



Management of the Mediterranean fruit fly, *Ceratitis capitata*: past, present, and future

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With 2 figures and 1 table

Abstract: Population monitoring and management of the Mediterranean fruit fly (medfly), *Ceratitis capitata* (Diptera: Tephritidae), are still challenging, and are tightly connected to a deep understanding of its biology and ecology. Within this framework, new innovative control approaches and tools are frequently proposed and developed to integrate the available techniques and to overcome the difficulties involved in designing effective Integrated Pest Management programs. Indeed, some biological, ecological, and genetic characteristics of *C. capitata* can limit the efficacy of classical pest management strategies. This article provides a comprehensive review of the currently available tools, devices and approaches used to monitor and control medfly populations worldwide.

Keywords: medfly; Area-Wide Integrated Pest Management; biological control; entomopathogen; lure-and-kill; pest forecasting; Sterile Insect Technique; Tephritidae

1 Introduction

Ceratitis capitata (Wiedemann) (Diptera: Tephritidae), commonly known as the Mediterranean fruit fly or medfly, is among the most destructive pests worldwide due to its high polyphagy and invasive ability (Giunti et al. 2023). Medfly has dispersed, from the ancestral habitats of the eastern sub-Saharan Africa to almost all African continent, Mediterranean and Middle East, north and south America, west Australia and islands of the Pacific, Atlantic and Indian ocean. The control of this tephritid pest is still challenging in many parts of the globe and relies mainly on application

of synthetic pesticides. There are several innovative control approaches and tools that have been developed, tested, and adopted over the last decades (Boulahia-Kheder 2021; Dias et al. 2022a). For example, the Sterile Insect Release Technique (SIT) has been perfected and currently used for area-wide management and eradication purposes (Enkerlin 2021). On the other hand, lure and kill systems have been developed and currently implemented in the framework of Integrated Pest Management (IPM) programs, while biological control is also considered (El-Sayed et al. 2009). In the framework of invasion dynamics, the use of effective and selective monitoring approaches is crucial for the timely

detection of the medfly in non-endemic areas and, thus, to immediately design adequate eradication and/or containment programs. In this scenario, a detailed understanding of the biology, ecology and invasiveness of this species is needed in planning effective surveillance and IPM programs (Dias et al. 2022b; Giunti et al. 2023).

In the present review, we critically describe the baseline knowledge and challenges for medfly monitoring and examine medfly prevention and management techniques, including trapping surveys, forecasting and decision-making, as well as its chemical control, insecticide resistance management, use of green insecticides, cultural control, biological control, and area-wide IPM programs (e.g., including the Sterile Insect Technique (SIT)).

2 Monitoring, trapping surveys, forecasting and decision making

Population monitoring is a central aspect of true fruit flies (Diptera: Tephritidae) pest management. Medflies and other fruit flies can be monitored at the larval stage by sampling fruits, and at the adult stage by trapping. Fruit sampling provides an indication of fruit infestation, while trapping provides information on the presence and population density and dynamics of adults. In both cases, limitations to their performances, such as zero catches and the probability of capturing low numbers of adult medflies during the season (Clift & Meats 2004; Manoukis et al. 2014), should be taken into consideration. Recent guidelines for fruit sampling and monitoring and for trapping adults can be found in FAO/IAEA (2018) and (2019) respectively.

There is a long list of trapping systems developed and tested for medfly adults (FAO/IAEA 2018) including bucket, McPhail type, color-sticky and Delta type traps. Male target trapping systems rely mainly on Jackson traps baited with the parapheromone trimedlure, while female trapping rely on bucket or McPhail type of traps baited with food attractants. Jackson traps with trimedlure are easy to use and quite selective on attracting only male medflies. Food lures attract both sexes but are rather female-specific and provide important information for early detection of the medfly activity in temperate areas (Papadopoulos et al. 2001). The development of the three-component female targeted lure (ammonium acetate, trimethylamine and putrescine packaged in slow-release dispensers) was a breakthrough in medfly trapping (Epsky et al. 1999; Katsoyannos et al. 1999). Early detection of females during the spring-summer is of importance in the successful management of the medfly populations and damage avoidance later in the season (Miranda et al. 2001). Detection of low populations early in the spring is challenging and the most efficient trapping systems deployed in high-risk areas should be considered. The performance of male and female targeted systems may vary during the season and hence both should be considered for a more accurate depiction of the population in a specific area (Papadopoulos

et al. 2001, 2003). In this respect, recent developments with smart-trapping devices (smart traps, e-traps) and automatic image analysis may improve the ability of early detection of female medflies (Diller et al. 2023), positively affecting area-wide management of the pest. Monitoring of females in SIT projects also provides an indication of the results of control efforts and allows to fine-tune releases of sterile males (Katsoyannos et al. 1999).

During the last decade, “smart” traps (i.e., electronic trapping devices) to monitor/survey fruit flies have been developed, tested and, a few of them, commercially implemented (Cardim Ferreira Lima et al. 2020; Schellhorn & Jones 2021; Preti et al. 2021). Smart traps utilize different types of electronic and optical sensors (e.g., laser light beam, automated recognition of images of trapped adults) to count adult flies entering the trap, determining the identity of the captured individuals with a relatively high accuracy (Goldshtein et al. 2017; Potamitis et al. 2018; Diller et al. 2023). Smart traps have not yet been implemented in routine monitoring/surveillance practices due to several technical problems (e.g., wireless communications, quality of sensors, stability of the system) and costs. These issues, however, are expected to be solved in the future. For medfly, several smart trap models have been developed (Goldshtein et al. 2017; Shaked et al. 2018; Diller et al. 2023), and some of them are in the process of commercialization (Goldshtein E. & Cohen Y. Personal Communications). Although smart traps and identification algorithms require further development and improvement, the future of monitoring/surveillance will undoubtedly use these devices to monitor and manage medfly and other fruit fly pests.

Trapping surveys have been classified into four types: detection, delimitation verification, and monitoring (FAO/IAEA 2018). The aim of detection is to determine if the pest is present in an area. The goal of delimitation is to establish boundaries of a pest incursion. Concerning verification, the aim is to confirm the pest status, while in monitoring the goal is to characterize the target population and determine efficacy of control measures. FAO/IAEA (2018) provides a classification of pests’ situations and the type of trapping surveys suggested for each pest situation.

Optimization of trapping systems requires traps to be deployed in space and time in such a way that the probability of capturing and detecting fruit flies is maximized, even with low or incipient populations, and that costs are kept within certain affordable limits. Optimization of trapping systems to detect invasive and incipient medfly populations in the time-dimension has been recently suggested. Kean & Stringer (2019), for instance, modeled and simulated the population dynamics of the medfly using current climatic patterns (and expected future scenarios) in New Zealand. They determined optimal trapping periods, and specific dates to initiate trapping, to detect medfly incursions and low populations. Climatic modeling is also being used and proposed to determine suitable geographic areas for medfly and other fruit flies, and for the optimization of detection surveys. For

instance, Szyniszewska & Tatem (2014) and Szyniszewska et al. (2020) have used several modeling approaches (e.g., CLIMEX, MED-FOES and MAX-ENT) that include biological information of medfly and of the habitat (e.g., host suitability, irrigation, Normalized difference vegetation index NDVI) to determine suitable geographic areas worldwide for medfly development. This type of modeling approach and forecasting is currently being implemented and tested in a Horizon 2020 project, *FF-IPM* (<https://fruitflies-ipm.eu/>), to track the range expansion of medfly in Europe. *FF-IPM* is also implementing smart traps to optimize surveillance in large geographic areas. Monitoring/surveillance optimization also includes the “optimal” deployment of traps in space including large geographic areas. Fang et al. (2022) recently investigated current deployment schemes in delimitation surveys of medfly in the USA using a simulation approach. Their simulation proposed to further optimize the surveillance schemes that are currently used with medfly incursions in the USA, and to reduce costs by 86% (Fang et al. 2022). Optimization of trap deployment in the geographic space is also being approached from the host-habitat suitability perspective by using Bayesian network to model the drivers of habitat aptness as a directive to deploy traps for fruit fly management (van Klinken et al. 2019). Trap-deployment optimization for medfly surveillance can be highly achieved by using the recently proposed Host Reproduction Number (HRN) index (Dominiak & Taylor-Hukins 2022). Lux (2019) provided a modeling and simulation approach to evaluate detectability and dispersion of invasive medflies in complex landscapes (e.g., urban) and changing climates using insect behavioral data that may also guide deployment of traps in the geographic space for medfly management. Currently, the *FF-IPM* Horizon 2020 (<https://fruitflies-ipm.eu/>) project is deriving and testing risk-maps and trap deployment scenarios and algorithms for medfly, and other invasive fruit flies for Europe, using experts’ information and risk-weighting procedures.

