Fruit Flies: Challenges and Opportunities to Stem the Tide of Global Invasions

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Abstract

Global trade in fresh fruit and vegetables, intensification of human mobility, and climate change facilitate fruit fly (Diptera: Tephritidae) invasions. Life-history traits, environmental stress response, dispersal stress, and novel genetic admixtures contribute to their establishment and spread. Tephritids are among the most frequently intercepted taxa at ports of entry. In some countries, supported by the rules-based trade framework, a remarkable amount of biosecurity effort is being arrayed against the range expansion of tephritids. Despite this effort, fruit flies continue to arrive in new jurisdictions, sometimes triggering expensive eradication responses. Surprisingly, scant attention has been paid to biosecurity in the recent discourse about new multilateral trade agreements. Much of the available literature on managing tephritid invasions is focused on a limited number of charismatic (historically high-profile) species, and the generality of many patterns remains speculative.

INTRODUCTION

Globally, there are more than 5,000 fruit fly species (Diptera: Tephritidae) (6), including approximately 200 species of economic significance (133). In a recent pest categorization, over 250 species of tephritids were considered as potential quarantine pests threatening the European Union (6), and tephritids top the lists of quarantine pests for Australia, China, New Zealand, Africa, South America, Asia, and North America (5, 53, 86). In many fruit-producing areas, fruit flies are considered to be one of the main threats to economic production and trade in horticultural crops, and consequently pose a huge challenge for regulators, legislators, and managers (23).

The global trade in fresh fruits and vegetables and the intensification of human mobility have increased the rate of biological invasions, including those of fruit flies (36). Incursions and invasions are increasing in frequency (89; **http://b3.net.nz/gerda**), stimulating intense debates regarding establishment versus eradication success (8–10, 69, 89, 102, 137). Fruit flies are the most frequently intercepted organisms in fruit and vegetable commodities in European ports of entry (**https://food.ec.europa.eu/plants/plant-health-and-biosecurity/europhyt_en**). The recent detections and outbreaks of the Oriental fruit fly (*Bactrocera dorsalis*) in Italy and France exemplify their invasiveness (27, 78). Climatic changes are shifting the potential ranges of fruit flies, exposing new jurisdictions to invasion threats, especially in middle latitudes.

SOCIOECONOMIC IMPACTS OF FRUIT FLY INVASIONS

Tephritids can cause substantial direct production losses, impede noncommercial horticultural activities, and severely impact small growers' incomes in developing countries if their produce becomes unmarketable.

Estimating the social and economic impacts of invasive fruit flies is challenging, since these impacts encompass (*a*) severe reduction of the agricultural produce; (*b*) the huge costs of interception, detection (extensive surveillance), eradication, and containment; and (*c*) impacts on fruit-trading and -exporting industries. The addition of a new pest species to a single export fruit incurs enormous expense when it is added to existing disinfestation protocols, especially if a new technology is required. Information on the costs of fruit fly invasions is scattered and disparate (**Supplemental Table 1**). Most estimates are imprecise; cannot be compared; and refer to different currencies, countries, and continents. The cost categories include (*a*) production, including direct fruit infestation, reduced shelf life of fresh fruit, qualitative degradation, and price reduction; (*b*) trading, including postharvest treatments, rejection of consignments, market loss, and interception and identification costs; (*c*) surveillance, including predictive modeling, trapping, fruit sampling, and identification tools; (*d*) eradication, including insecticide application, the sterile insect technique (SIT), the male annihilation technique (MAT), communication campaigns, and certifications of absence; (*e*) containment, including insecticide application, the SIT, the MAT, and intense population monitoring; and (*f*) management, including population monitoring, mass trapping, insecticide application, area-wide integrated pest management (IPM), and the SIT.

Direct Loss of Fruit Produce

Fruit and vegetables constitute major agricultural produce annually valued at more than €21 billion in the European Union, US$22.5 billion for African countries in 2007 (3), US$25 billion in California, and AU$1 billion in Australia (86). Loss in production due to fruit flies may range from 10% to 30% (77). For example, fruit flies are estimated to cause an economic loss of more than US$2 billion across Africa (23, 77). Similar estimates have been reported for Brazil (68, 82), Pakistan (110), Egypt (139 and references therein), India (135), China (97), La Reunion, France (33), and Taiwan (50). Losses can be high even with well-coordinated management interventions

such as that executed against the Mediterranean fruit fly (medfly), *Ceratitis capitata*, in Valencia, Spain, which consisted mainly of aerial malathion spraying; despite the intervention, the pest caused an estimated loss of up to approximately 4% of Oriental persimmon production (76). In contrast, a well-coordinated area-wide management project against several fruit flies in Hawaii reduced field infestation rates dramatically; these rates often ranged above 10–20% before the intervention (38, 125).

