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Empirical evidence of the mediterranean fruit fly movement between orchard types

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Abstract

Understanding species movement in the agroecological system is an important theme in ecology. A mark–release–capture experiment was conducted to study the dispersion behaviour of the Mediterranean fruit fly, *Ceratitis capitata* (Wied.; Diptera: Tephritidae; Medfly) in northern Israel. Four pairs of pear and citrus orchards were selected for the field experiments. Sterile flies dyed with different colours were released in three seasons during 2015 and 2016, based on the phenological stages of the hosts. The total number of captured marked sterile flies per trap (FT) was approx 300 in both April and August. In November, FT values decreased by about 35% to approximately 200. The wild Medfly that were also captured showed an opposite trend, from an FT of 1.8 and 6.4 in April and August, respectively, to an FT of about 330 in November. Marked sterile flies were captured in both the release and the neighbouring orchard sites. We found that the Medfly migrates from pear to citrus orchards during spring and from citrus to pear during summer, when there are no fruit-bearing trees in the orchards. However, during November, when the wild Medfly population prevails in the area, a clear pattern of migration is hard to identify, perhaps because of a possible interaction with the wild fly's population.

KEYWORDS

citrus, dispersion, mark–release, medfly, orchards, phenology

1 | INTRODUCTION

Major aspects in ecology include species spatial distribution and movement dynamics. Understanding such distribution and movement is crucial in managing species, either for conservation or control. Understanding how movement is triggered and distribution shaped is also of great importance (Firester et al., 2018; Kershenbaum et al., 2014; Kremen & Ostfeld, 2005; Macfadyen et al., 2015; Marmen et al., 2016, 2020; Rand et al., 2006; Thomson & Hoffmann, 2013). For pests that persist in the agroecological systems, movement is essential for reproduction and survival (e.g. finding food and shelter; Papadopoulos et al., 2003), especially when a large proportion of the movement occurs within a confined range, to locate resources (Thomas & Kunin, 1999).

The agricultural system is complex and encompasses heterogeneous landscapes, which might also change over time due to crop rotation and other managerial activities. The influence of the availability of vital resources, such as hosts, has recently received attention for pest dynamics (Ben-Hamo et al., 2020; Blank et al., 2019; Goldshtein et al., 2020; Krasnov et al., 2019). Statistical and spatial analysis was used in several studies to forecast pest population dynamics in complex heterogeneous landscapes, (Ives et al., 2017; Ricci et al., 2009; Rusch et al., 2016; Tsafack et al., 2016). Nonetheless, empirical data in commercial fields were rarely examined (Gavriel et al., 2012; Prasifka et al., 2009; Rahman & Broughton, 2019).

The Mediterranean fruit fly, *Ceratitis capitata* (Wied.; Diptera: Tephritidae; Medfly) is a major pest of more than 250 species of fruits, among them, all citrus species and a variety of deciduous fruits (Rossler et al., 2000). Various aspects of the survivability and nature of the Medfly's dispersion have been studied in places around the world (Meats & Smallridge, 2007; Papadopoulos et al., 2003), including in Israel (Gavriel et al., 2010, 2012; Mendelsohn et al., 2018). Recently, Medfly population growth and spatial dispersion patterns were posited to be determined by the abundance and distribution of host trees and fruit availability (Flores et al., 2016; Israely et al., 2005; Papadopoulos et al., 2003; Sciarretta & Trematerra, 2011; Vera et al., 2002). The Medfly is a polyphagous fly with over 250 known hosts, and it can potentially move freely between them. Migration of insects between hosts has been widely studied, primarily focusing on its effect on ecosystem services and disservices in agroecosystems (Blitzer et al., 2012; Oerke, 2006; Rand et al., 2006). The movement between hosts may be driven by abiotic factors, such as temperature and moisture; and biotic factors, like host suitability and crop type (Fahrig et al., 2011; Ojiambo & Kang, 2013). In addition, pest populations are affected by each grower's agricultural practices and management decisions, for example selection of crop type, source of the seedlings, chemical application and the time between crop cycles (Thébaud et al., 2006). Therefore, host preference may change throughout the season. For example, harvesting may force pests to move to alternate hosts (Altieri & Letourneau, 1982). Another factor in pest movement to a different host is that population density in the host trees can increase beyond the trees' capacity to endure the pests (Goldshtein et al., 2020).

