo, sete na vegetação) no P. E. Cristalino. Nidificam tanto no solo quanto na vegetação, sendo as espécies tropicais quase exclusivamente arborícolas (MacKay 1993). Alimentam-se de pequenos artrópodes, de líquidos açucarados excretados por hemípteros ou por nectários (Fernández 2003a).

Tapinoma Foerster, 1850: Distribuição cosmopolita. Possui 69 espécies descritas (Bolton 2015) sendo duas amostradas na vegetação do P. E. Cristalino. Podem apresentar dieta baseada principalmente em líquidos açucarados (Fernández 2003a), porém, as que habitam ambientes urbanos possuem hábitos omnívoros, podendo apresentar saprofagia ou

necrofagia (David & Venkatesha 2013; Bonacci & Vercillo 2015).

SUBFAMÍLIA DORYLINAE

Eciton Latreille, 1804 (fig. B): Distribuição Neotropical. Possui 12 espécies descritas (Bolton 2015) e uma foi amostrada no solo do P. E. Cristalino. Todas as espécies conhecidas do gênero são nômades (Longino 2010).

Neivamyrmex Borgmeier, 1940: Distribuição Neotropical e Neártica. Possui 127 espécies descritas (Bolton 2015) sendo duas amostradas, uma no solo e uma na vegetação do P. E. Cristalino. São formigas nômades com colônias numerosas e são predadoras de artrópodes, especialmente de insetos eussociais (LaPolla et al. 2002).

SUBFAMÍLIA ECTATOMMINAE

Ectatomma Smith, 1858: O gênero ocorre na região Neotropical, possui 15 espécies descritas (Bolton 2015) sendo três amostradas (três no solo e uma na vegetação) para o P. E. Cristalino. Nidificam no solo e possuem hábitos generalistas e oportunistas, são predadores de artrópodes e consomem líquidos açucarados de hemípteros e de nectários extraflorais além de restos orgânicos de animais, plantas e frutas (Fernández 1991; Fernández 2003a).

Gnamptogenys Roger, 1863 (fig. C): Possui ampla distribuição (Neártica, Neotropical, Oriental e Australiana) com 137 espécies descritas (Bolton 2015) sendo oito amostradas (sete no solo e uma na vegetação) no P. E. Cristalino. Nidificam no solo, troncos podres caídos ou então podem ser arborícolas. Possuem colônias relativamente pequenas (Lattke 2008). Podem ser predadoras generalistas, enquanto outras espécies são predadoras especialistas de besouros e milípedes (Brown 1993; Brandão et al. 2009).

SUBFAMÍLIA FORMICINAE

Acropyga Roger, 1862: O gênero possui distribuição cosmopolita, com 40 espécies descritas (Bolton 2015) e uma amostrada em solo para o P. E. Cristalino. São formigas que nidificam e forrageiam no solo se alimentando do líquido açucarado excretado por hemípteros que sugam seiva das raízes de plantas (Fernández 2003a).

Brachymyrmex Mayr, 1868: Distribuição Neártica e Neotropical. Possui 44 espécies (Bolton 2015) sendo três amostradas (1 no solo e 3 na vegetação) para o P. E. Cristalino. Nidificam em pequenas cavidades de plantas, em epífitas e na serapilheira (Longino 2010).

Camponotus Mayr, 1861 (fig. D): Distribuição cosmopolita. Possui 1,096 espécies descritas (Bolton 2015) sendo 16 amostradas (sete no solo e 13 na vegetação) no P. E. Cristalino. No geral são espécies omnívoras, que nidificam no solo, em raízes ou copas das árvores (Fernández 2003a). Algumas constroem ninhos de cartão associados à epífitas, interação conhecida como Jardins-de-formigas (Vicente et al. 2014). *Camponotus femoratus* (Fabricius, 1804) é um exemplo frequentemente encontrado nessa região.

Gigantiops Roger, 1863 (fig. E): Distribuição Neotropical. Possui uma espécie descrita (Bolton 2015) que foi amostrada no solo e na vegetação do P. E. Cristalino. Nidificam no solo, em troncos podres ou em galerias escavadas por outros insetos (Mariano et al. 2011).

Myrmelachista Roger, 1863: Distribuição Neotropical. Possui 56 espécies descritas (Bolton 2015) e uma foi amostrada na vegetação do P. E. Cristalino. Forrageiam na vegetação e nidificam em cavidades de plantas ou em troncos caídos (Davidson & McKey 1993; Nakano et al. 2013).

Nylanderia Emery, 1906: Distribuição cosmopolita, com 108 espécies descritas (Bolton 2015). Cinco morfoespécies foram amostradas (cinco no solo e quatro na vegetação) no P. E. Cristalino. Habitam desde desertos à florestas tropicais, podendo nidificar na serapilheira, no solo ou em troncos podres (LaPolla et al. 2011).

SUBFAMÍLIA MYRMICINAE

Apterostigma Mayr, 1865 (fig. F): Distribuição Neotropical. Possui 45 espécies descritas (Bolton 2015) e quatro foram amostradas (três em solo e uma na vegetação) no P. E. Cristalino. São formigas micetófagas que nidificam em troncos podres, debaixo de pedras, entre as folhas na serapilheira, em epífitas e nas bases de folhas de bromélias (Longino 2010).

Atta Fabricius, 1804: Distribuição Neotropical e Neártica (Bolton 1995). Possui 17 espécies descritas (Bolton 2015) e duas amostradas em solo para o P. E. Cristalino. São conhecidas popularmente como Saúvas e transportam folhas, frutos, galhos e partes de flores para o interior do ninho, onde elas cultivam os fungos dos quais se alimentam (Fernández 2003a).

Carebara Westwood, 1840: Distribuição cosmopolita, com 200 espécies descritas (Bolton 2015) sendo duas amostradas em solo para o P. E. Cristalino. São formigas relativamente pequenas de hábitos crípticos. Alimentam-se de pequenos invertebrados (Fischer 2014) podendo ser oportunistas (Fernández 2010).

Cephalotes Latreille, 1802 (fig. G): Distribuição Neotropical. Possui 118 espécies descritas (Bolton 2015) e cinco amostradas (1 no solo e 5 na vegetação) para o P. E. Cristalino. São formigas arborícolas que nidificam em troncos vivos ou mortos (Longino 2010). Alimentam-se principalmente de pólen (Prado & Brandão 2013) e em nectários extraflorais ou de secreção de hemípteros, frutas caídas, fezes de aves, matéria orgânica animal e de pequenos insetos (Corn 1980; Moretti & Ribeiro 2006).

Crematogaster Lund, 1831 (fig. H): O gênero possui distribuição cosmopolita, com 487 espécies descritas (Bolton 2015) e 10 foram amostradas (seis em solo e nove na vegetação) no P. E. Cristalino. Nidificam em galhos vivos ou mortos, troncos de árvores caídos, ou ainda constroem seus ninhos na vegetação, que em alguns casos estão associados à epífitas (Longino 2003), conhecidas como Jardins-de-formigas (Vicente et al.

2014). Muitas espécies se alimentam do líquido açucarado de nectários ou excretado por hemípteros, ou então de animais mortos (Longino 2003).

Cyphomyrmex Mayr, 1862: Distribuição Neártica e Neotropical. Possui 39 espécies descritas (Bolton 2015) e sete amostradas (seis em solo e uma na vegetação) para o P. E. Cristalino. Nidificam em pequenas câmaras no solo, debaixo de pedras, em pequenos troncos caídos na serapilheira, entre raízes de plantas (Snelling & Longino 1992), ou ainda em amontoados de terra suspensos (Adams & Longino 2007). São formigas micetófagas e cultivam os fungos com fezes de insetos e detritos vegetais (Snelling & Longino 1992).

Daceton Perty, 1833 (fig. I): Distribuição restritas às florestas da América do Sul. Duas espécies simpátricas são conhecidas (Vicente et al. 2011; Bolton, 2015). Uma espécie foi amostrada (solo) no P. E. Cristalino. São formigas arborícolas generalistas cuja dieta é composta por pequenos artrópodes e secreções açucaradas de hemípteros (Dejean et al. 2012). *Hylomyrma* Forel, 1912: Distribuição Neotropical. Possui 13 espécies descritas (Bolton 2015) e uma amostrada em solo para o P. E. Cristalino. Possui a biologia relativamente pouco conhecida, mas sabe-se que algumas espécies podem nidificar na serapilheira e em troncos podres caídos (Fernandez 2003a).

Megalomyrmex Forel, 1885: O gênero ocorre na região Neotropical. Possui 44 espécies descritas (Bolton 2015) e quatro foram amostradas no solo do P. E. Cristalino. Podem nidificar no solo ou em troncos podres caídos na serapilheira (Brandão 2003).

Mycetarotes Emery, 1913: Distribuição Neotropical. Possui quatro espécies descritas (Bolton 2015) e uma foi amostrada no solo do P. E. Cristalino. São formigas micetófagas e cultivam os fungos do qual se alimentam utilizando matéria orgânica vegetal como sementes e hastes florais (Mayhé-Nunes & Brandão 2006).

Mycocepurus Forel, 1893: Distribuição Neotropical. Possui seis espécies descritas (Bolton 2015) e uma amostrada (solo) para o P. E. Cristalino. São formigas micetófagas que nidificam no solo (Rabeling et al. 2007).

Myrmicocrypta Smith, 1860: Distribuição Neotropical. Possui 27 espécies descritas (Bolton 2015) sendo duas amostradas (solo) no P. E. Cristalino. São formigas micetófagas que nidificam no solo ou madeira podre (Leal & Oliveira 2000; Sosa-Calvo & Schultz 2010).

Nesomyrmex Wheeler, 1910: Distribuição cosmopolita. Possui 51 espécies descritas (Bolton 2015) sendo cinco amostradas (vegetação) no P. E. Cristalino. O gênero é arborícola e nidifica em cavidades de plantas e forrageiam de modo solitário (Longino 2010).

Ochetomyrmex Mayr, 1878: O gênero é restrito as florestas da América do Sul (Fernández 2003b). Possui duas espécies descritas (Bolton 2015), ambas amostradas no P. E. Cristalino (solo e vegetação).

Octostruma Forel, 1912: O gênero ocorre na região Neotropical, possui 34 espécies descritas (Bolton 2015) e uma espécie foi amostrada no solo do P. E. Cristalino. Nidificam na serapilheira, em pequenos troncos podres e em epífitas e são geralmente predadoras de pequenos artrópodes (Brown & Kempf 1960).

Pheidole Westwood, 1839 (fig. J, K): Este é o gênero mais abundante e diverso de formigas (Wilson 2003). Distribuição cosmopolita. Possui 1.007 espécies descritas (Bolton 2015) e trinta e oito foram amostradas (35 em solo e 11 em vegetação) no P. E. Cristalino. As espécies possuem os mais variados hábitos de nidificação e alimentação (Wilson 2003).