Trapping in time and space is also an important tool in the development of Decision Support Systems (DSS) for medfly, and in the application of precision pest management approaches (“precision Targeting”). For instance, the MedCila spatial DSS for medfly uses data on a number of flies in neighboring traps, and the history of captures, to derive decisions on the application of control measures in area-wide projects (Cohen et al. 2008). Other uses of medfly population monitoring in DSS include the approach of Sciarretta et al. (2019) to direct intervention in relatively small farms.

3 Control strategies

3.1 Chemical control

The control of the Mediterranean fruit fly has been traditionally accomplished using synthetic insecticides either as cover sprays, targeting adults on foliage and immatures

within fruit (systemic action), or bait sprays against adults (Baronio et al. 2018).

In Europe and North Africa the traditional medfly control has been based on cover sprays, especially using organophosphates (i.e., malathion and dimethoate) (Kheder et al. 2012). Both malathion and dimethoate are banned in Europe for use in open field conditions but are still used in other parts of the globe (<https://ec.europa.eu/food/plant/pesticides/eu-pesticides-database/start/screen/active-substances>). In some cases (i.e., Tunisia), terrestrial or airlift malathion and dimethoate spray treatments are applied up to 10 times per season on a crop (Magaña et al. 2007; Kheder et al. 2012). Frequent spraying should be closely monitored for residues on the fruit, and special attention should be placed to avoid applications of insecticides close to harvest. Although the number of authorized active ingredients has been reduced in various parts of the world, organophosphates, pyrethroids, chitin synthesis inhibitors, Spinosad and neonicotinoids are still used for the control of medfly. The new EU policy targets major reduction of pesticide use, including complete ban of major pesticide categories such as organophosphates (IARC 2017).

Cover sprays with appropriate/registered pesticides may be considered, to control medfly populations, considering the mode of exposure and the systemicity of the formulations. Indeed, some active ingredients (e.g., pyrethroids) are non-systemic and thus present contact, ingestion and respiratory action only against adult medflies, while other pesticides can penetrate the plant tissues targeting eggs and larvae inside the fruits by cytotoxic (e.g., spinosad, malathion) and/or systemic action (e.g., dimethoate, neonicotinoids).

However, the excessive use of cover sprays and the negative effects that these substances have on the environment and human health, as well as on the development of insecticide resistance to different active ingredients, stimulated a targeted and selective use of pesticides. A generalized trend in many parts of the world has been a transition from diffuse aerial or ground-based treatments to localized applications and the reinforcement of bait spray application with new classes of insecticides (Boulahia-Kheder 2021).

In this scenario, bait sprays, consisting of an attractant (e.g., protein hydrolysate, sugarcane molasses or syrup, Maillard reaction of fructose, urea and others) coupled with appropriate insecticides, are gradually replacing the cover-sprays of the entire crop canopy (Baronio et al. 2019; Sciarretta et al. 2019; Kouloussis et al. 2022). However, bait sprays target only adult medflies aiming to suppress population densities below the economic injury level, while they have no direct effect on eggs or larvae. Bait sprays contribute to reduction of both the amount of active ingredient applied and the residues on the fruit (El-Sayed et al. 2009). Bait spray products using phosmet, etofenprox, deltamethrin, lambda-cyhalothrin, acetamiprid, etofenprox and spinosad are commercially available and represent viable options for IPM programs, although their potential side effects towards non-target organisms, such as the natural enemies *Aphidius cole-*

mani Viereck (Hymenoptera: Braconidae), *Cryptolaemus montrouzieri* Mulsant (Coleoptera: Coccinellidae), *Neoseiulus californicus* (McGregor), should be considered (Urbaneja et al. 2009).

3.2 Resistance to insecticide and resistance management

Medfly control is undergoing a series of practical limitations due to the emergence of resistance phenomena to different active ingredients used both as sprays and in lure and kill approaches. As an example, strategies based on deltamethrin were expected to grow significantly in the coming years because of the high efficacy of this molecule against medflies. Unfortunately, resistance to deltamethrin was recently detected both in Spanish and Brazilian medfly populations (Lisi Demant et al. 2019; Castells-Sierra et al. 2022).

The potential of medfly to develop resistance to different insecticidal classes has been demonstrated for various insecticides, including malathion and lambda-cyhalothrin, (Magaña et al. 2007; Couso-Ferrer et al. 2011; Arouri et al. 2015). Resistance development of medfly and other pests to specific pesticides is related to the selection pressures of frequent use on a specific population. As an example, wild medfly populations subjected to frequent treatments with malathion were 2–30-fold less susceptible to this insecticide than populations from non-treated fields, and about 100 times more resistant than a laboratory susceptible strain (Magaña et al. 2008). Moreover, cross resistance may occur without a specific insecticide pressure, such as the resistance to deltamethrin and etofenprox in lambda-cyhalothrin resistant strains (Arouri et al. 2015). In addition, several malathion resistant populations developed cross-resistance to fenthion and other insecticides (lambda-cyhalothrin, lufenuron, and methyl-chlorpyrifos) (Magaña et al. 2007; Couso-Ferrer et al. 2011; Vontas et al. 2011). The alternance and integration of insecticides with different modes of action is considered the best strategy to avoid or delay the occurrence of resistant medfly strains. In this context, the use of mass trapping strategy could be a solution when the availability of different formulations is limited, since the poisoned specimens can be retained inside the devices (Kouloussis et al. 2022).

3.3 Lure and kill

From a practical point of view, there are different tactics to reduce insecticide treatments. Lure and kill in a broader sense includes mass trapping, bait dispensers or bait stations. In mass trapping the pest is retained by adhesive, the structure of the trapping device, killed by a pesticide or drawn in water, while in bait stations or bait dispensers the pest is killed by a pesticide or chemosterilized (El-Sayed et al. 2009; Navarro-Llopis et al. 2013).

The lure and kill strategy has extensively adopted worldwide and a series of attractants, traps and attract-and-kill

devices to control medflies are available (Economopoulos & Haniotakis 2019; Boulahia-Kheder 2021). Lure and kill has been acknowledged as an alternative to the insecticide control approach for many fruit flies, although its efficacy is difficult to prove in field conditions. Usually, mass-trapping and bait dispenser approaches can effectively and timely suppress medfly populations, although low efficacy is revealed with high populations. However, long-term applications of lure and kill over wide areas may significantly reduce medfly populations (Navarro-Llopis et al. 2013).

Most lure and kill devices used against medfly rely on food attractants and mainly target the adult females before oviposition. Among the lure components, ammonium acetate, trimethylamine and putrescine are the most used (Bali et al. 2021), but additional new-generation baits (e.g., Biodelear, a mixture of pyrazines, pyranones and amorphous nitrogen-based polymers) are also available on the market (Kouloussis et al. 2022). The success of lure and kill approaches to suppress medfly populations are directly related with the density of deployed devices.

3.4 Cultural control

Cultural practices are commonly acknowledged to reduce medfly populations in Area-Wide IPM programs, although few studies are available on this specific topic.

Sanitation (i.e., the disposal of host fruit from the ground or from host trees, either from crops or hedges and borders) can reduce further infestation, although it cannot eliminate the pests (Zavala-López et al. 2021). Fruit removal and destruction can be particularly useful in controlling the overwintering medfly population. Indeed, medfly females can continue laying eggs in non-harvested fruits, and infested fruits harboring larvae may either remain on the trees or fall to the ground during autumn and winter. Larvae may overwinter in such late season infested fruits and produce the first spring generation of adults (Papadopoulos et al. 1996, 1998). Sanitation of these overwintering refugia may have a large impact on the spring population of medfly. Infested fruit can be buried in the soil to impair the emergence of adult medflies, although newly emerged adults can reach the soil surface without injuries from 40 cm deep in loose soil (Chueca et al. 2013). Similarly, mechanized grinding of fallen fruit using a wood shredder in winter can reduce medfly populations in spring by 27–46% in citrus orchards in Spain (Chueca et al. 2013). This technique can significantly reduce the cost of cultural practice compared to the traditional ones, which involve manual gathering or burial of the fruit.

