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ARTICLE

# Mycophagous Drosophilidae (Diptera) guild and their hosts in the Brazilian Amazon

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**Abstract.** The composition and potential hosts of mycophagous Drosophilidae from a section of the Brazilian Amazon forest in the Caxiuanã National forest were investigated. Sampling was performed in three different periods at long the wet season (January (beginning) and July (end) 2013 and May (middle) 2014). The samples were collected from existing trails by actively searching for fungal fruiting bodies where Drosophilidae were present. We present composition and richness analysis over two years of sampling sampling Drosophilidae and Fungi. We evaluate sampling completeness using asymptotic species richness estimators. Out of 159 fruiting body samples and 64 fungal species, 5,124 drosophilids belonging to 55 species and 5 genera were collected. The mycophagous Drosophilidae richness values estimated by Jackknife 1 and Bootstrap were 69 and 61, respectively. The estimated fly richness correlated positively with fungal richness and abundance. Among the Drosophilidae species identified in this study, approximately 5% represent new occurrences for Brazil and 56% represent new species. Four genera belonging to the *Zygothrica* genus group are found in the Amazon region, and these genera represent 80% of the fungus-associated fauna known to date for the tropics. In conclusion, our results show that the fungal richness and abundance were the factors that determined the high diversity of mycophagous Drosophilidae.

**Key-Words.** Agaricales; Basidiomycota; *Drosophila;* Fungal composition; *Hirtodrosophila;* Insects; *Mycodrosophila;* Polyporaceae; Species richness; *Zygothrica.*

## INTRODUCTION

Community ecology aims to understand species abundance and distribution, which depend on biotic and abiotic variables (Diamond, 1986). One of the main challenges in the study of communities is the appropriate delimitation of a community, which is necessary to understand the processes that condition a given group of organisms. One way of facilitating the understanding of community organization processes is to focus on a group of species. One way to select a reference group is to focus on the guilds. Guilds are defined as groups of organisms that use same resource category (Root, 1967; Fauth *et al.,* 1996; Magurran, 2011), and the species can or not be phylogenetically related (Magurran, 2011). Considering these concepts, mycophagous Drosophilidae are phylogenetically related species that can be classified as a guild, considering that they are organisms are strongly associated based on the use of the same group of resources.

Sturtevant (1921) was the first to register that many species of Drosophilidae used fungi for reproduction. Since then, other studies have described in more detail species that use fungi not only to reproduce but also to feed adults, while they eat microorganisms (yeasts or bacteria) present in the fruiting bodies (Courtney *et al.,* 1990; Powell, 1997), larvae feed on the hyphae and microorganisms (Kimura, 1976; Martin, 1979; Lacy, 1984; Hosaka & Uno, 2012). In other species like *Hirtodrosophila polypori* (Malloch) the males use the hosts to court (Parsons, 1977).

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In the Neotropics, few studies have widely and systematically addressed Drosophilidae mycophagy. The taxonomy of this group, however, is quite well understood than other drosophilids (Sturtevant, 1920; Hendel, 1936; Frota-Pessoa, 1945, 1951; Cordeiro, 1952; Burla, 1956; Brncic, 1957; Wheeler & Takada, 1963; Mourão *et al.,* 1965, 1967; Grimaldi, 1987; Junges *et al.,* 2016). The descriptions of *Hirtodrosophila* Duda, *Mycodrosophila* Oldenberg and *Zygothrica* Wiedemann species were, most of them from specimens in entomological collections. Heed (1957) and Grimaldi (1987) studied ecological aspects of feeding, breeding and mating. In Brazil, mycophagous species have been identified in the Cerrado (Roque *et al.,* 2006; Roque & Tidon, 2008), Atlantic Rainforest (Gottschalk *et al.,* 2009) and Pampas biomes (Valer *et al.,* 2016). Among these studies, Gottschalk *et al.* (2009) and Valer *et al.* (2016) focused more specifically on fungus hosts of flies. These studies contributed to our understanding of the mycophagous fauna in these regions and the natural history of these groups.

The mycophagy probably evolved from detritivory in drosophilids and may have appeared independently in different lineages within the group (Throckmorton, 1975; Powell, 1997). Grimaldi (1990) proposed that mycophagy may represent a synapomorphy for the *Zygothrica* genus group clade (*Hirtodrosophila* + *Mycodrosophila* + *Zygothrica* + *Paraliodrosophila* Duda + *Paramycodrosophila*) but there are other mycophagous groups that derived this trait independently like some species of *Drosophila, Leucophenga* and *Scaptomyza* (Courtney *et al.,* 1990).

The data published on the natural history of mycophagous drosophilids are mostly fragmented. These works in general approach the mycophagy of groups of insects or Dipetra that use the fruiting bodies for its development (Burla & Bächli, 1968; Buxton, 1954, 1960; Ackerman & Shenefelt, 1973; Jaenike, 1978; Shorrocks & Charlesworth, 1980; Coutin, 1982; Worthen, 1989; Wertheim *et al.,* 2000; Yamashita & Hijii, 2003; Takahashi *et al.,* 2005; Kadowaki, 2010) or specifically related to the genus *Drosophila* (Bock & Parsons, 1978; Shorrocks & Charlesworth, 1982; Lacy, 1984; Grimaldi *et al.,* 1992; Heard, 1998). Courtney *et al.* (1990) studied mycophagous Drosophilidae ecology and classified the relevant species based on the type of feeding, grouping species that feed solely on fungi as strictly mycophagous and those that can feed on fungi or other resources as facultative mycophagous. Initially, mycophagous Drosophilidae were considered to be generalists with respect to their feeding and reproductive habits (Lacy, 1984; Hanski, 1989; Courtney *et al.,* 1990). However, a recent study suggested that some species of *Hirtodrosophila, Leucophenga* and *Zygothrica* are specialists with respect to reproduction (Valer *et al.,* 2016).

