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► To cite this version:

Emily Silva Araujo, Lino B. Monteiro, Rodrigo S. Monteiro, Guilherme Nishimura, Pierre Franck, et al.. Impact of native forest remnants and wild host plants on the abundance of the South American fruit fly, *Anastrepha fraterculus* in Brazilian apple orchards. *Agriculture, Ecosystems & Environment*, 2019, 275, pp.93-99. 10.1016/j.agee.2019.02.007 . hal-02618023

HAL Id: hal-02618023

<https://hal.inrae.fr/hal-02618023v1>

Submitted on 22 Oct 2021

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

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21

22 **Abstract**

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

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

45

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

47

48 **1. Introduction**

49 In Paraná, southern Brazil, agricultural areas devoted to apple production are commonly
50 bordered by Atlantic Forest. This biome stretches over 3,500 km across equatorial, tropical
51 and subtropical latitudes in Brazil and is renowned worldwide for being one of the 35
52 biodiversity hotspots of conservation priority (Myers et al. 2000). In addition to its intrinsic
53 value, the conservation of Atlantic forest remnants in agricultural areas may contribute to
54 the biological control of pests in orchards. Indeed, increasing or maintaining (semi)natural
55 habitats, such as forests, within croplands or in their proximity, generally increases the
56 abundance of pest enemies by providing them with refuges, resources and alternative hosts
57 (Chaplin-Kramer et al. 2011; Gurr et al. 2017; Holland et al. 2016; Landis et al. 2000; Marko
58 et al. 2017). The effects of (semi)natural habitats on pest abundance in crops are, however,
59 equivocal (Chaplin-Kramer et al. 2011; Veres et al. 2013; Karp et al. 2018). This is possibly
60 due to the poor consideration of the appropriate time or spatial scales (Chaplin Kramer et al.
61 2013), with many studies not considering pest dynamics. The composition and structure of
62 (semi)natural habitats are also seldom considered, even though (semi)natural habitats can
63 not only act as a source of natural enemies but also as a source of pests, depending on the

64 plant species composition and phenology (Blitzer et al. 2012; Parry et al. 2015; Tschardt et
65 al. 2016).

66 Tephritid flies are a serious problem in fruit production worldwide (Clarke et al. 2014;
67 Henri et al. 2015; Verghese et al. 2004). *Anastrepha* (Schiner) is the largest genus of
68 Tephritidae in the Americas, causing major economic losses (Norrbon and Korytkowski
69 2011). Within this genus, the South American fruit fly species complex *Anastrepha*
70 *fraterculus* (Wiedemann, 1830) (Diptera: Tephritidae) is the most critical insect pest in the
71 apple orchards of southern Brazil (Rosa et al. 2017). The females cause damage by laying
72 eggs in ripening fruits (Härter et al. 2015), which become unmarketable (Querino et al.
73 2014). At a very low pest density, this species also causes important income losses for
74 farmers and dealers due to its quarantine status in several countries.

75 *A. fraterculus* completes 6 to 11 generations per year in southern Brazil, depending on
76 climatic conditions, particularly temperature (Machado et al. 1995), requiring constant
77 insecticide use during the apple growing season (Rosa et al. 2017). *A. fraterculus* is highly
78 polyphagous, feeding on 114 different botanical species, among which 33% are Myrtaceae,
79 11% Rosaceae, 9% Rutaceae and 6% Annonaceae (Zucchi, 2008). In Brazil, in addition to
80 apple, *A. fraterculus* is a pest of other Rosaceae species, such as peach and loquat trees, but
81 prefers the fruits of wild plants (Rosa et al. 2017), particularly those of *Psidium araca*, *P.*
82 *cattleyanum*, *P. guajava*, *P. sellowiana*, *Eugenia uniflora*, *Campomanesia xanthocarpa* and
83 *Eriobotrya japonica* (Garcia and Norrbom 2011). *A. fraterculus* populations can thus be
84 observed both in cultivated and natural habitats (Querino et al. 2014).