Fruit bagging is a physical protection technique that may offer direct and almost full protection from medfly attacks by preventing oviposition inside the fruit (Raga et al. 2020). Pre-harvest bagging is mainly used to produce quality and high-value fruit and is based on the use of different types of fruit covers, including nets placed directly on the plants or over individual tree branches and bags covering single fruit.

Lastly, the high polyphagy of this species should be considered. The presence of key or alternative (wild growing, no crop hosts) host plants in the surroundings of crop fields (i.e., abandoned orchards, backyards in suburban areas, field margins) is important for the maintenance and development of medfly populations, thus should also be considered in IPM programs, and also in effort to extirpate, contain or eradicate medfly.

3.5 Botanicals

Although medfly is a highly polyphagous pest, it is acknowledged that its development and survival is more difficult in *Citrus* fruit, mainly because of the essential oil (EO) rich peel (Salvatore et al. 2004; Papachristos et al. 2008). Furthermore, petroleum extracts from *Citrus aurantium* L. showed contact toxicity toward adult medfly (Siskos et al. 2009), while linalool, a component of citrus EOs, showed oviposition deterrent properties (Papanastasiou et al. 2020). On this basis, several studies have investigated the insecticidal effects of plant extracts against medfly, though their use in the field is still limited due to applicative constraints, such as water immiscibility and low persistence, and the scarce efficacy of commercial products, like neem derivatives (Silva et al. 2013).

The most promising results have been produced by formulating botanicals in baits for lure-and-kill programs (Benelli et al. 2012; Stupp et al. 2020). A recent study reported high toxicity of *Mentha suaveolens* Ehrh. EO ($LD_{50} = 0.9 \mu\text{L}/\text{mL}$) on adults following ingestion of the compound (Zerkani et al. 2022). Furthermore, several EOs showed combined effects, such as ingestion toxicity and ovideterrence of *Lavandula coronopifolia* Poir. EO ($LC_{50} = 86.34 \mu\text{L}/\text{g}$ and 94% egg reduction at $55 \mu\text{L}/\text{g}$) (Ouarhach et al. 2022), or contact and oral toxicity of *Melaleuca alternifolia* (Maiden & Betche) Cheel EO ($LC_{50} = 0.117 \mu\text{L}/\text{cm}^2$ and $LD_{50} = 0.269\%$ w/w, respectively) (Benelli et al. 2013). Nevertheless, EO bioactivity can be altered by formulation with other bioactive botanicals, either by increasing or decreasing the whole insecticidal activity (Alves et al. 2019).

The oral administration of botanicals to medfly adults can also affect behavioral and biological traits other than survival, including oogenesis and fecundity (Di Ilio & Cristofaro 2021; Oviedo et al. 2020). Benelli et al. (2021) reported high ingestion toxicity for both sexes fed on *Carlina acaulis* L. EO ($LC_{50} = 1094 \text{ ppm}$) and its major compound, carlina oxide, can substantially decrease aggressive interactions, which are crucial for securing reproductive success in both sexes (Benelli et al. 2022). However, several botanical extracts demonstrated attractive activity towards medfly, which can be exploited for lure-and-kill formulations (Ghabbari et al. 2018; Blythe et al. 2020; Luu-Dam et al. 2021) or for aromatherapy to enhance the effectiveness of sterile males in SIT programs (Yuval et al. 2007; Shelly et al. 2014; Pereira et al. 2021).

3.6 Area-wide integrated pest management (AW-IPM)

The concept of Area Wide-Integrated Pest Management (AW-IPM) differs from conventional IPM in that the total population or metapopulations of the target pest is considered. This means that control measures, instead of being applied plot by plot, are applied throughout the landscape, considering areas that are not cultivated, but that can be refuge or reproduction sites for the pest. This approach is required when applying control methods such as biological control and the SIT. The latter is an environmental-friendly insect pest control method involving the mass-rearing and sterilization, using radiation, of a target pest, followed by the systematic area-wide release of the sterile males by air over defined areas, where they mate with wild females resulting in no offspring and a declining pest population. AW-IPM can be considered as a preventive strategy whereas IPM alone is a rather reactive one (Hendrichs et al. 2021a). Despite the scale that differs between AW-IPM and classical IPM, the management of a pest in a broad area results in a substantial population suppression eliminating the farm-to-farm interventions that are part of the classical IPM. Tephritid flies are the pest group with the largest number of AW-IPM programs using SIT worldwide (Fig. 1). Among them, medfly is by far the species with the higher number of programs and mass rearing facilities (Table 1).

SIT-AW-IPM approach has been used for prevention (exclusion from entry into pest free area), eradication, containment, or population suppression purposes as far as medfly is concerned. The adopted strategy mainly depends on the pest and the control program goal (Enkerlin 2021; Hendrichs et al. 2021b).

Medfly eradication using SIT-AW-IPM was first attempted in pilot projects in some Mediterranean (De Murtas et al. 1970) and South Pacific islands (Vargas 1993) with limited success. More recently, AW-IPM, combining SIT with cultural control, baiting and quarantine/border inspections, was successful to eradicate the medfly from the Dominican Republic (Zavala-López et al. 2021) and Colima state in Mexico (Pérez-Staples et al. 2021; Juárez et al. 2022). A common factor in these two last programs was that there were new invasions in pest-free areas.

Suppression has been the strategy adopted in areas where the pest is already present. Examples of successful SIT-AW-IPM suppression programs are ongoing in Spain (Plá et al. 2021) South Africa (Venter et al. 2021) and Croatia (Bjeliš et al. 2010). In Israel, the SIT-AW-IPM program successfully run for more than 20 years, was recently discontinued (Nestel D., personal communication).

In pest-free areas that are vulnerable to medfly introduction, either due to the frequency of events (human-assisted introduction) or the proximity to infested areas (natural dispersion), prevention or containment strategies have been applied. The California preventive release program is an example of a

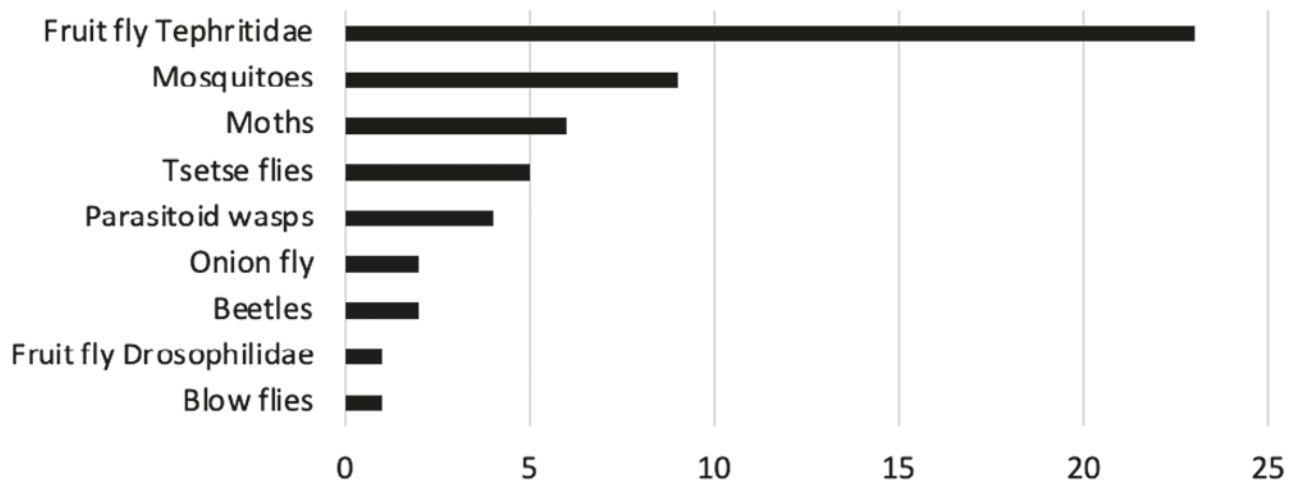


Fig. 1. Current (2022) number of SIT facilities per group of insect pests (source: FAO/IAEA DIR-SIT, World-Wide Directory of SIT Facilities).

Table 1. Tephritid mass-rearing facilities for SIT applications and production of sterile males per week (source: FAO/IAEA DIR-SIT, World-Wide Directory of SIT Facilities).

