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Impact of native forest remnants and wild host plants on the abundance of the South American fruit fly, *Anastrepha fraterculus* in Brazilian apple orchards.

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Abstract

In Paraná, southern Brazil, apple orchards are commonly bordered by highly biodiverse Atlantic Forest remnants. The main insect pest in these orchards is the highly polyphagous South American fruit fly, *Anastrepha fraterculus*. Technical advisers recommend that farmers remove wild host plants of *A. fraterculus* around orchards, which is at odds with the need for forest conservation. We thus investigated whether the presence of Atlantic Forest remnants and *A. fraterculus* host plants surrounding commercial apple orchards affect *A. fraterculus* populations in apple orchards in Paraná, southern Brazil. For this purpose, we monitored *A. fraterculus* using McPhail traps in a total of 67 100 m x 200 m apple orchard plots that differed in their adjacent landscape (forest with *A. fraterculus* host plants, forest without host plants, open areas). In total, we captured 6,412 *Anastrepha* fruit flies during four growing seasons. At the time when the apple fruits were susceptible to *A. fraterculus,* the probability of occurrence (i.e. of presence or absence) of *A. fraterculus* did not differ among the adjacent landscape types and was not affected by the presence of specific host plants. Its abundance in traps where at least one individual was found was also not affected. In contrast, at the time when the apple fruits were absent or not susceptible to *A. fraterculus, A. fraterculus* probability of occurrence was significantly higher in plots adjacent to open area than in plots adjacent to native forest remnants and intermediate in plots adjacent to native forest remnants with *A. fraterculus* host plants. At that time, its probability of occurrence and its abundance increased only with the presence of *Psidium cattleyanum* in these forest remnants. These results indicate that forest remnants had a limited impact on

A. fraterculus abundance in orchards and do not support the recommendation to indiscriminately remove wild host plants adjacent to apple orchards.

Key words: Atlantic Forest; Landscape; *Malus domestica* L.; Pest; Spillover.

1. Introduction

In Paraná, southern Brazil, agricultural areas devoted to apple production are commonly bordered by Atlantic Forest. This biome stretches over 3,500 km across equatorial, tropical and subtropical latitudes in Brazil and is renowned worldwide for being one of the 35 biodiversity hotspots of conservation priority (Myers et al. 2000). In addition to its intrinsic value, the conservation of Atlantic forest remnants in agricultural areas may contribute to the biological control of pests in orchards. Indeed, increasing or maintaining (semi)natural habitats, such as forests, within croplands or in their proximity, generally increases the abundance of pest enemies by providing them with refuges, resources and alternative hosts (Chaplin-Kramer et al. 2011; Gurr et al. 2017; Holland et al. 2016; Landis et al. 2000; Marko et al. 2017). The effects of (semi)natural habitats on pest abundance in crops are, however, equivocal (Chaplin-Kramer et al. 2011; Veres et al. 2013; Karp et al. 2018). This is possibly due to the poor consideration of the appropriate time or spatial scales (Chaplin Kramer et al. 2013), with many studies not considering pest dynamics. The composition and structure of (semi)natural habitats are also seldom considered, even though (semi)natural habitats can not only act as a source of natural enemies but also as a source of pests, depending on the plant species composition and phenology (Blitzer et al. 2012; Parry et al. 2015; Tscharntke et al. 2016).

Tephritid flies are a serious problem in fruit production worldwide (Clarke et al. 2014; Henri et al. 2015; Verghese et al. 2004). *Anastrepha* (Schiner) is the largest genus of Tephritidae in the Americas, causing major economic losses (Norrbom and Korytkowski 2011). Within this genus, the South American fruit fly species complex *Anastrepha fraterculus* (Wiedemann, 1830) (Diptera: Tephritidae) is the most critical insect pest in the apple orchards of southern Brazil (Rosa et al. 2017). The females cause damage by laying eggs in ripening fruits (Härter et al. 2015), which become unmarketable (Querino et al. 2014). At a very low pest density, this species also causes important income losses for farmers and dealers due to its quarantine status in several countries.

A. fraterculus completes 6 to 11 generations per year in southern Brazil, depending on climatic conditions, particularly temperature (Machado et al. 1995), requiring constant insecticide use during the apple growing season (Rosa et al. 2017). *A. fraterculus* is highly polyphagous, feeding on 114 different botanical species, among which 33% are Myrtaceae, 11% Rosaceae, 9% Rutaceae and 6% Annonaceae (Zucchi, 2008). In Brazil, in addition to apple, *A. fraterculus* is a pest of other Rosaceae species, such as peach and loquat trees, but prefers the fruits of wild plants (Rosa et al. 2017), particularly those of *Psidium araca*, *P. cattleyanum*, *P. guajava*, *P. sellowiana*, *Eugenia uniflora*, *Campomanesia xanthocarpa* and *Eriobotrya japonica* (Garcia and Norrbom 2011). *A. fraterculus* populations can thus be observed both in cultivated and natural habitats (Querino et al. 2014).

