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NOTAS

Vertical stratification of ant assemblage in Brazilian Savanna phytophysiognomies

Estratificación vertical de ensamble de hormigas en fitofisionomías de sabana brasileña

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SUMMARY

Spatial distribution of arthropods in forests has crucial implications for biodiversity conservation and forest management. In this environment, ants represent a good model for studies on vertical stratification of fauna. They are abundantly found in soil and well distributed in all vegetation strata. Factors determining the diversity and distribution of ant communities have deserved attention for years due to the essential role of these insects in many ecological processes such as nutrient cycling, energy turnover, herbivory, seed dispersal and seed predation. The aim of this study was to compare the richness and structure of ant assemblages among vertical strata (soil, shrubs and trees) in two phytophysiognomies of the Brazilian Savanna. The capture of ground-dwelling ants and arboreal ants was carried out with traps containing attractive baits. Sixty-six ant species were identified, and in both phytophysiognomies. Soil (litter) showed higher richness of ant species when compared to the others (Jackkinife 1). There was a distinction between soil and canopy (shrubs/trees) strata, shown in the composition and capture frequency of ant species (ANOSIM, $P = 0.001$), therefore, evidencing the vertical stratification of the ant assemblage.

Key words: myrmecofauna, arboreal ants, epigeic ants, similarity, richness.

RESUMEN

La distribución espacial de artrópodos en los bosques tiene implicaciones cruciales para la conservación de la biodiversidad y la gestión forestal. En este ambiente, las hormigas representan un buen modelo para los estudios de estratificación vertical de la fauna. Se encuentran abundantemente en el suelo y están bien distribuidos en todos los estratos de la vegetación. Los factores que determinan la diversidad y distribución de las comunidades de hormigas han merecido atención durante años debido al papel esencial de estos insectos en muchos procesos ecológicos, como el ciclo de nutrientes, el recambio de energía, la herbivoría, la dispersión de semillas y la depredación de semillas. El objetivo del presente trabajo fue comparar la riqueza y la estructura del ensamble de hormigas entre los estratos verticales (suelo, arbustos y árboles) en dos fitofisionomías de la sabana brasileña. La captura de hormigas que viven en el suelo y hormigas arbóreas se llevó a cabo con trampas que contenían cebos atractivos. Se identificaron sesenta y seis especies de hormigas, y en ambas fitofisionomías, el estrato del suelo (epigeo) mostró una mayor riqueza de especies de hormigas en comparación con los otros (Jackkinife 1). Se encontró una distinción entre los estratos de suelo y dosel (arbustos/árboles), que se muestran en la composición y frecuencia de captura de las especies de hormigas (ANOSIM, $P = 0,001$), lo que evidencia la estratificación vertical de los ensambles de hormigas.

Palabras clave: mirmecofauna, hormigas arbóreas, hormigas epigeas, similitud, riqueza.

INTRODUCTION

Brazilian Cerrado as a whole, is not exactly a synonym of savanna since forests (for instance, gallery forest, dry forest and Cerradão), as well as pure field, are merged with pure grasslands. Cerradão has flora formed by a mixture of elements from savanna and forest formations. Its trees reach up to 20 meters, with the degree of canopy cover varying from 30 to 60 %. Cerrado *stricto sensu* is a savanna woodland physiognomy, with the degree of canopy cover varying from 10 to 60 % (frequently below 30 %) at a site with trees reaching up to seven meters high (Eiten 1994, Felfili 2002).

The different phytophysiognomies of Brasilian Cerrado contain extremely rich and diverse flora and fauna (Strassburg *et al.* 2017, Tibcherani *et al.* 2018). It has a significant number of endemic species and is considered a hotspot for the conservation of biodiversity in Brazil (Myers *et al.* 2000). Recent estimates indicate that in Cerrado biome there are approximately 13,140 species of plants, although its invertebrate fauna is not very well known (Fernandes 2016). Invertebrates are of fundamental importance for terrestrial ecosystem processes, according to Kuchenbecker and Fagundes (2018), which accounts for the growing number of studies on invertebrate communities and the use of this data for the formulation and testing of different hypothesis.

