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Research article

# Co-Infestation and Spatial Distribution of *Bactrocera carambolae* and *Anastrepha* spp. (Diptera: Tephritidae) in Common Guava in the Eastern Amazon

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## Abstract

Field infestation and spatial distribution of introduced *Bactrocera carambolae* Drew and Hancock and native species of *Anastrepha* in common guavas [*Psidium guajava* (L.)] were investigated in the eastern Amazon. Fruit sampling was carried out in the municipalities of Calçoene and Oiapoque in the state of Amapá, Brazil. The frequency distribution of larvae in fruit was fitted to the negative binomial distribution. *Anastrepha striata* was more abundant in both sampled areas in comparison to *Anastrepha fraterculus* (Wiedemann) and *B. carambolae*. The frequency distribution analysis of adults revealed an aggregated pattern for *B. carambolae* as well as for *A. fraterculus* and *Anastrepha striata Schiner*, described by the negative binomial distribution. Although the populations of *Anastrepha* spp. may have suffered some impact due to the presence of *B. carambolae*, the results are still not robust enough to indicate effective reduction in the abundance of *Anastrepha* spp. caused by *B. carambolae* in a general sense. The high degree of aggregation observed for both species suggests interspecific co-occurrence with the simultaneous presence of both species in the analysed fruit. Moreover, a significant fraction of uninfested guavas also indicated absence of competitive displacement.

**Key words**: invasive species, fruit flies, negative binomial distribution, Brazil

Habitat invasion by exotic species is a global problem (Davis 2009). Although only a small fraction of the introduced species reach high population levels, when they do so, they can cause substantial ecological and economic impact, thus posing serious challenges to such diverse areas as biology, agriculture, transportation, and economy (Pimentel et al. 2000, Mooney and Cleland 2001, Peterson 2003, Liebhold and Tobin 2007). In the last decades, biological invasions have become the focus of a growing number of studies involving ecology, economics, evolution, biogeography, and genetics (Malacrida et al. 2007, Lockwood et al. 2013).

Once established, exotic species can impact native biodiversity by altering habitats, spreading diseases, hybridising with or competing with native species (Davis 2009). Interspecific competition is one of the most important interactions resulting from biological invasions and also one of the main factors responsible for the success of invasive species (Holway and Suarez 1999, Parker et al. 2006, Romero et al. 2014, Devescovi et al. 2015, Park and Potter 2015). Interspecific competition can either result in the complete displacement of one of the species or the evolution of a stable coexistence between the two species. In fact, it has been demonstrated that there are several mechanisms that are important in the invasion process as they can keep interspecific competition under a tolerable threshold (cf. Duyck et al. 2004, 2006a; Davis 2009; Ekesi et al. 2009; Devescovi et al. 2015).

Most agricultural pests are invasive exotic species (Lockwood et al. 2013). Multiple cases of invasion of new areas by tephritids have been reported, such as *Bactrocera dorsalis* (Hendel) in Hawaii, Australia (as *Bactrocera papayae* Drew and Hancock; subsequently eradicated), and Africa *Bactrocera invadens* Drew, Tsuruta and White; both *B. invadens* and *B. papayae* are now considered synonyms of *B. dorsalis* according to Schutze et al. (2015); *Ceratitis capitata* (Wiedemann), *Ceratits rosa* (Karsch), and *Bactrocera zonata*

(Saunders) on the island of La Réunion; and *Bactrocera carambolae* Drew and Hancock in Suriname, French Guyana, and northern Brazil (Sauers-Muller 1991, Lux et al. 2003, Duyck et al. 2006a, De Meyer et al. 2010, Lemos et al. 2014).