In southern Brazil, knowledge about the diversity of the plant hosts of *A. fraterculus* drove technical advisers to advocate for the elimination of native or exotic plants known to be hosts of tephritid flies from orchard surroundings, assuming that the presence of these hosts would increase fly abundance in orchards (Nava and Botton 2010). Such recommendations hamper conservation efforts targeting native forest remnants of high biodiversity value. Actual evidence about the impact of adjacent forests on *A. fraterculus* abundance in orchards is still needed. Only one study carried out in Rio Grande do Sul, southern Brazil, demonstrated the movement of *A. fraterculus* into apple orchards from a forest fragment surrounded by pasture (Kovaleski et al. 1999). Numerous studies also investigated the seasonal population fluctuations of *A. fraterculus* in orchards, but these fluctuations were related to climatic conditions or cultivated host plant phenology and not to the presence of adjacent vegetation (Malawasi and Morgante 1981; Rosa et al. 2017). Lastly, the infestation levels of cultivated and wild fruits have also been investigated (Raga et al. 2011; Souza-Filho et al. 2009; Taira et al. 2013), but none of these studies assessed the impact of the presence of these alternative host plants on orchard populations. Infestation levels of wild fruits are not sufficient information to conclude that spillover occurs from wild host plants to crops. A recent study on the tephritid fly *Ceratitis cosyra* even showed that infestation of wild host plants by this fruit fly may result from spillover from the crop to the wild hosts (Moxley et al. 2017).

The current study aimed to investigate whether the presence of Atlantic Forest and of plants known to be hosts of *A. fraterculus* within the forest surrounding apple orchards affect *A. fraterculus* populations in apple orchards, with an attempt to distinguish the effects on its occurrence that may indirectly reflect orchard colonization from the effects on its abundance when present. Special attention was also paid to the timing of the observed effects.

For this purpose, we monitored *A. fraterculus* populations in commercial apple orchards during four growing seasons. Specifically, we tested the hypotheses that *A. fraterculus* probability of occurrence and abundance in the apple orchards depended on (1) the adjacent landscape type, and (2) the presence of specific wild hosts within the adjacent landscape.

2. Materials and Methods

2.1. Study area

The abundance of fruit flies was monitored during four consecutive growing seasons (S1-S4, from September 2012 to August 2016) in commercial apple orchards within an apple production area located approximately 100 km southwest of the city of Curitiba, Paraná state, South Brazil. The climate is humid temperate with moderately hot summers and no dry season (Aparecido et al. 2016). During the study period, the average annual temperature was 17.5 °C and varied very little among seasons (from 17.3 °C in S1 to 17.9 °C in S3). The total rainfall per season varied from 1371 mm (S2) to 1942 mm (S4). The lowest temperatures occurred during the months of May, June and July (Fig. 1).

2.2. Characterization and delimitation of study plots

The study was conducted on 6 apple-growing farms growing both the ‘Gala’ and ‘Eva’ cultivars and varying between 150 and 250 ha in area. The apple growing areas were continuous, except in one farm, and only crossed by narrow paths. The cultivar ‘Eva’ is early-maturing and has low chilling requirements, whereas the cultivar ‘Gala’ is mid-maturing and produces fruits later than ‘Eva’, allowing farmers to extend their production for a longer period (Hauagge and Tsuneta 1999). Horticultural practices (fertilization, pesticide application, thinning and pruning) differed among farms for a given cultivar and included 6 to 14 insecticide applications from July to harvest, depending on the farm and year. Usually, three of these insecticides are organophosphates targeting *A. fraterculus* in November and December. The native vegetation in this area is mixed-ombrophilous forest and is considered to be a part of the southern Atlantic Forest biome.

Our aim was to delimit 100 m wide and 200 m long plots within apple orchards, with different landscape types adjacent to each plot: 1) forest with wild host plants for *A. fraterculus* females, 2) forests without host plants, and 3) open land cover (e.g., meadows, arable crops… all without host plants), hereafter named open area. These habitat types were determined based on the hypotheses that forests without host plants are a barrier to fly immigration in orchards, in contrast to open areas, while forests with wild host plants may themselves be a source of flies for the orchard. To characterize the adjacent landscapes, we first noted the presence or absence of forest. We then noted the presence of species of wild fruit tree hosts for *A. fraterculus* from the border of all the apple orchards up to 50 m within the forest by walking along and within the forest once during each season during the year preceding the beginning of the experiment. This distance ensured that no host plant grew in close proximity to apple trees. We considered wild hosts tree species to be those belonging to either Myrtaceae (*P. cattleyanum*, *C. xanthocarpa*, *Annona* aff. *neosericea* and *E. uniflora*) or Rosaceae (*E. japonica*) (Zucchi 2008). These host plants have mature fruits at different periods during the season: August to October (*E. japonica),* October-December *(E. uniflora*), October-November (*C. xanthocarpa*), and March to April (*P. cattleyanum*, *A*. *neosericea*,).