The Brazilian Drosophilidae fauna is extremely rich and widely distributed among all biomes (Val *et al.,* 1981). However, this group is poorly studied in some of the country's Northern and Northeastern states and regions. Even in states where the group is well studied, species that inhabit substrates other than fruits represent a knowledge gap, given that most sampling approaches utilize fermenting banana as the attractant (Gottschalk *et al.,* 2008). Mycophagous Drosophilidae can be attracted by commercial mushroom bait, which is a successful technique that is used in community studies in temperate regions (Shorrocks & Charlesworth, 1980). By contrast, data on tropical mycophagous Drosophilidae guild are from samples collected from naturally occurring fungi in the areas of Cerrado, the Atlantic Rainforest and Pampas (Roque *et al.,* 2006; Roque & Tidon, 2008; Gottschalk *et al.,* 2009).

We investigated the composition and richness of the mycophagous Drosophilidae guild and their potential hosts in a region of the Brazilian Amazon forest.

## MATERIALS AND METHODS

### Study area

Sampling was performed in the Caxiuanã National Forest Reserve in the eastern Amazon (01°43'S, 51°27'W), in a portion of the Amazon biome located in the municipalities of Melgaço and Portel in Pará State, Brazil. Caxiuanã National Forest Reserve contains approximately 300,000 ha and comprises 80% dense ombrophilous forest and 20% patches of savanna, Capoeira (low vegetation), Igapó (seasonally flooded vegetation), Várzea (floodplain) and vast aquatic vegetation (Lisboa *et al.,* 2007). According to the Köppen classification, the climate is hot and humid, with climate subtype 'Am' (tropical monsoon climate). The region experiences a short dry season and recurrent rain throughout the year (Oliveira *et al.,* 2008). Seasonality is defined by the amount of rain, with a lower rainfall index from July to November (27.5% rain) and a wet season from December to June (72.5% rain) (Oliveira *et al.,* 2008). The mean annual temperature is 26°C, with little variability (minimum of 22°C and maximum of 32°C) (Costa *et al.,* 2009).

### Sampling method and identification

Three Caxiuanã National Forest Reserve sampling expeditions were performed during the wet season, with two expeditions in 2013 (January and July) and one expedition in May 2014. Samples were collected by actively searching existing trails for fungal fruiting bodies with the presence of Drosophilidae for a total of 18 days, with six days per expedition. In this study we defined a sample corresponding to the conjunct of fruit body of one fungal species (Fig. 3). A total of 27 km (A total of 9 km field of trails was surveyed in each field trip, totaling 18 hs of sampling per field trip) of trails was surveyed.

Sampling was performed between 8 am and 11 am, when Drosophilidae are more active (Pavan *et al.,* 1950). Flies on the fungal surface were collected using a mechanical aspirator or entomological nets and stored in labeled tubes containing absolute ethanol. Following the collection of the adult flies hovering over the fungi, the exposed fruiting bodies and the fungal substrate were

photographed, and fungal specimens were collected for identification.

Flies were identified based on external morphology and when possible, male and female terminalia, based on the literature (Hendel, 1936; Frota-Pessoa, 1945; Burla, 1956; Wheeler & Takada, 1963, 1971; Grimaldi, 1987, 1990; Vilela & Bächli, 1990, 2004, 2007). Dissections of terminalia were performed following Wheller & Kambysellis (1966), as modified by Kaneshiro (1969). The material is housed at the Entomological Collection of the Museu Paraense Emílio Goeldi (MPEG) Entomological Collection in the city of Belém in Pará State, Brazil, and at the Padre Jesus Santiago Moure Entomological Collection of the Zoology Department of the Federal University of Paraná (Departamento de Zoologia, Universidade Federal do Paraná – DZUP) in the city of Curitiba in Paraná State, Brazil.

Fungal fruiting body sampling was performed according to the documentation and preservation methods cited by Fidalgo & Bononi (1989). Macroscopic and microscopic analyses were performed, and microstructure analysis was accomplished using sample slices mounted between a slide and a slide cover with a solution of 3% KOH, 1% phloxine and Melzer's reagent (Teixeira, 1995). The identification and/or confirmation of species were performed based on the specialized literature (*e.g.,* Ryvarden & Johansen, 1980; Furtado, 1981; Ryvarden, 1991, 2004). The mycological nomenclature and classification follow Kirk *et al.* (2008).