The impact of invasive fruit flies on native species has been intensively studied on the island of La Réunion, where *Ceratitis catoirii* Guérin-Méneville (native), *C. capitata*, *C. rosa*, and *B. zonata* (exotic) currently occur. These studies indicate that the pattern of interaction observed suggests hierarchical competition, a mode in which one of the species dominates and influences the abundance of other species (Duyck et al. 2006a,b, 2008). In most cases studied so far, complete exclusion after tephritid invasions has not been observed. However, competitive displacements and a significant decline in the abundance of native species have been reported, particularly in the case of *C. catoirii*, which is nearly extinct in La Réunion (Duyck et al. 2004, 2006a, 2008). Invasion processes, even though many times may result in the displacement of native species, do not always do so instantly as they depend on the action of different competition mechanisms also including the mediation by noncompetitive factors, e.g., lack of an alternative host, differential impact of natural enemies, metapopulation structure, and adaptation to local conditions (Reitz and Trumble 2002).

Niche partitioning and refuge use by native species may result from competition and have been largely used to explain the coexistence of species at a regional scale. At the smallest scale (e.g., host plant), it is possible that the coexistence of invasive and native species is related to the ability of species to exploit different climates and to avoid fruit previously infested by exotic invasive species (Duyck et al. 2004, Devescovi et al. 2015).

Spatial distribution can have a substantial effect in allowing the coexistence of Tephritidae species that share the same resource. In the model proposed by Atkinson and Shorrocks (1981) for insects that feed on discrete and ephemeral habitats (e.g., fruit, dead wood, carrion), aggregation seems to be paramount for coexistence. The authors suggest that two processes can lead to a more prolonged coexistence in a two-species system, namely increased resource division and increased aggregation of the competitors (Atkinson and Shorrocks 1981). If we suppose that two species can use distinct nutritional resources when sharing the same substrate, then intraspecific aggregation could help each species to better exploit the available resources, which in its own turn would allow cooccurrence and potentialize stable coexistence. Also, there are various evidences indicating that larval aggregation is important in Diptera to improve burrowing, reduce parasitism, and increase the efficiency of the feeding process by the simultaneous movement of mouth hooks and secretion of salivar and proteolytic enzymes by multiple individuals (Goodbrod and Goff 1990, Durisko et al. 2014). Studies aimed at ascertaining the spatial distribution of fruit flies using both adult trapping and fruit sampling have showed different levels of aggregation. However, the mechanisms responsible for this pattern within Tephritidae are still not completely understood (cf. Satarkar et al. 2009, Birke and Aluja 2011, Soemargono et al. 2011, Jahnke et al. 2014, Devescovi et al. 2015).

*Bactrocera carambolae*, the carambola fruit fly, is native to Indonesia, Malaysia, and Thailand. It has invaded Suriname (Paramaribo in 1975) and is now found in Guyana, French Guiana, and northern Brazil (Sauers-Müller 2005, Godoy et al. 2011). This species infests more than 150 fruit species and is considered a quarantine pest insect in the Caribbean region (Malavasi et al. 2000a, Haq et al. 2015).

In Brazil, *B. carambolae* was first reported in 1996 in the municipality of Oiapoque, state of Amapá, where it occurs in sympatry with native species in the genus *Anastrepha*, even sharing the same host species (Godoy et al. 2011, Lemos et al. 2014). In recent studies in Brazil, *B. carambolae* has been reported infesting guava (*Psidium guajava* L.) at a relatively high abundance when compared with *Anastrepha* species, except for *Anastrepha striata* Schiner (Lemos et al. 2014). However, despite being in the country for 20 years and its significant economic importance, data on *B. carambolae* population dynamics, demography, host preference, and its impact on the community of native tephritids are scarce.

In this study, we evaluated field infestation and spatial distribution of *B. carambolae* and native species of *Anastrepha* in common guava in the eastern Amazon, where the carambola fruit fly was detected for the first time in Brazil. We hypothesized that the spatial distribution pattern of fruit fly species infesting guavas in the studied area is aggregated.

## Materials and Methods

### Study Area and Sampling

Fruit sampling was carried out in the municipalities of Calçoene (02°33′N, 50°56′W) and Oiapoque (03°50′N, 51°50′W) in the northernmost region of the state of Amapá, in the Brazilian Amazon. The climate is defined as Am (monsoon) with annual rainfall over 3,000 mm (Alvares et al. 2013). The native vegetation in the region is typical of upland forest (IEPA 2002).

