Sociobiology
An international journal on social insects

RESEARCH ARTICLE - WASPS

# Is the social wasp fauna in the tree canopy different from the understory? Study of a particular area in the Brazilian Amazon Rainforest

A Somavilla, RNM Moraes Junior, JA Rafael

Instituto Nacional de Pesquisas da Amazônia, Coordenação de Biodiversidade, Manaus, Amazonas, Brazil

**Article History**

**Edited by**
Gilberto M. M. Santos, UEFS, Brazil
Received 09 July 2018
Initial acceptance 06 September 2018
Final acceptance 14 October 2018
Publication date 25 April 2019

**Keywords**
Amazonas, *Malaise* trap, Polistinae wasps.

**Corresponding author**
Alexandre Somvilla
Instituto Nacional de Pesquisas da Amazônia
Coordenação de Biodiversidade
Av. André Araújo nº 2936, CEP: 69067-375
Manaus, Amazonas, Brasil.
E-Mail: alexandresomavilla@gmail.com

**Abstract**

Most studies about the insect community in rainforests only focus on the forest understory, and even though the rainforest canopy is one of the most fascinating and diverse environments, it remains poorly explored. Therefore, we analyzed the difference between the social wasp composition in these two strata at the ZF-2 Station in the Brazilian Amazon Rainforest, Amazonas, Manaus, using flight interception *Malaise* traps, in the rainforest understory and canopy. We collected ninety-two species belonging to 18 genera; *Polybia* was the richest genera (22 species), followed by *Mischocyttarus* (14) and *Agelaia* (13). Forty-four species were exclusively collected in the understory, twenty exclusively collected in the canopy, and twenty-eight in both strata. The understory was distinctly more diverse and more abundant than the canopy, while some rare or poorly collected species were only found in the canopy. We found a relationship between the species composition at the ZF-2 Station and the Ducke Reserve, Manaus. Therefore, we suggest using traps in canopy in the Amazon biome as an effective method for collecting a higher diversity of social wasps.

## Introduction

The Polistinae social wasps are comprised of 26 genera and 958 species widely distributed in the Neotropical region (Pickett & Carpenter, 2010). These wasps are important components of Neotropical ecosystems due to their ubiquity and diversity, as well as their complex interactions with other organisms (Silveira et al., 2012). The Amazon Rainforest is the largest biome in Brazil, covering an area of 4,196,943 $Km^2$ within the Brazilian territory, and is one of the most biodiverse places in the world, presenting the highest diversity of social wasps (Silveira, 2002; Somavilla et al., 2014; Barbosa et al., 2016). Silveira (2002) highlighted that 200 species have been recorded in the Brazilian Amazon, which represents about two-thirds of all Brazilian Polistinae fauna. However, Somavilla and Oliveira (2013) emphasized the need for more studies focusing on wasp distribution in the region. Furthermore, the richness of social wasps in the Brazilian Amazon Forest is still underestimated (Somavilla & Oliveira, 2017).

Some studies about social wasps have been carried out in the Brazilian Amazon, as follows: Maracá Ecological Station, Roraima State with 36 species (Raw, 1998) and four other locations in Roraima with 85 species (Barroso et al., 2017); Caxiuanã Reserve, Pará State with 79 species (Silveira, 2002) and 65 species (Silva & Silveira, 2009); Serra do Divisor National Park, Acre State with 20 species and three fragments close to Rio Branco with 36 species (Morato et al., 2008; Gomes et al., 2018); Lakes of Amapá, Amapá State with 31 species (Silveira et al., 2008); Gurupi Biological Reserve, Maranhão State with 38 species (Somavilla et al., 2014); and three localities in North of Rondônia State with 76 species (Gomes, 2013). In the state of Amazonas, six surveys have been carried out: Mamirauá and Alvarães Reserves, with 46 and 42 species, respectively (Silveira et al., 2008), Jaú National Park with 49 species (Somavilla et al., 2015), Madeira-Purus rivers with 38 species (Oliveira et al., 2015), Embrapa-Manaus with 52 species (Somavilla et al., 2016), and Ducke Reserve with 103 species (Somavilla & Oliveira, 2017).

Despite the contributions of these works, Somavilla et al. (2014) stated "there are many sample gaps in the Amazon region and distribution and occurrence studies are necessary for improving this prior knowledge". This may be due to limited exploration in the rainforest understory (Somavilla et al., 2014). Inventories from the Amazon show that some Polistinae species have been represented by one or a few specimens with all collections carried out in understories only, while tree canopies have been poorly explored by researchers. The previously mentioned studies from understories, and only two studies used the suspended trap method in tree canopies (Roraima State and Ducke Reserve), but only as a complementary method and reaching low height, reaching at most 20 meters (Barroso et al., 2017; Somavilla & Oliveira, 2017).

