



The effect of local and landscape variables on Mediterranean fruit fly dynamics in citrus orchards utilizing the ecoinformatics approach

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Abstract

The Mediterranean fruit fly, *Ceratitis capitata* (Wied.) (Diptera: Tephritidae) (medfly), is a major pest among all varieties of citrus. Despite advances in recent years, knowledge about the effects of various variables on the spatiotemporal spread of the medfly is still limited. The goal of this study was to characterize the effects of various local and landscape variables on the population density of medfly in citrus orchards in Israel, utilizing the ecoinformatics approach. Data were collected during three citrus growing seasons (years). The medfly population data consisted of a weekly inspection of ~2300 traps. Thirteen potentially explanatory variables believed to influence the medfly populations were quantified. The contributions of the explanatory variables were analyzed using multimodel inference. Results show that the medfly population is affected by both local and landscape variables. Further analysis was focused on the data from November (representing the fall peak) and April (representing the beginning of the spring peak). The major findings were: Medfly population was higher in plots that were closer to human communicates, presumably due to their proximity to private gardens; the medfly population was negatively affected by the proportion of the surrounding crop; larger plots with lower perimeter-to-area ratio and plots inside large citrus clusters had smaller populations of medflies; variety had inconsistent effect; and elevation showed inverse response (positive in November and negative in April). Additionally, during the fall peak, the medfly population was positively affected by the proportion of the surrounding deciduous orchards and negatively affected by pest aerial spraying rounds up to a certain number. The results of this study demonstrate that the medfly populations in citrus are affected by the composition of the external landscape. Thus, similar to other studies, this study encourages the adoption of area-wide integrated pest management protocols.

Keywords Area-wide integrated pest management · Ecoinformatics · Multivariable analysis · Spatiotemporal analysis · *Ceratitis capitata*

Key messages

- The study used the ecoinformatics approach, which utilizes large databases collected from commercial agriculture to study medfly spatiotemporal dynamics.

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- This study examined 13 local and landscape variables in more than 2000 citrus plots over three years in Israel.
- Medfly population in citrus orchards is affected by the agricultural landscape surrounding the plot.
- The results of this study provide a better understanding of the variables affecting medfly distribution and can lead to recommendations regarding spraying implications and future netting of host and removal of the medfly.

Introduction

Many factors and interactions influence the development of pest populations in space and over time. Among them are abiotic factors, e.g., temperature and moisture, and biotic factors, e.g., host sensitivity and crop type. Pest distribution is also affected by various landscape-scale factors, such as landscape heterogeneity and the degree of connectivity of hosts (Fahrig et al. 2011; Beckler et al. 2005; Noda and Kiritani 1990; Ojiambo and Kang 2013; Thrall and Burdon 2002). In addition, pest populations are affected by the agricultural practices employed and the management decisions made by each grower, such as selection of crop type, source of the seedlings and the time between cropping cycles (Thébaud et al. 2006; Blank et al. 2016). The agro-biological system is even more complex, because there is a transition of pests between the agricultural areas and nearby natural and inhabited environments. All this suggests that studying the processes affecting the distribution of pests in space and over time is a great challenge (Ostfeld et al. 2005; Brévault et al. 2008; Parsa et al. 2012; Riley and Ciomperlik 1997).

The “classical” research approach is based on testing, using experimental methods, and of hypotheses related to factors affecting the system under study. The main drawback of this approach is the need to focus on the effect of only one or a small number of variables. In addition, in most cases it is limited in space and time. Ecoinformatics is a different approach, which seeks to examine the whole biological system (Michener and Jones 2012; Rosenheim 2013). In this approach, a large number of factors can be included in the analysis without the need to select only a few. Ecoinformatics in agriculture was driven by the development of technologies for collecting and sharing data, and the development of advanced and innovative statistical tools for data analysis, including spatial data from geographical information systems (GIS) (Rosenheim et al. 2011; Rosenheim and Gratton 2017). According to this approach, numerous observations collected in an agricultural system and in the adjacent natural system are analyzed along with the germane geographical and meteorological data. Increase in the availability of geospatial data and rich ecological databases are providing new sources of valuable information for landscape-scale research. This enables characterizing the factors

affecting pest development in space and over time. Despite advances in recent years, studies that use ecoinformatics in order to gain knowledge about the effects of various factors on the spatiotemporal heterogeneity and dynamics of pests remained limited.

The Mediterranean fruit fly, *Ceratitis capitata* (Wied.) (Diptera: Tephritidae) (medfly), is a major pest of more than 250 species of fruits, among which are all the citrus and a variety of deciduous fruits (Rossler et al. 2000). In the absence of controls, medflies could damage up to 100% of the yield (Allwood and Leblanc 1997). Economic impacts can be enormous, and the costs of control or eradication are substantial. In experiments carried out worldwide (Papadopoulos et al. 2003; Meats and Smallridge 2007), and in recent years in Israel (Gavriel et al. 2010, 2012; Cohen and Yuval 2000), various topics related to the survivability and nature of dispersion of sterilized medflies have been investigated. Many studies on medfly tend to focus on a local plot and on a radius of up to a few hundred meters of a specific area (Carey 1982; Harris and Lee 1986, 1987, 1989; Hendrichs and Hendrichs 1990; Israely et al. 1997; Warburg and Yuval 1997; Papadopoulos et al. 2001; Mendelsohn et al. 2018). In recent years, the effects of landscape on medfly population are the focus of an increasing number of studies (Papadopoulos et al. 2001; Vera et al. 2002; Meats and Smallridge 2007; Gutierrez and Ponti 2011; Flores et al. 2016). Kounatidis et al. (2008; De Meyer et al. 2008) showed that clustering of trapped flies was significantly related to elevation and that the effect of elevation upon clustering depended on seasonal climatic patterns. Studies by Puche et al. (2005) and Flores et al. (2016) in Guatemala related the captured medflies to host availability in the proximal area. Studies by Nestel et al. (2004) in Greece and Sciarretta and Trematerra (2011) in Central Italy using adult trapping and GIS analysis also attributed the medfly distribution in space to crop ripping, degree of susceptibility of hosts and their geographic location. Nonetheless, most studies on medflies still focus on only one or a few landscapes or local variables, mostly based on experimental data collection.