Collections were carried out in April, June, July, and December of 2013. In each site, six guava trees ~100 m from each other were randomly selected. A total of 30 fruit equally distributed among trees was collected at each sampling occasion, totalling 90 fruit per municipality. Fruit were collected both from the trees and from the ground among those that had recently fallen. The fruit collected from trees were completely ripe, a criterion that was adopted to reduce the probability of understimating infestation, as such fruit were about to fall from the tree. Fruit collected from the ground were carefully examined and those that had holes or cuts in the peel were not sampled as the larvae could have already left the fruit. The collected fruit were placed individually in plastic containers with a layer of sterelized sand. Every 3 d, all containers were checked and all puparia obtained were counted and transferred into 30-ml plastic containers with a layer of moist vermiculite at the bottom and covered with voile cloth until adults emerged. The containers were placed in a growth chamber at controlled temperature (26.5 ± 0.3°C), RH (70 ± 5%), and a photoperiod of 12:12 (L:D) h and checked daily for emerged adults.

Guava was chosen as substrate to investigate larval distribution per fruit as it is the preferred tephritid host in northern Brazil (Zucchi et al. 2011). Moreover, previous studies carried out in the state of Amapá verified that *B. carambolae* has frequently shared this host with native *Anastrepha* spp. (Lemos et al. 2014). Additionaly, guava is widespread in the state of Amapá fruiting from December to June and it is either cultivated without any phytosanitary management in backyards in urban and rural areas or grows along roads near the native vegetation.

### Insect Identification

*Anastrepha* and *Bactrocera* specimens were identified according to Zucchi (2000) and Drew and Hancock (1994), respectively. Voucher specimens were deposited at the Laboratório de Entomologia, Empresa Brasileira de Pesquisa Agropecuária - Embrapa, Amapá, Brazil.

### Data Analysis

*Fruit Infestation and Fruit Fly Abundance*. The average levels of infestation were calculated dividing the number of puparia by the mass (grams) of the fruit. We quantified the percentage of fruit infested by only one species of fruit fly, the percentage of coinfested fruit (fruit infested by more than one species), and the percentage of noninfested fruit. Abundance was considered as the proportion of individuals within the same species relative to the total number of individuals in the sample.

*Spatial Distribution of Fruit Flies*. In order to quantify spatial distribution, fruit infestation levels and abundance were described considering the collection sites, i.e., compiling data from different trees. Males and females were grouped together in the analysis and a table of frequency distribution considering the fruit as the sampling unit was constructed. A frequency class interval was constructed considering data of the total absence of individuals from zero (i.e., uninfested fruit) to the highest abundance of tephritids per fruit. Frequency distribution graphs were prepared for both *B. carambolae* and *Anastrepha* spp. and the mean and variance of the distribution were estimated considering the number of sampling units and the frequency of each unit. To evaluate aggregation level, the $k$ parameter of the negative binomial distribution was also estimated (Southwood and Henderson 2000). The highest aggregation level occurs when the value of $k$ tends towards zero. The best estimate of $k$ was also determined by the method of maximum likelihood (Ludwig and Reynolds 1988). The fit of the negative binomial distribution was tested by comparing the observed frequencies with the expected frequencies by the Pearson $\chi^2$ test (Crawley 2007). The algorithm was written in the R statistical programming language based on Crawley (2007). The analyses were carried out using R software (R Core Team 2014).