A three-year study by Israely et al., (1997) in northern Israel indicated that Medfly population dynamics were primarily driven by the sequential ripening of suitable hosts. Krasnov et al., (2019) analysed over 2000 citrus plots in Israel and found that Medfly populations were positively affected by the extent of deciduous orchards surrounding each citrus orchard. This study used the ecoinformatics approach, which is capable of examining the whole biological system by including a large number of factors (Michener & Jones, 2012; Rosenheim & Gratton, 2017; Rosenheim et al., 2011). It is nonetheless a statistical approach, providing only an indication of a phenomenon, without the ability to prove it. Based on this information, we decided to conduct a mark–release–capture experiment that is widely used to study insect dispersion behaviour (Meurisse & Pawson, 2017) including that of Medfly (Wong et al., 1982; Gavriel et al., 2010; Hendrichs et al., 1993; Meats & Smallridge, 2007; Shelly et al., 2014).

The goal of this study was to use this methodology to examine possible movement of Medfly between deciduous and citrus orchards in relation to host phenology and Medfly preference. We examined two mutually exclusive hypotheses; the purpose of our study was to find out which of the two accounted for Medfly infestation of deciduous and citrus trees. Our hypotheses: (a) Citrus orchards might deter Medfly infestation, because they exhibit a number of antagonistic mechanisms, that is the physicochemical characteristics of citrus peels. This mechanisms may affect the Medfly survival, fecundity, and longevity (Aluja & Mangan, 2008). If so, the Medfly might actively search for a less hostile host nearby. Thus, we expect to see a migration of the Medfly from the citrus orchard to an adjacent host throughout the season, unaffected by the phenological stages of either the citrus or the other host(s); (b) Or, the dynamics of Medfly dispersion will correspond to the phenological stage of each host. Thus, we expect to see the Medfly move between the citrus and deciduous orchards depending on the availability of ripe fruit on the trees.

To our knowledge, this is the first study that evaluated the capture of marked sterile Medfly in two specific hosts during different stages of the hosts' phenology. Knowing the Medfly preference and the possible migration behaviour during the season is valuable information for Medfly population monitoring and control.

2 | MATERIALS AND METHODS

2.1 | Study area

The agricultural landscape of northern Israel is characterized by a mixture of deciduous and citrus orchards, providing an ideal opportunity to explore Medfly dynamics in the context of different orchards types (Figure 1). The climate is Mediterranean, characterized by a short winter season (from October to March) and a long summer.

Deciduous orchards in Northern Israel include several dominant types: pear, peach, plum and pecan. Pear was the most abundant deciduous orchard in proximity to citrus orchards in our study area (27%; Figure 2). In addition, citrus growers in the area reported an increase in Medfly populations at specific periods during the season and attributed it to migration from pear orchards.

2.2 | Study design

Four pairs of pear and citrus orchards were selected for the field experiments (Figure 3). The orchards chosen were similar in size and shape, and the orchards in each pair shared a border (Table 1; Figure 4).

2.2.1 | Medfly origin and maintenance

Sterile male flies (Vienna 8 strain) supplied as pupae by Bio-Fly Inc., Sde Eliyahu, Israel, were used for the field experiments. The pupae were dusted with fluorescent dye powders of two distinguishable colours, using two grams of marking powder (DayGLo®; DayGlo Color) per litre of pupae. (Figure 5a) This marking method was developed by Norris, (1957) for calliphorid flies and modified by Steiner et al., (1965) and Schroeder and Mitchell, (1981). It is widely used in

