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## **RESEARCH ARTICLE - ANTS**

# Arboreal Ant Assemblages Respond Differently to Food Source and Vegetation Physiognomies: a Study in the Brazilian Atlantic Rain Forest

JJ RESENDE<sup>1</sup>, PEC PEIXOTO<sup>1</sup>, EN SILVA<sup>1</sup> JHC DELABIE<sup>2,3</sup> & GMM SANTOS<sup>1</sup>

- 1 Universidade Estadual de Feira de Santana, Feira de Santana, Bahia, Brazil
- 2 Universidade Estadual de Santa Cruz / CEPLAC/CEPEC, Ilhéus-Itabuna, Bahia, Brazil
- 3 CEPLAC/Centro de Pesquisas do Cacau, Itabuna, Bahia Brazil

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#### **Corresponding author**

Janete Jane Resende Departamento de Ciências Biológicas Universidade Estadual de Feira de Santana Av. Transnordestina s/n Novo Horizonte Feira de Santana, Bahia, Brazil 44036-900 E-Mail: antforjane@gmail.com

#### Introduction

Abstract

This study aimed to analyze assemblages of arboreal ants in different vegetation physiognomies within the Tropical Moist Forest (Atlantic Rain Forest) domain. The study was carried out at the Michelin Ecological Reserve, State of Bahia, Northeast of Brazil. We used sardine (protein resource) and honey (carbohydrate resource) baits to collect ants foraging in three vegetation types: (1) preserved native forest, (2) forest in regeneration (capoeira) with many invasive plants and (3) a mixed agroystem of rubber and cocoa tree plantation. We recorded 69 ant species attracted to the baits, 21 of them exclusive to honey bait and 25 exclusive to the sardine baits. The vegetation physiognomies preserved forest and rubber/cacao agrosystem showed higher species richness in relation to the forest in regeneration (capoeira), suggesting that rubber tree plantations can be a good matrix for the maintenance of some ant species typical of the forest matrix. The type of resource used is important for the structuring of the arboreal ant assemblages. The ants that were attracted to protein resources showed a guild composition that is more differentiated between vegetation types that of ants attracted to glucose resources.

The richness and composition of ant assemblages have been related to the different structural aspects or the level of habitat preservation (Schoener 1971, Greenslade & Greenslade 1977, Levings 1983 & Andersen 1995). Ants are frequently chosen for studies that focus on the understanding of the effects of repetitive events of man-made habitat or ecosystem simplification on biodiversity (Matos *et al.* 1994, Majer 1996, Perfecto *et al.* 1997). Several studies have shown significant correlations between ant assemblages and habitat structural complexity, particularly in the tropics (Andersen & Majer, 2004, Delabie *et al.* 2006). For example, the richness of ants in the forest leaf litter has a strong correlation with plant diversity (Pereira *et al.* 2005) and in coffee agrosystems, the diversity of twig dwelling ants increases in habitats with more diverse shade tree cover (Armbrecht *et al.* 2004).

Human activities have often caused the simplification of natural environments, leading to local extinction of popula-

tions and species and, consequently, could negatively impact important ecological processes such as nutrient cycling, seed dispersal and pollination (Thomas 2000, De Marco & Coelho 2004). Simplified environments often harbor a lower richness and diversity of ants, with an ant fauna consisting of generalist species (Sobrinho & Schoereder 2006), unlike forested habitats that harbor ant assemblages with higher levels of diversity, consistent with the characteristics and the complexity of the vegetation (Majer 1996, Pereira *et al.* 2007).

