Araujo, Mayara Ribeiro de; Martins, David dos Santos; Fornazier, Maurício José; Uramoto, Keiko; Ferreira, Paulo Sérgio Fiuza; Zucchi, Roberto Antonio; Godoy, Wesley Augusto Conde

Aggregation and spatio-temporal dynamics of fruit flies (Diptera, Tephritidae)
in papaya orchards associated with different area delimitations in Brazil

Aggregation and spatio-temporal dynamics of fruit flies (Diptera, Tephritidae) in papaya orchards associated with different area delimitations in Brazil

Mayara Ribeiro de Araujo[1*] , David dos Santos Martins[2], Maurício José Fornazier[2], Keiko Uramoto[1], Paulo Sérgio Fiuza Ferreira[3], Roberto Antonio Zucchi[1] and Wesley Augusto Conde Godoy[1]

[1]Departamento de Entomologia e Acarologia, Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo, Av. Pádua Dias, 11, 13418-900, Piracicaba, São Paulo, Brazil. [2]Departamento de Entomologia, Instituto Capixaba de Pesquisa, Assistência Técnica e Extensão Rural, Vitória, Espírito Santo, Brazil. [3]Departamento de Entomologia, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil. * Author for correspondence. E-mail: mayara_araujo@usp.br

ABSTRACT. We investigated aggregation patterns in three fruit fly species economically important in Brazil, namely *Ceratitis capitata*, *Anastrepha fraterculus*, and *A. obliqua*. The study was carried out in a buffer zone and two neighbourhoods by comparing two-time series associated with the management strategy of fruit flies (systems approach). The abundance of these three species significantly decreased over the years with a negative binomial regression model describing the relationship between abundance and time in the entire area, buffer zone, and their neighbourhoods. In addition, the negative binomial model was also well fitted to the frequency distribution data of fruit flies in all analyzed scenarios. *Anastrepha obliqua* showed the highest aggregation degree, considering both the entire area and time series. *A. fraterculus* exhibited the lowest aggregation level, and *C. capitata* showed an intermediate degree. The buffer zone exhibited the highest aggregation degree for all species, and neighbourhood 2 exhibited the lowest aggregation degree. The aggregation degree was higher in the time series impacted by the systems approach than the series in the first years of its implementation.

Keywords: *Ceratitis capitata*; *Anastrepha fraterculus*; *Anastrepha obliqua*; buffer zone; regression models; frequency distribution.

Introduction

The main tephritid species distributed across the Neotropical Region include two taxonomic groups, *Anastrepha*, which comprises 328 species native to the Americas (Norrbom et al., 2021) and occurs in all regions of Brazil (Zucchi & Moraes, 2021a), and *Ceratitis capitata*, a species with worldwide distribution (Vera, Rodriguez, Segura, Cladera, & Sutherst, 2002), and widely distributed in Brazil (Zucchi & Moraes, 2021b). The genus *Anastrepha* is distributed from a latitude of 35ºN to 35ºS, in different environments, from the sea level to an altitude of 3,000 m or more. *Anastrepha* spp. are classified in several infrageneric groups (Norrbom, Zucchi & Hernández-Ortiz, 1999), among which the *fraterculus* group has several economically important species. To understand the distribution of fruit flies, it is essential to associate them with their host plants, emphasizing the fruit-growing regions, making this interpretation a biogeographical criterion (Aluja & Liedo, 1986). A significant diversity of fruits is generally infested by fruit flies, including papaya, a fruit with a high production on a commercial scale (Martins, Uramoto, & Malavasi, 2000).

The papaya-producing areas in Brazil contribute significantly to the international market, owing to the annual production capacity and for currently being in areas considered to have a low prevalence of fruit flies (Martins, Fornazier, Ventura, Malavasi, & Ferreira, 2011). Papaya exports have been possible due to the implementation of an export program in the USA. The program, recognized as systems approach, includes a set of actions during the pre- and post-harvest periods of papaya for the management of fruit flies (Martins & Malavasi, 2003b; 2003a). It started approximately 25 years ago in the state of Espírito Santo, Brazil, following the requirements for quarantine security.

In Brazil, some species of *Anastrepha* and *Ceratitis capitata* are the most economically important flies because they attack various commercial orchards and are widely distributed in the country (Zucchi, 2000). The geographical distribution of these species is strongly linked to the distribution of their hosts (Selivon, 2000). However, the degree of association between host plants and fruit flies varies between regions (Malavasi, Morgante, & Zucchi, 1980). *Anastrepha fraterculus* and *A. obliqua* exhibit the highest

degree of polyphagy (159 and 70 associated hosts, respectively) in Brazil (Zucchi & Moraes, 2021a). *Ceratitis capitata*, an exotic species, also has a wide range of hosts, being associated with 115 plant species in Brazil (Zucchi & Moraes, 2021b).

Recent studies have been conducted with fruit flies to better understand their spatial distribution in several areas of Brazil (Garcia, Araujo, Uramoto, Walder, & Zucchi, 2017; Frighetto, Machota Junior, Bortoli, Botton, & Guerra, 2019; Santos, Silva, & Miranda, 2020). These studies have taken into account landscape arrangement as one of the factors determining species distribution in different parts of the world (Meyer, Robertson, Peterson, & Mansell, 2008; Kounatidis et al., 2008; Gutierrez & Ponti, 2011; Flores et al., 2016). In general, changes in natural ecosystems, when converting them into agroecosystems, have intensified questions on how to better understand the community structure of pests and their natural enemies as well as investigating the processes determining the abundance of species in different areas (Vandermeer, 1995; Altieri & Nicholls, 2004). Therefore, studies on the spatio-temporal distribution pattern associated with environmental conditions are of high relevance in fruit fly management (Aluja et al., 2003; Aluja & Mangan, 2008; Rull et al., 2018).

Spatio-temporal patterns of distribution in fruit flies have been investigated using different statistical tools such as geostatistics and exponential family models to investigate the frequency distribution of species and populations (Garcia et al., 2017; Nicácio et al., 2019; Oliveira, Uchoa, Pereira, Nicácio, & Faccenda, 2019). These include Poisson and negative binomial functions, usually employed to investigate random and clumped ecological distribution patterns. Insects, in general, particularly fruit flies, tend to exhibit clumped distribution because of the common aggregation of larvae in fruits (Deus et al., 2016). Understanding the aggregation patterns of insects may be useful for pest management in critical areas, such as orchards infested by fruit flies. As for fruit flies in Brazil, this knowledge is still scarce, especially when it involves a time series reflecting real conditions in orchards.

In this study, a long-term time series of *C. capitata*, *A. fraterculus,* and *A. obliqua* was analyzed to investigate the aggregation patterns of fruit fly species, taking into account spatio-temporal distribution in different area delimitations and a time series associated with a management strategy of fruit flies (systems approach). We aim to compare the time series of the three fruit fly species in different spatial delimitations, namely a buffer zone and neighbourhoods 1 and 2, to verify the spatio-temporal distribution patterns in the areas. Therefore, we analyzed the influence of the native forest on the distribution of fruit fly species by comparing the abundance distribution for the three species as a function of time, and under different spatial delimitations in a distance gradient from the Atlantic rainforest remnant. Although previous studies have investigated aspects of population dynamics in fruit flies (Aluja, Ordano, Guillén, & Rull, 2012; Raga, Paula, Souza-Filho, & Castro, 2017; Galli, Michelotto, Bernardes-Soares, Mello-Martins, & Fischer, 2019), a comparative spatio-temporal distribution, taking into account the distance from the native forest as well as pest management, has yet to be performed, especially for the three most important fruit flies (*C. capitata*, *A. fraterculus* and *A. obliqua*).