The orchards were then divided in 100 m x 200 m plots, with the narrowest edge facing the forest or open area. A total of 67 different plots were selected over the four seasons (2012-2016). All plots were more than 100 m apart. The number of plots was balanced as much as possible among farms and types of adjacent landscape. Not all plots, however, were monitored during the four seasons: 27 plots were evaluated in the first season, 60 in the second, 45 in the third and 36 in the last season (Table 1).

2.3. Delimitation of periods of crop susceptibility to *Anastrepha fraterculus*

Apple fruits are increasingly susceptible to *A. fraterculus* as they develop, so the abundance of flies in orchards is not a problem of equal importance for farmers across the season. Two phenological stages of apple trees are considered to define the beginnings of the periods of crop susceptibility to *A. fraterculus*: 1) 30 days after full bloom, when the apples are at the “J” stage of development (i.e., fruits are between 20 to 25 mm in diameter) and 2) 45 days before harvest. During the earliest susceptibility period, pricks by *A. fraterculus* can cause apple deformation and dropping (Sugayama et al. 1997). During the later susceptibility period, attacks by *A. fraterculus* can result in larval development and losses in apple production. These two phenological stages were used to determine the start of the ‘early’ and 'late' fruit susceptibility periods in subsequent analyses. These two periods extend until the end of harvest. The period extending from the end of harvest to stage J was defined as the 'insusceptibility' period. Dates for these two phenological stages were recovered from the observations at one studied farm each season for the 'Gala' and 'Eva' cultivars (Table A1).

2.4. *A. fraterculus* sampling and identification

Three McPhail traps (Biocontrole, Sâo Paulo, Brazil) baited with hydrolysed protein of plant origin (BioAnastrepha, Biocontrole, Sâo Paulo, Brazil) diluted to 5% were placed in each plot. They were located at distances of 0, 40 and 80 metres from the adjacent habitat along a transect perpendicular to the edge of the plot and starting on the middle edge point, ensuring that the adjacent habitat extended at least 50 m on both sides of the 0 m point. The traps were hung in the inner part of the tree canopy, at 1.7 m above ground level. Insect collection, trap cleaning and food lure replacement were performed weekly from spring to autumn and every two weeks during the winter (mid-June to mid-September). In total, we assessed 10,882 trap samples during the four growing seasons.

The number of individuals was recorded, and specimens were preserved in a 70% alcohol solution and subsequently sent to the Laboratory of Insect Pest Management (LAMIP) at the Federal University of Paraná for identification. The fruit fly specimens of the genus *Anastrepha* Schiner were sexed and identified according to Steykal (1977) and Zucchi (2000). Females were identified to the species level and males to the genus level because males do not present specific morphological characteristics allowing species identification (Zucchi, 2000). Only females of *A. fraterculus* and all males of the *Anastrepha* genus were considered for subsequent analyses. We assumed that the captured males belonged to *A. fraterculus* because almost all the captured females were identified to this species (see Results).

2.5. Statistical analyses

The number of captures was highly variable, and no *A. fraterculus* individuals were found in many traps on numerous sampling dates. Therefore, for each growing season, the number of individuals per trap was summed up over four different periods: over the whole season (*i=1*), over the 'early' (*i*=2) and 'late' (*i*=3) susceptibility periods and over the 'insusceptibility' period (*i=4*).

To assess the effect of landscape type and presence of specific host plant species on *A. fraterculus* populations, we performed two sets of independent analyses with R.3.4.1 software (R Core Team, 2017).

First, to assess whether landscape type affected colonization into the orchards, the sums of *A. fraterculus* individuals captured over each period *i* (*i* in [1,4]) were converted into a binary variable, '*Pflyi*', which took a value of 1 when the number of flies in a trap was positive and 0 when no flies were captured. The variable '*Pflyi*' was considered to follow a binomial distribution; it was analysed using a generalized linear mixed-effects model (glmm) with a logit link function (package *lme4,* Bates et al. 2015). Then, to assess whether landscape type affected the abundance of *A. fraterculus* when *A. fraterculus* was present (variable '*Abundi*'), we analysed the log-transformed average number of individuals per trap per day over each period *i* for traps with *Pflyi*=1 (named positive traps) (package *lme4*) with linear mixed models (lmms). This first set of analyses was performed on data from the 2nd and the 3rd growing seasons only to avoid confounding effects of 'landscape' and 'season' due to the small number of sampled farms with plots adjacent to open areas during the 1st and 4th season (Table 1). Independent factors were the same in the glmm and lmm regressions: the factors considered were the landscape type (*landscape*, 3 levels), the farm (*farm,* 5 levels) and the season (*season*, 2 levels). A random *plot within farm* effect was included in all the models to account for the sampling design. The significance of the fixed effects was assessed using chi-square tests to compare models with or without factors of interest with the *Anova* function (package *car,* Fox and Weisberg 2011). When significant differences were detected, pairwise comparisons among factor levels were performed using post hoc Tukey tests (package *multcomp*). Model residuals were inspected using the R package *DHARMa* (Harting 2018)