Tropical savannas are structurally complex and show significant vertical stratification in the quality and quantity of resources. Canopy contains complex tree architecture, flowering and fruiting phenology, while at the ground-level woody debris, decaying leaves, fruits, flowers, dung and carrion accumulate (Grimbacher and Stork 2007). Information of presence and abundance of species and the structure of their assemblages can be easily biased when relying on data not taking into account vertical stratification (Wilkie *et al.* 2010, Procházka *et al.* 2018). Kaspari *et al.* (2015) emphasize the considerable thermal heterogeneity existing in different latitudes (with different niche spaces) of the forest ecosystem. Yamazaki *et al.* (2016) and Conceição *et al.* (2019) report that the mosaic of arboreal ants is continuously restructured by specificities of the host plant (*e.g.* plants age), seasonal periods and also local microclimatic conditions.

Classical hypotheses suggest that communities become more vertically stratified with increasing species richness, owing to reduced competition or finer niche subdivision (Oliveira and Scheffers 2018). Even though stratification of the ant assemblage is not so evident in Cerrado, some species may have become specialized in foraging or nesting in the soil and elsewhere in the vegetation, promoting high species diversities, as well as allowing their coexistence (Campos *et al.* 2008).

The number of studies of arthropod vertical stratification in tropical forests is still rather limited. The present study identified and compared the diversity of ant species among vertical strata (on the soil, shrubs and trees) in two phytophysiognomies in Brazilian Savanna (seasonal forest, known in Brazil as Cerradão and Cerrado *stricto sensu*).

METHODS

Experimental area. The sampling of ant was carried out in an area known as "*Morro do Microondas"*, located in Ipameri, state of Goiás, Brazil (Lat. 17º39' S; Long. 48º10' W). This region has continuous native vegetation of Cerrado with an area of around six thousand hectares. The ants were collected in two phytophysiognomies: Cerradão and Cerrado *stricto sensu*. The climate of the region is classified as Aw (Köppen), with annual precipitation of approximately 1,600 mm, being characterized by two distinct seasons: a dry season during the winter, and a rainy season during the summer, with average temperature of 23 °C (Alvares *et al.* 2013). A list of common arboreal and shrub species can be found in Medeiros (2011). A floristic and phytosociological study of the arboreal community in our experimental area can be consulted in Vaz *et al.* (2015). In this region, the Fabaceae, Vochysiaceae and Dilleaceae families are predominant. The most frequent species are *Davilla elliptica* A.St.-Hil., *Tachigali rugosa* (Mart. ex Benth.) Zarucchi *et* Pipoly. and *Qualea parviflora* Mart.

Sampling and identification of ants. In each phytophysiognomies, two 100-meter parallel transects were drawn, about 10 meters apart. In one of these areas, 30 ant sampling sites were randomly placed in the soil. In the second transect, 30 plants were also randomly selected for ant sampling.

In each site selected, baited pitfall traps were placed on the soil. The trap consisted of a plastic cup (200 mL) fixed in the soil by a metal clamp, containing sardine, biscuits and honey, to attract the ants, following the methodology adapted from Rodrigues *et al.* (2008). Depending on the plants, the capture of ants was done directly on the trunk or branches with the same traps used for the soil, attached on plants, at 1.0 m from the ground surface (16 trees and 14 shrubs in Cerradão and in Cerrado *stricto sensu*, 11 trees and 19 shrubs). All traps (soil and plants) were operated for one hour during the morning, as recommended by Rodrigues *et al.* (2008). Prolonged exposure times of attractive baits to capture ants should be avoided, since some species recruit nest mate more quickly, thus dominating the space occupied by the bait. Ant sampling was repeated monthly for one year. The ants were identified by the last author (JHCD) and vouchers of the ants were deposited in the collection of the Myrmecology Laboratory in Cocoa Research Center, Ilhéus, BA, Brazil under the number #5705.

Statistical analyses. The ant species richness per sampled stratum was estimated by Jackknife 1 estimator, using the software EstimateS version 9.1 (Colwell 2013). The data obtained were summarized using the Nonmetric Multidimensional Scaling (NMDS), aiming at ordering the samples based on the similarity concerning the composition of species in each stratum. To test if there was significant difference between the groups formed in the ordination [soil and canopy (shrubs/trees)] ANOSIM (Analysis of Similarities) was applied. The statistical analyses of the data were carried out with the aid of software R version 3.4 (R Core Team 2017).