Material and methods

Data set

The data set was obtained from the monitoring of fruit flies in commercial papaya crops in the State of Espírito Santo, Brazil. This monitoring is part of a set of measures adopted for the management of fruit flies in papaya orchards, the systems approach, which aims to maintain crops with a low prevalence of tephritids, i.e., below seven fruit flies per trap per day (FTD), thus enabling the export of fruits to the USA (Martins & Malavasi, 2003b; Martins et al., 2011).

The study region is located in the vicinity of the municipality of Linhares, 33 m of altitude, and it is considered a production center for papaya in the state of Espírito Santo, Brazil, with a mean production of 50 t ha^{-1} year (Instituto Capixaba de Pesquisa, Assistência Técnica e Extensão Rural [Incaper], 2020). In the region, Ombrophilous Dense Forest, also known as Tableland Forest, is prevalent and the predominant climate is warm tropical, and humid, with a rainy season in summer and dry season in winter, reaching a mean annual temperature of 23ºC (Instituto Chico Mendes de Conservação da Biodiversidade [ICMBio], 2020).

The fruit flies were collected weekly using McPhail traps, with 300 mL of an attractive solution of hydrolyzed corn protein (5%) for collection of *Anastrepha* specimens, and Jackson traps with the sex pheromone Trimedlure were used to capture males of *C. capitata*. The traps were distributed at 1 trap per 1

ha of cultivated area, using 50 McPhail traps and 50% Jackson traps, interspersed, at different georeferenced points (18° 02' 35.7" to 20° 33' 58.3" S and 39° 13' 00.7" to 41° 09' 16.1" W) in commercial papaya production fields in Espírito Santo State (Figure 1). Incaper – *Instituto Capixaba de Pesquisa, Assistência Técnica e Extensão Rural* – provided us with a time series from 1998 to 2010, containing abundant data for *C. capitata*, *A. fraterculus,* and *A. obliqua*. The nominal *A. fraterculus* is used here in sensu lato, as it comprises a complex of cryptic species.

Time series with different area delimitations

The dataset was analyzed in different area delimitations to investigate the relationship between abundance and time. Additionally, the frequency distribution patterns of fruit fly species were analyzed in papaya orchards close and distant from the Reserva Natural Vale, an Atlantic forest remnant that is highly biodiverse with approximately 23,000 ha of protected area (Kierulff, Avelar, Ferreira, Povoa, & Bérnils, 2015). The area delimitations were classified as a buffer zone, neighbourhood 1, and neighbourhood 2 (Figure 1). The buffer zone is a delimitation of the Ministry of Environment of Brazil, an area established around a conservation unit to filter the negative impacts of activities occurring outside it, such as pollution, invasive species, and the advancement of human occupation, especially in units close to intensely occupied areas. Neighbourhood 1 borders the buffer zone and neighbourhood 2 is the pool of all areas further from the buffer zone.

As the present study aimed to investigate temporal space aggregation over a wide area regarding landscape composition, the delimited regions were investigated concerning the distance from the Atlantic forest remnant because it is the main element of the landscape capable of significantly influencing the distribution of fruit flies. Considering the center of the Atlantic Forest Reserve, the distances to the buffer zone, neighbourhood 1, and neighbourhood 2 are 9, 17, and 50 km, respectively.

The papaya orchards are randomly distributed in these regions with sizes between 2 and 275 ha, with a density of 1,100 to 1,500 plants ha^{-1} (Alves, 2003). A total of 332 orchards were studied in the buffer zone, 251 in neighbourhood 1, and 378 in neighbourhood 2, from 1998 to 2010.
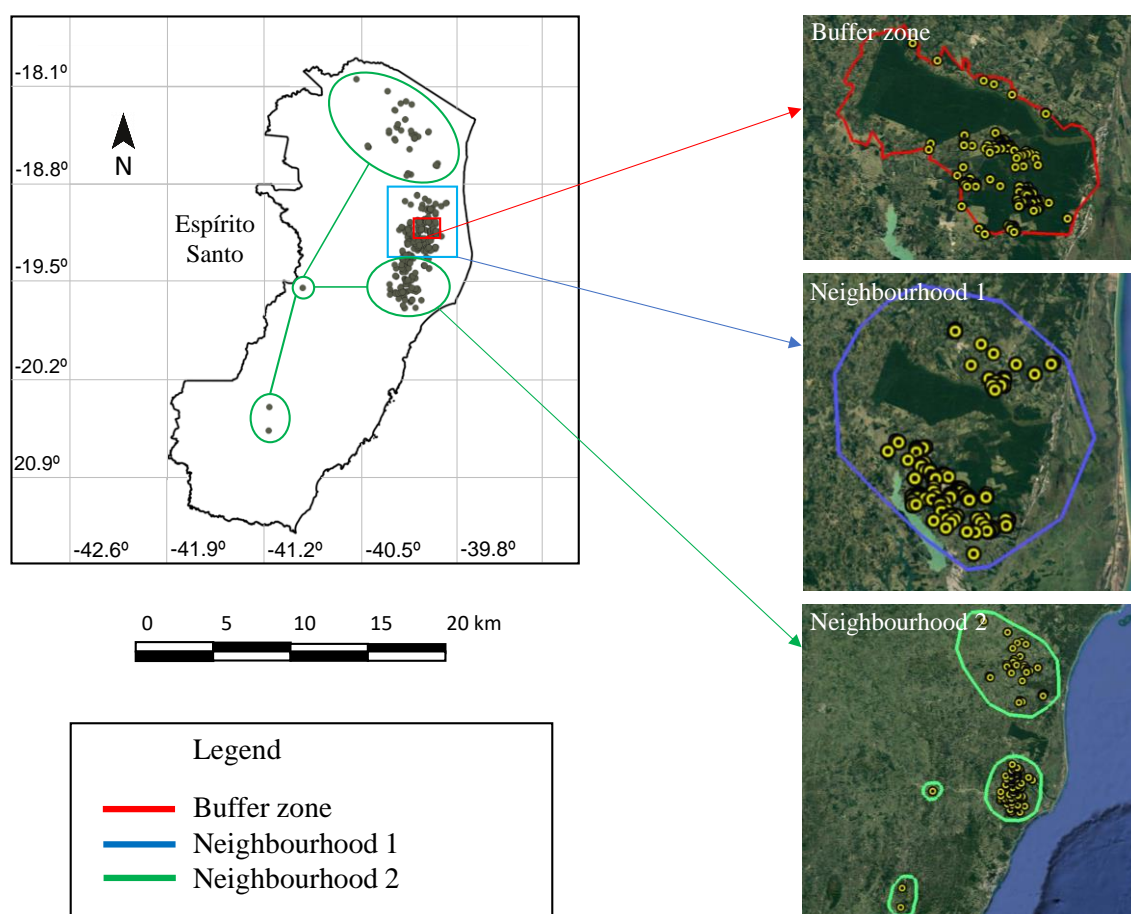

Figure 1. Maps of fruit fly collection sites in the state of Espírito Santo, Brazil, from 1998 to 2010.