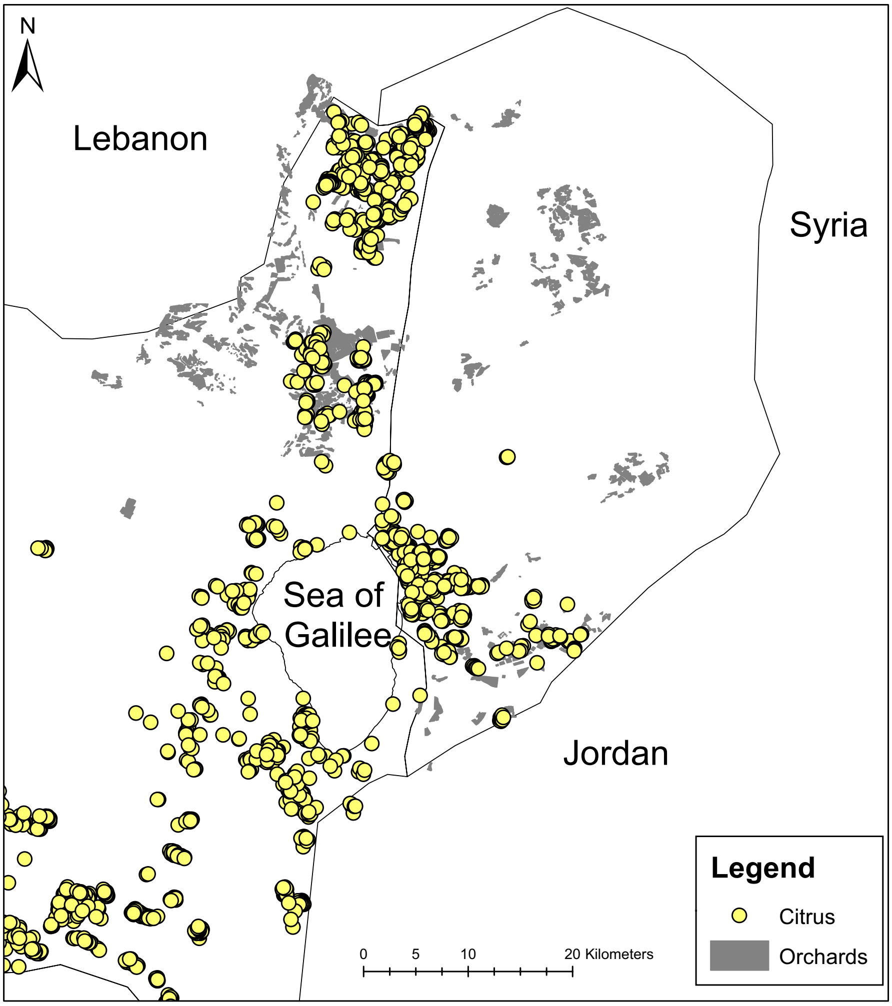

FIGURE 1 Distribution of the citrus orchards (yellow) and the deciduous orchards (grey) in northern Israel

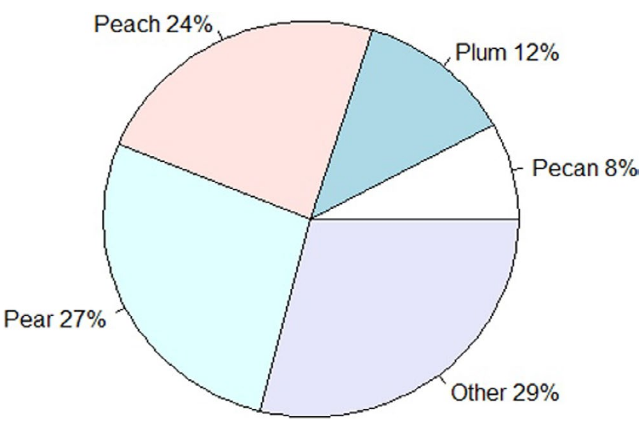

FIGURE 2 Proportion of the different deciduous orchards in the proximity (up to 1 km.) of citrus orchards in northern Israel. Only orchard types that exceeded 5% were included

tephritid fruit fly Sterile Insect Technique (SIT) programs. A study by Dominiak et al., (2003) revealed that the colour had no significant effect on the pupae upon emergence. The pupae were divided into doses of about 7,000 each (FAO/IAEA/USDA, 2014) and put into paper bags measuring 30 × 17 × 30 cm, which are used for ground release of flies, and supplied with a tray containing sugar gel (15% sucrose in 1% agar). The flies were incubated at controlled conditions of 24 ± 1°C with 60% ± 10% Relative Humidity (RH) for 6 days (four days after emergence), ensuring that all adults reached sexual maturity.

