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Biology, ecology and invasiveness of the Mediterranean fruit fly, *Ceratitis capitata*: a review

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With 2 figures

Abstract: The Mediterranean fruit fly (medfly), *Ceratitis capitata*, is a highly polyphagous pest that is economically important for fruit production in tropical, subtropical and temperate regions. It is considered a cosmopolitan pest due to its extreme invasiveness and has established populations in all continents except Antarctica. The medfly's broad range of host plants and distinctive biological, behavioral, and genetic traits help it easily adapt to and colonize novel environments. This review provides an overview of the specific characteristics of this species and its current distribution and invasiveness. It also outlines future challenges for medfly bioecology and invasiveness.

Keywords: medfly; biological invasion; chemical ecology; frugivorous pest; invasive species; morphology; pheromone; systematics; Tephritidae; true fruit flies

1 Introduction

The Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann) (Diptera Tephritidae), is a key frugivorous pest in many subtropical and tropical regions in the world (White & Elson-Harris 1992). Native to Sub-Saharan Africa, medfly has dispersed in almost all continents. It is a multivoltine polyphagous species that can feed on more than 300 host plants (Liquido et al. 1991; Papadopoulos et al. 2001), and it is considered one of the most important fruit pests worldwide (Boulahia-Kheder 2021). Despite a long history of outstanding research efforts to fully understand its biology and management, sustainable control of medfly is still challenging, due to its polyphagy, invasiveness, the high eradication and containment costs, and development of insecticide resistance in targeted populations (Dominiak & Daniels 2012; Szyniszewska & Tatem 2014; Pinto Dias et al. 2022; Giunti et al. 2023). In as much as a comprehensive review examining all facets of medfly bioecology is not available, herein we analyzed available knowledge on the morphology, taxonomy, biology, ecology, and genomics of the medfly, and provide an updated synthesis of its distribution and invasiveness.

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2 Taxonomy

The medfly belongs to the Afrotropical genus *Ceratitis* MacLeay. The latter comprises 100 valid species, which are native to Sub-Saharan Africa and some of the islands in the Western Indian Ocean. Only medfly, within the *Ceratitis* genus, has been introduced in other zoogeographical regions (White & Elson-Harris 1992). The genus *Ceratitis* is subdivided into six subgenera (De Meyer 2005): *Ceratitis* s.s., *Pterandrus* Bezzi, *Pardalaspis* Bezzi, *Ceratalaspis* Hancock, and the monotypic genera *Acropteromma* Bezzi and *Hoplolophomyia* Bezzi. *Ceratitis capitata* belongs to the subgenus *Ceratitis* s.s., which was revised by De Meyer (2000) and is considered to comprise eight species. The monophyly of several of these subgenera, including *Ceratitis* s.s., has been questioned and an overview of the different proposed classifications is given by Barr & McPheron (2006) and Barr & Wiegmann (2009). The consensus proposed by the latter is that *Ceratitis* s.s. is a monophyletic group, when combined with the so-called '*Pterandrus* B' group. Within this cluster some of the *Ceratitis* s.s. that were examined (i.e., *C. capitata, C. caetrata* Munro and *C. pinax* Munro) form a distinct monophyletic subcluster, except for *C. cornuta* (Bezzi), which conversely groups with some representatives of the subgenus *Pterandrus*. De Meyer (2000) and De Meyer et al. (2004) proposed that there are two lineages within *Ceratitis* s.s.: one distributed along eastern to southern Africa and a second one restricted to Madagascar and the Mascarenes. *Ceratitis capitata* belongs to the former and has probably spread from eastern Africa into other parts of the continent (Malacrida et al. 1998; Ruiz-Arce et al. 2020). An alternative hypothesis placed the origin of the species in western Africa (Gasparich et al. 1997). The closest relative of *C. capitata* is *Ceratitis caetrata* that is restricted to Kenya and recorded only a few times from a limited range of host plants (De Meyer et al. 2002). Barr et al. (2012) demonstrated that the traditional COI barcode region fails to discern *C. capitata* from *C. caetrata*, although adults can be easily morphologically differentiated, in particular the males (De Meyer 2000). The medfly does not seem to comprise cryptic species, and its worldwide population structure and phylogeography have recently been analyzed using a number of markers such as mitochondrial DNA (Ruiz-Arce et al. 2020) and microsatellite loci (Deschepper et al. 2021).

3 Morphology

3.1 Egg

The medfly eggs are small in lenght (around 1 mm) and have a smooth shiny white surface and a slim curved shape (Fig. 1), with a tubercular micropylar region (White & Elson-Harris 1992).

3.2 Larva

The medfly has three larval instars. Descriptions are usually limited to the third instar and a detailed description is given by Steck & Ekesi (2015). Medfly larvae are white colored, cylindrical with a narrow anterior side and a flattened caudal part. The dimensions vary depending on the instar and a ready to pupate third instar larva can measure from 7 to 9 mm. The ventral side presents 8 fusiform areas, and the anterior side has the typical mouth hooks (Fig. 1) (White & Elson-Harris 1992; Steck & Ekesi 2015).

Medfly larvae can be distinguished from other fruit flies by the morphological characteristics of the anterior and caudal ends (White & Elson-Harris 1992). In detail, the anterior has spiracles with tubule edge dorsally straight and 9–10 tubules ranging from a minimum of 7 to a maximum of 11. Furthermore, medfly larvae typically have 9–10 buccal carinae. The accessory plates of the oral ridges are absent which contrasts with some of the other *Ceratitis* species (Steck & Ekesi 2015). The caudal tail has two prominent subspiracular tubercles with fused papillules and the anal lobe, which can be bifid or single. Other specific features are the cephalopharyngeal skeleton presenting a large subhypostomium and the shape of the sclerotized dorsal bridge (White & Elson-Harris 1992). The pre-apical tooth can be either absent or present (Steck & Ekesi 2015; Balmès & Mouttet 2017). From an anatomical point of view, medfly larvae possess a complex triphasic heartbeat with a characteristic flow (i.e.,

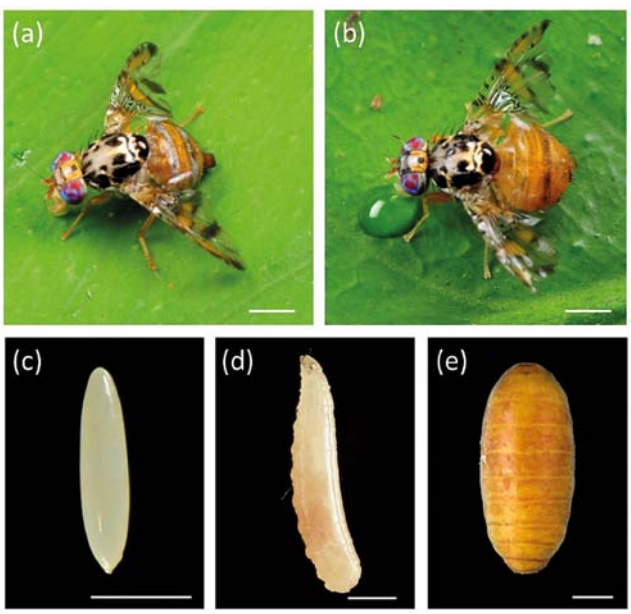

Fig. 1. Developmental stages of *Ceratitis capitata*: **(a)** female, **(b)** male, **(c)** egg, **(d)** third instar larva, and **(e)** puparium; the scale bar is 1 mm in all images, except for **(c)**, in which it corresponds to quarter mm (photo credit: P. Giannotti).

77 bmp heartbeat rate) from the abdomen to the head, which has been recently described using in vivo non-destructive echoentomography (Ricciardi et al. 2022).

3.3 Pupa

The pupa is enclosed by a puparium formed by the hardened exoskeleton of the last larval stage. This puparium is 4–4.3 mm long, dark red-brownish, cylindrical, barrel-like in shape, with smooth ends (Fig. 1) (White & Elson-Harris 1992).

3.4 Adult

Adults are usually 3–5 mm long and has the main characteristics found in all representatives of the genus *Ceratitis*: i.e. hyaline wings with yellow-brown to dark brown bandings comprised of a discal band, anterior apical band and subapical band, and a series of streaks and spots in the basal part; a wing cell bcu with sinusoid apex; scutellar pattern with three apical spots (separate or merged), and abdomen with bands on tergites 2 and 4. Also the male characteristics of the subgenus *Ceratitis* s.s. are present: i.e. the presence of a modified orbital bristle, and the fore femur posteriorly with a dense bush of long setae. They can be readily distinguished from other *Ceratitis* s.s. by thoracic patterns, and the shape of the modified orbital bristle (Fig. 1). The thorax coloration is creamy white to yellow with a distinctive pattern of black spots, The orbital bristle is black with a diamond-shaped apex. Adults have characteristic yellow wing patterns, a black scutellum on the apical side, and females possess a telescopic ovipositor that can extend up to 1.2 mm in length (White & Elson-Harris 1992; De Meyer 2000) (Fig. 1). Anatomical differences in wing shape have been reported depending on sex, i.e. with male wings wider and shorter in comparison to female ones (Siomava et al. 2016), as well as depending on the host plant from which the flies were reared (Pieterse et al. 2017). Sexual dimorphism of internal anatomy comprises the distinct size of specific glomeruli in the antennal lobes and the brain structures firstly processing the olfactory cues (Solari et al. 2016).

Like other fruit flies, medfly adults possess sucking and sponging mouthparts, consisting of a labellum with pseudotracheae in its inner surface, which convey food to the oral opening. The oral opening is never exposed during feeding, precluding the ingestion of food particles larger than the micropores in the pseudotracheae (i.e., 0.5 μm) (Coronado-Gonzalez et al. 2008). Furthermore, the pseudotracheae of medfly show sharp protrusions, which are probable ancestral organs used to abrade the food surface (Coronado-Gonzalez et al. 2008). Adult medflies possess strong stomodeal muscles covering the crop, probably playing a role in the typical feeding behavior of flies, which regurgitate their crop content in small droplets and then re-ingest it to eliminate the water excess from the diet (Caetano et al. 2017). The tarsal sensilla, of importance in taste and mechanoreception, have been described by Loy et al. (2016).

4 Biology

Because of its significance as a major pest and model species in aging research, there is an enormous number of publications addressing various aspects of the biology of medfly, including life history, demography and age-related behavioral and physiological traits, reproduction patterns and behavior, sexual selection, reproductive physiology and response to abiotic stresses. Its wide distribution and invasion dynamics over the last two centuries resulted in great diversity of geographically isolated populations, providing a fertile ground for studying divergence of biological traits as a consequence of its plastic and adaptive aspects.

4.1 Effect of host on life history traits and population growth rates

The medfly is a multivoltine species, with over 300 host plants (Liquido et al. 1991; Papadopoulos et al. 2001) (Fig. 2). The development in different host fruit and under variable controlled laboratory conditions generated a large number of phenotypes (Krainacker et al. 1987). The success of medfly as a major frugivorous generalist relies on its phenotypic plasticity in response to characteristics of different hosts to maintain relatively high intrinsic population growth rates. Pre-adult mortality depends on the host fruit and often exceeds 50% (Carey 1984; Krainacker et al. 1987; Papachristos et al. 2008). Larvae suffer higher mortality rate compared to pupae. Longevity and reproduction of emerging adults may also vary due to the breeding host of larvae. For example, female longevity and lifetime net fecundity rates range from approximately 38 to 62 days and from 155 to 456 eggs per female, respectively, for adults obtained from different citrus fruits in laboratory conditions (Papachristos & Papadopoulos 2009). The cultivar of host fruit, such as apples, may affect the performance of immatures and adults (Papadopoulos & Katsoyannos 2002).

Considering population growth, apples are not a preferred hosts for medfly (Papadopoulos & Katsoyannos 2002). However, these are important hosts for overwintering larvae in temperate Europe. Nutritional, chemical and physical properties of fruits can regulate the development and survival of larvae, and the adult performance. Extension of the larval stage due to the physical and chemical properties of apple fruit, combined with low winter temperatures, facilitates overwintering of medfly in cool temperate areas, such as northern Greece (Papadopoulos et al. 1996).