Different sampling methods have been used in surveys of ants and there is no direct means of comparison between different collection procedures (Romero & Jaffe 1989). There are several methods used for sampling ants such as oil sardine, carbohydrates, meat and cassava flour baits, Winkler extractor, pitfall or manual collection, each one of them suited to select different classes of ants (soil dwelling, carnivorous, detritivorous, omnivorous) (Bestelmeyer *et al.* 2000; Freitas *et al.* 2004). Each of the collection procedures sampled a different set of ant species (Romero & Jaffe 1989) and the foraging activities may reflect or indicate the nutrients that are most limiting to in the respective nesting habitats, some ants prefer honey baits (carbohydrate) and other ants set prefer fish baits (nitrogen- protein) (Hashimoto *et al.* 2010). Ants provide an ideal system to test how macronutrient availability affects the costs and benefits of competitive dominance (Grover et al., 2007). Considerable evidence suggests that resource competition strongly influences population and community dynamics in ants (Hölldobler & Wilson 1990)

This study aimed to analyze arboreal ant assemblages in different vegetation physiognomies within the Atlantic Rain Forest domain. We tested two hypotheses. First, if the agroforestry system constitutes a good matrix for the maintenance of ant species, richness of ants would be expected to be similar to or even greater than that found in forest like physiognomies. Second, since trophic groups of ants that are glycoside and protein consumers are generalist and specialist, respectively, the ant assemblages of generalist ants are expected to be more similar while the second ones would be more dissimilar between habitats.

#### **Material and Methods**

#### Study area

The study was conducted at the Michelin Ecological Reserve (headquarters: 13° 50'S, 39° 10' W) Ituberá, state of Bahia, Brazil. The climate is of the type As according to the Köppen classification, tropical, rainy, hot, characterized by rainfall concentrated in summer and autumn, and average temperatures are never below 20° C. The landscape of the region is characterized by the dominance of cacao agroforestry, mixed rubber/cacao plantations, pastures and forest fragments with natural vegetation comprising primary forest (a small percentage) and different stages of forest regeneration (with a large proportion of secondary forest).

We collected ants in six different periods between October 2007 and September 2008. Ant assemblies attracted to carbohydrate and protein baits were collected in three vegetation physiognomies: (I) Conserved Atlantic Forest Fragment (PF), a typical Low Land Humid Tropical Forest measuring about 550 ha comprising blocks of native forest canopy of 15-25 m in height, with isolated trees reaching 30-40 m; (II) Forest Regeneration Fragment (Capoeira - SF), an early to intermediate stage of secondary succession tract of land, measuring about 10 ha of contiguous forest in regeneration, characterized by the presence of lianas, bromeliads, orchids, rocky ground, shrub vegetation and invasive plants and (III) agrosystem of mixed rubber tree/cacao plantation (AG), with over 20 years of age and 12 ha of area.

#### Sampling methods

The sampling consisted of 18 transects distributed among three vegetation types. In each vegetation type six After installation, the baits remained on the plants for about 30 min. They were then collected and the ants present were fixed in alcohol 70%. In total, 120 baits were placed in each vegetation type. The sorting, assembly and morphospeciation of ant specimens occurred in the Laboratory of Entomology, at Feira de Santana State University (UEFS). For the identification of ant species we used the classification of Bolton (2003), except for the genus *Nylanderia* (based on Lapolla *et al.* 2010), and the genera *Strumigenys* e *Basiceros* (based on Baroni-Urbani & De Andrade 2007).

Vouchers were deposited in the Entomological Collection Prof. Johann Becker, Museum of Zoology - UEFS (MZFS) at Feira de Santana and the collection of the Myrmecology Laboratory of CEPEC/CEPLAC (CPDC) at Ilhéus, state of Bahia.

#### Data analyses

cm away from one another.

The analyses of data took into consideration only presence or absence of the species as usual in ant community ecology studies (Longino 2000). The observed species richness was calculated using the rarefaction curve (Mao Tau) (Colwell *et al.* 2004). The total richness was estimated using the 1st order Jackknife estimator based on 50 randomizations (Heltshe & Forrester, 1983), performed with the program EstimateS, version 7.5.2 (Colwell, 2006).

