Research Article

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Carambola fruit fly in Brazil: new host and first record of associated parasitoids

https://doi.org/10.1515/flaent-2024-0053
Received July 14, 2024; accepted October 15, 2024;
published online January 22, 2025

Abstract: *Bactrocera carambolae* Drew & Hancock (Diptera: Tephritidae), the Carambola fruit fly, is an invasive species in South America. This work aims to confirm the expansion of the host range of *B. carambolae* and report the occurrence of its parasitism in Brazil. The study was carried out in the Jari Valley region, Pará, Brazil. Two types of sampling of *Terminalia catappa* L. (Combretaceae) were carried out: one with grouped fruits to verify if they were infested by *B. carambolae* (Sites A, B, C) and the other with individualized fruits to investigate parasitism (Site C). Morphological analysis was done to confirm parasitism, based mainly on the cephalopharyngeal skeleton embedded in the opercula of the puparia. From the sampling with grouped *T. catappa* fruit, 2,841 fruit fly puparia were obtained, from which 480 *B. carambolae* specimens and 1,228 specimens of *Anastrepha* spp. Schiner (Diptera: Tephritidae) emerged. Site C was the one with the highest fruit fly infestation of *T. catappa* fruits. We conclude that *T. catappa* is a moderately good host at Site A and a good host at Sites B and C. From the samplings with individualized fruits of *T. catappa*, an adjusted parasitism index of 21.2 % was obtained for *Anastrepha* spp. and 1.8 % for *B. carambolae*, confirming the presence of the parasitoids *Doryctobracon areolatus* (Szépligeti), *Utetes anastrephae* (Viereck) (Hymenoptera: Braconidae), and *Aganaspis pelleranoi* (Brèthes) (Hymenoptera: Figitidae). The native parasitoids *D. areolatus*, *U. anastrephae*, and *A. pelleranoi* were reported for the first time parasitizing *B. carambolae* larvae in Brazil.

Keywords: Amazon; fruit flies; *Bactrocera carambolae*; parasitism

Resumo: *Bactrocera carambolae* Drew & Hancock (Diptera: Tephritidae), a mosca-da-carambola, é uma espécie invasora na América do Sul. Este trabalho tem como objetivo confirmar a expansão da gama de hospedeiros da *B. carambolae* e relatar a ocorrência de seu parasitismo no Brasil. O estudo foi realizado na região do Vale do Jari, Pará, Brasil. Foram realizados dois tipos de amostragem de *Terminalia catappa* L. (Combretaceae): uma com frutos agrupados para verificar se estavam infestados por *B. carambolae* (locais A, B, C) e outra com frutos individualizados para investigação de parasitismo (local C). Foi realizada uma análise morfológica para confirmar a ocorrência de parasitismo, baseada principalmente no esqueleto cefalofaríngeo incrustado nos opérculos dos pupários. Da amostragem com frutos agrupados de *T. catappa* foram obtidos 2.841 pupários de moscas-das-frutas, dos quais 480 exemplares de *B. carambolae* e 1.228 exemplares de *Anastrepha* spp. Schiner (Diptera: Tephritidae). O local C foi o que apresentou maior infestação

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de frutos de *T. catappa*. Concluímos que *T. catappa* é um hospedeiro moderadamente bom no local A, e um bom hospedeiro nos locais B e C. A partir das amostragens dos frutos individualizados de *T. catappa*, foi obtido um índice de parasitismo ajustado de 21,2 % para *Anastrepha* spp. e 1,8 % para *B. carambolae*, confirmando a presença dos parasitoides *Doryctobracon areolatus* (Szépligeti), *Utetes anastrephae* (Viereck) (Hymenoptera: Braconidae) e *Aganaspis pelleranoi* (Brèthes) (Hymenoptera: Figitidae). Os parasitoides nativos *D. areolatus*, *U. anastrephae* e *A. pelleranoi* foram relatados pela primeira vez parasitando larvas de *B. carambolae* no Brasil.

Palavras-Chave: Amazônia; Moscas-das-frutas; *Bactrocera carambolae*; parasitismo

1 Introduction

Bactrocera carambolae Drew & Hancock (Diptera: Tephritidae), commonly known as the Carambola fruit fly, is native to Southeast Asia, specifically in the region formed by Indonesia, Malaysia, and Thailand (Vijaysegaran and Oman 1991). In South America, it is an invasive species reported in Suriname, French Guiana, Guyana, and Brazil (Malavasi 2015). In Brazil, *B. carambolae* was first recorded in 1996 in the municipality of Oiapoque, Amapá. It is currently distributed in restricted areas of Amapá, Pará and Roraima and is classified as a quarantine pest present in the country (Castilho et al. 2019; MAPA - Ministry of Agriculture and Livestock 2018). This pest is considered as the main phytosanitary barrier to the export of fruits produced in Brazil as its simple presence in production areas can lead to the loss of important import markets (Garcia et al. 2024; Miranda and Adami 2015). The dispersion of *B. carambolae* to other fruit-producing regions in Brazil could generate an estimated loss of US$ 35.7 million (R$ 175 million) in its first three years, taking into account only national mango production. Regarding exports, the estimated loss would be approximately US$ 38.7 million (R$ 190 million), starting from the fourth year of the phytosanitary embargo (Lima et al. 2018; Miranda et al. 2015).

The Regional Program for the Eradication of *B. carambolae* in South America was created in 1996, which involved the four South American countries affected by this pest (Brazil, French Guiana/France, Guyana, and Suriname). Because of a reduction in funding, the program ended in 2001, coinciding with a new spread of the pest species (Godoy et al. 2011a; Midgarden et al. 2016). In Brazil, immediately after the first detection of *B. carambolae*, The National Carambola Fruit Fly Eradication Program was created, coordinated by the Department of Plant Health, linked to the Agricultural Defense Secretariat of the Ministry of Agriculture and Livestock (MAPA), with the objective of monitoring and controlling *B. carambolae*, aiming at its eradication (Godoy et al. 2011a). Nowadays this program is called Suppression Subprogram for the Eradication of *B. carambolae* (SSEBC).

The selection of a host plant by a pest involves a dynamic hierarchy of various aspects (Aluja and Mangan 2008). According to Aluja and Mangan (2008), a natural host is a fruit or plant species that is unequivocally found infested under completely natural field conditions, i.e., where nothing is manipulated. Identifying natural hosts by sampling fruit allows for identification of various ecological traits of the pest, which is fundamental for establishing management strategies. Furthermore, knowing the plant species used by *B. carambolae* for the development of its larvae is crucial for the inspection and control actions carried out by official plant health defense agencies in Brazil. On the other hand, sampling fruits enables the determination of the presence of fruit fly natural enemies (Malavasi et al. 2013).

In Brazil, intense fruit collection in natural conditions has already been conducted by the Amazon Fruit Fly Research Network between 2004 and 2024, and 35 host plant species of *B. carambolae* have been identified and confirmed, belonging to 14 botanical families, with a preference for Myrtaceae (nine species) (Adaime et al. 2023; Costa et al. 2023a, 2023b, 2024; Lemos et al. 2024).

According to Wharton (1989), Ovruski (1994), and Dias et al. (2022), the most important natural enemies of fruit flies are parasitoid species in the subfamily Opiinae (Hymenoptera, Braconidae). In the Brazilian Amazon, two families of fruit fly parasitoids stand out: Braconidae, represented by the subfamilies Alysiinae (*Asobara*) and Opiinae (*Doryctobracon*, *Opius* and *Utetes*), and Figitidae whose highlight is the Eucoilinae subfamily (*Aganaspis* and *Odontosema*) (Silva et al. 2011a). Eleven species of fruit fly parasitoids have been recorded, eight of which belong to the Braconidae family. The opiines *Doryctobracon areolatus* (Szépligeti) and *Opius bellus* Gahan are the most widely distributed species, reported in all the region states of the Brazilian Amazon (Sousa et al. 2021a). Specifically in the state of Amapá, seven other species of fruit fly parasitoids have been identified [see details in Sousa et al. (2021a)]. Undeniably, *D. areolatus* is the predominant species, representing more than 50 % of the specimens in different studies conducted in the state, and is associated with various species of fruit flies in wild and cultivated hosts. The other parasitoid species are considered to be frequent, but are generally fewer (Deus and Adaime 2013).

In 2000, there have been attempts to release the exotic parasitoid *Diachasmimorpha longicaudata* (Ashmead) to control *B. carambolae* at the border between Amapá and French Guiana (Vayssières et al. 2013). In 2013, Embrapa, in cooperation with MAPA imported the parasitoid *Fopius arisanus* (Sonan) (Hymenoptera: Braconidae), from the United States Department of Agriculture (USDA), as an alternative for the biological control of *B. carambolae* (Lima et al. 2017). The research is still in the laboratory phase.