RESULTS

In both physiognomies studied in Brazilian Cerrado, 66 ant species were identified, divided into 23 genera and seven subfamilies (appendix 1). Even taking into account the use of attractive baits in the sampling in the canopy, the highest richness was found in the soil (figure 1). It was observed that the canopy (shrubs and trees) in both physiognomies presented similar estimated species richness according to the confidence intervals overlap with the richness average. However, such overlap has not been noted between the soil and the canopy, thus, one can infer that soil presented higher richness of ant species than that presented by shrubs and trees (figure 1).

The formation of two well-defined groups was clear through the NMDS analysis, one aggregating soil samples and the other, canopy samples (shrubs and trees) (figure 2). ANOSIM analysis, based on the composition and the frequency of occurrence of ant species, indicated that both groups formed (canopy and soil strata) presented significant difference in both areas: Cerradão (R = 0.883; *P* = 0.001), and also in Cerrado *stricto sensu* (R = 0.752; *P* = 0.01). In Cerradão and Cerrado *stricto sensu*, richness and community composition of arboreal ants were not significantly influenced by plant size (trees or shrubs) (figures 1 and 2).

DISCUSSION

The highest richness of ant species in the soil may be related to its higher environmental complexity, which provides more food resources and nesting sites in the soil rather than in trees or shrubs (Campos *et al.* 2008). Dantas *et al.* (2011) also observed higher ant richness in the epigeic stratum, when compared to the soil (soil without litter) and tree in a transition zone between Cerrado and the biome Caatinga. Another explanation for this result may be the fact that about 50 % of the myrmecofauna is associated with leaf-litter (on the surface of the soil) in tropical forests (Delabie and Fowler 1995). For this reason, studies of the ant assemblages of this stratum generally present high richness of species.

The specificity of some ant species concerning the areas of foraging and nesting may also explain the high occurrence of ants at the soil surface, as well as the formation of two distinct groups in this study, soil and canopy, in both phytophysiognomies. *Acromyrmex*, *Atta*, *Cyphomyrmex* and *Trachymyrmex* are genera exemplifying such, whose ants are known for fungi cultivation and nesting in the soil, which were predominant in this stratum. The same has occurred with other species such as *Odontomachus bauri*, *Odontomachus chelifer* and *Gnamptogenys sulcata*. This amplitude in the use of different habitats may be understood when considering that a wide number of ant species have a great capacity to adapt to all types of environments and feeding sources (Wilkie *et al.* 2010).