Time series with different periods

The full-time series (1998-2010) was subdivided into two subseries, 1998 to 2003 and 2004 to 2010, to document and compare the evolution of the systems approach, and their effects on the abundance of *C. capitata*, *A. fraterculus,* and *A. obliqua*. The systems approach is a set of actions during the pre- and post-harvest periods, implemented in 1990s to improve production, harvesting, packaging, and transport of a commodity that meets the requirements for quarantine security (Martins & Malavasi, 2003b; Malavasi & Martins, 2005). For convenience, we named the time series as 'continuous implementation of the systems approach' for the series between 1998 and 2003, and 'impact on abundance' for the series between 2004 and 2010. Continuous implementation of the systems approach determines sequential, permanent, and uninterrupted management actions since the beginning of its implementation. The impact on abundance describes years after which abundance was visibly influenced by the systems approach.

Data analysis

The Shapiro-Wilk test was used to evaluate data normality, with results indicating that the relationship between abundance and rainfall, temperature, and humidity did not follow a normal distribution. Then, Spearman's correlation was applied to investigate the correlation between the variables mentioned above. Generalized linear models (GLMs) with Poisson and negative binomial errors were used to analyze the relationship between fruit fly abundance and time, according to the series and subseries mentioned above. The Akaike information criterion (AIC) was used to select the best GLM model to fit the fruit fly dataset.

Based on the results obtained with the GLM models, the frequency distribution of fruit flies was fitted to the negative binomial distribution models to confirm whether the spatio-temporal distribution of *C. capitata*, *A. fraterculus*, and *A. obliqua* followed a clumped pattern, and also to compare the degree of aggregation among areas and time subseries. The number of flies per sampling unit was summarized as a frequency distribution, described as the area delimitations with 0, 1, 2, 3, …*n* fruit flies. The *k* parameter in the negative binomial distribution was used to estimate the spatial aggregation degree of flies. The value of *k* indicates the highest aggregation with *k* tending to zero. *K* was calculated by computing the maximum likelihood estimate for aggregation, and the fit of the negative binomial model was tested using the Pearson's χ^2 statistic (Crawley, 2007).

Results and discussion

A total of 13,889 adults of *C. capitata* (FTD = 0.007), 2,999 of *A. fraterculus* (FTD = 0.006), and 797 of *A. obliqua* (FTD = 0.006) were collected in papaya orchards in the State of Espírito Santo, during a 13-year monitoring period. The three-time series for the three fruit fly species from 1998 to 2010 described the population dynamics of *C. capitata*, *A. fraterculus*, and *A. obliqua*, indicating a decreasing trend in abundance for the species, particularly visible after 2003 (Figure 2). Regression analyses with Poisson and negative binomial errors were performed for the three datasets showing a significant relationship between time (years) and abundance when data were fitted to the two functions (Table 1). However, the AIC value indicated that the negative binomial model was the best regression function to explain the abundance variation in response to the time series for *C. capitata*, *A. fraterculus*, and *A. obliqua*.
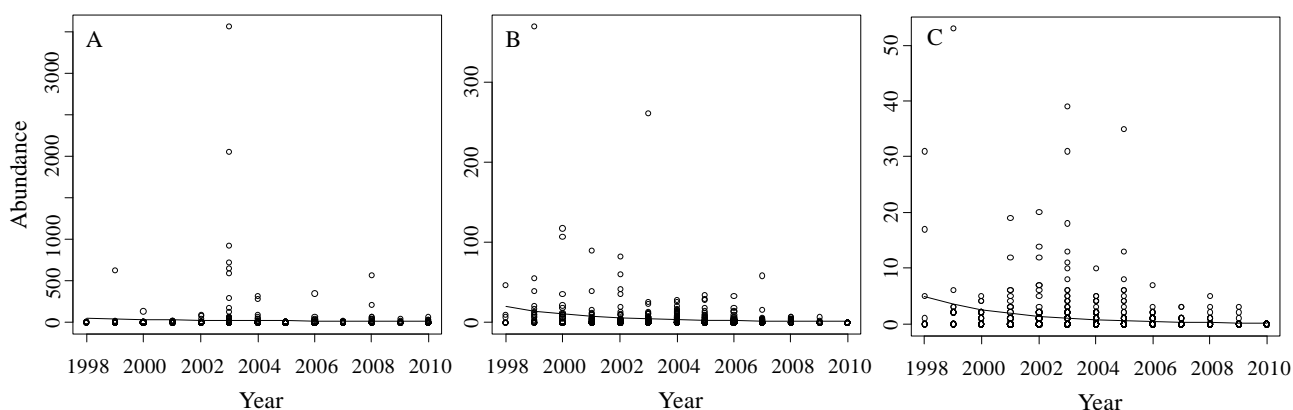

Figure 2. Time series for *C. capitata* (A)*, A. fraterculus* (B) and *A. obliqua* (C) describing the variation of abundance in response to time.

Table 1. Regressions with Poisson and Negative binomial errors taking into account fruit fly abundance variation in response to time (1998-2010).

Coefficients	Estimate	Standard error	z value	Pr(>|z|)
Regression with Poisson errors for C. capitata				
Intercept	287.22	6.44	44.61	< 2e-16
Time	-0.14	0.003	-44.19	< 2e-16
				AIC 101672
Regression with negative binomial errors for C. capitata				
Intercept	406.30	87.83	44.61	3.73e-06
Time	-0.20	0.043	-4.59	4.29e-06
				AIC 3426*
Regression with Poisson errors for A. fraterculus				
Intercept	672.09	14.83	45.31	< 2e-16
Time	-0.33	0.007	-45.21	< 2e-16
				AIC 12297
Regression with negative binomial errors for A. fraterculus				
Intercept	687.59	58.33	11.79	< 2e-16
Time	-0.34	0.03	-11.77	< 2e-16
				AIC 3189*
Regression with Poisson errors for A. obliqua				
Intercept	579.42	28.25	20.51	< 2e-16
Time	-0.28	0.01	-20.50	< 2e-16
				AIC 3593
Regression with negative binomial errors for A. obliqua				
Intercept	650.86	71.26	9.13	< 2e-16
Time	-0.32	0.03	-9.13	< 2e-16
				AIC 1848*

*Best model.

The abundance variation of the three species in response to time was also significant when fly abundances were compared within the entire area from 1998 to 2010 (Table 1). This result was also observed in the delimitated areas, buffer zone (Table 2), neighbourhood 1 (Table 3), and neighbourhood 2 (Table 4).

Spearman's correlation analysis between the abundance of fruit flies and the variables temperature, humidity, rainfall, and time (1998-2010) indicated a single negative significant correlation (rho = -0.14 p < 0.001), i.e., between abundances of *C. capitata* and humidity.