85 In southern Brazil, knowledge about the diversity of the plant hosts of *A. fraterculus* drove
86 technical advisers to advocate for the elimination of native or exotic plants known to be
87 hosts of tephritid flies from orchard surroundings, assuming that the presence of these hosts
88 would increase fly abundance in orchards (Nava and Botton 2010). Such recommendations
89 hamper conservation efforts targeting native forest remnants of high biodiversity value.
90 Actual evidence about the impact of adjacent forests on *A. fraterculus* abundance in
91 orchards is still needed. Only one study carried out in Rio Grande do Sul, southern Brazil,
92 demonstrated the movement of *A. fraterculus* into apple orchards from a forest fragment
93 surrounded by pasture (Kovaleski et al. 1999). Numerous studies also investigated the
94 seasonal population fluctuations of *A. fraterculus* in orchards, but these fluctuations were
95 related to climatic conditions or cultivated host plant phenology and not to the presence of
96 adjacent vegetation (Malawasi and Morgante 1981; Rosa et al. 2017). Lastly, the infestation
97 levels of cultivated and wild fruits have also been investigated (Raga et al. 2011; Souza-Filho
98 et al. 2009; Taira et al. 2013), but none of these studies assessed the impact of the presence
99 of these alternative host plants on orchard populations. Infestation levels of wild fruits are
100 not sufficient information to conclude that spillover occurs from wild host plants to crops. A
101 recent study on the tephritid fly *Ceratitis cosyra* even showed that infestation of wild host
102 plants by this fruit fly may result from spillover from the crop to the wild hosts (Moxley et al.
103 2017).

104 The current study aimed to investigate whether the presence of Atlantic Forest and of
105 plants known to be hosts of *A. fraterculus* within the forest surrounding apple orchards
106 affect *A. fraterculus* populations in apple orchards, with an attempt to distinguish the effects

107 on its occurrence that may indirectly reflect orchard colonization from the effects on its
108 abundance when present. Special attention was also paid to the timing of the observed
109 effects.

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

115

116 **2. Materials and Methods**

117 2.1. Study area

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

126

127 2.2. Characterization and delimitation of study plots

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

139 Our aim was to delimit 100 m wide and 200 m long plots within apple orchards, with
140 different landscape types adjacent to each plot: 1) forest with wild host plants for *A.*
141 *fraterculus* females, 2) forests without host plants, and 3) open land cover (e.g., meadows,
142 arable crops... all without host plants), hereafter named open area. These habitat types were
143 determined based on the hypotheses that forests without host plants are a barrier to fly
144 immigration in orchards, in contrast to open areas, while forests with wild host plants may
145 themselves be a source of flies for the orchard. To characterize the adjacent landscapes, we
146 first noted the presence or absence of forest. We then noted the presence of species of wild
147 fruit tree hosts for *A. fraterculus* from the border of all the apple orchards up to 50 m within
148 the forest by walking along and within the forest once during each season during the year
149 preceding the beginning of the experiment. This distance ensured that no host plant grew in

150 close proximity to apple trees. We considered wild hosts tree species to be those belonging
151 to either Myrtaceae (*P. cattleianum*, *C. xanthocarpa*, *Annona* aff. *neosericea* and *E. uniflora*)
152 or Rosaceae (*E. japonica*) (Zucchi 2008). These host plants have mature fruits at different
153 periods during the season: August to October (*E. japonica*), October-December (*E. uniflora*),
154 October-November (*C. xanthocarpa*), and March to April (*P. cattleianum*, *A. neosericea*).

155 The orchards were then divided in 100 m x 200 m plots, with the narrowest edge facing
156 the forest or open area. A total of 67 different plots were selected over the four seasons
157 (2012-2016). All plots were more than 100 m apart. The number of plots was balanced as
158 much as possible among farms and types of adjacent landscape. Not all plots, however, were
159 monitored during the four seasons: 27 plots were evaluated in the first season, 60 in the
160 second, 45 in the third and 36 in the last season (Table 1).

161

162 2.3. Delimitation of periods of crop susceptibility to *Anastrepha fraterculus*

163 Apple fruits are increasingly susceptible to *A. fraterculus* as they develop, so the abundance
164 of flies in orchards is not a problem of equal importance for farmers across the season. Two
165 phenological stages of apple trees are considered to define the beginnings of the periods of
166 crop susceptibility to *A. fraterculus*: 1) 30 days after full bloom, when the apples are at the
167 “J” stage of development (i.e., fruits are between 20 to 25 mm in diameter) and 2) 45 days
168 before harvest. During the earliest susceptibility period, pricks by *A. fraterculus* can cause
169 apple deformation and dropping (Sugayama et al. 1997). During the later susceptibility
170 period, attacks by *A. fraterculus* can result in larval development and losses in apple
171 production. These two phenological stages were used to determine the start of the ‘early’

172 and 'late' fruit susceptibility periods in subsequent analyses. These two periods extend until
173 the end of harvest. The period extending from the end of harvest to stage J was defined as
174 the 'insusceptibility' period. Dates for these two phenological stages were recovered from
175 the observations at one studied farm each season for the 'Gala' and 'Eva' cultivars (Table
176 A1).