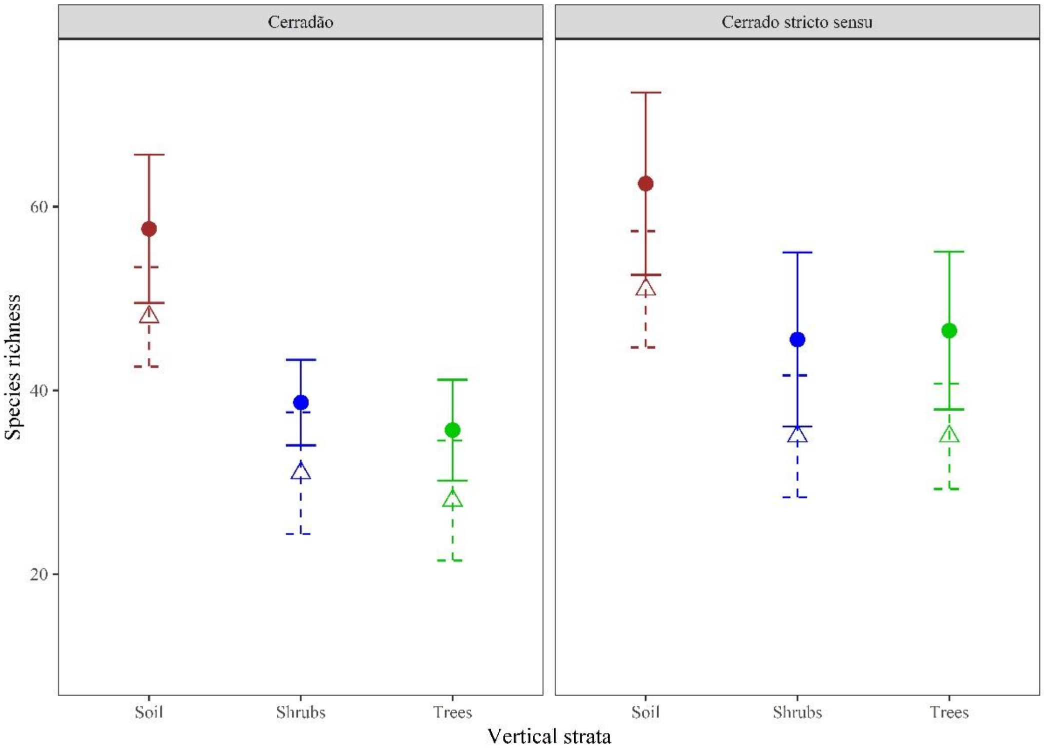

Figure 1. Richness of species observed (triangles) and estimated (dots) in the three strata sampled in Cerradão and Cerrado *stricto sensu*. The bars represent their respective confidence intervals (Jackkinife 1).

Riqueza de especies observadas (triángulos) y estimadas (puntos) en los tres estratos muestreados en Cerradão y Cerrado *stricto sensu*. Las barras representan sus respectivos intervalos de confianza (Jackkinife 1).