2.2.2 | Experimental design

We released sterile flies in three different seasons during 2015 and 2016 (Figure 5b). The timing was based on the different phenological stages of the hosts during the year. During April, citrus trees do not bear fruit, but good sanitation is not applied during this period, so some fruit remains on the ground and is available to Medfly. By contrast, pear trees flower at this time. Pear trees reach their production peak in August, when citrus trees still do not bear fruit. The situation is reversed in November, when the pear trees do not produce any fruit, while citrus cultivation is at its peak fruit production, and the Medfly population is thriving.

The flies that were released in the pear orchards were marked with yellow dye; those released in the citrus orchards were marked with the pink dye. In each pair of orchards, two different people opened the bags, to avoid accidental human assistance in the flies'

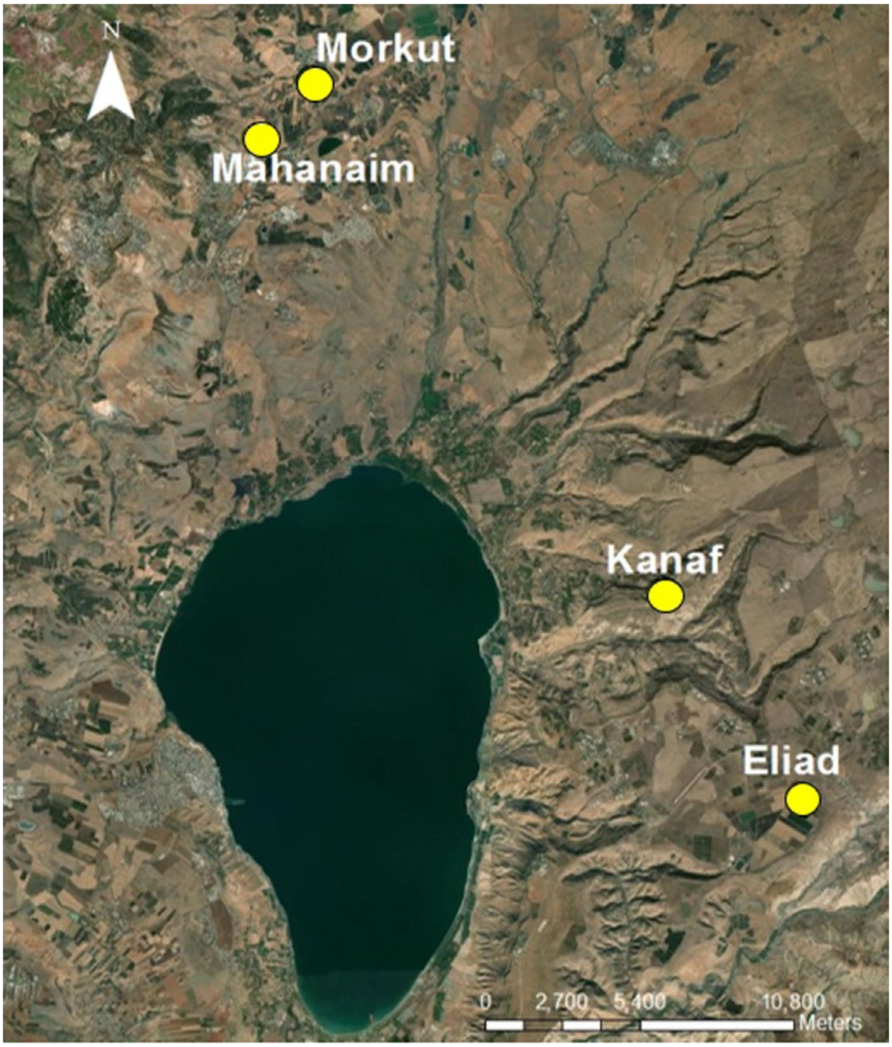

FIGURE 3 Location of the four citrus-pear orchard pairs

TABLE 1 Location and description of the eight orchards studied. All plots were 15 years or older