The rainforest canopy is one of the most fascinating environments to develop studies about arthropod communities (Erwin, 2013; Nakamura et al., 2017). Although the tropics hold the highest species diversity (Erwin, 2013), many interactions in tropical forests are made in the canopies, due to the high number of species that inhabit canopies and the large amount of biomass that is generated in this stratum (Nakamura et al., 2017). Compared to other rainforest strata, the rainforest canopy presents higher illumination, temperatures, wind speeds, and relative humidity (Nakamura et al., 2017).

In this way, we asked: Is the social wasp fauna different between the tree canopy and the understory? Which environment/strata has the highest richness of social wasps? Herein, we present a list of species and discuss the use of interception traps, *Malaise* traps mounted in the canopy and understory, for collecting social wasps (Polistinae) at the ZF-2 Station in the Brazilian Amazon Rainforest.

## Methods

### *Study area*

The study site is located inside one of the National Institute for Amazonian Research (INPA) reserves - Tropical Silviculture Experimental Station, at Km 934 of BR 174 on the road ZF-2 (2°35'21"S – 60º06'55"W), herein called ZF-2 station. This area is about 50 km North of Manaus in Amazonas, Brazil and is managed by the project: The Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA-INPA), which is the largest study about climate change in the Amazon region.

According to the Köppen (1948) climate classification, the climate at the station is Am type, with low annual thermic range and average monthly rainfall over 60 mm. The average annual temperature is 26.7 ºC, ranging between 23.3 ºC and 31.4 ºC, while average annual rainfall is 2286 mm and relative humidity is around 80%. The rainy season is from December to May, and the dry season from June to November (Barbosa et al., 2015). The topography in this area is undulating with elevation ranging from 50 to 140 meters above sea level.

### *Wasp collection*

Currently, Brazil holds one of the largest research programs that uses towers as a standard structure to reach the tree canopy. Such sampling tower is metallic and 40 m high, located inside a typical Amazonian landscape, which is comprised of an ombrophilous dense forest with a canopy reaching 40 m, or even 50 m due to emergent trees. In this type of forest, it is difficult to distinguish between median and lower strata, but the mean canopy height in the Amazon is 28.6 m (Higuchi et al., 2009). A description of the flora at the research station can be found in Martins et al. (2006). In the forest understory and canopy, we used a modified *Malaise* trap Gressit and Gressit model (1972) that was 6-meter long with two collector vials (Figure 1). In the canopy, the trap was mounted 32 meters from the ground in a metallic tower (6m wide x 6m length) to collect wasps and in understory on the forest floor. Both traps were active for fifteen consecutive days each month, for a period of eight months between July 2016 to March 2017.

The Polistinae specimens were sorted and identified at the Hymenoptera Laboratory of the National Institute of Amazonian Research (INPA). The vouchers were deposited into the INPA's Invertebrate Collection. Specimens were identified using the keys proposed by Richards (1978),


**Fig 1**. Sampling method at the ZF-2 Station (LBA/INPA): (A) *Malaise* trap in the understory and (B) *Malaise* trap in the canopy at 32 m high.

Carpenter and Marques (2001), and Carpenter (2004) and were compared to previously identified species from the INPA Invertebrate Collection.

*Data analysis*

We used Nonmetric Multidimensional Scaling (NMDS) (Minchin, 1987) to ordinate the inventories carried out in the Brazilian Amazon (see Introduction topic) according to their species composition and to verify whether species displayed a preference for a particular area and used dissimilarity coefficient for the species composition from the ZF-2 Station compared to other inventories in the Brazilian Amazon. This analysis was conducted in R version 3.3.3. (R Core Team, 2017) using vegan package 2.4-0 (Oksanen et al., 2016). For this analysis, we excluded the specimens identified as "morphospecies" or "varieties" and we used only the species collected in *Malaise* or suspended traps, and we exclude the species of active search, light trap or attractive trap.

## Results

The survey from ZF-2 station revealed a rich fauna of social wasps. We found 1.548 specimens in ninety-two species belonging to 18 genera (Table 1). *Polybia* Lepeletier was the richest genera (22 species), followed by *Mischocyttarus* de Saussure (14) and *Agelaia* Lepeletier (13). Together, these three genera comprised about 55% of the species listed. The only Brazilian Polistinae genera we did not collect from in the area were *Asteloeca* Raw, *Chartergus* Lepeletier, and *Protonectarina* Ducke, the first two not specious genera with three described species and *Protonectarina* with occurrence only for the Atlantic Forest.

In terms of specimens' numbers collected, 870 were from understory and 678 from canopy. Forty-four species were exclusively collected in the trap mounted in understory, twenty species were exclusively collected in the trap mounted in the tree canopy, and twenty-eight species were found in both traps (Table 1). All species of *Agelaia*, *Apoica,* and *Pseudopolybia* were collected in the understory. Species of *Metapolybia*, *Nectarinella*, and *Synoeca* were collected in the canopy. *Polybia* species were collected in both strata.