177

178 2.4. *A. fraterculus* sampling and identification

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

188 The number of individuals was recorded, and specimens were preserved in a 70% alcohol
189 solution and subsequently sent to the Laboratory of Insect Pest Management (LAMIP) at the
190 Federal University of Paraná for identification. The fruit fly specimens of the genus
191 *Anastrepha* Schiner were sexed and identified according to Steykal (1977) and Zucchi (2000).
192 Females were identified to the species level and males to the genus level because males do
193 not present specific morphological characteristics allowing species identification (Zucchi,

194 2000). Only females of *A. fraterculus* and all males of the *Anastrepha* genus were considered
195 for subsequent analyses. We assumed that the captured males belonged to *A. fraterculus*
196 because almost all the captured females were identified to this species (see Results).

197

198 2.5. Statistical analyses

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

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

207 First, to assess whether landscape type affected colonization into the orchards, the sums
208 of *A. fraterculus* individuals captured over each period i (i in $[1,4]$) were converted into a
209 binary variable, '*Pflyi*', which took a value of 1 when the number of flies in a trap was
210 positive and 0 when no flies were captured. The variable '*Pflyi*' was considered to follow a
211 binomial distribution; it was analysed using a generalized linear mixed-effects model (glmm)
212 with a logit link function (package *lme4*, Bates et al. 2015). Then, to assess whether
213 landscape type affected the abundance of *A. fraterculus* when *A. fraterculus* was present
214 (variable '*Abundi*'), we analysed the log-transformed average number of individuals per trap
215 per day over each period i for traps with $Pflyi=1$ (named positive traps) (package *lme4*) with

216 linear mixed models (lmm). This first set of analyses was performed on data from the 2nd
217 and the 3rd growing seasons only to avoid confounding effects of 'landscape' and 'season'
218 due to the small number of sampled farms with plots adjacent to open areas during the 1st
219 and 4th season (Table 1). Independent factors were the same in the glmm and lmm
220 regressions: the factors considered were the landscape type (*landscape*, 3 levels), the farm
221 (*farm*, 5 levels) and the season (*season*, 2 levels). A random *plot within farm* effect was
222 included in all the models to account for the sampling design. The significance of the fixed
223 effects was assessed using chi-square tests to compare models with or without factors of
224 interest with the *Anova* function (package *car*, Fox and Weisberg 2011). When significant
225 differences were detected, pairwise comparisons among factor levels were performed using
226 post hoc Tukey tests (package *multcomp*). Model residuals were inspected using the R
227 package *DHARMA* (Harting 2018)

228 In a second step, we assessed the effect of the presence of each of the five most frequent
229 host plant species: *P. cattleyanum* (5 plots), *C. xanthocarpa* (3 plots), *A. neosericea* (8 plots),
230 *E. uniflora* (2 plots), and *E. japonica* (4 plots). For this purpose, we performed randomization
231 tests on the subset of the 17 different plots bordered by forest with wild host plants.
232 Distributions of variables *Pflyi* and *Abundi* under the null hypothesis of no effect of the
233 presence of specific host plant species were obtained from 1000 random permutations of
234 traps between plots within farms and growing seasons. The test statistic used to analyse
235 *Pflyi* was a chi-square distance calculated on the contingency table describing the numbers
236 of times that *Pflyi* took values 0 and 1 in presence or absence of each tested host plant
237 species. The test statistic used to analyse *Abundi* was the absolute value of the difference of

238 the mean numbers of flies per trap per day in plots adjacent to forest with or without the
239 tested plant species. For both *Pflyi* and *Abundi*, we reported the proportion of permutations
240 for which the test statistic was higher than the observed value.