## Results

### Infestation Levels and Abundance

In Calçoene, a total of 910 puparia was obtained and there was emergence of fruit flies from 58.8% of them and from the remaining 41.2% no emergence was registered. The species reared from the collected fruit were *Anastrepha fraterculus* (Wiedemann) (5, 0.9%), *A. striata* Schiner (397, 74.2%), and *B. carambolae* (133, 24.9%). Fruit infestation in this locality ranged from 0.02 to 1.21 puparia/g of fruit (mean 0.34). In Oiapoque, a total of 1,090 puparia was obtained and fruit flies emerged from 76.1% of them and there was no emergence out of the remaining 23.9%. The species reared from the collected fruit were *A. fraterculus* (3, 0.4%), *A. striata* (650, 78.3%), and *B. carambolae* (177, 21.3%). Fruit infestation in this locality ranged from 0.02 to 2.94 puparia/g of fruit (mean 0.41). The abundance of *A. striata* was higher than that of *A. fraterculus* and *B. carambolae* in both sampling areas. No parasitoid emergence was observed in either collection site. The proportion of noninfested fruit was higher in Calçoene, which had a direct impact on the number of puparia obtained. The pattern of fruit infestation observed in both sites is shown on Table 1.

Considering only the coinfested fruit, there was a change in pattern, in which *B. carambolae* became the more abundant species accounting for >50% of the individuals in both sampling areas (Table 2). In Calçoene, *A. striata* and *B. carambolae* co-occurred in eight fruit and *A. striata* and *A. fraterculus* in three fruit. In Oiapoque, *A. striata* and *B. carambolae* co-occurred in 13 fruit, *A. fraterculus* and *A. striata* in one fruit, *A. fraterculus* and *B. carambolae* in one fruit and *A. fraterculus*, *A. striata*, and *B. carambolae* in one fruit.

**Table 1.** Proportion of infested fruit

| Locality | Number of infested fruit | | | | |
|---|---|---|---|---|---|
| | Only by *A. fraterculus* | Only by *A. striata* | Only by *B. carambolae* | Coinfested | Uninfested |
| Calçoene | 0 (0%) | 48 (53.3%) | 4 (4.4%) | 11 (12.2%) | 27 (30%) |
| Oiapoque | 0 (0%) | 59 (65.6%) | 4 (4.4%) | 16 (17.8%) | 11 (12.2%) |

**Table 2.** Abundance of *A. fraterculus*, *A. striata*, and *B. carambolae* in coinfested fruit

| | Number of coinfested fruit | Puparia | *A. fraterculus* | *A. striata* | *B. carambolae* |
|---|---|---|---|---|---|
| Calçoene | 11 | 185 | 5 (3.7%) | 28 (20.7%) | 102 (75.6%) |
| Oiapoque | 16 | 342 | 3 (1.3%) | 85 (35.7%) | 150 (63%) |

### Spatial Distribution

The observed distribution frequency of *A. fraterculus*, *A. striata* e *B. carambolae* is shown in Figure 1 for both sampling areas. In all cases, the variance was higher than the mean, which suggests an aggregated distribution pattern described by the negative binomial distribution.

The values estimated for the aggregation coefficient ($k$) are close to zero, which also suggests that the fruit fly community distribution in guava is aggregated in both areas sampled, despite the difference in magnitude between them, since the population of *A. striata* in Oiapoque showed a lower degree of aggregation when compared with the others (Table 3).

In both areas, the chi-square values were lower than the critical value in the table ($\chi^2 = 0$, df = 34; $\chi^2 = 0$, df = 34 e $\chi^2 = 0$, df = 25 in Calçoene and $\chi^2 = 0$, df = 3; $\chi^2 = 0$, df = 30; $\chi^2 = 0$, df = 53 in Oiapoque for *A. fraterculus*, *A. striata*, and *B. carambolae*, respectively), indicating that the observed values are significantly explained by the negative binomial distribution, which suggests an aggregated distribution. The expected and observed values of frequency distributions are shown in Figure 2.

## Discussion

This is the first study to evaluate the infestation pattern and spatial distribution of *B. carambolae* and *Anastrepha* spp. in areas where there is host overlap. Previous studies carried out in the state of Amapá revealed that *B. carambolae* infests fruit commonly used by *Anastrepha* species (Lemos et al. 2014).