Several species are new records for Brazil or Amazonas state: *Agelaia pallidiventris* (new record for Brazil), *Nectarinella manauara* and *Protopolybia rugulosa* (second time both species were collected for Amazonian Rainforest), *A. flavipennis*, *Polybia affinis*, *Po. minarum*, *Pr. nitida*, *Pr. rotundata* and *Pr. sedula* (new records for Amazonas State). The following specimens could not be determined to the species level: one species of *Agelaia*, one species of *Polybia* (*Myrapetra*), and two species of *Mischocyttarus* (*Haplometrobius*).

According to the dissimilarity analysis between the social wasps' composition from different areas in the Amazon, we found a relationship between the species composition of ZF-2 Station andDucke Reserve (Figures 02, 03). The same relationship was found for Alvarães and Mamirauá Reserve (AM) and Caxuanã Reserve (PA). However, the composition of wasp fauna from the Rio Branco region (AC), Serra do Divisor National Park (AC), Maracá Ecological Station (RR), and Lagos Region (AP) were dissimilar from the ZF-2 Station.

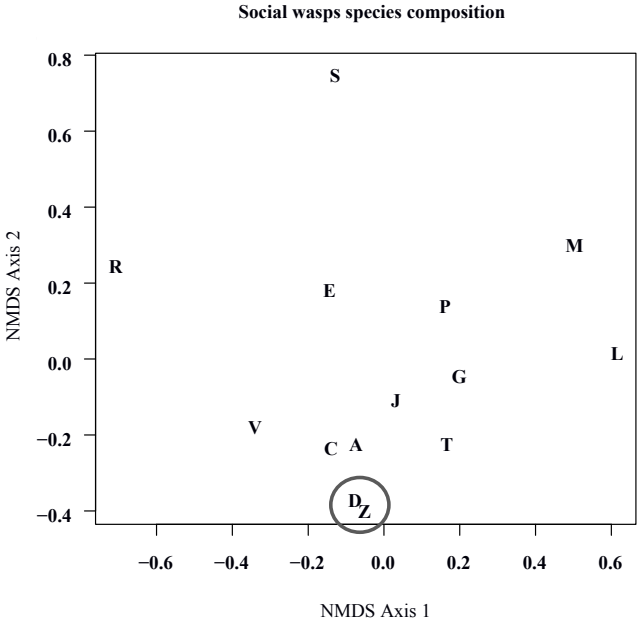


**Fig 2**. First two NMDS ordination axes considering social wasp species composition from inventories in the Amazon Region. Legend: Z (ZF-2 Station - AM), D (Ducke Reserve - AM), E (Embrapa - AM), J (Jaú National Park - AM), P (Purus-Madeira rivers - AM), A (Alvarães and Mamirauá Reserve - AM), M (Maracá Ecological Station - RR), T (Tepequém, Mocidade, Viruá - RR), R (Rio Branco region - AC), S (Serra do Divisor National Park - AC), C (Caxiuanã Reserve - PA), V (Porto Velho region - RO), L (Região dos Lagos - AP) and G (Gurupi Biological Reserve - MA).

## Discussion

In surveys conducted in the Amazon rainforest, the diversity of social wasps is generally higher than in other biomes. Surprisingly, we collected 92 species from the ZF-2 Station in only eight months, using two passive collection trap sin two strata (understory and canopy 32 meters high). The 92 species from the ZF-2 station were distributed into 18 genera, mainly *Polybia* (22 species), *Mischocyttarus* (14), and *Agelaia* (13).

In other areas of Amazonas State, as the Ducke Reserve, 103 social wasp species were collected from the understory stratum only, however, six types of collection methods were used during several years of collection and different methods. At Ducke Reserve, 19 genera were collected, mainly *Polybia* (28 species), *Agelaia* (12 species) and *Mischocyttarus* (12 species). Therefore, the results of species composition from both the ZF-2 Station and the Ducke Reserve were very similar.

Silva and Silveira (2009) and Somavilla et al. (2014) showed that fast inventories were efficient for sampling the most abundant species, recording three genera: *Agelaia, Polybia* and *Mischocyttarus*. Herein, we found, the same