The frequency distribution analysis (Table 5) shows significant clumped patterns for the three fruit fly species in all the areas studied. When studying the influence on each area, the three species were more aggregated in the buffer zone. Observing each species separately, it was noticed that the aggregation degree was practically the same for *C. capitata* in the entire area, neighbourhoods 1, and 2, but the buffer zone exhibited its highest aggregation, reaching $k = 0.08$ (Table 5). *Anastrepha fraterculus* also exhibited the maximum aggregation degree in the buffer zone, but with $k = 0.13$, and in neighbourhood 2, it showed its lowest aggregation degree, with $k = 0.25$. *Anastrepha obliqua* exhibited its maximum aggregation in the buffer zone, with $k = 0.03$, and its lowest aggregation level in neighbourhood 2.

The comparison between the continuous implementation of the systems approach and the impact on abundance also revealed that the two times series exhibited clumped frequency distribution for the three species analyzed (Table 6). The species showed more aggregated patterns during the impact on abundance when the entire area was evaluated. Further evidence of an increase in aggregation can be observed when comparing the *C. capitata* time series in the buffer zone, with $k = 0.13$ for the series between 1998 and 2003, $k = 0.07$ for the series between 2004 and 2010, and *A. fraterculus* when the k value decreased from 0.2 (1998-2003) to 0.09 (2004-2010; Table 6). Although *A. obliqua* has exhibited a clear trend to increase its aggregation in the entire area, in the buffer zone, and neighbourhoods 2, its aggregation degree trended to decrease. In both areas, a loss of aggregation was observed, with k values increasing from the 1998-2003 series to the 2004-2010 series. An increase in aggregation was only observed for the entire area and neighbourhood 1.

Among the species of Tephritidae reported in agricultural orchards in Brazil, *C. capitata*, *A. fraterculus,* and *A. obliqua* have been dominant (Querino, Maia, Lopes, Alvarenga, & Zucchi, 2014; Lopes et al., 2015; Duarte, Garcia, & Andaló, 2016; Rosa et al., 2018). These species are widely distributed in the Brazilian territory, are

highly polyphagous, and have a wide range of hosts already registered (Zucchi & Moraes, 2021a; 2021b). As observed in surveys of fruit flies in commercial plantations (Aluja et al., 1996), also in the areas of commercial production of papaya in the state of Espírito Santo, Brazil, few species of fruit flies are common.

Table 2. Regressions with Poisson and negative binomial errors taking into account fruit fly abundance variation in response to time (1998-2010) in the buffer zone.

Coefficients	Estimate	Standard error	z value	Pr(>|z|)
Regression with Poisson errors for C. capitata				
Intercept	243.43	14.78	16.48	< 2e-16
Time	-0.12	0.007	-16.36	< 2e-16
				AIC 13010
Regression with negative binomial errors for C. capitata				
Intercept	584.97	143.39	4.08	4.51e-05
Time	-0.29	0.07	-4.07	4.70e-05
				AIC 848*
Regression with Poisson errors for A. fraterculus				
Intercept	904.25	24.80	36.46	< 2e-16
Time	-0.45	0.01	-34.38	< 2e-16
				AIC 4293
Regression with negative binomial errors for A. fraterculus				
Intercept	776.93	99.14	7.84	4.64e-15
Time	-039	0.05	-7.83	4.83e-15
				AIC 910*
Regression with Poisson errors for A. obliqua				
Intercept	940.10	72.56	12.96	< 2e-16
Time	-0.47	0.04	-12.96	< 2e-16
				AIC 651
Regression with negative binomial errors for A. obliqua				
Intercept	757.53	138.27	5.48	4.28e-08
Time	-0.37	0.07	-5.48	4.07e-08
				AIC 349 *

*Best model.

Table 3. Regressions with Poisson and negative binomial errors taking into account fruit fly abundance variation in response to time (1998-2010) in the neighbourhood 1.

Coefficients	Estimate	Standard error	z value	Pr(>|z|)
Regression with Poisson errors for C. capitata				
Intercept	-399.76	24.28	-16.47	< 2e-16
Time	0.20	0.01	16.53	< 2e-16
				AIC 5942
Regression with negative binomial errors for C. capitata				
Intercept	-511.19	149.91	-3.41	6.5e-04
Time	0.25	0.07	3.42	6.3e-04
				AIC 804*
Regression with Poisson errors for A. fraterculus				
Intercept	813.32	25.47	31.93	< 2e-16
Time	-0.40	0.01	-31.85	< 2e-16
				AIC 4263
Regression with negative binomial errors for A. fraterculus				
Intercept	826.54	117.16	7.05	1.73e-12
Time	-0.41	0.06	-7.04	1.85e-12
				AIC 923*
Regression with Poisson errors for A. obliqua				
Intercept	589.71	50.69	11.63	< 2e-16
Time	-0.29	0.02	-1163	< 2e-16
				AIC 1170
Regression with negative binomial errors for A. obliqua				
Intercept	607.87	143.33	4.24	2.22e-05
Time	-0.30	0.07	-4.24	2.22e-05
				AIC 538*

*Best model.

Table 4. Regressions with Poisson and negative binomial errors taking into account fruit fly abundance variation in response to time (1998-2010) in the neighbourhood 2.

Coefficients	Estimate	Standard error	z value	Pr(>|z|)
Regression with Poisson errors for *C. capitata*				
Intercept	183.04	9.02	20.29	<2e-16
Time	-0.09	0.004	-19.91	<2e-16
				AIC 74733
Regression with negative binomial errors for *C. capitata*				
Intercept	873.57	168.30	5.19	2.10e-07
Time	-0.43	0.08	-5.17	2.33e-07
				AIC 1690*
Regression with Poisson errors for *A. fraterculus*				
Intercept	250.70	32.04	7.82	5.14e-15
Time	-0.12	0.02	-7.79	6.36e-15
				AIC 2866
Regression with negative binomial errors for *A. fraterculus*				
Intercept	326.10	102.06	3.19	1.40e-03
Time	-0.16	0.05	-3.18	1.44e-03
				AIC 1335*
Regression with Poisson errors for *A. obliqua*				
Intercept	439.62	46.08	9.54	<2e-16
Time	-022	0.02	-9.54	<2e-16
				AIC 1627
Regression with negative binomial errors for *A. obliqua*				
Intercept	541.18	117.12	4.62	3.82e-06
Time	-0.27	0.06	-4.62	3.82e-06
				AIC 934*

*Best model

Table 5. Fits of the negative binomial distribution model to the frequency of *C. capitata, A. fraterculus* and *A. obliqua* in entire area, buffer zone, neighbourhood 1 and neighbourhood 2 from 1998-2010.

	$\bar{x}$	s^2	k	$\chi^{2(*)}$	df
Entire area					
C. capitata	7.18	309.21	0.14	6.00	60
A. fraterculus	2.71	100.61	0.15	3.07	117
A. obliqua	0.83	11.26	0.13	5.23	53
Buffer zone					
C. capitata	2.31	73.88	0.08	0.01	60
A. fraterculus	1.93	48.43	0.13	0.05	58
A. obliqua	0.37	8.90	0.03	0.80	53
Neighbourhood 1					
C. capitata	2.35	67.47	0.13	0.03	65
A. fraterculus	4.12	194.80	0.17	0.24	91
A. obliqua	1.06	16.98	0.13	0.01	39
Neighbourhood 2					
C. capitata	5.97	319.20	0.14	0.10	88
A. fraterculus	2.30	27.90	0.25	5.54	41
A. obliqua	1.08	9.34	0.20	1.28	31

*$p < 0.05$.