Fruit Trade

Horticultural trade implications encompass various geographically distinct regions of the world. An embargo by Asian countries on fruit commodities from California was estimated to cost US$564 million and over 15,000 jobs in 1990 (103). The outbreak of *B. dorsalis* in only one county in Florida in 2015–2016, because of the costs of quarantine implementation and the losses from not planting, was estimated to cost tens of millions of US dollars in losses for the fruit-production sector and up to 726 jobs (110). Interception of medfly-infested Spanish clementines in the United States in 2001 resulted in a ban on imports, with an estimated loss of €300 million (93). Additional examples of bans on imports exist for avocado exports from Kenya (83), banana exports from Mozambique (13, 40), and mango exports from West Africa (75) (for additional details, see **Supplemental Table 1**). Bans on fruit exports because of fruit fly interceptions may have dramatic consequences for small- and medium-scale farmers in developing countries. For example, as Europe is the main destination for tropical fruits like mangoes from Africa, high numbers of interceptions of fruit flies at EU points of entry can lead to the destruction of full shipments and import bans (**https://food.ec.europa.eu/plants/plant-health-and-biosecurity/europhyt/interceptions_en**). The presence of an invasive fruit fly can even have an impact on the export industry of nonsusceptible commodities such as kiwi fruit (85).

Interception

The costs of interceptions are related to regular inspection activities conducted at ports of entry or devanning sites by authorized personnel and include inspection of fruit commodities, parcel shipments, and passengers' luggage (84) (**Supplemental Table 1**). Adoption of noninvasive sensing technologies, such as scanning systems (e.g., spectroscopic techniques, visible light sensing, hyperspectral imaging, X-ray imagining), and electronic noses, to detect volatiles of infested fruit; development and use of identification tools; and expert consultation to identify intercepted specimens all carry costs (1 and references therein). Delays in completing an inspection event may result in large costs, as sensitive crops may deteriorate and/or completely lose their value.

Surveillance and Detection

Surveillance activities to detect invasive fruit flies are costly operations, since several species are considered in most countries, and dense trapping networks (using protein-baited or male-attractant lures) are established and serviced year-round or during a period of several months. For example, since 1989, New Zealand has deployed traps in more than 3,450 sites for the detection of three fruit fly species, at a cost of more than NZ$1 million (106). The fruit fly detection program in California deploys more than 94,000 traps state-wide each year, and has run for several decades at a huge cost to taxpayers (102).

Eradication

An eradication attempt is the most common response to incursions of invasive fruit flies. The cost of eradication programs against medfly in California is estimated at US$500 million over

the past 25 years (120). Incursions by alien tephritids typically elicit expensive control campaigns. These campaigns often cost millions of US dollars and involve intense insecticide spraying even in residential areas, with direct negative health and environmental effects, as well as the long-term danger of insecticide resistance. The cost of a typical fruit fly eradication campaign is estimated to be US$12 million but may exceed US$100 million (113). There are several examples of costly eradication campaigns against fruit flies, e.g., in Australia against *B. dorsalis* (7), Japan against *B. dorsalis* and *Zeugodacus cucurbitae* (81), and California and Florida against several species (9, 119), and these campaigns may run for decades (e.g., the regional program for the eradication of medfly from Mexico and Guatemala) (26).

Increased Cost of Interventions

The failure to eradicate or contain a fruit fly pest results in permanent population establishment that requires continuous management input. Large commodity losses are frequently avoided with pesticide use, but this comes at a high cost. In the European Union, costs of control are estimated from a few to several hundred euros/ha. The regional government of Valencia spends €9.5 million a year on the control of medfly, but the costs are much higher without a centrally organized IPM program (93). Additional estimates regarding costs of interventions have been obtained for the control of medfly in the Hex River valley in South Africa and in Israel, Jordan, and the Palestinian Authority (25, 74). The invasion of the Nearctic species *Rhagoletis completa* into Europe is associated with an increase of 13% and 430% in the costs of pest management in conventional and organic walnut orchards, respectively, making the production costs for organic farmers uneconomical (128).

INVASION PROCESS: BARRIERS, RISKS, AND MANAGEMENT

Transport

Interception data in Europe and the United States suggest that long-distance fly movement is mostly associated with commercial or passengers' importation of plant material (e.g., fruits, soil) (6, 56). Thus, greater trade and transport connectivity allows fruit flies to overcome geographical barriers to spread. Importantly, despite the strong focus on developing greater trade connectivity, the concomitant need for increased biosecurity measures has not featured in discussions about new initiatives such as the Belt and Road Initiative (**https://www.ebrd.com/what-we-do/belt-and-road/overview.html**) or the Trans-Pacific Partnership (80).

Risk assessments for fruit flies vary in scope and breadth. Most risk assessments have focused on the climate suitability dimension of the problem, using bioclimatic models to estimate the potential distribution under historical and, in some cases, future climate scenarios (14–16, 48, 49, 52, 57, 58, 116, 118, 127, 134). Kriticos (46) examined the potential for each of six *Bactrocera* species to establish in New Zealand under current and future climate scenarios, concluding that, under historical climate conditions, New Zealand was at least marginally suitable for establishment for half of the species, and under the future climate scenario, another two could potentially establish. Subsequently, one of these species, *Bactrocera tryoni*, was detected and eradicated from the Auckland area of New Zealand (**http://b3.net.nz/gerda**).