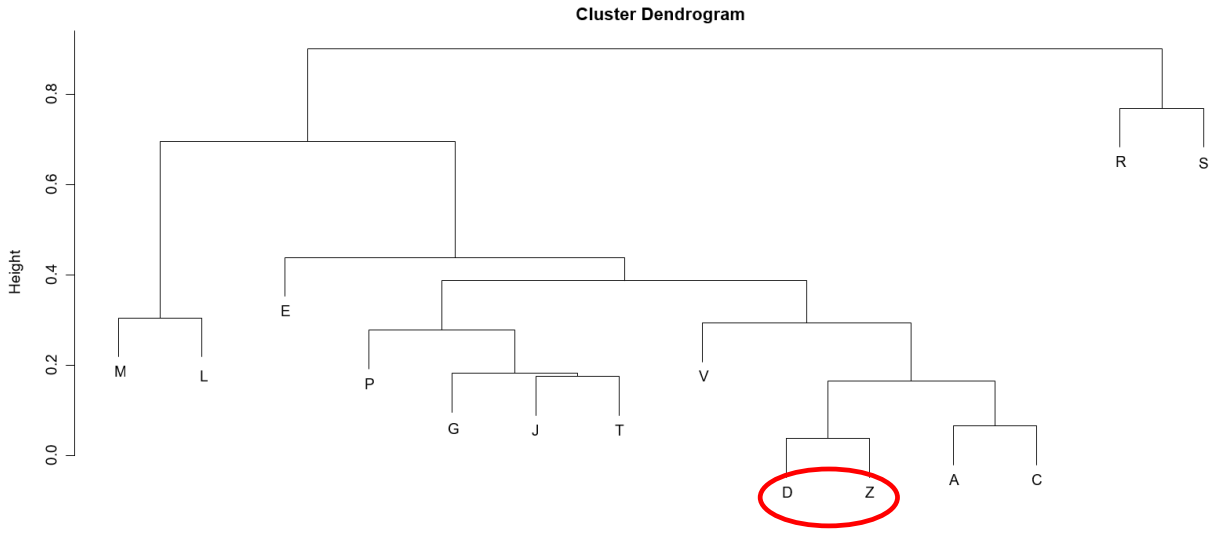


**Fig 3**. Cluster dendrogram generated dissimilarity coefficient for the species composition from the ZF-2 Station compared to other inventories in the Amazon Region. Legend: Z (ZF-2 Station - AM), D (Ducke Reserve - AM), E (Embrapa - AM), J (Jaú National Park - AM), P (Purus-Madeira rivers - AM), A (Alvarães and Mamirauá Reserve - AM), M (Maracá Ecological Station - RR), T (Tepequém, Mocidade, Viruá - RR), R (Rio Branco region - AC), S (Serra do Divisor National Park - AC), C (Caxiuanã Reserve - PA), V (Porto Velho region - RO), L (Região dos Lagos - AP) and G (Gurupi Biological Reserve - MA).

most abundant genera, which constituted more than 50% of the specimens collected specimens. *Agelaia* species usually form large colonies with millions of individuals (Zucchi et al., 1995), and, consequently, are more likely to be captured (Silva & Silveira, 2009). *Mischocyttarus* is the genus with more described species in social wasps, that can support the high diversity in this study. (Silveira, 2002) and *Polybia* has a very active foraging behavior, which facilitates the collection of these species in traps (Carpenter & Marques, 2001).

Most species of Epiponini, belonging to *Apoica*, *Brachygastra*, *Clypearia*, *Leipomeles*, *Polybia,* and *Protopolybia,* were only collected in *Malaise* traps. Conversely, this method was less efficient for capturing *Polistes*, a pattern that has also been reported by other researchers (Silveira, 2002; Silva & Silveira, 2009). *Polistes* nests at lower height and has usually small nests with few individuals, they are more difficult to be seen in forest (Carpenter & Marques, 2001). Therefore, using only *Malaise* traps to collect social wasps may underestimate the actual richness of *Polistes*.

Conversely, there was a strong relationship of nesting in the forest canopy, as the rare species *Clypearia duckei*, *Epipona tatua*, and *Polybia depressa* were only recorded in the canopy stratum at the ZF-2 Station and the Ducke Reserve (Somavilla & Oliveira, 2017). Furthermore, Richards (1978) recorded an *E. tatua* nest that was over 12 meters above ground in Mato Grosso, and Somavilla (2013) photographed a nest above 20 meters at the Ducke Reserve. *Synoeca*, and some *Brachygastra* and *Polybia* nests are also common in canopy, Richards (1978) recorded a *B. bilineolata* nest above 13 meters above ground and Somavilla et al. (2012) recorded a *S. surinama* and *P. liliacea* nest about 20 meters above ground.

Insects inhabiting the canopy of the Amazon rainforest strata are poorly represented in collections, with many unknown specimens in these habitats (Rafael & Gorayeb, 1982). From inventories in the Amazon, some Polistinae species are represented by only one or a few specimens in the collections and occur in the tree canopy, a habitat that has been poorly explored by collectors. For example, in the two works they explored the canopy, 25 species in Ducke Reserve and seven in Roraima State, manly *Agelaia*, *Clypearia*, *Metapolybia* and *Polybia* (Barroso et al., 2017; Somavilla & Oliveira, 2017). Likewise, there are few methods for collecting insects in these strata, that are often times costly and impractical. Based on this observation and the need for collections in these environments, traps mounted in the canopy are efficient ways of collecting and improving knowledge about social wasp species, mainly in the Amazon rainforest. Furthermore, such methods should be used in conjunction with *Malaise* traps mounted on the forest floor and active search. Finally, our study shows that some species were only collected in the canopy (Table 1).