Species	Countries	Production (millions/week)
<i>Anastrepha fraterculus</i>	Peru	25
<i>Anastrepha ludens</i>	Guatemala, Mexico, USA	30
<i>Anastrepha obliqua</i>	Mexico	30
<i>Bactrocera correcta</i>	Thailand	10
<i>Bactrocera dorsalis</i>	Mauritius, Thailand	21
<i>Bactrocera latifrons</i>	Japan	0.3
<i>Bactrocera oleae</i>	Israel	0.12*
<i>Bactrocera tryoni</i>	Australia	30
<i>Ceratitis capitata</i>	Argentina, Australia, Brazil, Chile, Costa Rica Guatemala, Israel, Mexico, Peru, South Africa, Spain, Tunisia, USA	2,683
<i>Zeugodacus cucurbitae</i>	Japan, Mauritius	65

*: the production of sterile olive fruit flies was stopped some years ago due to the lack of funds (D. Nestel, pers. comm.)

preventive AW-SIT program to address incursions of medfly. The high frequency of medfly detections in the Los Angeles Basin, whether due to multiple entries or the establishment of the pest in the area (Papadopoulos et al. 2013; Carey et al. 2017; McInnis et al. 2017), pushed to release sterile males throughout the year in a large area (Dowell et al. 2000). Up to date, preventive releases are kept aiming to both eliminate any incursion (Hendrichs et al. 2021b) and suppress possible existing low density populations.

The medfly presence in Central America represents a high risk for the Mexican fruit industry. For this reason, since the early 1980s a SIT-AW-IPM program (Moscamed) was established. Over 500 million sterile flies have been

released every week at the border between Guatemala and Mexico, to prevent the spread of the pest and its introduction into Mexican territory. So far, this program has been successful in preventing the introduction and establishment of the medfly in Mexico (Enkerlin et al. 2015, 2017; Liedo 2016). In Australia, AW-IPM have been widely applied against fruit flies, including the medfly, which is now established in Western Australia; AW-IPM involving the SIT, the male annihilation technique (MAT), as well as the chemical control, baiting and trapping techniques and the border inspections were used to reduce the incidence of pest damages on crops in this regions and to prevent its spread to pest-free areas (Jessup et al. 2007).

3.6.1 Technological developments

Since the first SIT application for medfly control, continuous improvements have been sought. Among them, larval diets stand out, whose ingredients represent the highest cost of mass-rearing. These improvements include the evaluation of lower-cost alternative ingredients (e.g., Vargas et al. 1983; Silva Neto et al. 2012), diet recycling (e.g., Bruzzone et al. 1990), and use of symbiotic microorganisms (e.g., Augustinos et al. 2015, 2021; Kyritsis et al. 2019). An important development was the genetic sexing strain, which allowed the production and release of only males. Vienna 7 and Vienna 8 genetic sexing strains are currently reared at almost all mass-rearing facilities (Augustinos et al. 2017). These strains have two sexing traits, i.e., different pupal colors and lethal temperatures; the development of these strains, achieved through classical genetic methods is described by Franz et al. (2021).

Medfly mass-rearing has important effects on its behavior. In its lek mating system, the male courtship affects female choices, and this directly influences SIT effectiveness (Hendrichs et al. 2002; Robinson et al. 2002). Developing the “filter system” to rear genetic sexing strains (Fisher & Cáceres 2000) opened the possibility of designing colony management systems that minimize adverse changes in sexual behavior, the ability to evade predators, and other attributes that affect the performance of sterile insects in the field. Some colony management strategies are (a) refreshing the strain by backcrossing with wild insects (Cáceres 2022), (b) hybridization (Shelly 2001) and (c) selection (McInnis et al. 2002).

Post-irradiation treatments have been developed with the aim of overcoming the issues caused by mass-rearing and the irradiation adverse effects (Lux et al. 2002). These treatments contribute to improving the sexual competitiveness of sterile males and boost their field performance. Within these treatments, manipulating the diet of adults and exposing flies to aromatherapy play a major role (Yuval et al. 2007; Shelly et al. 2014; Pereira et al. 2021).

The AW-IPM approach with the SIT application allows the integration with other control methods in a synergistic manner. A good example is mass-trapping using female attractants (Navarro-Llopis et al. 2008), since it has no effect on sterile males, and the wild population is affected by trapping, as well as by the induction of sterility. Another example is the use of sterile insects as vectors of entomopathogenic fungi (EPF) (Flores et al. 2013). Here, EPF conidia are transmitted through intraspecific interactions. A limiting factor of this strategy is the effect of the EPF on vectors, i.e., the sterile males. During the first 5 days after release, there are no effects on the performance of the sterile males, but there is a gradual decrease after this period (Ramírez et al. 2022). An alternative to overcome this disadvantage is the use of auto-inoculation devices, baited with a female attractant (Toledo et al. 2017).

3.7 Biological control

3.7.1 Predators and parasitoids

Biological control is among the safest, most environmentally benign, and cost-effective methods for long-term and landscape-level management of invasive pests. Biological control alone may not result in the desired level of management for tephritid pests because of an extreme low tolerance for damaged fruit for a marketable crop or exported fruits. However, it may contribute effectively to reduce fly populations that may constantly spill over treated crops from non-crop habitats, making other management strategies more efficient and economical. The greatest benefits of effective biological control also extend to other potential insect pests in commercial orchards, as reduced insecticide usage leads to increased activity of the natural enemies of secondary pests. Therefore, biological control as a fundamental component of Area-Wide pest management would provide a valuable ecosystem service, improves environmental quality, and lowers growers' management costs.

One of the major challenges for managing extremely polyphagous and highly mobile pests such as medfly is that non-crop habitats often provide reservoirs for fly populations to reinvade crops after they have been treated (Aluja & Rull 2009). Although, as discussed above, various on-farm control methods can be effective targeting adult flies (Dias et al. 2018), natural enemies especially parasitoids can play a unique role not only because they can attack immature flies inside the fruit, but can reduce fly densities at the landscape level as well. Indeed, most efforts of biological control of medfly have made to explore, introduce, and establish exotic parasitoids in the fly's invaded regions in Australia, Hawaii, parts of the Mediterranean areas and throughout Latin America (Wharton 1989; Sivinski 1996; Purcell 1998; Ovruski et al. 2000; Garcia et al. 2020; Clarke et al. 2022; Dias et al. 2022b).

3.7.1.1 Predators

Various species of predators, including ants, arachnids, birds, carabids, crickets, earwigs, lizards, predatory wasps, rodents, rove beetles, spiders and true bugs have been reported to prey upon tephritids (Hendrichs et al. 1994; van Mele & Cuc 2003; Garcia et al. 2020). However, predators have been rarely used in classical or augmentative biological control of medfly, except for a few early attempts in 1930s with the introduction of the rove beetles, *Belonuchus rufipennis* F. and *Thyreocephalus albertisi* (Fauvel) (Coleoptera: Staphylinidae) from Brazil into Hawaii (Clausen 1978). Ground dwelling predators, which are hard to rear, targeting wondering larvae before pupation are the most effective against medfly. Some ground-dwelling predators such as beetles, earwigs and ants can play a key role in reducing medfly populations in ground cover management (Cruz-Miralles et al. 2022). Ants is an important group of predators

and several studies have documented their impacts on the medfly in various agroecosystems (Campolo et al. 2015). For example, active predation was observed by *Pheidole megacephala* (Fabricius), *Linepithema humile* (Mayr) and *Solenopsis geminata* (Fabricius) on medfly larvae, pupae and teneral adults in guava orchards in Hawaii (Wong et al. 1984a); by *Tapinoma nigerrimum* (Nylander) on medfly larvae in citrus orchards in Spain (Urbaneja et al. 2006); and by *Monomorium subopacum* (Smith), *T. simrothi* Krausse, *Cataglyphis viatica* (Fabricius) and *Messor picturatus maura* Santschi on mature medfly larvae in the Argan forest in Morocco (El Keroumi et al. 2010). The fire ant *S. geminata* is most effective, killing 73.4% pupae and 31% teneral adults of medfly in guava orchards in Hawaii (Wong et al. 1984a), and 7–25% of mature larvae in coffee and citrus plantations in Guatemala (Eskafi & Kolbe 1990). The weaver ants of the genus *Oecophylla* also reduced the damage of *Ceratitis* and *Bactrocera* species in mango orchards in Africa, Asia, and Australia (van Mele et al. 2007). These studies show the potential of predators as conservative biocontrol agents for medfly (Abeijon et al. 2019; Cruz-Miralles et al. 2022).