Ceratitis capitata was more abundant than the other two species in papaya orchards in the State of Espírito Santo. Studies indicate that *C. capitata* prefers agricultural and/or anthropized environments when compared to *Anastrepha* species that prefer environments with native vegetation (Alvarenga, Alves, Silva, Lopes, & Lopes, 2010; Querino et al., 2014). The collection methods used in this study may also have influenced the abundance of fruit flies, mainly because *C. capitata* was captured with a trap using a sexual pheromone as bait, and *Anastrepha* species were collected using food attractive traps; however, both methods are usually used for fruit fly monitoring (Silva et al., 2011). Additionally, the eventual dominance of *C. capitata* in papaya orchards in Espírito Santo can also be interpreted from results showing temporal segregation between *C. capitata* and *A. obliqua*, as previously documented in loquat orchards (Lopes et al., 2015). There are also results showing high dominance of *C. capitata* when co-occurring with *A. fraterculus* in different localities of Argentina (Segura et al., 2006).

The decrease in the abundance of fruit flies, statistically confirmed with Poisson and negative binomial regressions, was potentially due to the impact of the systems approach applied in the studied area. Comparing

the abundance values during the years, the decrease in population size is easily noticeable for *A. fraterculus* and *A. obliqua*. However, although *C. capitata* also exhibited a significant decrease in abundance in response to time, it was not as visible as observed in the other species, potentially due to its high variation in abundance values. In 2003, *C. capitata* exhibited a significantly higher abundance than *A. fraterculus* and *A. obliqua,* alongside its abundance in other years. There is no specific reason for this outbreak, although *C. capitata* outbreaks have commonly been noticed in other parts of the world where outbreaks frequently occur (Montoya, Cancino, Zenil, Gómez, & Villaseñor, 2005; Barnes, Targovska, & Franz, 2006; Carey, 2010).

In the systems approach, papaya fruits are harvested at stages 1 and 2 of ripeness (Martins & Malavasi, 2003b; Brasil, 2008). In these stages, the fruits have high concentrations of benzyl-isothiocyanate (BITC), a natural chemical compound present in fruit latex, and its concentration decreases as the fruit ripen (Seo, Tang, Sanidad, & Takenaka, 1983; Nascimento, Frighetto, Malavasi, & Habibe, 2003). BITC acts as an ovicide, inhibiting oviposition, and killing the initial larvae of fruit flies (Seo & Tang, 1982). There is no risk of infestation by these insects when the papaya is harvested in the early stages of maturation.

Despite having two models to describe significantly the fruit fly dynamics for the three species, the AIC values indicated that the negative binomial model was the best regression function to explain the relationship between time and fly abundance. In addition, the analysis taking into account the frequency distribution of the fruit flies confirmed the suitability of the negative binomial model for all scenarios analyzed (different periods: 1998 to 2003, 2004 to 2010, and different areas: entire area, buffer zone, and neighbourhoods 1 and 2). Insect count data are generally not normally distributed (Sileshi, 2006), and there is evidence showing that the frequency distribution in this taxonomic group is ecologically described by a negative binomial distribution (Deus et al., 2016; Maldonado Jr, Barbosa, Costa, Gonçalves, & Santos, 2016; Nicácio et al., 2019). This function, characterized by variance significantly higher than the mean (Crawley, 2013), was observed in our results.

Table 6. Fits of the negative binomial distribution model to the frequency of *C. capitata*, *A. fraterculus* and *A. obliqua* in continuous implementation of Systems approach (1998-2003) and impact on abundance (2004-2010).

	$\bar{x}$	s^2	k	$\chi^{2(*)}$	Df
Entire area 1998-2003					
C. capitata	5.56	291.55	0.13	0.07	86
A. fraterculus	4.21	167.36	0.20	0.45	91
A. obliqua	1.37	18.77	0.20	0.04	53
Entire area 2004-2010					
C. capitata	2.88	123.58	0.10	0.06	88
A. fraterculus	1.55	20.57	0.18	4.39	58
A. obliqua	0.40	3.28	0.11	3.67	35
Buffer zone 1998-2003					
C. capitata	1.70	20.36	0.13	0.0008	22
A. fraterculus	3.83	75.22	0.2	0.003	40
A. obliqua	1.04	30.36	0.07	0.29	54
Buffer zone 2004-2010					
C. capitata	2.08	65.66	0.07	0.005	59
A. fraterculus	0.94	19.86	0.09	1.01	58
A. obliqua	0.23	0.48	0.16	4.51	03
Neighbourhood 1 1998-2003					
C. capitata	1.28	7.76	0.21	0.03	16
A. fraterculus	8.58	469.11	0.21	0.0001	91
A. obliqua	1.96	33.01	0.25	0.07	39
Neighbourhood 1 2004-2010					
C. capitata	3.01	111.39	0.12	0.04	66
A. fraterculus	1.60	15.60	0.21	0.01	34
A. obliqua	0.65	9.31	0.08	0.001	35
Neighbourhood 2 1998-2003					
C. capitata	8.44	444.72	0.15	0.06	86
A. fraterculus	2.37	32.03	0.26	0.12	41
A. obliqua	1.6	16.35	0.21	0.02	31
Neighbourhood 2 2004-2010					
C. capitata	3.23	152.54	0.13	0.04	88
A. fraterculus	2.18	23.72	0.24	0.015	29
A. obliqua	0.58	1.71	0.28	0.097	08

*p < 0.05.

Landscape heterogeneity in the buffer zone may have contributed to the greater aggregation of species, because it contains a large fragment of preserved natural vegetation exhibiting large quantities of resources available for fruit fly maintenance, which may dissipate the concentration of fruit flies in the same area. Fruit flies in agricultural areas tend to be influenced by the presence of fragments of adjacent native vegetation (Aluja et al., 1996; Uchôa & Nicácio, 2010). Forest fragments have contributed to the presence of *Anastrepha* species in adjacent guava orchards (Querino et al., 2014). According to Meats (2007), the conformation of the landscape is a relevant factor in the distribution of fruit flies. Natural environments may result in a more aggregated distribution of flies than other types of environments. In all the scenarios analyzed, *A. obliqua* exhibited abundances significantly lower than those of the other species, and under this condition, any movement of individuals among sampling units may proportionally influence the spatial pattern of distribution. Furthermore, this can result in a decrease in empty units, making the system prone to random occupancy, characterized by *k* parameter exhibiting values more distant from zero (Reigada & Godoy, 2005).

In neighbourhood 1, the aggregation degree of *C. capitata* and *A. obliqua* increased from the first series to the second series, while *A. fraterculus* maintained the same *k* value. This result, when compared to the buffer zone, allows us to conclude that the population aggregation behavior may change in response to different local conditions, and this is potentially intrinsic to each species, with responses including intense variation regarding distribution among areas. The aggregation trend from the first to the second series was also maintained in neighbourhood 2, but similarly to the buffer zone, *A. obliqua* decreased its aggregation from the first to the second series.