The goal of this study was to characterize the effects of both the local and landscape variables on the population density of *Ceratitis capitata* in citrus orchards. In turn, these variables can be used to formulate general rules that can help growers control medfly population size. The data for this study were collected from commercial plots over the years and therefore represent real management and growth under various conditions. The database is broad and comprehensive, but has not been studied yet (3 years with over 2000 monitored plots); it provides an exceptional opportunity to characterize spatial variables that influence the distribution of medfly. The results of this work can help to better understand the ecology of the species and the factors affecting its distribution. Recommendations to help minimize the

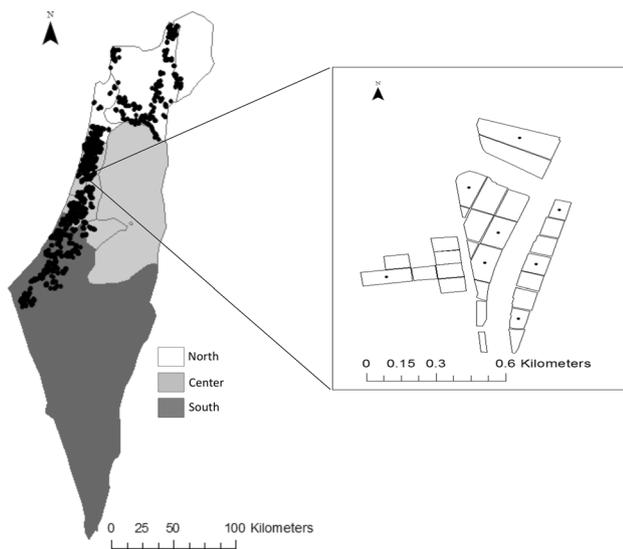


Fig. 1 Map of the study area (Israel) and location of all monitored citrus plots (on the left); enlarged citrus aggregate plots and location of traps. Polygon = citrus plot. Dot = center of monitored plot

damage that the medfly generates can therefore be made. Such recommendations could be relevant to other regions with similar conditions and landscapes (Fig. 1).

Materials and methods

Medfly data

Medfly control in citrus in Israel is centralized by the Israel Cohen Institute for Biological Control (ISCIBC). Approximately 2300 Steiner traps baited with trimedlure dispensers were distributed in 14,000 citrus orchards. On average, the density of the trap distribution is one trap per seven ha. One trap is placed at the edge of a plot and attracts males from up to 20 m away. The traps catch male medfly adults and are manually monitored every 7–10 days during the citrus growing year, which starts in August and ends in May. As the year progresses and the fruits are picked, the number of monitored traps decreases (Fig. 2). More details about the trap monitoring and control system can be found in Cohen (2007) and Cohen et al. (2008).

The study was conducted on data collected during three citrus growing years in Israel: 2013–2014, 2014–2015 and 2015–2016. Captures are expressed as flies per trap per day (FTD), which is a recognized international reference value (FAO/IAEA/USDA 2003). Five months, characterizing different periods of the medfly yearly patterns, were selected for analysis: September, representing the beginning of the monitoring year when the medfly population is beginning to increase; October, with increasing medfly populations;

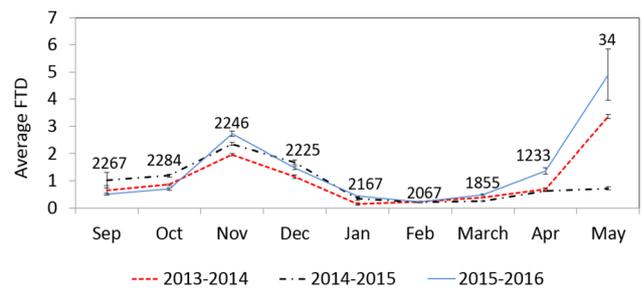


Fig. 2 Medfly yearly pattern (with error) for the 3 years studied. The citrus growing year starts in August and ends in May. The average number of monitored plots per month (examples from 2015 to 2016) is presented above the graph line. FTD = flies per trap per day

November, the fall peak in medfly populations; February, during which the medfly populations decrease; and April, during which medfly populations increase (see results and Fig. 2).

Explanatory variables

Thirteen available explanatory variables, which we hypothesized influence the medfly population, were quantified. The variables were categorized into local and landscape variables (Table 1S). Information regarding descriptive statistics is presented for November 2015 in Table 1S. The citrus spatial layer and information about the local variables were provided by the ISCIBC. The location of deciduous orchards for northern Israel is available since 2012 (over 6.5 thousand ha) from the Northern R&D station through the Agritask online farm data management system (AgriTask, Israel). The locations and borders of human communities were obtained from the Israel's national GIS database (Survey of Israel). The 25-m Digital Terrain Model (DTM) of Israel created by Hall (2008) was used for deriving the orchards elevation.

Local variables (variables that characterize the plot)

1. *Citrus plot perimeter-to-area ratio* Larger fields have lower perimeter-to-area ratios; it has been suggested that they have lower infestations of various pests (Parsa et al. 2011, 2012). Plot dimensions were calculated from the GIS layer provided by the ISCIBC.
2. *Citrus variety type* Although all citrus fruits may be heavily infested by fruit flies, different varieties might exhibit different resistance mechanisms that affect survival, fecundity and longevity of the attacking flies (Staub et al. 2008; Papachristos et al. 2009; Ioannou et al. 2012). This study examined seven citrus groups while accounting for their ripening period and infestation sensitivity: white grapefruit (*Citrus paradisi*) (considered to be very sensitive to medfly infestation); early

- grapefruit; late grapefruit; early orange; late orange; pomelo (*Citrus grandis*); Valencia (*Citrus sinensis*).
3. *Plot age* Various studies have shown the effect of plant age on pest species' richness and population fluctuations (Guedes et al. 2000; Lee et al. 2018). The age of the citrus plot might also have an effect on the condition of the fruit and its attractiveness to the medfly.
 4. *Pest control type* Different types of pest control might have different levels of medfly control efficacy. Four main pest control types were recorded: aerial spraying, ground spraying, mass trapping and other (used mainly for organic plots or for plots under environmentally friendly control projects).
 5. *Number of medfly aerial spraying rounds* The number of medfly aerial spraying rounds during the year was expected to affect medfly control efficacy. The medfly aerial spraying data were available only from August 2015 until December 2015. Despite its limited availability, it was examined for its important and direct effect. The variable is calculated as the number of medfly aerial spraying rounds accumulated until the end of a specific month (e.g., the number of medfly aerial spraying rounds in November is the sum of medfly aerial spraying rounds in August, September, October and November).

Landscape variables (variables representing the surrounding area of each plot)

1. *Aggregated areas of clusters of citrus plots* Citrus plots in Israel are usually grown in close proximity to each other, forming clusters; thus, the plots are spatially linked to each other. This might affect the population size and survival probability of medflies, similar to the citrus perimeter-to-area ratio variable, but at a greater spatial scale. Plots at a distance of up to 10 m from each other were considered to belong to the same cluster.
2. *Distance from nearest human community* A common assumption among farmers and pest scouts is that trees in human communities constitute a source of medfly populations, since regular control measures against the medfly are not used. Citrus plot layers were overlaid on layers of human communities, and the distances between the plots' borders and the borders of the closest human communities were evaluated.
3. *Area of the nearest human community* The area of the nearest community served as a proxy to the type of community (e.g., village, town, city) and the total area of the source of medfly populations (private gardens).
4. *Elevation* Previous studies showed that elevation affects crop yields and pest populations (Kounatidis et al. 2008; Flores et al. 2016). For each plot, the average DTM pixels contained within it was used.