241

242 **3. Results**

243 3.1. Species trapped and abundance of fruit flies in traps

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

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

260

261 3.2. Effects of the growing season and farms on the occurrence and abundance of *A.*

262 *fraterculus*

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

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

271

272 3.3. Effect of landscape type on the occurrence and abundance of *A. fraterculus*

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

280

281 3.4. Effect of the presence of specific hosts in the adjacent forest

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

287

288 **4. Discussion**

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

300

301 Like other fruit flies, the abundance of *Anastrepha* species is known to vary among years
302 depending on broad-scale climatic variables (Aluja et al. 2012) and within year depending on
303 the local temperature and rainfall (Rosa et al. 2017). The seasonal pattern observed in the

304 present study was very typical, with peaks in the number of flies in traps following the
305 warmest months and fly number decreases following cold temperatures, except in the first
306 growing season (2012-2013), which was atypical. This pattern also matched the known
307 effects of temperature on *A. fraterculus* development. Mean air temperatures lower than 10
308 °C, which are limiting for *A. fraterculus* development (Machado et al. 1995), were observed
309 around the months of July and indeed corresponded to the lowest population abundance
310 (except in the 2012-2013 season). Further, the ideal temperature for *A. fraterculus*
311 development ranges from 15.3 °C to 26.8 °C (Cardoso et al. 2002; Taufer et al. 2000), and we
312 indeed observed a sharp decrease in *A. fraterculus* captures starting in March, when
313 minimum temperatures lower than 15 °C were recorded. Note, however, that McPhail traps
314 that, like many trapping methods, record a combination of fly abundance and activity
315 (activity-density), so that the weekly observed variation in FTD may reflect variation in
316 activity rather than abundance. Lower abundance in traps at low temperature may thus
317 reflect lower activity. Pooling the data per month or over longer periods allowed the
318 smoothing of the short-term variation in activity so that abundances in traps could be
319 compared among locations.

320

321 Beyond climatic conditions, the landscape surrounding cultivated crops can affect pest
322 abundance, being a source for the spillover of pests or pest enemies (Aluja et al. 2014).
323 Spillover is particularly expected in pests, such as *A. fraterculus*, that are both generalist
324 (Aluja et al. 2012) and mobile (Schliserman et al. 2014). Moreover it is suspected that there

325 are no resident fly populations in commercial apple orchards, probably because of the poor
326 quality of apples as larval hosts and the use of insecticides (Kovaleski 1999).

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

344 The probability of occurrence of flies was intermediate in plots bordered by forests with
345 host plant species, indicating that some spillover may happen from the forest to the orchard.
346 The specific analysis on host plant species indicates that *P. cattleyanum* appears as a

347 candidate source. *P. cattleyanum* is known to be a very favourable host for *A. fraterculus*
348 (Garcia and Norrbom 2011) and can produce very large numbers of fruits. The observed
349 effect is moreover consistent with its fruiting period that occurs after harvest of apples.

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

367

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

386

387 **5. Acknowledgements**

388 The authors are grateful to Edson Chappuis and José A. S. Tomba for help with field work
389 and to the farmers of Paraná for providing access to the orchards. E.A. benefited from a

390 post-doc grant from the National Council for the Improvement of Higher Education (CAPES)
391 [grant 57/2012] for her stay in France. This work was funded by Agropolis Fondation [grant
392 1203-002] and CAPES [14/13].

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560

561 **Figure legends**

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

567

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

571

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

576

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

580

581

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

Farm	Landscape type											
	Open area				Forest with hosts				Forest without hosts			
	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

584

585

586 **Table 2** – Effects of landscape type, growing season and distance to the edge of the plot on
 587 *A. fraterculus* probability of occurrence and abundance during four specific periods of the
 588 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
<i>Occurrence</i>									
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
<i>Abundance</i>									
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