In Brazil, there is no record of a native parasitoid associated with *B. carambolae* (Adaime et al. 2023). Over almost two decades of work by the Amazon Fruit Fly Research Network and more than 3,000 kg of fruit sampled in Amapá, no native parasitoid species have been observed associated with *B. carambolae* (Costa et al. 2022). Additionally, in French Guiana, no native parasitoid species emerged from samples of *B. carambolae* from 2001 to 2003, with the exception of some specimens of *Aganaspis pelleranoi* (Brèthes) (Hymenoptera: Figitidae) (Vayssières et al. 2013). The authors argue that there is no evidence that local parasitoids have not developed the ability to detect and attack immature stages of *B. carambolae*. So, it is possible that parasitoids attack the larvae but fail to develop due to poor suitability of the host fruit or a strong response from the immune system of *B. carambolae*. In Suriname, van Sauers-Muller (2005) collected fruit from various plant species, including native species, over a 16-year period (from 1986 to 2002), and did not observe parasitism in *B. carambolae*. Thus, there are no reports of native parasitoids of *B. carambolae* from the Braconidae family on the American continent.

Studies conducted in the native range of *B. carambolae*, including Thailand and Malaysia, report parasitoids from the Opiinae subfamily, especially *D. longicaudata*, *F. arisanus*, *Fopius vandenboschi* (Fullaway), *Psyttalia incisi* (Silvestri), *Psyttalia makii* (Sonan), *Psyttalia* sp. nr. *fletcheri*, and *Psyttalia* sp. nr. *makii* (Chinajariyawong et al. 2000). In addition, *D. longicaudata* has been identified in Malaysia as a solitary endoparasitoid of *B. carambolae* larvae (Ibrahim et al. 1994; Stibick 2004). In Malaysia, Yaakop and Aman (2013) demonstrated a tritrophic association between *F. arisanus*, *B. carambolae*, and *Syzygium samarangense* (Blume) Merr. & L. M. Perry (Myrtaceae); however, these findings were not seen in Thailand (Yu et al. 2005).

In Brazil, mainly in Amapá, further studies should be conducted to verify the possible existence of new parasitoid associations, especially for the biological control of *B. carambolae*. This work aims to confirm the expansion of the host range of *B. carambolae* and report the occurrence of parasitism by native parasitoids.

2 Materials and methods

Fruit sampling was carried out based on the suspicion that *B. carambolae* could have expanded its host range in Brazil and suggests the possible occurrence of parasitism.

2.1 Study area

The study was carried out in the Jari Valley region, located between the south of the state of Amapá and the north of the state of Pará, Brazil. The fruit was sampled in the municipality of Laranjal do Jari (Amapá) and in the district of Monte Dourado, in the municipality of Almeirim (Pará) (Figure 1). Laranjal do Jari is 275 km from the capital, Macapá, via the BR-156 highway. The district of Monte Dourado, in Almeirim, is approximately 450 km from the capital, Belém (Godoy et al. 2011b).

The climate in the region is characterized as hot, humid equatorial (Am-Köppen-Geiger classification) (Peel et al. 2007), with a rainfall regime marked by two well-defined seasons: rainy (January–July) and dry (August–December). The average annual temperature is approximately 26 °C (minimum 22 °C and maximum 34 °C). Vegetation includes various forest and non-forest formations, the most representative of which is dense forest (Godoy et al. 2011b; Souza 2009).

It should be noted that the region sampled is covered by the control actions of the SSEBC. The main actions are: monitoring using Jackson and McPhail traps, other control actions include collecting and destroying host fruit, spraying hosts with spinosad-based toxic baits, and the male annihilation technique (MAT), which uses the parapheromone methyl-eugenol associated with an insecticide, in a ratio of 6:1, respectively (Garcia et al. 2024).

2.2 Sampling procedures for grouped fruit

The fruits of *Terminalia catappa* L. (Combretaceae), known as chestnut, sun hat, or tropical almond, were collected in February and March 2022. In general, in Brazil, the fruiting period of this species runs from February to September (Reyes 1996). The samples were collected in the municipality of Laranjal do Jari (Amapá) and district of Monte Dourado, municipality of Almeirim (Pará). In Laranjal do Jari, the collections were concentrated in the urban area (Site A). In Monte Dourado, samples were collected in the village of Munguba (Site B) and in the private area of the company Jari Celulose S.A. (Site C), where there were a group of *T. catappa* plants (Figure 1 and Table 1).

In each site, samples were taken randomly, collecting ripened or ripening fruit directly from the plants or freshly

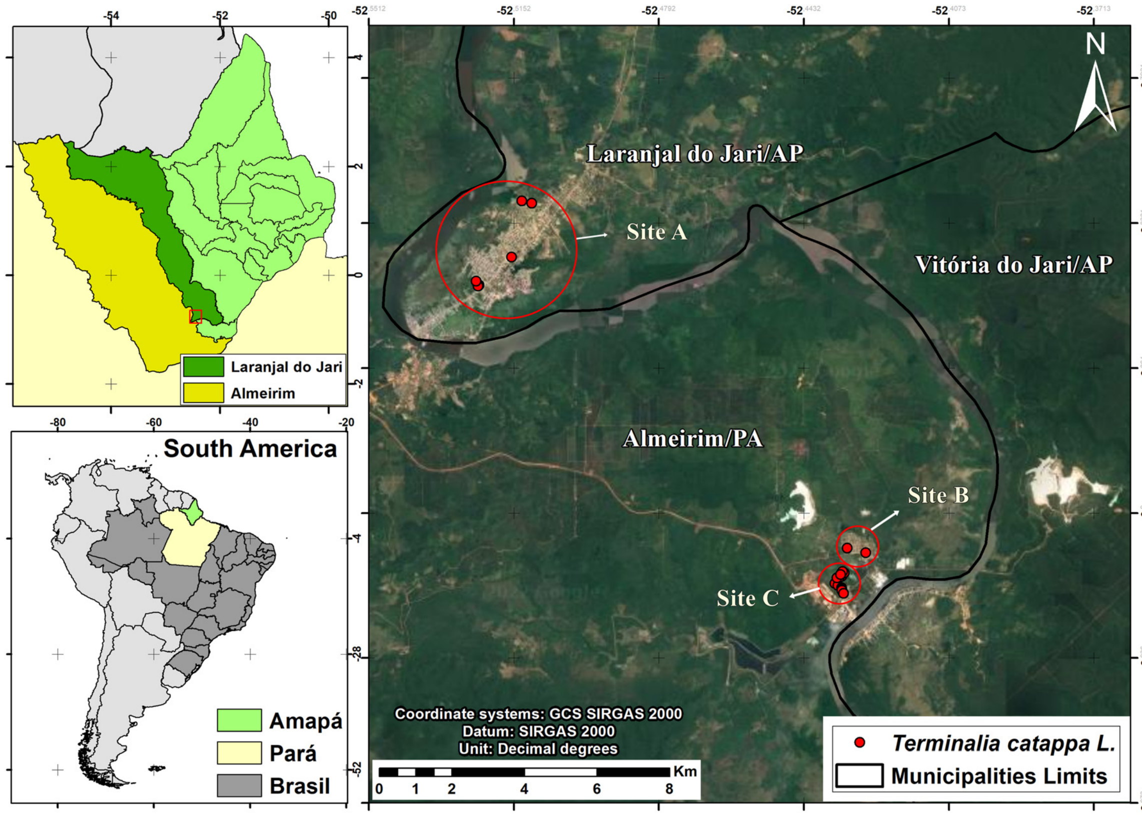

Figure 1: Location map of the *Terminalia catappa* fruit sampling points in the Jari Valley. Site A (Laranjal do Jari, Amapá): collections concentrated in the urban area (single plants of *T. catappa*); Site B (village of Munguba, Monte Dourado District, Almeirim, Pará): collections concentrated in the urban area (single plants of *T. catappa*) and Site C (private area of the company Jari Celulose S.A., Monte Dourado District, Almeirim, Pará): group of plants of *T. catappa*.

fallen to the ground. Each sample was composed of an amount of fruits evaluated in groups, following the method described by Silva et al. (2011b). After being weighed on a digital scale, they were placed in plastic trays (30.3 length × 22.1 width × 7.5 height cm), over a 2 cm layer of moistened vermiculite, covered with organza, which was secured with an elastic band.

The sampled material was transported to the Plant Protection Laboratory at Embrapa Amapá, in Macapá, where the trays with the fruit were kept for 28 days and examined every seven days to collect puparia. To avoid desiccation of the puparia, humidity was maintained in the trays by replacing water with a spray bottle. The puparia obtained from each sample were stored in plastic jars (8 diameter × 6 height cm), which contained a thin layer of moistened vermiculite.

2.3 Sampling procedures for individualized fruits

To confirm the possible occurrence of parasitism of *B. carambolae* larvae from *T. catappa* fruit, a new fruit collection was carried out in February 2023, in Site C, wherein 12 plants (samples) were randomly selected (Tables 2). Forty fruits (sub-samples) were collected from each tree and evaluated individually, according to the methods of Silva et al. (2011b), totaling 480 fruits. A minimum distance between plants of 100 m was adopted to reduce the possibility of selecting related specimens (Capelanes and Biella 1986).