While there are some invasive temperate fruit flies (e.g., *Rhagoletis cerasi*, *Rhagoletis cingulata*, *R. completa*, and *Rhagoletis suavis*), most fruit flies are adapted to tropical or subtropical climates. In recent times, probably due in part to climatic changes and changes in host availability, many tropical fruit flies have been observed expanding their ranges poleward into cooler Mediterranean and warm temperate regions. Examples include *B. tryoni* in southern Australia (20); *C. capitata* in France, Italy, and possibly Austria and Germany (22, 30, 44); and *B. dorsalis* in northern China (98).

Introduction

Once a non-native fruit fly has overcome geographical barriers via human-induced transport or natural dispersal and avoided interception at points of entry, it can potentially spread into a novel habitat. Studies have been conducted on how to detect and track these new introductions (64, 101). Given the adult stage's relatively mobile and exposed life history, it is predominantly this stage that is targeted for detection. However (and excluding natural dispersal from adjacent areas), as anthropogenic transport is predominantly of the juvenile stage (either as larvae inside infested fruit or, less often, as pupae in soil), the moment that an adult is captured will likely lag far behind the actual introduction event. Given the developmental time for most (sub)tropical pests, this detection lag is usually a matter of weeks or months (but see the discussion on lag phase in the section titled Establishment), but for fruit flies with an overwintering diapause, such as representatives of the genus *Rhagoletis* (73, 90, 129), it can be several seasons long. This time lag has substantial consequences for mitigation and control measures (**Figure 1**). For example, traceback to understand the likely invasion pathway may be difficult or impossible due to the passage of time.

Trapping efficiency depends on the type of trap, the attractant used, and the emission time and efficiency of the attractant carrier, along with species' biology (e.g., temperature dependence
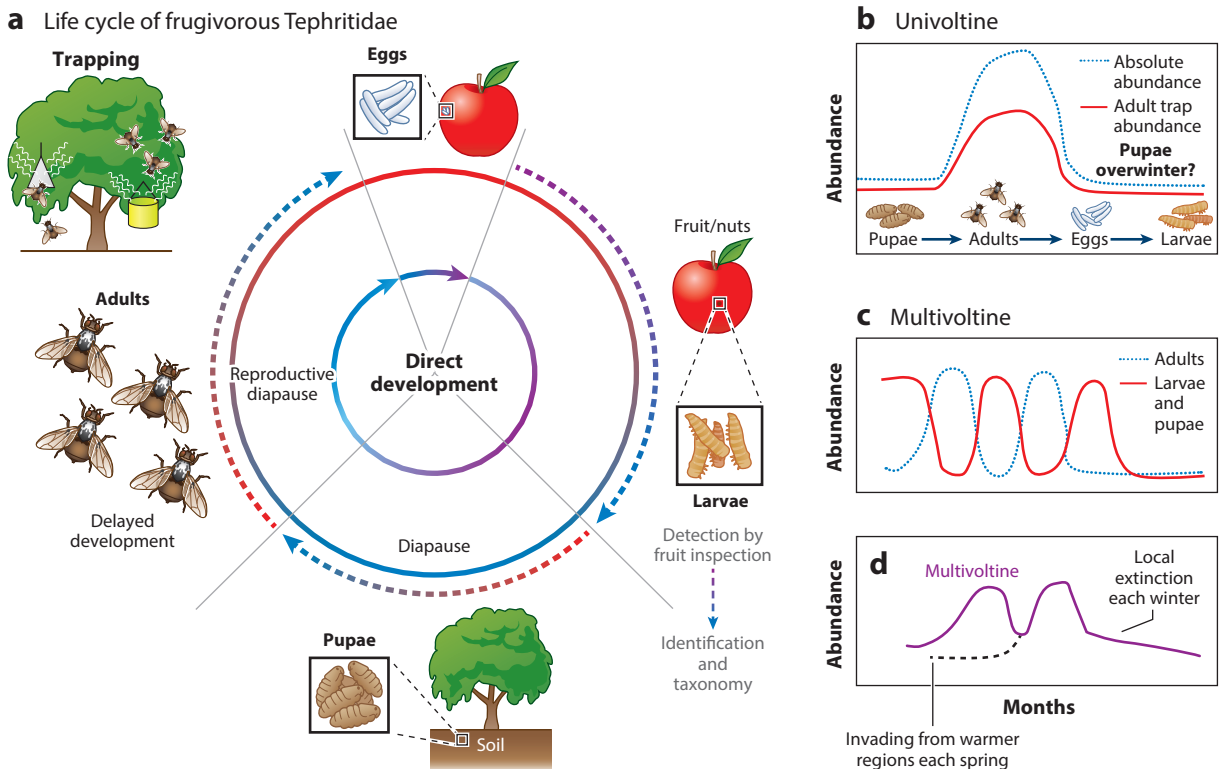
Figure 1