### Assemblage characterization

A Whittaker graphical representation showing absolute species abundance (Log N) was used to display guild dominance patterns (Krebs, 1999). The following four models were tested to identify the model that best describes the abundance distribution data: (1) Geometric Series: assumes that each species in the community utilizes a fraction of the resource according to its dominance (McGill, 2011); (2) Logarithmic Series (Log-series): the model with the most uniform abundance distribution, in which resources are randomly and sequentially shared among niches (Magurran, 2011); (3) Broken stick: a model without a predominant species, based on the random and simultaneous sharing of resources among species (Pielou, 1975); and (4 Log-normal: a model that describes most of the species abundance distribution within the community and similar to the logarithmic series model, is associated with the community equilibrium, with small proportions of rare species (Sugihara, 1980). Modeling was performed using Past 3.05 (Hammer *et al.,* 2001). To choose of the model that better adjusted the distribution, was considered as parameter the significance. Models that were significant or presented high values were considered models that did not good fit.

Species accumulation curves for Drosophilidae (observed species richness, Sobs) and Jackknife 1 and Bootstrap estimation curves were built (Smith & van Belle, 1984). These methods account for sampling size

**Table 1.** Drosophilidae abundance for I = 1st expedition (January 2013), II = 2nd expedition (July 2013) and III = 3rd expedition (May 2014); F = Frequency. Morphospecies are referenced according to listings from the DZUP and MPEG entomological collections.

| Genus | Species/Morphospecies | I | II | III | F(%) | Total |
|---|---|---|---|---|---|---|
| *Drosophila* | *D. atrata* Burla & Pavan | | | 4 | 30 | 4 |
| *Drosophila* | (SB13005) | 34 | 1 | | 60 | 35 |
| *Drosophila* | (SB13009) | 51 | 160 | 6 | 100 | 217 |
| *Drosophila* | (SB14051) | | | 11 | 30 | 11 |
| *Hirtodrosophila* | *H. clypeata* (Wheeler) | 45 | 61 | 1 | 100 | 107 |
| *Hirtodrosophila* | *H. minuscula* Vilela & Bächli | | | 12 | 30 | 12 |
| *Hirtodrosophila* | *H. morgani* Mourão, Gallo & Bicudo) | 6 | | 3 | 60 | 9 |
| *Hirtodrosophila* | *H. subflavohalterata* (Burla, 1956) | 19 | | 1 | 60 | 20 |
| *Hirtodrosophila* | (SB13010) | 88 | 3 | 52 | 100 | 143 |
| *Hirtodrosophila* | (SB13011) | 419 | 17 | 327 | 100 | 763 |
| *Hirtodrosophila* | (SB14003) | 5 | | 15 | 60 | 20 |
| *Hirtodrosophila* | (SB14004) | 2 | | | 30 | 2 |
| *Hirtodrosophila* | (SB14005) | 1 | | | 30 | 1 |
| *Hirtodrosophila* | (SB14006) | 1 | | | 30 | 1 |
| *Hirtodrosophila* | (SB14007) | 5 | 2 | 64 | 100 | 71 |
| *Hirtodrosophila* | (SB14009) | 1 | | | 30 | 1 |
| *Hirtodrosophila* | (SB14010) | 1 | | | 30 | 1 |
| *Hirtodrosophila* | (SB14011) | 1 | | 23 | 60 | 24 |
| *Hirtodrosophila* | (SB14033) | 2 | | | 30 | 2 |
| *Hirtodrosophila* | (SB14034) | 22 | | | 60 | 22 |
| *Hirtodrosophila* | (SB14035) | | | 136 | 30 | 136 |
| *Hirtodrosophila* | (SB14041) | | | 9 | 30 | 9 |
| *Hirtodrosophila* | (SB14049) | | | 1 | 30 | 1 |
| *Mycodrosophila* | *M. brunnescens* Wheeler & Takada | 2 | | | 30 | 2 |
| *Mycodrosophila* | *M. elegans* Wheeler & Takada | 12 | 2 | 23 | 100 | 37 |
| *Mycodrosophila* | *M. neoprojectans* Wheeler & Takada | 162 | | 105 | 60 | 267 |
| *Mycodrosophila* | *M. projectans* (Sturtevant) | 81 | 7 | 107 | 100 | 195 |
| *Mycodrosophila* | *M. pseudoprojectans* Wheeler & Takada | 84 | 2 | 52 | 100 | 138 |
| *Paraliodrosophila* | *P. antennata* Wheeler | 137 | 17 | 8 | 100 | 162 |
| *Zygothrica* | *Z. atriangula* Duda | | 1 | 288 | 60 | 289 |
| *Zygothrica* | *Z. caudata* Hendel | | | 1 | 30 | 1 |
| *Zygothrica* | *Z. dimidiata* Duda | | | 1 | 30 | 1 |
| *Zygothrica* | *Z. joeyesco* Grimaldi | | | 1 | 30 | 1 |
| *Zygothrica* | *Z. microeristes* Grimaldi | | 5 | 269 | 60 | 274 |
| *Zygothrica* | *Z. orbitalis* (Sturtevant) | | 140 | | 30 | 140 |
| *Zygothrica* | *Z. poeyi* (Sturtevant) | 165 | 4 | 105 | 100 | 274 |
| *Zygothrica* | *Z. prodispar* Duda | | | 1 | 30 | 1 |
| *Zygothrica* | *Z. radialis* Grimaldi | | | 30 | 30 | 30 |
| *Zygothrica* | *Z. subcandens* Burla | | | 4 | 30 | 4 |
| *Zygothrica* | *Z. virgatalba* Burla | 10 | | 165 | 60 | 175 |
| *Zygothrica* | *Z. virgatinigra* Burla | | | 18 | 30 | 18 |
| *Zygothrica* | *Z. zygia* Grimaldi | | | 224 | 30 | 224 |
| *Zygothrica* | (SB14002) | 1 | | 2 | 60 | 3 |
| *Zygothrica* | (SB14003) | | | 154 | 30 | 154 |
| *Zygothrica* | (SB14016) | | | 243 | 30 | 243 |
| *Zygothrica* | (SB14025) | | | 104 | 30 | 104 |
| *Zygothrica* | (SB14028) | | | 1 | 30 | 1 |
| *Zygothrica* | (SB14037) | | | 34 | 30 | 34 |
| *Zygothrica* | (SB14038) | | | 283 | 30 | 283 |
| *Zygothrica* | (SB14042) | | | 78 | 30 | 78 |
| *Zygothrica* | (SB14043) | | | 3 | 30 | 3 |
| *Zygothrica* | (SB14047) | | | 1 | 30 | 1 |
| *Zygothrica* | (SB14052) | | | 1 | 30 | 1 |
| *Zygothrica* | (SB14022) | | | 8 | 30 | 8 |
| *Zygothrica* | (SB14017) | | | 366 | 30 | 366 |
| | | **1357** | **422** | **3345** | | **5124** |