Freshly fallen fruits were collected directly from the ground, individually packed in plastic jars (8 diameter × 6 height cm) containing vermiculite. Plastic jars were covered with organza fabric and a vented lid and taken to the Plant Protection Laboratory at Embrapa Amapá. In the laboratory, the fruits were weighed using a precise electronic scale and then placed in plastic jars, which contained a thin layer of moistened vermiculite. Each fruit was reviewed every 7 days for 28 days. The puparia were removed and individually packaged in colorless gelatin capsules (no. 00, 1,000 mg), properly identified with the number of the sample (plant) and sub-sample (fruit) and the number of the puparium. The capsules containing the puparia obtained from the same fruit were

Table 1: Sample number, location data, elevation and geographic coordinates of *Terminalia catappa* in the grouped fruit experiment collected in the Jari Valley, Amapá/Pará, Brazil.

Sample number	Sites	Collection date	State	Municipality	Locality	Elevation (m a.s.l.)	Geographic coordinates	
							Latitude	Longitude
1	C	3 Feb 2022	Pará	Almeirim	Jari Celulose S.A.	19	0.9157 °S	52.4338 °W
2	C	3 Feb 2022	Pará	Almeirim	Jari Celulose S.A.	22	0.9175 °S	52.4355 °W
3	C	3 Feb 2022	Pará	Almeirim	Jari Celulose S.A.	20	0.9180 °S	52.4348 °W
4	C	3 Feb 2022	Pará	Almeirim	Jari Celulose S.A.	24	0.9162 °S	52.4345 °W
5	C	28 Feb 2022	Pará	Almeirim	Jari Celulose S.A.	21	0.9161 °S	52.4350 °W
6	C	28 Feb 2022	Pará	Almeirim	Jari Celulose S.A.	15	0.9151 °S	52.4336 °W
7	C	28 Feb 2022	Pará	Almeirim	Jari Celulose S.A.	12	0.9149 °S	52.4333 °W
8	C	28 Feb 2022	Pará	Almeirim	Jari Celulose S.A.	15	0.9150 °S	52.4339 °W
9	C	28 Feb 2022	Pará	Almeirim	Jari Celulose S.A.	12	0.9146 °S	52.4336 °W
10	C	28 Feb 2022	Pará	Almeirim	Jari Celulose S.A.	17	0.9153 °S	52.4341 °W
11	C	28 Feb 2022	Pará	Almeirim	Jari Celulose S.A.	19	0.9186 °S	52.4339 °W
12	C	28 Feb 2022	Pará	Almeirim	Jari Celulose S.A.	15	0.9190 °S	52.4338 °W
13	C	28 Feb 2022	Pará	Almeirim	Jari Celulose S.A.	15	0.9193 °S	52.4338 °W
14	C	28 Feb 2022	Pará	Almeirim	Jari Celulose S.A.	12	0.9200 °S	52.4334 °W
15	B	28 Feb 2022	Pará	Almeirim	Village of Munguba	9	0.9099 °S	52.4279 °W
16	B	28 Feb 2022	Pará	Almeirim	Village of Munguba	21	0.9088 °S	52.4325 °W
17	A	28 Feb 2022	Amapá	Laranjal do Jari	Municipal headquarters	10	0.8435 °S	52.5238 °W
18	A	28 Feb 2022	Amapá	Laranjal do Jari	Municipal headquarters	8	0.8438 °S	52.5241 °W
19	A	28 Feb 2022	Amapá	Laranjal do Jari	Municipal headquarters	10	0.8425 °S	52.5245 °W
20	A	28 Feb 2022	Amapá	Laranjal do Jari	Municipal headquarters	37	0.8227 °S	52.5132 °W
21	A	28 Feb 2022	Amapá	Laranjal do Jari	Municipal headquarters	9	0.8365 °S	52.5157 °W
22	C	5 Oct 2022	Pará	Almeirim	Jari Celulose S.A.	18	0.9154 °S	52.4341 °W
23	C	5 Oct 2022	Pará	Almeirim	Jari Celulose S.A.	11	0.9144 °S	52.4334 °W
24	C	5 Oct 2022	Pará	Almeirim	Jari Celulose S.A.	20	0.9158 °S	52.4337 °W

Table 2: Sample number, location data, elevation and geographic coordinates of *Terminalia catappa* in the individualized fruit experiment collected in the Jari Valley, Amapá/Pará, Brazil.

Sample number	Sites	Collection date	State	Municipality	Locality	Elevation (m a.s.l.)	Geographic coordinates	
							Latitude	Longitude
1	C	16 Feb 2023	Pará	Almeirim	Jari Celulose S.A.	11	0.9205 °S	52.4333 °W
2	C	16 Feb 2023	Pará	Almeirim	Jari Celulose S.A.	11	0.9203 °S	52.4332 °W
3	C	16 Feb 2023	Pará	Almeirim	Jari Celulose S.A.	17	0.9186 °S	52.4342 °W
4	C	16 Feb 2023	Pará	Almeirim	Jari Celulose S.A.	23	0.9161 °S	52.4345 °W
5	C	16 Feb 2023	Pará	Almeirim	Jari Celulose S.A.	24	0.9162 °S	52.4342 °W
6	C	16 Feb 2023	Pará	Almeirim	Jari Celulose S.A.	19	0.9157 °S	52.4337 °W
7	C	16 Feb 2023	Pará	Almeirim	Jari Celulose S.A.	16	0.9152 °S	52.4338 °W
8	C	16 Feb 2023	Pará	Almeirim	Jari Celulose S.A.	15	0.9152 °S	52.4336 °W
9	C	16 Feb 2023	Pará	Almeirim	Jari Celulose S.A.	13	0.9148 °S	52.4338 °W
10	C	16 Feb 2023	Pará	Almeirim	Jari Celulose S.A.	12	0.9145 °S	52.4337 °W
11	C	16 Feb 2023	Pará	Almeirim	Jari Celulose S.A.	8	0.9136 °S	52.4340 °W
12	C	16 Feb 2023	Pará	Almeirim	Jari Celulose S.A.	17	0.9186 °S	52.4339 °W

stored in plastic containers properly identified with the sample information and the date the puparia were collected.

The jars containing puparia from the grouped fruits and the jars containing the capsules with puparia from the individualized fruits were kept in a room with controlled conditions of temperature (26 ± 0.5 °C), relative humidity (70 ± 10 %), and photoperiod (12 h, light: dark), being observed daily for 30 days, a period sufficient for the emergence of all viable insects (Silva et al. 2011b; Souza-Adaime et al. 2017). The fruit flies and parasitoids that emerged were preserved in 70 % ethanol for later identification.

2.4 Taxonomic identification of insects

The adult specimens of *Anastrepha* were identified using the illustrated dichotomous key by Zucchi et al. (2011). Identification was based on examination of the terminalia of the females by examining the apex of the extroverted aculeus using a stereomicroscope and an optical microscope (40×). Other features such as wing pattern, mesonotum, mediotergite, and subscutellum also were examined. The identification of *B. carambolae* was based on Zucchi (2000) and Plant Health Australia (2018). To identify the parasitoids (Braconidae), we used the works of Canal and Zucchi (2000) and Marinho et al. (2011). Voucher specimens were deposited at the Plant Protection Laboratory of Embrapa Amapá.

2.5 Morphological analysis of puparia

To confirm parasitism, morphological analysis was based mainly on the cephalo-pharyngeal skeleton embedded in the opercula of the puparia from which parasitoids emerged and of the puparia with no insect emergence. The tritrophic relationship (host fruit/fruit flies/parasitoids) was considered when the parasitoid species naturally emerged from the puparia identified as being of the genus *Anastrepha* or *Bactrocera*.

After dissection, the puparia were identified according to genus (*Anastrepha* and *Bactrocera*), and the parasitoids were removed and later identified to determine the percentage of apparent parasitism. Fruit fly puparia show morphological differences (coloration and size) depending on the genus (*Anastrepha* and *Bactrocera*) (Figure 2A).

At the Centro Avançado de Pesquisa em Proteção de Plantas e Saúde Animal do Instituto Biológico, in Campinas, São Paulo, reference images were taken (puparia, cephalo-pharyngeal skeleton, and mandible of the larvae adhered in the operculum). The larval mandibles of the puparia from which parasitoids emerged were then compared with the reference images. In addition, reference images of parasitoids from *B. carambolae* puparia were depicted.

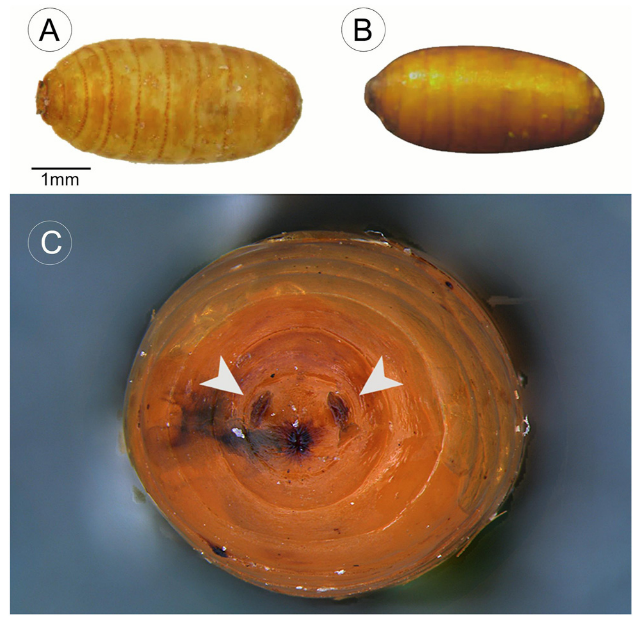

Figure 2: Comparative analysis of fruit fly puparia. (A) Side view of *Anastrepha* (left) and *Bactrocera* (right) puparia. (B) Details of the anterior region of *Bactrocera carambolae* showing the blackened spiracles (possible distinctive character).