		Morkut	Eliad	Kanaf	Mahanaim
Location (N, E)	Citrus	33.023, 35.574	32.806, 35.736	32.817, 35.698	32.984, 35.567
	Pear	33.023, 35.576	32.806, 35.737	32.817, 35.721	32.984, 35.568
Cultivar	Citrus	Or	Or	Or	Star Rubi
	Pear	Spadona	Spadona	Spadona	Spadona
Plot size (ha)	Citrus	2.8	2	1	2
	Pear	3	3.8	0.9	2
Plot age (years)	Citrus	NA	15	>15	15
	Pear	>15	>15	>15	>15

travelling from one orchard to the other. Jackson traps baited with Trimedlure (Chemtica International S.A.) were placed in each orchard one day after the release. This was done to minimize an artificial "blast effect" from the sudden release of flies (initially creating dense clouds of flies) and to avoid immediate capture of flies. We placed ten traps in two lines in each of the plots in the study, which we determined would enable us to catch the migrating male Medfly in each plot. The distance between the traps in each line of traps was 25 m to minimize any possible effect one trap might have on the other. The lines were set up 50 m from each other, one row of trees in from the edge of each plot. Thus, the line of traps in each plot was at least 25 m from the closest line of traps in the adjacent plot; the two most distant lines of traps were a minimum of 125 m from each other.

The point of release was in the centre of the rectangle forming each plot, that is 25 m from the centre of each line of traps in that

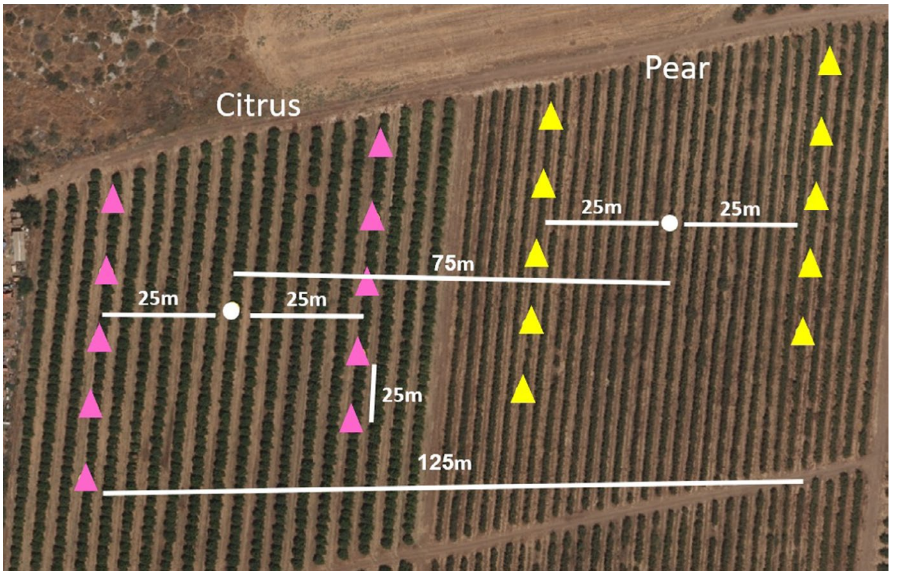

FIGURE 4 Illustration of the location of Jackson traps (white triangles) placed one day after the flies were released in the Morkut pair. Yellow and pink triangles represent the location of release points

plot. Thus, the points of release in adjacent plots were a minimum of 75 m from each other.

To provide the flies enough time to move and disperse, the traps were collected two days after their placement in the orchards. Many capture–release studies found that the great majority of captures occur within several days of release (Andress et al., 2013). All marked flies were counted and recorded according to their colour, a day or two after the traps were collected, using binocular microscopes equipped with Black Light (Superlight™ Model 18; StockerYale; Figure 5d). Wild flies that were captured, that is non-dyed flies were also counted, to gain insight regarding Medfly populations in the area.

2.2.3 | Additional data and statistical analysis

The Medfly in each trap were counted, and the totals were obtained for each plot and divided by ten to get the average number of flies per trap (FT) in each plot. The average number of FT of the four plots per host was used for the statistical analysis.