Rogeria Emery, 1894: Distribuição conhecida para o Novo Mundo e Australásia (LaPolla & Sosa-Calvo 2006). Possui 40 espécies descritas (Bolton, 2015) e uma amostrada em solo do P. E. Cristalino. São espécies crípticas que nidificam na serapilheira, em troncos caídos, debaixo de rochas e em galhos de árvores (LaPolla & Sosa-Calvo 2006).

Sericomyrmex Mayr, 1865 (fig. L): Distribuição Neotropical. Possui 19 espécies descritas (Bolton 2015) sendo duas amostradas no solo do P. E. Cristalino. São micetófagas

e nidificam no solo (Longino 2010).

Solenopsis Westwood, 1840: Distribuição cosmopolita. Possui 196 espécies descritas (Bolton 2015) e oito foram amostradas (oito em solo e duas na vegetação) no P. E. Cristalino. As formigas deste gênero, em sua maioria onívoras, alimentando-se de carcaças de vertebrados, invertebrados vivos ou mortos, frutos e sementes caídos, néctar de plantas (Trager 1991; Pacheco & Mackay 2013). Nidificam no solo e algumas espécies vivem associadas a ninhos de outras formigas, para predação da prole de sua hospedeira (Pacheco & Mackay 2013).

Strumigenys Smith, 1860 (fig. M): Distribuição cosmopolita. Possui 836 espécies descritas (Bolton 2015) e oito amostradas (cinco em solo e três na vegetação) para o P. E. Cristalino. Habitam a serapilheira, podendo nidificar em galhos podres e no solo. São predadores de pequenos artrópodes (Wilson 1953).

Trachymyrmex Forel, 1893: Distribuição cosmopolita, com 47 espécies descritas (Bolton 2015) e cinco amostradas (cinco em solo e uma em vegetação) no P. E. Cristalino. São micetófagas e nidificam no solo (Longino 2010).

Wasmannia Forel, 1893: Gênero endêmico da região Neotropical, porém, *W. auropunctata* foi introduzida ao longo de outras regiões tropicais (Longino & Fernández 2007), possui 10 espécies descritas (Bolton 2015) e três foram amostradas (três em solo e duas na vegetação) no P. E. Cristalino. As espécies deste gênero nidificam em folhas e galhos mortos caídos, debaixo de pedras, em domáceas de mirmecófitas e em epífitas (Longino & Fernández 2007). São onívoras e sua dieta é composta de animais mortos, secreções de plantas e hemípteros (Armbrecht & Ulloa-Chacón 2003; Longino & Fernández 2007).

SUBFAMÍLIA PONERINAE

Anochetus Mayr, 1861: Regiões tropicais, subtropicais e temperadas (Schmidt &

Shattuck 2014). Possui 114 espécies descritas (Bolton 2015) e duas amostradas em solo no P. E. Cristalino. São predadoras e utilizam de um tipo de armadilha mandibular para subjugar suas presas (Fernández 2003a). Nidificam em galhos podres, sob a casca dos troncos das árvores e no solo. Algumas espécies são arborícolas e outras vivem associadas a Isoptera (Schmidt & Shattuck 2014).

Dinoponera Roger, 1861: Distribuição Neotropical. Possui oito espécies descritas (Bolton 2014) e uma morfoespécie amostrada em solo no P. E. Cristalino. São formigas que possuem colônia com cerca de 100 indivíduos e forrageiam de forma solitária. Nidificam no solo, são predadoras generalistas de insetos, mas consomem frutas e outras fontes de alimento (Paiva & Brandão 1995; Araújo & Rodrigues 2006; Monnin & Peeters 2008).

Hypoponera Santschi, 1938: Distribuição cosmopolita. Dentre as 148 espécies descritas (Bolton 2015) três foram amostradas em solo no P. E. Cristalino. Nidificam no solo, em troncos podres e na serapilheira. São predadores generalistas de pequenos artrópodes (Brandão *et al.* 2009; Schmidt & Shattuck 2014).

Leptogenys Roger, 1861: Distribuição cosmopolita, com 307 espécies descritas (Bolton 2015) e uma amostrada em solo no P. E. Cristalino. Nidificam no solo, debaixo de pedras, em troncos podres, em cavidades de galhos ou sob a casca de troncos (Longino 2010). São predadoras de invertebrados, especialmente isópodos e Dermaptera (Brandão *et al.* 2009).

Mayaponera Schmidt & Shattuck, 2014: Distribuição Neotropical. Possui uma espécie descrita, *M. constricta* (Mayr, 1884) (Bolton 2015), que foi amostrada no solo e na vegetação do P. E. Cristalino. Nidificam no solo, debaixo de pedras ou em troncos podres, são predadoras e forrageiam durante a noite (Schmidt e Shattuck 2014).

Neoponera Emery, 1901 (fig. N): Distribuição Neotropical. Possui 57 espécies descritas (Bolton 2015) e nove amostradas (quatro em solo e seis na vegetação) no P. E.

Cristalino. Nidificam no solo, em troncos podres e galhos mortos. Algumas espécies são predadoras generalistas enquanto outras espécies são predadoras especialistas de Isoptera (Schmidt e Shattuck 2014).

Odontomachus Latreille, 1804 (fig. O): Distribuição Neotropical. Possui 67 espécies descritas (Bolton 2015) e três amostradas em solo no P. E. Cristalino. Nidificam no solo, serapilheira, troncos podres e algumas espécies são arborícolas (Brown 1976). São predadoras generalistas de pequenos artrópodes (Brown 1976; Jiménez et al. 2008).

Pachycondyla Smith, 1858: Distribuição Neotropical. Possui 17 espécies descritas (Bolton 2015) e duas amostradas em solo no P. E. Cristalino. As formigas deste gênero nidificam no solo e são predadoras generalistas e detritívoras (Schmidt & Shattuck 2014).

Pseudoponera Emery, 1900: Distribuição cosmopolita. Possui seis espécies descritas (Bolton 2015) e uma amostrada em solo no P. E. Cristalino. Nidificam no solo, troncos em decomposição e forrageiam solitariamente, sendo provavelmente predadoras generalistas e necrófagas (Schmidt & Shattuck 2014).

SUBFAMÍLIA PSEUDOMYRMECINAE

Pseudomyrmex Lund, 1831 (fig. P): Distribuição Neotropical. Possui 134 espécies descritas (Bolton 2015) e oito amostradas (uma em solo e oito na vegetação) no P. E. Cristalino. São arborícolas de hábitos generalistas ou se alimentam de secreções de cochonilhas, nidificam na cavidade de troncos, em galhos de plantas ou em troncos podres (Ward 1985, Ward 1991).

Este trabalho traz dois diferenciais em relação a inventários de formigas disponíveis na literatura. O primeiro é a listagem de formigas tanto que forrageiam pela vegetação do subbosque quanto ao nível do solo. A grande maioria dos inventários trazem registros de espécies que habitam o solo, sendo a fauna sub-arborícola negligenciada na maioria desses

estudos, principalmente na Amazônia (e.g. Ryder-Wilkie et al. 2010, Monteiro et al. 2013). Esses poucos estudos tem demonstrado a importância de amostrar ambos os estratos, visto o considerável acréscimo na contribuição para o conhecimento da fauna local. O segundo diferencial deste trabalho é a compilação de informações biológicas locais e disponíveis na literatura sobre os gêneros de formigas, que é extremamente escasso quando se trata da fauna Neotropical (e.g. Fernández 2003; Suguituru et al. 2015). Tanto essa listagem que refleta melhor a biodiversidade local por amostrar formigas de solo e vegetação, juntamente com as informações biológicas desses grupos, são informações importantes e podem auxiliar tanto em outros estudos com formigas, bem como as tomadas de decisões conservacionistas regionais.

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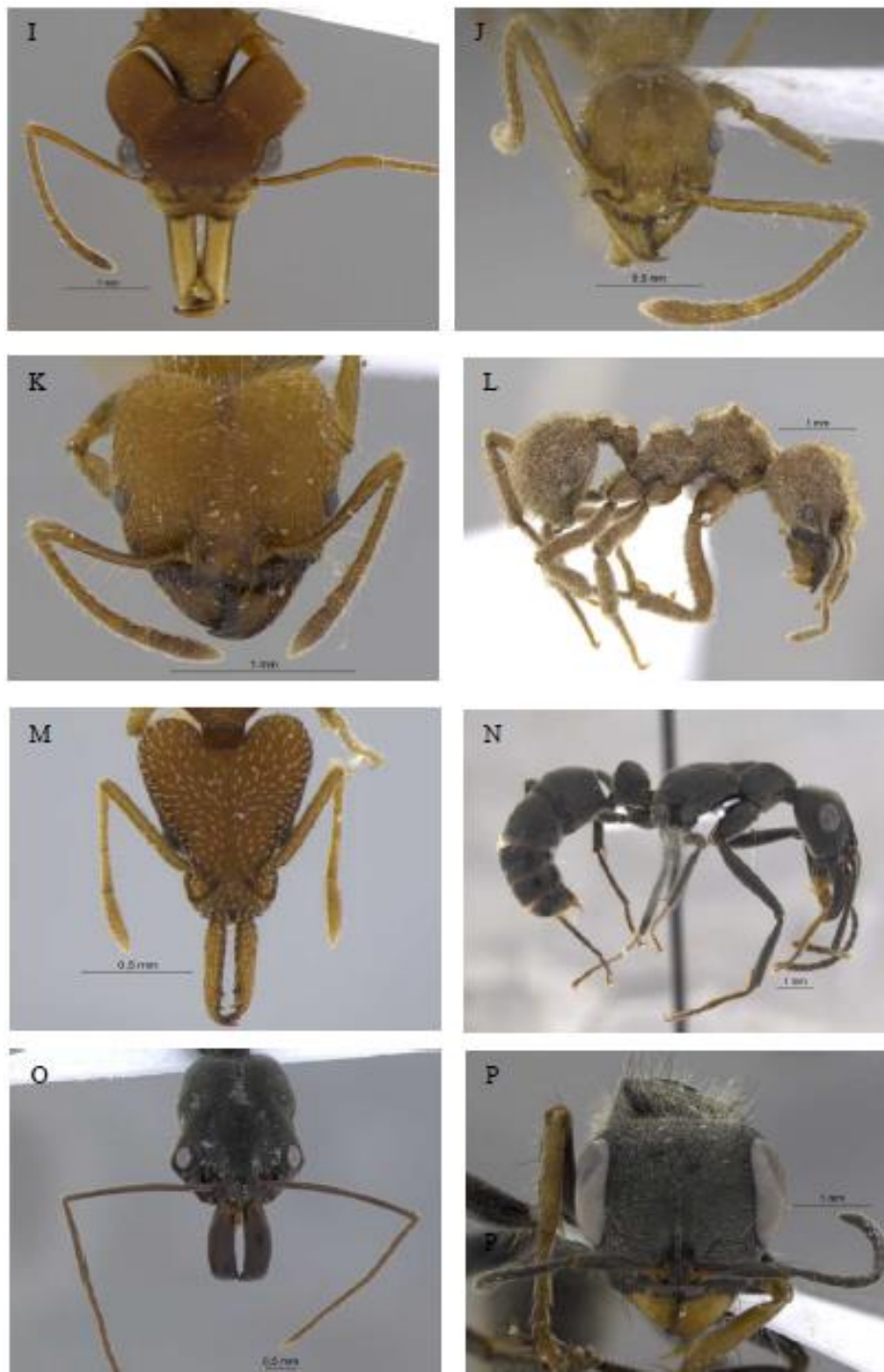
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Fauna de formigas do Parque Estadual do Cristalino: Figura A) *Dolichoderus* sp., B) *Eciton* sp., C) *Gnamptogenys* sp., D) *Camponotus* sp., E) *Gigantiops* sp., F) *Apterostigma* sp., G) *Cephalotes* sp., H) *Crematogaster* sp.