589

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

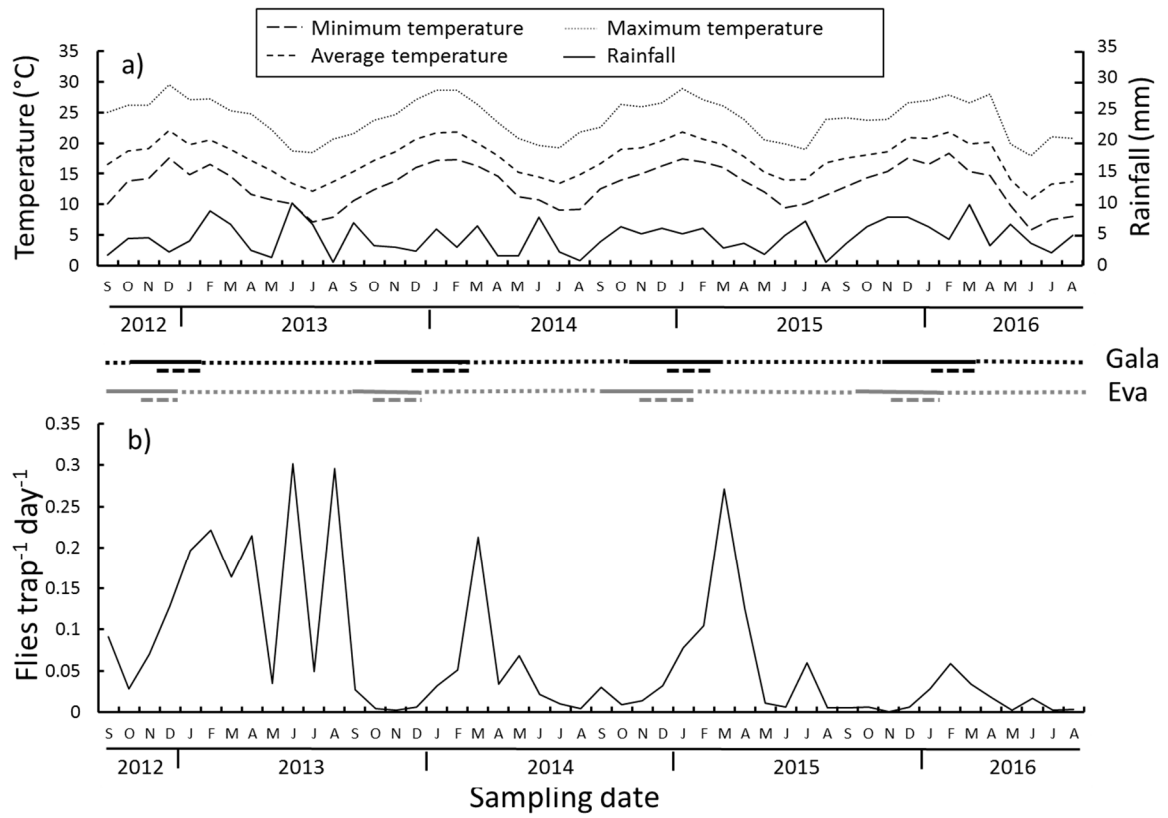
	Whole season	Not susceptible	Early susceptible	Late susceptible
Occurrence				
<i>Annona aff. neosericea</i>	0.75	1	0.76	0.67
<i>Campomanesia xanthocarpa</i>	0.15	0.31	0.81	1
<i>Eugenia uniflora</i>	0.44	0.57	1	0.98
<i>Eriobotrya japonica</i>	1	1	0.63	0.65
<i>Psidium cattleianum</i>	0.15	0.04	0.29	0.30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

593

594

595

596 **Fig. 1**



597

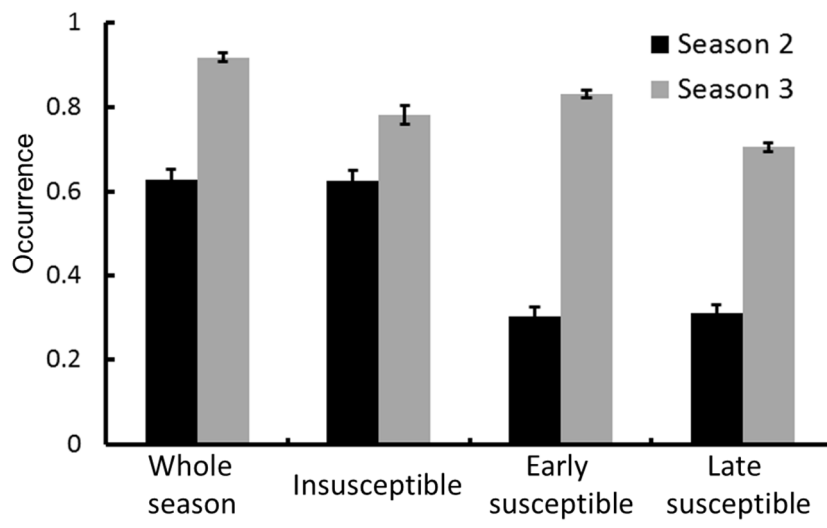
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Fig. 2