In addition to the field experiment, we obtained data of Medfly captures from over 2000 Steiner traps in deciduous and citrus orchards collected by the Northern Agriculture R&D Centre and the Israel Cohen Institute for Biological Control (ISCIBC). These data were analysed during 2015–2018, to extrapolate wild Medfly population dynamics in northern Israel in citrus and pear orchards. Results were presented by flies per trap per day (FTD), with a design of 1–2 traps per plot. The flies in each trap were counted at ten-day intervals.

Statistical analyses were performed using R statistics software (R Core Team, 2017). A non-parametric one-factor analysis of variance, the Kruskal–Wallis test, was conducted twice, to assess whether the magnitude of Medfly movement (average number of flies captured for each crop) could be explained by the phenology (month). The first test represents the analysis between months in each category, while the second test analysed two sets of citrus and pear orchards per month (explained in the results section).

3 | RESULTS

The temporal changes in flies per trap per day (FTD) of Medfly in northern Israel in pear and citrus orchards were slightly different (Figure 6). The mean FTD in the citrus orchards during the winter, January-March, was very low (0.75 ± 0.1), and increased in April (1.5 ± 0.25). By contrast, the FTD in the pear orchards was almost zero during March-May and increased during the summer, June-September, (1.7 ± 0.02) and peaked in October (7.9 ± 0.5). The citrus traps are not monitored by the ISCIBC from mid-May to mid-August, because it is off season for citrus, and no Medfly control is undertaken. During the fall, the FTD in the citrus orchards increased and reach its highest level in November (8.2 ± 0.58).

In our experiment, the FT of marked sterile male Medfly was approximately 300 in both April and August (blue bar in Figure 7) for both citrus and pear. In November, the FT decreased by about 35% to approximately 200.

A contrasting trend was found in the wild Medfly (orange bar in Figure 7), from FT of 1.8 and 6.4 in April and August, for both citrus and pear orchards, to about FT of 330 in November (Figure 7).

In all 3 months of the experiment, marked sterile flies from the release site and from the adjacent orchard were captured in both citrus and pear plots (Figure 8, Table 2). However, a larger number of the marked sterile flies were captured in the plot in which they were released than were captured in the adjacent orchard, regardless of the month or season. The average FT of marked flies captured in the plot in which they were released ranged between 8.6 and 53.7 in the citrus orchards, and 28.9 to 65.2 in the pear orchards (Table 2). The average FT of marked flies released and captured in the citrus orchards was similar during April and August and was significantly lower in November. The average number of marked sterile flies

FIGURE 5 Four stages of the field mark–release–capture experiment

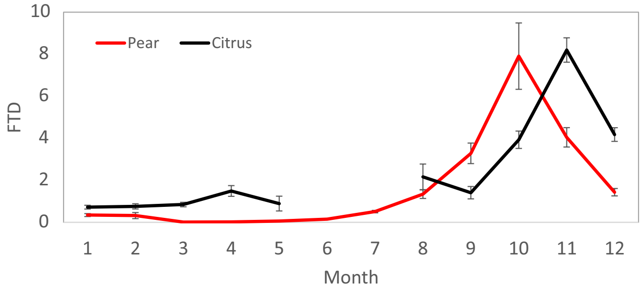

FIGURE 6 Medfly mean yearly pattern (presented as flies per trap per day) in citrus and pear orchards in northern Israel (±SE) in four seasons 2015–2018

TABLE 2 Total average number of flies per trap captured by the experiment calculated for all four plots

	April	August	November
Released flies captured in citrus	53.7	41.2	8.6
Released flies captured in pear	28.9	65.4	38.2
Released flies migrated to pear	2.7	14.2	10.0
Released flies migrated to citrus	10.8	8.3	7.1
Wild flies in citrus	1	1.8	50.1
Wild flies in pear	0.6	1.7	60.4