5. *Region in Israel (District)* Israel is located between 29° and 33° north of the equator, which is characterized as a subtropical region, between the temperate zone and the tropical zone. This unique location creates a situation whereby the north of Israel has a Mediterranean climate, characterized by hot and dry summers and cool rainy winters, whereas the southern areas are characterized by an arid climate. These climatic differences might directly affect the abundance of medfly populations. Thus, the study area was divided into three regions (north, center and south) based on general climate characteristics.

Agricultural area around the plot The agricultural area surrounding the plot was shown to have an effect on pest population in previous studies, such as Carrière et al. (2006, 2012) and Blum et al. (2018). Each citrus plot was considered to be the center for a series of 100-m-wide concentric rings, starting at 100 m and reaching 600 m. The total area of the field crops was calculated for each buffer. The radius of each ring was calculated from the citrus plot borders. Thus, the buffers are not round rings but rather ellipsoids. The agricultural area was separated into three types:

6. *Field crops* Field crops that are not considered to be medfly hosts, such as wheat and vegetables.
7. *Deciduous orchards* Crops that are considered to be medfly hosts, such as fruits of all types.
8. *Other types of agriculture* Crops such as fish farms and flower greenhouses.

Information regarding natural and seminatural areas covering the study area was not available and therefore could not be included in the analyses.

Data analysis

First, for every monitored trap, a mean FTD per month was calculated and used as the response variable. Additionally, the general average FTD of all traps was evaluated using descriptive statistics for each of the 3 years.

We tested all the variables for multicollinearity by conducting Spearman cross-correlations among the continuous variables (Graham 2003) (Table 2S). All the variables studied (continuous and categorical) had low cross-correlations ($r < 0.45$), and the highest variance inflation factor (VIF) calculated was 1.82. Neter et al. (1989) suggested that multicollinearity is considered severe when $VIF > 10$. Next, the FTD values were cubic root transformed to meet the assumption of normality and a Gaussian distribution was used in the models.

The contributions of the independent variables were studied using the “glmulti” package in R Documentation

(Calcagno and de Mazancourt 2010), which creates multiple regression models representing alternative explanations for the observed patterns. The multiple models are compared in order to evaluate which one is best supported by the data. The various models were compared using the Akaike information criterion (AIC); the degree of importance of each variable was found by averaging their contribution and importance in the different models, thus obtaining a weighted average. This approach is thought to be less vulnerable to finding spurious effects due to over-fitting and is more informative than methods based on null hypothesis testing (Anderson et al. 2000). Variable estimates are averaged across all models, weighted by the probability that their originating model is the best in the set. Hence, the relative importance of a variable is not based on p-values, but rather on its occurrence in the models that is best supported by the data. The importance value for a particular predictor is equal to the sum of the weights/probabilities for the models in which the variable appears. Thus, a variable that shows up in many of the models with large weights will receive a high importance value. In that sense, these values can be regarded as the overall support for each variable across all the models in the candidate set.

We conducted three separate analyses for each year. The first one used the local variables, and the second used the landscape variables (Tables 3 and 4). Both analyses were performed in order to find the variables that had the greatest effect (importance) on the FTD. To select the most important variables, only those with importance values of 90% (or above) and found to be consistent among years were used. The effect of the surrounding field crops at various distances was also evaluated using the *glmulti* analysis. The distance (100–600 m) that was found to have the highest importance was later incorporated into the landscape analysis. The effect of spatial autocorrelation of FTD was tested and incorporated into each analysis, using the function *autocov_dist* in the “*sqdep*” package (Bivand et al. 2009). The goal of the third model (GLM model) was to envisage the change in FTD based on the important variables found from the local and landscape models. A pseudo-R-squared value was calculated for each month using *NagelkerkeR2* from the “*fmsb*” package (Nagelkerke 1991). Note that Nagelkerke’s pseudo- R^2 ranges from 0 to 1 and summarizes the variance accounted for by the model but is not interpreted as the percentage of variance accounted for by the predictor variables.

The variables found to be the most important in the GLM model were divided into groups (a minimum of 20 observations per group), and a nonparametric Kruskal–Wallis with post hoc (*kruskalmc* in R package) was conducted for each variable. While the model located the variables that significantly affected the medfly population and their general trends, the purpose of this analysis was to figure out which groups in the variables differ from each other and to outline

general rules for growers and extension that can be used in their decision-making process.

Results

Medfly temporal pattern

The yearly changes in FTDs (for the 3 years) are presented in Fig. 2. The temporal pattern was repeated in all 3 years. For example, the mean FTD (and standard error) for the 2015–2016 growing year at the beginning of the year (September–October) was low (0.59 ± 1.8); increased in the fall (2.73 ± 4.21 for November); and then dropped to very low levels in the winter (0.37 ± 1.08 for January–March). In April, the FTD started to increase (1.34 ± 3.8) toward the spring peak, which in general occurs in May and June (Papadopoulos et al. 2001; Goldshtein et al. 2017). This peak was not evident in the trapping loads, because it occurs at the end of the citrus growing year and thus trap monitoring has ended.

Model averaging

Tables 3S and 4S present the variables that were found to be important in at least two out of the 3 years studied. The first model type included the local variables. The results show that overall, the most important local variables were *citrus variety* with inconsistent trend with FTD, the *plot perimeter-to-area ratio* (except for September) which had a positive relationship with FTD and *Pest control type* (except for April) that in general demonstrate that lower FTDs were found in plots under aerial spraying compared to plots underground spraying and mass trapping and higher FTD compared to plots with organic/unknown pests control (labeled other). In addition, the number of *aerial spraying rounds* had a negative effect on medfly population in November 2015.

The most important landscape variables were: The *area of aggregated citrus plots* and the *area of crop in a 300-m buffer* around citrus plots were both found important in all months with consistent negative relationships with FTD. The *elevation* was found important in all 5 months, but with positive relationships with FTD from September to November and negative relationships for February and April; The *area of deciduous orchards in a 300-m buffer* around citrus plots was found important from September to February and had a positive relationship with FTD; the *distance from the nearest human community* was found important for September, with a positive relationship with FTD and from November to April with a negative relationship; The *district* was found important for September in which the northern district had lower FTD values compared to the other districts, and in November and April with higher FTD values.

The third model included all the important variables found in the local and landscape models for each month studied and each year. The calculated pseudo- R^2 (Nagelkerke R^2) for each month in every year is presented in Fig. 3.

Further analysis was conducted to November and April representing the peak fall and the beginning of the spring peak. The FTD was plotted as a function of the important variables: *distance to human community*; *pest control type* (only November); *number of medfly aerial spraying rounds* (only November); *district*; *area of deciduous orchards in a*

300-m buffer (only November); *area of crops in a 300-m buffer*; *area of aggregated citrus plots*; *plot perimeter-to-area ratio and elevation* (Fig. 4 and fig 5S in supplementary section).