(*a*) Generalized frugivorous fruit fly life cycle, illustrating key life stages and the main microhabitat sites and typical detection or trapping methods associated with each of them. (*b*–*d*) Adult trap abundance and absolute population abundance may be related and (*b*) synchronized (for univoltine adults) or (*c*) asynchronized (for multivoltine adults), which introduces lags between the event and the detection thereof, thus limiting inference of key invasion processes or population dynamics. (*d*) A population may appear multivoltine when in fact it is simply invading from a warmer region each spring.

of flight ability, age of flight maturation, senescence rates, age structure of wild populations). A plethora of trapping devices are available commercially, and more are in development (65, 99). There are two major groups of attractants: protein-based lures (providing a protein source for both sexes but predominantly targeting females) and male-specific attractants (often referred to as para-pheromones) (28, 101, 121). The former are more general in their attractiveness but less effective in that they attract flies over shorter distances. Male-specific lures attract a smaller range of taxa but can be effective over longer distances. They are mainly based on natural compounds found in the wild and naturally sourced by males. Several new lures that are chemically related to the traditional ones but more efficient for targeted taxa are being developed and tested (65, 99). Nevertheless, even the most efficient lures and traps still capture only a small proportion of the fly population (an overview of surveillance sensitivity tests through release-recapture gives an exceptional maximum recapture percentage of close to 23%, but the percentage is usually between 1–4%; see 101).

Another limiting factor is the time and costs (transport, personnel) required to maintain trapping surveys. Currently, automated systems (including electronic traps furnished with digital cameras that can send images through mobile networks) that detect, identify, and report the presence of target species are being developed (17, 18). Other automated traps that have been developed for fruit flies use optoelectronic sensors to count and detect species-specific patterns of wing beat (96, 100) and light-sensing transistors (infrared LED emitters and receivers) to count captured insects that break a light beam (31). When these automated trapping systems are commercially available and deployed at scale, they promise to substantially improve the detection and response times for insect invasions and the associated costs.

Establishment

Establishment can be hard to define and quantify, especially given the trapping and detection issues discussed above; its identification typically follows a long, unpredictable lag phase (89). Survival, self-propagation, and persistence in a novel area are challenging and involve an interaction among several biological, climatic, social, and stochastic factors that have been poorly disentangled for tephritids to date.

Propagules that escape interceptions may end up in a hostile environment (e.g., unfavorable climate, lack of host, lack of mating partners, and management aimed at extirpation) and thus become locally extinct or remain undetected. Initial breeding populations are typically small and genetically restricted. Although they form the first main step in establishment and spread, they do not ensure establishment in a novel environment, since additional biological processes need to be achieved; these processes include year-round survival in an environmental mosaic of stochastic resources and breeding opportunities (59). To establish in marginally suitable novel environments, such as temperate areas, tropical invasive fruit flies must survive cold winters, with limited breeding opportunities (e.g., lack of host fruits) for several months (87). The existence of established populations at low levels that fall below detection densities for several months has been shown for several species, including medfly in northern Greece and the Queensland fruit fly in southeastern Australia (12, 88). Furthermore, individual-based stochastic modeling considering various degrees of site fragmentation and cool environmental conditions demonstrated variable population growth rates and fluctuations that can remain at low densities for months to a few years (59). Thus, the exponential population growth of the r-selected invasive tropical fruit flies is rarely achieved in the wild, at least within several generations following an invasion event (69). There can be a long lag between an introduction or invasion event and the population building up to a level detectable through trapping. Thus, the lag phase from arrival to establishment, population

growth to detectable levels, and dispersion may well hold for fruit flies (9, 54, 89). Between the Allee effect (i.e., lower population density that still leads to establishment and population viability) and exponential population growth, there are several processes that can suppress population densities of invasive fruit flies to low levels even in climatically suitable environments. Preventive management efforts, such as the sterile insect release program that has been executed for decades in Southern California against the establishment of *C. capitata*, may further contribute to hindering innate population growth, suppressing populations below detection levels but above levels that lead to stochastic extinction (for an extended review, see 137). Eradication campaigns involving the extensive use of pesticides may also suppress populations to low densities. Repeated invasion events, occurring within a reasonable amount of time to allow overlapping reproduction or mating events, may further facilitate naturalization by contributing fresh genetic material that could enhance adaptation to a new environment (55).