3.7.1.2 Parasitoids

Over 60 hymenopteran species of Braconidae, Chalcididae, Diapriidae, Eulophidae, Figitidae, and Pteromalidae have

been reported to attack medfly, including 26 species recorded from the fly's native range in Africa, 15 species endemic to the Indomalayan and Australasia realms and 21 Neotropical native species (Table S1). Most of them are members of the braconid subfamily Opiinae in the genera *Diachasmimorpha*, *Fopius*, *Opius*, *Psytalia* and *Uletes* that are of Afrotropical, Australasia or Indomalayan origin (Wharton 1989; Ovruski et al. 2000; Wharton et al. 2000). All opiine parasitoids are solitary koinobiont endoparasitoids, oviposit in host eggs or larvae, and emerge as adults from the host puparium. The most important parasitoids for biological control of medfly include three egg parasitoids, *F. arisanus* (Sonan), *F. ceratitivorus* Wharton and *F. caudatus* (Szépligeti) and six larvae-attacking parasitoids, *D. longicaudata* (Ashmead), *D. kraussii* (Fullaway), *D. tryoni* (Cameron), *F. vandenboschi* (Fullaway), *P. concolor* (Szépligeti) and *P. humilis* (Silvestri) (Wharton 1989; Purcell 1998; Ovruski et al. 2000; Bokonon-Ganta et al. 2005; 2019; Wang et al. 2021) (Fig. 2). The neotropical figitid larval parasitoid *Aganaspis pelleranoi* (Brèthes) and diapriid pupal parasitoid *Coptera haywardi* (Oglobin) are also important biological control agents for medfly in South America (Garcia & Corseuil 2004; Ovruski et al. 2004), while parasitization of *Coptera occidentalis* Muesebeck in medfly pupae has been tested in laboratory in Europe (Fig. 2) (Kazimírová & Vallo 1999;

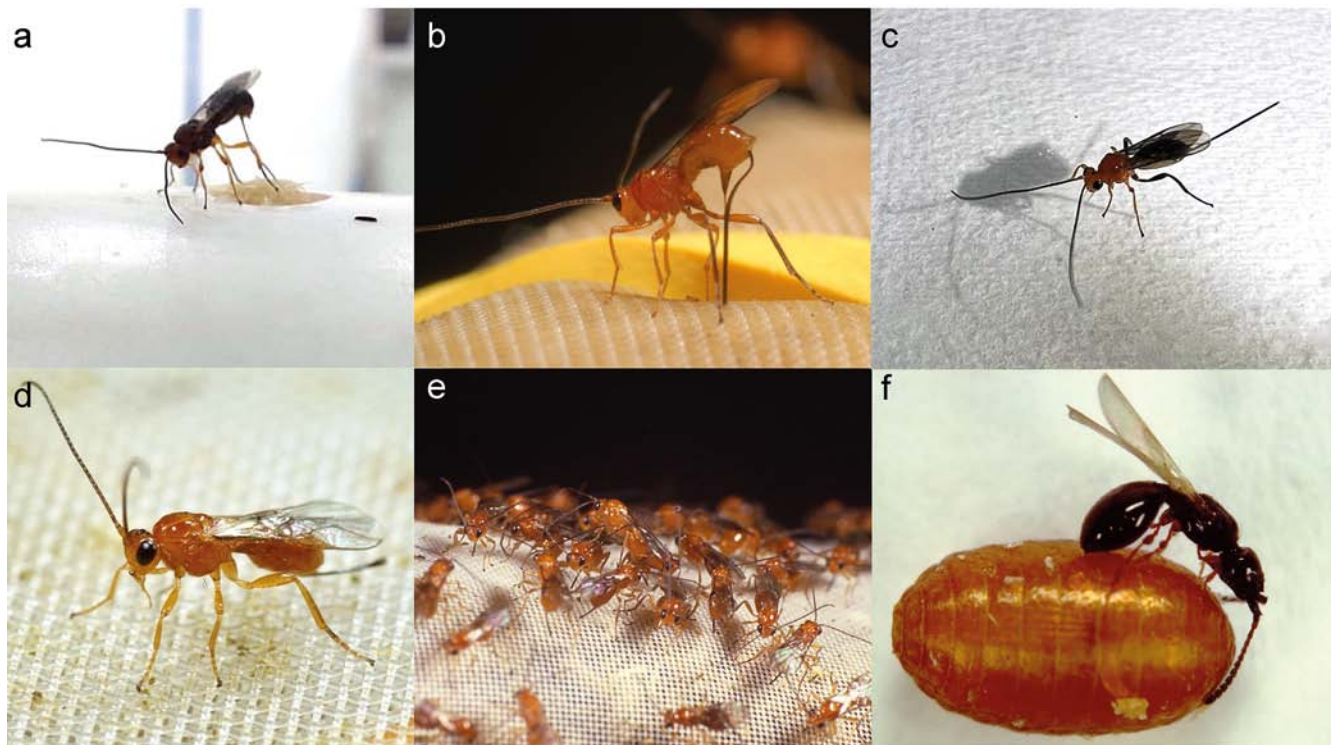


Fig. 2. Several hymenopteran parasitoids of *Ceratitis capitata*: (a) the braconid *Fopius arisanus* (Sonan) ovipositing in a medfly egg, the larval-pupal braconid parasitoids (b) *Diachasmimorpha longicaudata* (Ashmead), (c) *Diachasmimorpha tryoni* (Cameron), and (d) *Psytalia concolor* (Szépligeti), and (e) a detail of *P. concolor* mass-rearing, (f) the driapriid *Coptera occidentalis* Muesebeck parasitizing a medfly pupa (photo credit: a,c Pablo Liedo; b,d,e: Paolo Giannotti, f: Patrizia Sacchetti).

Granchietti et al. 2012). Most chalcidids such as *Dirhinus giffardii* Silvestri and pteromalids such as *Pachycrepoideus vindemiae* (Rondani) are generalist pupal idiobiont ectoparasitoids and can act as hyperparasitoids of other primary parasitoids (Wang & Messing 2004a; 2004b).

3.7.1.2.1 Australia

The first biological control project of medfly was undertaken in Western Australia in 1900s, where the neotropical larval parasitoids *Doryctobracon areolatus* (Szepligeti), *Opius bellus* Gahan, and *Ganaspis brasiliensis* Ihering were imported from Brazil and one eulophid larval parasitoid *Aceratoneuromyia indica* (Silvestri) was also brought from India, but none became established (Wharton 1989). *Aceratoneuromyia indica* was also introduced to South Africa from Western Australia in the 1900s without establishment (Wharton 1989; Ovruski et al. 2000). Later, more attempts have been made to introduce several important parasitoids, including *F. arisanus*, *F. vandenboschi* and *D. longicaudata* from Hawaii and *D. tryoni* from Eastern Australia into Western Australia, but these efforts have resulted in no documented establishment (Clarke et al. 2022).