There are different methods for sampling social wasps, however, few studies have attempted to standardize these methods or establish comparable and adequate protocols to survey the fauna at a given site. One important factor to consider when implementing new social wasp sampling protocols is the distribution pattern of these organisms (Silveira, 2002; Somavilla et al., 2014). Similarly, it is also important to determine the most efficient traps to collect the target group and dispose of them in a standardized manner (Noll & Gomes, 2009). Through this study, we verified, that using traps in the upper forest canopy is very important for collecting social wasp species. Furthermore, such method should be included in the collection protocol for the Amazon biome.

**Table 1**. Species of social wasps collected at the Estação ZF-2 (LBA/INPA), as along with the method used to capture every species. *Malaise* understory trap and *Malaise* suspended trap.

| Taxa | *Malaise* understory | *Malaise* canopy |
|---|---|---|
| **Epiponini** | | |
| *Agelaia angulata* (Fabricius, 1804) | X | |
| *Agelaia cajennensis* (Fabricius, 1798) | X | X |
| *Agelaia centralis* (Cameron, 1907) | X | |
| *Agelaia constructor* (de Saussure, 1854) | X | X |
| *Agelaia flavipennis* (Ducke 1905) | X | |
| *Agelaia fulvofasciata* (DeGeer, 1773) | X | X |
| *Agelaia hamiltoni* (Richards, 1978) | X | |
| *Agelaia myrmecophila* (Ducke, 1905) | X | |
| *Agelaia pallidiventris* (Richards, 1978) | X | |
| *Agelaia pallipes* (Olivier, 1791) | X | X |
| *Agelaia ornata* (Ducke, 1905) | X | |
| *Agelaia testacea* (Fabricius, 1804) | X | X |
| *Agelaia* sp.1 | X | X |
| *Angiopolybia pallens* (Lepeletier, 1836) | X | X |
| *Angiopolybia paraensis* (Spinola, 1851) | X | |
| *Apoica arborea* de Saussure, 1854 | X | |
| *Apoica gelida* van der Vecht, 1898 | X | |
| *Apoica pallens* (Fabricius, 1804) | X | |
| *Apoica pallida* (Olivier, 1791) | X | |
| *Apoica strigata* Richards, 1978 | X | |
| *Apoica thoracica* Du Buysson, 1906 | X | X |
| *Brachygastra bilineolata* Spinola, 1841 | | X |
| *Brachygastra lecheguana* (Latreille, 1824) | | X |
| *Brachygastra scutellaris* (Fabricius, 1804) | X | |
| *Chartergelus amazonicus* Richards, 1978 | | X |
| *Chartergelus nigerrimus* Richards, 1978 | X | |
| *Charterginus fulvus* Fox, 1898 | X | |
| *Clypearia apicipennis* (Spinola, 1851) | X | |
| *Clypearia duckei* Richards, 1978 | | X |
| *Clypearia sulcata* (de Saussure, 1854) | X | X |
| *Epipona tatua* (Cuvier, 1797) | | X |
| *Leipomeles dorsata* (Fabricius, 1804) | X | |
| *Leipomeles spilogastra* Cameron, 1912 | X | X |
| *Metapolybia decorata* (Gribodo, 1896) | X | |
| *Metapolybia nigra* Richards, 1978 | X | X |
| *Metapolybia rufata* Richards, 1978 | | X |
| *Metapolybia unilineata* (R. Von Ihering, 1904) | | X |
| *Nectarinella manauara* Silveira & Santos Jr., 2016 | | X |
| *Parachartergus amazonensis* (Ducke, 1905) | X | |
| *Parachartergus fraternus* (Gribodo, 1892) | X | X |
| *Parachartergus richardsi* Willink, 1951 | X | X |
| *Polybia belemensis* Richards, 1970 | | X |
| *Polybia bifaciata* de Saussure, 1854 | | X |
| *Polybia bistriata* (Fabricius, 1804) | X | X |
| *Polybia depressa* (Ducke, 1905) | | X |
| *Polybia dimidiata* (Olivier, 1792) | X | X |
| *Polybia dimorpha* Richards, 1978 | X | X |
| *Polybia emaciata* Lucas, 1879 | X | |
| **Epiponini** | | |
| *Polybia incerta* Ducke, 1907 | X | |
| *Polybia jurinei* de Saussure, 1854 | X | X |
| *Polybia juruana* R. von Ihering, 1904 | | X |
| *Polybia liliacea* (Fabricius, 1804) | X | X |
| *Polybia minarum* Ducke, 1906 | X | |
| *Polybia occidentalis* (Olivier, 1791) | X | X |
| *Polybia parvulina* Richards, 1970 | X | |
| *Polybia platycephala* Richards, 1951 | | X |
| *Polybia procellosa* Zavattari, 1906 | X | X |
| *Polybia rejecta* (Fabricius, 1798) | X | X |
| *Polybia scrobalis* Richards, 1970 | X | X |
| *Polybia signata* Ducke, 1905 | X | |
| *Polybia singularis* Ducke, 1905 | X | X |
| *Polybia striata* (Fabricius, 1787) | X | X |
| *Polybia* (*Myrapetra*) sp. | X | |
| *Protopolybia bituberculata* Silveira & Carpenter, 1995 | | X |
| *Protopolybia emortualis* (de Saussure, 1855) | X | X |
| *Protopolybia exigua* (de Saussure, 1954) | | X |
| *Protopolybia holoxantha* (Ducke, 1904) | X | |
| *Protopolybia nitida* (Ducke, 1904) | | X |
| *Protopolybia rotundata* Ducke, 1910 | X | |
| *Protopolybia rugulosa* Ducke, 1907 | X | |
| *Pseudopolybia compressa* (de Saussure, 1854) | X | |
| *Pseudopolybia dificcilis* (Ducke, 1905) | X | |
| *Pseudopolybia langi* Bequaert, 1944 | X | |
| *Pseudopolybia vispiceps* (de Saussure, 1863) | X | |
| *Synoeca surinama* (Linnaeus, 1767) | | X |
| *Synoeca virginea* (Fabricius, 1804) | | X |
| **Mischocyttarini** | | |
| *Mischocyttarus bertonii* Ducke, 1918 | X | |
| *Mischocyttarus collaris* (Ducke, 1904) | X | |
| *Mischocyttarus drewseni* (de Saussure, 1857) | X | |
| *Mischocyttarus imitator* (Ducke, 1904) | | X |
| *Mischocyttarus labiatus* (Fabricius, 1804) | X | |
| *Mischocyttarus lecointei* (Ducke, 1898) | X | |
| *Mischocyttarus metathoracicus* (de Saussure, 1854) | X | |
| *Mischocyttarus punctatus* (Ducke, 1904) | X | X |
| *Mischocyttarus smithii* de Saussure, 1853 | X | |
| *Mischocyttarus surinamensis* (de Saussure, 1854) | X | X |
| *Mischocyttarus synoecus* Richards, 1940 | | X |
| *Mischocyttarus tomentosus* Zikán, 1935 | X | |
| *Mischocyttarus* (*Haplometrobius*) sp.1 | X | |
| *Mischocyttarus* (*Haplometrobius*) sp.2 | X | |
| **Polistini** | | |
| *Polistes claripennis* Ducke, 1904 | X | X |
| *Polistes versicolor* (Olivier, 1792) | X | |
| TOTAL = 92species | 72 | 47 |