Results from Kruskal–Wallis test show that for both months, plots located inside human communities (Fig. 4a) had significantly higher FTD values compared to the rest of the distance categories. Outside the community, the FTD decreases with the increase in distance, yet it seems to level off at a distance of 250 m from the community. A significant lower FTD was found for plots that were managed with aerial spraying in November compared to both ground and mass trapping. A significant and clear decrease in FTD was also found between plots that were not sprayed compared to plots that were sprayed at least once (Fig. 4b). Among plots that were sprayed, there is an ambiguous decrease in FTD with the increase in spraying rounds. The average FTD was significantly larger in the northern region compared to the other two regions in both November and April (Fig 5Sd). In November, the lower elevation areas were generally characterized by lower values of FTD. However, from an elevation of 150 m there was a major increase in FTD (Fig 5Se). In April, while a decreasing trend was found with elevation, it

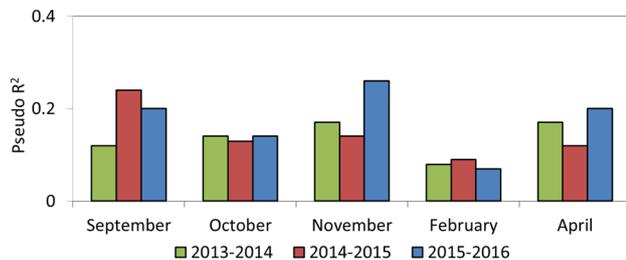


Fig. 3 Pseudo- R^2 of the generalized linear models (GLM) for the 3 years studied, based on the local and landscape variables that were found to be important

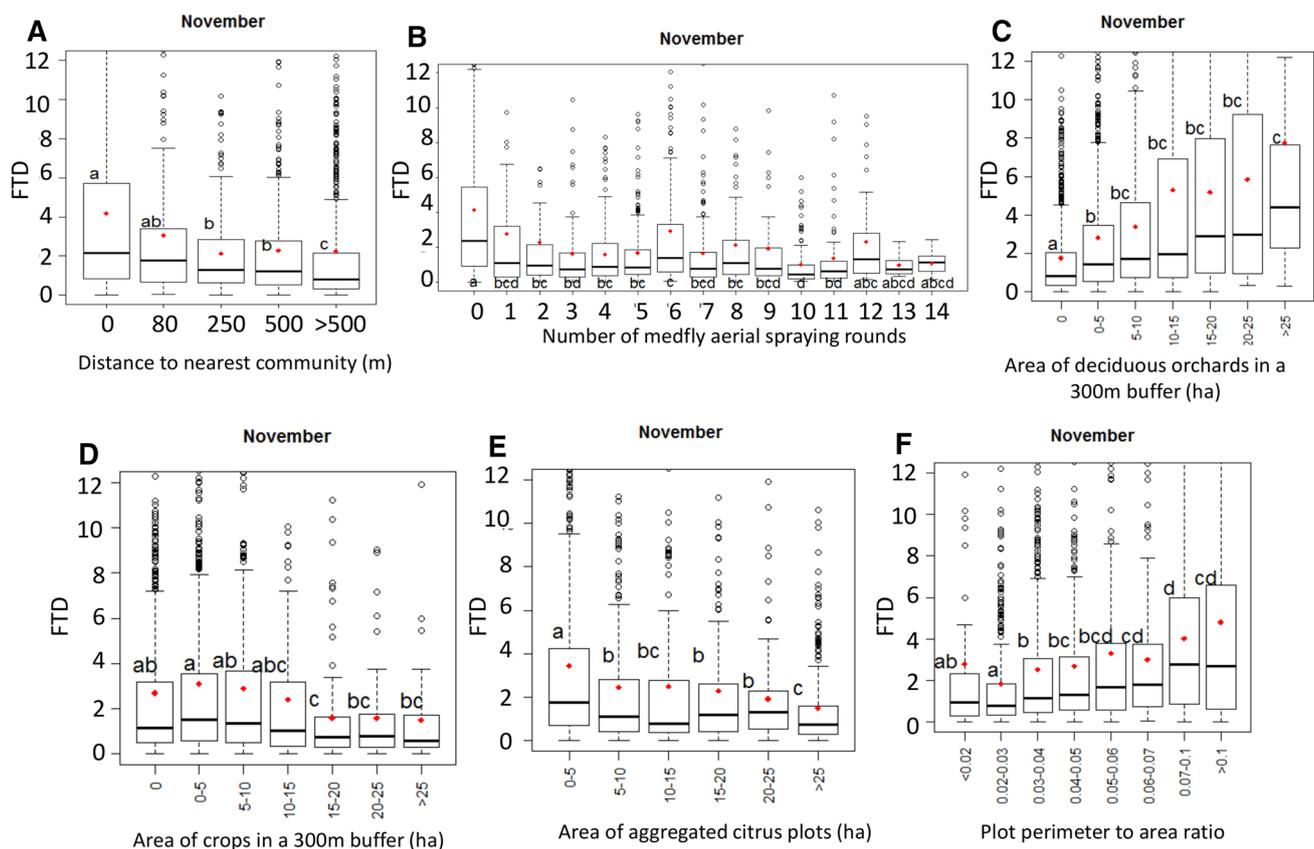


Fig. 4 FTD (flies per trap per day) values as a function of the important variables. **a** Distance from community (m). **b** Number of medfly aerial spraying rounds. **c** Area of deciduous orchards (ha). **d** Area of crops (ha). **e** Area of aggregated citrus plots (ha). **f** Plot-to-perimeter area

seems that the larger FTD values were found in the -50-0 m asl category compared to all the other elevation categories. During November, there is a general trend of increase in FTD as the area of the deciduous orchards around the citrus plot increases (Fig. 4c). Plots with no deciduous orchards around them had significantly lower FTD compared to plots that were surrounded with deciduous orchards, and plots with more than 25 ha had significantly higher FTD than plots with less than 5 ha. As for the other categories of this variable, despite the positive relationship, there were no significant differences. In both months, citrus plots surrounded by large areas of crop fields (Fig. 4d; Fig 5Sg)) were characterized with smaller FTD. Significant lower FTDs were found in November in plots with more than 15 ha of surrounding crops compared to plots with less than 5 ha. Plots that were part of large clusters of citrus plots (Fig. 4e; Fig 5Sh) were characterized by smaller FTD. Plots, with a cluster smaller than 5 ha, had significantly higher FTD than those in clusters larger than 5 ha both in November and in April. Larger-perimeter-to-area (PTA) ratio characterized plots with larger FTD (Fig. 4f). In November, plots with PTA larger than 0.07 had significantly higher FTD than those with a PTA of less than 0.03, while in April, a significant increase in FTD was in PTA larger than 0.04 (Fig 5Si).