Host fruit used for larvae breeding affects various aspects of the demography of adults. For example, longevity and fecundity of females obtained from the sweet orange cultivar

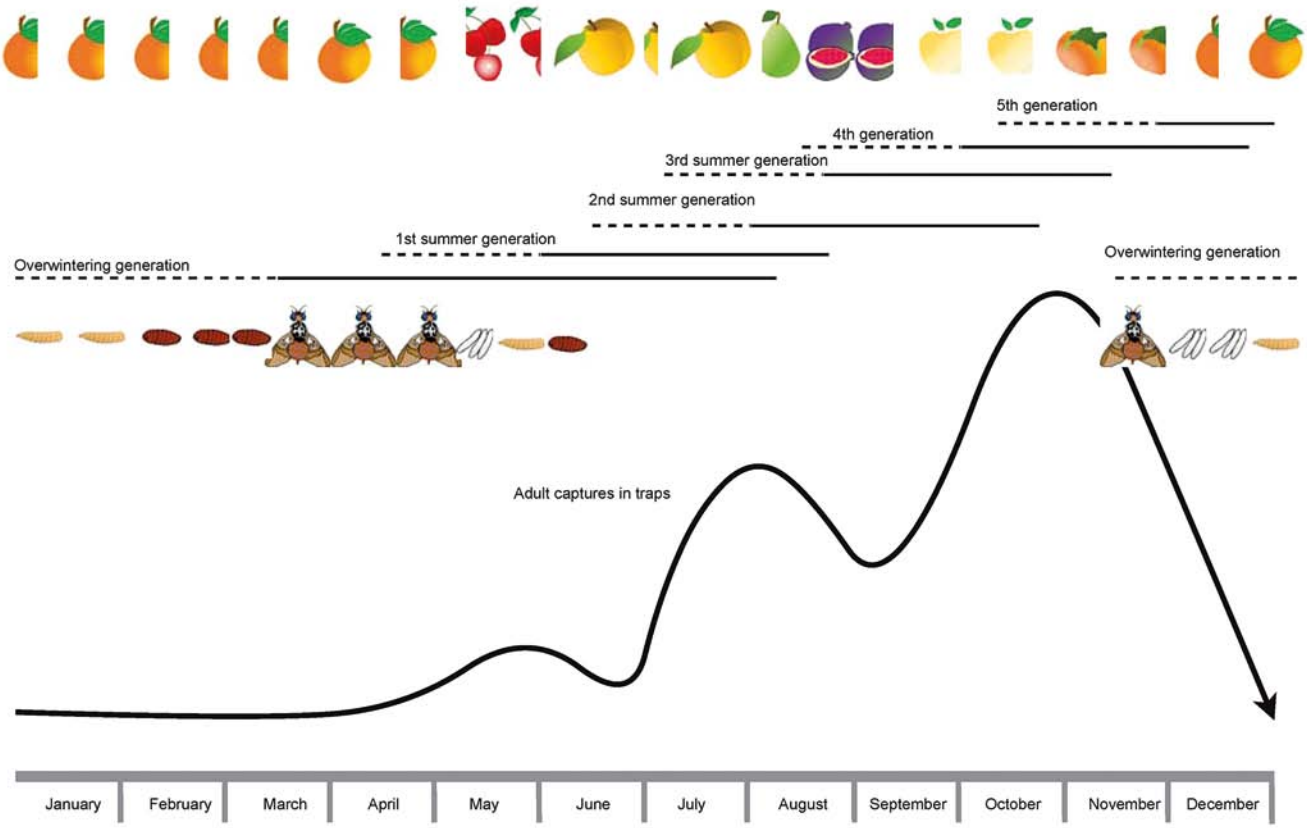

Fig. 2. Seasonal patterns of the life cycle of *C. capitata* in Mediterranean climates. The temporal ripening seasons of the main hosts, that facilitate successive and overlapping population growth, are given. Straight lines stand for the different overlapping generations.

"Artas" were higher than those obtained from bitter oranges under controlled laboratory conditions (Papachristos & Papadopoulos 2009). The same study also demonstrated that adults emerging from the bitter oranges laid slightly lower number of eggs in neutral artificial substrates (pre-punctured plastic domes) compared to intact fruit, while those obtained from the sweet oranges "Artas" produced approximately five times fewer eggs in fruits compared to plastic domes. Similar trends have been also reported for adult longevity (Papachristos & Papadopoulos 2009). The plastic response of medfly to different host fruit generates a long list of phenotypes (Krainacker et al. 1987) and results in variable population growth rates that assure persistence in variable environmental conditions and explain both outbreaks and endemic population configurations.

The quality and the quantity of proteins and carbohydrates in larval diet regulate survival and development of immatures as well as the size of individuals (Nash & Chapman 2014). Larval nutrition may significantly affect the performances of adults, including longevity and sexual performance (Yuval et al. 1998; Leftwich et al. 2017). These results highlight the high adaptive plasticity of medfly to hosts with different nutritional quality and explain the colonization success of medfly, although obtained under controlled laboratory conditions with defined artificial diets.

4.2 Life history evolution

Although tropical in origin, from the ancestral area of east Sub-Saharan Africa (Malacrida et al. 1998; De Meyer et al. 2004; Ruiz-Arce et al. 2020), medfly has dispersed, over the last two centuries, in all African countries and invaded all continents (except Antarctica), becoming established in a huge variety of habitats. Genetic drift and natural selection, operating individually, sequentially or even simultaneously, have shaped life histories of geographically distant medfly populations (Diamantidis et al. 2008a). Following a common garden experimental approach with medfly populations originating from Kenya (ancestral), Greece, Portugal (Madeira), Guatemala, Brazil and USA (Hawaii), Diamantidis et al. (2009) revealed large differences in their life history traits, including longevity of males and females, reproductive periods, age-specific and lifetime oviposition rates. Female and male longevity ranged from approximately 48 to 75 and 68 to

122 days for the different populations, respectively, and the flies obtained from Guatemala were the shortest-lived ones. Differences in lifetime fecundity were less pronounced, but age-specific patterns greatly differed. Seasonal and temporal patterns of host fruit resources as well as climatic particularities in the newly invaded areas are among the factors that contribute to the observed differences. The evolutionary and invasion history of medfly might regulate the performance in captivity and hence breeding in a novel environment, although the ancestral Kenyan population expresses a stable profile as far as longevity and reproduction in captivity (Diamantidis et al. 2011).

Artificial selection experiments conducted under laboratory conditions demonstrated the adaptability of medfly larvae to diets with different nutritional values and, at the same time, the adult plasticity concerning behavioral traits (Leftwich et al. 2017).

4.3 Medfly as a demographic model of aging and gerontology

Since the early 90s, medfly has been recognized as model species for demographic and aging research, revealing significant biological patterns. Carey and coworkers (Carey et al. 1992) assembled life tables of millions of adult medflies and demonstrated that age-specific mortality rates do not follow an exponential increase in relation to aging, slowing down or becoming constant at older ages. This finding questioned several central concepts in aging research and gerontology. In addition, aging in the medfly is characterized by two distinct demographic/physiological states: a waiting mode associated with low mortality and reproduction, and a reproductive one that begins with low mortality while it accelerates as reproduction progresses (Carey et al. 1998). Thus, female medflies respond plastically to resource availability (proteinaceous food) regulating reproduction and aging accordingly.

In most animal species, the longevity of females is higher than males. However, this is not the case in medfly, with males outliving females in most laboratory experimental trials. Gender-related mortality patterns are context-dependent, and can change in relation to aging; for example, mortality in females compared to that of males is higher at the beginning of adult life and lower in more advanced ages (Carey et al. 1995). The linkage between reproduction and longevity has been also addressed for both sexes and the respective tradeoffs have been identified and discussed (Müller et al. 2009; Papadopoulos et al. 2010).

Age-specific patterns of the expression of innate behaviors and their relationship to life span and health have been studied both in male and female medflies (Papadopoulos et al. 2002, 2011). The supine behavior (temporarily upside-down orientation) of males is directly related to mortality risk and can be used as a biomarker of aging and health, broadening the use of medfly as model species in biodemographic research (Papadopoulos et al. 2002).

4.4 Response to abiotic stress

The response to abiotic stress has been extensively studied mainly under controlled conditions to understand and predict the limits of the geographical dispersion of medfly in the frameworks of its invasion potential. Medfly is a tropical insect that has invaded many temperate areas, expressing a remarkable ability to cope with harsh winter conditions, whilst it can thrive and persist in extremely hot and dry deserting environments, such as southern Israel and oases in Tunisia (Carey et al. 2014 and references therein). It is characterized as a chill-susceptible insect, expressing a Supercooling Points (SCP) much lower than subfreezing temperatures causing death (Nyamukondiwa et al. 2013). The SCP differs among different developmental stages and geographically isolated populations and is generally lower than −16 ºC (Papadogiorgou et al. 2023). Exposure for a few hours at chilling temperatures kills all developmental stages of the medfly in laboratory trials (Nyamukondiwa & Terblanche 2010). The critical thermal limits, both maximum and minimum, as well as chill coma recovery times, have been studied in medfly populations of the southern and northern hemispheres revealing high variability among populations. However, it does not follow a linear latitudinal trend (Weldon et al. 2018; Moraiti et al. 2022). The most southern and northern populations considered in the previous study (Yotvata, Israel and Vienna, Austria) expressed the longest chill coma recovery time following exposure to 0 ºC. Thus, it seems that there are high levels of local adaptation that regulate the chill coma recovery time, which is an important metric to understand survival of adults in cold conditions (Weldon et al. 2011; Pujol-Lereis et al. 2016). Differences among populations in SCP and thermal tolerance has been also demonstrated for populations from the northern hemisphere (Papadogiorgou et al. 2023). Plastic response to thermal acclimation or hardening generates phenotypes that tolerate exposure to low temperatures.

In addition to response to thermal stress, there is a substantial amount of information that has been recently generated regarding the desiccation and starvation resistance of adult medflies. Similar to thermal response, high among-populations variability in time to death following hydric and starvation stress has been found for adults of several South African populations (Weldon et al. 2018). Thermal acclimation affects both response to desiccation and starvation in a population-specific manner also in populations originating from the northern hemisphere (Papadopoulos NTP, unpublished).

4.5 Symbiotic bacteria

The multidimensional contribution of symbiotic bacteria in several biological processes of insects, including medfly, is currently well appreciated. The nitrogen-fixing bacteria of the Enterobacteriaceae family dominate the gut of the medfly and may contribute to an equivalent of 6 mg of protein per day, approximately 1/3 of the protein consumed by adult females

(Behar et al. 2005). Symbiotic bacteria are maternally and vertically transmitted to eggs and introduced to fruit during oviposition. Symbiotic bacteria communities (e.g. *Klebsiella oxytoca* and *Pectobacterium cypripedii*) of medflies express pectinolytic activities, contributing to fruit decay and facilitating the development of the young larvae (Behar et al. 2008). Hence, as it suggested by Behar and colleagues, medfly "… larvae receive from their mother a 'survival pack' of pectinolytic and nitrogen-fixing Enterobacteriaceae that are amplified by the host fruit and subsequently maintained throughout the fly's life". The gut bacteria affect the reproductive success of adults and have been considered as a tool to increase the performance of sterile males in SIT programs (Ben-Yosef et al. 2008; Gavriel et al. 2011; Augustinos et al. 2015; Kyritsis et al. 2019). Recently, it was demonstrated that gut bacteria regulate the foraging behavior of medfly larvae which can be attracted to commensal bacteria and avoid putative pathogens (Sivakala et al. 2022).

5 Ecology

5.1 Landscape ecology

The observed population spatio-temporal patterns of a species in a given time and geographic-space are the synthesis of the ecological processes occurring at the organismal and population levels in a specific period and landscape. The ecological and physiological mechanisms operating at the individual level and expressed in a patchy environment produce ecological phenomena that can be observed at the population level of the species, and are sensitive to the effects of the environmental spatial variation (Wiens et al. 1993). The medfly lays eggs in fruits that are suitable for larvae to develop, pupates in the soil, and forages for nutritional resources, mates and refuges as adults. All medfly stages are also prone to be "attacked" by other organisms, serving as a nutritional resource for other species in the habitat. The aggregated interaction of individual medflies to the distribution in space and time of all these environmental factors, as well as of climatic factors affecting the rate of development of the individual insect (i.e., temperature and humidity), will result in population patterns on the landscape that can be partially measured and tracked.

Studies on the spatio-temporal patterns of medfly populations have been focused on adults using captures in lured traps. It seems that larval-host availability and suitability, as well as temperature, regulate spatial and temporal dynamics of populations. Similarly, agronomic practices are also perceived as important drivers of medfly trapping patterns. In temperate regions with cold winter, deciduous fruit hosts prevail and medfly population patterns, as detected by trapping, are rather low to moderate during summer and peak in autumn. In a study conducted near Jerusalem, Israel, in the 1990s, Israely et al. (1997) described a temporal pattern of male medflies (trapped with trimedlure lured traps) with three main waves, each with a larger amplitude than the preceding, that extend from the spring to the autumn. Medfly captures decline towards the winter, and completely cease from December to April. This temporal pattern and disappearance of males in traps coincided with the drastic drop of average air temperature to less than 10°C, which is common during winter months at these latitudes and elevations (ca. 700 m above sea level). Male medflies started to be trapped again when average temperatures increased above 15°C (Israely et al. 1997). Similar population patterns have been described in northern Greece (Papadopoulos et al. 2001), and Chios island (in eastern central Greece) (Katsoyannos et al. 1998). Conversely, in the coastal areas of Israel, where fall and winter temperatures are on average above 15°C, medfly males continue to be captured at very low number throughout winter and spring in citrus orchards (Krasnov et al. 2019). In tropical warmer regions, medfly trapping continues throughout the year and the levels of trapping are mainly driven by nearby host phenology and precipitation patterns (e.g., Hentze 1993). By using machine learning algorithms (Random Forest), Bekker et al. (2019) demonstrated that the main environmental factors explaining medfly spatio-temporal patterns in temperate Southern Africa were precipitation (inversely related) and minimal and maximal temperatures. Papadopoulos et al. (2003) also characterized the effects of the sporadic availability of suitable host upon adult medfly trapping. In their study, they showed how a mosaic of mixed host-fruit in a relatively small orchard affects male and female medflies captures: males generally showed a more random dispersion in all sectors of the mixed orchard, while females were aggregated in areas with ripe or ripening fruit. Sciarretta et al. (2018) reported a similar differential spatial pattern in a mixed deciduous orchard in Central Italy. However, while gravid females did not aggregate at the same time in the same locations as males, unmated females aggregated with males (Sciarretta et al. 2018). At a larger geographic scale (several square km), Israely et al. (1997) showed that trapping was related to the presence of host fruit suitable for egg-laying and to the availability of nutritional resources for adults, such as honey-dew from aphids in non-host orchards like English walnut (*Juglans regia*).