The definitive confirmation of the morphometric characters of the puparia was based on comparative images of *B. carambolae* puparia obtained using a motorized stereomicroscope system Leica M205C (as shown in Figure 2B). This examination involved a detailed comparison with puparia from other genera. Also, Figures 3A and B and 4 were made in stereomicroscope. Plates were prepared to illustrate the anatomical structures removed from the puparia (Figures 3 and 4) that make up the cephalo-pharyngeal skeleton. The distinction between the species *Anastrepha fraterculus* (Wiedemann) and *B. carambolae* was made mainly by comparing the mandibles.

To obtain the cephalo-pharyngeal skeletons, the puparia were immersed in 70 % ethanol solution for at least 72 h. Subsequently, the skeleton was carefully separated from the puparium, removing as much adhered tissue as possible. This structure was positioned in profile on a glass slide for verification purposes. The mandible was then removed and placed laterally to visualize the structures.

To confirm the identification of the puparia at genus level, the key to third-stage larvae of economically important genera of American frugivorous tephritids by Frías et al. (2006) was used, exclusively in aspects related to the cephalo-pharyngeal skeleton and the mandible. The cephalo-pharyngeal skeleton was studied using an optical microscope (40×), and the following structures were observed:

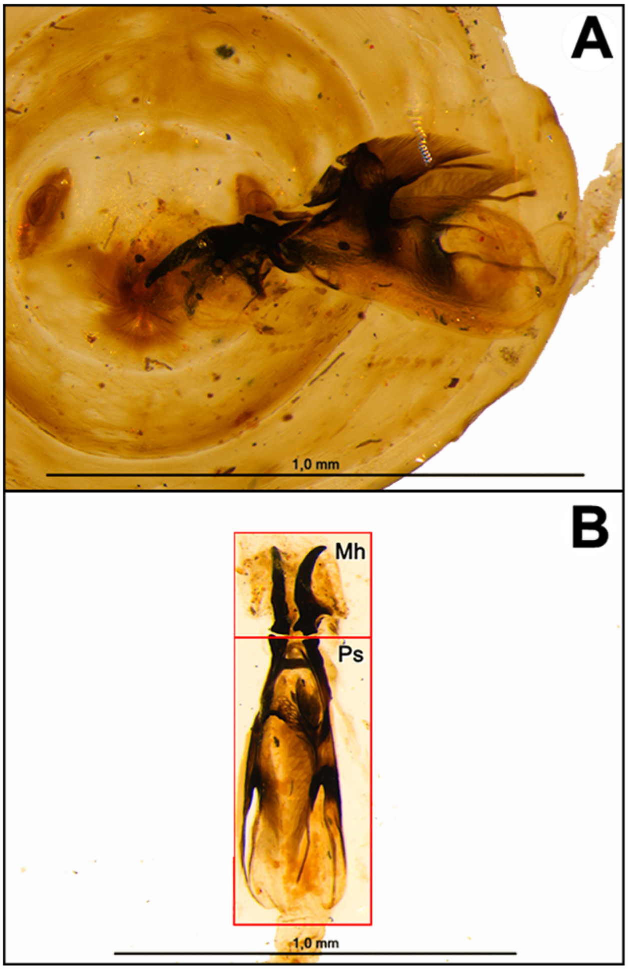

Figure 3: Morphological analysis of puparia of *Bactrocera carambolae*. (A) Cephalo-pharyngeal skeleton inserted into the operculum. (B) Cephalo-pharyngeal skeleton, dorsal view. Mh: mouth hooks; Ps: pharyngeal sclerite.

mandibles, ventral and dorsal apodemes of the mandible, neck of the mandible, dental sclerite, labial sclerite, hypopharyngeal sclerite, sclerite, parasternal bar, hypopharyngeal bridge, dorsal and ventral horns, anterior sclerite, ventral and dorsal bridges of the ventral and dorsal horns, oral and pre-oral teeth.

2.6 Obtaining images

To create the location map (Figure 1), Arcgis 10.8 software was used. For Figures 2B, 3A and B, 4 and 6A it is noteworthy that the images are a compilation of photos taken layer by layer, edited in the LAS v4.1 software, to become a single image. Figures 2, 6 and 7 were assembled using Photoscape v3.7 software. The diagram in Figures 6B and 7A and B was created using Photoshop.

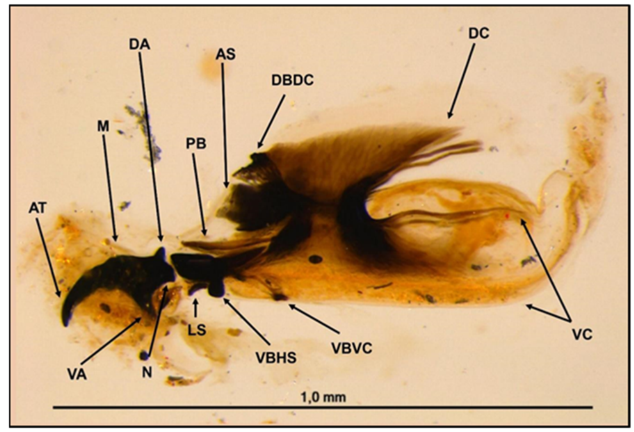

Figure 4: Diagram of the cephalo-pharyngeal skeleton of *Bactrocera carambolae* identifying the morphology of the structures, lateral view. Anterior sclerite (AS); apical tooth (AT); dorsal apodeme (DA); dorsal bridge of the dorsal cornu (DBDC); dorsal cornu (DC); labial sclerite (LS); mandible (M); neck (N); parastomal bar (PB); ventral apodeme (VA); ventral bridge of the hypopharyngeal sclerite (VBHS); ventral bridge of the ventral cornu (VBVC) and ventral cornu (VC).

2.7 Data analysis

To assess the fruit fly infestation index and apparent parasitism from the grouped fruit samples, we performed the following calculations: (I) infestation index = (number of puparia obtained in the sample/sample mass in kilograms), expressed as the number of puparia per kg of fruit; (II) emergence percentage [(number of adults emerged/number of puparia obtained in the sample) × 100]; and (III) apparent parasitism percentage [(number of parasitoids emerged/number of puparia obtained) × 100] (Carvalho 2005).

For the individual fruit samples, we presented parasitism percentages in two ways. The percentage of apparent parasitism, according to Blais (1960), when only parasitoids that actually emerged from the puparia collected were considered, given by the formula: (I) percentage of apparent parasitism [(number of parasitoids emerged/number of puparia obtained) × 100]. The percentage of adjusted parasitism, when those puparia already formed but not emerged, observed from the dissection of the puparia, were counted in addition to the emerged parasitoids, is given by the formula: (II) percentage of adjusted parasitism = [(number of parasitoids emerged + number of parasitoids formed but not emerged/number of puparia obtained) × 100] (Gattelli 2006).

To identify differences between locations (sites) in relation to fruit fly infestation we used the Host Reproduction Number (HRN) proposed by Dominiak (2022). HRN is the capacity of the host fruit to support the entire life cycle of fruit flies and is measured by the number of adults obtained from one kg of fruit. HRN values range from zero for nonhosts to many hundreds for highly suitable hosts. For each sampling site, we calculated the Host Suitability Index proposed by Follett et al. (2021) and assigned one of six potential categories: HRN = 0 is non-host; HRN = <0.1 is very poor; HRN = 0.1–1.0 is poor; HRN = 1.1–10.0 is moderately good; HRN = 10.1–100 is good; and HRN > 100 is very good.

To examine the number of specimens that emerged from individualized samples in the experiment, we generated tables based on fruit fly genus, identified and grouped by the number of the sample (plant) and the sub-sample (fruit). Another table was created to identify the emergence of the total number of specimens and whether different genera occurred in the same subsample. A Venn diagram was prepared based on the data from this table, using the ggvenn package (Linlin 2021) in software R version 4.1.0 (R Core Development Team 2021).

3 Results

3.1 *T. catappa* as a host plant for *B. carambolae*

Twenty-four samples of *T. catappa* were collected, 19 in Almeirim/Pará and five in Laranjal do Jari/Amapá (Tables 1 and 2) (Figure 1), comprising 1,139 fruits, totaling 20.16 kg (Table 3). A total of 2,841 fruit fly puparia were obtained from 21 of the 24 samples. From the puparia, 480 specimens of *B. carambolae* and 1,228 specimens of *Anastrepha* spp. emerged [323♀ *Anastrepha turpiniae* Stone; 137♀ *Anastrepha zenildae* Zucchi; 131♀ *A. fraterculus*, as well as 637 ♂]. The infestation levels in the samples varied, ranging from 2.8 to 415.9 puparia per kg of fruit. The highest infestation percentages were observed in areas with a high concentration of host plants, as indicated in Table 3.