Fauna de formigas do Parque Estadual do Cristalino: Figura I) *Daceton* sp., J) *Pheidole* sp. (operária menor), K) *Pheidole* sp. (operária menor), L) *Sericomyrmex* sp., M) *Strumigenys* sp., N) *Neoponera* sp., O) *Odontomachus* sp., P) *Pseudomyrmex* sp.

**ANEXO 2 - Amazon rainforest ant-fauna of Parque Estadual do Cristalino:
Understory and ground-dwelling ants**

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**Amazon Rainforest Ant-Fauna of Parque Estadual do Cristalino: Understory
and Ground-Dwelling Ants**

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Abstract - Ants are ecologically dominant and have been used as valuable bio-indicators of environmental change or disturbance being used in monitoring inventories. However, the majority of inventories have concentrated on ground-dwelling ant fauna disregarding arboreal fauna. This paper aimed to list the ant species collected both on the ground and in the vegetation of the Parque Estadual do Cristalino, an important protected site in the center of the southern Amazon. Moreover, we compared the composition of the ground dwelling and vegetation foraging ants. Two hundred and three (203) species distributed among 23 genera and eight subfamilies were sampled, wherein 34 species had not yet been reported in the literature for Mato Grosso State. As expected, the abundance and richness of ants was higher on the ground than in the understory. Also, the composition of the ant assemblages was different between these habitats (with only 20% occurring in both) indicating that complementary methods which include arboreal and terrestrial ants are indicated for efficient inventory. This study provides an inventory of the arboreal and ground ant fauna contributing to the knowledge and conservation of Amazonian ant fauna.

Keywords: Arboreal ants; Conservation; Diversity; Formicidae; Inventory.

INTRODUCTION

Ants are ecologically dominant, playing several ecosystem services in the environment (Del Toro *et al.*, 2012) and occupying the most varied habitats (Bruhl *et al.*, 1998; Dejean *et al.* 2015; Rocha *et al.* 2015; Pape *et al.*, 2016). Ants strongly influence several terrestrial communities due to their abundance and potential relationships with various biological groups. The interactions of ants can be positive or negative, ranging from interactions with microorganisms (Hanshew *et al.*, 2014; Sanders *et al.*, 2014), plants (Izzo & Vasconcelos, 2009; Vicente *et al.*, 2012, 2014; Koch *et al.*, 2015) and other invertebrates (Dáttilo *et al.*, 2012a; Freitas & Rossi, 2015; Puker *et al.*, 2015), even other ants (Adams *et al.*, 2007; Sanhudo *et al.*, 2008; Gallego-Roperero & Feitosa, 2014). Therefore, ants have been used as a model to understand the various ecological patterns and as valuable bio-indicators of environmental change or disturbance (Andersen *et al.*, 2002; Bruna *et al.*, 2014; Falcão *et al.*, 2015).

Regardless of their ecological importance and diversity, studies on Brazilian ant fauna were usually concentrated in the Atlantic Forest (Feitosa & Ribeiro, 2005; Figueiredo *et al.*, 2013; Silva *et al.*, 2007), the Cerrado (Dáttilo *et al.*, 2012b; Silva & Brandão, 2014; Camacho & Vasconcelos, 2015), and Pantanal (Ribas & Schoereder, 2007; Silva *et al.*, 2013; Meurer *et al.*, 2015). Although the Amazon is one of the largest and heterogeneous tropical forests remaining, the panorama is not different. The studies of Amazonian ants in Brazil are generally concentrated in small parts of the Central region (e.g. Vasconcelos *et al.*, 2006, 2010; Santos *et al.*, 2007; Baccaro *et al.*, 2013; Souza *et al.*, 2012). Studies in the southern Amazon region are few, and because they focus on local ecological patterns, the list of species therein usually does not have confirmation of specialists and comprises a large number of morphospecies (for example: Dáttilo *et al.*, 2013; Falcão *et al.*, 2015). The absence of surveys in this area is particularly problematic to the knowledge of the distribution of ant diversity in the tropics. More than being a frontier

between the Amazonia and Cerrado biomes, the south of Amazonia is a frontier of fast agricultural expansion, being subject to enormous rates of deforestation (Fearnside, 2005). In such a scenario, several species could become, and probably some already have become extinct without being known by science. This is worrying in a region that has many species with unknown distribution (Vicente et al. 2011, 2012, 2015, 2016; Prado et al. 2016).

Whereas inventories are fundamental to promote conservation of tropical forest remnants and the ants are important components of biodiversity, this work aims to contribute to the knowledge of the Amazonian ground-dwelling and arboreal ant fauna. The reserve is a *terra firme* Tropical Rainforest located in the Southern Amazon, but with little known diversity of various taxa. In this study, we list the fauna of ground-dwelling ants and the assemblages of ants foraging on lower vegetation in the same site. We compared the difference between the strata in order to demonstrate the increase in local biodiversity by using a simple additional method.

MATERIAL AND METHODS

Study area

The surveys were conducted in an Amazonian Research Program Station in Biodiversity in the Brazilian Parque Estadual do Cristalino (henceforward PEC), with RAPELD methodology (see Magnusson *et al.*, 2005). The park is a large protected area defined as “Priority for Conservation Site” (Ministério do Meio Ambiente [MMA], 2001) that hosts an area of 184,900 ha, situated in the middle of an area called “Arc of Deforestation” (Fearnside, 2005), comprising the Brazilian municipality of Alta Floresta and Novo Mundo, state of Mato Grosso bordering on Pará state. The research study was carried in a station installed in the north of the park (9° 32'47 "S, 55° 47'38" W) (Fig 1) in the municipality of Novo Mundo. The vegetation is characterized as transition zones between ombrophilous and seasonal forest, seasonal forest and savanna (Cerrado), and

ombrophilous and savanna (Cerrado) (Instituto Brasileiro de Geografia e Estatística [IBGE], 2004).

Ant sampling

The inventory of ants was conducted between November 2012 (beginning of the rainy season with sporadic rains) and May 2013 (end of the rainy season with sporadic rains) in 11 trails 250m long, with a distance between sites of at least 1 km. In each trail, ants were collected every 25m, resulting in 20 samples per trail (10 samples of the ground-dwelling ants and 10 samples of the arboreal ants) and totaling 220 samples (110 samples of ground-dwelling ants and 110 samples of arboreal ants). The collection of the ground ant assemblages was made using a single pitfall trap that remains installed for 48 hours in each sample point. For sampling arboreal ants a beating-tray method was used in vegetation of understory. In each of these points, we selected the four treelets equidistant of about 2 m of the pitfall. Under each treelet, a white canvas was installed to prevent some ants from jumping and getting away from the sampling (Dáttilo *et al.*, 2013), and about one meter from the ground to prevent ants from walking on the ground and climbing on the canvas. Then all vegetation in each treelet within 1m² with between 1-3 meters in height was steadily shaken and the ants that fell on the canvas were properly collected. The sampling of ground and arboreal ants was carried out concomitantly, so the sampling of arboreal ants was performed between 9 am and 3 pm on the same day that the pitfall was removed.

Ant identification

Ants collected initially were identified using dichotomous key for subfamilies and genera available in Baccaro *et al.* (2015). So as to separate into morphospecies and identify to a specific level we used several taxonomic keys (Brandão, 1990; Fernández, 2003; Longino, 2003a; MacKay & MacKay, 2010; Fernandes *et al.*, 2014). Posteriorly we made comparisons with specimens deposited at the Laboratório de Ecologia de Comunidades from the Centro de Biodiversidade da Universidade Federal de Mato Grosso (UFMT) and

the ant collection from the Laboratório de Sistemática, Evolução e Biologia de Hymenoptera from the Museu de Zoologia da Universidade de São Paulo (MZSP). We also consulted specialists to confirm species identification (see acknowledgments). Vouchers were deposited in the collections mentioned above. After the identification and confirmation by specialists we consulted the distribution of each species using the AntMaps (Janicki *et al.*, 2016), a new interactive tool recently used by taxonomists and ecologists (Gérnard & Economo, 2015; Vicente *et al.*, 2015; Santos-Silva *et al.* 2016; Wepfer *et al.*, 2016). This tool comprises the geographic distributions of more than 15,000 species/subspecies in over 1.7 million records of about 8,650 publications, museum collections and specimen databases (Janicki *et al.*, 2016). Furthermore, we researched in bibliographic references related to taxonomy of species or lists of ants from region.

Data analysis

We carried out a t-test to access the difference of ant abundance and richness patterns between ground and understory. Because ants are social insects, the sampled abundance of workers in pitfalls may be strongly related to the proximity to the nest (Gotelli *et al.*, 2011) or workers' number in a colony, which varies greatly between species (Baccaro *et al.*, 2015). To minimize this effect, we treated the abundance as sample-based occurrences (Gotelli *et al.*, 2011) as is commonly done in studies with ants (Ryder-Wilkie *et al.*, 2010; Dáttilo & Izzo, 2012; Baccaro *et al.*, 2013). To access the distribution patterns of the ant assemblages we performed an ordination with Principal Coordinate Analysis (PCoA) technique based on a matrix of Raup-Crick dissimilarity measures calculated in a binary matrix with presence and absence date. Raup-Crick was used because it is a robust index that calculates how different pairwise samples are than expected by chance implementing null models which consider the variation in the number of local species and alpha diversity (Chase *et al.*, 2011). This index is frequently used to compare the dissimilarity of invertebrate communities between different habitats (Ryder-Wilkie *et al.*,

2010; Ribas *et al.*, 2012; Reis *et al.*, 2013). We utilized the first two PCoA axis (which represented 66.76 % of explication) in a Multivariate Analysis of Variance (MANOVA) as dependent variables and vertical habitat (ground and understory) as a factor. All analysis were performed with R-software (R Core Team, 2015) using the Vegan-package (Oksanen *et al.*, 2015).