In this study, we verified that *A. striata* is the most abundant species in both areas, and most fruit were infested only by this species (Table 1). In Brazil, *A. striata* is the most abundant species in guava only in the Amazon region, where it is commonly reported as either the only species infesting guavas or the most abundant when other fruit fly species are also present (cf. Silva et al. 2007a,b; Deus et al. 2009; Pereira et al. 2010; Jesus-Barros et al. 2012; Marsaro-Júnior et al. 2013).

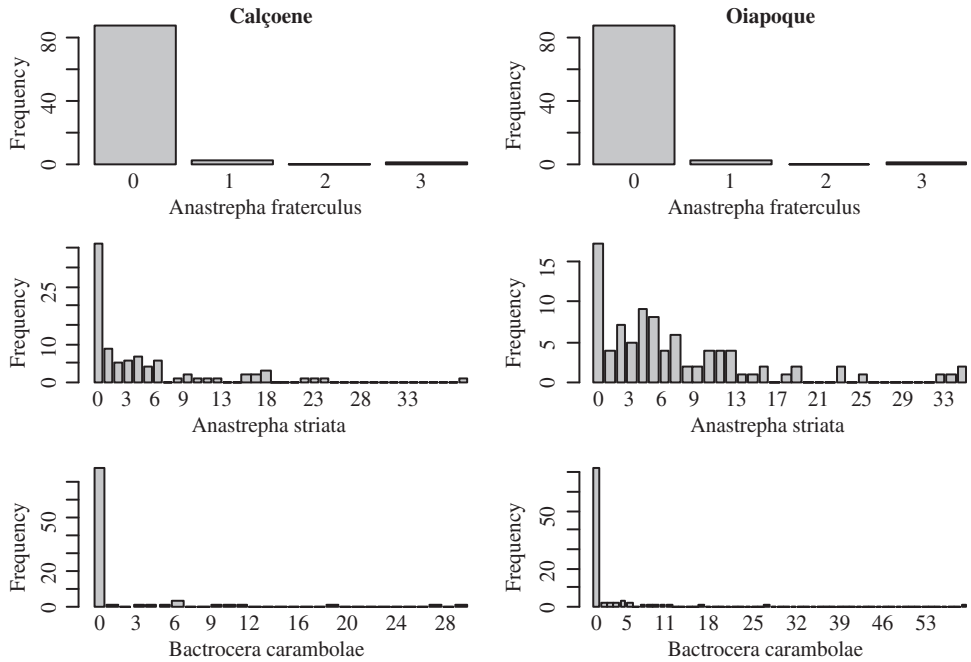


**Fig. 1.** Frequency of *A. fraterculus*, *A. striata*, and *B. carambolae* in the sampling areas indicating the distribution of emerging adults (x axis) from the fruits. Numbers on the x axis determine the class interval, showing data from the total absence of individuals (i.e., uninfested fruit) to the highest abundance of tephritids per fruit.

**Table 3.** Frequency distribution of *A. fraterculus*, *A. striata*, and *B. carambolae* in guava

| Species and locality | Mean ($\bar{x}$) | Variance ($s^2$) | $K^a$ | $K^b$ |
|---|---|---|---|---|
| *A. fraterculus* in Calçoene | 0.05 | 0.12 | 0.047 | 0.039 |
| *A. striata* in Calçoene | 4.4 | 45.07 | 0.475 | 0.396 |
| *B. caramboale* in Calçoene | 1.47 | 23.01 | 0.101 | 0.084 |
| *A. fraterculus* in Oiapoque | 0.06 | 0.12 | 0.06 | 0.06 |
| *A. striata* in Oiapoque | 7.2 | 60.70 | 0.968 | 0.852 |
| *B. caramboale* in Oiapoque | 1.94 | 47.38 | 0.083 | 0.071 |

[a]initial estimate of $K\left(\frac{\bar{x}}{(s^2-\bar{x})}\right)$.

[b]estimated using the method of maximum likelihood $\left(\log_{10}\left(\frac{N}{N_0}\right) = K^*\log_{10}\left[1+\left(\frac{\bar{x}}{k}\right)\right]\right)$, where $N$ is the total number of sampling units and $N_0$ is the number of sampling units with zero individuals.