Discussion

Medfly dynamics in time

Our objective in this study was to identify the set of variables which could explain the change in FTD in citrus plots throughout Israel. The yearly pattern is well documented in several areas around the world (Mavrikakis et al. 2000; Papadopoulos et al. 2001; Maelzer et al. 2004; Martínez-Ferrer et al. 2010) including Israel (Israely et al. 2005; Goldshtein et al. 2017). The FTD was low in August–September, which is the beginning of the citrus growing and monitoring year in Israel. The peak in November was attributed to the ripening of most of the citrus varieties, together with the temperate temperatures prevailing during that time of the year. Due to the decrease in the temperature during the winter months, the FTD levels decreased in the months of December through March. Papadopoulos et al. (2001) suggested that low winter temperatures and the absence of host fruits for a long period of time are the two main factors determining medfly population density in Northern Greece. In their study, adult activity ceases at the end of November and adults were not detected in traps from December (when temperatures are very low and hosts are absent) until the following June. In contrast to the region that Papadopoulos et al. (2001) studied, in our study area, different hosts are available all year round. Approximately 2000 traps were still

monitored during the winter months, demonstrating that citrus hosts are available for the medfly during this time. In comparison, toward the spring, around 50% of the citrus plots are already harvested (the number of traps decreased to around 1200; Fig. 2) but the medfly population increased (Fig. 2). This is the first generation of medflies after the cold winter, which are generated despite the decrease in citrus hosts. These findings indicate that the medfly pattern of increasing and decreasing populations is primarily due to temperature changes (Israely et al. 2005). In addition, bad sanitation after harvesting may contribute to the medfly development. Another variable that might have a positive relationship with the FTD is the decrease in medfly aerial spraying toward the end of the citrus year.

Medfly dynamics in space

Results of the multivariable regression model showed that the medfly population in the fall and at the beginning of the spring was affected by both local and landscape variables. Among the variables that were examined, three main local and six landscape variables were found to be important during both periods.

Our data revealed a significant effect of the citrus variety. This finding coincides with results of recent and older studies which demonstrated a variable degree of sensitivity of citrus species to medfly (Papadopoulos et al. 2015). For example, Staub et al. (2008) demonstrated in a field and laboratory experiments that oranges were more susceptible to medfly than mandarins and lemons. This variable, however, was not included in the final model as its trend was not consisted among the years. The inconsistency should be further examined in future studies. In our study, in November, larger medfly populations were found in plots wherein ground spraying or mass trapping devices were utilized, than in those that were sprayed aurally. This finding may suggest that medfly aerial spraying is more efficient in the fall than the other two control/management measures. Despite the apparent advantage of the aerial spraying upon the ground spraying, in November, it should be noted that ground spraying is conducted in plots located in human communities and up to 80 m from a community. From Fig. 4a, it is evident that a relatively high medfly population exists in close proximity to a community. This means that the ground spraying is applied in a priority more infected regions, and the higher trapping loads are not necessarily an evident for its efficacy.

We also succeeded to demonstrate the common assumption of scouts, farmers and extension that the proximity to a community had a positive effect on medfly trapping loads. A possible explanation for that is the existence of private gardens that contain various fruit-bearing host plants, including Citrus spp. and deciduous trees, with ripe fruits. Because these private gardens can be found in all regions of

the country and in all years, including winter, they constitute a source of medfly populations in citrus orchards surrounding settled communities. It should be noted that an opposite trend was found with the distance to a community, suggesting that trapping loads decrease with the increase from a community. With caution, we may suggest that it may be attributed to the intensive preventive spraying control that might be more intensive in proximity to communities.

At the autumn peak, after preventive spraying was carried out as required in September–October, the medfly population seems to be affected by the deciduous orchards especially in the higher altitudes as deciduous orchards are confounded with elevation. The elevation in the study area ranges from 50 to 360 m asl. Yet, the average area of deciduous orchards (which are located 300 m around the monitored citrus plot) in the higher altitudes (above 200 m) is 10.9 ha compared to 3.1 ha in the lower altitudes (up to 150 m). Studies in Guatemala by Puche et al. (2005) and Flores et al. (2016) also related the capture of medfly at a specific elevation to host availability. These findings are supported by other studies of *Ceratitis capitata* (Katsoyannos et al. 1998; Papadopoulos et al. 2003; Appiah et al. 2009) and on other species of *Anastrepha* fruit flies (Celedonio-Hurtado et al. 1995) and *Bactrocera dorsalis* (Jayanthi and Verghese 2011). The interpretation that deciduous orchards may contribute to the medfly population in citrus may be supported by another results in this study: Where the area of other crops was large, the FTD was relatively low. This highlights the possible tradeoff between field crops, which are not suitable hosts for the medfly and thus do not contribute to the medfly population in citrus, and deciduous orchards, which are suitable hosts, serve as one of the sources for the citrus medfly population.

The findings of this study generally suggest that during the fall, the medfly population partly comes from outside the plot, and thus, its effect is expected to be greater in isolated small plots (plots with higher perimeter-to-area ratios) and in plots at the outer ring of large citrus clusters (larger aggregated area). The latter edge effect was not studied in this work and should be examined in future studies. A study by Alonso-Muñoz and Garcia-Marí (2013) also showed that the establishment of a network of traps causes a barrier effect, with a gradual and rather constant reduction in medfly captures from the periphery to the interior of the area covered. A study by Parsa et al. (2011) also observed a strong negative association between potato weevil infestations and the abundance of potato in the agricultural landscape and predicted that aggregating potato fields may outperform the management of Andean potato weevils by IPM and chemical control. With the arrival of spring and the rise in temperature, we would expect the medfly population to be larger in later ripening citrus varieties that are still attractive to the medfly as was suggested by Rosenheim et al. (2017)

that showed preferences to late-maturing varieties. Valencia is the main citrus cultivar that is ripe during April; it is grown in central and southern Israel which are characterized by lower altitudes. Yet, according to our results we do not see a higher FTD in these districts in April. The effect of Valencia on FTD (although found important) is not stable (Table 3). We subject that citrus varieties should be further studied. During the spring, higher FTDs were found in large citrus clusters (Fig. 4e). The effect of the citrus aggregation on FTDs in April is probably related to the new medfly generation. As the medfly settles into the cluster for the winter, there will be enough eggs inside the cluster in early spring, and they will be the source of the population rise in April, when the population in the surrounding deciduous orchards is still very low.

The principal hypothesis drawn from this study, which should be examined further, is that medfly populations in citrus are affected by the composition of the external landscape and not only the presence of citrus hosts. The results of this study can provide a better understanding of the ecology of the species, and the variables affecting its distribution, which can lead to recommendations for minimizing the damage it inflicts. The recommendations for the most part call for closer monitoring of medfly in proximity to human communities, as well as raising public awareness in these communities regarding their role in increasing medfly population in nearby orchards.