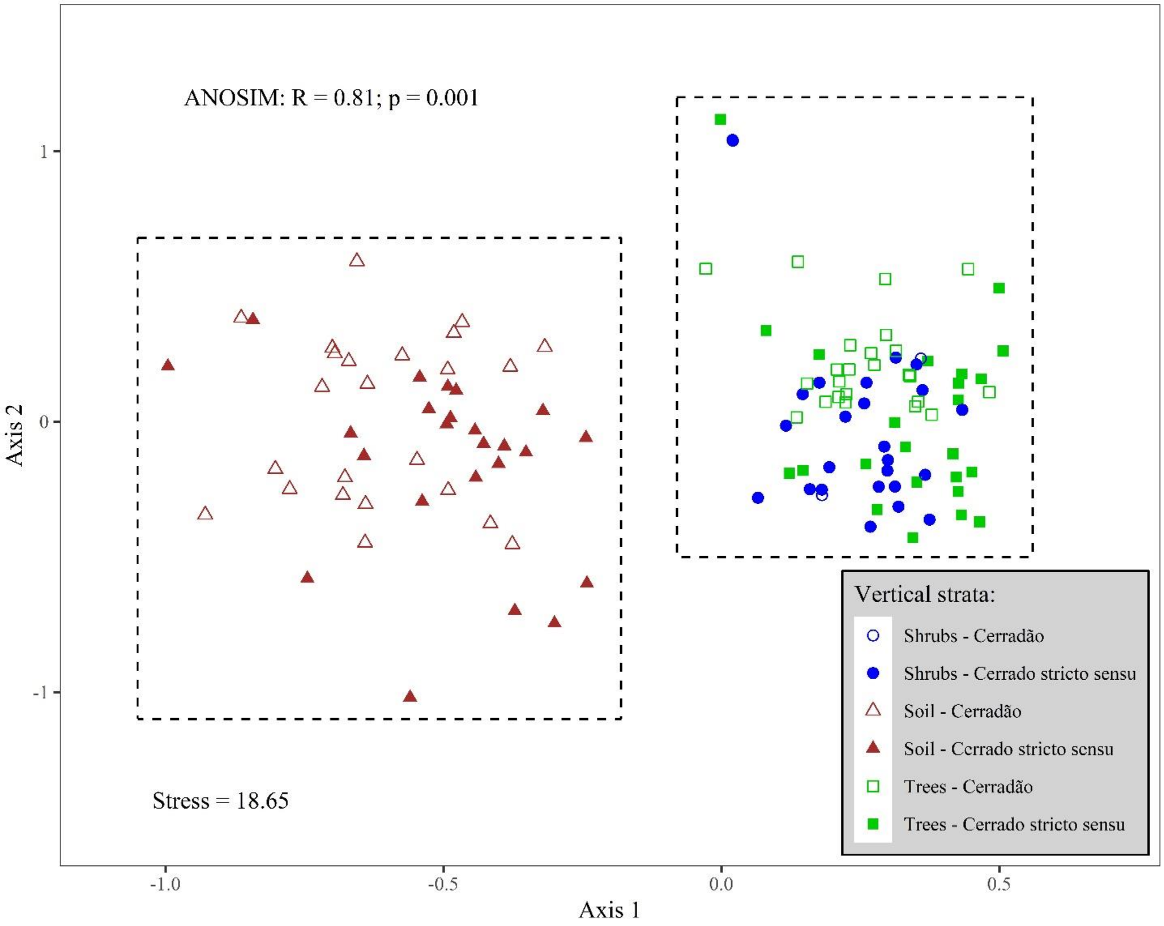

Figure 2. Ordination of the resulting analysis scores nonmetric multidimensional scaling (NMDS) of the data of composition and frequency of ants in the strata in Cerradão and Cerrado *stricto sensu*. The dotted lines represent the confidence intervals for the soil strata *versus* shrubs/trees which were compared by the similarity test-ANOSIM.

Ordenación de las puntuaciones de análisis resultantes escalamiento multidimensional no métrico (NMDS) de los datos de composición y frecuencia de las hormigas en los estratos de Cerradão y Cerrado *stricto sensu*. Las líneas de puntos representan los intervalos de confianza para los estratos del suelo versus arbustos/árboles que se compararon mediante la prueba de similitud ANOSIM.

The genera *Ectatomma* and *Pseudomyrmex* are examples of this diversification regarding the use of habitats, and are the most representative in this study, in all strata. Unlike *Pogonomyrmex,* which is a typical granivore that builds its nest in the soil (Baccaro *et al.* 2015). Wilkie *et al.* (2010) mention the genus *Pheidole* as dominant in soil and *Camponotus* as dominant in canopy. In our study, the genus *Pheidole* occurred predominantly in ground and *Camponotus* did not present prominence by strata. Some species such as *Camponotus bladus*, *Camponotus novograndensis*, *Camponotus rengerri* and *Camponotus senex* were captured in all strata, also indicating the ability of this group of ants to explore all types of environmental. In general (see appendix 1), only 25.75 % of the identified species were found in all extracts of Cerradão and Cerrado *stricto sensu*.

According to Izzo and Vasconcelos (2005), the size and ages of the tree can modify the richness and composition of arboreal ants. For these authors, a reduction of the number of species in older plants can be due to demarcation of territories by colonies, established for longer periods of time and, in opposite situation, young plants would have species still in competition, trying to establish their territory. However, in our study, richness and composition of ant communities were not significantly different for tree and shrub. The size of trees not influencing the richness of ant species was mentioned by Rodrigues *et al.* (2008).

This study demonstrates clearly the vertical stratification of ant assemblages, especially in Cerradão, suggesting local specificity for foraging of some groups of ants. It also corroborates the hypothesis that richness and diversity of ants in the soil extract are higher than in the tree extract. By improving our understanding of the diversity of ants, we can advance our knowledge of the causes that maintain biodiversity in exceptionally rich savanna habitats.

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Appendix 1. Ant species collected in three strata (soil, shrubs and trees) in Cerradão and Cerrado *stricto sensu*. Goiás, Brazil.

Especies de hormigas recolectadas en tres estratos (suelo, arbustos y árboles) en Cerradão y Cerrado *stricto sensu*. Goiás, Brasil.