RESULTS

We recorded 1,581 occurrences of ants in the 220 samples. The ants collected belong to 203 species, 45 genera and eight subfamilies. Subfamilies with greater richness were Myrmicinae with 23 genera and 113 species, Ponerinae with eight genera and 23 species and Formicinae with five genera and 27 species. The genus with greater richness was *Pheidole* (37 species), *Camponotus* (17), *Neoponera* and *Crematogaster* (both 10 species).

Both abundance ($p < 0.001$) and richness ($p < 0.001$) of ants were different between the vertical strata (Table 1 – Fig 2), being greater on the ground than on the understory. We collected almost 63.4% of ant occurrences (total: 1,002, mean: 89.1, SD: ± 26.3 per sample) and 65% of ant species (total: 143 species, mean: 47.91, SD: ± 10.26) on the ground stratum. The understory showed a total of 579 occurrences (mean: $51 \pm$, SD: 15.1) and a total of 100 species (mean: 26.6, \pm SD: 6.67). Of these 203 species, 164 species were restricted to a vertical stratum with 104 species collected only on the ground and 60 only on the understory, and just 39 species collected in both strata (Table 2). Although on average 41.09 species by trail (\pm SD: 9.07) were exclusive to the ground, there is a mean increase of 19.73 species by trail (\pm SD: 5.85) by adding beating tray in the ant collection. Only one subfamily (Amblyoponinae) was sampled exclusively on the ground. Consequently, the species composition was different between the habitats (MANOVA - Pillai-Trace: 0.852, $F_{1,20}$: 54.873, $p < 0.001$ – Fig 3). Among the species sampled, 34 were recorded for the first time for Mato Grosso State, Brazil (Table 2).

DISCUSSION

Of the inventories on ant assemblages conducted in the Amazon, the major part of the studies focused just on ground-dwelling ants (Miranda *et al.*, 2012; Souza *et al.*, 2012, 2015; Baccaro *et al.*, 2013) and few comprised both terrestrial and arboreal ant fauna detailing the strata in which each species was collected (e.g.: Vasconcelos & Vilhena, 2006; Ryder-Wilkie *et al.*, 2010). These few studies carried out in the Amazon embracing both soil and vegetation ants have demonstrated extremely different ant assemblages between these habitats (Vasconcelos & Vilhena, 2006; Ryder-Wilkie *et al.*, 2010). The methods employed here are very different. The both methods capture active foraging ants, however the pitfall traps were active during day and night whereas the beating tray method was used only during the day. This can explain the small number of species collected on vegetation, preventing strong inferences towards the patterns of species richness. However we observed a strong turnover on ant composition, since only about 20% of all collected species were sampled both on the ground and on vegetation. Hence, even missing several nocturnal species on vegetation strata, the species collected just on vegetation were certainly absent on ground strata. Therefore, the vertical stratification in the ant fauna is a robust ecological pattern found in both the Amazon forest and in other biomes (Bruhl *et al.*, 1998; Vasconcelos & Vilhena, 2006; Neves *et al.*, 2013; Camacho & Vasconcelos, 2015). Additionally our results indicate that, using an additional simple method focusing on vegetation foraging ants, as beating-tray, one can increase the number of collected species. Therefore, besides the vegetation foraging ant community can show different ecological patterns they contribute to our understanding of the real ant biodiversity in an area and, as well as the knowledge of biogeographical patterns.

The Amblyoponinae subfamily, considered as a basal group in the evolution of ants (Saux *et al.*, 2004), as well as the 18 other genera were sampled exclusively on the ground.

Among these genera collected only in soil are the fungus-growing ants *Atta*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta* and *Sericomyrmex*. These ants nest directly on the ground or in rotten wood in contact with the soil (Baccaro *et al.*, 2015). Except for the *Atta* species which climbs into vegetation to cut fresh vegetable matter, the other abovementioned species take advantage of organic matter found in litter such as fallen leaves, fruits, flowers, feces and corpses (Leal & Oliveira, 2000; Mayhé-Nunes & Brandão, 2006). *Hylomyrma immans*, *Octostruma balzani*, *Rogeria scobinata* and three unidentified *Hypoponera* species also were collected exclusively in the soil. These genera have species with cryptic behavior (Lapolla & Sosa-Calvo, 2006; Longino, 2013b). The sampling of only one *Daceton armigerum* worker on the ground should be considered as an accidental record, since species of this genus have adaptations such as hook-shaped claws which provide remarkable adhesion to the arboreal substrate (Billen *et al.*, 2016) where they nest in tree branches (Azorsa & Sosa-Calvo, 2008; Vicente *et al.*, 2011) and forage (Dejean *et al.*, 2012).

Despite their hypogeal origin, ants diversify occupying other habitats (Lucky *et al.*, 2013) and the occupation of the arboreal environment resulted in morphological and behavioral adaptations both to get around and feed on available resources in vegetation (Orivel & Dejean, 1999; Dejean *et al.*, 2005). These adaptations were observed in the various *Neoponera* species sampled. *Neoponera* is composed mainly by arboreal behavior species (Schmidt & Shattuck, 2014) that live or forage on vegetation, and have morphological adaptations regarding modifications on claws, shape and adhesion (Orivel *et al.*, 2001). Four other genera were restricted to vegetation: *Azteca*, *Myrmelachista*, *Nesomyrmex* and *Tapinoma*. Species of these genera usually nest on plants (Longino, 2007; Nakano *et al.*, 2013; Longino, 2004). *Cephalotes* was another genus with a greater number of arboreal species, with just *C. atratus* being collected in both strata. The *Cephalotes* ant genus has as their main features a diet based largely on pollen and nectar and nesting in

pre-existing plant cavities (Byk & Del-Claro, 2010), however, *C. atratus* can often be found foraging on the ground (Corn, 1980). Although some subfamilies as Pseudomyrmecinae and Dolichoderinae had a large proportion of species collected in the vegetation, no subfamily has been sampled exclusively to only this vertical strata. In Pseudomyrmecinae, only *Pseudomyrmex tenuis* was collected in both soil (one worker) and vegetation (seven workers). *P. tenuis* is a widespread ant species, frequently sampled foraging in all strata as epigeaic, arboreal and canopy stratum (Vasconcelos & Vilhena, 2006; Neves *et al.*, 2013; Camacho & Vasconcelos, 2015; Souza *et al.*, 2015). Also, in a Dolichoderinae subfamily with 18 ant species, only five species of *Dolichoderus* genus, occurred also on the ground.

Camponotus genus was particularly representative (17 species; 84 samples) in relation to the total number of collected species (5.6%). In two areas of Central Amazon, both in Amazonas state, Brazil, *Camponotus* species comprises 2.7% and 2.3% of total species collect on the ground (Souza *et al.*, 2015). In addition, in the Central South Amazon this proportion ranges from 1.99% to 4.62% of ground ants in preserved areas of Rondônia state (Souza *et al.*, 2015). On the other hand, in samples made in ground and understory of patches of forest in Southern Amazon in Rondonia state and Central East Amazon in Pará state, both in Brazil, there was a ratio of 9.33% and 7.09%, respectively (Santos-Silva *et al.* 2016; Vasconcelos *et al.*, 2006). Therefore, this high proportion of *Camponotus* found in the Parque Estadual do Cristalino confirm that simple methodologies could sampled a greater number of considered arboreal ant species, such as *Camponotus*.

Mato Grosso State is the third largest state in Brazil, hosting three different Biomes and the many new records in an inventory (18 species collected in the soil, seven in vegetation and 10 in both strata) demonstrating a gap or shortcoming related mainly to the lack of surveys throughout the South American territory (but see: Kempf 1972; Brandão

1991; Silva *et al.*, 2013; Meurer *et al.*, 2015). Although there are a number of studies on the ecology and distribution of ants in the Amazon in northern Mato Grosso (Dáttilo *et al.*, 2013; Falcão *et al.*, 2015; Vicente *et al.*, 2011, 2012, 2014, 2015) this is the first list of ant species for the region, as well as being the most complete list published until now for the southern Amazon. In summary, this work demonstrates that inventories should consider ants of both ground and vegetation for a better sampling of local ant diversity. In addition, the number of new records of ant fauna (35 species) for Mato Grosso state and the number of unnamed species (97 morphospecies), show that the ant fauna of the Amazon in general are not common or are extremely unknown. The tropical forests are being increasingly threatened by anthropic activities and Mato Grosso state in particular because they are located in a region with a historically strong pressure for disturbance, being an agricultural frontier. Therefore, efforts should be made to understand ant diversity distribution patterns and propose conservation strategies in this region.

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Table 1: Test-t measures for difference in abundance and richness between ground and arboreal ant assemblages.

Parameters	t	df	p-value
Abundance	4.1599	15.979	<0.001
Richness	5.7656	17.167	<0.001

Table 2: List of species recorded at the Parque Estadual do Cristalino. Numbers represent the total number of occurrences in strata. *First record in literature from Mato Grosso state.

Subfamily/Genus/Species	Ground (pitfall trap)	Understory (beating-tray method)	Total
Amblyoponinae			
<i>Prionopelta</i>			
<i>Prionopelta punctulata</i> Mayr, 1866*	4	-	4
Dolichoderinae			
<i>Azteca</i>			
<i>Azteca alfari</i> Emery, 1893	-	4	4
<i>Azteca prox. aurita</i> Emery, 1893	-	3	3
<i>Azteca</i> INPA01	-	19	19
<i>Azteca</i> TJI02	-	5	5
<i>Azteca</i> TJI04	-	2	2
<i>Azteca</i> TJI05	-	1	1
<i>Azteca</i> TJI07	-	4	4
<i>Azteca</i> TJI08	-	2	2
<i>Azteca</i> TJI09	-	3	3
<i>Dolichoderus</i>			
<i>Dolichoderus abruptus</i> (Smith, 1858)*	-	1	1
<i>Dolichoderus attelaboides</i> (Fabricius, 1775)*	2	3	5
<i>Dolichoderus bidens</i> (Linnaeus, 1758)*	1	2	3
<i>Dolichoderus bispinosus</i> (Oliver, 1792)	1	-	1
<i>Dolichoderus gagates</i> Emery, 1890	1	5	6
<i>Dolichoderus ghilianii</i> Emery, 1894	-	1	1
<i>Dolichoderus imitator</i> Emery, 1894	3	2	5
<i>Tapinoma</i>			
<i>Tapinoma</i> CR1	-	12	12
<i>Tapinoma</i> CR2	-	5	5
Dorylinae			
<i>Eciton</i>			
<i>Eciton burchellii</i> (Westwood, 1842)	3	-	3
<i>Neivamyrmex</i>			
<i>Neivamyrmex prox. pilosus</i>	1	-	1