In a second step, we assessed the effect of the presence of each of the five most frequent host plant species: *P. cattleyanum* (5 plots), *C. xanthocarpa* (3 plots), *A. neosericea* (8 plots), *E. uniflora* (2 plots), and *E. japonica* (4 plots). For this purpose, we performed randomization tests on the subset of the 17 different plots bordered by forest with wild host plants. Distributions of variables *Pflyi and Abundi* under the null hypothesis of no effect of the presence of specific host plant species were obtained from 1000 random permutations of traps between plots within farms and growing seasons. The test statistic used to analyse *Pflyi* was a chis-square distance calculated on the contingency table describing the numbers of times that *Pflyi* took values 0 and 1 in presence or absence of each tested host plant species. The test statistic used to analyse *Abundi* was the absolute value of the difference of the mean numbers of flies per trap per day in plots adjacent to forest with or without the tested plant species. For both *Pflyi* and *Abundi*, we reported the proportion of permutations for which the test statistic was higher than the observed value.

3. Results

3.1. Species trapped and abundance of fruit flies in traps

In total, 6,412 fruit flies of the *Anastrepha* genus were trapped over the four growing seasons; 59.2% were females and 40.8% were males. Of the trapped females, 99% were identified as *A. fraterculus*. The remaining trapped females were *A. dissimilis* Stone (5 individuals), *A. grandis* Macquart (24 individuals) and *Ceratitis capitata* Wiedemann (35 individuals), which were not considered in subsequent analyses.

A. fraterculus were observed in 14.2 % of the total trap surveys. Only six traps did not capture any individual during the whole experiment. The monthly mean number of *A. fraterculus* per trap per day (FTD) ranged between 0 and 0.30, with a very marked seasonal pattern. The number of FTD peaked during the month of March, for all the growing seasons, after the periods of highest temperatures. Patterns were similar among the four growing seasons, although the maximum number of individuals was very different, with maximum values of 0.30, 0.21, 0.27 and 0.06, respectively. Note, however, that all farms were not sampled each season. During the winter, the number of *A. fraterculus* was almost zero in all growing seasons. In 2013, two large secondary peaks were recorded in June (0.30) and August (0.29), although the climatic pattern did not differ markedly from those in the other growing seasons (Fig. 1).

3.2. Effects of the growing season and farms on the occurrence and abundance of *A. fraterculus*

A. fraterculus probability of occurrence and abundance in positive traps significantly differed between the growing seasons S2 and S3 considering the periods when fruits were susceptible or not (Table 2, Figs. 2 and A1). Probability of occurrence and abundance were much lower in 2013-2014 (S2) than in 2014-2015 (S3). Differences during the periods when fruits were not susceptible were small compared to the differences observed during fruit susceptibility (Fig 2).

A. fraterculus probability of occurrence and abundance in positive traps also significantly differed among farms for all considered periods (Table 2, Figs. A2, A3).

3.3. Effect of landscape type on the occurrence and abundance of *A. fraterculus*

A. fraterculus probability of occurrence did not significantly differ among plots with different adjacent landscape types when the probability of occurrence was calculated over the periods of fruit susceptibility (Table 2), and it was higher in plots bordered by open areas than without host plants over the whole growing season and in the insusceptibility period, plots bordered by forests with host plants being intermediate (Fig. 3). In contrast, *A. fraterculus* abundance in positive traps, i.e., traps that had successfully trapped *A. fraterculus*, was not affected by adjacent landscape type (Table 2, Fig. 4).

3.4. Effect of the presence of specific hosts in the adjacent forest

The probability of occurrence of *A. fraterculus* and its abundance in positive traps, were significantly higher in the presence of *P. cattleyanum* during the insusceptibility period (Table 3). *A. fraterculus* was present in 83 % of the traps and its abundance in positive traps was of 1.6 10^{-2} in the presence of *P. cattleyanum,* while it was present in 69 % of the traps and its abundance was of 0.9 10^{-2} in its absence.

4. Discussion

Understanding the determinants of fruit fly abundance in orchards is key for the development of knowledge-based crop protection strategies that rely less on broad-spectrum insecticide treatments (Rosa et al. 2017). In the present study, the dominant fruit fly was *A. fraterculus*. This complex of cryptic species has already been reported to be the main dipteran pest of fruit trees in southern Brazil (Härter et al. 2015, Monteiro et al. 2018). We found that the probability of occurrence of flies and, particularly, their abundance in traps were low but, when summed over growing periods, nevertheless largely differed among farms and between growing seasons. In contrast, differences in probability of occurrence or abundance of flies were rare between plots adjacent to different landscape types and were only observed at the period when apple fruits were either absent or not susceptible to *A. fraterculus*.