The ecoinformatics approach implemented in this work has the unique ability to create a large database, with the data collected from commercial agriculture, and process it so as to present true spatial and temporal changes (Cohen 2007; Rosenheim and Gratton 2017). As digital data sharing becomes more widespread, the ecoinformatics methods will become even more useful. Although such databases are vulnerable to errors resulting from combining multiple sources of data that use different sampling methods, once these issues are overcome, the method is particularly helpful when studying the effect of a large number of different independent variables.

Authors' contribution

YC, HK, LB and OM developed the ideas and concepts. YG, MS and EG supplied the data and the entomological knowledge. HK, YC and LB analyzed data. HK wrote the manuscript. All authors read and approved the manuscript.

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Compliance with ethical standards

Conflict of interest All authors declare that he/she has no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

References

- Allwood AJ, Leblanc L (1997) Losses caused by fruit flies (Diptera: Tephritidae) in seven Pacific Island Countries. In: Allwood AJ, Drew RAI (eds) Management of fruit flies in the Pacific. ACIAR proceedings. pp 21–29
- Alonso-Muñoz A, Garcia-Marí F (2013) Mass-trapping of *Ceratitis capitata* (diptera: Tephritidae) in citrus: how it works and factors to improve its efficacy. IOBC WPRS Bulletin 95:43–50
- Anderson DR, Burnham KP, Thompson WL (2000) Null hypothesis testing: problems, prevalence, and an alternative. J Wildl Manag 64:912–923. <https://doi.org/10.2307/3803199>
- Appiah E, Afreh-Nuamah K, Obeng-Ofori D (2009) Abundance and distribution of the Mediterranean fruit fly *ceratitis capitata* (diptera: Tephritidae), in late valencia citrus orchards in ghana. Int J Trop Insect Sci 29:11–16. <https://doi.org/10.1017/S1742758409351036>
- Beckler AA, Wade French B, Chandler LD (2005) Using GIS in area wide pest management: a case study in south dakota. Trans GIS 9:109–127
- Bivand R, Anselin L, Berke O, Bernat A, Carvalho M, Chun Y, Dormann C, Dray S, Halbersma R, Lewin-Koh N (2009) Spdep: spatial dependence: weighting schemes, statistics and models. R package version 0.4-56. <http://CRAN.R-project.org/package=spdep>
- Blank L, Cohen Y, Borenstein M, Shulhani R, Lofthouse M, Sofer M, Shtienberg D (2016) Variables associated with severity of bacterial canker and wilt caused by *Clavibacter michiganensis* subsp. *michiganensis* in tomato greenhouses. Phytopathology 106:254–261. <https://doi.org/10.1094/PHYTO-07-15-0159-R>
- Blum M, Nestel D, Cohen Y, Goldshtein E, Helman D, Lensky IM (2018) Predicting heliothis (*Helicoverpa armigera*) pest population dynamics with an age-structured insect population model driven by satellite data. Ecol Model 369:1–12. <https://doi.org/10.1016/j.ecolmodel.2017.12.019>
- Brévault T, Carletto J, Linderme D, Vanlerberghe-Masutti F (2008) Genetic diversity of the cotton aphid *gossypii* in the unstable environment of a cotton growing area. Agric Entomol 10:215–223
- Calcagno V, de Mazancourt C (2010) Glmulti: an R package for easy automated model selection with (generalized) linear models. J Stat Softw 34:1–29. <https://doi.org/10.18637/jss.v034.i12>
- Carey JR (1982) Demography and population dynamics of the Mediterranean fruit fly. Ecol Model 16:125–150. [https://doi.org/10.1016/0304-3800\(82\)90005-9](https://doi.org/10.1016/0304-3800(82)90005-9)
- Carrière Y, Ellsworth PC, Dutilleul P, Eilers-Kirk C, Barkley V, Antilla L (2006) A GIS-based approach for areawide pest management: the scales of *Lygus hesperus* movements to cotton from alfalfa, weeds, and cotton. Entomol Exp Appl 118:203–210. <https://doi.org/10.1111/j.1570-7458.2006.00384.x>
- Carrière Y, Goodell PB, Eilers-Kirk C, Larocque G, Dutilleul P, Naranjo SE, Ellsworth PC (2012) Effects of local and landscape factors on population dynamics of a cotton pest. PLoS ONE 7:e39862. <https://doi.org/10.1371/journal.pone.0039862>
- Celedonio-Hurtado H, Aluja M, Liedo P (1995) Adult population fluctuations of *Anastrepha* species (diptera: Tephritidae) in tropical orchard habitats of Chiapas, Mexico. Environ Entomol 24:861–869. <https://doi.org/10.1093/ee/24.4.861>
- Cohen H (2007) Development and evaluation of improved Mediterranean fruit fly attractants in Israel. Development of Improved Attractants and their Integration into Fruit Fly SIT Management Programmes: 43
- Cohen H, Yuval B (2000) Suppressing medfly populations by using the mass trapping strategy in apple orchards located at the northern region of Israel. Alon Hanotea 54:212–216
- Cohen Y, Cohen A, Hetzroni A, Alchanatis V, Broday D, Gazit Y, Timar D (2008) Spatial decision support system for medfly control in citrus. Comput Electron Agric 62:107–117. <https://doi.org/10.1016/j.compag.2007.12.005>
- De Meyer M, Robertson M, Peterson A, Mansell M (2008) Ecological niches and potential geographical distributions of Mediterranean fruit fly (*Ceratitis capitata*) and natal fruit fly (*Ceratitis rosa*). J Biogeogr 35:270–281. <https://doi.org/10.1111/j.1365-2699.2007.01769.x>
- Fahrig L, Baudry J, Brotons L, Burel FG, Crist TO, Fuller RJ, Sirami C, Siriwardena GM, Martin J (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol Lett 14:101–112. <https://doi.org/10.1111/j.1461-0248.2010.01559.x>
- Flores S, Montoya P, Ruiz-Montoya L, Villaseñor A, Valle A, Enkerlin W, Liedo P (2016) Population fluctuation of *Ceratitis capitata* (diptera: Tephritidae) as a function of altitude in eastern Guatemala. Environ Entomol 45:802–811
- Food and Agriculture Organization of the United Nations/International Atomic Energy Agency/United States Department of Agriculture (FAO/IAEA/USDA) (2003) FAO/IAEA/USDA manual for product quality control and shipping procedures for sterile mass-reared tephritid fruit flies. Version 5. IAEA, Vienna, Austria
- Gavriel S, Gazit Y, Yuval B (2010) Effect of diet on survival, in the laboratory and the field, of sterile male Mediterranean fruit flies. Entomol Exp Appl 135:96–104. <https://doi.org/10.1111/j.1570-7458.2010.00972.x>
- Gavriel S, Gazit Y, Leach A, Mumford J, Yuval B (2012) Spatial patterns of sterile Mediterranean fruit fly dispersal. Entomol Exp Appl 142:17–26. <https://doi.org/10.1111/j.1570-7458.2011.01197.x>
- Goldshtein E, Cohen Y, Hetzroni A, Gazit Y, Timar D, Rosenfeld L, Grinshpon Y, Hoffman A, Mizrach A (2017) Development of an automatic monitoring trap for Mediterranean fruit fly (*Ceratitis capitata*) to optimize control applications frequency. Comput Electron Agric 139:115–125. <https://doi.org/10.1016/j.compag.2017.04.022>
- Graham MH (2003) Confronting multicollinearity in ecological multiple regression. Ecology 84:2809–2815. <https://doi.org/10.1890/02-3114>
- Guedes R, Zanuncio T, Zanuncio J, Medeiros A (2000) Species richness and fluctuation of defoliator lepidoptera populations in Brazilian plantations of *Eucalyptus grandis* as affected by plant age and weather factors. For Ecol Manag 137:179–184. [https://doi.org/10.1016/S0378-1127\(99\)00326-6](https://doi.org/10.1016/S0378-1127(99)00326-6)
- Gutierrez AP, Ponti L (2011) Assessing the invasive potential of the Mediterranean fruit fly in California and Italy. Biol Invasions 13:2661–2676. <https://doi.org/10.1007/s10530-011-9937-6>
- Hall JK (2008) The 25-m DTM (digital terrain model) of Israel. Isr J Earth Sci 57:145–147. <https://doi.org/10.1560/IJES.57.3-4.145>
- Harris EJ, Lee CY (1986) Seasonal and annual occurrence of Mediterranean fruit flies (diptera: Tephritidae) in Makaha and Waianae valleys, Oahu, Hawaii. Environ Entomol 15:507–512. <https://doi.org/10.1093/ee/15.3.507>
- Harris EJ, Lee CY (1987) Seasonal and annual distribution of the Mediterranean fruit fly (diptera: Tephritidae) in Honolulu and