(Smith, 1858)			
<i>Neivamyrmex</i> INPA02	-	1	1
Ectatomminae			
<i>Ectatomma</i>			
<i>Ectatomma edentatum</i> Roger, 1863	14	-	14
<i>Ectatomma lugens</i> Emery, 1894*	65	-	65
<i>Ectatomma tuberculatum</i> (Olivier, 1792)	3	31	34
<i>Gnamptogenys</i>			
<i>Gnamptogenys</i> prox. <i>ericae</i> (Forel, 1912)	5	-	5
<i>Gnamptogenys horni</i> (Santschi, 1929)*	17	-	17
<i>Gnamptogenys kempfi</i> Lenko, 1964*	1	-	1
<i>Gnamptogenys moelleri</i> (Forel, 1912)*	10	-	10
<i>Gnamptogenys pleurodon</i> (Emery, 1896)	-	1	1
<i>Gnamptogenys striatula</i> Mayr, 1884	5	13	18
<i>Gnamptogenys</i> prox. <i>sulcata</i> (Smith, 1858)	1	-	1
<i>Gnamptogenys</i> TJ14	1	-	1
Formicinae			
<i>Acropyga</i>			
<i>Acropyga</i> TJ11	3	-	3
<i>Brachymyrmex</i>			
<i>Brachymyrmex</i> CR1	4	41	45
<i>Brachymyrmex</i> CR2	-	1	1
<i>Brachymyrmex</i> CR3	-	13	13
<i>Camponotus</i>			
<i>Camponotus atriceps</i> (Smith, 1858)	1	1	2
<i>Camponotus diversipalpus</i> Santschi, 1922	3	-	3
<i>Camponotus femoratus</i> (Fabricius, 1804)	13	10	23
<i>Camponotus latangulus</i> Roger, 1863	-	8	8
<i>Camponotus mus</i> Roger, 1863	-	1	1
<i>Camponotus nidulans</i> (Smith, 1860)	-	5	5
<i>Camponotus</i> <i>novogranadensis</i> Mayr, 1870	1	-	1
<i>Camponotus scissus</i> Mayr, 1887*	-	1	1
<i>Camponotus trapezoideus</i>	-	5	5

Mayr, 1870			
<i>Camponotus</i> CR02	-	2	2
<i>Camponotus</i> CR06	-	1	1
<i>Camponotus</i> CR07	-	2	2
<i>Camponotus</i> CR11	-	8	8
<i>Camponotus</i> CR16	3	2	5
<i>Camponotus</i> CR19	2	-	2
<i>Camponotus</i> TJI01	-	3	3
<i>Camponotus</i> TJI04	10	2	12
Gigantiops			
<i>Gigantiops destructor</i> (Fabricius 1804)	2	1	3
Nylanderia			
<i>Nylanderia</i> prox. <i>caeciliae</i> (Forel, 1899)	15	11	26
<i>Nylanderia</i> prox. <i>fulva</i> (Mayr, 1862)	4	1	5
<i>Nylanderia</i> CR1	26	16	42
<i>Nylanderia</i> CR5	1	-	1
<i>Nylanderia</i> TJI2	17	3	20
Myrmicinae			
Apterostigma			
<i>Apterostigma urichii</i> Forel, 1893	9	-	9
<i>Apterostigma</i> CR1	-	2	2
<i>Apterostigma</i> INPA01	4	-	4
<i>Apterostigma</i> INPA04	5	-	5
Atta			
<i>Atta cephalotes</i> (Linnaeus, 1758)	13	-	13
<i>Atta sexdens</i> (Linnaeus, 1758)	1	-	1
Carebara			
<i>Carebara urichi</i> (Wheeler, 1922)	13	-	13
<i>Carebara</i> JT11	2	-	2
Cephalotes			
<i>Cephalotes atratus</i> (Linnaeus, 1758)	3	3	6
<i>Cephalotes oculatus</i> (Spinola, 1851)*	-	5	5
<i>Cephalotes pallens</i> (Klug, 1824)	-	1	1
<i>Cephalotes</i> CR1	-	2	2
<i>Cephalotes</i> CR3	-	1	1
Crematogaster			
<i>Crematogaster arcuata</i> Forel, 1899	-	2	2

<i>Crematogaster brasiliensis</i> Mayr, 1878	-	14	14
<i>Crematogaster carinata</i> Mayr, 1862*	-	1	1
<i>Crematogaster curvispinosa</i> Mayr, 1862*	-	1	1
<i>Crematogaster erecta</i> Mayr, 1866	3	8	11
<i>Crematogaster levior</i> Longino 2003*	8	7	15
<i>Crematogaster limata</i> Smith, 1858*	6	23	29
<i>Crematogaster nigropilosa</i> Mayr, 1870*	3	26	29
<i>Crematogaster stollii</i> Forel, 1885	1	-	1
<i>Crematogaster tenuicula</i> Forel, 1904*	32	24	56
Cyphomyrmex			
<i>Cyphomyrmex laevigatus</i> Weber, 1938*	7	-	7
<i>Cyphomyrmex peltatus</i> Kempf, 1966	5	-	5
<i>Cyphomyrmex prox. rimosus</i>	-	3	3
<i>Cyphomyrmex</i> CR7	1	-	1
<i>Cyphomyrmex</i> TJI02	1	-	1
<i>Cyphomyrmex</i> TJI03	9	-	9
<i>Cyphomyrmex</i> TJI06	1	-	1
Daceton			
<i>Daceton armigerum</i> (Latreille, 1802)	1	-	1
Hylomyrma			
<i>Hylomyrma immanis</i> Kempf, 1973*	8	-	8
Megalomyrmex			
<i>Megalomyrmex ayri</i> Brandão, 1990	16	-	16
<i>Megalomyrmex cuatiara</i> Brandão, 1990*	1	-	1
<i>Megalomyrmex drifti</i> Kempf, 1961	2	-	2
<i>Megalomyrmex</i> CR3	1	-	1
Mycetarotes			
<i>Mycetarotes</i> CR1	1	-	1
Mycocepurus			
<i>Mycocepurus smithii</i> (Forel, 1893)	4	-	4
Myrmelachista			
<i>Myrmelachista</i> TJI01	-	1	1
Myrmicocrypta			

<i>Myrmicocrypta</i> INPA01	2	-	2
<i>Myrmicocrypta</i> INPA02	1	-	1
Nesomyrmex			
<i>Nesomyrmex</i> prox. <i>asper</i> (Mayr, 1887)	-	1	1
<i>Nesomyrmex</i> prox. <i>pleuriticus</i> (Kempf, 1959)	-	1	1
<i>Nesomyrmex tonsuratus</i> (Kempf, 1959)	-	1	1
<i>Nesomyrmex</i> CR1	-	1	1
<i>Nesomyrmex</i> TJI2	-	1	1
Ochetomyrmex			
<i>Ochetomyrmex neopolitus</i> Fernández, 2003	18	8	26
<i>Ochetomyrmex semipolitus</i> Mayr, 1878	3	56	59
Octostruma			
<i>Octostruma balzani</i> (Emery, 1894)	1	-	1
Pheidole			
<i>Pheidole biconstricta</i> Mayr, 1870*	4	4	8
<i>Pheidole bufo</i> Wilson, 2003	1	-	1
<i>Pheidole gertrudae</i> Forel, 1886*	1	-	1
<i>Pheidole</i> prox. <i>gilva</i> Wilson, 2003	-	2	2
<i>Pheidole nitella</i> Wilson, 2003*	22	-	22
<i>Pheidole radoszkowskii</i> Mayr, 1884*	17	7	24
<i>Pheidole transversostriata</i> Mayr, 1887*	65	2	67
<i>Pheidole vorax</i> (Fabricius, 1804)*	1	-	1
<i>Pheidole</i> CR16	22	-	22
<i>Pheidole</i> CR44	2	-	2
<i>Pheidole</i> INPA008	2	2	4
<i>Pheidole</i> INPA019	6	-	6
<i>Pheidole</i> INPA020	4	-	4
<i>Pheidole</i> INPA025	1	-	1
<i>Pheidole</i> INPA026	1	-	1
<i>Pheidole</i> INPA037	5	-	5
<i>Pheidole</i> INPA045	3	2	5
<i>Pheidole</i> INPA048	8	-	8
<i>Pheidole</i> INPA049	2	-	2
<i>Pheidole</i> INPA051	13	-	13
<i>Pheidole</i> TJI02	16	1	17
<i>Pheidole</i> TJI07	-	1	1
<i>Pheidole</i> TJI09	10	1	11
<i>Pheidole</i> TJI10	2	2	4

<i>Pheidole</i> TJI17	6	-	6
<i>Pheidole</i> TJI21	22	-	22
<i>Pheidole</i> TJI22	8	-	8
<i>Pheidole</i> TJI23	2	-	2
<i>Pheidole</i> TJI24	3	-	3
<i>Pheidole</i> TJI26	3	-	3
<i>Pheidole</i> TJI28	5	-	5
<i>Pheidole</i> TJI29	6	-	6
<i>Pheidole</i> TJI30	4	-	4
<i>Pheidole</i> TJI31	4	-	4
<i>Pheidole</i> TJI33	3	-	3
<i>Pheidole</i> TJI40	1	-	1
<i>Pheidole</i> TJI41	1	-	1
Rogeria			
<i>Rogeria scobinata</i> Kugler, 1994	3	-	3
Sericomyrmex			
<i>Sericomyrmex</i> INPA001	14	-	14
Solenopsis			
<i>Solenopsis</i> prox. <i>geminata</i> (Fabricius, 1804)	4	-	4
<i>Solenopsis</i> CR1	2	44	46
<i>Solenopsis</i> CR6	18	-	18
<i>Solenopsis</i> CR7	6	-	6
<i>Solenopsis</i> CR8	8	-	8
<i>Solenopsis</i> CR9	6	-	6
<i>Solenopsis</i> TJI2	22	6	28
<i>Solenopsis</i> TJI4	1	-	1
Strumigenys			
<i>Strumigenys alberti</i> Forel, 1893	-	1	1
<i>Strumigenys beebei</i> (Wheeler, 1915)*	2	-	2
<i>Strumigenys elongata</i> Roger, 1863	3	-	3
<i>Strumigenys fairchildi</i> Brown, 1961	-	1	1
<i>Strumigenys trinidadensis</i> Wheeler, 1922	-	3	3
<i>Strumigenys vilhenai</i> Bolton, 2000*	8	-	8
<i>Strumigenys</i> INPA03	1	-	1
<i>Strumigenys</i> TJI8	1	-	1
Trachymyrmex			
<i>Trachymyrmex</i> INPA03	8	-	8
<i>Trachymyrmex</i> INPA05	6	-	6
<i>Trachymyrmex</i> INPA10	5	-	5
<i>Trachymyrmex</i> TJI1	33	1	34