Like other fruit flies, the abundance of *Anastrepha* species is known to vary among years depending on broad-scale climatic variables (Aluja et al. 2012) and within year depending on the local temperature and rainfall (Rosa et al. 2017). The seasonal pattern observed in the present study was very typical, with peaks in the number of flies in traps following the warmest months and fly number decreases following cold temperatures, except in the first growing season (2012-2013), which was atypical. This pattern also matched the known effects of temperature on *A. fraterculus* development. Mean air temperatures lower than 10 °C, which are limiting for *A. fraterculus* development (Machado et al. 1995), were observed around the months of July and indeed corresponded to the lowest population abundance (except in the 2012-2013 season). Further, the ideal temperature for *A. fraterculus* development ranges from 15.3 °C to 26.8 °C (Cardoso et al. 2002; Taufer et al. 2000), and we indeed observed a sharp decrease in *A. fraterculus* captures starting in March, when minimum temperatures lower than 15 °C were recorded. Note, however, that McPhail traps that, like many trapping methods, record a combination of fly abundance and activity (activity-density), so that the weekly observed variation in FTD may reflect variation in activity rather than abundance. Lower abundance in traps at low temperature may thus reflect lower activity. Pooling the data per month or over longer periods allowed the smoothing of the short-term variation in activity so that abundances in traps could be compared among locations.

Beyond climatic conditions, the landscape surrounding cultivated crops can affect pest abundance, being a source for the spillover of pests or pest enemies (Aluja et al. 2014). Spillover is particularly expected in pests, such as *A. fraterculus*, that are both generalist (Aluja et al. 2012) and mobile (Schliserman et al. 2014). Moreover it is suspected that there are no resident fly populations in commercial apple orchards, probably because of the poor quality of apples as larval hosts and the use of insecticides (Kovaleski 1999).

Our results indeed indicate that *A. fraterculus* probability of occurrence was affected by the adjacent landscape type, but only during the insusceptibility period, i.e., between harvest and the beginning of apple fruit susceptibility. In contrast, its abundance in positive traps was not affected at that period. These results are consistent with the fact that populations of *A. fraterculus* in orchards depend largely on colonization from the environment during that period, since fruit fly reproduction within the apple orchard can only occur when fruits are present and sufficiently mature (Sugayama et al. 1997). Further, the probability of occurrence of *A. fraterculus* in orchards was higher when the adjacent landscape was open area, rather than forest without host plants. This may indicate that the forest limits movements of flies into the orchard, either through a barrier effect or because flies find a more suitable environment and more resources in the forest than in the orchards during that period. Flies may also be more frequently predated by natural enemies in the proximity of the forest. Pupae in particular are prey of ants which may cause high mortality (Aluja et al. 2005). Alternatively, open areas may act as a barrier, limiting fly movements out of the orchard after apple harvest. Lastly, traps next to open areas may be particularly attractive because open areas are resource free. Direct movement observations would be necessary to further investigate these processes.

The probability of occurrence of flies was intermediate in plots bordered by forests with host plant species, indicating that some spillover may happen from the forest to the orchard. The specific analysis on host plant species indicates that *P. cattleyanum* appears as a candidate source. *P. cattleyanum* is known to be a very favourable host for *A. fraterculus* (Garcia and Norrbom 2011) and can produce very large numbers of fruits. The observed effect is moreover consistent with its fruiting period that occurs after harvest of apples.

We found no effect of adjacent landscape type or of presence of specific host plant species on fly populations during the susceptibility period, although this period overlapped with the fruiting periods of *E. uniflora*, *E. japonica* and *C. xanthocarpa* in the study area. The abundance and probability of occurrence of flies were lower at that period than during the insusceptibility period, particularly during the second growing season. It is possible that the traps were less attractive during the susceptibility period due to the high abundance of fruits that may have distracted the flies from the traps. Such decrease, however, more likely results from insecticide treatments within the orchards. Investigating pest abundance variation in crops treated with pesticides is difficult because the pest abundance is mainly governed by insecticide treatments, but may not relate directly to the number of treatments if farmers adopt calendar strategies. In the present study, we had only partial information on farmers' treatment calendars. Farmers generally treat their apple growing area as a whole against *A. fraterculus*. We thus considered treatments indirectly in the analyses by including a 'farm' effect. This farm effect, however, was highly significant also when fruits were not susceptible, so that it may not be a good proxy of insecticide treatments and better knowledge of calendar treatments may have been necessary to analyze data from the fruit susceptibility period.

The significance of our results for crop management purposes should be taken cautiously since they may only apply to intensive orchards where pest populations depend more on recolonization from the surroundings (Roschewitz et al. 2005). More research is needed in less intensive orchards that may not only be less affected by the spillover of flies but may also benefit from wild host plants that are multipliers of *A. fraterculus* parasitoids (Nunes et al. 2012). Moreover, the taxonomy of *Anastrepha* flies still needs to be clarified (e.g., Dias et al. 2016 for Brazil) since there is evidence that three cryptic species of *A. fraterculus* occur in southern Brazil (Vaníčková et al. 2015). These cryptic species may all be attracted to the traps but may have different preferred host plants, as host preference may be one of the drivers of species radiation in *A. fraterculus (*Oroño et al. 2013). Further investigations are thus needed to assess the extent to which populations from different native host plants are also strongly attracted to apple. In any case, the effect of landscape type was rarely and only marginally significant (p=0.04 and p=0.05) for the occurrence of *A. fraterculus*. Similarly, the presence of *P. cattleyanum* had a marginally significant effect on fly occurrence. Our results thus indicate that adjacent landscape type had a minor role, compared to season and farm effects, in shaping *A. fraterculus* occurrence and abundance and do not support the recommendation of indiscriminate wild host plant removal in forests adjacent to apple orchards.