**Table 2.** Fungal species and morphospecies recorded at Caxiuanã FLONA showing families, the number of collected fruiting bodies (samples (S)), Drosophilidae abundance (DA) and number of Drosophilidae species (RD) collected from each fungal species.

| Order | Family | Genus | Species/Morphospecies | S | DA | RD |
|---|---|---|---|---|---|---|
| Agaricales | Agaricaceae | *Leucocoprinus* | *L. cretaceous* (Bull.) Locq | 1 | 20 | 2 |
| | Marasmiaceae | *Crinipellis* | sp. | 1 | 1 | 1 |
| | | *Lactocollybia* | sp. | 3 | 216 | 10 |
| | | *Marasmius* | sp. | 2 | 144 | 4 |
| | | *Nothopanus* | sp. | 1 | 1 | 1 |
| | Mycenaceae | *Heimiomyces* | sp. | 1 | 4 | 2 |
| | Omphalotaceae | *Gymnopus* | sp. 1 | 6 | 16 | 5 |
| | | *Gymnopus* | sp. 2 | 1 | 20 | 5 |
| | | *Gymnopus* | sp. 3 | 3 | 33 | 4 |
| | | *Hydropus* | sp. | 1 | 7 | 2 |
| | | *Marasmiellus* | *M.* cf. *volvatus* | 3 | 20 | 6 |
| | | *Marasmiellus* | sp. 4 | 1 | 139 | 16 |
| | Physalacriaceae | *Oudemansiella* | sp. | 1 | 17 | 4 |
| | Pleurotaceae | *Hoehnbuehelia* | sp. | 2 | 2 | 2 |
| | | *Pleurotus* | *P.* cf. *djamor* | 1 | 8 | 4 |
| | | *Pleurotus* | sp. | 1 | 1 | 1 |
| | Strophariaceae | | Agaricales sp. 1 | 1 | 36 | 6 |
| | | *Gymnopilus* | sp. 1 | 1 | 22 | 5 |
| | Tricholomataceae | | Agaricales sp. 4 | 1 | 121 | 7 |
| | | *Collybia* | *C. aurea* (Beeli) Pegler | 2 | 198 | 16 |
| | | *Filoboletus* | *F. gracilis* (Klotzch ex berk.) | 1 | 4 | 2 |
| | | *Hemimycena* | sp. 1 | 3 | 27 | 5 |
| | | *Hemimycena* | sp. 2 | 1 | 41 | 3 |
| | | *Hemimycena* | sp. 13 | 2 | 9 | 2 |
| | | *Hygrocybe* | *H. occidentalis* (Dennis) Pegler | 1 | 2 | 1 |
| Agaricales | | | sp. 2 | 1 | 6 | 1 |
| Agaricales | | | sp. 5 | 3 | 5 | 3 |
| Agaricales | | | sp. 6 | 1 | 1 | 1 |
| Agaricales | | | sp. 10 | 2 | 185 | 12 |
| Auriculariales | Auriculariaceae | *Auricularia* | *A. mesenterica* (Dicks.) Pers. | 1 | 4 | 4 |
| Cantharellales | Hydnaceae | | sp. 1 | 1 | 57 | 9 |
| Geastrales | Geastraceae | *Geastrum* | sp. 1 | 1 | 1 | 1 |
| Hymenochaetales | Hymenochaetaceae | *Hymenochaete* | *H. damicornis* (Link) Lév. | 1 | 3 | 1 |
| | | *Phellinus* | *P. baccharidis* (Pat.) Pat. | 1 | 1 | 1 |
| | | *Phellinus* | *P. fastuosus* (Láv.) S. Ahmad | 1 | 7 | 2 |
| | | *Phellinus* | *P. gilvus* (Schwein) Pat. | 1 | 1 | 1 |
| | | *Phellinus* | *P. rimosus* (Berk.) Pilát | 1 | 1 | 1 |
| Polyporales | Ganodermataceae | *Amauroderma* | sp. 1 | 1 | 1 | 3 |
| | | *Ganoderma* | *G. australe* (Fr.) Pat. | 41 | 690 | 21 |
| | Meripilaceae | *Rigidoporus* | *R. biokoensis* (Bres. ex Lloyd) Ryvarden | 4 | 89 | 13 |
| | | *Rigidoporus* | *R. lineatus* (Pers.) Ryvarden | 11 | 209 | 17 |
| | | *Rigidoporus* | *R. microporus* (Sw.) Overeem | 4 | 150 | 11 |
| | Meruliaceae | *Cymatoderma* | sp. 1 | 1 | 38 | 5 |
| | | *Flaviporus* | *F. liebmannii* (Fr.) Ginns | 2 | 4 | 1 |
| | Phanerochaetaceae | *Antrodiella* | sp. 1 | 1 | 3 | 2 |
| | | *Inflatostereum* | *I. glabrum* (Pat.) D.A. Reid | 2 | 64 | 2 |
| | Polyporaceae | *Echinochaete* | *E. brachypora* (Mont.) Ryvarden | 1 | 72 | 9 |
| | | *Fomes* | *F. fasciatus* (Sw.) Cooke | 2 | 5 | 2 |
| | | *Microporellus* | *M. obovatus* (Jungh.) Ryvarden | 4 | 45 | 7 |
| | | *Nigroporus* | *N. vinosus* (Berk.) Murril | 1 | 1 | 1 |
| | | *Perenniporia* | *P. inflexibilis* (Berk.) Ryvarden | 1 | 1 | 1 |
| | | *Perenniporia* | *P. martia* (Berk.) Ryvarden | 2 | 9 | 4 |
| | | *Polyporus* | *P. guianensis* Mont. | 2 | 11 | 3 |
| | | *Favolus* | *F. tenuiculus* P. Beauv. | 10 | 2163 | 32 |
| | | *Trametes* | *T. lactinea* (Berk.) Sacc. | 1 | 9 | 3 |
| | | *Trametes* | *T. máxima* (Mont.) A. David & Rajchenb. | 1 | 7 | 2 |
| | | *Trametes* | *T. modesta* (Kunze ex Fr.) Ryvarden | 2 | 26 | 3 |
| | | *Trametes* | *T. pavonia* (Berk.) Fr. | 1 | 2 | 1 |
| | | *Trametes* | sp. 1 | 1 | 4 | 2 |
| Polyporales | | | Polyporales sp. 3 | 1 | 13 | 3 |
| Polyporales | | | Polyporales sp. 4 | 1 | 51 | 6 |
| Stereales | Stereaceae | | Stereaceae sp. 1 | 4 | 58 | 2 |
| Tremellales | Tremellaceae | *Tremella* | *T. fuciformis* Berk. | 1 | 1 | 1 |
| Xylariales | Xylariaceae | *Xylaria* | sp. 1 | 1 | 4 | 3 |
| **Total** | | | | **159** | **5124** | |