At the global scale, it is usual to observe changes in aggregation in insects described by outbreaks over time, mainly in response to climatic changes, with important implications for pest management (Williams & Liebhold, 1995). However, at the local scale, the spectrum of variable values changes, such as temperature and others generally investigated, is much more restricted, making the influence of temperature or other variables less impactful, as observed in our correlation tests. Therefore, at the local scale, there are potentially other factors capable of influencing the spatial distribution of insects. Changes in the spatial distribution patterns of host plants can influence the intensity of ecological interactions between plants and herbivorous insects (Hakes, Halpern, & Underwood, 2018). Papaya orchards in the investigated areas were not distributed significantly far from each other. This condition may be associated with the general aggregation pattern discussed here. However, distance and size are not homogeneous among the orchards, and these factors certainly influenced each species differently, explaining the small differences in aggregation observed in the three fruit fly species, with particular emphasis on *A. obliqua*.

Comparing the two periods in the entire area, a slight aggregation trend was found for the three species in the series 2004-2010. This result may be due to the management actions implemented in the papaya orchards in Espírito Santo State (Martins & Malavasi, 2003b), mainly because the fruit fly species aggregation is implied in several areas with zero individuals. The decrease in fruit flies in response to the systems approach implementation resulted in more empty areas when compared with the previous condition. This information is relevant, mainly for when sequential sampling plans are implemented to monitor critical population sizes, with direct implications for decisions based on economic threshold and/or prediction of pest outbreaks (Ferreira & Godoy, 2014; Nicácio et al., 2019).

Our results can also be useful as subsidies to optimize monitoring plans and risk mapping in orchards. In this sense, studies should be carried out to discuss the possibility of sampling plans suitable to local realities and critical areas to minimize the costs of installing traps and/or enhancing pest control in locations with a higher risk of infestation.

Conclusion

The aggregation pattern of fruit fly species was significantly influenced by area and time. The buffer zone and the impact on the abundance period provided a maximum aggregation of populations of *C. capitata*, *A. fraterculus,* and *A. obliqua*, indicating a significant association between aggregation degrees and a decrease in the abundance of fruit flies.

Acknowledgements

References

Altieri, M. A., & Nicholls, C. I. (2004). An agroecological basis for designing diversified cropping systems in the tropics. *Journal of Crop Improvement, 11*(1-2), 81-103. DOI: https://doi.org/10.1300/J411v11n01_05

Aluja, M., & Liedo, P. (1986). Future perspectives on integrated management of fruit flies in Mexico. In M. Mangel, J. R. Carey, & R. E. Plant (Eds.), *Pest control: operations and systems analysis in Fruit Fly management* (p. 12-48). New York, NY: Springer.

Aluja, M., & Mangan, R. L. (2008). Fruit fly (Diptera: Tephritidae) host status determination: critical conceptual, methodological, and regulatory considerations. *Annual Review of Entomology, 53*(1), 473-502. DOI: https://doi.org/10.1146/annurev.ento.53.103106.093350

Aluja, M., Celedonio-Hurtado, H., Liedo, P., Cabrera, M., Castillo, F., Guillén, J., & Rios, E. (1996). Seasonal population fluctuations and ecological implications for management of *Anastrepha* fruit flies (Diptera: Tephritidae) in commercial mango orchards in southern Mexico. *Journal of Economic Entomology, 89*(3), 654-667. DOI: https://doi.org/10.1093/jee/89.3.654

Aluja, M., Ordano, M., Guillén, L., & Rull, J. (2012). Understanding long-term fruit fly (Diptera: Tephritidae) population dynamics: implications for areawide management. *Journal of Economic Entomology, 105*(3), 823-836. DOI: https://doi.org/10.1603/EC11353

Aluja, M., Rull, J., Sivinski, J., Norrbom, A. L., Wharton, R. A., Macías-Ordóñez, R., ... López, M. (2003). Fruit flies of the genus *Anastrepha* (Diptera: Tephritidae) and associated native parasitoids (Hymenoptera) in the tropical rainforest biosphere reserve of Montes Azules, Chiapas, Mexico. *Environmental Entomology, 32*(6), 1377-1385. DOI: https://doi.org/10.1603/0046-225X-32.6.1377

Alvarenga, C. D., Alves, D. A., Silva, M. A., Lopes, E. N., & Lopes, G. N. (2010). Moscas-das-frutas (Diptera: Tephritidae) em pomares da área urbana no norte de Minas Gerais. *Revista Caatinga, 23*(2), 25-31.

Alves, F. L. (2003). A cultura do mamão *Carica papaya* no mundo, no Brasil e no estado do Espírito Santo. In D. S. Martins, & A. F. S. Costa (Eds.), *A cultura do mamoeiro: tecnologias de produção* (p. 11-34). Vitória, ES: Incaper.

Barnes, B. N., Targovska, A., & Franz, G. (2006). Origin of a Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), outbreak determined by DNA analysis. *African Entomology, 14*(2), 205-209.

Brasil. (2008). *Instrução normativa nº 5, de 22 de Janeiro de 2008*. Brasília, DF: Diário Oficial da União.

Carey, J. R. (2010). The Mediterranean fruit fly (*Ceratitis capitata*). *American Entomologist, 56*(3), 158-163. DOI: https://doi.org/10.1093/ae/56.3.158

Crawley, M. J. (2007). *The R book*. Silwood Park, UK: Wiley-Blackwell.

Crawley, M. J. (2013). *The R book* (2nd ed.). Silwood Park, UK: Wiley-Blackwell.

Deus, E. G., Godoy, W. A. C., Sousa, M. S. M., Lopes, G. N., Jesus-Barros, C. R., Silva, J. G., & Adaime, R. (2016). Co-infestation and spatial distribution of *Bactrocera carambolae* and *Anastrepha* spp. (Diptera: Tephritidae) in common guava in the eastern Amazon. *Journal of Insect Science, 16*(1), 88. DOI: https://doi.org/10.1093/jisesa/iew076

Duarte, P. A. S., Garcia, F. R. M., & Andaló, V. (2016). Faunal analysis and population density of fruit flies (Diptera: Tephritidae) in an orchard located in the central western region of Minas Gerais, Brazil. *Bioscience Journal, 32*(4), 960-968. DOI: https://doi.org/10.14393/BJ-v32n4a2016-33321

Ferreira, C. P., & Godoy, W. A. C. (2014). *Ecological modelling applied to entomology*. Cham, CH: Springer.