The dissimilarity of ant assemblages between vegetation types was assessed by performing a Principal Coordinate Analysis (PCoA) using the program R (R Development Core Team 2010). This analysis was preceded of the calculation of the Jaccard similarity index for the pair-wise combination of data collected in all transects, considering as a transect the 20 samples collected by vegetation type and sampling date. Therefore, the analyses were based on 18 transects (three vegetation types times six dates).

#### Results

We recorded 69 species of ants attracted to the baits. Out of this total, 21 species were exclusive to honey baits and 25 to sardine baits (Table 1). With respect to vegetation types, 17 species were exclusive to Conserved Forest, 16 to the agrosystem and seven to the "Capoeira". Regarding the frequency of species, *Solenopsis* sp.2 was the most frequent on both sardine (31.6%) and honey (20%) baits in rubber/cacao tree agroforestry. The second most frequent species in this physiognomy was *Camponotus* sp.5 which was recorded on 11.6% of sardine baits.

In the Conserved Forest physiognomy, the most fre-

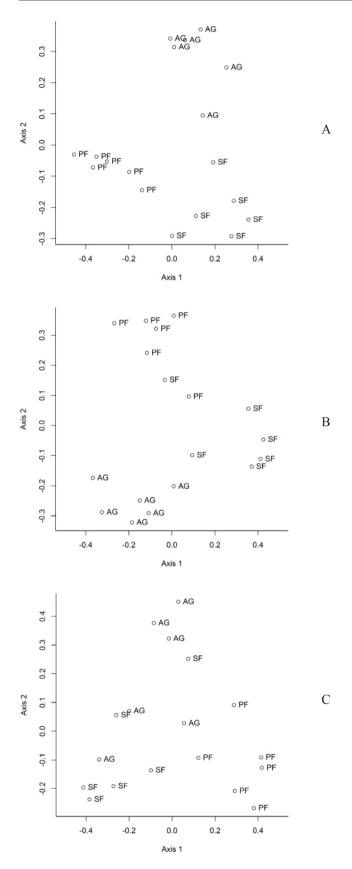


Fig. 1. Ordination by PCoA of species of ants collected in different phytophysiognomies, Reserva Ecológica da Michelin, Ituberá e Igrapiúna municipalities Bahia, Brazil. PF – Conserved forest; SF - Capoeira; AG– Agrosystem of mixed rubber tree/cacao plantation. (A) ants collected in honey and sardine baits; (B) ants collected in sardine baits and (C) ants collected in honey baits.

quent ants on sardine baits were *Crematogaster* sp.1 (9.1% of the baits) and *Ectatomma tuberculatum* (8.3%). The same happened in the "Capoeira" area with *Crematogaster* sp.1 present on 10% of the baits and *E. tuberculatum* in 9.1%. For honey baits, *Strumigenys* sp.9 (5.8%) was the most frequent species in conserved forest while *Crematogaster* sp.1 (6.6%) was the most abundant in "Capoeira".

Among the most speciose genera, *Pheidole* (14 species), *Pachycondyla* (8), *Camponotus* (7) and *Solenopsis* (5) were the most rich. The proportion of species belonging to these genera present in both types of baits remained very close, except for *Camponotus* which had two and seven species recorded on honey and sardine baits, respectively.

The two axis extracted from the PCoA analyses with data from the two bait types grouped explained 34.3% of the total variation in ant composition among samples (18.6% of variation explained by axis 1 and 15.6% of variation explained by axis 2). According to this analysis, the species collected in sardine differed from the species collected in honey baits. Considering only ants collected in sardine baits, there was also a very clear separation between vegetation types, indicating that the composition of ant species differs between vegetation types (17.6% of variation explained by axis 1 and 17.1% of variation explained by axis 2). On the other hand, the analysis including only ants collected in honey baits demonstrated a low distinction between vegetation types (18.4% of variation explained by axis 1 and 11.7% of variation explained by axis 2), indicating that the assemblage of species that visited the baits rich in carbohydrates were similar among the three habitats (Fig. 1).