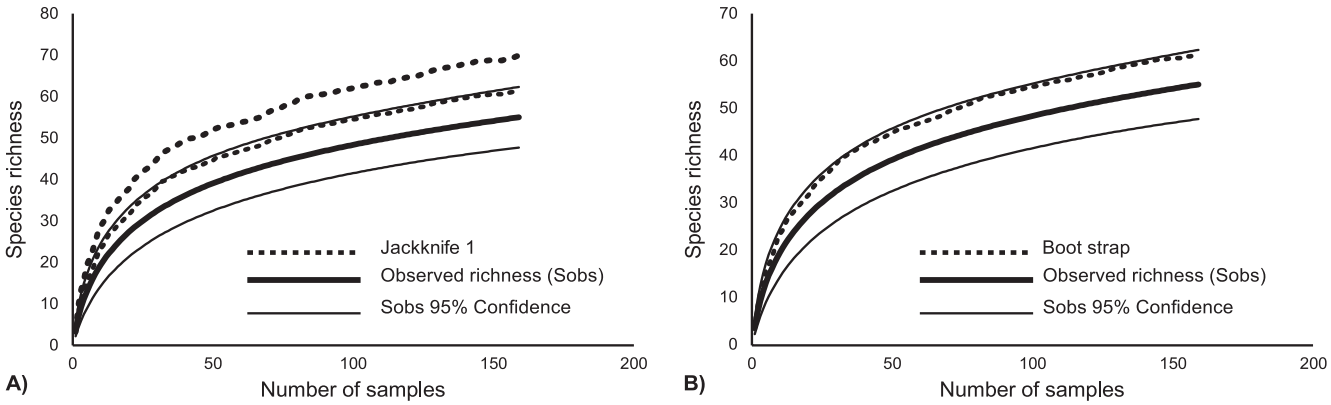


**Figure 1.** Species accumulation curves for the observed richness of the Drosophilidae guild from Caxiuanã National Forest Reserve relative to curves generated using Jackknife 1 (A) and Bootstrap (B) estimators.