The spatial patterns of medfly male trapping in this large heterogeneous landscape (with commercial fruit orchards, residential areas and unplanted bare areas) seems to be related to agronomic practices. Male flies aggregated during the commercial production season in the "safe" residential home-gardens, where pesticides are not used (Israely et al. 1997; unpublished results). This effect of human activities (e.g., release of sterile flies and pesticide use) as a driver of medfly distribution seems to be more important under certain circumstances than temperature. Less wild adults were trapped in SIT (Sterile Insect Technique)-treated areas than

in the non-SIT-treated ones, regardless of elevation and temperatures in the coffee growing regions of Guatemala and Southern Mexico (Midgarden et al. 2014).

Few studies have investigated the distribution patterns of medfly larvae and pupae. Most of the studies dealing with immatures (i.e., larvae) correlate abundance and dispersion mainly to season, fruit receptivity and susceptibility (i.e., the period of time, or date, at which a fruit becomes susceptible to egg-laying and larval development, or the receptivity of a fruit species or variety to medfly larval development). For example, Papadopoulos et al. (1996) demonstrated that medfly larvae develop at a slow rate during the cold winter months in late ripening apple cultivars in Greece, allowing the local medfly population to overcome the winter. This same conclusion was reached for medfly populations overwintering in Western Australia (Rahman & Broughton 2019). Nestel et al. (2004) studied the medfly larval-damage distribution in a heterogeneous citrus-growing landscape and found that the spatial distribution of infested fruit was associated with citrus variety and their susceptibility, and with the distance from residential home gardens. This last observation was also confirmed by Krasnov et al. (2019), strengthening the importance of the growing interaction that exists between urban areas and agricultural settings, and the relevance of this interaction in the medfly population dynamics, endurance and dissemination into new areas.

5.2 Behavioral ecology: sexual, chemical and oviposition ecology

The medfly expansion into a wide diversity of new areas worldwide over the last few centuries led the species to encounter a variety of environmental conditions. In different ecosystems, abiotic factors such as temperature, relative humidity and light intensity, as well as biotic parameters, including vegetation features and distribution and predation pressure, may have produced shifts in natural and sexual selection, thus affecting the evolution of the mating system (Thornhill & Alcock 1983). On this basis, life history traits such as those related to reproductive behavior, including male signaling activity, may have evolved differently within the species' geographical range (Diamantidis et al. 2008b), affecting mating strategy and remating frequencies. For instance, Diamantidis et al. (2008b) detected significant differences in male signaling behavior among four medfly populations from Greece, Portugal, Kenya and Brazil. Variations were reported both in terms of daily rhythm and quantity of sexual signaling in response to adult diet. Similarly, the progress of sexual maturity (measured by the mean number of males involved in sexual signaling) was different among the considered populations (Diamantidis et al. 2008b).

Sexual signaling plays a major role in the fitness of medfly males and is directly related to mating success (Whittier et al. 1994; Shelly 2000). The emission of a volatile pheromone by males is a key step in a complex mating behavior, which is based on arboreal leks (Prokopy & Hendrichs 1979; Arita & Kaneshiro 1985; Whittier et al. 1992). Males aggregate on the undersurface of leaves of host trees and perform sexual signaling, which comprises the emission of a complex mixture of volatile-chemicals attractive to females (Arita & Kaneshiro 1986; Heath et al. 2000). The pheromone blend includes major, minor and trace compounds and the medfly females display a different response to mixtures of the major pheromone components than to the complete blend (Light et al. 1999). In the last five decades, several studies contributed to the characterization of the medfly pheromone by sampling the headspace of calling males, and 71 chemicals have been identified in the medfly male pheromone blend, with prenol lipids being the most represented class (Scolari et al. 2021a). In particular, (*E,E*)-α-farnesene, together with the fatty acyls geranyl acetate, ethyl (*E*)-3-octenoate, and 2-ethylhexanoic acid, are regarded as the main components of the pheromone blend in this species (Alfaro et al. 2011). The biological role of such male-emitted compounds has been studied both at the antennal and behavioral level. Indeed, gas chromatography coupled to electroantennographic detection (GC-EAD) analyses have been performed on male (Vanickova et al. 2012; Cossè et al. 1995), but also female emissions (Siciliano et al. 2014a) to identify "antennally-active" chemicals. Behavioral assays further proved the role of a few compounds in the biology of the species, revealing that synthetic blends of three male pheromone compounds (i.e., ethyl (*E*)-oct-3-enoate, geranyl acetate and (*E,E*)-α-farnesene) (Heath et al. 1991), and of the five most abundant male-emitted chemicals (Jang et al. 1994), are attractive to females. These findings greatly contributed to applied research studies aimed at improving the current strategies for medfly trapping in the field (see Scolari et al. 2021a for a review). A thorough evaluation of the differences in male signaling levels, as well as in antennal sensitivity, is essential not only for the abovementioned applied purposes, but also to achieve a wider knowledge of the medfly adaptation to different environments.

In these regards, qualitative and quantitative differences have been detected between wild populations of the medfly and laboratory strains in terms of the composition of the male volatile pheromone blend (Vanickova et al. 2012). In this study the pheromone composition of males from a laboratory colony and two wild populations originating from different host plants (apple and fig) collected in Greece during August–September 2008 was compared. Their results showed that laboratory males produce more pheromone than their wild counterparts, probably due to the higher nutritional levels of laboratory-reared flies. Moreover, interpopulation differences in female antennal sensitivity to the major pheromone component (*E,E*)-a-farnesene were also observed (Vanickova et al. 2012).

Within a lek, only a small proportion of males accounts for most of the matings (Whittier et al. 1994), with a posi-

tive correlation between sexual calling propensity and male mating success (Whittier et al. 1994; Shelly 2000, 2018). In addition to high sexual signaling, enhanced male sexual performance is also associated with increased lek participation, higher mating success, longer mating duration and inhibition of female remating (see Kyritsis et al. 2022 for a review). From an evolutionary perspective, the influence on female remating in the field may affect sperm competition and use, with an impact on gene flow and genetic diversity (Bloem et al. 1993; Bonizzoni et al. 2006).

Female multiple-mating behavior in laboratory conditions and field cage experiments has been widely reported since the '70s in the medfly (Nakagawa et al. 1971; McInnis et al. 2002; Vera et al. 2002, 2003; Shelly et al. 2004; Kraaijeveld & Chapman 2004; Gavriel et al. 2009; Bertin et al. 2010; Leftwich et al. 2014; Scolari et al. 2014; Abraham et al. 2021; Pogue et al. 2022), although these studies were performed using flies from laboratory strains, either wild-type, transgenic, or genetic sexing strains, often reared in massive conditions and after irradiation. Only in 2002 samples collected in the field were used to determine the level of multiple-mating, proving that remating also occurs in natural conditions (Bonizzoni et al. 2002). This study used microsatellite markers to compare the genotypes of wild females and their offspring (obtained under laboratory conditions), allowing to estimate a remating frequency ranging from 3.8 to 21%. Remating was detected early in the season, when the size of the population was low and potential mates were few. Afterwards, Kraaijeveld et al. (2005) confirmed that remating in wild medfly females captured in Chios, Greece ranges from 4 to 28% during the fruiting season. Polyandry in different wild populations was then estimated by comparing remating levels in populations from Chios, Greece and Rehovot, Israel, where slightly different climatic patterns occur (Bonizzoni et al. 2006). Differences in remating frequencies (5.5% in Chios and 50% in Rehovot) and paternity skew suggest that the observed remating rates are the effect of distinct genetic backgrounds, as well as of diverse climatic conditions affecting the seasonal fluctuations of the two populations.

Due to the intrinsic difficulty of collecting reproductive data from medfly individuals under natural conditions, few studies are currently available about reproductive parameters in the field. A good example is the study by Kouloussis et al. (2011), who collected medfly females in Chios, Greece during two field seasons and then monitored oviposition patterns in the laboratory. Using this approach, the authors managed to compare reproductive rates and found differences in oviposition and captive lifespan both within- and between-seasons. Apparently, reproductive maturity of adult medflies may vary considerably in the wild, being longer in cooler periods of the year compared to warmer ones and depending also on breeding hosts (Krainacker et al. 1987; Papadopoulos et al. 1996). Under optimal laboratory conditions (25 ºC), progress of female ovarian maturity and mating follow similar patterns (Papadopoulos et al. 2002). It takes almost two weeks for all females, obtained from filed infested fruit, to reach ovarian maturity, become inseminated and initiated egg-laying. Pre-oviposition period is much shorter for laboratory adapted populations because of selection for early breeding under crowded conditions (Bravo & Zucoloto 1998).

Selection of oviposition sites may be challenging for a highly polyphagous species such as medfly and may involve chemical and physical stimuli. Female medfly lay eggs in ripe or ripening fruit following a sequence of behavioral steps defining the preoviposition behavior (Levinson et al. 2003; Papachristos & Papadopoulos 2009). Fruit odor and color are both involved in the selection of the oviposition sites. As recently shown, fruit odor, including essential oils, attracts gravid females and stimulates oviposition in medfly (Antonatos et al. 2021, 2023). Females may lay eggs in existing oviposition holes or other injuries on the fruit and the clutch size is adjusted by females depending on fruit physical and chemical properties (Papaj et al. 1989). Furthermore, an oviposition marking pheromone is applied on the fruit following completion of oviposition (Arredondo & Díaz-Fleischer 2006).

5.3 Genomics

The medfly was one of the 30 arthropod species sequenced in the pilot project for the i5K 5,000 arthropod genomes sequencing initiative at the Baylor College of Medicine Human Genome Sequencing Center. In this initial work, genomic DNA was isolated from embryos of the well-established laboratory strain Ispra, reared at the University of Pavia (Italy) since 1979, and without additional inbreeding to increase homozygosity. This first sequencing was based on a Roche 454 approach and resulted in a low contiguity of the assembly. To reduce the heterozygosity most likely responsible for such a weak initial assembly, a second attempt using the Illumina HiSeq2000 platform was initiated and resulted in a high-quality genome that was published in 2016 (Papanicolaou et al. 2016). In this second project, DNA derived from an individual offspring of sibling matings after 12–20 generations was used. This strategy increased the contig N50 (from 3.1 Kb to 45.8 Kb) and scaffold N50 (from 29.4 Kb to 4.1 Mb) compared to the previous assembly. Moreover, the automated structural annotations were complemented by RNA-Seq data that allowed a joint manual annotation effort by 20 research groups. This resulted in the production of both extensive high-quality genome resources for this model species as well as of an established protocol that served as a reference for the subsequent genome sequencing initiatives for, but not limited to, all species in the i5k initiative.

After removal of contaminant bacterial sequences, the new assembly resulted in a final genome size of 479.1 Mb, thus being slightly smaller than previous estimates based on qPCR assays (591 Mb) (Tsoumani & Mathiopoulos

2012). This difference can be explained in light of the difficulties of assembling highly repetitive heterochromatic regions. A total of 14,547 genes were identified and 23,075 CDSs following annotation. Comparative genomics analysis involving medfly, *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) and *Musca domestica* L. (Diptera: Muscidae) genomes evidenced the presence of expansions in gene families potentially related to medfly host adaptation and invasive ability. Indeed, similarly to *Drosophila* and differently from *Musca*, the medfly genome showed expansions in the ionotropic and taste receptor gene families and in pheromone attractant receptors. Moreover, the higher number of cytochrome P450 and immunity genes with respect to *Drosophila* may be indicative of the medfly cosmopolitan distribution and relevance as a pest. Ceratotoxin genes, previously found to encode antibacterial peptides expressed in the medfly female accessory glands (Rosetto et al. 2003), were confirmed to be medfly-specific, and they may contribute to protect the eggs deposited in different substrates and environments.

The medfly is so far the insect species with the highest number of aquaporin genes. Aquaporins are involved in the formation of channels facilitating water transport across cell membranes and, in insects, are essential for water management in stress conditions, including drought and cold (Campbell et al. 2008). The aquaporin gene expansion in the medfly may be related to the success of this species in exploiting a wide range of food resources and surviving in new, potentially hostile, environments.

Such interesting findings stimulated further research in the field of functional genomics, contributing to expanding the knowledge achieved by studies in the pre-genome era that targeted different developmental, behavioral and reproductive traits using gene expression and protein analyses (Gomulski et al. 2008, 2012; Gabrieli et al. 2010; Scolari et al. 2012; Calla et al. 2014; Salvemini et al. 2014; San Andrés et al. 2013; Siciliano et al. 2014b). The availability of the reference genome sequence, coupled with newly generated transcriptomic resources, favored the characterization of the medfly RNA virome and viral sRNA profile, which is of relevance for medfly fitness in a mass-rearing context (Hernández-Pelegrín et al. 2022). A recent study analyzed Spanish medfly populations distributed in a SIT-target area since 2007 to identify the presence of Vienna GSS genetic markers and introgression events in wild populations (Sancho et al. 2021). In addition to available nuclear and mitochondrial Vienna GSS genetic markers (Gasparich et al. 1995; Spanos et al. 2000; San Andrés et al. 2007; Sim et al. 2017), in this research novel nuclear polymorphisms were used to assess the presence Vienna GSS genetic markers in wild medfly individuals. The novel nuclear markers were selected based on RNA-Seq analysis, which could be mapped to the medfly reference genome, amplification and Sanger sequencing. This study showed the presence of Vienna GSS sequences in the field, stimulating further studies to validate the presence of introgression events, with relevance to the successful application of the SIT technology.