Flores, S., Montoya, P., Ruiz-Montoya, L., Villaseñor, A., Valle, A., Enkerlin, W., & Liedo, P. (2016). Population fluctuation of *Ceratitis capitata* (Diptera: Tephritidae) as a function of altitude in eastern Guatemala. *Environmental Entomology, 45*(4), 802-811. DOI: https://doi.org/10.1093/ee/nvw051

Frighetto, J. M., Machota Junior, R., Bortoli, L. C., Botton, M., & Guerra, A. C. B. (2019). Spatial and temporal distribution of South American fruit fly in vineyards. *Revista Ceres, 66*(4), 287-296. DOI: https://doi.org/10.1590/0034-737X201966040007

Galli, J. A., Michelotto, M. D., Soares, M. B. B., Martins, A. L. M., & Fischer, I. H. (2019). Population fluctuation of fruit fly *Anastrepha* spp. (Díptera: Tephritidae) in guava *(Psidium guajava* L.) accesses produced in organic system. *Acta Agronómica, 68*(1), 9-15. DOI: https://doi.org/10.15446/acag.v68n1.66263

Garcia, A. G., Araujo, M. R., Uramoto, K., Walder, J. M. M., & Zucchi, R. A. (2017). Geostatistics and geographic information system to analyze the spatial distribution of the diversity of *Anastrepha* species (Diptera: Tephritidae): the effect of forest fragments in an urban area. *Environmental Entomology, 46*(6), 1189-1194. DOI: https://doi.org/10.1093/ee/nvx145

Gutierrez, A. P., & Ponti, L. (2011). Assessing the invasive potential of the Mediterranean fruit fly in California and Italy. *Biological Invasions, 13*(12), 2661-2676. DOI: https://doi.org/10.1007/s10530-011-9937-6

Hakes, A. S., Halpern, S., & Underwood, N. (2018). Insect herbivores increase the spatial aggregation of a clonal plant. *International Journal of Plant Sciences, 179*(3), 209-216. DOI: https://doi.org/10.1086/696685

Instituto Capixaba de Pesquisa, Assistência Técnica e Extensão Rural [Incaper]. (2020). *Polos de fruticultura – mamão*. Incaper. Recuperado de https://incaper.es.gov.br/fruticultura-mamao

Instituto Chico Mendes de Conservação da Biodiversidade [ICMBio]. (2020). *Aspectos físicos e biológicos*. ICMBio. Recuperado de https://www.icmbio.gov.br/rebiosooretama/aspectos-fisicos-e-biologicos.html

Kierulff, M. C. M., Avelar, L. H. S., Ferreira, M. E. S., Povoa, K. F., & Bérnils, R. S. (2015). Reserva Natural Vale: história e aspectos físicos. *Ciência & Ambiente, 49*, 7-40.

Kounatidis, I., Papadopoulos, N. T., Mavragani-Tsipidou, P., Cohen, Y., Tertivanidis, K., Nomikou, M., & Nestel, D. (2008). Effect of elevation on spatio-temporal patterns of olive fly (*Bactrocera oleae*) populations in northern Greece. *Journal of Applied Entomology, 132*(9-10), 722-733. DOI: https://doi.org/10.1111/j.1439-0418.2008.01349.x

Lopes, G. N., Souza-Filho, M. F., Gotelli, N. J., Lemos, L. J. U., Godoy, W. A. C., & Zucchi, R. A. (2015). Temporal overlap and co-occurrence in a guild of sub-tropical tephritid fruit flies. *PLoS One, 10*(7), e0132124. DOI: https://doi.org/10.1371/journal.pone.0132124

Malavasi, A., & Martins, D. S. (2005). Origem e aplicações futuras do conceito de systems approach. In D. S. Martins (Ed.)*, Papaya Brasil: mercado e inovações tecnológicas para o mamão* (2nd ed., p. 43-53). Vitória, ES: Incaper.

Malavasi, A., Morgante, J. S., & Zucchi, R. A. (1980). Biologia de "moscas-das-frutas" (Diptera, Tephritidae).: I. listas de hospedeiros e ocorrência. *Revista Brasileira de Biologia, 40*(1), 9-16.

Maldonado Jr, W., Barbosa, J. C., Costa, M. G., Gonçalves, P. C. T., & Santos, T. R. (2016). Spatial distribution and sequential sampling of *Brevipalpus phoenicis* in citrus. *Revista Brasileira de Fruticultura, 38*(4), e-085. DOI: https://doi.org/10.1590/0100-29452016

Martins, D. S., & Malavasi, A. (2003a). Aplicação do "System Approach" para a exportação de frutas: mamão brasileiro para os Estados Unidos. In L. Zambolim (Ed.)*, Manejo integrado: produção integrada, fruteiras tropicais, doenças e pragas* (p. 7-35). Viçosa, MG: UFV.

Martins, D. S., & Malavasi, A. (2003b). Systems Approach na produção de mamão do Espírito Santo, como garantia de segurança quarentenária contra moscas-das-frutas. In D. S. Martins, & A. F. S. Costa (Eds.), *A cultura do mamoeiro: tecnologias de produção* (p. 347-372). Vitória, ES: Incaper.

Martins, D. S., Fornazier, M. J., Ventura, J. A., Malavasi, A., & Ferreira, P. S. F. (2011). Caracterização da cultura de mamão na região norte do Espírito Santo como área de baixa prevalência de moscas-das-frutas. *Simpósio do Papaya Brasileiro: Inovação e Sustentabilidade, 5*, 12.

Martins D.S., Uramoto K., & Malavasi A. (2000) Espírito Santo. In: A. Malavasi & R.A. Zucchi (eds), *Moscas-das-frutas de importância econômica no Brasil: conhecimento básico e aplicado* (p. 253-258). Ribeirão Preto, SP: Holos.

Meats, A. (2007). Dispersion of fruit flies (Diptera: Tephritidae) at high and low densities and consequences of mismatching dispersions of wild and sterile flies. *Florida Entomologist, 90*(1), 136-146. DOI: https://doi.org/10.1653/0015-4040(2007)90[136:DOFFDT]2.0.CO;2

Meyer, M., Robertson, M. P., Peterson, A. T., & Mansell, M. W. (2008). Ecological niches and potential geographical distributions of Mediterranean fruit fly (*Ceratitis capitata*) and Natal fruit fly (*Ceratitis rosa*). *Journal of Biogeography, 35*(2), 270-281. DOI: https://doi.org/10.1111/j.1365-2699.2007.01769.x

Montoya, P., Cancino, J., Zenil, M., Gómez, E., & Villaseñor, A. (2005). Parasitoid releases in the control of Ceratitis capitata (Diptera: Tephritidae) outbreaks, in coffee growing zones of Chiapas, Mexico. *Vedalia, 12*(1), 85-89.

Nascimento, A. S., Frighetto, R. T. S., Malavasi, A., & Habibe, T. C. (2003). Avaliação dos teores de benzil isotiocinato (BITC) em mamoeiros sadios e infectados pela meleira sob condições de campo e telado. In D. S. Martins (Ed.)*, Papaya Brasil: qualidade do mamão para o mercado interno* (p. 609-612). Vitória, ES: Incaper.

Nicácio, J., Oliveira, I., Uchoa, M. A., Faccenda, O., Abot, A. R., Fernandes, M. G., & Garcia, F. R. M. (2019). Spatial distribution and control levels of *Anastrepha* spp. (Diptera: Tephritidae) in guava orchards. *Anais da Academia Brasileira de Ciências, 91*(3), e20180428. DOI: https://doi.org/10.1590/0001-3765201920180428

Norrbom, A.L., Muller, A., Gangadin, A., Sutton, B.D., Rodriguez, E.J., Savaris, M., Lampert, S., Rodriguez-Clavijo, P.A., Steck, G.J., Moore, M.R., Nolazo, N., Troya, H., Keil, C.B., Padilla, A., Wiegmann, B.M., Cassel, B., Branham, M. & Ruiz-Arc, R. (2021). New species and host plants of *Anastrepha* (Diptera: Tephritidae) primarily from Suriname and Pará, Brazil. *Zootaxa 5044* (1): 001–074. DOI: https://doi.org/10.11646/zootaxa.5044.1.1

Norrbom, A.L., Zucchi, R.A. & Hernández-Ortiz, V. (1999). Phylogeny of the genera *Anastrepha* and *Toxotrypana* (Trypetinae: Toxotrypanini) based on morphology. In: M. Aluja & A.L. Norrbom (Eds.), *Fruit flies (Tephritidae): Phylogeny and evolution of behavior* (p. 299–342). Boca Raton, FL: CRC Press.