The greatest observed and expected richness of ants were recorded in the preserved forest fragment and in the agrosystem of mixed rubber/cacao plantation (Fig. 2, Table 1).

The observed richness curves (Mao Tau) showed no stabilization in any of phytophysiognomies (Fig. 2). Never-

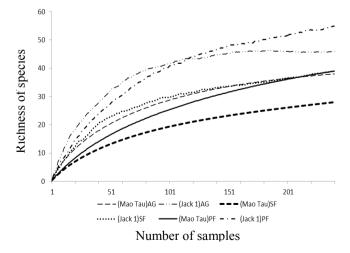


Fig. 2. Expected (Jack1) and observed (Mao Tau) richness curves for species of ants collected in a total of 240 samples. Reserva Ecológica da Michelin, Ituberá e Igrapiúna municipalities, Bahia, Brazil. **PF** – Conserved forest; **SF**- Capoeira; **AG** – Agrosystem of mixed rubber tree/cacao plantation.

theless, the expected richness according to the species accumulation curve (jack1) showed a sharp increase in the number of species as a function of sample size, followed by an asymptote in the agrosystem habitat. The shape of the curve suggests that in the agrosystem the sampled fauna is more homogeneous than in "Capoeira" and conserved forest. Therefore the majority of the species is sampled with a lower number of samples. Extrapolation of the curves also suggests that the number of total species in the agrosystem is lower than the two other habitats.

#### Discussion

According to our results, the vegetation physiognomies of conserved forest and agrosystem presented species richness highest than "Capoeira", showing that agricultural habitats including the association between cacao and rubber trees forms a suitable matrix for the maintenance of ant species typical of forest environment. However, the juxtaposition of forest areas close to the agrosystem is an important point allowing to maintain the ant diversity (Delabie *et al.* 2007).

#### Similarity between bait types and vegetation physiognomies

The similarity between the ant assemblages sampled in sardine baits among the studied vegetation physiognomies, is probably a result of the shared occurrence of species of the genera *Azteca*, *Camponotus*, *Crematogaster*, *Pheidole* and *Solenopsis* which are considered dominant or subdominant if considering the structure of arboreal ant fauna (Wilson 1976; Majer *et al.* 1994; Brandão *et al.* 2009). Some species of these genera can significantly influence the structure of the arthropod community, exercising strong predation, especially on larvae of Lepidoptera and Coleoptera (Majer & Delabie 1993, Floren *et al.* 2002; Philpott & Armbrecht 2006).

This same ecological context may apply to explain the great similarity between the ant assemblages attracted to honey and sardine baits within the agrosystem, because almost the same species were present in both types of baits. Other species that were recorded in this physiognomy such as E. tuberculatum, Pachycondyla venusta and Odontomachus haematodus belong to genera typically considered as those of generalist predator species. Except for P. venusta, these ants may supplement their diet with nectar exudates from plants and honoydew producer insects (Hölldobler & Wilson 1990, Delabie 2001). An additional outcome supporting this explanation is the occurrence of the species Tapinoma sp.1 in the agrosystem of mixed rubber/cacao plantation. This species has as main feature the generalist behavior, being undemanding in terms of habitat quality and shifting easily from one food source to another.

The numerous species of ants visiting sardine baits in each vegetation physiognomy, such as those of the genera *Hypoponera*, *Megalomyrmex*, *Nylanderia*, *Wasmannia* in Conserved Forest, *Linepithema* in Capoeira and *Dorymyrmex* in the agroystem, has an important ecological implication. In case where protein-based resources are scarce in these habitats, they will be almost exclusively used by specialist species that tend to defend this resource with aggressive behaviors, by exhibiting a rapid recruitment of workers and thus preventing access of other species. The species of the genus *Solenopsis*, for instance, have aggressive behavior and are common in disturbed habitats. On the other hand, carbohydrate-based resources are more common and visited by generalist species, which do not have any preference to the types of bait used, such as those of the genera *Camponotus*, *Pheidole* and *Solenopsis* (Hölldobler & Wilson 1990).