While the functional annotation of the medfly reference genome requires further improvement (Nash et al. 2019), this resource is fundamental to investigate processes such as the molecular stress response to heat and cold (Anantanawat et al. 2020, 2022), or to process restriction site-associated DNA sequencing (RADseq) data, which were recently used to investigate genomic structure and phylogeographic history of medfly populations worldwide, tracing potential links between invasion routes and the microbiota (Arias et al. 2022). The medfly reference genome was also used in a study aimed at investigating the phylogenetic relationships within the *Ceratitis* FARQ complex (previously known as FAR complex) and between the four *Ceratitis* subgenera using mitogenome and genome-wide SNPs (Zhang et al. 2021). This study further contributed to resolving the FARQ taxa and detected gene flow from *C. quilici* to *C. fasciventris*, providing evidence of introgression events in the complex.

Recently, long-read PacBio sequencing was used to develop a male genome assembly from the *Fam18* medfly strain (Meccariello et al. 2019). Through the integration of this resource with i) analysis of transcripts in the 4 to 8 hours after egg laying (i.e. when sex determination is first established in the males), ii) production of an XX-only embryo RNA-Seq dataset, and iii) comparative analysis among tephritid species, *Maleness-on-the-Y* (*MoY*), a Y-linked gene determining the male sex in the medfly and in several other tephritids, was identified. This study sheds new light on the primary signal of the sex determination cascade, paving the way to the development of novel control strategies against major agricultural pests belonging to the Tephritidae family.

Moreover, a re-assembly of the medfly genome obtained with PacBio and Hi-C data was instrumental to identify and functionally characterize mutations responsible for the white pupae phenotype, which is currently used to remove females in a selective manner in genetic sexing strains before release (Ward et al. 2021). This genome assembly was also used to begin characterizing the origin and structure of X-linked repeat sequences that, when targeted with components of CRISPR (a genome engineering approach)- gRNAs and Cas9, lead to sex ratio distortion towards males, with promising perspectives for the development of alternative methods of medfly control (Meccariello et al. 2021).

6 Distribution and invasiveness

6.1 The current scenario

Because of its extreme invasiveness, the medfly is currently exhibiting a cosmopolitan distribution, except for Antarctica. Established populations exist in West Australia, Asia (Middle and near East), whole of Africa, Southern Europe, most of South America, and islands of the Pacific, Indian and

Atlantic Ocean. The species is still detected in South Mexico (e.g. Chiapas) and mainland United States of America (e.g. California), despite the costly and long-lasting eradication campaign that has operated for decades. Several biological traits can explain the invasion success of medfly, including its capacity to adapt to new habitats, to respond plastically to environmental and nutritional challenges, to express a wide range of phenotypes, and to exploit several hosts including some that are marginal for its survival and development.

Older and recent studies on the structure of global and regional populations identify the sub-Saharan Africa and, more specifically, Kenya as the ancestral area of the medfly diversification (Bonizzoni et al. 2004; Malacrida et al. 2007; Ruiz-Arce et al. 2020; Deschepper et al. 2021). Within Africa, dispersion seems to be more complicated, involving range expansion and long-distance trading and travel in the historic and contemporary times. For example, the genetic relatedness of the South African populations with those of Western Africa may be linked to long-distance trading activities (Deschepper et al. 2021). Invasion of the Indian Ocean islands (i.e. Madagascar, Reunion and Mauritius) seems to involve multiple arrival and/or establishment events from African and Mediterranean origin. Colonization of Europe and Mediterranean countries has been accomplished either through western Africa, first to the Iberian Peninsula (first record in 1842) and then eastwards, or through the Nile valley followed by a westward expansion (Bonizzoni et al. 2004; Malacrida et al. 2007). A secondary invasion event from South America to Portugal (i.e. Madeira island) have been also supported by recent genetic analyses (Deschepper et al. 2021). Medfly invasion of Americas is quite complicated and involves links between Central and South American populations and considerable gene flow between these two regions and within South America. Genetic relatedness between Brazilian, Guatemalan and East Mediterranean populations suggests a European origin for both central and south America (Deschepper et al. 2021). South America seems to be the source of the colonization of Hawaii. The medfly was detected first in South Brazil in 1901 and then in 1934 in Northeast Argentina (Dias et al. 2022). Although the fly has been detected multiple times in Chile since 1963, from recent reports it has been eradicated and the country is considered free from medfly (Dias et al. 2022). The invasion history of medfly in central America is more recent, with first detection in Costa Rica in the 1950s and then progressively in other neighboring countries. The fly invaded Guatemala, El Salvador and Mexico in the 1970s, dispersing widely in the southwest parts of the country. Following intensive eradication campaigns based on SIT programs, Mexico is considered free of medfly (Enkerlin et al. 2017). However, there are still sporadic detections of the fly recorded in Chiapas south Mexico and the recent outbreaks reported in central east Mexico (Manzanillo) are currently under eradication (Dias et al. 2022). Medfly was detected in the mainland United States of America first in Florida in 1929. The next detection was reported in 1956, a few more in 1960s, and sporadically since then (Szyniszewska et al. 2016). Aggressive and costly eradication campaigns have been executed to address these outbreaks. For example, the eradication campaigns executed against the major outbreaks of 1997 and 1998 cost in total approximately $37.5 million (Silva et al. 2003). Genetic analysis revealed the existence of breeding, overwintering populations from 1997 to 1998 in central Florida, which, however, were not related to the invasion events in the area of Miami. Thus, both persistent population and re-invasions should be considered to explain the invasion patterns of medfly in Florida during these years. Repeated detections of medfly in California (USA), since its first occurrence in 1975 and the big outbreaks in the early 1980s, have been reported. The frequency of medfly detection in California, especially in the area of Los Angeles, is quite high (i.e. 1417 detections from 1975 to 2012) (Papadopoulos et al. 2013), and expensive eradication campaigns have been implemented (Macaluso et al. 2020). Regardless, of the number and frequency of detections, medfly occurrence has been legally considered transient in California (McInnis et al. 2017); however, there is evidence supporting the existence of established, breeding populations and multiple invasion events (Carey 1991; Bonizzoni et al. 2001; Meixner et al. 2002; Gutierrez & Ponti 2011; Papadopoulos et al. 2013). The importance of medfly invasion in California is also supported by the fact that a "Preventive Sterile Insect Release Program" has been running in the area of Los Angeles since 1993.

In Australia, the medfly was first detected in 1895 in Perth, the Western part of the continent, at around the same time in Tasmania and later in eastern Australia (Bonizzoni et al. 2004 and references therein). Medfly has been eradicated from Tasmania in the 1940s and has disappeared from the eastern parts of the continent. Competitive displacement and even eradication of the medfly from eastern Australia due to the southwards range expansion of the Queensland fruit fly *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) has been proposed, although no solid evidence exists (Clarke & Measham 2022). In South Australia, there were sporadic detections from 1946s to the 1990s that continued since 1994. The area of Perth is the main source of propagules for detections in South Australia and also for medfly expansion along the coast (Bonizzoni et al. 2004). Genetic analyses suggest that the colonization of Australia is a secondary invasion event that is most probably related to propagules from Mediterranean countries. Although the medfly has been frequently intercepted in China since 1993, there are no reports of detections (Li et al. 2010). More than 80% of all interceptions are recorded at Guangzhou and interestingly almost all of them are from fruits carried by travelers. A pathway analysis indicated the volume of imported fruits to be a significant predictor of the risk of introducing

medfly throughout trading, but confirmed that passengers' luggage are the main pathway for introduction for medfly larvae (Li et al. 2010). Overall, medfly represents a high risk for Chinese horticulture, especially in parts of South-East China, such as Yunnan and Hainan (Li et al. 2009).

6.2 Range expansion in Europe

Medfly has been reported in the Mediterranean countries since 1842 and it is a major pest of many fruit commodities in the coastal areas, posing a huge havoc to the fruit growing and trading industry. In recent years, there have been frequent reports on the occurrence of medfly populations in more continental areas of the Mediterranean countries, such as central Macedonia (northern Greece), the area of Lombardy and Trentino in Italy (Zanoni et al. 2020), northeast Spain (Escudero-Colomar et al. 2008) and mainland France, as well as in central European countries such as Austria and Germany (Egartner et al. 2019; König et al. 2022) and Romania (Chireceanu et al. 2013). In recent years, sporadic detection have become frequent in central Europe and breeding populations may have succeeded to establish. For example, in the area of Vienna (Austria), medfly has been captured every year since 2009 (Egartner A. personal communication), with fly infestation in pome and stone fruits being reported at the end of the growing season. Likewise, extensive detections have been reported in recent official surveys conducted in Germany. The genetic analysis of specimens detected in Germany in 2016 and 2017 revealed the structure and genetic relatedness with flies captured in France and some Mediterranean countries (König et al. 2022). The possibility of survival of low numbers of individuals in protected areas cannot be excluded, although the status of the fly in Germany is still considered transient.

Recent modeling simulations demonstrated that established medfly populations exist up to North Italy and Southern France (46º North Latitude) and temporarily breeding populations may reach 48º North latitude (Gilioli et al. 2021). Overwintering in cooler areas seems to be accomplished in immature stages (mainly larvae), aligned with earlier empirical studies (Papadopoulos et al. 1996; Israely et al. 1997), and might be related to urban areas and protected refugia availability. Besides latitudinal limits in the northward distribution of medfly in Europe, altitudinal limits exist. The range expansion of medfly in more temperate areas of the southern European countries and in warmer areas of central Europe poses an additional hazard on the pome and stone fruit industry. In most marginal areas, the population growth of medfly is very slow in most of the fruiting season and increases in autumn (Papadopoulos et al. 2001). Infestation rates may still remain low, and sporadically increase above the economic thresholds. Nevertheless, the presence of medfly in these areas may strongly affect the fruit trading industry and individual farmers who may suffer high infestation rates.

7 Conclusions and research challenges

Despite the long history of research on medfly biology, ecology and invasiveness, there is a long and windy road to shed light on the related research challenges, which are deeply connected to the development and implementation of sustainable pest management tools (see Giunti et al. 2023 for a dedicated review). Further studies are essential to improve our knowledge of the environmental features affecting reproductive potential in the medfly with respect to its spatio-temporal patterns. Reproduction-related parameters, such as remating rates and paternity skew, should be monitored across different seasons, in multiple geographic areas. The studies performed on the Greek island of Chios, which harbors an established medfly population well characterized from the behavioral point of view (Katsoyannos et al. 1998), opened the way to this challenging research, with key applied relevance for medfly control. A particularly promising field for insect reproductive studies is metabolomics, which allows the comprehensive analysis of the metabolites in a given system (Snart et al. 2015). Metabolomics-based studies may provide a global picture of the effects of development, diet, mating, aging and other important physiological traits and it holds great potential for the characterization of seminal fluid components and post-mating female responses (Scolari et al. 2021b). The interpretation of metabolomics data in an ecological context is extremely challenging, but exploring the relationships between metabolic signatures and environmental conditions is of great basic and applied relevance.

Although difficult to perform, behavioral studies (in space and time) investigating habitat preferences by individual or group of medflies, and environmental factors affecting such preferences, may also allow us to deepen our understanding of the ecology of the species. For instance, studying the physical (e.g., illumination, chemical composition of the resting-foraging surfaces, localized temperature, etc.) and biotic (e.g., bacterial arrays on the resting and foraging substrate, etc.) parameters can advance our understanding on the complexity of environmental interactions of the medfly, and if some factors are important drivers of its behavior, and spatio-temporal patterns. Moreover, the combination of individual behavioral studies with genomics, may greatly advance our understanding of the interactions between the environment and the genome, and the dynamic interactions occurring in this interphase. In this respect, research efforts should be devoted to study the epigenetic mechanisms that may be involved in the regulation of mating and reproduction, as suggested for *B. tryoni*. In this species, Kumaran & Clarke (2014) found that a lure-foraging trait was passed from males fed on phytochemicals to their progeny, suggesting the presence of epigenetic changes mediated by these compounds. Histone modifications have been later identified also in lure-mated Qfly females (Kumaran et al. 2018). Due

to its applied relevance, this field deserves to be explored also in the medfly.

Major advances in the quality of insect genome assemblies expanded the toolbox available for the study of multiple biological traits in the medfly. Third-generation sequencing techniques, which are able to produce long reads, have been shown useful in this species, for which it was possible to obtain the required quantity of high-molecular-weight DNA (Meccariello et al. 2019, 2021; Ward et al. 2021). Importantly, combining medfly genomics, genetics, transcriptomics, bioinformatics and cytogenetics has proven successful in providing answers to complex biological longstanding questions (Ward et al. 2021). The integration of different techniques and resources remains a big challenge in the field of gene discovery and the medfly will continue to be a fruitful target to develop effective approaches with relevance to pest control.

Expanding the investigation of medfly male pheromone and other volatile organic compounds (VOCs) involved in insect-insect as well as medfly-plant communication is essential not only from the biological, but also from the pest management perspective, due to the key roles these chemicals play in medfly ecology. Given the chemical diversity of the volatiles produced by the medfly, a holistic approach integrating metabolomics, genomics and behavioral studies in different environmental conditions, will facilitate the investigation of the biological functions of this species in the ecosystems. Moreover, a deeper characterization of the medfly pheromone composition in response to environmental parameters may help developing improved (species- and sex-specific) semiochemicals for medfly management in the field. Successful implementation of such novel semiochemicals will require a strong interaction among researchers, farmers, agricultural extension officers and the semiochemical supply industry, further suggesting the urge for collaborative interdisciplinary initiatives.