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Figure legends

Figure 1 – Monthly air temperatures (°C) and rainfall (mm) (a) and *A. fraterculus* population dynamics (b) in the study apple plots over four growing seasons, from September 2012 to August 2016. Continuous and dotted lines delinate the insusceptibility and susceptibility periods for the Gala and Eva apple cultivars: insusceptible ▪▪▪▪▪ , early susceptible ▬▬▬ , late susceptible ▬ ▬ ▬ .

Figure 2 – Predicted probability of occurrence of *A. fraterculus* in plots during season 2 and season 3; (a) whole season, (b) insusceptibility period, (c) early susceptibility period, (d) late susceptibility period. Error bars represent standard errors.

Figure 3 – Predicted probability of occurrence of *A. fraterculus* in plots bordered by different landscape types considering only season 2 and season 3; (a) whole season, (b) insusceptibility period, (c) early susceptibility period, (d) late susceptibility period. Error bars represent standard errors.

Figure 4 – Predicted abundance of *A. fraterculus* (flies trap^{-1} day^{-1}) in positive traps in plots adjacent to different landscape types; (a) whole season, (b) insusceptibility period, (c) early susceptibility period, (d) late susceptibility period. Error bars represent standard errors.

Table 1 – Number of apple orchard plots surveyed during the study period for each farm and each growing season (S1-S4) according to their adjacent landscape type.

	Landscape type											
	Open area				Forest with hosts				Forest without hosts			
Farm	S1	S2	S3	S4	S1	S2	S3	S4	S1	S2	S3	S4
Bor		5	5	7		5	6	6		2	3	3
Bou		2	2						6	11	6	6
Con					2	2	2		4	11	7	7
Fru					2	2	2		5	5	5	
Pom	1	1			5	5			2	2		
Pos		3	3	3		2	2	2		2	2	2
Total	1	11	10	10	9	16	12	8	17	33	23	18

Table 2 – Effects of landscape type, growing season and distance to the edge of the plot on *A. fraterculus* probability of occurrence and abundance during four specific periods of the apple growing cycle. Bold values indicate the significance of a given factor.

		Whole season		Not susceptible		Early susceptible		Late susceptible	
		Chisq	P	Chisq	P	Chisq	P	Chisq	P
Occurrence									
Landscape	2	6.3	**0.04**	6.1	**0.05**	1.0	0.59	0.5	0.76
Farm	5	16.7	**5.1 10^{-3}**	29.4	**1.9 10^{-5}**	12.2	**0.03**	13.9	**0.016**
Season	1	33.6	**6.8 10^{-9}**	16.7	**4.3 10^{-5}**	21.6	**3.3 10^{-6}**	12.8	**3.5 10^{-5}**
Abundance									
Landscape	2	0.6	0.74	0.3	0.85	1.0	0.59	1.0	0.59
Farm	3	72.4	**3.2 10^{-14}**	79.2	**1.2 10^{-15}**	19.4	**1.6 10^{-3}**	21.3	**7.1 10^{-4}**
Season	1	15.4	**8.8 10^{-5}**	15.9	**6.5 10^{-5}**	3.5	0.06	3.4	0.06

Table 3 – Significance (p-values) of the effects of the presence of specific host plant species on *A. fraterculus* probability of occurrence and abundance in positive traps during four different periods of the apple growing cycle. Bold p-values <0.05.

	Whole season	Not susceptible	Early susceptible	Late susceptible
Occurrence				
Annona aff. *neosericea*	0.75	1	0.76	0.67
Campomanesia xanthocarpa	0.15	0.31	0.81	1
Eugenia uniflora	0.44	0.57	1	0.98
Eriobotrya japonica	1	1	0.63	0.65
Psidium cattleyanum	0.15	**0.04**	0.29	0.30
Abundance				
Annona aff. *neosericea*	0.40	0.26	0.27	0.19
Campomanesia xanthocarpa	0.49	0.34	0.91	0.90
Eugenia uniflora	0.32	0.54	0.26	0.23
Eriobotrya japonica	0.76	0.45	0.87	0.83
Psidium cattleyanum	0.05	**0.02**	0.97	0.78