Detections of only a few individuals are often officially reported as a transient population, i.e., nonbreeding and established populations that require no further action as far as eradication and containment are concerned. For example, the detections of *B. dorsalis* in Naples, Italy in 2018 and in France in 2019 were both reported as "transient actionable, under surveillance" (78). The subsequent outbreak of 2022 in the same area of Naples (**https://gd.eppo.int/taxon/DACUDO/distribution/IT**) may have been related to previous detections stemming from a cryptic (undetected) population that went through a naturalization process after a lag phase of a few years. Misclassification of populations as transient may lead to poor control and delayed intervention. Detection of invasive fruit flies is often followed by aggressive eradication campaigns that aim to extirpate any breeding population in a large area; it is widely accepted that an early detection, rapid response strategy is a cost-effective management approach for invasive species, but this strategy has not been widely adopted for fruit fly control (54). Successful eradication is often declared if no detection in the specific area is recorded for at least three life cycles, considering prevailing temperatures and generic degree-day growth models [e.g., Measure 26 of the FAO International Standards for Phytosanitary Measures (ISPMs)]. For example, the eradication campaign against *B. dorsalis* in South Africa in 2010 was officially declared successful four months after the end of the campaign (66). Later work on the *B. dorsalis* invasion in South Africa revealed a sequence of several isolated male detections before any action was initiated (2007 and 2008), as well as an increase in incursions following the eradication campaign that changed the status of the pest in the area from "eradicated" to "present" and that ultimately raised questions about the apparent eradication achieved by the previous campaigns (67). The northern parts of South Africa border Botswana, Zimbabwe, and Mozambique, each of which experienced *B. dorsalis* invasions. In Mauritius, eradication was attempted following detections of *B. dorsalis* in 1996 and 2013 and was declared successful in 1999 and 2013, respectively, following the international standards. Nevertheless, additional detections in 2015, followed by major outbreaks since 2016, revealed that the fly was established on the island (104). Repeated detections of *B. dorsalis*, *C. capitata*, and a few other fruit flies in the same areas of California over decades, based on recurrence and spatial and demographic analysis, have been interpreted as stemming from established, self-sustained, low-density populations (9, 51, 89, 138, 139); however, others argue that these are the result of repeated introductions (69, 102, 137).

The existence of endemic or established fruit fly species in an area may also affect the establishment of arriving propagules of an invasive pest, especially if a superior competitor is present (12). The fruit fly literature includes several interesting cases of competitive displacement of resident species by invaders (72, 137). The presence of a superior competitor such as *B. dorsalis* may lower the risk of establishment of inferior competitors such as *C. capitata* (35).

Spread

Factors influencing the dispersal of fruit flies have been the subjects of great interest for a long time (e.g., 19, 132). Natural dispersal of larvae is likely insignificant; thus, the focus has been on understanding the movement of adult flies, particularly (*a*) propensity to move and explore the local environment (perhaps equivalent to boldness in behavioral syndromes) (108); (*b*) ability, performance, and proportion of the population that typically moves under various conditions; and (*c*) duration of (and recovery from) walking and flying various distances. There are two major factors that are widely accepted as influencing local adult dispersal: population density and nutrition. Low density plays a key role via Allee effects but also because flies need other flies to mate with (and rarely travel in pairs), and moving away from others in a population translates into a lower probability of finding mates (19). Adequate nutrition via larval host resources can result in a vigorous, flight-capable, and sexually mature fly that can withstand relatively long periods of resource limitation (either water or adult food) during dispersal (132), while low host availability promotes dispersal to new areas if environmental conditions are permissive. Consequently, while poor nutrition might create a greater propensity to move, it also likely results in a less physiologically robust fly that is incapable of long-distance, self-sustained movement. It is widely expected that sexes differ in dispersal propensity and ability, although this is not the case in *B. tryoni* and *B. dorsalis* (61). Flight mill studies often find sex effects in morphology or performance. While many studies have sought morphological correlates or biomarkers of dispersal-prone flies (e.g., 11, 62), dispersal syndromes remain poorly studied to date (see, e.g., 108), especially across the key traits that might translate into invasion success through fragmented landscapes.

KEY ELEMENTS IN FRUIT FLY BIOLOGY THAT FACILITATE INVASION

The invasiveness and overall ability of Tephritidae to occupy diverse hosts and a broad range of environments may be facilitated by a range of intrinsic and extrinsic factors, such as (*a*) life-history traits, (*b*) environmental stress response traits, (*c*) dispersal traits, and (*d*) a novel genetic admixture aiding in establishment and spread (45, 126) (**Supplemental Table 2**). The literature is patchy, and the traits that can confer an advantage to specific invasive taxa remain unclear. This advantage predominantly includes traits of fecundity, temperature dependence of growth rate and reasonably broad lower and upper developmental temperature thresholds, and early onset and delayed duration of reproductive maturity, in addition to stress resistance to, recovery from, or tolerance of stress perturbations (e.g., climatic factors such as seasonality, brief or repeated high-temperature events). Life-history traits have been demonstrated to have a strong impact on invasiveness, although, to our knowledge, there are no formal systematic comparative studies or meta-analyses of effect sizes for different traits (but see, e.g., 131, 39 for broader comparisons).