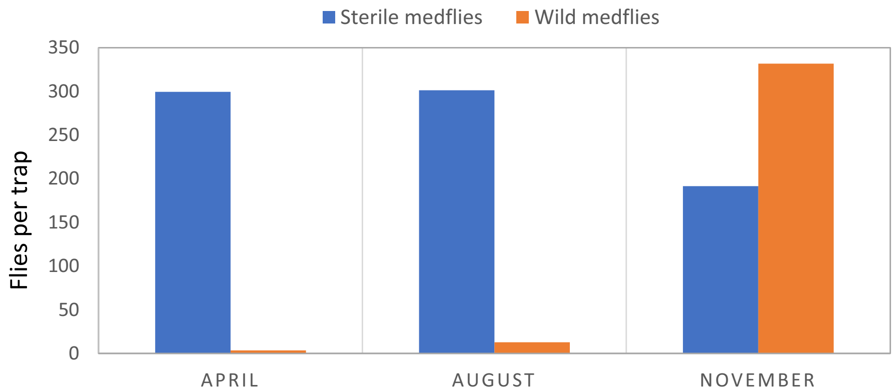

FIGURE 7 Number of captured male flies per trap in the mark–release–capture experiment. Both the flies that had migrated and flies that were recaptured in the released orchard are presented, as well as wild flies captured in the study area

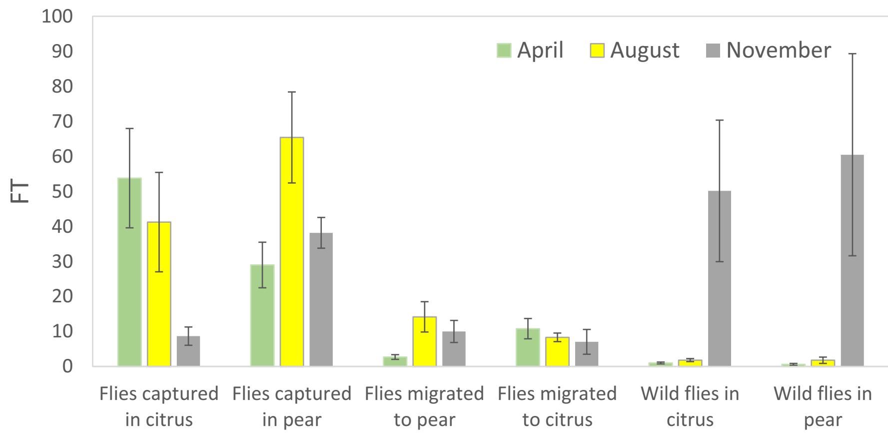

FIGURE 8 Average number of trapped flies per trap for each month of sampling, for the citrus and pear orchards, with error bars

that were captured in the pear orchards after having been released there was significantly higher during August than in April. Similarly, the number was higher in August than in November. The number of marked sterile flies that were captured in the orchard in which the flies were released was higher for citrus during April, but significantly higher in pear orchards than in citrus orchards during August and November.

The FT values of marked flies that migrated to the citrus orchards ranged between 7.1 and 10.8, while the FT of flies that moved from the citrus to the pear orchards ranged between 2.7 and 14.2. No significant difference was found in the FT value of migrated marked flies from pear to citrus orchards between the 3 months. However, the FT of marked flies that moved from citrus to pear orchards was lower during April than in August and November. The FT of marked flies migrating between the hosts during the 3 months was always different, that is the FT of marked flies migrating to the pear was significantly lower than the FT of marked flies migrating to the citrus orchards during April, but higher during August and November.

The FT values of the wild flies the citrus orchards ranged between 1 and 50.1, while the FT of flies in the pear orchards ranged between 0.6 and 60.4 (Figure 8 and Table 2). No significant differences in the number of captured wild flies in the citrus orchard compared with the pear orchards during the 3 months were found.