<i>Trachymyrmex</i> TJI4	7	-	7
<i>Trachymyrmex</i> sp.	3	-	3
Wasmannia			
<i>Wasmannia auropunctata</i> (Roger, 1893)	22	9	31
<i>Wasmannia rochai</i> Forel, 1912*	2	-	2
<i>Wasmannia scrobifera</i> Kempf, 1961*	24	4	28
Ponerinae			
Anochetus			
<i>Anochetus diegensis</i> Forel, 1912*	1	-	1
<i>Anochetus horridus</i> Kempf, 1964*	1	-	1
Dinoponera			
<i>Dinoponera quadriceps</i> Kempf, 1971*	4	-	4
Hypoponera			
<i>Hypoponera</i> TJI1	1	-	1
<i>Hypoponera</i> TJI2	2	-	2
<i>Hypoponera</i> TJI3	2	-	2
Leptogenys			
<i>Leptogenys</i> INPA02	2	-	2
Mayaponera			
<i>Mayaponera constricta</i> (Mayr, 1884)	10	1	11
Neoponera			
<i>Neoponera apicalis</i> (Latreille, 1802)	4	-	4
<i>Neoponera commutata</i> (Roger, 1860)	2	-	2
<i>Neoponera crenata</i> (Roger, 1861)	-	2	2
<i>Neoponera globularia</i> (MacKay & MacKay, 2010)*	-	1	1
<i>Neoponera inversa</i> (Smith, 1858)	1	3	4
<i>Neoponera striatinodis</i> (Emery, 1890)*	-	2	2
<i>Neoponera unidentata</i> (Mayr, 1862)	-	4	4
<i>Neoponera verena</i> Forel, 1922*	14	-	14
<i>Neoponera villosa</i> (Fabricius, 1804)	-	1	1
<i>Neoponera</i> TJI8	-	4	4
Odontomachus			
<i>Odontomachus haematodus</i> (Linnaeus,	1	-	1

1758)			
<i>Odontomachus meinerti</i>	2	-	2
Forel, 1905			
<i>Odontomachus</i> TJI1	3	-	3
<i>Pachycondyla</i>			
<i>Pachycondyla crassinoda</i>	31	-	31
(Latreille, 1802)			
<i>Pachycondyla harpax</i>	6	-	6
(Fabricius, 1804)			
<i>Pseudomyrmecinae</i>			
<i>Pseudomyrmex</i>			
<i>Pseudomyrmex oculatus</i>	-	2	2
(Smith, 1855)			
<i>Pseudomyrmex tenuis</i>	1	7	8
(Fabricius, 1804)			
<i>Pseudomyrmex tenuissimus</i>	-	2	2
(Emery, 1906)			
<i>Pseudomyrmex unicolor</i>	-	1	1
(Smith, 1855)			
<i>Pseudomyrmex</i> INPA001	-	1	1
<i>Pseudomyrmex</i> TJI3	-	3	3
<i>Pseudomyrmex</i> TJI8	-	1	1
Total occurrences	1002	579	1581

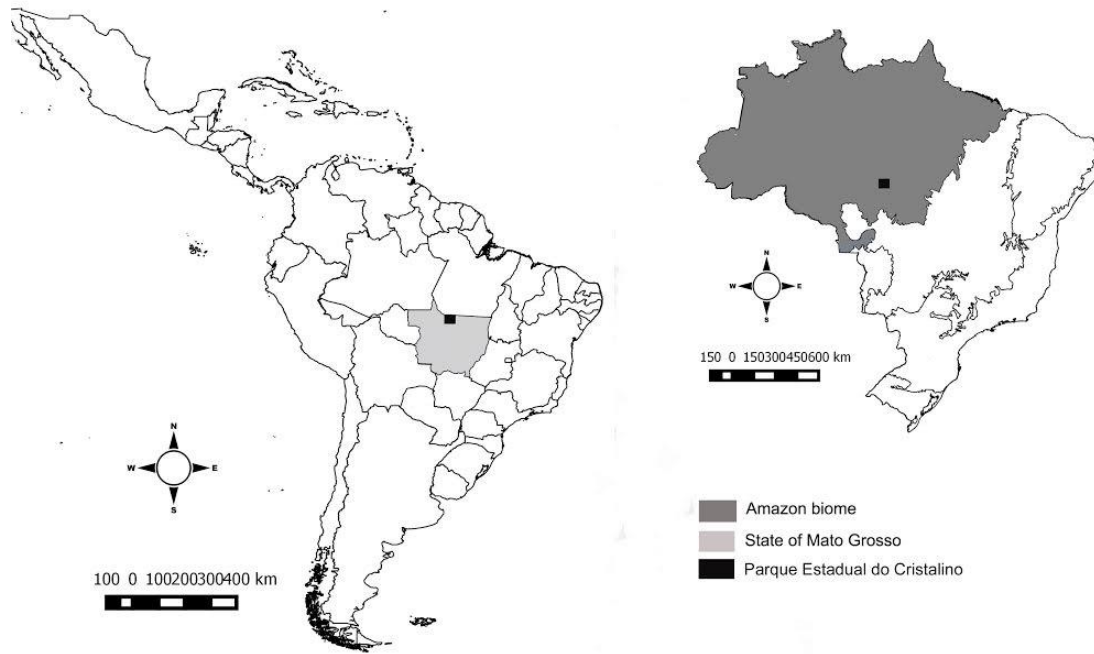


Fig 1. Location map of the Parque Estadual do Cristalino (filled circle).

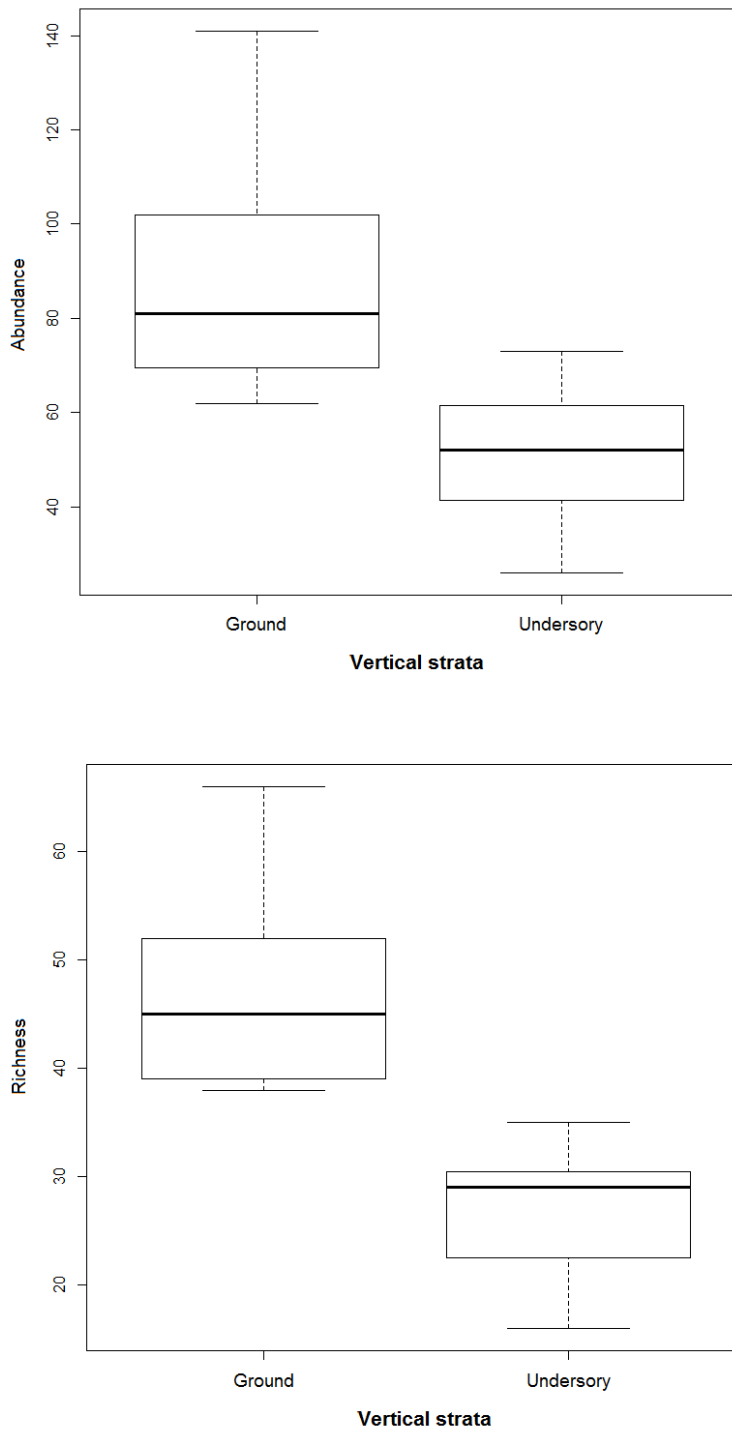


Fig 2. (a) Abundance mean of ants and (b) richness of ant species in vertical strata (ground and understory).