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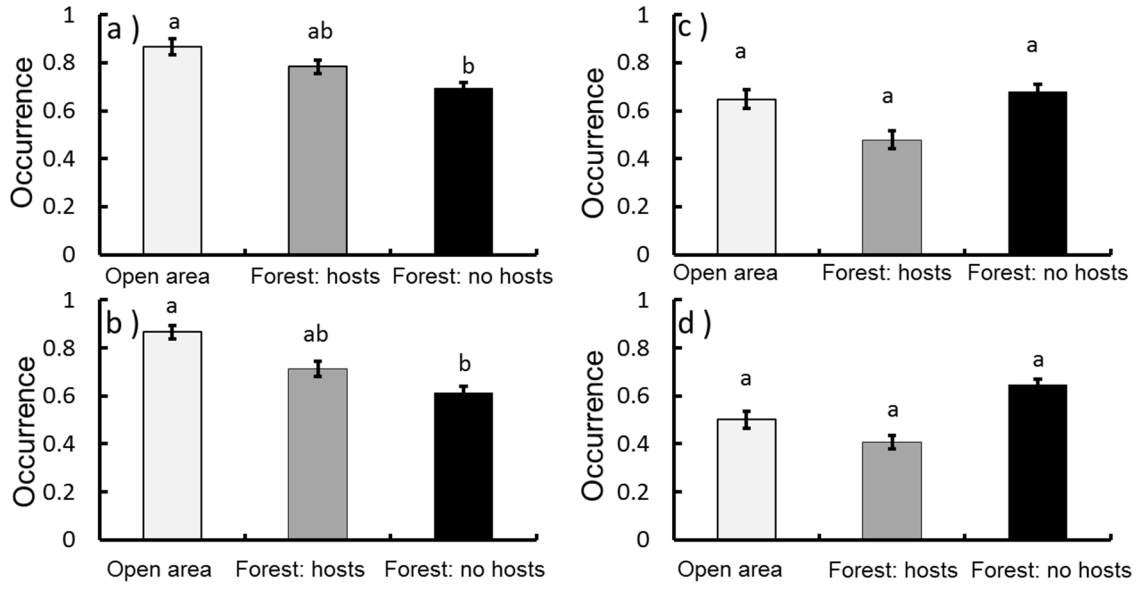
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Fig. 3

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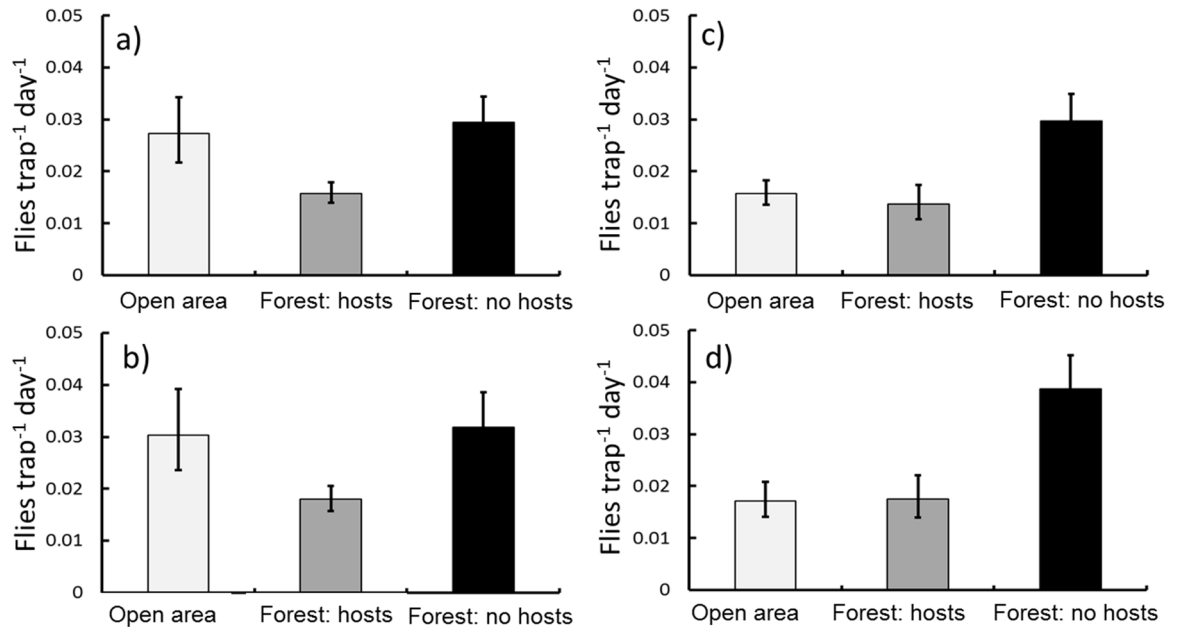


608

609

Fig. 4

610



611