4 | DISCUSSION

In this study, we conducted a mark–release–capture experiment to track the possible movements of Medfly between adjacent citrus and deciduous orchards in relation to the hosts' phenology. Marked sterile flies were captured in both release and neighbouring orchards, but throughout the study, the number of flies captured in the adjacent orchard was lower compared to the number of flies captured in the plot in which they were released. Studies show that released Medfly can fly to distances of about 300 m from the release site (Dominiak et al., 2003; Gavriel et al., 2012; Vargas et al., 1995) and that they migrate from habitat to habitat (Oerke, 2006; and Rand et al., 2006; Blitzer et al., 2012). We found that migration occurs in both directions, but at different magnitudes and different times. During April, when the citrus is in the final stages of the harvest season and the grounds are not cleaned, (Krasnov et al., 2019) but pear is flowering, three times more marked sterile flies migrated to citrus from pear orchard, than did those from the citrus to the pear orchard, a difference that is statistically significantly. During August, citrus trees do not bear fruit but fruits are abundant on the pear trees, significantly more sterile flies moved to the pear orchards (Figure 8 and Table 2). However, contrary to our expectation, during November, when there is no fruit in the pear orchards while the citrus has ripe fruit, more flies moved to the pear orchards than did those in the opposite direction, that is from the pear orchards to the citrus orchards.

We also noted that the temporal trend in the sterile marked Medfly captured in citrus orchards during November, where they were released, was not in line with the trend in the wild Medfly population captured in these plots. The wild Medfly population in the citrus in our experiments follows the yearly pattern of the Medfly population in the area (Figure 6). We also saw that apparently; it is only the citrus orchards that have lower numbers of sterile Medfly. We cautiously suggest that there might be a possible interaction (e.g. antagonism, competitiveness) between the sterile marked flies and the wild fly population in citrus during November. In fact, some studies reported that the mass-rearing process may alter the behaviour of the male Medfly, and especially their reproductive behaviour (Cayol, 2000; Liimatainen et al., 1997; Rendon, 2000; Rossler et al., 2000). This subsequently can reduce the sexual competitiveness of mass-reared males relative to their wild counterparts and thus impair their success with females and may motivate them to leave. We do not have data regarding females captured in our experiment, but studies show that male and female populations are approximately equal (Leza et al., 2008; Miranda et al., 2001). Therefore, we assume that the female population also exists in our plots. A study by Liedo et al., (2007) showed that it is possible to improve mating performance of mass-reared sterile Medfly through changes in adult holding conditions: demography and mating competitiveness. We suspect that during November, the wild flies can inhabit the unripe pear orchards by consuming honey dew and move randomly to the citrus orchard for sexual relationship with the females. November is the citrus-growing season, and the female will later use the fruit to lay eggs. Interestingly, though, we see only migration to the pear orchards.

Overall, the results of our study reinforce our second hypothesis, that, the dynamics of the Medfly dispersal is affected by the phenological stage of each host. Our main reservation in this study is the use of males to follow phenology, because males might be attracted to other characteristics in the plot such as sexual attraction and honey dew (Broughton et al., 2015). The framework of this study suggests that females follow the phenology of the crops, and specifically the presence of fruits, and the males follow this pattern while searching for females to mate with. Nonetheless, we found that the Medfly migrates from pear to citrus orchards during spring and from the citrus to pear during the summer, when there are no fruits on the trees in the orchards. However, during November when the wild Medfly population prevails in the area, a clear pattern of migration in the sterile Medfly is hard to discern, perhaps because of a possible interaction between them and the wild Medfly. A technical problem may also be affecting the outcome: space in the Jackson trap is limited. Thus, the more flies that are trapped, the less room there is, and the less effective the trap is. When there are large numbers of wild Medfly in the orchard (as is the case in November), they quickly fill the trap, and at the possible expense of capturing sterilized flies.

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CONFLICT OF INTEREST

The research was conducted in the absence of any commercial or financial relationships that could be a potential conflict of interest.

AUTHOR CONTRIBUTIONS

HK, YC, MS, YG and LB conceived research. MS, EG and YG conducted experiments. HK, YC, EG, YG and LB analysed data and conducted statistical analyses. HK wrote the manuscript. MS, YG, LB and YC secured funding. All authors read and approved the manuscript.

DATA AVAILABILITY STATEMENT

All relevant data are available at Helena Furman (2020) Medfly dataset. https://doi.org/10.17632/x2jxhx6rhw.1 (https://data.mendeley.com/datasets/x2jxhx6rhw/1).

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