3.7.1.2.2 Hawaiian Islands

Following the invasion of medfly in Hawaii in 1910, foreign explorations were conducted for the first time throughout the fly's aboriginal home in Africa (Silvestri 1914; Bess et al. 1961; Gilstrap & Hart 1987; Clausen 1978; Mohamed et al. 2016). A dozen parasitoids were introduced into Hawaii and five of them become established at least initially: *P. humilis*, *Coptera silvestrii* Kieffer, *D. giffardii*, *Tetrastichus giffardianus* Silvestri and *Diachasmimorpha fullaway* (Silvestri) (Table S1). Among them, *P. humilis* effectively reduced medfly abundance in several fruit crops (Bess et al. 1961). However, *P. humilis* became rare after *D. tryoni* was introduced from Australia, while *D. tryoni* contributed to the reduction of medfly populations (Bess et al. 1961; Wong & Ramadan 1987). *Diachasmimorpha tryoni* was later used successfully in augmentative release concurrently with sterile fly release to suppress medfly populations in Hawaii (Wong et al. 1991; 1992). The invasion of *B. dorsalis* led to subsequent introduction of 24 Asian opiine parasitoid species including *D. longicaudata*, *F. arisanus* and *F. vandenboschi* (Bess et al. 1961). These three species became widespread and also parasitized medfly across the Hawaiian Islands (Wong et al. 1984b; Wong & Ramadan 1987; Vargas et al. 1995). *Diachasmimorpha longicaudata* was largely replaced by *F. vandenboschi* and subsequently both *F. vandenboschi* and *D. longicaudata* declined following the establishment of *F. arisanus* (van den Bosch & Haramoto 1953; Bess et al. 1961; Stark et al. 1991). The medfly was also outcompeted by *B. dorsalis* but was still the dominant species in coffee plantations (Vargas et al. 1995). The abundance of *D. tryoni* declined sharply after *F. arisanus* became established on medfly populations, while *D. tryoni* apparently

has shifted to higher elevation where *F. arisanus* is unable to colonize (Messing & Wang 2009). *Fopius arisanus* has replaced all early or concurrently introduced larval parasitoids and accounted for 70–90% of the total parasitism of the major fruit flies throughout the Hawaiian Islands (Stark et al. 1991; Vargas et al. 1995; 2001). The success of *F. arisanus* in Hawaii may be attributed to its competitive superiority as an early-attacking parasitoid against all the larval parasitoids (Wang & Messing 2002, 2003; Wang et al. 2003). A recent analysis suggests a global pattern of the intrinsic competitive superiority of the early acting species in opiine parasitoids through physiological suppression or physical combat against other parasitoids (Wang et al. 2021). Egg-attacking fruit fly parasitoids may also pose an ecological superiority as they attack hosts when the hosts are near the fruit surface as some larval parasitoids may be unable to locate their hosts especially in large fruits (e.g., Sivinski et al. 2001; Wang et al. 2009, 2021). This has led to a resurgence of efforts recently to explore, introduce, and evaluate two African egg parasitoids *F. ceratitivorus* and *F. caudatus* for their suitability and compatibility with *F. arisanus* and other parasitoids (Wang et al. 2004; Bokonon-Ganta et al. 2005, 2007, 2019). Laboratory tests showed that *F. ceratitivorus* specifically attacks medfly (Wang et al. 2004) and poses similar competitive superiority as *F. arisanus* against larval fruit fly parasitoids (Wang et al. 2008). These new parasitoids have not yet been released in Hawaii and may have the potential to improve overall suppression of medfly in Hawaii (Kroder & Messing 2010).

Early success in Hawaii triggered the introduction of many parasitoids from Hawaii to the Mediterranean Basin and Latin America for biological control of medfly (Table S1).

3.7.1.2.3 Mediterranean basin

In the Mediterranean areas, several important species were introduced into Italy (e.g., *D. longicaudata* and *P. concolor*), Spain (e.g., *P. concolor* and *P. humilis*) and Greece (e.g., *D. giffardii*), but only *P. concolor* (obtained from Tunisia and repeatedly released since 1900s) has established mainly on the olive fruit fly *Bactrocera oleae* (Rossi) in some southern regions (Greathead & Greathead 1992; Miranda et al. 2008). Many parasitoid species, including *A. indica*, *D. longicaudata*, *D. kraussii*, *D. giffardii*, *D. tryoni*, *F. arisanus*, *F. ceratitivorus*, *P. concolor* and *P. vindemiae* have been introduced into Israel from 1960s to 2000s (Argov & Gazit 2008). Only *D. giffardii*, *P. concolor*, *F. ceratitivorus* and *D. kraussii* apparently have become established (Argov & Gazit 2008). The Asian larval parasitoid *Aganaspis daci* (Weld) (Hymenoptera: Eucolidae) has been reported parasitizing medfly in Greece (Papadopoulos & Katsoyannos 2003) and Spain (de Pedro et al. 2018). This species was introduced and released for the control of medfly in France in the 1970s, but its origin in Greece and Spain is unknown. Both field parasitism and laboratory evaluations showed the

potential of *A. daci* as a biological control agent for medfly (Papadopoulos & Katsoyannos 2003, de Pedro et al. 2018).

3.7.1.2.4 Central and Southern America

In Latin America, several parasitoids such as *D. tryoni*, *D. fullawayi* (Silvestri), *Psytalia fletcheri* (Silvestri) and *T. giffardianus* were introduced from Hawaii into Brazil in 1930s (Table S1) and only *T. giffardianus* was recovered from medfly 60 years later (Garcia & Ricalde 2012). With the northward expansion of medfly during 1950–60s, most of these major parasitoids were introduced from Hawaii to Mexico and Costa Rica and some of them were re-distributed to Argentina, Bolivia, Colombia, El Salvador, Guatemala, Nicaragua, Panama, Perú, Trinidad and Tobago, and Venezuela (Table S1). *Diachasmimorpha longicaudata* is the only introduced parasitoid established throughout Latin America (Ovruski et al. 2000). *Fopius arisanus* has established only sporadically on medfly on coffee in Costa Rica with low impact on the medflies (Wharton et al. 1981). *Fopius arisanus* appears not to adapt well to *Anastrepha* (Zenil et al. 2004; Paranhos et al. 2021). Because it does not show a diapause, lack of alternative tephritid hosts in the neotropics might have affected its establishment (Ovruski et al. 2000). Western Australia, parts of the Mediterranean areas and Central and South America seem not climatically suitable for *F. arisanus* based on a climatic model (Lane et al. 2018). In addition, *A. indica* and *P. vindemiae* also became established in parts of Latin America (Ovruski et al. 2000), though the latter species is cosmopolitan (Ovruski et al. 2004).

Diachasmimorpha longicaudata has well adapted to various *Anastrepha* and outcompeted common neotropical larval parasitoids (Miranda et al. 2015; Murillo et al. 2019; Paranhos et al. 2021). In addition, the relatively long ovipositor of *D. longicaudata* enables it to attack hosts in various sizes of fruits (Sivinski et al. 2001; Miranda et al. 2015). However, *D. longicaudata* was generally recovered in low numbers from medfly in various regions. Therefore, augmentative release of *D. longicaudata* has been applied to suppress medfly populations in coffee in Guatemala (Cancino et al. 2019), Southern Mexico (reaching up to 69% parasitism) (Montoya et al. 2005), and Peru (reaching over 50% parasitism) (Garcia et al. 2020). In Argentina, *D. longicaudata* has been mass-reared on the larvae of a temperature-sensitive lethal genetic sexing strain of medfly and released in large numbers in couple with SIT to suppress or eradicate medfly in central-eastern Argentina (Albornoz Medina et al. 2014; Sánchez et al. 2016). Post-release showed up to 75% and 50% of medfly mortality by *D. longicaudata* in figs and peaches, respectively (Suárez et al. 2019a; 2019b). The feasibility of augmentative releases of *D. tryoni*, *D. kraussii*, *F. arisanus*, *G. pelleranoi* and *Coptera haywardi* to control medfly has also been evaluated (Núñez-Campero et al. 2020). Both *D. kraussii* and *F. arisanus* showed significant suppression of medfly in field cages in Guatemala (Rendón

et al. 2006). Augmentative releases of *D. tryoni* in coffee orchards led to 84% parasitism of medfly in Guatemala (Sivinski et al. 2000). As the most abundant native parasitoid species associated with medfly in Argentina (Ovruski et al. 2004; Schliserman et al. 2003), *G. pelleranoi* can discriminate against medfly larvae previously parasitized by *D. longicaudata* and both species could be compatible for the control of medfly (Buonocore Biancheri et al. 2022).

3.7.1.2.5 Worldwide outlook

In conclusion, the biological control of medfly has achieved partial success in Hawaii and Latin America, mainly with *D. longicaudata* and *F. arisanus*. However, the majority of introduced parasitoids did not establish, especially in Western Australia and the Mediterranean Basin (Wharton 1989; Ovruski et al. 2000). The reasons behind the failures may be due to introduction of unsuitable agents in early days or agents that were not capable to adapt to local conditions, and/or to undesired interactions with other introduced parasitoids (Wharton 1989; Wang et al. 2021). Many environmental factors, such as local climatic conditions or habitat mismatching, might pose ecological constraints on the establishment of introduced parasitoids. The success of both *D. longicaudata* and *F. arisanus* stems from their competitive superiority against other parasitoids and a high adaptability of *D. longicaudata* (Wang et al. 2021).