It is generally accepted that environmental stress tolerance provides an advantage during the transport, establishment, and spread phases of biological invasions. In *C. capitata*, which possesses broad thermal tolerance and great flexibility to adjust tolerances upon exposure to novel conditions, there is good evidence of broader tolerance, more rapid thermal acclimation, and longer persistence of an acquired stress response, and evolutionary adaptation to climate stress could perhaps yield comparable fitness benefits over congeners such as *Ceratitis rosa* (79). Adult *C. capitata* also possesses the overwintering capacity to persist in many temperate environments, giving them a springtime or early season advantage as soon as temperature increases (87). By contrast, *B. dorsalis*, while considered by some to be an exemplar invader and able to outcompete *C. capitata* in tropical Africa, does not appear to have an exceptionally pronounced thermal advantage over *Ceratitis* species when thermal limits for activity and survival are compared (92).

Some research groups working on the functional genomics of *B. dorsalis* suggest that it is genetically predisposed to and has unusually high adaptive capacity for thermal stress tolerance (e.g., 136). However, the whole-animal phenotypes assayed to date do not necessarily support such a view, finding thermal tolerances are inferior compared to several *Ceratitis* species. Regardless, at present, no studies have determined whether the native-range populations underwent a fundamental climatic niche shift or tested whether niche shifts are typical of the genus or characteristic of highly invasive tephritid species more generally.

In the case of dispersal, only a subset of individuals in a tephritid population exhibit dispersal behavior. Of those that disperse willingly, most individuals fly a few hundred meters over several small flight bouts, but a rather small proportion of the population (<10%) will engage in sustained, long-distance dispersal of several kilometers (11–35 km) in their lifetime (61). Long-distance dispersal is also likely to come with substantial costs; it remains unknown whether body condition is depleted so far as to impact fitness upon arrival in a poor-quality environment, so the invasion significance of such events is unclear. Automatic flight mills can log distance traveled under controlled conditions over a short timeframe and have frequently been used to assess dispersal ability and the effects of temperature, body size, irradiation, and mating status (e.g., 61). In the field, flies are typically marked with, e.g., fluorescent powder; released at a central location; and then recaptured at a range of distances to infer dispersal patterns under varying conditions or over longer timescales (21). Studies of Tephritidae have increasingly probed the impact of different handling protocols or thermal treatments on recapture rates or dispersal patterns (107). For invasiveness, the evidence is mixed or weak, and it is therefore rather unclear if dispersal traits play a strong role in tephritid invasions; indeed, we are unaware of any studies that have directly compared the relevant traits across populations or species varying in invasion success.

One mechanism proposed to explain the invasiveness of several cosmopolitan insects is the invasion bridgehead hypothesis, where successive introductions result in a novel genetic admixture that gives rise to a population with fitness advantages in the invasive range, increasing its invasiveness (137). However, Bertelsmeier & Keller (4) argue that this observed increase in invasiveness has more to do with the increased abundance at the bridgehead population and emphasized that adequate tests of this hypothesis are lacking. In Tephritidae, there is some weak evidence to suggest that genetically unusual or atypical populations with high levels of heterozygosity were the source for a particular geographic range expansion or niche shift (42); in other words, novel genetic mixture may have contributed some key genetic material to the invasion process. However, this idea is contentious and requires further testing coupled with comparisons of functional traits. In addition to novel genetic admixtures of the metazoan organism, the role of host–microorganism interactions in the invasion process is a relatively new field of investigation. Recent studies show that microorganism commensals contribute to the feeding success of phytophagous organisms such as fruit flies by supporting rapid diet shifts (41), which could allow fruit flies to exploit novel hosts in their newly invaded environment (2).

MODELING FRUIT FLY POPULATIONS TO INFORM TEPHRITID INVASIONS

There has been considerable effort applied to modeling fruit flies to inform management questions at different stages of the invasion process (**Supplemental Table 3**). Interestingly, much of this effort has been focused on a few high-profile, charismatic species, with different modeling groups completing similar models on the same few species.

Bioclimatic models are used to understand the potential distribution of invasive fruit flies. This knowledge allows each jurisdiction to understand what invasion hazard they face. Combined with

information on the distribution of assets at risk, invasion pathways, and propagule pressure, this understanding allows a full estimate of the invasion risks. These bioeconomic assessments are frequently used to justify phytosanitary and other measures to attenuate the risks or surveillance and reporting measures to maintain market access.

There are two paradigms in bioclimatic modeling (115): process-based or process-oriented niche models such as CLIMEX (34, 47, 117) and correlative species distribution models (SDMs) such as GARP (109) and MaxEnt (91). Niche models can draw on information from multiple knowledge domains to achieve robust cross-validation (e.g., 134). In contrast, SDMs are trained solely on species distribution data and thus are sensitive to the frequent errors or biases in these data (32). A frequent problem in tephritid modeling is the inclusion of location records from xeric locations where flies and their hosts only persist because of artificial irrigation, with the resulting model overstating the risks of invasion into xeric habitats. SDMs are also prone to overfitting, where the modeler makes a choice to use more covariates than is prudent, resulting in a model that fits the input data (too) closely and consequently understates the establishment risks elsewhere (e.g., 60).