- suburban areas of Oahu, Hawaii. *Environ Entomol* 16:1273–1282. <https://doi.org/10.1093/ee/16.6.1273>
- Harris EJ, Lee CY (1989) Development of *Ceratitis capitata* (diptera: Tephritidae) in coffee in wet and dry habitats. *Environ Entomol* 18:1042–1049. <https://doi.org/10.1093/ee/18.6.1042>
- Hendrichs J, Hendrichs MA (1990) Mediterranean fruit fly (diptera: Tephritidae) in nature: Location and diel pattern of feeding and other activities on fruiting and nonfruiting hosts and nonhosts. *Ann Entomol Soc Am* 83:632–641. <https://doi.org/10.1093/aesa/83.3.632>
- Ioannou CS, Papadopoulos NT, Kouloussis NA, Tananaki CI, Katsoyannos BI (2012) Essential oils of citrus fruit stimulate oviposition in the Mediterranean fruit fly *Ceratitis capitata* (diptera: Tephritidae). *Physiol Entomol* 37:330–339
- Israely N, Yuval B, Kitron U, Nestel D (1997) Population fluctuations of adult Mediterranean fruit flies (diptera: Tephritidae) in a Mediterranean heterogeneous agricultural region. *Environ Entomol* 26:1263–1269. [https://doi.org/10.1603/0013-8746\(2005\)098\[0077:SDPOMF\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2005)098[0077:SDPOMF]2.0.CO;2)
- Israely N, Ziv Y, Oman SD (2005) Spatiotemporal distribution patterns of Mediterranean fruit fly (diptera: Tephritidae) in the central region of Israel. *Ann Entomol Soc Am* 98:77–84. <https://doi.org/10.1093/ee/26.6.1263>
- Jayanthi PK, Verghese A (2011) Host-plant phenology and weather based forecasting models for population prediction of the oriental fruit fly, *Bactrocera dorsalis* Hendel. *Crop Prot* 30:1557–1562. <https://doi.org/10.1016/j.cropro.2011.09.002>
- Katsoyannos BI, Kouloussis NA, Carey JR (1998) Seasonal and annual occurrence of Mediterranean fruit flies (diptera: Tephritidae) on Chios island, Greece: differences between two neighboring citrus orchards. *Ann Entomol Soc Am* 91:43–51. <https://doi.org/10.1093/aesa/91.1.43>
- Kounatidis I, Papadopoulos N, Mavragani-Tsipidou P, Cohen Y, Terivanidis K, Nomikou M, Nestel D (2008) Effect of elevation on spatio-temporal patterns of olive fly (*Bactrocera oleae*) populations in northern Greece. *J Appl Entomol* 132:722–733. <https://doi.org/10.1111/j.1439-0418.2008.01349.x>
- Lee M, Campbell JW, Miller DA, Martin JA (2018) Insect community response to switchgrass intercropping and stand age of loblolly pine (*Pinus taeda*) plantations. *Agric For Entomol* 20:217–227. <https://doi.org/10.1111/afe.12247>
- Maelzer D, Bailey PT, Perepelicia N (2004) Factors supporting the non-persistence of fruit fly populations in south Australia. *Aust J Exp Agric* 44:109–126. <https://doi.org/10.1071/EA01128>
- Martínez-Ferrer M, Navarro C, Campos J, Marzal C, Fibla J, Bargues L, García-Marí F (2010) Seasonal and annual trends in field populations of Mediterranean fruit fly, *Ceratitis capitata*, in Mediterranean citrus groves: comparison of two geographic areas in eastern Spain. *Span J Agric Res* 8:757–765. <https://doi.org/10.5424/sjar/2010083-1275>
- Mavrikakis PG, Economopoulos AP, Carey JR (2000) Continuous winter reproduction and growth of the Mediterranean fruit fly (diptera: Tephritidae) in Heraklion, Crete, southern Greece. *Environ Entomol* 29:1180–1187. <https://doi.org/10.1603/0046-225X-29.6.1180>
- Meats A, Smallridge C (2007) Short- and long-range dispersal of medfly, *Ceratitis capitata* (dipt., tephritidae), and its invasive potential. *J Appl Entomol* 131:518–523. <https://doi.org/10.1111/j.1439-0418.2007.01168.x>
- Mendelsohn O, Dayan T, Aidlin-Harari S, Silberstein M, Orlov V, Blank L (2018) Mediterranean fruit fly subplot hot spots prediction by experts' experience. *J Appl Entomol* 142:371–379
- Michener WK, Jones MB (2012) Ecoinformatics: supporting ecology as a data-intensive science. *Trends Ecol Evol* 27:85–93
- Nagelkerke NJ (1991) A note on a general definition of the coefficient of determination. *Biometrika* 78:691–692. <https://doi.org/10.1093/biomet/78.3.691>
- Nestel D, Katsoyannos B, Nemny-Lavy E, Mendel Z, Papadopoulos N, Barnes BN (2004) Spatial analysis of medfly populations in heterogeneous landscapes. In Proceedings of the 6th international symposium on fruit flies of economic importance. Isteg Scientific Publications, Irene, South Africa, pp 35–43
- Neter J, Wasserman W, Kutner MH (1989) Applied linear regression models. Irwin, Homewood
- Noda T, Kiritani K (1990) Landing places of migratory planthoppers. *Nilaparvata lugens* (Stål) and *Sogatella furcefera* (Horváth) (Homoptera: Delphacidae) in Japan. *Appl Entomol Zool* 24:59–65. <https://doi.org/10.1303/aez.24.59>
- Ojiambo P, Kang E (2013) Modeling spatial frailties in survival analysis of cucurbit downy mildew epidemics. *Phytopathology* 103:216–227. <https://doi.org/10.1094/PHYTO-07-12-0152-R>
- Ostfeld RS, Glass GE, Keesing F (2005) Spatial epidemiology: an emerging (or re-emerging) discipline. *Trends Ecol Evol* 20:328–336. <https://doi.org/10.1016/j.tree.2005.03.009>
- Papachristos D, Kimbaris A, Papadopoulos N, Polissiou M (2009) Toxicity of citrus essential oils against *Ceratitis capitata* (diptera: Tephritidae) larvae. *Ann Appl Biol* 155:381–389. <https://doi.org/10.1111/j.1744-7348.2009.00350.x>
- Papadopoulos N, Katsoyannos B, Carey J, Kouloussis N (2001) Seasonal and annual occurrence of the Mediterranean fruit fly (diptera: Tephritidae) in northern Greece. *Ann Entomol Soc Am* 94:41–50. [https://doi.org/10.1603/0013-8746\(2001\)094\[0041:SAOOT\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2001)094[0041:SAOOT]2.0.CO;2)
- Papadopoulos NT, Katsoyannos BI, Nestel D (2003) Spatial autocorrelation analysis of a *Ceratitis capitata* (diptera: Tephritidae) adult population in a mixed deciduous fruit orchard in northern Greece. *Environ Entomol* 32:319–326. <https://doi.org/10.1603/0046-225X-32.2.319>
- Papadopoulos NT, Papachristos DP, Ioannou C (2015) Citrus fruits and the Mediterranean fruit fly. *Acta Hort* 1065:1009–1018. <https://doi.org/10.17660/ActaHortic.2015.1065.126>
- Parsa S, Ccanto R, Rosenheim JA (2011) Resource concentration dilutes a key pest in indigenous potato agriculture. *Ecol Appl* 21:539–546. <https://doi.org/10.1371/journal.pone.0036533>
- Parsa S, Ccanto R, Olivera E, Scurrah M, Alcázar J, Rosenheim JA (2012) Explaining Andean potato weevils in relation to local and landscape features: a facilitated ecoinformatics approach. *PLoS ONE* 7:36533. <https://doi.org/10.1371/journal.pone.0036533>
- Puche H, Midgarden DG, Ovalle O, Kendra PE, Epsky ND, Rendon P, Heath RR (2005) Effect of elevation and host availability on distribution of sterile and wild Mediterranean fruit flies (diptera: Tephritidae). *Fla Entomol* 88:83–90. [https://doi.org/10.1653/0015-4040\(2005\)088\[0083:EOEAHA\]2.0.CO;2](https://doi.org/10.1653/0015-4040(2005)088[0083:EOEAHA]2.0.CO;2)
- Riley D, Ciomperlik M (1997) Regional population dynamics of whitefly (homoptera: Aleyrodidae) and associated parasitoids (hymenoptera: Aphelinidae). *Environ Entomol* 26:1049–1055. <https://doi.org/10.1093/ee/26.5.1049>
- Rosenheim JA (2013) Costs of lygus herbivory on cotton associated with farmer decision-making: an ecoinformatics approach. *J Econ Entomol* 106:1286–1293. <https://doi.org/10.1603/EC12511>
- Rosenheim JA, Gratton C (2017) Ecoinformatics (big data) for agricultural entomology: pitfalls, progress, and promise. *Annu Rev Entomol* 62:399–417. <https://doi.org/10.1146/annurev-ento-031616-035444>
- Rosenheim JA, Parsa S, Forbes AA, Krimmel WA, Law YH, Segoli M, Segoli M, Sivakoff FS, Zaviezo T, Gross K (2011) Ecoinformatics for integrated pest management: expanding the applied insect ecologist's tool-kit. *J Econ Entomol* 104:331–342. <https://doi.org/10.1603/EC10380>
- Rosenheim JA, Higbee BS, Ackerman JD, Meisner MH (2017) Ecoinformatics can infer causal effects of crop variety on insect attack by capitalizing on 'pseudoeperiments' created when different crop varieties are interspersed: a case study in almonds.