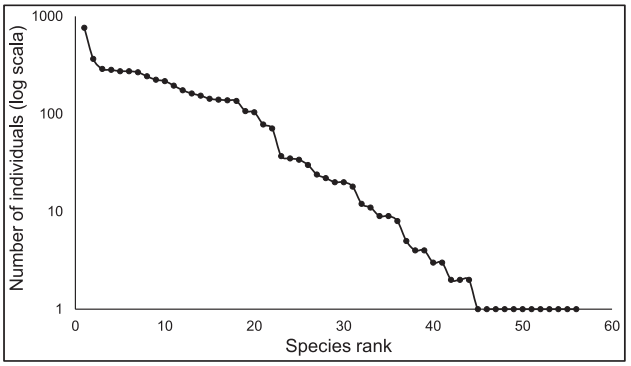


**Figure 2.** Ranking of the Log (N) abundance distributions of 55 mycophagous Drosophilidae species at Caxiuanã National Forest Reserve.

and were thus used to support the guild sampling effort. Jackknife 1 and Bootstrap estimators consider the incidence data (Magurran, 2011). Species richness curves and estimators were calculated (following 1,000 sample randomizations) using EstimateS 9.1.0 (Colwell, 2016).

The potential associations between Drosophilidae richness and fungal richness and/or abundance were evaluated using Spearman's correlation analysis. Evaluations were performed to investigate associations between the species richness of the two groups and between Drosophilidae richness and fungal abundance per sampling day. These analyses were performed using the Car package (Fox & Weisberg, 2018) of R statistical software (R Development Core Team, 2018). To assess the species temporality, the relative frequency of fungal species was calculated as the ratio between the number of collections in which the species were observed and total number of collections (collections tree).

## RESULTS

The samples consisted of 5,124 Drosophilidae specimens, which belongs to 55 species (including those identified as morphospecies), and 159 fruiting body samples, which belongs to 64 fungal species (including those identified as morphospecies) (Table 2). The collected species belongs to *Zygothrica* (26 species), *Hirtodrosophila* (19 species), *Mycodrosophila* (five species), *Drosophila* (four species) and *Paraliodrosophila* (one species) (Table 1). The fungal species were members of the orders Agaricales (eight families and 29 species), Polyporales (five families and 24 species), Hymenochaetales (one family and five species), Auriculariales, Cantharellales, Geastrales, Stereales, Tremellales and Xylariales (one species each) (Table 2).

The richness values estimated by Jackknife 1 and Bootstrap were 69 and 61 mycophagous Drosophilidae species, respectively, for the 159 fruiting bodies observed. The curves were ascending but showed signs of approaching an asymptote (Fig. 1).

The observed abundance distribution was the best fitting by Log-series model ($\alpha = 48.58$, $x^2 = 3.42$, $x = 0.59$, $p = 0.94$), which characterizes few very abundant species and many rare species (Fig. 2). The 22 most abundant species accounted for 93% of the individuals, while 22 out of the 55 species (40%) were represented by less than 40 individuals, including 11 singletons (20%). The most abundant species were *Hirtodrosophila* (SB13011) (15% of all Drosophilidae), *Zygothrica* (SB14017) (7%), *Z. atriangula* and *Zygothrica* (SB14024) (6%). *Z. zygia, Z. microerites, Z. atriangula, M. neoprojectans, Z. poeyi, Zygothrica* (SB14016), *Zygothrica* (SB14038) and *Drosophila* (SB13009) displayed abundances representing 3% to 5% of all Drosophilidae (Table 1).

Drosophilidae richness and abundance correlated positively with fungal richness and abundance ($\rho = 0.64$, $p = 0.004$ and $\rho = 0.73$, $p = 0.004$, respectively).

Among the collected fungi, *Favolus tenuiculus* (Fig. 3a) had the highest abundance and richness of Drosophilidae visitors, with 42% of the drosophilid abundance and 32 species, followed by *Ganoderma australe* (Fig. 3b) with 13% abundance and 21 species (Table 2). Furthermore, considering the relative frequency of fungal species as a measure of temporal availability, *Ganoderma australe* and *Rigidoporus biokoensis* were the most common species at a relative frequency of 100%, and it was followed by seven species (Agaricales sp. 10, *Gymnopus* sp. 1, *Gymnopus* sp. 3, *Favolus tenuiculus, Rigidoporus lineatus, Rigidoporus microporus* and *Trametes modesta*), had a relative frequency of 60% and 86% of the collected fungi species were sampled in a single collection.