The spread of medfly in cooler, more temperate areas in response to climate change is ongoing and needs to be further documented by population modeling and empirical studies. Overwintering in the novel cooler areas is a prerequisite for establishment, and needs to be locally investigated. The effect of anthropogenic environment (urban and suburban areas) on the colonization of medfly in cooler areas needs to be addressed as well. The impact of medfly on the deciduous fruit production and trading industry of the northern hemisphere should be explored as well. Lastly, regardless of the enormous amount of work conducted on the biology of the Mediterranean fruit fly, there are still gaps concerning field biology and responses of wild populations. Hence, considering current technological advances, research should focus on the wild trying to understand the persistence at marginal areas and survival at low population densities.

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References

Abraham, S., Díaz, V., Moyano, A., Castillo, G., Rull, J., Suárez, L., … Ovruski, S. M. (2021). Irradiation dose does not affect male reproductive organ size, sperm storage, and female remating propensity in *Ceratitis capitata*. *Bulletin of Entomological Research, 111*(1), 82–90. https://doi.org/10.1017/S0007485320000437

Alfaro, C., Vacas, S., Zarzo, M., Navarro-Llopis, V., & Primo, J. (2011). Solid phase microextraction of volatile emissions of *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae): Influence of fly sex, age, and mating status. *Journal of Agricultural and Food Chemistry, 59*(1), 298–306. https://doi.org/10.1021/jf104183c

Anantanawat, K., Papanicolaou, A., Hill, K., & Xu, W. (2020). Molecular response of the Mediterranean fruit fly (Diptera: Tephritidae) to heat. *Journal of Economic Entomology, 113*(5), 2495–2504. https://doi.org/10.1093/jee/toaa147

Anantanawat, K., Papanicolaou, A., Hill, K., & Xu, W. (2022). Mediterranean fruit fly genes exhibit different expression patterns between heat and cold treatments. *Bulletin of Entomological Research, 112*(2), 236–242. https://doi.org/10.1017/S000748532100078X

Antonatos, S., Papadopoulos, N. T., Anastasaki, E., Kimbaris, A., & Papachristos, D. P. (2021). Oviposition responses of female Mediterranean fruit flies (Diptera: Tephritidae) to fruit volatile compounds. *Journal of Economic Entomology, 114*(6), 2307–2314. https://doi.org/10.1093/jee/toab178

Antonatos, S., Anastasaki, E., Balayiannis, G., Michaelakis, A., Magiatis, P., Milonas, P., … Papachristos, D. P. (2023). Identification of volatile compounds from fruits aroma and citrus essential oils and their effect on oviposition of *Ceratitis capitata* (Diptera: Tephritidae). *Environmental Entomology, 52*(3), 327–340. https://doi.org/10.1093/ee/nvad024

Arias, M. B., Hartle-Mougiou, K., Taboada, S., Vogler, A. P., Riesgo, A., & Elfekih, S. (2022). Unveiling biogeographical patterns in the worldwide distributed *Ceratitis capitata* (medfly) using population genomics and microbiome composition. *Molecular Ecology, 31*(18), 4866–4883. https://doi.org/10.1111/mec.16616

Arita, L. H., & Kaneshiro, K. Y. (1985). The dynamics of the lek system and mating success in males of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). *Proceedings of the Hawaiian Entomological Society, 25*, 39–48.

Arita, L. H., & Kaneshiro, K. Y. (1986). Structure and function of the rectal epithelium and anal glands during mating behavior in the Mediterranean fruit fly male. *Proceedings of the Hawaiian Entomological Society, 26*, 27–30.

Arredondo, J., & Díaz-Fleischer, F. (2006). Oviposition deterrents for the Mediterranean fruit fly, *Ceratitis capitata* (Diptera:

Tephritidae) from fly faeces extracts. *Bulletin of Entomological Research, 96*(1), 35–42. https://doi.org/10.1079/BER2005399

Augustinos, A. A., Kyritsis, G. A., Papadopoulos, N. T., Abd-Alla, A. M. M., Cáceres, C., & Bourtzis, K. (2015). Exploitation of the medfly gut microbiota for the enhancement of sterile insect technique: Use of *Enterobacter* sp. in larval diet-based probiotic applications. *PLoS One, 10*(9), e0136459. https://doi.org/10.1371/journal.pone.0136459

Balmès, V., & Mouttet, R. (2017). Development and validation of a simplified morphological identification key for larvae of tephritid species most commonly intercepted at import in Europe. *Bulletin OEPP. EPPO Bulletin. European and Mediterranean Plant Protection Organisation, 47*(1), 91–99. https://doi.org/10.1111/epp.12369

Barr, N. B., & McPheron, B. A. (2006). Molecular phylogenetics of the genus *Ceratitis* (Diptera: Tephritidae). *Molecular Phylogenetics and Evolution, 38*(1), 216–230. https://doi.org/10.1016/j.ympev.2005.10.013

Barr, N. B., & Wiegmann, B. M. (2009). Phylogenetic relationships of *Ceratitis* fruit flies inferred from nuclear CAD and tango/ARNT gene fragments: Testing monophyly of the subgenera *Ceratitis (Ceratitis)* and *C. (Pterandrus). Molecular Phylogenetics and Evolution, 53*(2), 412–424. https://doi.org/10.1016/j.ympev.2009.07.008

Barr, N. B., Islam, M. S., De Meyer, M., & McPheron, B. A. (2012). Molecular identification of *Ceratitis capitata* (Diptera: Tephritidae) using DNA sequences of the COI barcode region. *Annals of the Entomological Society of America, 105*(2), 339–350. https://doi.org/10.1603/AN11100

Behar, A., Yuval, B., & Jurkevitch, E. (2005). Enterobacteria-mediated nitrogen fixation in natural populations of the fruit fly *Ceratitis capitata. Molecular Ecology, 14*(9), 2637–2643. https://doi.org/10.1111/j.1365-294X.2005.02615.x

Behar, A., Jurkevitch, E., & Yuval, B. (2008). Bringing back the fruit into fruit fly-bacteria interactions. *Molecular Ecology, 17*(5), 1375–1386. https://doi.org/10.1111/j.1365-294X.2008.03674.x

Bekker, G. F. H. G., Addison, M., Addison, P., & van Niekerk, A. (2019). Using machine learning to identify the geographic drivers of *Ceratitis capitata* trap catch in an agricultural landscape. *Computers and Electronics in Agriculture, 162*, 582–592. https://doi.org/10.1016/j.compag.2019.05.008

Ben-Yosef, M., Jurkevitch, E., & Yuval, B. (2008). Effect of bacteria on nutritional status and reproductive success of the Mediterranean fruit fly *Ceratitis capitata. Physiological Entomology, 33*(2), 145–154. https://doi.org/10.1111/j.1365-3032.2008.00617.x

Bertin, S., Scolari, F., Guglielmino, C. R., Bonizzoni, M., Bonomi, A., Marchini, D., … Matessi, C. (2010). Sperm storage and use in polyandrous females of the globally invasive fruit fly, *Ceratitis capitata. Journal of Insect Physiology, 56*(11), 1542–1551. https://doi.org/10.1016/j.jinsphys.2010.05.006

Bloem, K., Bloem, S., Rizzo, N., & Chambers, D. (1993). Female Medfly Refractory Period: Effect of Male Reproductive Status. In M. Aluja & P. Liedo (Eds.), *Fruit flies*. New York, NY: Springer; https://doi.org/10.1007/978-1-4757-2278-9_35

Bonizzoni, M., Zheng, L., Guglielmino, C. R., Haymer, D. S., Gasperi, G., Gomulski, L. M., & Malacrida, A. R. (2001). Microsatellite analysis of medfly bioinfestations in California. *Molecular Ecology, 10*(10), 2515–2524. https://doi.org/10.1046/j.0962-1083.2001.01376.x

Bonizzoni, M., Katsoyannos, B. I., Marguerie, R., Guglielmino, C. R., Gasperi, G., Malacrida, A., & Chapman, T. (2002). Microsatellite analysis reveals remating by wild Mediterranean fruit fly females, *Ceratitis capitata. Molecular Ecology, 11*(10), 1915–1921. https://doi.org/10.1046/j.1365-294X.2002.01602.x

Bonizzoni, M., Guglielmino, C. R., Smallridge, C. J., Gomulski, M., Malacrida, A. R., & Gasperi, G. (2004). On the origins of medfly invasion and expansion in Australia. *Molecular Ecology, 13*(12), 3845–3855. https://doi.org/10.1111/j.1365-294X.2004.02371.x

Bonizzoni, B., Gomulski, L. M., Mossinson, S., Guglielmino, C. R., Malacrida, A. R., Yuval, B., & Gasperi, G. (2006). Is polyandry a common event among wild populations of the pest *Ceratitis capitata? Journal of Economic Entomology, 99*(4), 1420–1429. https://doi.org/10.1093/jee/99.4.1420

Boulahia-Kheder, S. (2021). Advancements in management of major fruit flies (Diptera: Tephritidae) in North Africa and future challenges: A review. *Journal of Applied Entomology, 145*(10), 939–957. https://doi.org/10.1111/JEN.12938 https://doi.org/10.1111/jen.12938

Bravo, I. S. J., & Zucoloto, F. S. (1998). Performance and feeding behavior of *Ceratitis capitata:* Comparison of a wild population and a laboratory population. *Entomologia Experimentalis et Applicata, 87*(1), 67–72. https://doi.org/10.1046/j.1570-7458.1998.00305.x

Caetano, F. H., Solferini, V. N., de Britto, F. B., …. (2017). Ultra morphology of the digestive system of *Anastrepha fraterculus* and *Ceratitis capitata* (Diptera Tephritidae). *Journal of Morphological Sciences, 23*(3–4), 455–462.

Calla, B., Hall, B., Hou, S., & Geib, S. M. (2014). A genomic perspective to assessing quality of mass-reared SIT flies used in Mediterranean fruit fly (*Ceratitis capitata*) eradication in California. *BMC Genomics, 15*(1), 98. https://doi.org/10.1186/1471-2164-15-98

Campbell, E. M., Ball, A., Hoppler, S., & Bowman, A. S. (2008). Invertebrate aquaporins: A review. *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology, 178*(8), 935–955. https://doi.org/10.1007/s00360-008-0288-2

Carey, J. R. (1984). Host specific demographic studies of the Mediterranean fruit fly *Ceratitis capitata. Ecological Entomology, 9*(3), 261–270. https://doi.org/10.1111/j.1365-2311.1984.tb00850.x

Carey, J. R. (1991). Establishment of the Mediterranean fruit fly in California. *Science, 253*(5026), 1369–1373. https://doi.org/10.1126/science.1896848

Carey, J. R., Liedo, P., Orozco, D., & Vaupel, J. W. (1992). Slowing of mortality-rates at older ages in large medfly cohorts. *Science, 258*(5081), 457–461. https://doi.org/10.1126/science.1411540

Carey, J. R., Liedo, P., Orozco, D., Tatar, M., & Vaupel, J. W. (1995). A male-female longevity paradox in medfly cohorts. *Journal of Animal Ecology, 64*(1), 107–116. https://doi.org/10.2307/5831

Carey, J. R., Liedo, P., Muller, H. G., Wang, J. L., & Vaupel, J. W. (1998). Dual modes of aging in Mediterranean fruit fly females. *Science, 281*(5379), 996–998. https://doi.org/10.1126/science.281.5379.996

Carey, J. R., Plant, R. E., & Papadopoulos, N. T. (2014). Response to commentary by Gutierrez et al. *Proceedings. Biological Sciences, 281*(1782), 20132989. https://doi.org/10.1098/rspb.2013.2989

Chireceanu, C., Iamandei, M., Stanica, F., & Chiriloaie, A. (2013). The presence of the Mediterranean fruit fly *Ceratitis capitata* (Wied.), (Diptera: Tephritidae) in Romania. *Romanian Journal of Plant Protection, 6*, 92–97.

Clarke, A. R., & Measham, P. F. (2022). Competition: A missing component of fruit fly (Diptera: Tephritidae) risk assessment and planning. *Insects, 13*(11), 1065. https://doi.org/10.3390/insects13111065

Coronado-Gonzalez, P. A., Vijaysegaran, S., & Robinson, A. S. (2008). Functional morphology of the mouthparts of the adult Mediterranean fruit fly, *Ceratitis capitata. Journal of Insect Science, 8*(1), 73. https://doi.org/10.1673/031.008.7301

Cossé, A. A., Todd, J. L., Millar, J. G., Martinez, L. A., & Baker, T. C. (1995). Electroantennographic and coupled gas chromatographic-electroantennographic responses of the mediterranean fruit fly, *Ceratitis capitata*, to male-produced volatiles and mango odor. *Journal of Chemical Ecology, 21*(11), 1823–1836. https://doi.org/10.1007/BF02033679

De Meyer, M. (2000). Systematic revision of the subgenus *Ceratitis* MacLeay s.s. (Diptera, Tephritidae). *Zoological Journal of the Linnean Society, 128*(4), 439–467. https://doi.org/10.1111/j.1096-3642.2000.tb01523.x

De Meyer, M. (2005). Phylogenetic relationships within the fruit fly genus *Ceratitis* MacLeay (Diptera: Tephritidae), derived from morphological and host plant evidence. *Insect Systematics & Evolution, 36*, 459–480. https://doi.org/10.1163/187631205794761012

De Meyer, M., Copeland, R. S., Lux, S., …. (2002). Annotated check list of host plants for Afrotropical fruit flies (Diptera: Tephritidae) of the genus *Ceratitis. Zoologische Documentatie Koninklijk Museum voor Midden Afrika, 27*, 1–92.