The *Malaise* trap in the understory captured more specimens and social wasp species when compared to the *Malaise* trap in the canopy. Probably because much of the foraging of social wasps happen in the understory, in addition to various feeding and nesting resources found near the forest floor (Somavilla et al., 2012). In this study, we did not use the active search collection method. However, Silveira (2002) concluded that the active search method was more efficient than traps, when they only used understory *Malaise* trap. In order to determine which species were unique to the two traps, we note the importance of working with different stratum. In the Amazon, where the forest canopy can reach great heights, using *Malaise* traps in the forest canopy could be a good method for capturing social wasps.

The similarities of social wasp species composition between ZF-2 Station and Ducke Reserve was not surprising since they are geographically close (50 km apart) and both areas have the same phytophysiognomy characteristics (ombrophilous dense and humid forest). In addition, these two sites, as well as some localities in Roraima State, are the only places where canopy fauna was collected. The species composition between Alvarães and Mamirauá in Amazonas and Caxiuanã in Pará were very similar, with both reserves located in lowland areas.

The sites with different phytophysiognomies and that were geographically distant were the most dissimilar sites. The Maracá Ecological Station with savanna formations, Serra do Divisor with more open and elevated vegetation, Rio Branco Region and the Amapá Lake Region, were the most dissimilar from the ZF-2 Station. Collection efforts were discontinuous in these places.

Unfortunately, different methods and collection efforts in surveys are complicated, as Silveira (2002) pointed out: "Comparisons of local fauna by the use of information in collections always confront obstacles arising from unsystematic collecting methodologies. In general, appropriate information about the effort spent in finding a certain number of species is not available, and data about the relative abundance of the species are hardly recoverable". We hope that this work stimulates other standardized surveys that explore the canopy fauna in the Amazon Region.

Finally, in this study we found that the social wasp fauna in the canopy is slightly different from the fauna of the understory, with many similar species in both forest strata. In addition, when comparing the strata, the understory had more diverse fauna than the canopy, while the canopy had some rare and poorly collected species. In this way, we suggest using traps suspended in the Amazon biome to collect a high diversity of social wasps. In addition, continuous collection efforts are important for better sampling in a particular area.