3.7.2 Entomopathogens

The entomopathogenic activity of various viruses, bacteria, fungi, and nematodes against medfly has been documented in numerous studies, with the entomopathogenic fungi (EPF) and entomopathogenic nematodes (EPN) being the most promising. These biocontrol agents in some cases can be effectively combined with pesticides, parasitoids and predators within IPM programs (Ekesi et al. 2005; Jean-Baptiste et al. 2021).

3.7.2.1 Entomopathogenic fungi (EPFs)

Several fungal entomopathogens (EPFs), that are naturally found in agroecosystems, show positive effects against medfly. Among these, the most studied are *Beauveria bassiana* (Balsamo) Vuillemin and *Metarhizium anisopliae* (Metschnikoff) Sorokin, besides some other relevant species belonging to the same genera, i.e., *B. brongniartii* (Sacc.), *B. pseudobassiana* Rehner et Humber, *M. brunneum* (Metschnikoff) Sorokin, or other genera including *Lecanicillium*, *Purpureocillium*, *Isaria*, and *Paecilomyces* (Beris et al. 2013).

With regard to the wide variety of *Beauveria* and *Metarhizium* strains studied on medfly, albeit with all due differences and specificities, their typical mechanism of pathogenic action occurs through the following main steps: a) contact with the host and adhesion of aerial conidia on the insect body surface; b) germination of conidia under specific environmental conditions; c) penetration of the fungus

through the cuticle by a combined mechanical and enzymatic action; d) development of infection with mycelial colonization of the insect body, evading the immune system and spreading via a second type of conidia (blastoconidia) into the host hemocoel; e) emergence from the dead insect (normally mummified and covered by the mycelium), with the development of conidiophores carrying new aerial conidia (dispersion phase) (Mascarin & Jaronski 2016). It follows that the efficacy of each fungal strain of *Beauveria* and *Metarhizium* spp. against different life stages of medfly will depend on its intrinsic (genomic) characteristics and environmental conditions, according to a triangular pathogen-host-environment interaction. A plethora of bioactive compounds are normally involved in the pathogenesis. These include hydrophobins covering conidia surface and involved in the adhesion to insect cuticle, chitinases and proteases responsible for the cuticle degradation, and various secondary metabolites mostly produced inside the insect body during infection (Xiao et al. 2012; Pattemore et al. 2014).

Entomopathogenic fungal strains' diversity translates into variable virulence degrees, so that continued research and screening of new fungal isolates for their efficacy against medfly larvae have led to the identification of new protein toxins (Ortiz-Urquiza et al. 2009) involved in the mechanism of action, highlighting the importance of the microbial culture method to enhance the fungus virulence by overexpressing these proteins (Ortiz-Urquiza et al. 2013).

Besides the insecticidal potential of a specific EPF strain, environmental factors play a crucial role in pathogenicity. For instance, moisture conditions are critical to favour conidia mobility in the soil facilitating contact with pupariating larvae and puparia, and for their germination once host adhesion has occurred (Garrido-Jurado et al. 2011; Gava et al. 2021). Conidia viability is moreover affected by pH, temperature, and UV-solar radiation, which stimulates the continuous search for EPF strains with adaptations to specific environmental conditions, such as UV-resistance or suitability for drier conditions (Fernández-Bravo et al. 2017; Gava et al. 2022).

Increasing the shelf-life and mobility of aerial conidia is of considerable importance in promoting horizontal transmission of infections in epigeal field conditions (Dimbi et al. 2013). Another factor significantly affecting the success of an EPF application against the medfly is the conidia-based formulation (e.g., suspension concentrate, granular) (Ekesi et al. 2005).

Numerous studies on autochthonous EPF highlighted significant mortality of different medfly stages by contact and ingestion, reporting also sublethal effects on adult reproductive potential (Ortiz-Urquiza et al. 2010). However, in compliance with legislative frameworks on pre-market authorization of biopesticides, only few products are available to farmers.

In the face of a wide variety of studies conducted in different parts of the world, employing diverse strains and dos-

ages, mostly in the laboratory, but also under semi-field and field conditions, the following main strategies of EPF used against medfly emerge: (1) Distribution in the upper soil layer (within 7 cm depth), preferably employing granular formulations that are more persistent than aqueous or oil/aqueous suspensions, to target pupariating larvae and puparia (Ekesi et al. 2005). (2) Cover spray or protein bait applications (normally using oil-based formulations with a concentration of 10 million conidia/ml and a dosage in the order of 1–2 l/ha), leveraging the direct effect on adults or indirectly protecting fruits from female oviposition (Bedini et al. 2018; Falchi et al. 2015). (3) Conidia autodissemination by specific auto-inoculative devices containing fungal conidia and a medfly food lure, which exploits the successive horizontal transmission of EPFs in the population (Navarro-Llopis et al. 2015). This technique has also been experimentally applied in combination with SIT inoculating sterile males for a synergistic biocontrol effect (Toledo et al. 2017).

Various plant protection products based on EPFs are commercially available and approved for use against medfly in orchards. Accordingly, several field trials proved the ability of EPF-formulations to contain fruit infestations with efficacy levels comparable to chemical insecticides, although to achieve such result multiple applications are often needed in the same season (Ortu et al. 2009; Qazzaz et al. 2015).

3.7.2.2 Entomopathogenic nematodes (EPNs)

The use of EPN for biological control of medfly has been explored as early as the 1980s with studies indicating a significant potential of the nematodes in reducing medfly populations in some cases >80% (Poinar & Hislop 1981; Lindegren et al. 1990; Gazit et al. 2000). Mostly larvae and, to a lesser degree pupae, are the stages of medfly susceptible to the infective juvenile nematodes (IJs) (Gazit et al. 2000; Jean-Baptiste et al. 2021; Shaurub 2023). There have been numerous studies examining the efficacy and the potential of EPN for controlling not only medfly but also other fruit flies as well (reviewed in Shaurub 2023). Most of these studies were conducted in the laboratory, sometimes in artificial conditions that depart significantly from natural conditions (e.g., bioassays in Petri dishes or application of nematodes in media that does not approximate soil conditions). Moreover, the different experimental conditions, different strains and doses of nematodes, make the comparisons between studies very difficult, but nonetheless clearly demonstrate the potential of EPN for medfly control. Some limited field studies showed that the nematodes *Heterorhabditis baujardi* Phan, Subbotin, Nguyen & Moens LPP7 and *H. indica* IBCB n5 reduced the population of medfly larvae in Guava by >87% and 93% respectively when applied in doses of 25,000–100,000 infective juveniles (IJs)/m² of soil, whereas a Mexican strain of *Steinernema feltiae* Filipjev applied at 5×10^6 IJs/m² resulted to 86% mortality of medflies in papaya trees in Hawaii (Dolinski 2016; Minas et al. 2016; Lindegren et al. 1990).

Furthermore, both laboratory studies and limited field trials, although promising, concern species and/or strains of EPN such as *S. riobravae* Cabanillas, Raulston and Poinar, *S. yirgalemense* Mráček, Tesfamariam, Gozel, Gaugler and Adams, *H. baujardi* strain LPP7, *H. noenieputensis* Malan, Knoetze and Tiedt that are not commercially produced (Lindegren et al. 1990; Gazit et al. 2000; Minas et al. 2016; James et al. 2018; Mokrini et al. 2020). However, it has been shown that commercially produced *S. feltiae* can greatly suppress medflies in the laboratory and in the field (Karagoz et al. 2009; Kapranas et al. 2021; 2023). Even more, the same species is capable of actively searching and parasitizing medfly and other tephritid fly larvae inside fruits such as oranges, apples and apricots (Sirjani et al. 2009; Mokrini et al. 2020; Kapranas et al. 2021), thus serving as a sanitation measure off-season.