Table 4 shows the HRN for *T. catappa*, according to fly genus and collection site. There was a difference in obtaining specimens according to the sampling sites, with the HRN being higher for site C, for both, *Anastrepha* and *Bactrocera*. The Host Suitability Index was moderately good for site A and good for sites B and C.

3.2 Parasitoids obtained from grouped fruit samples of *T. catappa*

A total of 525 parasitoid specimens were obtained, belonging to three species: *D. areolatus* (96.8 %), *O. bellus* (2.3 %), and *Asobora anastrephae* (0.9 %). No parasitoids were recovered from nine of the samples (Table 3). The percentage of apparent parasitism ranged from 4.3 % to 52.0 %.

3.3 Individualized fruit samples of *T. catappa* and tritrophic associations

The assessment of emergence was conducted on 12 samples of *T. catappa*, with 40 repetitions each, resulting in a total of 480 subsamples (Supplementary Material). In every sample collected, at least one specimen of *B. carambolae* and *Anastrepha* species successfully emerged. Additionally, parasitoids were obtained from all collected samples (Table 5). Of the 480 subsamples (fruits), at least one specimen emerged in 333 of them (69.4 %). The percentage of emergence ranged from 37.5 % to 92.5 % (Table 5).

A total of 6,461 puparia were obtained from the individualized samples, from which emerged 808 specimens of *B. carambolae* and 389 specimens of *Anastrepha* spp. (112♀ *A. turpiniae*; 19♀ *A. fraterculus*; 30♀ *A. zenildae*, as well as 228♂; Table 5). In addition, 501 parasitoid specimens were obtained, belonging to four species: *D. areolatus* (91.4 %), *A. anastrephae* (4.0 %), *Utetes anastrephae* (Viereck) (3.8 %), and *O. bellus* (0.8 %). Parasitoids were recovered from all the samples (Table 5).

It should be noted that of the 333 fruits with emergence, only specimens of the genus *Anastrepha* emerged in 10.3 % of fruits; *B. carambolae* emerged in 16.2 % and only parasitoids (*D. areolatus*, *A. anastrephae*, *U. anastrephae*, and *O. bellus*) emerged in 17.1 %. We recorded co-infestations between *Anastrepha* and *B. carambolae* from 11.4 % of the *T. catappa* fruits. Parasitoids and specimens of *B. carambolae* also coexisted in 22.2 % of fruits. In 10.8 % *Anastrepha* specimens coexisted with parasitoids. Parasitoids and both species of fruit flies emerged from 12.0 % of fruits (Figure 5).

Analysis of the mandibles removed from the puparia in which emergence occurred showed that 441 specimens of *D. areolatus* (96.3 %) were obtained from *Anastrepha* puparia, while 3.7 % were obtained from *B. carambolae* puparia. For *A. anastrephae* and *O. bellus*, 100 % of the specimens were obtained from *Anastrepha*. For *U. anastrephae*, 11 specimens were obtained from *Anastrepha* (57.9 %) and eight from *B. carambolae* (42.1 %) (Table 6).

When only the emerged parasitoids were considered, an apparent parasitism percentage of 11.9 % was observed for *Anastrepha* spp. and 1.0 % for *B. carambolae* (Table 6). The puparia dissection indicated 372 parasitoids from *Anastrepha* puparia, of which 77 were *D. areolatus*, three were *O. bellus*, 11 were *A. anastrephae*, three were *U. anastrephae*, 11 were Figitidae, and 267 could not be identified as they were not fully developed (Table 6). From *Bactrocera* puparia,

Table 3: Species of fruit flies and parasitoids obtained from grouped fruit samples of *Terminalia catappa*, in the Jari Valley, Amapá/Pará, Brazil (February and March 2022).

CS	S[a]	Fruits (n)	Mass (kg)	PP (n)	*Anastrepha fraterculus*	*Anastrepha turpiniae*	*Anastrepha zenildae*	*Anastrepha*	*Bactrocera carambolae*		Infestation PP/kg	*Doryctobracon areolatus*		*Opius bellus*		*Asobara anastrephae*		Parasitoids (total)	AP (%)	E (%)
					♀	♀	♀	♂	♀	♂		♀	♂	♀	♂	♀	♂			
1	C	31	0.57	57	2	1	0	2	3	5	100	19	6	0	0	0	0	25	43.9	66.7
2	C	30	0.55	76	0	5	3	13	7	9	138.2	10	10	0	1	0	0	21	27.6	76.3
3	C	42	0.76	88	0	14	0	13	2	4	115.8	22	9	0	0	0	0	31	35.2	72.7
4	C	48	0.90	33	0	7	0	12	3	0	36.7	0	8	0	0	0	0	8	24.2	90.9
5	C	40	0.83	346	0	20	5	39	33	24	416.9	41	51	0	2	0	1	95	27.5	62.4
6	C	31	0.55	188	6	21	4	35	31	32	341.8	13	13	0	0	0	0	26	13.8	82.4
7	C	32	0.46	106	0	12	0	16	4	4	230.4	17	23	0	0	0	0	40	37.7	71.7
8	C	152	2.68	543	17	38	19	62	100	132	202.6	30	18	0	0	0	0	48	8.8	76.6
9	C	11	0.27	75	3	3	2	9	5	5	277.8	10	23	1	2	0	3	39	52.0	88.0
10	C	56	0.98	180	6	11	6	21	32	31	183.7	27	15	0	0	0	0	42	23.3	82.8
11	C	47	0.86	224	20	49	22	87	0	0	260.5	13	6	0	0	0	0	19	8.5	87.9
12	C	21	0.37	79	11	17	7	30	2	1	213.5	0	0	0	0	0	0	0	0.0	86.1
13	C	56	0.76	208	13	45	16	73	0	0	273.7	17	20	2	2	0	0	41	19.7	90.4
14	C	68	1.33	385	35	53	35	139	0	0	289.5	21	45	0	2	1	0	69	17.9	86.0
15	B	86	1.24	62	7	11	7	19	2	2	50.0	0	0	0	0	0	0	0	0.0	77.4
16	B	68	1.41	132	11	14	9	52	0	1	93.6	11	9	0	0	0	0	20	15.2	81.1
17	A	16	0.29	0	0	0	0	0	0	0	0.0	0	0	0	0	0	0	0	–	–
18	A	12	0.29	0	0	0	0	0	0	0	0.0	0	0	0	0	0	0	0	–	–
19	A	17	0.36	1	0	0	0	0	1	0	2.8	0	0	0	0	0	0	0	0.0	100.0
20	A	22	0.46	0	0	0	0	0	0	0	0.0	0	0	0	0	0	0	0	–	–
21	A	12	0.34	3	0	0	0	0	1	2	8.8	0	0	0	0	0	0	0	0.0	100.0
22	C	81	1.19	23	0	0	2	9	0	0	19.3	1	0	0	0	0	0	1	4.3	52.2
23	C	66	1.30	19	0	2	0	3	2	0	14.6	0	0	0	0	0	0	0	0.0	36.8
24	C	94	1.40	13	0	0	0	3	0	0	9.3	0	0	0	0	0	0	0	0.0	23.1
Total		1,139	20.16	2,841	131	323	137	637	228	252		252	256	3	9	1	4	525		

[a]Site A (Laranjal do Jari, Amapá): collections concentrated in the urban area (single plants of *T. catappa*); Site B (village of Munguba, Monte Dourado District, Almeirim, Pará): collections concentrated in the urban area (single plants of *T. catappa*); and Site C (private area of the company Jari Celulose S.A., Monte Dourado District, Almeirim, Pará): group of plants of *T. catappa*. CS, collected samples; S, site; PP, puparia; AP (%), percentage of apparent parasitism; E, emergence.

Table 4: Host Reproduction Number (HRN) and Host Suitability Index (HSI) for *Terminalia catappa* fruits in three sampling sites in the Jari Valley, Amapá/Pará, Brazil (February and March 2022 and February 2023).

Site[a]	Fruits (n)	Mass (kg)	Puparia (n)	*Anastrepha* spp. (n)	HRN[b] (*Anastrepha*)	*Bactrocera carambola* (n)	HRN[b] (*Bactrocera*)	HRN[b] (fruit flies)	HSI[c] (site)
A	79	1.74	4	0	0.0	4	2.3	2.3	Moderately good
B	154	2.65	194	130	49.1	5	1.9	50.9	Good
C	906	15.76	2,643	1,098	69.7	471	29.9	99.6	Good

[a]Site A (Laranjal do Jari, Amapá): collections concentrated in the urban area (single plants of *T. catappa*); Site B (village of Munguba, Monte Dourado District, Almeirim, Pará): collections concentrated in the urban area (single plants of *T. catappa*); and Site C (private area of the company Jari Celulose S.A., Monte Dourado District, Almeirim, Pará): group of plants of *T. catappa*. [b]Host Reproduction Number (HRN), proposed by Dominiak (2022); [c]Host Suitability Index (HSI), proposed by Follett et al. (2021): HSI categories: HRN = 0 is non-host; HRN = <0.1 is very poor; HRN = 0.1–1.0 is poor; HRN = 1.1–10.0 is moderately good; HRN = 10.1–100 is good; and HRN > 100 is very good.

we obtained two *D. areolatus*, six *A. pelleranoi* and 11 specimens were not identified (Table 6). Consequently, by adding up the number of naturally emerging parasitoids and those obtained after dissection, an adjusted parasitism of 21.2 % was obtained for *Anastrepha* spp. and 1.8 % for *B. carambolae* (Table 6).