Although, in general, species richness correlates positively with habitat complexity, this correlation seems to depend on the habitat, because the agrosystem had a higher observed richness compared to "Capoeira", which is considered structurally more complex than the former. Lassau & Hochuli (2004) found similar results with a greater richness in less complex habitats, believing that the movement of ants may be more efficient in terms of energy, in less complex habitats. Gomes et al (2010) demonstrates that ant fauna is more influenced by vegetation integrity than by fragment size, distance to edge or forest cover surrounding fragments. Lopes et al (2012) shows that the species that compose the ant assemblies in different phytophysiognomies are a reflex of the environment, especially of the plant species, supporting the hypothesis that differences in the vegetational composition result in different position of the ant assembly.

The higher number of species in the agrosystem in comparison to "Capoeira" suggests the occurrence of occasional species with low occurrence, sometimes called "tourists". These species are treated by the estimators of richness as singletons or doubletons and can boost the expected richness estimation. In spite of this, a greater number of species considered dominant (genera *Camponotus*, *Crematogaster*, *Solenopsis* and *Pheidole*) was recorded for the agrosystem in comparison to "Capoeira".

It is important to remark that although the species accumulation curve based on Jack1 reached an asymptote in the agrosystem, the estimated richness in the Capoeira is in an ascending trend and could surpass the estimated richness of the agrosystem if the sampling effort were increased. This leaves the inference on the quality of the rubber/cacao agrosystem as a good matrix open, from the perspective of which habitat is richer.

However, looking at the list of species in Table 1, the following results are found. Out of the 69 ant species collected in all habitats, 13 (18.84%) are common to both conserved forest and agrosystem. Six species are protein consumers and seven carbohydrate consumers. Furthermore, the relative frequencies of most of these species are low and very similar in forest and agrosystem habitats. Thus, from the point of view of life history, we can infer that the agrosystem is a good qual-

ity matrix for at least some rare species that also occur in forest vegetation.

The choice of food resource (honey or sardine baits) by the ant assemblages, clearly differentiate the three vegetation physiognomies.

Both proteins and carbohydrates are of paramount importance for maintenance of ant populations. Hashimoto et al. (2010) demonstrated that different populations of ants forage more actively on these resources when they are scarce. On one hand, the proteic resources are fundamental for brood development and tissue synthesis (Hölldobler & Wilson 1990). On the other hand, carbohydrates are key resources for the maintenance of the ant activity (Davidson, 1998). Byk and Del-Claro (2011) demonstrated the benefits of the carbohydrate resources to ant populations. The glucidic foods influence ant species composition, abundance, number of individuals per colony, body weight, survivorship, growth, reproduction and interactions at the community level. Bihn et al. (2008) examined bait preferences of litter ants along a successional gradient of forests in the Atlantic Forest of Brazil and observed that ants preferred protein-based baits in secondary forests, and carbohydrate-based baits in old-growth forests. In addition, the ant preference for carbohydrate or protein is subject to change individually according a previous ingestion of one of this food source, extrafloral nectar or insect. This is the theory of ecological stoichiometry, which relates nutrient balance to ecological processes (Sterner & Elser 2002). Such nutritional complexity can mediate patterns of ecological interactions (Anderson et al. 2004). Therefore, if an ant individual is consuming extrafloral nectar, it is more propable it attacks a herbivore on the host plant aiming to balance the ingestion of protein after too much ingestion of carbohydrate (Grover et al., 2007).