Mathematical models can inform biosecurity management at multiple points in the invasion process. For example, phenological models can be used to inform border surveillance, as well as the seasonal timing of scouting and pesticide application. Similarly, analytical models of life stage vulnerability can be used to target control efforts during eradication campaigns, as well as in post-border pest management.

Kean & Stringer (43) developed a growth index–style model to inform the seasonal deployment of traps to detect flies at the biosecurity border, delivering significant surveillance savings by not maintaining the surveillance during inclement seasons. The same type of model could be used to inform post-border pest surveillance.

The SIT is a mainstay of eradication and suppression programs (21, 111). To be effective, the ratio of sterile male to wild male flies must be maintained at high levels throughout the area of the infestation. Variance in this ratio in time or space can rapidly undermine the system (94). Models have been developed to inform the spatial and temporal deployment of SIT releases. The relatively poor dispersal of released flies and their short lifespan indicate that releases should be made every 200–400 m (70, 95). Roving releases and aerial releases could improve the coverage and reduce the spatial variance in the overflooding ratio substantially (71). Because of the negative exponential nature of the survival and dispersal factors, reducing the variance in coverage is far more cost effective than increasing the numbers of sterile flies released (95).

There are several techniques available to control tephritid incursions. The challenge is to understand when it is appropriate to deploy each technique and how it should be deployed. Modeling has suggested that management actions targeted at interfering with egg laying are the methods that are most likely to be effective at reducing populations of *B. tryoni* (111). This is logical, since adult female flies are numerically the smallest component of the population, and they are accessible and relatively detectable. When used concurrently, the MAT interferes with the SIT because it kills the sterile males. However, if deployed prior to the SIT, the MAT can reduce the number of wild males, improving the overflooding ratio for the SIT. Protein bait sprays targeting both males and females can enhance control slightly over the SIT alone (111).

An important question for eradication campaigns is the stopping rule, i.e., how to define the end of the campaign. MED-FOES (63) is an agent-based model designed to dynamically simulate the eradication of *C. capitata* in California. Modeling using MED-FOES suggests that the regulatory rule for declaring eradication success after three generations, estimated by degree-day modeling, likely resulted in premature cessation in some cases, while other campaigns were prolonged unnecessarily (63).

Wang and colleagues (130) describe an individual-based model focused on *B. tryoni* host-finding behavior to inform the spatial deployment of fruit fly traps. The model indicated that the best location to place a trap depended primarily on the fly species and the canopy architecture. Placing the trap as high in the canopy as practicable and on the edge of the canopy should maximize fly catch for closed-canopy trees, while placing the trap in the mid- to upper canopy should maximize catch for vase-shaped trees.

In a tephritid surveillance program, it is often economically desirable to survey for multiple species at the same time, to reduce the average cost of servicing traps for each species (112). While there is more work to be done on this topic, it appears possible to combine male lures for some tephritid species. System-wide sensitivity can be maintained by increasing the density of the traps, but this will reduce the cost savings; in addition, attention needs to be paid to potential interference between lures (112).

A critical element of creating mass trapping networks is to understand the effective area of a trap. Suckling et al. (114) describe a simple method for assessing the appropriate trap density, identifying the critical density at which trap interference occurs.

Degree-day phenological models have been developed for several tephritid species to inform pesticide applications (**Supplemental Table 3**). In other settings, this style of modeling could be used to inform pest scouting and trapping, as well as IPM decision making.

CURRENT METHODS TO MANAGE FRUIT FLY INVASIONS

For many geographical regions, regulations or strategies for tephritid management are not clearly defined or publicly available. In cases where they are available, the interpretation can vary by country and at different governmental levels, making a standardized approach difficult. Internationally, the International Plant Protection Convention (IPPC), an intergovernmental treaty, plays an important role in setting out global standards for plant health management. This is the result of the Sanitary and Phytosanitary Agreement, which defined the role of the IPPC in the development and harmonization of such regulations and standards (29). These are presented as ISPMs. While most of the ISPMs are generic, many of these standards apply specifically to fruit flies (e.g., ISPM26, concerning the establishment of pest-free areas for fruit flies; ISPM35, concerning a systems approach for pest risk management of fruit flies; and ISPM37, concerning determination of the host status of different fruit species for fruit flies). In addition, several appendices to ISPM27 (diagnostic protocols for regulated pests) and ISPM28 (phytosanitary treatments for regulated pests) deal with specific fruit fly taxa. In the United States, the Plant Protection Act of 2000 (also called the Agriculture Risk Protection Act; Public Law 106–224) regulates all activities at the federal level to prevent the introduction into or dissemination within the United States of invasive species. This act combines responsibilities that were previously dispersed over several pieces of legislation. This federal act can be supplemented by additional legislation at the state level. For the European Union, the most important recent regulation is EU 2016/2031 on protective measures against pests of plants (officially in place since December 2019 and introducing a proactive approach to prevent introduction of non-EU pest organisms into the European Union). One of the requirements of this regulation is that member states develop a surveying program in their territory that will allow rapid detection of the presence of specified non-EU pest organisms if they pose a threat of establishment to the member state. The European Union also provides a listing of quarantine organisms, with regulation EU 2021/2285 including 75 tephritid taxa. In addition, the delegated regulation EU 2019/1702 dealing with priority organisms includes four tephritids (*Anastrepha ludens*, *B. dorsalis*, *Bactrocera zonata*, and *Rhagoletis pomonella*). Any actions and the ways in which they are developed are the responsibility of the individual member state, but several