Taxa	Cerradão			Cerrado *stricto sensu*		
	Soil	Shrubs	Trees	Soil	Shrubs	Tree
Myrmicinae						
Acromyrmex balzani (Emery, 1890)	x	-	-	x	-	-
Acromyrmex niger (Smith, 1858)	x	x	-	x	-	-
Atta sexdens (Linnaeus, 1758)	-	-	-	x	-	-
Cephalotes depressus (Klug, 1824)	-	x	x	-	x	x
Cephalotes pinelii (Guérin-Méneville, 1844)	x	x	x	x	x	x
Cephalotes pusillus (Klug, 1824)	-	x	x	-	x	x
Crematogaster stollii (Forel, 1885)	x	x	x	x	x	x
Crematogaster victima (Smith, 1858)	x	-	-	x	-	-
Crematogaster sp.A	-	-	-	x	-	-
Cyphomyrmex transversus (Emery, 1894)	x	-	-	x	-	-
Pogonomyrmex naegelii (Forel, 1878)	-	-	-	x	-	-
Pheidole diligens (Smith, 1858)	x	x	x	x	x	x
Pheidole midas (Wilson, 2003)	-	-	-	x	-	-
Pheidole obscurithorax (Naves, 1985)	x	x	x	x	x	x
Pheidole radoszkowskii (Mayr, 1884)	x	-	x	x	-	x
Pheidole valens (Wilson, 2003)	x	-	-	x	-	-
Pheidole wallacei (Mann, 1916)	x	-	x	-	-	x
Pheidole tristis Group sp.A	x	-	x	-	-	x
Pheidole fallax Group sp.B	x	x	x	x	-	x
Pheidole fallax Group sp.C	x	-	-	x	x	-
Pheidole flavens Group sp.D	x	-	-	-	-	-
Pheidole near *terribilis*	-	-	-	x	-	-
Solenopsis substituta (Santschi, 1925)	x	-	x	x	x	-
Solenopsis sp.A	-	x	x	-	x	-
Trachymyrmex fuscus (Emery, 1834)	x	-	-	x	-	-
Xenomyrmex sp.A	x	x	x	x	x	x
Formicinae						
Brachymyrmex heeri (Forel, 1874)	x	x	x	x	x	x
Brachymyrmex patagonicus (Mayr, 1868)	x	x	x	x	x	x
Brachymyrmex sp.A	-	x	x	x	-	-
Brachymyrmex sp.B	x	x	-	-	-	x
Brachymyrmex sp.C	x	x	x	x	x	x
Camponotus blandus (Smith, 1858)	x	x	x	x	x	x
Camponotus cingulatus (Mayr, 1862)	x	x	-	x	-	-
Camponotus leydigi (Forel, 1886)	-	x	x	-	x	-
Camponotus melanoticus (Emery, 1894)	x	x	x	x	-	-
Camponotus novogranadensis (Mayr, 1870)	x	x	x	x	x	x
Camponotus renggeri (Emery, 1894)	x	x	x	x	x	x
Camponotus senex (Smith, 1858)	x	x	x	x	x	x
Camponotus sericeiventris (Guérin-Méneville, 1838)	-	x	-	-	-	-

Continue

Continue Appendix 1

Camponotus vittatus (Forel, 1904)	x	-	x	x	x	-
Camponotus (*Hypercolobopsis*) sp.A	-	x	x	-	-	x
Camponotus (*Myrmaphaenus* sp.B)	-	-	-	-	x	-
Camponotus (*Myrmaphaenus* sp.C)	-	-	-	x	x	-
Nylanderia sp.A	x	-	-	x	-	-
Paratrechina longicornis (Latreille, 1802)	x	-	-	-	-	-
Ectatomminae						
Ectatomma brunneum (Smith, 1858)	x	x	x	x	x	x
Ectatomma opaciventre (Roger, 1861)	x	x	x	x	-	x
Ectatomma permagnum (Forel, 1908)	x	-	-	x	-	-
Ectatomma planidens (Borgmeier, 1939)	x	-	-	-	-	-
Ectatomma suzanae (Almeida, 1986)	x	-	-	-	-	-
Ectatomma tuberculatum (Olivier, 1792)	x	x	x	x	x	x
Gnamptogenys sulcata (Smith, 1858)	-	-	-	x	-	-
Pseudomyrmecinae						
Pseudomyrmex curacaensis (Forel, 1912)	x	x	x	x	x	x
Pseudomyrmex gracilis (Fabricius, 1804)	x	x	x	x	x	x
Pseudomyrmex termitarius (Smith, 1855)	x	x	x	x	x	x
Pseudomyrmex tenuis (Fabricius, 1804)	x	-	-	-	-	-
Pseudomyrmex urbanus (Smith, 1877)	x	x	-	x	x	x
Pseudomyrmex pallidus Group sp.A	x	-	-	-	-	-
Dolichoderinae						
Dorymyrmex goeldii (Forel, 1904)	x	x	x	x	x	x
Dorymyrmex pyramicus (Roger, 1863)	x	x	x	x	x	-
Forelius maranhaoeusis (Cuezzo, 2000)	x	-	-	x	-	-
Linepithema cerradense (Wild, 2007)	x	x	x	x	x	x
Ponerinae						
Odontomachus bauri (Emery, 1892)	x	-	-	x	-	-
Odontomachus chelifer (Latreille, 1802)	x	-	-	x	-	-
Neoponera villosa (Fabricius, 1804)	x	x	x	-	x	x
Dorylinae						
Neivamyrmex carettei (Forel, 1913)	x	-	-	-	-	-