A comprehensive overview of the fruit fly and associated parasitoid occurrences is shown in the Supplementary Material. Emergence of parasitoids was observed in the puparia of *B. carambolae* in 20 subsamples (fruits), 17 of which were *D. areolatus* and three were *U. anastrephae*. From the puparia of *B. carambolae*, it was observed that the parasitoid *U. anastrephae* emerged exclusively in one fruit and the parasitoid *D. areolatus* emerged exclusively in five fruits. Parasitoids of *B. carambolae* and *Anastrepha* spp. emerged simultaneously in 14 fruits, and parasitoids exclusively of *Anastrepha* emerged in 186 fruits (Supplementary Material). Figure 6 offers a visual representation of a *D. areolatus* specimen formed in a *B. carambolae* puparium, confirmed by analysis of mandible morphology.

4 Discussion

The tropical almond (*T. catappa*) is native to coastal areas of East Asia (Sanches et al. 2007; Thomson and Evans 2006). It has become an invasive species in coastal regions, particularly along the Brazilian coastline, a presence that dates back to the arrival of Europeans. The dispersal of its seeds is facilitated by water currents and bats (Plucênio et al. 2013). In Brazil, although there are no commercial plantations, this species is present throughout the country, especially in urban afforestation, in some cases representing many specimens (Malentachi 2013; Ribeiro et al. 2022).

As highlighted by Nascimento and Carvalho (2000), the presence of this plant species was decisive for the predominance of the exotic fruit fly species, *Ceratitis capitata* (Wiedemann) to the detriment of *Anastrepha* spp. in an urban area in Bahia State. Therefore, the presence of *T. catappa* could pose a similar risk for the dispersal of *B. carambolae*.

Internationally, there are reports of *B. carambolae* occurring on *T. catappa*, for example in Suriname (van Sauers-Muller 1991, 2005), French Guiana (Vayssières et al. 2013), Thailand, and Malaysia (Southeast Asia) (Allwood et al. 1999; Chinajariyawong et al. 2000). In Brazil, *T. catappa* is infested by six species of fruit flies: *A. fraterculus*, *A. obliqua* (Macquart), *A. sororcula* Zucchi, *A. turpiniae*, *A. zenildae*, and *C. capitata* (Zucchi and Moraes 2024). Hence, this manuscript marks the first documented occurrence of *B. carambolae* on *T. catappa* in Brazil. Furthermore, the results represent the initial recorded cases of infestation of this plant species by *A. fraterculus*, *A. turpiniae*, and *A. zenildae* in Amapá. These three species have already been identified on this host in other states, namely *A. turpiniae* in Amazonas (Silva 1993), *A. zenildae* in Mato Grosso do Sul (Uchôa-Fernandes et al. 1997), and *A. fraterculus* in São Paulo (Souza-Filho et al. 1997).

In Suriname, van Sauers-Muller (2005) obtained 132 specimens of *B. carambolae*, in 10.7 % of the samples, totaling 19.71 kg of *T. catappa*, between 1986 and 2002. In French Guiana, Vayssières et al. (2013) obtained an average of eight *B. carambolae* adults per kg of *T. catappa* host fruit between 2001 and 2003. Allwood et al. (1999) and Chinajariyawong et al. (2000) also indicated *T. catappa* as a host plant for *B. carambolae* in field studies conducted between 1986 and 1994 in Thailand and Malaysia (Southeast Asia).

In our study, the HRN was higher in sites B and C, where there was a higher concentration of *T. catappa* plants (Table 4). This probably facilitated the reproduction of flies and the recolonization of the fruits. Consequently, the Host Suitability Index was good at sites B and C and only moderately good at site A. The higher incidence of fruit flies

Table 5: Species of fruit flies and parasitoids obtained from individual fruit samples of *Terminalia catappa* in the Jari Valley (Site C), Amapá/Pará, Brazil (February 2023).

Sample number	Fruits with emerged insects		Number of puparia	*Anastrepha fraterculus*	*Anastrepha turpiniae*	*Anastrepha zenildae*	*Anastrepha*	*Bactrocera carambolae*		*Doryctobracon areolatus*		*Opius bellus*		*Asobara anastrephae*		*Utetes anastrephae*	
	number (*N* = 40)	%		♀	♀	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
1	27	70.0	552	0	3	1	9	36	45	14	8	0	0	0	0	0	0
2	37	92.5	621	4	20	10	49	49	67	17	21	0	0	1	1	0	1
3	30	75.0	583	6	7	6	18	22	30	13	22	0	0	1	0	0	0
4	25	62.5	359	0	6	3	12	5	4	14	18	0	0	0	0	0	0
5	22	55.0	560	0	6	0	4	9	25	5	8	0	0	1	0	3	2
6	34	85.0	581	0	8	2	13	62	63	36	21	0	0	4	1	0	0
7	29	72.5	759	0	3	1	10	24	27	29	41	0	0	0	0	2	0
8	15	37.5	157	1	3	3	6	7	4	5	9	0	0	0	1	0	0
9	27	67.5	668	6	9	1	20	53	53	17	22	0	0	0	0	0	0
10	30	75.0	445	0	20	3	37	52	39	44	23	1	0	0	1	0	0
11	22	55.0	315	1	20	0	38	5	4	7	16	2	0	0	0	0	0
12	35	87.5	861	1	7	0	12	64	59	29	19	0	1	6	3	5	6
	333	69.4	6,461	19	112	30	228	388	420	230	228	3	1	13	7	10	9

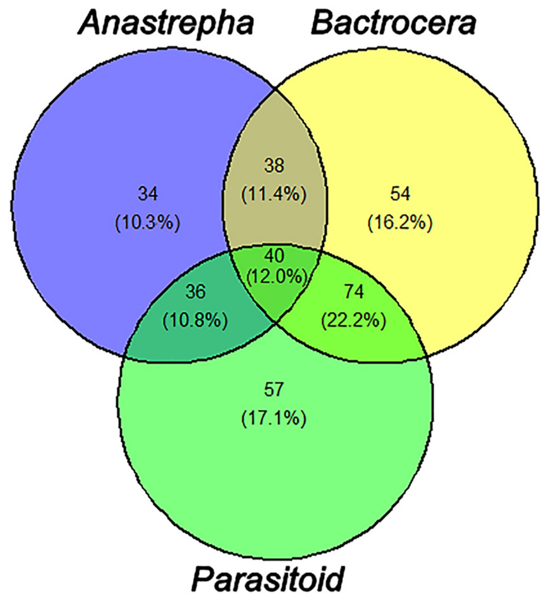

Figure 5: Venn diagram of the association between the specimens obtained from the 333 fruits of *Terminalia catappa* in which there was parasitoid or fruit fly emergence.

in the samples collected from the Jari Celulose (Site C) can be primarily attributed to the fact that the area is difficult to access and is made up of a large density of hosts, especially *T. catappa* (Table 3). Moreover, as this is a private area, SSEBC control actions at this location were only recently initiated following the suspicion of an outbreak of the pest nearby. On the other hand, the samples with the lowest fruit fly infestations were obtained from the urban areas of Laranjal do Jari (Site A) and the village of Munguba (Site B), where control actions are more intensive and there is a lower density of *B. carambolae* host plants.

Given that *B. carambolae* dominates urban areas and is occasionally identified in tropical forests undisturbed by human activity (Almeida 2016; Costa et al. 2022; Vijaysegaran and Oman 1991) and that *T. catappa* is present in an urban environment in Amapá (Soares et al. 2021), this species should be regarded as a potential reservoir for this pest. In this context, it is advisable to carry out phenological studies to determine the period of greatest fruiting.

Although effective containment and control measures have been taken since the detection of *B. carambolae* in Brazil, it must be considered that there is a risk of the pest spreading to other Brazilian regions. In this context, Marchioro (2016), using ecological niche models using the maximum entropy algorithm, identified climatically suitable areas for *B. carambolae* in tropical and subtropical regions of South America, including Brazil. Considering nine host crops and the variables relative humidity, temperature and soil texture, Mingoti et al. (2023) indicated 1,877 Brazilian

Table 6: Number of parasitoids emerged and dissected from puparia of *Bactrocera carambolae* and *Anastrepha* and apparent and adjusted parasitism in individualized fruits of *Terminalia catappa* in Vale do Jari (Site C), Amapá/Pará, Brazil (February 2023).