Our data support our working hypothesis that the type of resource used by ant species is important in structuring the community. The distribution of ant species that are specialist and consumers of protein-based resources (sardine baits) differed more between the vegetation types than the distribution of ant species that are generalist and consumers of carbohydrate-based resources. The similarity of species collected in each vegetation physiognomy was higher among ant assemblages that use carbohydrate-based resources (Fig. 1c) than among ant assemblages that use protein-based resources, in an exclusive manner (Fig. 1b) or together with carbohydrate sources (Fig. 1c).

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**Table 1.** Number of records and relative frequency (%) of ants collected in honey and sardine baits in three vegetation physiognomies in the Reserva Ecológica da Michelin. Ituberá e Igrapiúna municipalities, Bahia, Brazil **PF** – Preserved forest; **SF** - Secondary Forest (Capoeira); **AG** – Agrosystem of mixed rubber tree/cacao plantation. Food Preferences (C= Primarily Carbohydrate consumer, P= Primarily Protein consumer, C/P = Both; *sensu* Brandão et al. 2009).

Sampled Species	Food	Honey bait			Sardine bait		
	Preferences	PF	SF	AG	PF	SF	AG
AMBLYOPONINAE							
Prionopelta sp.1	Р	-	1 (0.8)	-	-	-	-
ECTATOMMINAE							
Ectatomma sp.1	Р	-	2 (1.6)	-	-	-	-
Ectatomma brunneum F. Smith, 1858	Р	-	3 (2.5)	-	-	-	-
Ectatomma tuberculatum F. Smith, 1858	Р	-	4 (3.3)	8 (6.6)	10 (8.3)	11 (9.1)	7 (5.8)
Gnamptogenys sp.3	Р	-	-	-	3 (2.5)	-	-
DOLICHODERINAE							
Azteca sp.1	C/P	2 (1.6)	-	3 (2.5)	7 (5.8)	1 (0.8)	6 (5)
Azteca sp.28	C/P	4 (3.3)	-	-	3 (2.5)	2 (1.6)	3 (2.5)
Azteca sp.3	C/P	-	-	-	-	-	2 (1.6)
Azteca sp.4	C/P	-	-	3 (2.5)	-	-	-
Dorymyrmex sp.1	С	-	-	-	-	-	4 (3.3)
<i>Linepithema</i> sp.1	С	-	3 (2.5)	4 (3.3)	-	2 (1.6)	-
Linepithema sp.3	С	-	-	-	-	1 (0.8)	-
Tapinoma sp.1		1 (0.8)	2 (1.6)	4 (3.3)	-	-	1 (0.8)
FORMICINAE							
Camponotus sp.2	С	-	-	-	-	5 (4.1)	-
Camponotus sp.3	С	1 (0.8)	-	-	-	4 (3.3)	-
Camponotus sp.4	С	-	-	-	3 (2.5)	-	-
Camponotus sp.5	С	-	-	3 (2.5)	-	-	14 (11.6)
Camponotus sp.6	С	-	-	-	-	-	5 (4.1)
Camponotus sp.7	С	-	-	-	-	-	3 (2.5)
Camponotus sp.8	С	-	-	-	-	-	1 (0.8)
Brachymyrmex sp.1	C/P	3 (2.5)	-	3 (2.5)	-	-	-
Brachymyrmex sp.4	C/P	-	3 (2.5)	-	1 (0.8)	1 (0.8)	-
<i>Nylanderia</i> sp.2	C/P	-	-	-	1 (0.8)	-	-
<i>Nylanderia</i> sp.3	C/P	-	-	1 (0.8)	-	-	-
<i>Nylanderia</i> sp.4	C/P	-	-	1 (0.8)	3 (2.5)	-	-
MYRMICINAE							
Cephalotes atratus (Linneus, 1758)	С	-	1 (0.8)	-	-	-	-
Cephalotes sp.1	С	-	-	-	-	3 (2.5)	-
Cephalotes sp.2	С	1 (0.8)	-	-	-	-	-
Crematogaster sp.1	С	-	8(6.6)	3 (2.5)	11 (9.1)	12 (10)	8 (6.6)
Crematogaster sp.2	С	1 (0.8)	-	2 (1.6)	1 (0.8)	1 (0.8)	-
Crematogaster sp.3	С	-	-	3 (2.5)	-	1 (0.8)	12 (10)
Crematogaster sp.5	С	-	-	-	2 (1.6)	1 (0.8)	-
Crematogaster sp.6	С	-	-	10 (8.3)	-	-	-
Pheidole sp.1	C/P	2 (1.6)	1 (0.8)	-	-	-	-
Pheidole sp.2	C/P	-	-	_	1 (0.8)	-	-