Oliveira, I., Uchoa, M. A., Pereira, V. L., Nicácio, J., & Faccenda, O. (2019). *Anastrepha* species (Diptera: Tephritidae): patterns of spatial distribution, abundance, and relationship with weather in three environments of midwestern Brazil. *Florida Entomologist, 102*(1), 113-120. DOI: https://doi.org/10.1653/024.102.0118

Querino, R. B., Maia, J. B., Lopes, G. N., Alvarenga, C. D., & Zucchi, R. A. (2014). Fruit fly (Diptera: Tephritidae) community in guava orchards and adjacent fragments of native vegetation in Brazil. *Florida Entomologist, 97*(2), 778-786. DOI: https://doi.org/10.1653/024.097.0260

Raga, A., Paula, L. I. S., Souza-Filho, M. F., & Castro, J. L. (2017). Population dynamics and infestation rate of fruit flies in stone fruits in São Paulo State, Brazil. *Annual Research & Review in Biology, 14*(6), 1-11. DOI: https://doi.org/10.9734/ARRB/2017/34005

Reigada, C., & Godoy, W. A. C. (2005). Dispersal and predation behavior in larvae of *Chrysomya albiceps* and *Chrysomya megacephala* (Diptera: Calliphoridae). *Journal of Insect Behavior, 18*(4), 543-555. DOI: https://doi.org/10.1007/s10905-005-5611-0

Rosa, J. M., Nunes, M. Z., Boff, M. I. C., Garcia, F. R. M., Boff, P., & Franco, C. R. (2018). Ensamble de moscas de las frutas (Diptera: Tephiritidae) en huerto de feijoa en el Estado de Santa Catarina, Brasil. *Revista Colombiana de Entomología, 44*(1), 110-115. DOI: https://doi.org/10.25100/socolen.v44i1.6547

Rull, J., Tadeo, E., Lasa, R., Rodríguez, C. L., Altuzar-Molina, A., & Aluja, M. (2018). Experimental hybridization and reproductive isolation between two sympatric species of tephritid fruit flies in the *Anastrepha fraterculus* species group. *Insect Science, 25*(6), 1045-1055. DOI: https://doi.org/10.1111/1744-7917.12489

Santos, R. P. D., Silva, J. G., & Miranda, E. A. (2020). The past and current potential distribution of the fruit fly *Anastrepha obliqua* (Diptera: Tephritidae) in south America. *Neotropical Entomology, 49*(2), 284-291. DOI: https://doi.org/10.1007/s13744-019-00741-1

Segura, D. F., Vera, M. T., Cagnotti, C. L., Vaccaro, N., Coll, O., Ovruski, S. M., & Cladera, J. L. (2006). Relative abundance of *Ceratitis capitata* and *Anastrepha fraterculus* (Diptera: Tephritidae) in diverse host species and localities of Argentina. *Annals of the Entomological Society of America, 99*(1), 70-83. DOI: https://doi.org/10.1603/0013-8746(2006)099[0070:RAOCCA]2.0.CO;2

Selivon, D. (2000). Relações com as plantas hospedeiras. In A. Malavasi, & R. A. Zucchi (Eds.)*, Moscas-das-frutas de importância econômica no Brasil: conhecimento básico e aplicado* (p. 87-91). Ribeirão Preto, SP: Holos.

Seo, S. T., & Tang, C.-S. (1982). Hawaiian fruit flies (Diptera: Tephritidae): toxicity of benzyl isothiocyanate against eggs or 1st instars of three species. *Journal of Economic Entomology, 75*(6), 1132-1135. DOI: https://doi.org/10.1093/jee/75.6.1132

Seo, S. T., Tang, C.-S., Sanidad, S., & Takenaka, T. H. (1983). Hawaiian fruit flies (Diptera: Tephritidae): variation of index of infestation with benzyl isothiocyanate concentration and color of maturing papaya. *Journal of Economic Entomology, 76*(3), 535-538. DOI: https://doi.org/10.1093/jee/76.3.535

Sileshi, G. (2006). Selecting the right statistical model for analysis of insect count data by using information theoretic measures. *Bulletin of Entomological Research, 96*(5), 479-488. DOI: https://doi.org/10.1079/BER2006449

Silva, R. A., Deus, E. G., Raga, A., Pereira, J. D. B., Souza-Filho, M. F., & Costa Neto, S. V. (2011). Monitoramento de moscas-das-frutas na Amazônia: amostragem de frutos e uso de armadilhas. In R. A. Silva, W. P. Lemos, & R. A. Zucchi (Eds.)*, Moscas-das-frutas na Amazônia brasileira: diversidade, hospedeiros e inimigos naturais* (p. 33-50). Macapá, AP: Embrapa Amapá.

Uchôa, M. A., & Nicácio, J. (2010). New records of neotropical fruit flies (Tephritidae), lance flies (Lonchaeidae) (Diptera: Tephritoidea), and their host plants in the south pantanal and adjacent areas, Brazil. *Annals of the Entomological Society of America, 103*(5), 723-733. DOI: https://doi.org/10.1603/an09179

Vandermeer, J. (1995). The ecological basis of alternative agriculture. *Annual Review of Ecology and Systematics, 26*, 201-224. DOI: https://doi.org/10.1146/annurev.es.26.110195.001221

Vera, M. T., Rodriguez, R., Segura, D. F., Cladera, J. L., Sutherst. R. W. (2002). Potential Geographical Distribution of the Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae), with Emphasis on Argentina and Australia. *Environmental Entomology, 31*(6), 1009-1022.

Williams, D. W., & Liebhold, A. M. (1995). Herbivorous insects and global change: potential changes in the spatial distribution of forest defoliator outbreaks. *Journal of Biogeography, 22*(4-5), 665-671. DOI: https://doi.org/10.2307/2845968

Zucchi, R. A. (2000). Taxonomia. In A. Malavasi, & R. A. Zucchi (Eds.), *Moscas-das-frutas de importância econômica no Brasil: conhecimento básico e aplicado* (p. 13-24). Ribeirão Preto, SP: Holos.

Zucchi, R. A., & Moraes, R. C. B. (2021a). *Fruit flies in Brazil - Hosts and parasitoids of the Mediterranean fruit fly*. Retrieved on 10 July, 2020 from http://www.lea.esalq.usp.br/ceratitis.

Zucchi, R. A., & Moraes, R. C. B. (2021b). *Fruit flies in Brazil - Hosts and parasitoids of the Mediterranean fruit fly*. Retrieved on 10 July, 2020 from http://www.lea.esalq.usp.br/ceratitis.