## Acknowledgments

Specimens were collected during a project coordinated by JAR and financed by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, process: 407623/2013-2) through the program "Rede BIA – Biodiversidade de Insetos na Amazônia". We sincerely thank CNPq for the postdoctoral scholarship (PDJ – process number 150029/2017-9) of A. Somavilla and research productivity fellowship of J.A. Rafael, and Marlon Breno Graça helped with analysis.

## References

Barbosa, B.C., Detoni, M., Maciel, T.T. & Prezoto, F. (2016). Studies of social wasp diversity in Brazil: Over 30 years of research, advancements and priorities. Sociobiology, 63: 858-880. doi: 10.13102/sociobiology.v63i3.1031

Barbosa, P.H.D., Costa, A.C.L. da, Cunha, A.C. da & Silva Junior, J.A. (2015). Variabilidade de elementos meteorológicos e de conforto térmico em diferentes ambientes na Amazônia brasileira. Revista Brasileira de Climatologia, 17: 98-118.

Barroso, P.C.S., Somavilla, A. & Boldrini, R. (2017). Updating the geographic records of social wasps (Vespidae: Polistinae) in Roraima state. Sociobiology, 64: 339-346. doi: 10.13102/sociobiology.v64i3.1789

Carpenter, J.M. (2004). Synonymy of the genus *Marimbonda* Richards, 1978, with *Leipomeles* Mobius, 1856 (Hymenoptera: Vespidae: Polistinae), and a new key to the genera of paper wasps of the new world. American Museum Novitates, 3456: 1-16.

Carpenter J.M. & Marques, O.M. (2001). Contribuição ao Estudo dos Vespídeos do Brasil. Universidade Federal da Bahia, Departamento de Fitotecnia, Bahia, 147 pp.

Erwin, T. (2013). Forest Canopies, Animal Diversity, in: Levin, S., (Ed.), Encyclopedia of Biodiversity. Academic Press Elsevier, New Jersey, pp. 511-515.

Gomes, B. (2013). Diversidade de vespas sociais (Vespidae, Polistinae) na região norte de Rondônia e relação dos ciclos ambientais abióticos sobre o forrageio. Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, USP, 55 pp.

Gomes, B., Knidel, S.V.L., Moraes, H.S. & da Silva, M. (2018). Survey of social wasps (Hymenoptera, Vespidae, Polistinae) in Amazon rainforest fragments in Acre, Brazil. Acta Amazonica, 48: 109-116. doi: 10.1590/1809-4392201700913

Gressit, J.H. & Gressit, K.M. (1972). An improved *Malaise* trap. Pacific Insects, 4: 87-90.

Higuchi, N., Pereira, H.S., Santos, J., Lima, A.J.N., Higuchi, F.G., Higuchi, M.I.G. & Ayres I.G.S.S.(2009). Governos locais amazônicos e as questões climáticas globais. Manaus, 103 pp.

Köppen, W. (1948). Climatologia, conunestudio de los climas de latierra. Fondo de Cultura Economica, México, 479 pp.

Martins, U.R., Galileo, M.H.M., Santos-Silva, A. & Rafael, J.A. (2006). Cerambycidae (Coleoptera) coletados à luz a 45 metros de altura, no dossel da Floresta Amazônica, e a descrição de quatro espécies novas. Acta Amazonica, 36: 265-272.

Minchin, P.R.(1987). An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio, 69: 89-107.

Morato, E.F., Amarante, S.T. & Silveira, O.T. (2008). Avaliação ecológica rápida da fauna de vespas (Hymenoptera, Aculeata) do Parque Nacional da Serra do Divisor, Acre, Brasil. Acta Amazonica, 38: 789-798.

Nakamura, A., Kitching, R.L., Cao, M., Creedy, T.J., Fayle, T.M., Freiberg, M., Hewitt, C.N., Itioka, T., Koh, L.P., Ma, K., Malhi, Y., Mitchell, A., Novotny, V., Ozanne, C.M.P., Song, L., Wang, H. & Ashton, L.A. (2017). Forest canopy science: achievements and horizons. Trends in Ecology and Evolution, 36: 438-451.

Noll, F.B. & Gomes, B. (2009). An improved bait method for collecting Hymenoptera, especially social wasps (Vespidae: Polistinae). Neotropical Entomology, 38: 477-481.

Oliveira, M.L., Fernandes, I.O. & Somavilla, A. (2015). Insetos das Unidades de Conservação de Uso Sustentável no Interflúvio Madeira-Purus, in: Gordo, M. & Pereira, H.S., (Eds.), Unidades de Conservação do Amazonas no Interflúvio Purus-Madeira: Diagnóstico Biológico. Editora da Universidade Federal do Amazonas, Manaus, pp. 51-84.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P. & McGlinn, D. (2016). Vegan: Community ecology package. Avaliable at: http://cran.rproject.org/web/packages/vegan. (accessed 09 May 2018).