De Meyer, M., Copeland, R. S., Wharton, R. A., & McPheron, B. A. (2004). On the geographical origin of the medfly, *Ceratitis capitata* (Wiedemann). Proceedings 6th International Symposium on Fruit Flies of Economic Importance, Stellenbosch, South Africa, pp. 45–53.

Deschepper, P., Todd, T. N., Virgilio, M., De Meyer, M., Barr, N. B., & Ruiz-Arce, R. (2021). Looking at the big picture: Worldwide population structure and range expansion of the cosmopolitan pest *Ceratitis capitata* (Diptera, Tephritidae). *Biological Invasions, 23*(11), 3529–3543. https://doi.org/10.1007/s10530-021-02595-4

Diamantidis, A., Carey, J. R., & Papadopoulos, N. T. (2008a). Life history evolution of an invasive tephritid. *Journal of Applied Entomology, 132*(9-10), 695–705. https://doi.org/10.1111/j.1439-0418.2008.01325.x

Diamantidis, A. D., Papadopoulos, N. T., & Carey, J. R. (2008b). Medfly populations differ in diel and age patterns of sexual signalling. *Entomologia Experimentalis et Applicata, 128*(3), 389–397. https://doi.org/10.1111/j.1570-7458.2008.00730.x

Diamantidis, A. D., Papadopoulos, N. T., Nakas, C. T., Wu, S., Müller, H.-G., & Carey, J. R. (2009). Life history evolution in a globally invading tephritid: Patterns of survival and reproduction in medflies from six world regions. *Biological Journal of the Linnean Society. Linnean Society of London, 97*(1), 106–117. https://doi.org/10.1111/j.1095-8312.2009.01178.x

Diamantidis, A. D., Carey, J. R., Nakas, C. T., & Papadopoulos, N. T. (2011). Ancestral populations perform better in a novel environment: Domestication of Mediterranean fruit fly populations from five global regions. *Biological Journal of the Linnean Society, 102*(2), 334–345. https://doi.org/10.1111/j.1095-8312.2010.01579.x

Dias, N. P., Montoya, P., & Nava, D. E. (2022). A 30-year systematic review reveals success in tephritid fruit fly biological control research. *Entomologia Experimentalis et Applicata, 170*(5), 370–384. https://doi.org/10.1111/eea.13157

Dominiak, B. C., & Daniels, D. (2012). Review of the past and present distribution of Mediterranean fruit fly (*Ceratitis capitata* Wiedemann) and Queensland fruit fly (*Bactrocera tryoni* Froggatt) in Australia. *Australian Journal of Entomology, 51*(2), 104–115. https://doi.org/10.1111/j.1440-6055.2011.00842.x

Egartner, A., Lethmayer, C., Gottsberger, R. A., & Blümel, S. (2019). Recent records of the Mediterranean fruit fly, *Ceratitis capitata* (Tephritidae, Diptera), in Austria. *IOBC/WPRS Bulletin, 146*, 143–152.

Enkerlin, W. R., Gutiérrez Ruelas, J. M., Pantaleon, R., Soto Litera, C., Villaseñor Cortés, A., Zavala López, J. L., … Hendrichs, J. (2017). The Moscamed Regional Programme: Review of a success story of area-wide sterile insect technique application. *Entomologia Experimentalis et Applicata, 164*(3), 188–203. https://doi.org/10.1111/eea.12611

Escudero-Colomar, L. A., Vilajeliu, M., & Batllori, L. (2008). Seasonality in the occurrence of the Mediterranean fruit fly [*Ceratitis capitata* (Wied.)] in the north-east of Spain. *Journal of Applied Entomology, 132*(9-10), 714–721. https://doi.org/10.1111/j.1439-0418.2008.01372.x

Gabrieli, P., Falaguerra, A., Siciliano, P., Gomulski, L. M., Scolari, F., Zacharopoulou, A., … Gasperi, G. (2010). Sex and the single embryo: Early development in the Mediterranean fruit fly, *Ceratitis capitata. BMC Developmental Biology, 10*(1), 12. https://doi.org/10.1186/1471-213X-10-12

Gasparich, G. E., Sheppard, W. S., Han, H. Y., McPheron, B. A., & Steck, G. J. (1995). Analysis of mitochondrial DNA and development of PCR-based diagnostic molecular markers for Mediterranean fruit fly *Ceratitis capitata* populations. *Insect Molecular Biology, 4*(1), 61–67. https://doi.org/10.1111/j.1365-2583.1995.tb00008.x

Gasparich, G. E., Silva, J. G., Han, Y. Y., Mcpheron, B. A., Steck, G. J., & Sheppard, W. S. (1997). Population genetic structure of Mediterranean fruit fly (Diptera: Tephritidae) and implications for worldwide colonization patterns. *Annals of the Entomological Society of America, 90*(6), 790–797. https://doi.org/10.1093/aesa/90.6.790

Gavriel, S., Gazit, Y., & Yuval, B. (2009). Remating by female Mediterranean fruit flies (*Ceratitis capitata,* Diptera: Tephritidae): temporal patterns and modulation by male condition. *Journal of Insect Physiology, 55*(7), 637–642. https://doi.org/10.1016/j.jinsphys.2009.04.002

Gavriel, S., Jurkevitch, E., Gazit, Y., & Yuval, B. (2011). Bacterially enriched diet improves sexual performance of sterile male Mediterranean fruit flies. *Journal of Applied Entomology, 135*(7), 564–573. https://doi.org/10.1111/j.1439-0418.2010.01605.x

Gilioli, G., Sperandio, G., Colturato, M., Pasquali, S., Gervasio, P., Wilstermann, A., … Schrader, G. (2021). Non-linear physiological responses to climate change: The case of *Ceratitis capitata* distribution and abundance in Europe. *Biological Invasions, 24*(1), 261–279. https://doi.org/10.1007/s10530-021-02639-9

Giunti, G., Benelli, G., Campolo, O., Canale, A., Kapranas, A., Liedo, P., … Papadopoulos, N. (2023). (Manuscript submitted for publication). Management of the Mediterranean fruit fly, *Ceratitis capitata:* Past, present and future. *Entomologia Generalis*.

Gomulski, L. M., Dimopoulos, G., Xi, Z., Soares, M. B., Bonaldo, M. F., Malacrida, A. R., & Gasperi, G. (2008). Gene discovery

in an invasive tephritid model pest species, the Mediterranean fruit fly, *Ceratitis capitata. BMC Genomics, 9*(1), 243. https://doi.org/10.1186/1471-2164-9-243

Gomulski, L. M., Dimopoulos, G., Xi, Z., Scolari, F., Gabrieli, P., Siciliano, P., … Gasperi, G. (2012). Transcriptome profiling of sexual maturation and mating in the Mediterranean fruit fly, *Ceratitis capitata. PLoS One, 7*(1), e30857. https://doi.org/10.1371/journal.pone.0030857

Gutierrez, A. P., & Ponti, L. (2011). Assessing the invasive potential of the Mediterranean fruit fly in California and Italy. *Biological Invasions, 13*(12), 2661–2676. https://doi.org/10.1007/s10530-011-9937-6

Heath, R. R., Landolt, P. J., Tumlinson, J. H., Chambers, D. L., Murphy, R. E., Doolittle, R. E., … Calkins, C. O. (1991). Analysis, synthesis, formulation, and field testing of three major components of male mediterranean fruit fly pheromone. *Journal of Chemical Ecology, 17*(9), 1925–1940. https://doi.org/10.1007/BF00993739

Heath, R. R., Landolt, P. J., Robacker, D. C., Dueben, B. D., & Epsky, N. D. (2000). Sexual pheromones of tephritid flies: Clues to unravel phylogeny and behavior. In M. Aluja & A. L. Norrborm (Eds.), *Fruit flies (Tephritidae): phylogeny and evolution of behavior* (pp. 793–809). Boca Raton, FL, USA: CRC Press.

Hentze, F. (1993). Efficiency of Trimedlure for Medfly trapping. In M. Aluja, & P. Liedo (Eds.), *Fruit flies: biology and management*, pp. 227–234, Springer-Verlag, New York, Inc., USA. https://doi.org/10.1007/978-1-4757-2278-9_43

Hernández-Pelegrín, L., Llopis-Giménez, Á., Crava, C. M., Ortego, F., Hernández-Crespo, P., Ros, V. I. D., & Herrero, S. (2022). Expanding the medfly virome: Viral diversity, prevalence, and sRNA profiling in mass-reared and field-derived medflies. *Viruses, 14*(3), 623. https://doi.org/10.3390/v14030623

Israely, N., Yuval, B., Kitron, U., & Nestel, D. (1997). Population fluctuations of adult Mediterranean fruit flies (Diptera: Tephritidae) in a Mediterranean heterogeneous agricultural region. *Environmental Entomology, 26*(6), 1263–1269. https://doi.org/10.1093/ee/26.6.1263

Jang, E. B., Light, D. M., Binder, R. G., Flath, R. A., & Carvalho, L. A. (1994). Attraction of female mediterranean fruit flies to the five major components of male-produced pheromone in a laboratory flight tunnel. *Journal of Chemical Ecology, 20*(1), 9–20. https://doi.org/10.1007/BF02065987

Katsoyannos, B. I., Kouloussis, N. A., & Carey, J. R. (1998). Seasonal and annual occurrence of Mediterranean fruit flies (Diptera: Tephritidae) on Chios island: differences between two neighbouring citrus orchards. *Annals of the Entomological Society of America, 91*(1), 43–51. https://doi.org/10.1093/aesa/91.1.43

König, S., Steinmöller, S., & Baufeld, P. (2022). Origin and potential for overwintering of *Ceratitis capitata* (Wiedemann) captured in an official survey in Germany. *Journal of Plant Diseases and Protection, 129*(5), 1201–1215. https://doi.org/10.1007/s41348-022-00605-8

Kouloussis, N. A., Papadopoulos, N. T., Katsoyannos, B. I., Müller, H.-G., Wang, J.-L., Su, Y.-R., … Carey, J. R. (2011). Seasonal trends in *Ceratitis capitata* reproductive potential derived from live-caught females in Greece. *Entomologia Experimentalis et Applicata, 140*(3), 181–188. https://doi.org/10.1111/j.1570-7458.2011.01154.x

Kraaijeveld, K., & Chapman, T. (2004). Effects of male sterility on female remating in the mediterranean fruitfly, *Ceratitis capitata. Proceedings. Biological Sciences, 271*(suppl_4), S209–S211. https://doi.org/10.1098/rsbl.2003.0116

Kraaijeveld, K., Katsoyannos, B., Stavrinides, M., Kouloussis, N. A., & Chapman, T. (2005). Remating in wild females of the Mediterranean fruit fly, *Ceratitis capitata. Animal Behaviour, 69*(4), 771–776. https://doi.org/10.1016/j.anbehav.2004.06.015

Krainacker, D. A., Carey, J. R., & Vargas, R. I. (1987). Effect of larval host on life history traits of the Mediterranean fruit fly, *Ceratitis capitata. Oecologia, 73*(4), 583–590. https://doi.org/10.1007/BF00379420

Krasnov, H., Cohen, Y., Goldshtein, E., Mendelsohn, O., Silberstein, M., Gazit, Y., & Blank, L. (2019). The effect of local and landscape variables on Mediterranean fruit fly dynamics in citrus orchards utilizing the ecoinformatics approach. *Journal of Pest Science, 92*(2), 453–463. https://doi.org/10.1007/s10340-018-1023-8

Kumaran, N., & Clarke, A. R. (2014). Indirect effects of phytochemicals on offspring performance of Queensland fruit fly, *Bactrocera tryoni* (Diptera: Tephritidae). *Journal of Applied Entomology, 138*(5), 361–367. https://doi.org/10.1111/jen.12082

Kumaran, N., van der Burg, C. A., Qin, Y., Cameron, S. L., Clarke, A. R., & Prentis, P. J. (2018). Plant-mediated female transcriptomic changes post-mating in a tephritid fruit fly, *Bactrocera tryoni. Genome Biology and Evolution, 10*(1), 94–107. https://doi.org/10.1093/gbe/evx257

Kyritsis, G. A., Augustinos, A. A., Ntougias, S., Papadopoulos, N. T., Bourtzis, K., & Cáceres, C. (2019). Enterobacter sp. AA26 gut symbiont as a protein source for Mediterranean fruit fly mass-rearing and sterile insect technique applications. *BMC Microbiology, 19*(1), 288. https://doi.org/10.1186/s12866-019-1651-z

Kyritsis, G. A., Koskinioti, P., Bourtzis, K., & Papadopoulos, N. T. (2022). Effect of *Wolbachia* infection and adult food on the sexual signaling of males of the Mediterranean fruit fly *Ceratitis capitata. Insects, 13*(8), 737. https://doi.org/10.3390/insects13080737

Leftwich, P. T., Nash, W. J., Friend, L. A., & Chapman, T. (2017). Adaptation to divergent larval diets in the medfly, *Ceratitis capitata. Evolution; International Journal of Organic Evolution, 71*(2), 289–303. https://doi.org/10.1111/evo.13113

Leftwich, P. T., Koukidou, M., Rempoulakis, P., Gong, H.-F., Zacharopoulou, A., Fu, G., … Alphey, L. (2014). Genetic elimination of field-cage populations of Mediterranean fruit flies. *Proceedings. Biological Sciences, 281*(1792), 20141372. https://doi.org/10.1098/rspb.2014.1372