Results of natural emergence

Genus	*Doryctobracon areolatus*		*Asobara anastrephae*		*Utetes anastrephae*		*Opius bellus*		Figitidae	Not identified	Total number of puparia from which insects emerged	Total parasitoids emerged (1)	Apparent parasitism (%)
	♀	♂	♀	♂	♀	♂	♀	♂					
Anastrepha	219	222	13	7	8	3	3	1	2	–	867	478	11.9
Bactrocera	11	6	0	0	2	6	0	0	0	–	833	25	1.0
Subtotal	230	228	13	7	10	9	3	1	2	–	1,700	503	–

Puparium dissection results

Genus	*D. areolatus*		*A. anastrephae*		*U. anastrephae*		*O. bellus*		Figitidae	Not identified	Total number of puparia dissected	Total parasitoids obtained by dissection (2)
	♀	♂	♀	♂	♀	♂	♀	♂				
Anastrepha	48	29	6	5	3	0	2	1	11	267	3,142	372
Bactrocera	1	1	0	0	0	0	0	0	6	11	1,619	19
Subtotal	49	30	6	5	3	0	2	1	17	278	4,761	391

Results of natural emergences and dissected puparia

Genus	*D. areolatus*		*A. anastrephae*		*U. anastrephae*		*O. bellus*		Figitidae	Not identified	Grand total of puparia obtained	Grand total of parasitoids (3 = 1 + 2)	Adjusted parasitism (%)
	♀	♂	♀	♂	♀	♂	♀	♂					
Anastrepha	267	251	19	12	11	3	5	2	13	267	4,009	850	21.2
Bactrocera	12	7	0	0	2	6	0	0	6	11	2,452	44	1.8
Total	279	258	19	12	13	9	5	2	19	278	6,461	894	–

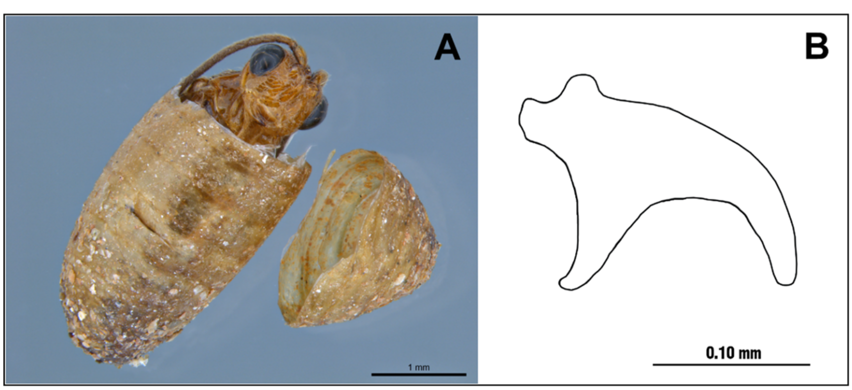

Figure 6: Proof of parasitism of *Bactrocera carambolae* larvae by *Doryctobracon areolatus*. (A) *Doryctobracon areolatus* semi-emerged in a puparium of *Bactrocera carambolae* obtained from *Terminalia catappa* fruit. (B) Characteristic mandible of *Bactrocera carambolae*, taken from the puparium (schematic drawing from the current authors).

municipalities favorable to better development of *B. carambolae* puparia. Soares et al. (2024) indicated that Brazil has a large part of its territory with high suitability for *B. carambolae*, especially the north, south, and southeast regions and the entire coastal area. Soares et al. (2023), analyzing pest population density data in the state of Roraima, Brazil, concluded that its abundance was positively correlated with relative air humidity.

This represents the initial documented occurrence in the Brazilian Amazon of the association between the parasitoid species *O. bellus* and *A. anastrephae* on *T. catappa* and the first report for Amapá of *D. areolatus* on this plant species (Canal et al. 1995; Dutra et al. 2013; Sousa et al. 2024). Until now, the tritrophic relationship between the parasitoid *D. areolatus* and *Anastrepha* species on this host plant only had been reported in the states of Amazonas and Rio Grande do Norte (Canal et al. 1994, 1995; Dutra et al. 2013; Silva et al. 2004; Zucchi and Moraes 2024).

The levels of parasitism observed in the grouped fruit samples are considered high according to the standards of Fletcher (1987), who states that parasitism levels exceeding 30 % are already regarded as substantial. The high levels of apparent parasitism, especially at Site C, are likely due to the characteristics of the site, such as the high density of hosts, the presence of alternative hosts, shading, many fruits available on the ground, and the hot and humid climate in the region. The presence of fallen fruit increases the likelihood of parasitoids locating and parasitizing larvae (Aguiar-Menezes and Menezes 2002). It is important to note that, at the time of collection, this area had seen only limited SSEBC control measures due to the recent discovery of the site.

A low percentage of apparent parasitism was obtained in the urban areas of the municipality of Laranjal do Jari and the village of Munguba, where more intensive SSEBC actions were carried out during the sampling period (Figure 1). A similar fact was reported by Meirelles (2015), who suggested that the absence of parasitoids in peaches (*Prunus persica* L., Rosaceae) could be associated with the use of insecticides to control fruit flies, through the application of toxic baits in the orchard where the study was carried out. Therefore, applying baits on a weekly basis can reduce the population of fruit flies in the orchard and limit the amount of hosts for the parasitoids.

Figure 3A illustrates the way in which the mouthparts of *B. carambolae* are inserted into the puparium. The removal of the mouthparts needs to be done so that the morphological structure becomes visible. Furthermore, Figure 3B provides a dorsal view of the cephalo-pharyngeal apparatus as this position of the structure helps in visualizing the distinctive characteristics for identification, as the dorsal and lateral views are completely different. Figure 4 presents a diagram with a side view of all the structures present in the cephalo-pharyngeal system, this is the most common way to make identifications. The presentation of images with this level of quality is important, as studies that present current, high-quality images in this area are scarce and normally focus on the larval stage. Furthermore, the present study is an exploratory work whose contributions can help the development of new identification methodologies.

Analysis of the morphological structures of the puparia of the genera *Bactrocera* and *Anastrepha* has revealed that the cephalo-pharyngeal skeleton, especially the mandible, is the main parameter for distinguishing between the two genus. According to Frías et al. (2006), the cephalo-pharyngeal skeleton of *B. carambolae* is described as having a black, heavily sclerotized mandible with a thin, strongly curved apical tooth. A small pre-apical tooth also is present. The ventral apodeme is pointed and projects posteriorly, while the dorsal apodeme is long and rounded apically. The dental sclerite present stands out. The mandibles of *B. carambolae* have a distinctive posterior neck, whereas this feature is absent in *Anastrepha*. Furthermore, in all studied *Anastrepha* species, the ventral apodeme is perpendicular to the dorsal margin of the mandibles or projects anteriorly (Frías et al. 2006, 2008). The dental sclerite is present in *Bactrocera* but absent in *Anastrepha* (Frías et al. 2006; White and Elson-Harris 1992).

Figure 7 provides a side-by-side comparison between the mandibles of *A. fraterculus* (Figure 7A) and *B. carambolae* (Figure 7B). In detail (red arrow) it is possible to see the ventral apodeme of the mandible projecting posteriorly in *B. carambolae* and absent in *A. fraterculus*.

The comparative study of the specific morphological aspects of the larvae plays a crucial role in taxonomy and quarantine measures (Dutra et al. 2018a; MAPA - Ministério da Agricultura e Pecuária 2007). To effectively employ all the available strategies and respond quickly and adequately to parasitism, it is essential to correctly and swiftly identify these insects, whether at the larval or pupal stage. Hence, further studies should be encouraged to develop comparative keys that encompass a broader range of species.

Even though *T. catappa* is a relatively small fruit (length 4.78 cm, width 3.6 cm, thickness 2.82 cm) a substantial emergence of fruit flies was observed. In this study, we obtained up to 36 specimens emerging from a single fruit (Supplementary Material, fruit 9 of plant 10). This infestation possibly reflected the parasitism identified in this study. Obtaining a percentage of adjusted parasitism of 21.2 % and 1.8 %, for *Anastrepha* and *Bactrocera*, respectively, is highly relevant information. It suggests that the parasitoids have adapted to the exotic *B. carambolae*, over the approximately 16 years since the species was first reported in the Monte Dourado region in Almeirim, Pará (Dutra et al. 2018b). On the other hand, it appears that the vast majority of unemerged host puparia were non-parasitized tephritid pupae (Table 6).

It should be noted that the exclusive association between parasitoids and *B. carambolae*, in the individualized samples experiment was observed in six fruits. It was also possible to identify parasitoids associated with the two genera in 14 other fruits (Supplementary Material).

Corroborating this information, the use of capsules to individualize puparia has proven to be a method capable of identifying the tritrophic associations of *B. carambolae* with the native parasitoids *D. areolatus* (12♀ and 7♂), *U. anastrephae* (2♀ and 6♂) and *A. pelleranoi* (2♀ and 4♂) for the host *T. catappa* in Brazil.