The current costs of commercially available EPN are about 0.2 €/million IJs (a price quite stable over the last years, Arne Peters personal communication), rendering repeated EPN applications for medfly control economically non-viable especially when considering other costs (labour). An alternative tested tactic using a single application of *S. feltiae* at rates of 1.5–2.5x 10⁶ IJs/m² beneath the canopy of citrus trees at the end of the season or early in season reduced medfly emergence by 65% (Kapranas et al. 2023). *Steinernema feltiae*, a widely commercially available EPN, can infect medflies and other tephritid flies at cool temperatures as low as 8°C that are representative to temperate climates (Hazir et al. 2001). Cooler autumn temperatures could improve the residual activity and therefore the efficacy of *S. feltiae* against medfly larvae in the soil and in fruits (Kapranas et al. 2021; 2023). EPN efficacy is greatly influenced by the soil characteristics such as moisture and texture. EPN mobility and infectivity of medfly larvae is decreased in extreme wet and dry conditions (Gazit et al. 2000; Rohde et al. 2010; Mokrini et al. 2020). Wetting the soil with adjuvants can increase EPN efficacy (Shapiro-Ilan et al. 2006) and remains to be tested in the case of medfly and given the great variability of cultivars and practices concerning cover management in different orchards/cultivars. Furthermore, EPN can survive better and be more infectious in well aerated soils, and therefore heavy silt or clay soils with reduced pore size and retaining high moisture, reduce their efficacy (Barbercheck & Kaya 1991; Rohde et al. 2010; Mokrini et al. 2020).

Lastly EPN can be combined with EPF, sometimes with additive or synergistic effects, as it has been shown for control of other fruit fly species (Usman et al. 2020; Wakil et al. 2022), but it remains to be demonstrated for medfly as well. Given the volume of all these studies, it is beyond doubt that EPN holds great potential as a biological control tool for medfly management. However, to fully explore this potential is essential to bring into mass production the appropriate strains/species that are quite infectious even at low dose or use off-season and/or early-season application of commercially produced EPN species. Both approaches require

extensive field trials which are still sought after. In addition, there is ongoing research on EPN formulations aiming at increasing their residual activity and infectivity and remains to be determined if they hold promise for improving the biological control of medfly with EPN.

4 Conclusions and research challenges

Overall, our literature analysis highlighted many important research challenges for sustainable medfly management. Since fruit crops are often subject to a wide range of pests and diseases, chemical control has become an essential component of production for decades. As the world's population continues to grow, the demand for fresh fruit is also expected to increase, presenting new challenges for chemical control in this industry. One of the main challenges facing chemical control in fruit crops is the development of resistance to commonly used pesticides. Overuse of these chemicals can lead to the selection of resistant populations, making control increasingly difficult over time. This can result in the need for more potent and/or toxic pesticides, which can have negative effects on both human health and the environment. To address this challenge, it is important to intensify the adoption of IPM approaches that include a range of control strategies, such as biological control, cultural practices, and the use of resistant crop varieties. Another challenge facing chemical control in fruit crops is the regulatory aspect. In many countries, strict regulations govern the use of pesticides in agriculture, including restrictions on certain active ingredients and application methods. This can limit the availability of effective chemical control options for growers and can also result in increased costs and bureaucratic hurdles. To address this challenge, it is important for growers, researchers, and regulatory agencies to work together to develop and implement sustainable pest management strategies that meet both economic and environmental goals. The future of chemical control in fruit crops will be shaped by a range of challenges, including resistance development, regulatory constraints, climate change, and health and safety concerns. Addressing these challenges will require a collaborative effort between growers, researchers, regulators, and consumers, and will likely involve a range of pest management strategies tailored to specific local conditions and goals. In this scenario, botanical pesticides are a promising alternative to synthetic pesticides in citrus crop management. While there are some challenges associated with their use, the benefits of botanical pesticides in terms of reduced impact on non-target organisms, shorter persistence, and reduced risk of pesticide resistance make them an attractive option for growers. As research in this area continues, it is likely that we will see increased use of botanical pesticides in fruit crop management in the future.

The SIT-AW-IPM approach has shown its effectiveness in the control of medfly. Knowledge on the biology, ecology, and

behavior of the target pest, as well as technological advances have made it possible to make the technique more effective and efficient. Nowadays, we have empirical evidence that the approach can be applied in eradication, suppression, containment, and prevention strategies. The advantages include a highly positive benefit:cost ratio when considering long-term effects (Enkerlin & Mumford 1997; Enkerlin 2021; Rendón & Enkerlin 2021). In the future, we can expect even a steady growth in the use of SIT-AW-IPM, especially considering the risk of new invasions, the issues connected with pesticide overuse, resistance development and non-target effects, and the growth in world demand for healthier fruits.

From a biological control perspective, future efforts should focus on entomophagous species, with special reference to parasitoid species or strains, with better inherent abilities to adapt to local climates and survive periods of low host density as well as the competitive risks of introducing parasitoids to extant species (Wang et al. 2021). On the other hand, the modern practice of classical biological control strongly emphasizes minimal non-target impacts of introduced agents, which further reduces the number of potential agents (Messing & Brodeur 2018). The two African parasitoids (*F. ceratitivorus* and *F. caudatus*) could be introduced and released into areas where *F. arisanus* does not thrive. Another larval parasitoid, *P. lounsburyi*, is also relatively host-specific to *B. oleae* but can readily attack medfly and could be a potential agent for areas where both pests have invaded (Wang et al. 2022). Future studies may also explore the potential of some indigenous parasitoids capable of attacking medfly such as *G. pelleranoi* and *C. haywardi* and augmentative biological control using these already established parasitoids. Lastly, the medfly is currently halted northward spreading in Guatemala and Mexico (Enkerlin et al. 2017) and poses a continued threat to the US. Some promising agents could be evaluated proactively to address the escalating threat of invasion and increase preparation to manage medfly in the event of the fly's invasion.

Still in the biocontrol scenario, we would like to highlight the need to develop and evaluate schemes of applying in the field commercially available EPF and EPN in conjunction with improved formulation and/or adjuvants. Further key challenges for EPF and EPN include (1) the mass rearing and field evaluation of new species and/or native EPF and EPN strains with improved intrinsic potential and adaptations to environmental conditions; (2) the development of new and more effective ways of application, increasing the chances of pathogen-host contact or increasing shelf-life of EPF conidia and EPN infective juveniles; and (3) the enhancement (protecting and creating ideal conditions) of the natural biocontrol activity of entomopathogens already present in the agroecosystem. It is also important to understand how different entomophagous insects and entomopathogens might interact antagonistically to reduce overall impacts on medfly, or synergistically to enhance medfly suppression. We emphasize a systematic approach towards the develop-

ment of biological control strategies that can stand alone or be used with other compatible control methods (e.g., SIT).

As it is explicitly stated earlier, medfly population monitoring is the cornerstone for any management project that spans from addressing invasion events (e.g. eradication or containment) to population suppression through structured IPM projects. Indeed, there is much attention on developing trapping systems, recently involving electronic systems for adult population monitoring as well. However, it seems there is still need for additional work as both abiotic and biotic factors affect efficacy and therefore seasonal performance of electronic trapping systems should be addressed (Bali et al. 2021). In addition, more research should be conducted on developing trapping strategies that should maximize efficacy at a reasonable cost. Population growth models and detailed analyses of the structure of the landscape and the orchards may contribute towards establishing more efficient trapping networks to detect and monitor low density medfly populations (see Lux 2019).

Medfly and fruit fly monitoring is expected to dramatically advance in the future by integrating the world of electronic-engineering, sensing-technology, meta-data sciences and artificial intelligence. This novel way of monitoring insect populations is still evolving, and is being integrated into IPM decision systems. Some challenges in the field of smart monitoring include its efficient integration and expansion into pest control. Smart-monitoring will become more widely used once a more effective integration between data-scientists, engineers and pest control people occurs. Another challenge for the adoption of this emerging technology is the need for a reduction in price, which at this stage is prohibitive for most growers in the world. Regarding SIT applications, the possibility of remote-sensing and integration of smart-traps able to discern between released, fluorescent, sterile medflies and wild flies, is a challenge. This aspect, which has been in the agenda for a long period of time, is now being tackled by several scientists. The ability to introduce SIT-tailored "smart-traps", into the operation of SIT-projects, will greatly increase the efficacy and management of this control strategy. Progress in the electronic trapping system is rapid, and several systems are reaching the market without proper testing that should include experimentation in different ecosystems and during several seasons. Also, more work is still required to compare the efficacy of electronic trapping systems against traditional traps.

Conceptual algorithms to support pest management of the Mediterranean fruit fly have been recently developed and tested (Sciarretta et al. 2019). Besides temporal elements, spatial components are included in these algorithms that constitute the foundation of spatial decision support pest management systems. Further efforts to incorporate population growth models into above systems should be conducted both within farms (Lux 2019) and also at a regional level to support the area wide IPM programs against the Mediterranean fruit fly.

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Table S1