*A. fraterculus* represented <1% of the specimens reared. Even though it is the fruit fly species with the widest geographical distribution in Brazil, its frequency and distribution are significantly reduced northwards. In the Southern region, this species has been reported to have a frequency higher than 95% in guava (Nunes et al. 2012, Jahnke et al. 2014). However, for the Northern region, *A. fraterculus* is a secondary species with marginal distribution (Malavasi et al. 2000b, Silva and Ronchi-Teles, 2000). In the state of Amapá, *A. fraterculus* has eight known hosts; however, it has low frequency and low abundance. The highest populational density was observed in fruit of *Mouriri acutiflora* Naudin (Melastomataceae), a typical species of the Amazon forest (Deus and Adaime 2013). So far, there are no studies that explain the low abundance of *A. fraterculus* and the high abundance of *A. striata* in guava in the Northern region, however, it is likely that behavioral aspects together with environmental factors are responsible for the pattern observed here. Therefore, additional studies are necessary to elucidate this question.

*B. carambolae* represented 24.9 and 21.3% of all fruit flies reared from fruit collected in Calçoene and Oiapoque, respectively, with a higher abundance in coinfested fruit (Table 2). Several studies have demonstrated that species within the *dorsalis* complex have a marked preference for ripe fruit (cf Alyokhin et al. 2000, Cornelius et al. 2000, Rattanapun et al. 2009, Quilici et al. 2014). Even though *B. carambolae* belongs to the *dorsalis* complex, there are no studies on the influence of the degree of fruit ripeness on female oviposition decision in this species. Thus, additional studies are necessary to test this hypothesis.

The high aggregation pattern observed in this study corroborates similar findings in other tephritids (cf. Dimou et al. 2003, Satarkar et al. 2009, Soemargono et al. 2011, Jahnke et al. 2014). The evaluation of the spatial distribution of species requires analytical tools that can estimate characteristic parameters and indicate dispersion patterns, which generally are the expression of individual behavior as evidenced by the magnitude of the values found (Taylor 1984). Additionally, factors such as the environmental heterogeneity, resource availability, and presence of natural enemies can influence spatial distribution (Waters 1959, Satarkar et al. 2009).

*A. fraterculus*, *A. striata*, and *B. carambolae* use guava as a host in their area of natural distribution. Thus, when there is resource overlap, the response of the native species to the presence of the potential exotic competitor is paramount for the persistence of the former. Likewise, the strategy employed by the invading species is crucial for its establishment in the presence of native species. As postulated by Atkinson and Shorrocks (1981), the increase in resource division and aggregation of competitors may decrease the effect of competitive displacement. When it comes to a specific and ephemeral resource, the high degree of aggregation of *A. fraterculus*, *A. striata*, and *B. carambolae* in the fruit indicates potential for the coexistence of tephritids in guava in the northern region of Brazil. There are probably other factors involved, including abiotic factors, which can have an influence upon the spatial distribution and that should be taken into account in future studies.

The results reported herein suggest that *A. striata* is the most abundant species in both sampling areas, even though other