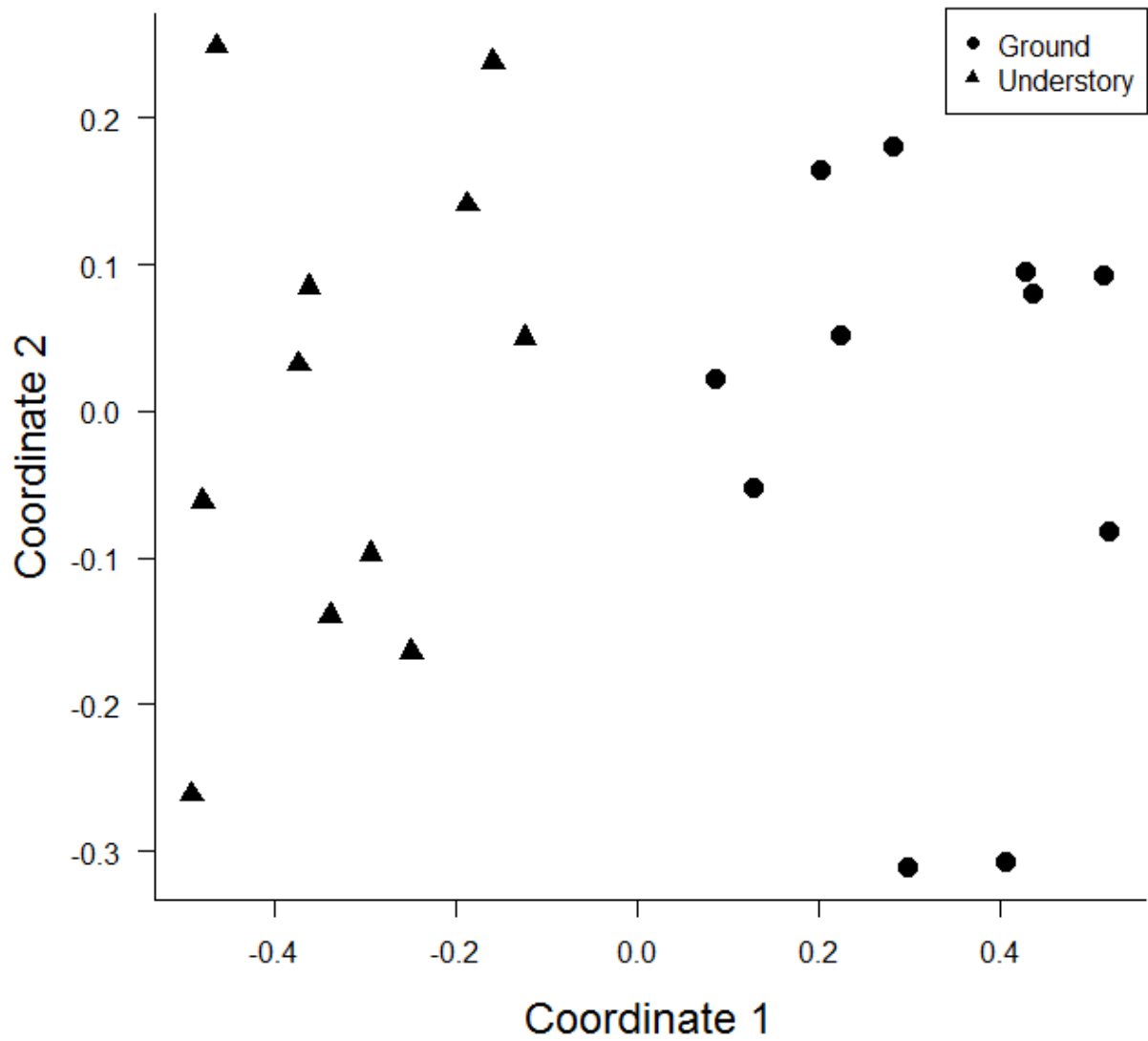


Fig 3. Composition of ground (filled circle) and understory (filled circle) ant community of the Parque Estadual do Cristalino. Principal Coordinate Analysis axis represented 71.6% of total ordination.

ANEXO 3 - *Strumigenys fairchildi* Brown, 1961 (Formicidae, Myrmicinae): first record of this rarely collected ant from Brazil

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Prado et al. | First record of *Strumigenys fairchildi* from Brazil

Strumigenys fairchildi Brown, 1961 (Formicidae, Myrmicinae): first record of this rarely collected ant from Brazil

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Abstract: *Strumigenys fairchildi* Brown, 1961 is recorded for the first time in Brazil. This ant species was previously known only from a few specimens collected in Costa Rica, Panama and Ecuador. The worker *S. fairchildi* was collected at the Parque Estadual do Cristalino, a continuous area of Amazon tropical rain forest protected for biodiversity conservation in the municipality of Novo Mundo, Mato Grosso state. In addition, we present a distribution map and high-resolution images of the worker.

Key words: Amazon basin; Brazilian ant fauna; distribution; Formicidae; Neotropical ants

<INTRODUCTION>

The ant genus *Strumigenys* Smith, 1860 (Formicidae: Myrmicinae), found worldwide, is represented by 838 extant species, and four fossil species (AntWeb 2016); 25% of the species occur in the Neotropics (Lattke and Aguirre 2015). Most species of this genus occur in tropical rainforest, some in grassland and scrub, usually nesting in soil and rotting wood, though a few species live in arboreal cavities in tropical rain forest (Brown and Wilson 1959; Bolton 2000). Besides the most common form of reproductive females (gyne) some species of *Strumigenys* have the ergatoid forms (Silva and Brandão 2014). Species of the genus are predators of Collembola, mites, insect larvae, and other small arthropods (Wilson 1953; Hölldobler and Wilson 1990; Bolton 1999; Kaufmann et al. 2003), although, some few species occasionally feed on sugary substances (Brown and Wilson 1959). To capture their prey, some species use a kinetic mode of attack (Gronenberg 1996; Bolton 1999).

Despite being a relatively speciose genus and commonly sampled in biodiversity surveys (Morini et al. 2007; Silva et al. 2007; Suguituru et al. 2013; Ulysséa and Brandão 2013; Camacho and Vasconcelos 2015; Souza et al. 2015) most species records are based upon a few specimens (Bolton 2000), as is the case with *S. fairchildi* Brown, 1961. *Strumigenys fairchildi* belongs to the *tococae*-group (comprised by *S. anthocera* Lattke & Goitía, *S. extirpa* Bolton, *S. fairchildi* Brown, *S. tococae* Wheeler & Bequaert, and *S. usbensis* Lattke & Goitía) and was originally described based on one worker collected in Panama (Brown 1961). Since then, the species has been recorded in Costa Rica (Bolton 2000) and most recently in Ecuador (Salázar et al. 2015). In the present paper we report the first record of *S. fairchildi* in Brazil, considerably extending the distribution limits for the species.

<MATERIALS AND METHODS>

One *S. fairchildi* worker (Figure 1) was collected in November 2013, during the beginning of the rainy season in a protected area for biodiversity conservation of the Parque Estadual do Cristalino (Figure 2), a continuous pristine forest in the Novo Mundo municipality, of Mato Grosso state (09°28' S, 055°50' W). In this region, known as the Arc of Deforestation (Michalski et al. 2008), the ant fauna is still not very well known with just a few studies contributing to expand our knowledge of the distribution of some rarely collected species (Vicente et al. 2011, 2012, 2015). According to the Köppen classification, the climate in this region is characterized as tropical humid (Am) with a mean annual temperature of 25°C and an annual precipitation ranging from 2,800mm to 3,100mm (Alvares et al. 2013). There are two well-defined seasons, a rainy season between November and April and a dry season between May and October (Vicente et al. 2014). The local altitude ranges from 100 to 400 m above sea level and the vegetation is classified as Open Ombrophilous Forest and ecological tension zones between the Ombrophilous Forest and Savanna (Cerrado), Savanna and Seasonal Forest, Seasonal Forest and Ombrophilous Forest (Instituto Brasileiro de Geografia e Estatística 2004). The specimen was collected in understory vegetation (plants 1–3 m high) using a beating tray in one trail of the Research Program in Biodiversity (Programa de Pesquisas em Biodiversidade, PPBio grid 09°28'29.2" S, 055°50'00.2" W, altitude 304 m as estimated in Google Earth™).

The specimen is deposited in the ant collection of the Laboratório de Sistemática, Evolução e Biologia de Hymenoptera of the Museu de Zoologia da Universidade de São Paulo (MZSP), SP, Brazil (the ant collection of the MZSP does not have numerical identifiers, therefore, the author's number is REV_Strumi001). It was photographed with a Leica Application Suite V3 system at the MZSP and edited in Adobe Photoshop® version 7.0. The distribution map was generated using the Quantum GIS 2.6.0 software, with shapes available at Natural Earth, the coordinates were imported from Google Earth™ after consulting the records for *S. fairchildi* in the literature (Bolton 2000;

Salazar et al. 2015).

<IDENTIFICATION>

To identify *Strumigenys* ant species we used the taxonomic key provided by Bolton (2000). According to Bolton (2000), *S. fairchildi* (Figure 1) is morphologically characterized by the combination of (1) first gastral tergite finely and very densely longitudinally costulate-striolate; (2) surface of this sclerite with minute inconspicuous appressed pubescence only, without spatulate hairs such as are present on the cephalic dorsum but with a few scattered flagellate hairs that are extremely fine, easily broken or lost; (3) apicoscrobial hair absent; (4) maximum diameter of eye ca 0.14; (5) propodeum in profile with a pair of long spines at top of declivity; (6) base of declivity with a pair of much shorter acute teeth that are narrowly triangular; (7) ventral surface of petiole with a narrow continuous strip of spongiform tissue.

The intraspecific morphological variability observed in specimens collected in Brazil and Costa Rica are variations in patterns of pilosity of the cephalic dorsum, waist and gaster. In addition, the body color is variable; the specimen collected in Brazil is slightly darker than the specimen collected in the Costa Rica.

Morphologically, *S. fairchildi* is very similar to *S. anthocera* and *S. usbensis*, species with a possible overlapping distribution. This species differs from the first by the apicoscrobial hair (absent in *S. fairchildi* and present in *S. anthocera*) and by the length of the spine at the propodeal lobe (shorter than the dorsal propodeal spine in *S. fairchildi* and as long as the dorsal propodeal spine in *S. anthocera*). In addition, *S. usbensis* differs from *S. fairchildi* by the modifications of the spongiform tissue on the ventral surface of the petiole (present in *S. fairchildi* and absent in *S. usbensis*) and shape of hairs in the first gastral surface (flagellate hairs in *S. fairchildi* and spatulate hairs in *S.*

usbensis).

<DISCUSSION>

Strumigenys fairchildi (Figure 1) was previously recorded in Cerro Campana, Panama (Brown 1961), Heredia province, Costa Rica (Bolton 2000) and recently in Sucumbios province, Ecuador (Salazar et al. 2015) (Figure 2). The new record of this work expands its occurrence to Parque Estadual do Cristalino (09°28' S, 055°50' W), a continuous Amazonian forest in the Novo Mundo municipality, of Mato Grosso state, Brazil (Figure 2). This is more than 2,000 km from the nearest record of this species.

Despite growing knowledge about the diversity of Neotropical ants (Silva et al. 2013; Baccaro et al. 2015; Bezděčková et al. 2015; Brandão et al. 2015; Delabie et al. 2015; Salazar et al. 2015), the distribution of many species, especially those primarily associated with the Amazonian biome, is still virtually unknown (Fernandes et al. 2015a, 2015b; Vicente et al. 2011, 2012, 2015). Several ground-dwelling ant inventories have been carried out in what can be now considered the range of *S. fairchildi* (Vasconcelos et al. 2006, 2010; Mertl et al. 2010; Miranda et al. 2012; Ryder-Wilkie et al. 2009; Souza et al. 2016) but they all failed to detect this species. Because *S. fairchildi* lives in vegetation and considering the scarcity of inventories of arboreal ants (but see: Vasconcelos and Vilhena 2006; Ryder-Wilkie et al. 2010), the distribution of this species is probably much broader than reported in the literature.

Furthermore, four ant collections (Museu de Zoologia da Universidade de São Paulo [MZSP], Instituto Nacional de Pesquisas da Amazônia [INPA], Laboratório de Ecologia de Comunidades da Universidade Federal do Mato Grosso [LEC/UFMT] and Collection Padre Jesus Santiago Moure of the Universidade Federal do Paraná [DZUP]) that house a large number of specimens of both the

Amazon and Brazilian ant fauna were consulted and no other specimen of *S. fairchildi* was found. Thus, the new record reported here suggests that more sampling efforts applying different techniques of sampling should be used to reveal the distribution of this species and contribute to increase the knowledge of the Brazilian ant fauna that remains underestimated, especially for species that inhabit vegetation strata. As seen in the present paper, the use of beating trays is a viable technique for sampling ants that live and forage in shrubby environments. Available information on niche preference is still scarce for most groups of this family of insects, hampering advances on studies such as behavioral ecology. Applying beating trays as a standardized technique in sampling inventories of ants, in this particular arboreal stratum, will certainly provide useful information to boost studies in disciplines in which knowledge regarding habitat preference is needed, especially in those genera believed to be exclusively epigaeic, such as *Strumigenys*.