Table 1 (continued)							
Pheidole sp.5	C/P	-	-	-	-	-	3 (2.5)
Pheidole sp.10	C/P	-	1 (0.8)	1 (0.8)	-	3 (2.5)	1 (0.8)
Pheidole sp.12	C/P	-	-	-	3 (2.5)	-	-
Pheidole sp.14	C/P	-	6 (5)	-	4 (3.3)	-	-
Pheidole sp.15	C/P	1 (0.8)	1 (0.8)	-	-	-	-
Pheidole sp.16	C/P	-	-	-	5 (4.1)	-	3 (2.5)
Pheidole sp.17	C/P	1 (0.8)	-	2 (1.6)	-	-	-
Pheidole sp.18	C/P	1 (0.8)	-	1 (0.8)	-	-	-
Pheidole sp.20	C/P	1 (0.8)	-	-	-	-	3 (2.5)
Pheidole sp.23	C/P	1 (0.8)	-	-	-	-	1 (0.8)
Pheidole sp.24	C/P	2 (1.6)	1 (0.8)	-	1 (0.8)	-	-
Pheidole sp.26	C/P	3 (2.5)	-	2 (1.6)	-	-	-
Carebara pilosa Fernández, 2004	Р	2 (1.6)	-	-	-	-	-
Megalomyrmex sp.1	Р	-	-	-	2 (1.6)	-	-
Solenopsis sp.1	Р	-	-	-	-	-	1 (0.8)
Solenopsis sp.2	Р	-	5 (4.1)	24 (20)	2 (1.6)	4 (3.3)	38 (31.6)
Solenopsis sp.3	Р	-	-	2 (1.6)	-	5 (4.1)	-
Solenopsis sp.4	Р	2 (1.6)	2 (1.6)	4 (3.3)	7 (5.8)	1 (0.8)	-
Solenopsis sp.5	Р	-	-	2 (1.6)	-	-	5 (4.1)
Strumigenys sp.8	Р	-	-	-	1 (0.8)	-	-
Strumigenys sp.9	Р	7 (5.8)					
Wasmannia auropunctata (Roger, 1863)	C/P	-	-	-	1 (0.8)	-	-
Basiceros (Octostruma) sp.2	Р	-	-	1 (0.8)	-	-	-
PONERINAE							
<i>Hypoponera</i> sp.1	Р	-	-	-	1 (0.8)	-	-
<i>Hypoponera</i> sp.2	Р	-	-	-	2 (1.6)	-	
Pachycondyla apicalis (Latreille, 1802)	Р	2 (1.6)	-	-	-	-	-
Pachycondyla constricta (Mayr, 1884)	Р	-	-	-	-	-	1 (1.6)
Pachycondyla complexo villosa (Fabricius, 1804)	Р	-	-	5 (4.1)	-	-	-
Pachycondyla harpax (Fabricius, 1804)	Р	-	-	-	1 (0.8)	-	-
Pachycondyla venusta (Forel, 1912)	Р	-	2 (1.6)	2 (1.6)	-	3 (2.5)	1 (0.8)
Pachycondyla villosa (Fabricius, 1804)	Р	-	-	-	-	-	2 (1.6)
Pachycondyla sp.1	Р	1 (0.8)	-	-	-	-	-