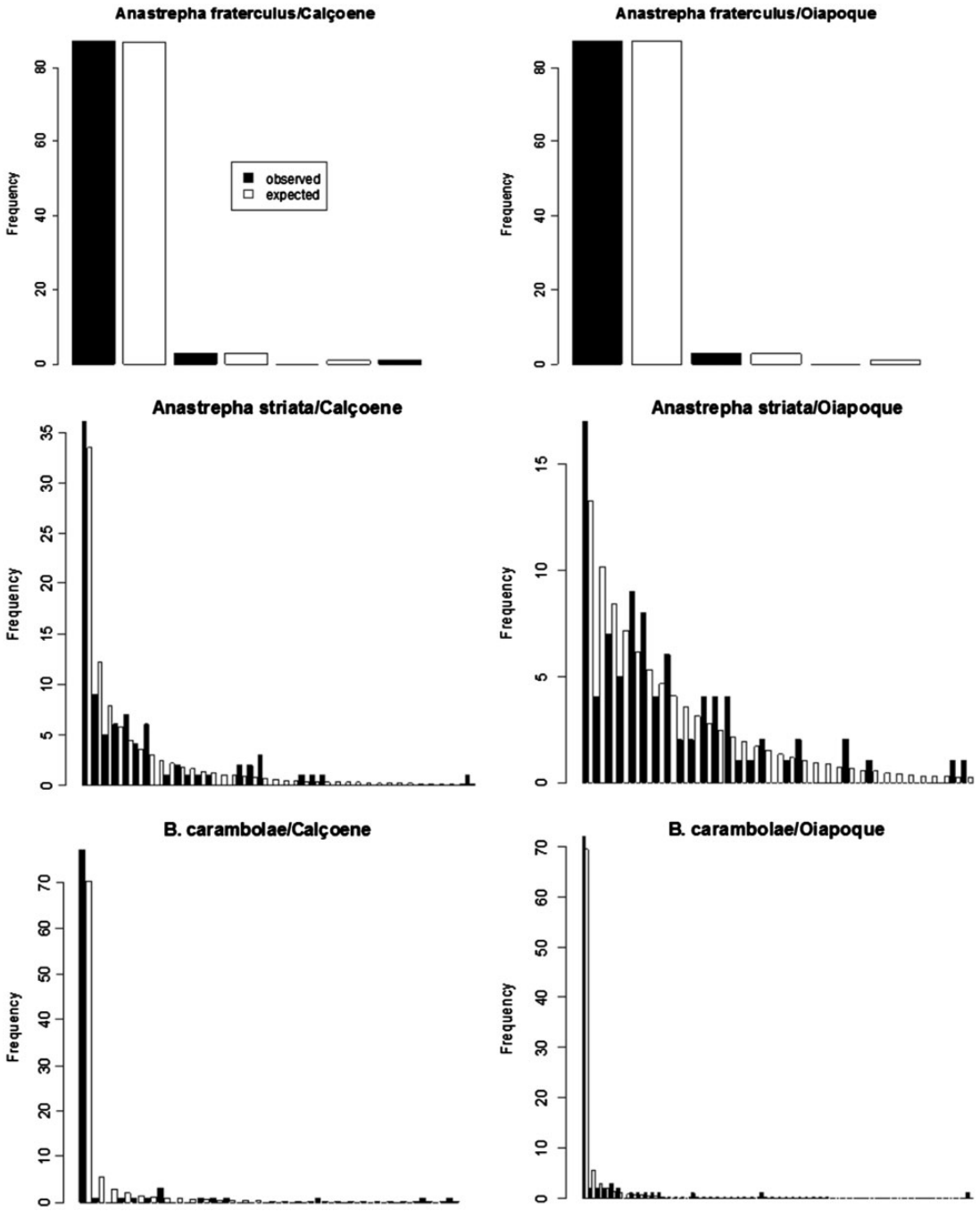


**Fig. 2.** Expected and observed frequency distribution of *A. fraterculus, A. striata,* and *B. carambolae* in the sampling areas.

Tephritidae species are also present. Our results also indicate that the spatial distribution of *Anastrepha fraterculus*, *A. striata*, and *B. carambolae* in guava follows a negative binomial distribution, i.e., it is aggregated.

Finally, we consider that basic biology studies are needed for the understanding of the mechanisms involved in the coexistence of species. Among these sudies, we could include the influence of coloration and degree of fruit ripeness in the preference and larval development of *B. carambolae*, the response of *B. carambolae* to volatiles of different fruit species, its distribution pattern in the presence and absence of competitors, and the influence of abiotic factors in community structuring. Such studies are paramount for the understanding of the processes driving fruit fly community dynamics on guava in the Amazon region. Moreover, the data generated will be a valuable tool for the development of management strategies.

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