Pickett, K.M. & Carpenter**,** J.M. (2010). Simultaneous analysis and the origin of eusociality in the Vespidae (Insecta: Hymenoptera). Arthropod Systematics and Phylogeny, 68: 3-33.

R Core Team.(2017). R: A language and environment for statisticalcomputing. Avaliable at: http://www.R-project.org. (accessed 09 May 2018).

Rafael, J.A. & Gorayeb, I.S. (1982). Tabanidae (Diptera) da Amazônia. I – Uma armadilha suspensa e primeiros registros de mutucas de copas de árvores. Acta Amazonica, 12: 232-236.

Raw, A. (1998). Social Wasps (Hymenoptera, Vespidae) of the Ilha de Maracá, in: Ratter, J.A. & Milliken, W. (Eds.), Maracá. Biodiversity and environment of an Amazonian Rainforest. Chichester, John & Sons, London, pp. 307-321.

Richards, O.W. (1978). The social wasps of the Americas (excluding the Vespinae).British Museum of Natural History, London, 580 pp.

Silva, S.S. & Silveira, O.T. (2009). Vespas sociais (Hymenoptera, Vespidae, Polistinae) de floresta pluvial Amazônica de terra firme em Caxiuanã, Melgaço, Pará. Iheringia, 99: 317-323.

Silveira, O.T. (2002). Surveying Neotropical Social Wasps. An Evaluation of Methods in the "Ferreira Penna" Research Station (ECFPn), in Caxiuanã, PA, Brazil (Hymenoptera, Vespidae, Polistinae). Papéis Avulsos de Zoologia, 42: 299-323.

Silveira, O.T., da Costa Neto, S.V. & da Silveira, O.F.M. (2008). Social wasps of two wetland ecosystems in Brazilian Amazonia (Hymenoptera, Vespidae, Polistinae). Acta Amazonica, 38: 333-344.

Silveira, O.T., Silva, S.S., Pereira, J.L.G. & Tavares, I.S. (2012). Local-scale spatial variation in diversity of social wasps in an Amazonian rain forest in Caxiuanã, Pará, Brazil (Hymenoptera, Vespidae, Polistinae). Revista Brasileira de Entomologia 56: 329-346. doi: 10.1590/S0085-56262012005000053

Somavilla, A., Oliveira, M.L. & Silveira, O.T. (2012). Guia de identificação dos ninhos de vespas sociais (Hymenoptera, Vespidae, Polistinae) na Reserva Ducke, Manaus, Amazonas, Brasil. Revista Brasileira de Entomologia, 56: 405-414.

Somavilla, A. & Oliveira, M.L. (2013). New Records of Social Wasps (Hymenoptera: Vespidae: Polistinae) in Amazonas State, Brazil. Entomo Brasilis, 6: 157-159.

Somavilla, A., Oliveira, M.L. & Silveira, O.T. (2014). Diversity and aspects of the ecology of social wasps (Vespidae, Polistinae) in Central Amazonian 'terra firme' forest. Revista Brasileira de Entomologia, 58: 349-355. doi: 10.1590/s0085-56262014005000007.

Somavilla, A., Marques, D.W.A., Barbosa, E.A.S., Pinto Jr, J.S. & Oliveira, M.L. (2014). Vespas Sociais (Vespidae: Polistinae) em uma Área de Floresta Ombrófila Densa Amazônica no Estado do Maranhão, Brasil. EntomoBrasilis, 7: 183-187. doi: 10.12741/ebrasilis.v7i3.404

Somavilla, A., Andena, S.R. & Oliveira, M.L. (2015). Social Wasps (Hymenoptera: Vespidae: Polistinae) of the Jaú National Park, Amazonas, Brazil. EntomoBrasilis, 8: 45-50. doi: 10.12741/ebrasilis.v8i1.447

Somavilla, A., Schoeninger, K., Castro, D.G.D., Oliveira, M.L. & Krug, C. (2016). Diversity of wasps (Hymenoptera: Vespidae) in conventional and organic guarana (*Paulliniacupana* var. sorbilis) crops in the Brazilian Amazon. Sociobiology, 63: 1051-1057. doi: 10.13102/sociobiology.v63i4.1178

Somavilla, A. & Oliveira, M.L. (2017). Social wasps (Vespidae: Polistinae) from Ducke Reserve, Amazonas, Brazil. Sociobiology, 64: 125-129. doi: 10.13102/sociobiology.v64i1.1215

Zucchi, R., Sakagami, S.F., Noll, F.B., Mechi, M.R., Mateus, S., Baio, M.V. & Shima, S.(1995). *Agelaiavicina*, a swarm-founding polistine with the largest colony size among wasps and bees (Hymenoptera: Vespidae). Journal of New York Entomological Society, 103: 129-137.