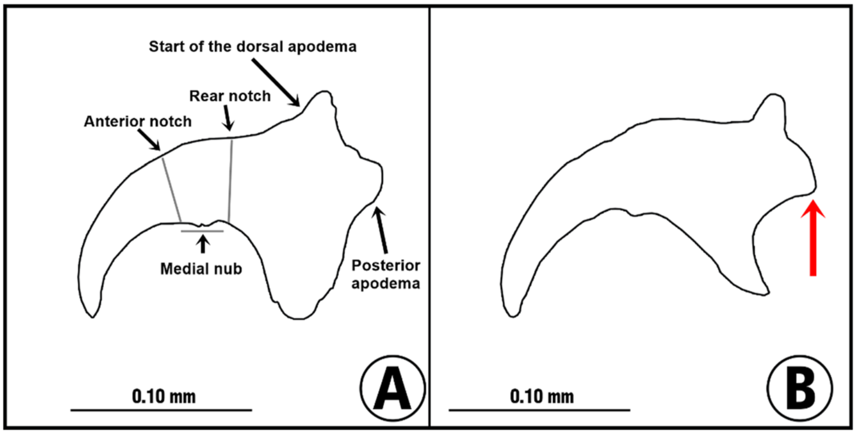

Figure 7: Comparison between *Anastrepha* and *Bactrocera* mandibles. (A) Mandible of *Anastrepha fraterculus* [schematic drawing adapted from Canal et al. (2015)]; (B) mandible of *Bactrocera carambolae* (schematic drawing from the current authors). In detail (red arrow), ventral apodeme of the mandible projecting posteriorly.

Previous suspicions of parasitism in *B. carambolae* by Almeida (2016) reported that two of the three samples of *Licania* sp. (Chrysobalanaceae) fruits were infested by fruit flies (presence of puparia), and in one of them four puparia were obtained from which two specimens of *B. carambolae* emerged. Only parasitoids emerged from the other sample (two specimens of *D. areolatus* and one unidentified specimen). Although significant, this observation was not enough to conclusively confirm parasitism. As a result, no native parasitoids had been reported for this species (Adaime et al. 2014; Adaime et al. 2023; Almeida et al. 2016).

According to van Sauers-Muller (2005), there is no evidence of parasitoid attack on the carambola fruit fly in Suriname. It should also be noted that no native parasitoid species emerged from *B. carambolae* samples collected during the period from 2001 to 2003 in French Guiana (Vayssières et al. 2013). The introduced parasitoid *D. longicaudata* was the only species to emerge from carambola fruit fly puparia, due to flood releases of millions of adults in the year 2000 along the Oiapoque River. The recorded percentage of parasitism varied between 0 % and 14.3 %.

Conversely, Guimarães et al. (2003) reported parasitism of *B. carambolae* larvae by *A. pelleranoi* in French Guiana. Vayssières et al. (2013) indicated that this same association was found in *B. carambolae* in French Guiana. In both cases, parasitism percentages and other details were not given, although these are considered as initial confirmation of the occurrence of native parasitoids from the Figitidae family on *B. carambolae* in South America.

Suputa et al. (2007) observed parasitism of *Aganaspis* sp., *F. arisanus*, and *Asobara* sp. on *B. carambolae* in the province of Yogyakarta, Java Island, Indonesia. Despite the indication of parasitism by *Asobara* sp. on carambola fruit flies, there was no record of parasitism by *A. anastrephae* on *B. carambolae* in this study.

D. areolatus was associated with *B. carambolae* in this study. This parasitoid already has been reported parasitizing *Anastrepha coronilli* Carrejo & González (on *Bellucia grossularioides* (L.) Triana, Melastomataceae), *A. fraterculus* (on *Spondias mombin* L., Anacardiaceae), and *A. striata* (on *Malpighia glabra* L., Malpighiaceae; *Psidium guajava* L., Myrtaceae; and *Psidium guineense* Sw., Myrtaceae), in the state of Pará (Zucchi and Moraes 2024). The limited reports of parasitism in the state of Pará suggest that the sampling effort was less extensive when compared to Amapá. The greater occurrence of *D. areolatus* in this study aligns with existing literature, indicating that this is one of the most widespread species, having been found in all the states of the northern region of Brazil (Barreto et al. 2022; Sousa et al. 2021a). The superior occurrence of *D. areolatus* is recurrent in Amapá (Deus and Adaime 2013; Sousa et al. 2021b). Another important ecological factor is that *D. areolatus* can find fruit fly larvae in unripe fruit (Carvalho et al. 2004).

The presence of *U. anastrephae* in carambola flies associated with *T. catappa* is unprecedented in Brazil. This parasitoid species had previously been linked to *A. turpiniae* (on *S. mombin*) in Amapá and to *A. obliqua* (on *Malpighia emarginata* D.C., Malpighiaceae) (Zucchi and Moraes 2024) in Pará. In addition, we identified six specimens of *A. pelleranoi* parasitizing *B. carambolae*, confirming the reports of Guimarães et al. (2003) and Vayssières et al. (2013).

Furthermore, the occurrence of parasitism involving native organisms may be attributed to their successful adaptation to the carambola fruit fly, which has been documented in Amapá since 1996. At the beginning of the introduction of *B. carambolae* on the continent, parasitoid surveys in the region of occurrence were scarce. In Amapá, the area with the highest incidence of fruit fly surveys, evidence of parasitism may not have occurred due to the existence of control actions recommended by the SSEBC and the parasitoids' inability to adapt to the newly introduced pest.

In French Guiana, Vayssières et al. (2013) reported a lack of evidence that local parasitoids have developed the ability to detect and attack immature stages of the invasive species *B. carambolae*. The authors point out that while they can attack, they can also fail to develop due to poor host suitability or a strong response from the host's immune system.

However, in the state of Pará the pest was first detected in the Monte Dourado region in 2007, the area where the samples were collected remained free from chemical or cultural control or monitoring, due to difficult access and the fact that it is a private area subject to entry controls. Therefore, it appears that the insects present there have lived together for several life cycles. The abundance of *T. catappa* fruits and the fact that the fruits remained on the ground for long periods may have facilitated parasitism.

It is important to consider that the parasitism percentages found in studies in which fruit was collected in the field and placed in laboratory conditions does not represent reality because the fruit is taken from the natural environment, possibly with eggs and first and second-stage larvae of fruit flies (Adaime et al. 2018). Thus, when immature fruits are removed from the field, they no longer have any chance of being parasitized (Uchôa-Fernandes et al. 2003). Therefore, the percentage of parasitism in *B. carambolae* larvae may be underestimated.

Considering the possibility of *B. carambolae* dispersing to other regions of Brazil, it is very important to analyze in detail the studies that report native parasitoids acting to control the pest in its center of origin, especially those carried out in Indonesia, Malaysia and Thailand (Juma 2015; Stibick 2004; Suputa et al. 2007; Yuliadhi et al. 2022). The information contained in these works may guide future classical biological control programs for the pest in Brazil.

On the other hand, it should be remembered that the exotic parasitoid *D. longicaudata* has already been released along the Oiapoque River and, although it is established in French Guiana, was ineffective in controlling fruit flies (Vayssières et al. 2013). On the Brazilian side, in the state of Amapá, no specimen of *D. longicaudata* was captured during fruit sampling activities carried out by Embrapa over the last 20 years (Adaime et al. 2023).

The use of native Brazilian parasitoids for biological control offers the advantage of simplifying the authorization process for registered techniques, as it would not involve the introduction of an exotic organism. Further studies are warranted to identify the feasibility of using *D. areolatus* as an applied biological control technique for *B. carambolae*. In general, additional studies should be carried out to confirm other parasitoid species and determine the parasitism percentages of native species on *B. carambolae* in Brazil.

T. catappa is reported for the first time as a host of *B. carambolae* in Brazil. The native parasitoids *D. areolatus*, *U. anastrephae*, and *A. pelleranoi* were reported for the first time parasitizing larvae of *B. carambolae* in Brazil.

Acknowledgments: To Alexon Bentes da Silva, Ederson Teles de Costa, Jhonata Filho Melo, Adriano Pinheiro Souza, André da Silva Vale, and Horlen Dias for their support during the fieldwork. To the pest control company Romar LTDA for supporting field collections. To Dr. Valmir Antônio Costa, Centro Avançado de Pesquisa e Desenvolvimento em Sanidade Agropecuária, Instituto Biológico, for providing some photos and for identifying the Figitidae specimens. To Adriana Bariani and Jacivaldo Barbosa, for their support in laboratory activities. To Embrapa Amapá, for providing the laboratory structure. The authors thank the Department of Plant Health and Agricultural Inputs of the Ministry of Agriculture and Livestock, for the authorization granted to carry out this research (Process 21008.000524/2022–14).
Research ethics: Not applicable.
Informed consent: Not applicable.
Author contributions: José V. T. A. Costa: Conceptualization, methodology, software, validation, formal analysis, investigation, data curation, writing – original draft preparation, visualization; Maria S. M. Sousa: Conceptualization, methodology, validation, formal analysis, investigation, data curation, writing – original draft preparation, visualization; Miguel F. Souza-Filho: Conceptualization, methodology, writing – original draft preparation, visualization; Caio G. Murbach: investigation, data curation; Jessica P. M. Oliveira: investigation, data curation; Tatiana P. Santos: investigation, data curation; Alain K. B. T. Matos: investigation, data curation; Dori E. Nava: writing – review and editing, visualization; Ricardo Adaime: Conceptualization, supervision, methodology, validation, formal analysis, writing – original draft preparation, writing – review and editing, visualization. The authors have accepted responsibility for the entire content of this manuscript and approved its submission.
Use of Large Language Models, AI and Machine Learning Tools: None declared.
Conflict of interest: The authors states no conflict of interest.
Research funding: None declared.
Data availability: Not applicable.

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Supplementary Material: This article contains supplementary material (https://doi.org/10.1515/flaent-2024-0053).