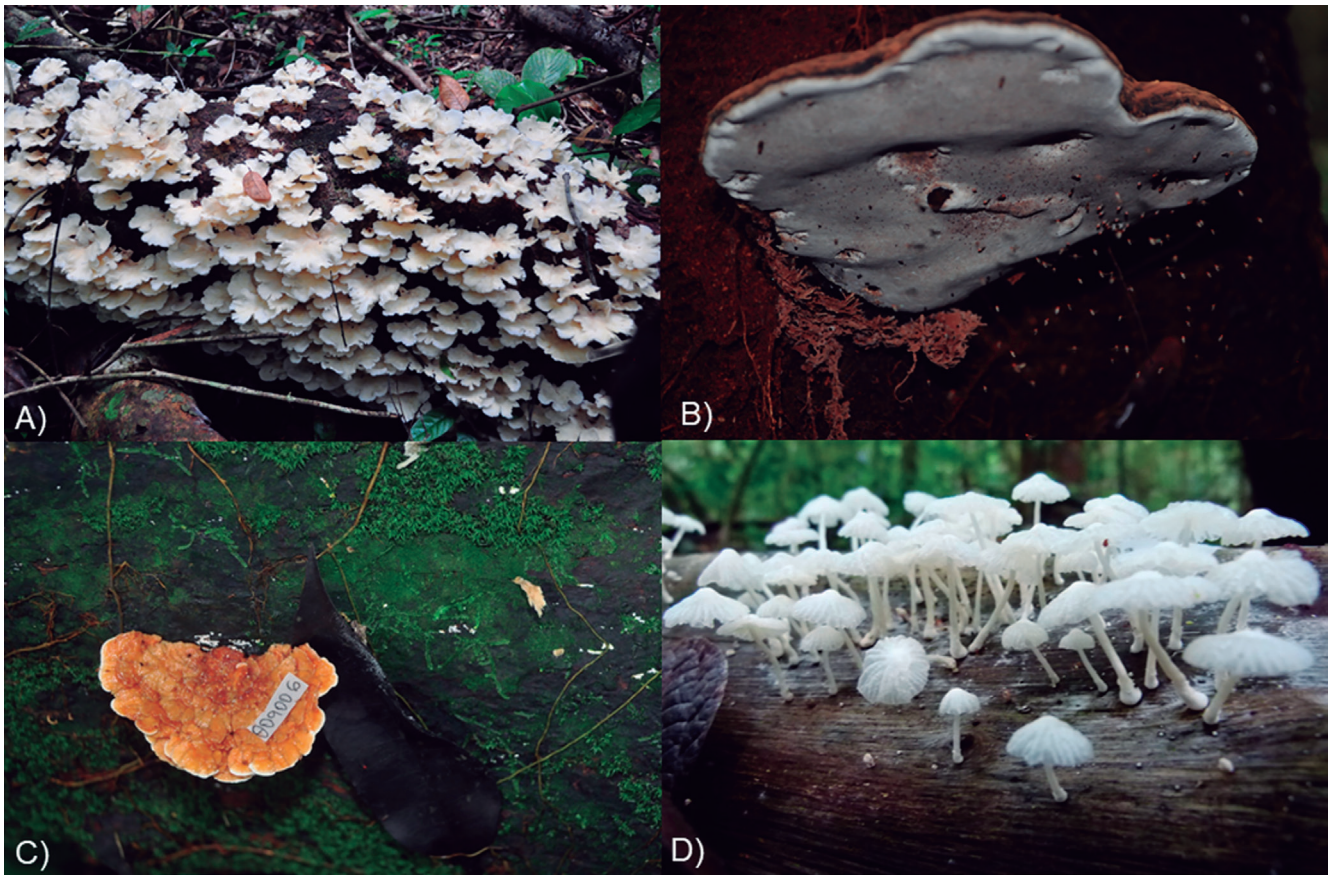


**Figure 3.** Examples of fungal species recorded for Caxiuanã National Forest Reserve: (A) *Favolus tenuiculus,* (B) *Ganoderma australe,* (C) *Rigidoporus lineatus* and (D) *Marasmiellus* sp. 4.

Out of the nine *Mycodrosophila* species found in the Neotropics, only five had been previously recorded in Brazil (Val *et al.,* 1981; Junges *et al.,* 2016). In this study, five *Mycodrosophila* species were observed (Table 1), including the first records of *M. neoprojectans* and *M. pseudoprojectans* to Brazil. Furthermore, our observation of *Z. dimidiata* was the first record of this species in Brazil, and (56%) morphospecies of *Drosophila Zygothrica* and *Hirtodrosophila* might represent new species.

Among the collected Basidiomycetes, the order Polyporales displayed the highest richness of associated Drosophilidae, with 51 species, followed by Agaricales, with 31 species. Among families, Polyporaceae was the most visited by Drosophilidae, with 37 species and 2,350 visitors, followed by Meripilaceae and Omphalotaceae, with 23 species each and drosophilids abundances of 235 and 448, respectively.

## DISCUSSION

The present study represents the largest survey of mycophagous Drosophilidae and their potential hosts in the Brazilian Amazon forest. The 55 species recorded at Caxiuanã National Forest Reserve represent 31% of the Drosophilidae species known to date for the Amazon forest (Bächli, 2017). This study reaffirms that Neotropical mycophagous Drosophilidae are represented primarily by species that belong to the *Zygothrica* genus group (Grimaldi, 1987; Remsen & O'Grady, 2002; Valer *et al.,* 2016). The Drosophilidae richness value obtained in this study was greater than those reported for Australia (van Klinken & Walter, 2001), Japan (Toda *et al.,* 1999), the United States (Lacy, 1984) and the Pampas biome in Southern Brazil (Valer *et al.,* 2016). The estimated richness data are consistent with previous studies (Burla, 1956; Grimaldi, 1987) that hypothesized that the mycophagous fauna might be richer in mature tropical forests.

The Log-Series Series model, which best described the mycophagous Drosophilidae abundance, indicates a guild structured by species dominance in resource utilization, predicts extremely unbalanced abundances among taxa (McGill *et al.,* 2007; McGill, 2011) and identifies the dominant species.

Recurrent records of *Hirtodrosophila, Mycodrosophila, Paraliodrosophila* and *Zygothrica* species in macroscopic fungi confirm mycophagy in these genera (Grimaldi, 1987; Val & Kaneshiro, 1988; Courtney *et al.,* 1990; Valer *et al.,* 2016), as well as their affinity for forest environments, as suggested by Spieth (1987).