- J Econ Entomol 110:2647–2654. <https://doi.org/10.1146/annurev-ento-031616-035444>
- Rössler Y, Ravins E, Gomes P (2000) Sterile insect technique (SIT) in the near east—a transboundary bridge for development and peace. *Crop Prot* 19:733–738. [https://doi.org/10.1016/S0261-2194\(00\)00097-1](https://doi.org/10.1016/S0261-2194(00)00097-1)
- Sciarretta A, Trematerra P (2011) Spatio-temporal distribution of *Ceratitidis capitata* population in a heterogeneous landscape in Central Italy. *J Appl Entomol* 135:241–251
- Staub CG, De Lima F, Majer JD (2008) Determination of host status of citrus fruits against the Mediterranean fruit fly, *Ceratitidis capitata* (Wiedemann)(diptera: Tephritidae). *Austral Entomol* 47:184–187. <https://doi.org/10.1111/j.1440-6055.2008.00646.x>
- Thébaud G, Sauvion N, Chadœuf J, Dufils A, Labonne G (2006) Identifying risk factors for European stone fruit yellows from a survey. *Phytopathology* 96:890–899. <https://doi.org/10.1094/PHTO-96-0890>
- Thrall P, Burdon J (2002) Evolution of gene-for-gene systems in metapopulations: the effect of spatial scale of host and pathogen dispersal. *Plant Pathol* 51:169–184. <https://doi.org/10.1046/j.1365-3059.2002.00683.x>
- Vera MT, Rodriguez R, Segura DF, Cladera JL, Sutherst RW (2002) Potential geographical distribution of the Mediterranean fruit fly, *Ceratitidis capitata* (diptera: Tephritidae), with emphasis on Argentina and Australia. *Environ Entomol* 31:1009–1022. <https://doi.org/10.1603/0046-225X-31.6.1009>
- Warburg M, Yuval B (1997) Effects of energetic reserves on behavioral patterns of Mediterranean fruit flies (diptera: Tephritidae). *Oecologia* 112:314–319. <https://doi.org/10.1007/s004420050314>