bodies within the European Union aim to coordinate some of the necessary tools and measures, such as pest survey cards for each priority pest compiled by the European Food Safety Agency or identification standards developed by the European Reference Laboratory for Insects and Mites. Other countries with large horticultural activities that are vulnerable to invasive plant pests have developed their own policies, such as Australia's Plant Quarantine Pest and Official Control National Policy (123). In developing countries in Africa, most management actions are at the national level, but the current state of development is variable from country to country. Such country-specific action programs are described by Ekesi et al. (24). In recent years, overarching regional programs have been developed, in particular in western Africa, by the Regional Agency for Agriculture and Food of ECOWAS, through the SyRIMAO program funded by the European Union and the French Government (**https://capacity4dev.europa.eu/projects/desira/info/syrimao**).

The first step to address fruit fly invasions is the development of a comprehensive pest risk assessment (PRA) to assess the risk, impact, pathways of introduction, and direct preventive interventions at point and time of entry (37). Scenario-based PRAs consider data regarding propagule pressure and potential for establishment and dispersion into new areas (see above) and may include assessment of the risk of importing infested fruit. A recent biosecurity PRA model has been developed for *B. zonata* in New Zealand considering two scenarios: (*a*) with current biosecurity measures and (*b*) an alternative with no management applied (37). Several other PRAs have been developed for other fruit flies, such as *B. zonata*, *Ceratitis quilicii*, and *C. rosa* (122, 139). Four elements to reduce risk (i.e., minimizing exposure and vulnerability of a host commodity to pests and reducing infestation rates and establishment risk) at three production stages (preharvest, at harvest, and postharvest) have been recently organized in a systems framework to address invasive fruit fly pests (124). Of the 60 protocols reviewed, 40 dealt with fruit flies and imposed measures and actions to put in place pest-free or low-prevalence areas, cover the crop (netting), harvest and trade fruits at early ripening stages (e.g., banana), and implement quarantine postharvest treatments (e.g., cold treatment, hot treatment, irradiation), among others. Detections of specimens that break the above barriers are categorized as either transient, requiring no actions, or incursions, often resulting from a breeding or an established population, which can trigger aggressive eradication or containment campaigns. The fruit fly invasion literature reports a list of eradication efforts that encompass different tools and approaches. The sterile insect release method has been used as the main management tool in short- and long-term eradication campaigns executed for medfly in California, Florida, South Australia, and Mexico (8, 25, 26). Male annihilation based on strong male-specific attractants in lure-and-kill methods has been used to eradicate *B. dorsalis* from California, Florida, northeastern Australia, Mauritius, and other areas (104, 105). Pesticides have also been used in eradication campaigns as a stand-alone tool or to reduce population densities before the application of the SIT. Likewise, inundative releases of parasitoids have been combined with the SIT.

FUTURE ISSUES

1. We recommend establishing a global database of fruit fly invasions, under the aegis of the International Plant Protection Convention, focused on post-border detections that includes details of each event in time and space (e.g., number of individuals, geographical coordinates, host, management tactics, cost of intervention) to support heuristic learning on how to best manage fruit fly invasions. An International Standard for Phytosanitary Measures could be developed to define data standards and reporting procedures.

2. We recommend investing in developing enhanced tools with sufficient geographical coverage to analyze local and global biological invasions (e.g., genetic and genomic tools) to (*a*) trace the geographic origin of intercepted or detected alien fruit flies, (*b*) resolve seasonal population dynamics, and (*c*) develop a reference genetic database covering the native and invaded range of the invasive fruit flies.

3. We recommend refining and developing modeling methods and establishing flexible systems to estimate dynamic spatiotemporal risks at various levels that are related to fruit fly invasion (e.g., *Bactrocera dorsalis* detection in Europe). This capability can inform efficient and effective border surveillance activities and aid in early detection and rapid response.

4. We recommend establishing comprehensive, real-time online platforms to share information on tephritids (and potentially other pests) and run identification, modeling, and management operations. For efficiency, these would ideally be global resources.

5. We recommend investing more in understanding the invasion traits and adaptive capacity of fruit fly species, including efforts on the lesser-studied species.

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