The world's records of *M. neoprojectans* were restricted to Central America and Northern South America (Val *et al.,* 1981), with records in Colombia (Bächli, 2017) that are now expanded to Brazil. This species abundance was proportionally high in two fungal species (*F. tenuiculus* and *G. australe*), but the species was also observed in 21 other fungi, showing host versatility. *Mycodrosophila pseudoprojectans,* which also represents a new record for

Brazil, occurs as well in Central America and Northern South America, Colombia and Peru (Bächli, 2017). In this study, *M. pseudoprojectans* exhibited high abundance in three fungal species (*G. australe, Rigidoporus microporus* and *F. tenuiculus*) and occurred in seven other host species, demonstrating polyphagy.

Our observation of *M. brunnescens* in this study is the first since 1952, when the first specimen was collected by Theodosius Dobzhansky in the city of Belém in Pará State, Brazil, although the substrate was not mentioned in that study (Wheeler & Takada, 1963). In the present study, two specimens were recorded, one specimen found in *R. lineatus* and the other found in *G. australe*. This low occurrence suggests that both species are rare and may associate with another substrate that was not recorded in this study.

Another new occurrence for Brazil was a single *Z. dimidiata* specimen found in *F. tenuiculus*. This species was previously recorded in Peru (Wheeler, 1970). In addition, 13 species of the genus *Zygothrica,* three of the genus *Drosophila* and 15 of the genus *Hirtodrosophila* are probably new species.

These results indicate that Drosophilidae that visit fungi in the Amazon forest are represented by species that belong to genera of known mycophagous habits (Throckmorton, 1975; Grimaldi, 1987; Remsen & O'Grady, 2002). This study highlights species of the *Zygothrica* genus group, confirming the hypothesis that genera in this group exhibit mycophagous habits in the Neotropics (Grimaldi, 1990; Remsen & O'Grady, 2002; Valer *et al.,* 2016). Moreover, as shown in the results, these genera are more representative in the Amazon biome.

*Hirtodrosophila* dominated the guild in a fly emergence dataset from the Pampas biome (Valer *et al.,* 2016). However, in the present study, this genus was the most generalist genus with respect to potential hosts, in contrast to observations made by Valer *et al.* (2016). Fly emergence studies for the Amazon biome are needed to corroborate the potential generalist character of *Hirtodrosophila*.

Among the 36 fungal genera recorded, 28 were visited by *Hirtodrosophila,* while *Mycodrosophila, Zygothrica* and *Drosophila* visited 22, 20 and 18 host genera, respectively. In this study and in a study performed by Grimaldi (1987), *Zygothrica* did not occur in fungi of the genera *Pleurotus*. Moreover, *Zygothrica* were not observed in any other genera of the Pleurotaceae. In the Holarctic region *Hirtodrosophila* is commonly recorded in *Collybia* (Yamashita & Hijii, 2007), in this study we recorded two species in *Collybia aurea*.

The family Polyporaceae attracted the highest diversity of flies. These results are in agreement with previous studies that suggested that this family is one of the most utilized by mycophagous Drosophilidae (Grimaldi, 1987; Lacy, 1984; Gottschalk *et al.,* 2009). Polyporaceae displays high species richness in the studied area (Sotão *et al.,* 2009). The Drosophilidae preference for Polyporaceae species may be due to the succulent basidiocarp of these fungi, which facilitates ovipositor penetration and allows more larval mobility, as well as representatives of the family do not present toxic compounds, which can favour the selection by Drosophilidae (Lacy, 1984). Furthermore, the fruiting bodies of these fungi can last for months, allowing the full development of the larvae, while the fruiting bodies of Agaricales are ephemeral, lasting only days or even a few hours (Gugliota & Capelari, 1998).

The availability of fungal species (measured by number of samples and relative frequency) contribute to increase the abundance and species richness of drosophilids visiting the fungi. In fact, Valadão *et al.* (2010) and Döge *et al.* (2015) observed that the availability of resources is the main factor affecting the size of the Drosophilidae populations. We observed that the highest drosophilid richness and abundance were recorded during the 3rd expedition (May, 2014), when *F. tenuiculus* was observed to have high fly abundances. The preference of flies for this species with fleshy basidiocarp could be due to the fungal quality (Courtney *et al.,* 1990) and with large fruiting bodies in the substrates (Fig. 3a). However, given that *F. tenuiculus* is ephemeral, heterogeneously distributed throughout the Caxiuanã National Forest Reserve and highly abundant at certain periods within the wet season (Medeiros *et al.,* 2015), it is not possible to state that this species is responsible for maintaining guild richness. It is possible that the high attractiveness of *F. tenuiculus* is the result of both substrate quality and the influence of rainfall. In fact, Valadão *et al.* (2010) and Carvalho (2014) observed that fruit substrates were more attractive to flies during high rainfall periods.

Finally, the fungal richness and abundance at Caxiuanã National Forest Reserve were the factors that determined the diversity of mycophagous Drosophilidae. This observation is consistent with the predicted outcome of a strategy that includes the utilization of a temporally and spatially unpredictable resource. Due to such unpredictability, the evolution of specialization mechanisms is unlikely (Kimura *et al.,* 1978; Jaenike, 1978). However, considering that fruiting bodies are nearly absent during periods of lower rainfall, the strategies employed by these species to survive the lack of resources remains unknown.

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