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[FIGURE CAPTIONS]

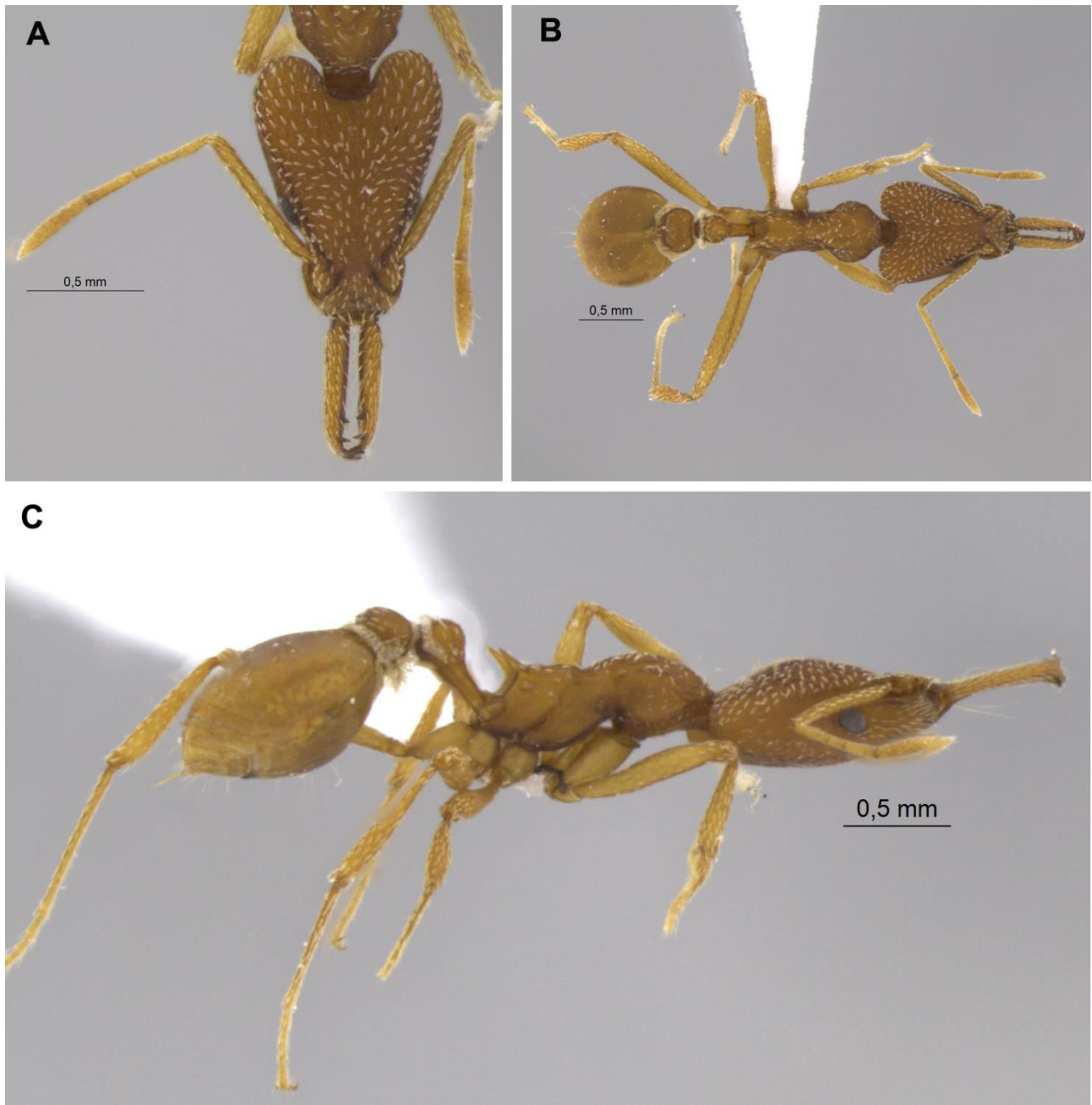


Figure 1. Worker of *Strumigenys fairchildi* from Mato Grosso, Brazil in full-face view (A), dorsal view (B) and lateral view (C).

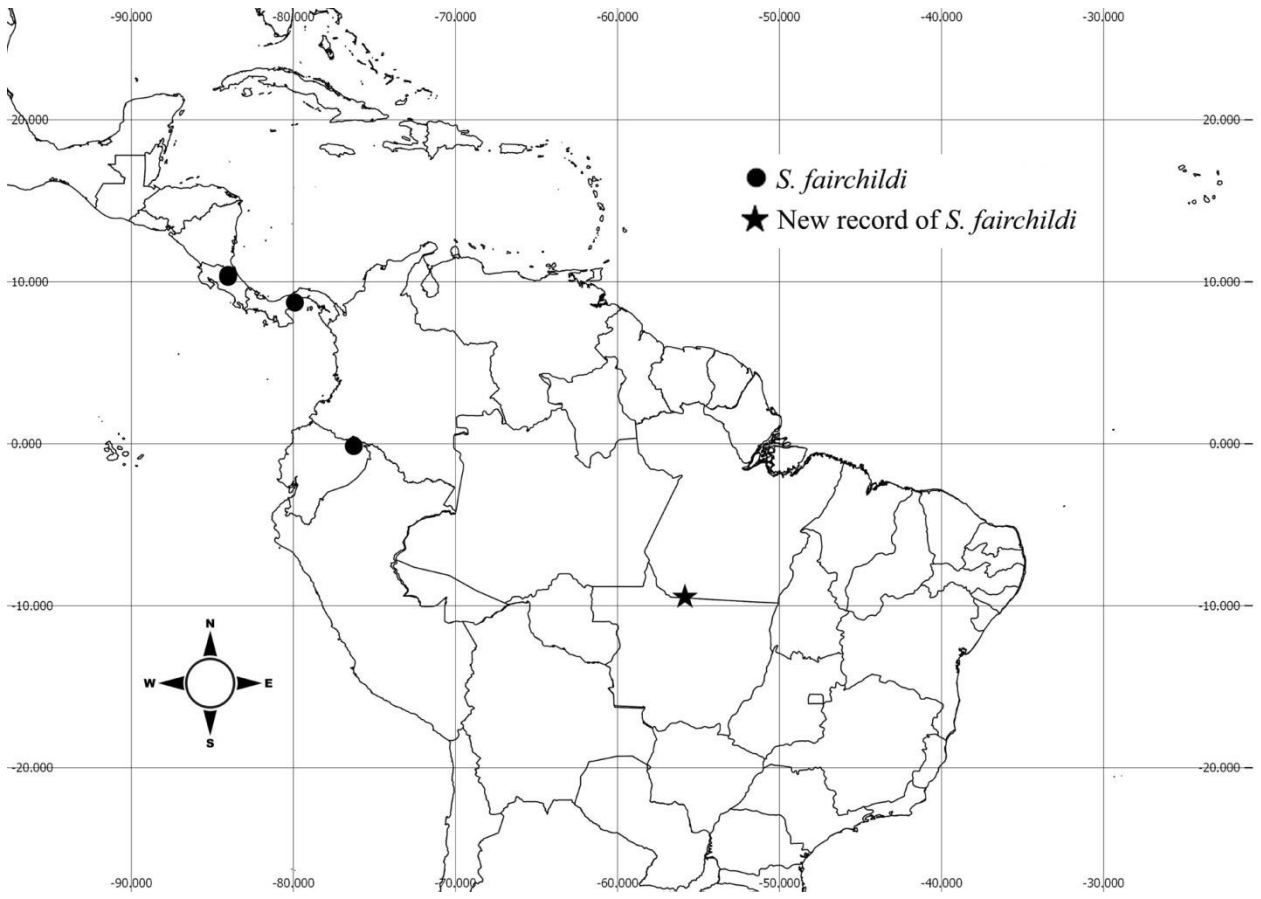


Figure 2. Distribution of *Strumigenys fairchildi*.

CONCLUSÃO GERAL

As epífitas mais abundantes nos Jardins-de-formigas foram *Peperomia macrostachya* (Piperaceae, presente em 88% dos JFs observados), *Codonanthe uleana* (Gesneriaceae - 41%), *Philodendron* sp. (Araceae - 18%) e *Markea longiflora* (Solanaceae - 6%). As formigas apresentaram recrutamento diferente entre as epífitas associadas e a planta não mutualista de subbosque. Os resultados demonstraram que as formigas parabióticas conseguem reconhecer os compostos químicos voláteis diferentes entre todas as espécies associadas. Além de reconhecer os voláteis químicos das epífitas, conseguem diferenciar entre epífitas habitantes obrigatórias de JFs e epífitas não obrigatórias. O fato de *Camponotus femoratus* reagir aos voláteis das epífitas obrigatórias, principalmente *P. macrostachya*, e não a da abundante planta de subbosque pertencente a mesma família botânica, reforça o refinamento do reconhecimento químico de *Camponotus*.

A presença, número e volume de Jardins-de-formigas foi afetado pelo tamanho da clareira mas não pela abertura de dossel, que influenciou somente o forrageamento das formigas parabióticas. As espécies *Ca. femoratus* e *Cr. levior* utilizam igualmente os estratos verticais sendo a frequência de ambas espécies no solo diminuída pela abertura do dossel. Porém, somente a frequência de *Cr. levior* no chão diminuiu com o aumento da complexidade da vegetação, demonstrando que o nicho de *Cr. levior* é mais ligado a vegetação do que o de *Ca. femoratus*.

A abundância, riqueza e composição da comunidade de formigas de solo é afetada pela presença das formigas parabióticas, sendo que, sua presença torna as comunidades presentes subamostras de comunidades onde as formigas parabióticas estão ausentes (Aninhamento). Por fim, nem a complexidade, bem como abertura do dossel influenciam a frequência de forrageamento dessas formigas no sub-bosque. Nem sua presença altera a comunidade de formigas arborícolas. Esses resultados demonstram que essas formigas

parabióticas podem retardar a recuperação da biodiversidade de formigas de solo em clareiras amazônicas, porém, não afetam a diversidade de formigas na vegetação. Isto demonstra que é importante compreender como as formigas parabióticas, dominantes nesses ambientes, impedem a colonização de espécies cosmopolitas comuns em ambientes degradados. Além disso, esses resultados ainda demonstram que, se deve empenhar esforços para compreender o padrão de dominância em formigas arborícolas na Região Neotropical e como estas interferem nos processos ecosistêmicos locais.