Levinson, H., Levinson, A., & Osterried, E. (2003). Orange-derived stimuli regulating oviposition in the Mediterranean fruit fly. *Journal of Applied Entomology, 127*(5), 269–275. https://doi.org/10.1046/j.1439-0418.2003.00750.x

Li, B., Ma, J., Hu, X., Liu, H., & Zang, R. (2009). Potential geographical distributions of the fruit flies *Ceratitis capitata, Ceratitis cosyra* and *Ceratitis rosa* in China. *Journal of Economic Entomology, 102*(5), 1781–1790. https://doi.org/10.1603/029.102.0508

Li, B. N., Ma, J., Hu, X. N., Liu, H., Wu, J., Chen, H., & Zhang, R. (2010). Risk of Introducing Exotic Fruit Flies, *Ceratitis capitata, Ceratitis cosyra,* and *Ceratitis rosa* (Diptera: Tephritidae), Into Southern China. *Journal of Economic Entomology, 103*(4), 1100–1111. https://doi.org/10.1603/EC09217

Light, D. M., Jang, E. B., Binder, R. G., Flath, R. A., & Kint, S. (1999). Minor and intermediate components enhance attraction of female Mediterranean fruit flies to natural male odor pheromone and its synthetic major components. *Journal of Chemical Ecology, 25*(12), 2757–2777. https://doi.org/10.1023/A:1020855625244

Liquido, N. J., Shinoda, L. A., & Cunningham, R. T. (1991). Host plants of the Mediterranean fruit fly (Diptera, Tephritidae) an annotated world review. *Entomological Society of America, 83*, 1863–1878. https://doi.org/10.4182/CMLT2950

Loy, F., Solari, P., Isola, M., Crnjar, R., & Masala, C. (2016). Morphological and electrophysiological analysis of tarsal sensilla in the medfly *Ceratitis capitata* (Wiedemann, 1824) (Diptera: Tephritidae). *The Italian Journal of Zoology, 83*(4), 456–468. https://doi.org/10.1080/11250003.2016.1241830

Macaluso, K., Bigsby, K. M., Kriticos, D. J., …. (2020). CLIMEX and MED-FOES models for predicting the variability in growth potential and persistence of Mediterranean fruit fly (Diptera: Tephritidae) populations. *Annals of the Entomological Society of America, 113*(2), 114–124. https://doi.org/10.1093/aesa/saz065

Malacrida, A. R., Marinoni, F., Torti, C., Gomulski, L. M., Sebastiani, F., Bonvicini, C., … Guglielmino, C. R. (1998). Genetic aspects of the worldwide colonization process of *Ceratitis capitata. The Journal of Heredity, 89*(6), 501–507. https://doi.org/10.1093/jhered/89.6.501

Malacrida, A. R., Gomulski, L. M., Bonizzoni, M., Bertin, S., Gasperi, G., & Guglielmino, C. R. (2007). Globalization and fruitfly invasion and expansion: The medfly paradigm. *Genetica, 131*(1), 1–9. https://doi.org/10.1007/s10709-006-9117-2

McInnis, D. O., Rendon, P., & Komatsu, J. (2002). Mating and remating of medflies (Diptera: Tephritidae) in Guatemala: individual fly marking in field cages. *The Florida Entomologist, 85*(1), 126–137. https://doi.org/10.1653/0015-4040(2002)085[0126:MAROMD]2.0.CO;2

McInnis, D. O., Hendrichs, J., Shelly, T., Barr, N., Hoffman, K., Rodriguez, R., … Tan, K. H. (2017). Can polyphhagous invasive tephritid pest populations escape detection for years under favorable climatic and host conditions? *American Entomologist (Lanham, Md.), 63*(2), 89–99. https://doi.org/10.1093/ae/tmx038

Meccariello, A., Salvemini, M., Primo, P., Hall, B., Koskinioti, P., Dalíková, M., … Saccone, G. (2019). Maleness-on-the-Y (MoY) orchestrates male sex determination in major agricultural fruit fly pests. *Science, 365*(6460), 1457–1460. https://doi.org/10.1126/science.aax1318

Meccariello, A., Krsticevic, F., Colonna, R., Del Corsano, G., Fasulo, B., Papathanos, P. A., & Windbichler, N. (2021). Engineered sex ratio distortion by X-shredding in the global agricultural pest *Ceratitis capitata. BMC Biology, 19*(1), 78. https://doi.org/10.1186/s12915-021-01010-7

Meixner, M. D., McPheron, B. A., Silva, J. G., Gasparich, G. E., & Sheppard, W. S. (2002). The Mediterranean fruit fly in California: Evidence for multiple introductions and persistent populations based on microsatellite and mitochondrial DNA variability. *Molecular Ecology, 11*(5), 891–899. https://doi.org/10.1046/j.1365-294X.2002.01488.x

Midgarden, D., Lira, E., & Silver, M. (2014). Spatial analysis of Tephritidae fruit fly traps. In T. Shelly, N. Epsky, E. B. Jang, J. Reyes-Flore, & R.Vargas (Eds.), *Trapping and the detection, control and regulation of Tephritid fruit flies* (pp. 277–320). USA: Springer. https://doi.org/10.1007/978-94-017-9193-9_9

Moraiti, C. A., Verykouki, E., & Papadopoulos, N. T. (2022). Chill coma recovery of *Ceratitis capitata* adults across the Northern Hemisphere. *Scientific Reports, 12*(1), 17555. https://doi.org/10.1038/s41598-022-21340-y

Müller, H. G., Wu, S., Diamantidis, A. D., Papadopoulos, N. T., & Carey, J. R. (2009). Reproduction is adapted to survival characteristics across geographically isolated medfly populations. *Proceedings. Biological Sciences, 276*(1677), 4409–4416. https://doi.org/10.1098/rspb.2009.1461

Nakagawa, S., Farias, G. J., Suda, D., Cunningham, R. T., & Chambers, D. L. (1971). Reproduction of the Mediterranean fruit fly; frequency of mating in the laboratory. *Annals of the Entomological Society of America, 64*(4), 949–950. https://doi.org/10.1093/aesa/64.4.949

Nash, W. J., & Chapman, T. (2014). Effect of dietary components on larval life history characteristics in the medfly (*Ceratitis capitata*: Diptera, Tephritidae). *PLoS One, 9*(1), e86029. https://doi.org/10.1371/journal.pone.0086029

Nash, W., Mohorianu, I., & Chapman, T. (2019). Mate choice and gene expression signatures associated with nutritional adaptation in the medfly (*Ceratitis capitata*). *Scientific Reports, 9*(1), 6704. https://doi.org/10.1038/s41598-019-42610-2

Nestel, D., Katsoyannos, B., Nemny-Lavy, E., Medel, Z., & Papadopoulos, N. (2004). Spatial analysis of medfly populations in heterogeneous landscapes. In B. N. Barnes (Ed.) *Proceedings of the 6th International Symposium of Fruit Flies of Economic Importance*, Stellenbosch, South Africa, May 6–10, 2002. Isteg Scientific Publications, Irene, South Africa.

Nyamukondiwa, C., & Terblanche, J. S. (2010). Within-generation variation of critical thermal limits in adult Mediterranean and Natal fruit flies *Ceratitis capitata* and *Ceratitis rosa*: Thermal history affects short-term responses to temperature. *Physiological Entomology, 35*(3), 255–264. https://doi.org/10.1111/j.1365-3032.2010.00736.x

Nyamukondiwa, C., Weldon, C. W., Chown, S. L., le Roux, P. C., & Terblanche, J. S. (2013). Thermal biology, population fluctuations and implications of temperature extremes for the management of two globally significant insect pests. *Journal of Insect Physiology, 59*(12), 1199–1211. https://doi.org/10.1016/j.jinsphys.2013.09.004

Papachristos, D. P., & Papadopoulos, N. T. (2009). Are citrus species favorable hosts for the Mediterranean fruit fly? A demographic perspective. *Entomologia Experimentalis et Applicata, 132*(1), 1–12. https://doi.org/10.1111/j.1570-7458.2009.00861.x

Papachristos, D. P., Papadopoulos, N. T., & Nanos, G. D. (2008). Survival and development of immature stages of the Mediterranean fruit fly (Diptera: Tephritidae) in citrus fruit. *Journal of Economic Entomology, 101*(3), 866–872. https://doi.org/10.1093/jee/101.3.866

Papadogiorgou, G. D., Moraiti, C. A., Nestel, D., Terblanche, J. S., Verykouki, E., & Papadopoulos, N. T. (2023). Acute cold stress and supercooling capacity of Mediterranean fruit fly populations across the Northern Hemisphere (Middle East and Europe). *Journal of Insect Physiology, 147*, 104519. https://doi.org/10.1016/j.jinsphys.2023.104519

Papadopoulos, N. T., & Katsoyannos, B. I. (2002). Development of *Ceratitis capitata* (Diptera: Tephritidae) in three apple varieties in the laboratory. Sixth International Symposium on Fruit Flies of Economic Importance, Stellenbosch, South Africa.

Papadopoulos, N., Carey, J., Katsoyannos, B., & Kouloussis, N. (1996). Overwintering of the Mediterranean fruit fly (Diptera:

Tephritidae) in northern Greece. *Annals of the Entomological Society of America, 89*(4), 526–534. https://doi.org/10.1093/aesa/89.4.526

Papadopoulos, N. T., Katsoyannos, B. I., Carey, J. R., & Kouloussis, N. A. (2001). Seasonal and annual occurrence of the Mediterranean fruit fly (Diptera:Tephritidae) in northern Greece. *Annals of the Entomological Society of America, 94*(1), 41–50. https://doi.org/10.1603/0013-8746(2001)094[0041:SAAOOT]2.0.CO;2

Papadopoulos, N., Carey, J., Katsoyannos, B., Kouloussis, N. A., Müller, H.-G., & Liu, X. (2002). Supine behaviour predicts the time to death in male Mediterranean fruit flies (*Ceratitis capitata*). *Proceedings. Biological Sciences, 269*(1501), 1633–1637. https://doi.org/10.1098/rspb.2002.2078

Papadopoulos, N. T., Katsoyannos, B. I., & Nestel, D. (2003). Spatial autocorrelation analysis of a *Ceratitis capitata* (Diptera: Tephritidae) adult population in a mixed deciduous fruit orchard in northern Greece. *Environmental Entomology, 32*(2), 319–326. https://doi.org/10.1603/0046-225X-32.2.319

Papadopoulos, N. T., Liedo, P., Muller, H. G., Wang, J.-L., Molleman, F., & Carey, J. R. (2010). Cost of reproduction in male medflies: The primacy of sexual courting in extreme longevity reduction. *Journal of Insect Physiology, 56*(3), 283–287. https://doi.org/10.1016/j.jinsphys.2009.10.014

Papadopoulos, N. T., Papanastasiou, S., Muller, H. G., Wang, J.-L., Yang, W., & Carey, J. R. (2011). Dietary effects on sex-specific health dynamics of medfly: Support for the dynamic equilibrium model of aging. *Experimental Gerontology, 46*(12), 1026–1030. https://doi.org/10.1016/j.exger.2011.08.013

Papadopoulos, N. T., Plant R. E., & Carey, J. R. (2013). From trickle to flood: the large-scale, cryptic invasion of California by tropical fruit flies. *Proceedings of the Royal Society B, 280*(1768). https://doi.org/10.1098/rspb.2013.1466

Papaj, D. R., Katsoyannos, B. I., & Hendrichs, J. (1989). Use of fruit wounds in oviposition by Mediterranean fruit flies. *Entomologia Experimentalis et Applicata, 53*(3), 203–209. https://doi.org/10.1111/j.1570-7458.1989.tb03567.x

Papanicolaou, A., Schetelig, M. F., Arensburger, P., Atkinson, P. W., Benoit, J. B., Bourtzis, K., … Handler, A. M. (2016). The whole genome sequence of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), reveals insights into the biology and adaptive evolution of a highly invasive pest species. *Genome Biology, 17*(1), 192. https://doi.org/10.1186/s13059-016-1049-2

Pieterse, W., Benitez, H. A., & Addison, P. (2017). The use of geometric morphometric analysis to illustrate the shape change induced by different fruit hosts on the wing shape of *Bactrocera dorsalis* and *Ceratitis capitata* (Diptera: Tephritidae). *Zoologischer Anzeiger, 269*, 110–116. https://doi.org/10.1016/j.jcz.2017.08.004

Pinto Dias, N., Montoya, P., & Nava, D. E. (2022). Historical invasion of medfly in the Neotropical region and adoption of management techniques. *Current Opinion in Insect Science, 50*, 100872. https://doi.org/10.1016/j.cois.2021.12.012

Pogue, T., Malod, K., & Weldon, C. W. (2022). Patterns of remating behaviour in *Ceratitis* (Diptera: Tephritidae) species of varying lifespan. *Frontiers in Physiology, 13*, 824768. https://doi.org/10.3389/fphys.2022.824768

Prokopy, R. J., & Hendrichs, J. (1979). Mating behaviour of *Ceratitis capitata* on a field-caged host tree. *Annals of the Entomological Society of America, 72*(5), 642–648. https://doi.org/10.1093/aesa/72.5.642

Pujol-Lereis, L. M., Fagali, N. S., Rabossi, A., Catalá, Á., & Quesada-Allué, L. A. (2016). Chill-coma recovery time, age and sex determine lipid profiles in *Ceratitis capitata* tissues. *Journal of Insect Physiology, 87*, 53–62. https://doi.org/10.1016/j.jinsphys.2016.02.002