Fig. 1

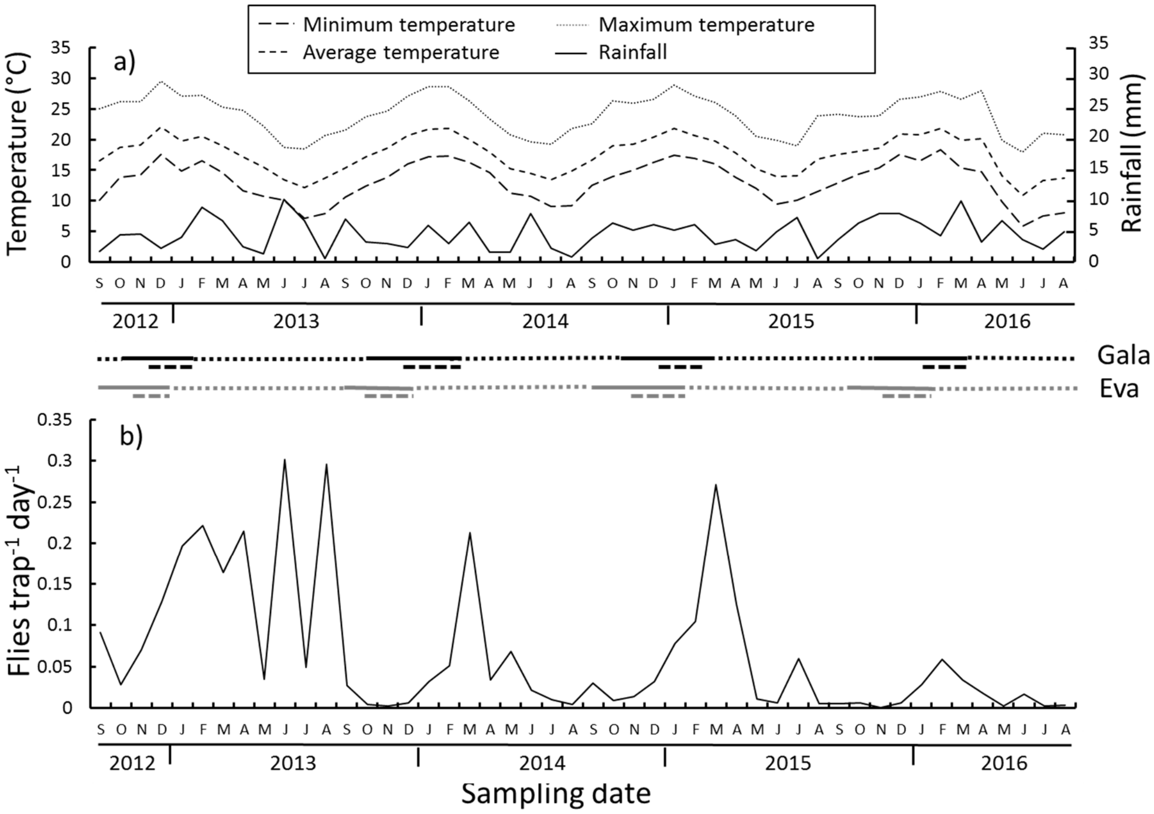

Minimum temperature
Maximum temperature
Average temperature
Rainfall
a)
Temperature (°C)
Rainfall (mm)
0
5
10
15
20
25
30
35
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
2012
2013
2014
2015
2016
Gala
Eva
b)
Flies trap^{-1} day^{-1}
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
2012
2013
2014
2015
2016
Sampling date

Fig. 2

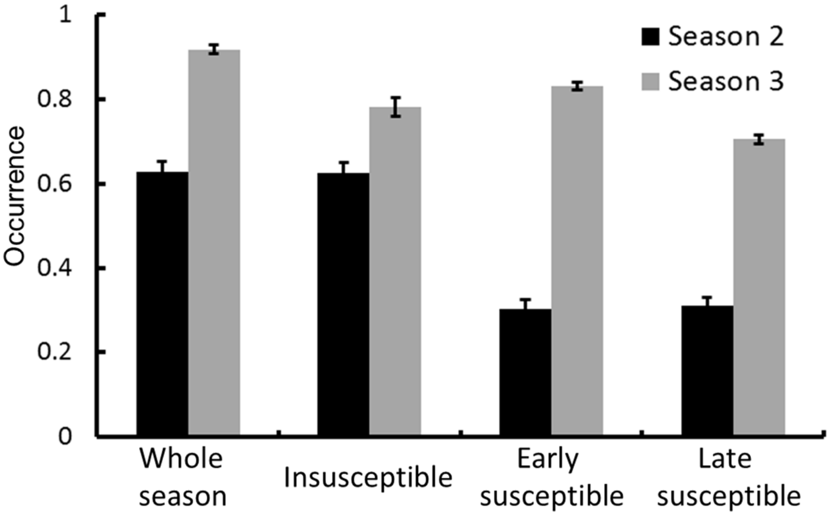

1
0.8
0.6
0.4
0.2
0
Occurrence
■ Season 2
■ Season 3
Whole season
Insusceptible
Early susceptible
Late susceptible