Rahman, T., & Broughton, S. (2019). The survival of Mediterranean fruit fly (Diptera: Tephritidae) over winter in Western Australia. *Environmental Entomology, 48*(4), 977–987. https://doi.org/10.1093/ee/nvz060

Ricciardi, R., Aringhieri, G., Faita, F., Benelli, G., Boccaccio, C., Lucchi, A., & Caramella, D. (2022). Echoentomography: A novel non-destructive imaging of soft-body insects through ultra-high frequency ultrasonography (UHFUS). *Entomologia Generalis, 42*(1), 147–161. https://doi.org/10.1127/entomologia/2021/1101

Rosetto, M., Marchini, D., de Filippis, T., Ciolfi, S., Frati, F., Quilici, S., & Dallai, R. (2003). The *ceratotoxin* gene family in the medfly *Ceratitis capitata* and the Natal fruit fly *Ceratitis rosa* (Diptera: Tephritidae). *Heredity, 90*(5), 382–389. https://doi.org/10.1038/sj.hdy.6800258

Ruiz-Arce, R., Todd, T. N., Deleon, R., Barr, N. B., Virgilio, M., De Meyer, M., & McPheron, B. A. (2020). Worldwide phylogeography of *Ceratitis capitata* (Diptera: Tephritidae) using mitochondrial DNA. *Journal of Economic Entomology, 113*(3), 1455–1470. https://doi.org/10.1093/jee/toaa024

Salvemini, M., Arunkumar, K. P., Nagaraju, J., Sanges, R., Petrella, V., Tomar, A., … Saccone, G. (2014). *De novo* assembly and transcriptome analysis of the Mediterranean fruit fly *Ceratitis capitata* early embryos. *PLoS One, 9*(12), e114191. https://doi.org/10.1371/journal.pone.0114191

San Andrés, V., Urbaneja, A., Sabater-Muñoz, B., & Castañera, P. (2007). A novel molecular approach to assess mating success of sterile *Ceratitis capitata* (Diptera: Tephritidae) males in sterile insect technique programs. *Journal of Economic Entomology, 100*(4), 1444–1449. https://doi.org/10.1093/jee/100.4.1444

San Andrés, V., Castañera, P., & Sabater-Muñoz, B. (2013). Transcriptome analysis in *Ceratitis capitata* to unveil genes involved in ageing-maturation process. *Spanish Journal of Agricultural Research, 11*(3), 842–854. https://doi.org/10.5424/sjar/2013113-3987

Sancho, R., Guillem-Amat, A., López-Errasquín, E., Sánchez, L., Ortego, F., & Hernández-Crespo, P. (2021). Genetic analysis of medfly populations in an area of sterile insect technique applications. *Journal of Pest Science, 94*(4), 1277–1290. https://doi.org/10.1007/s10340-021-01337-8

Sciarretta, A., Tabilio, M. R., Lampazzi, E., Ceccaroli, C., Colacci, M., & Trematerra, P. (2018). Analysis of the Mediterranean fruit fly [*Ceratitis capitata* (Wiedmann)] spatio-temporal distribution in relation to sex and female mating status for precision IPM. *PLoS One, 13*(4), e0195097. https://doi.org/10.1371/journal.pone.0195097

Scolari, F., Gomulski, L. M., Ribeiro, J. M., Siciliano, P., Meraldi, A., Falchetto, M., … Malacrida, A. R. (2012). Transcriptional profiles of mating-responsive genes from testes and male accessory glands of the Mediterranean fruit fly, *Ceratitis capitata. PLoS One, 7*(10), e46812. https://doi.org/10.1371/journal.pone.0046812

Scolari, F., Yuval, B., Gomulski, L. M., Schetelig, M. F., Gabrieli, P., Bassetti, F., … Gasperi, G. (2014). Polyandry in the medfly – shifts in paternity mediated by sperm stratification and mixing. *BMC Genomic Data, 15*(S2), S10. https://doi.org/10.1186/1471-2156-15-S2-S10

Scolari, F., Valerio, F., Benelli, G., Papadopoulos, N. T., & Vanickova, L. (2021a). Tephritid fruit fly semiochemicals: Current knowledge and future perspectives. *Insects, 12*(5), 408. https://doi.org/10.3390/insects12050408

Scolari, F., Khamis, F. M., & Pérez-Staples, D. (2021b). Beyond sperm and male accessory gland proteins: Exploring insect reproductive metabolomes. *Frontiers in Physiology, 12*, 729440. https://doi.org/10.3389/fphys.2021.729440

Shelly, T. E. (2000). Male signalling and lek attractiveness in the Mediterranean fruit fly. *Animal Behaviour, 60*(2), 245–251. https://doi.org/10.1006/anbe.2000.1470

Shelly, T. E. (2018). Sexual selection on leks: A fruit fly primer. *Journal of Insect Science, 18*(3), 9. https://doi.org/10.1093/jisesa/iey048

Shelly, T. E., Edu, J., & Pahio, E. (2004). Sterile males of the Mediterranean fruit fly exposed to ginger root oil induce female remating: implications for the sterile insect technique (Diptera: Tephritidae). *The Florida Entomologist, 87*(4), 628–629. https://doi.org/10.1653/0015-4040(2004)087[0628:SMOTMF]2.0.CO;2

Siciliano, P., He, X. L., Woodcock, C., Pickett, J. A., Field, L. M., Birkett, M. A., … Zhou, J. J. (2014a). Identification of pheromone components and their binding affinity to the odorant binding protein CcapOBP83a-2 of the Mediterranean fruit fly, *Ceratitis capitata. Insect Biochemistry and Molecular Biology, 48*, 51–62. https://doi.org/10.1016/j.ibmb.2014.02.005

Siciliano, P., Scolari, F., Gomulski, L. M., Falchetto, M., Manni, M., Gabrieli, P., … Malacrida, A. R. (2014b). Sniffing out chemosensory genes from the Mediterranean fruit fly, *Ceratitis capitata. PLoS One, 9*(1), e85523. https://doi.org/10.1371/journal.pone.0085523

Sim, S. B., Ruiz-Arce, R., Barr, N. B., & Geib, S. M. (2017). A new diagnostic resource for *Ceratitis capitata* strain identification based on QTL mapping. *G3 (Bethesda, Md.), 7*(11), 3637–3647. https://doi.org/10.1534/g3.117.300169

Silva, J. G., Meixner, M. D., Mcpheron, B. A., Steck, G. J., & Sheppard, W. S. (2003). Recent Mediterranean fruit fly (Diptera: Tephritidae) infestations in Florida – a genetic perspective. *Journal of Economic Entomology, 96*(6), 1711–1718. https://doi.org/10.1603/0022-0493-96.6.1711

Siomava, N., Wimmer, E. A., & Posnien, N. (2016). Size relationships of different body parts in the three dipteran species *Drosophila melanogaster, Ceratitis capitata* and *Musca domestica. Development Genes and Evolution, 226*(3), 245–256. https://doi.org/10.1007/s00427-016-0543-6

Sivakala, K. K., Jose, P. A., Shamir, M., C-N Wong, A., Jurkevitch, E., & Yuval, B. (2022). Foraging behaviour of medfly larvae is affected by maternally transmitted and environmental bacteria. *Animal Behaviour, 183*, 169–176. https://doi.org/10.1016/j.anbehav.2021.10.014

Snart, C. J., Hardy, I. C., & Barrett, D. A. (2015). Entometabolomics: Applications of modern analytical techniques to insect studies. *Entomologia Experimentalis et Applicata, 155*(1), 1–17. https://doi.org/10.1111/eea.12281

Solari, P., Corda, V., Sollai, G., Kreissl, S., Galizia, C. G., & Crnjar, R. (2016). Morphological characterization of the antennal lobes in the Mediterranean fruit fly *Ceratitis capitata. Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology, 202*(2), 131–146. https://doi.org/10.1007/s00359-015-1059-7

Spanos, L., Koutroumbas, G., Kotsyfakis, M., & Louis, C. (2000). The mitochondrial genome of the Mediterranean fruit fly, *Ceratitis capitata. Insect Molecular Biology, 9*(2), 139–144. https://doi.org/10.1046/j.1365-2583.2000.00165.x

Steck, G. J., & Ekesi, S. (2015). Description of third instar larvae of *Ceratitis fasciventris, C. anonae, C. rosa* (FAR complex) and *C. capitata* (Diptera, Tephritidae). *ZooKeys, 540*, 443–466. https://doi.org/10.3897/zookeys.540.10061

Szyniszewska, A. M., & Tatem, A. J. (2014). Global assessment of seasonal potential distribution of Mediterranean fruit fly *Ceratitis capitata* (Diptera: Tephritidae). *PLoS One, 9*(11), e111582. https://doi.org/10.1371/journal.pone.0111582

Szyniszewska, A. M., Leppla, N. C., Huang, Z., & Tatem, A. J. (2016). Analysis of seasonal risk for importation of the Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae), via air passenger traffic arriving in Florida and California. *Journal of Economic Entomology, 109*(6), 2317–2328. https://doi.org/10.1093/jee/tow196

Thornhill, R., & Alcock, J. (1983). *The evolution of insect mating systems*. Cambridge, MA: Harvard University Press; https://doi.org/10.4159/harvard.9780674433960

Tsoumani, K. T., & Mathiopoulos, K. D. (2012). Genome size estimation with quantitative real-time PCR in two Tephritidae species: *Ceratitis capitata* and *Bactrocera oleae. Journal of Applied Entomology, 136*(8), 626–631. https://doi.org/10.1111/j.1439-0418.2011.01684.x

Vanickova, L., do Nascimento, R. R., Hoskovec, M., Ježková, Z., Břízová, R., Tomčala, A., & Kalinová, B. (2012). Are the wild and laboratory insect populations different in semiochemical emission? The case of the medfly sex pheromone. *Journal of Agricultural and Food Chemistry, 60*(29), 7168–7176. https://doi.org/10.1021/jf301474d

Vera, M. T., Wood, R. J., Cladera, J. L., & Gilburn, A. S. (2002). Factors affecting female remating frequency in the Mediterranean fruit fly (Diptera, Tephritidae). *The Florida Entomologist, 85*(1), 156–164. https://doi.org/10.1653/0015-4040(2002)085[0156:FAFRFI]2.0.CO;2

Vera, M. T., Cladera, J. L., Calgano, G., Vilardi, J. C., & McInnis, D. O. (2003). Remating of wild *Ceratitis capitata* (Diptera: Tephritidae) females mated with wild or laboratory males during a single day trial in field cages. *Annals of the Entomological Society of America, 96*, 563–570. https://doi.org/10.1603/0013-8746(2003)096[0563:ROWCCD]2.0.CO;2

Ward, C. M., Aumann, R. A., Whitehead, M. A., Nikolouli, K., Leveque, G., Gouvi, G., … Schetelig, M. F. (2021). White pupae phenotype of tephritids is caused by parallel mutations of a MFS transporter. *Nature Communications, 12*(1), 491. https://doi.org/10.1038/s41467-020-20680-5

Weldon, C. W., Terblanche, J. S., & Chown, S. L. (2011). Time-course for attainment and reversal of acclimation to constant temperature in two *Ceratitis* species. *Journal of Thermal Biology, 36*(8), 479–485. https://doi.org/10.1016/j.jtherbio.2011.08.005

Weldon, C. W., Nyamukondiwa, C., Karsten, M., Chown, S. L., & Terblanche, J. S. (2018). Geographic variation and plasticity in climate stress resistance among southern African populations of *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae). *Scientific Reports, 8*(1), 9849. https://doi.org/10.1038/s41598-018-28259-3

White, I. M., & Elson-Harris, M. (1992). *Fruit flies of economic significance: their identification and bionomics*.

Wallingford, UK: CAB International. https://doi.org/10.1079/9780851987903.0000

Whittier, T. S., Kaneshiro, K. Y., & Prescott, L. D. (1992). Mating behavior of Mediterranean fruit flies (Diptera: Tephritidae) in a natural environment. *Annals of the Entomological Society of America, 85*(2), 214–218. https://doi.org/10.1093/aesa/85.2.214

Whittier, T. S., Nam, F. Y., Shelly, T. E., & Kaneshiro, K. Y. (1994). Male courtship success and female discrimination in the Mediterranean fruit fly (Diptera, Tephritidae). *Journal of Insect Behavior, 7*(2), 159–170. https://doi.org/10.1007/BF01990078

Wiens, J. A., Stenseth, N. C., Van Horne, B., & Ims, R. A. (1993). Ecological mechanisms and landscape ecology. *Oikos, 66*(3), 369–380. https://doi.org/10.2307/3544931

Yuval, B., Kaspi, R., Shloush, S., & Warburg, M. S. (1998). Nutritional reserves regulate male participation in Mediterranean fruit fly leks. *Ecological Entomology, 23*(2), 211–215. https://doi.org/10.1046/j.1365-2311.1998.00118.x

Zanoni, S., Baldessari, M., Chiesa, S., Angeli, G., & Ioriatti, C. (2020). Confronto di sistemi di monitoraggio di *Ceratitis capitata* su melo in Trentino. In *Giornate fitopatologiche 2020, 27 ottobre-12 novembre 2020* (pp. 133–140). Lazzaro, Italy: Bologna S.; http://hdl.handle.net/10449/65528

Zhang, Y., De Meyer, M., Virgilio, M., Feng, S., Badji, K., & Li, Z. (2021). Phylogenomic resolution of the *Ceratitis* FARQ complex (Diptera: Tephritidae). *Molecular Phylogenetics and Evolution, 161*, 107160. https://doi.org/10.1016/j.ympev.2021.107160

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