Fig. 3

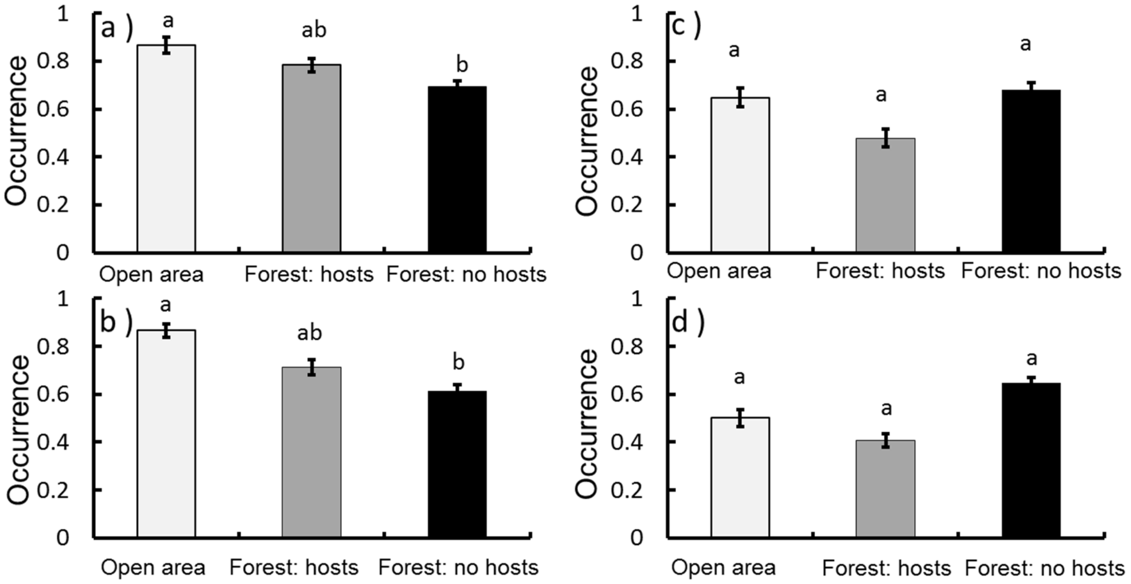
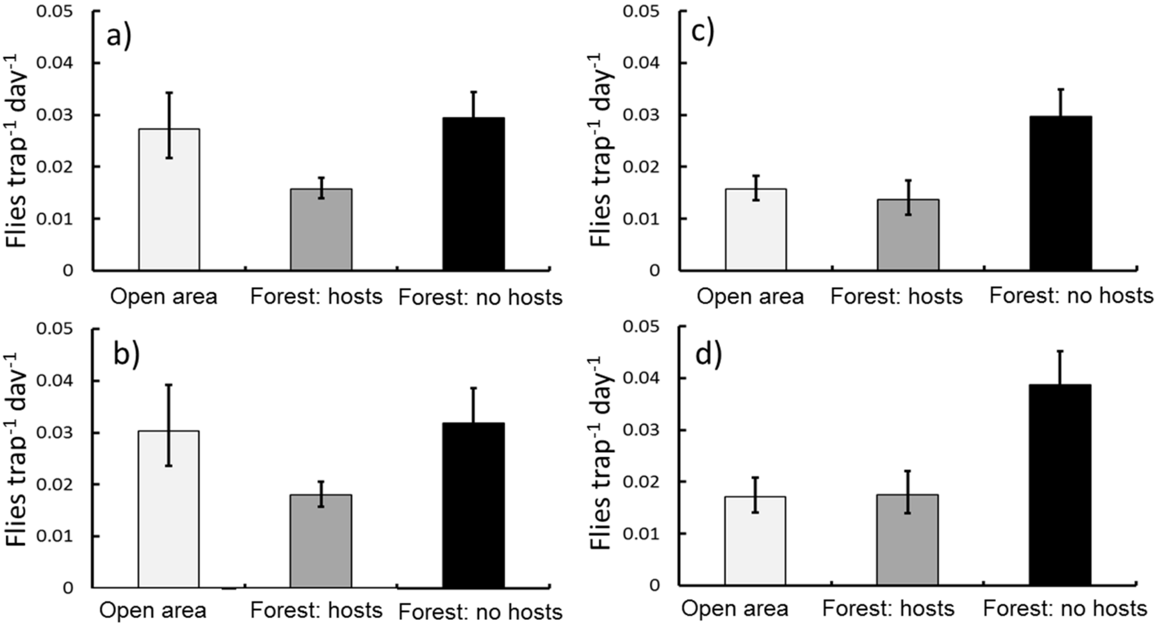

a)
b)
c)
d)
Occurrence
0
0.2
0.4
0.6
0.8
1
a
ab
b
a
a
a
Open area
Forest: hosts
Forest: no hosts

Fig. 4


a)
b)
c)
d)
Flies trap-1 day-1
0
0.01
0.02
0.03
0.04
0.05
Open area
Forest: hosts
Forest: no hosts