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Invasion biology of spotted wing *Drosophila* (*Drosophila suzukii*): a global perspective and future priorities

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Abstract The Asian vinegar fly *Drosophila suzukii* (spotted wing *Drosophila* [SWD]) has emerged as a major invasive insect pest of small and stone fruits in both the Americas and Europe since the late 2000s. While research efforts have rapidly progressed in Asia, North America, and Europe over the past 5 years, important new insights may be gained in comparing and contrasting findings across the regions affected by SWD. In this review, we explore common themes in the invasion biology of SWD

by examining (1) its biology and current pest status in endemic and recently invaded regions; (2) current efforts and future research needs for the development of predictive models for its geographic expansion; and (3) prospects for both natural and classical (=importation) biological control of SWD in invaded habitats, with emphasis on the role of hymenopteran parasitoids. We conclude that particularly fruitful areas of research should include fundamental studies of its overwintering, host-use, and dispersal capabilities; as well as applied studies of alternative, cost-effective management techniques to complement insecticide use within the integrated pest management framework. Finally, we emphasize that outreach efforts are critical to effective SWD management by highlighting successful

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strategies and insights gained from various geographic regions.

Keywords Biological control · *Drosophila* · Frugivore · Integrated pest management · Invasion biology

Key message

- Spotted wing *Drosophila* (SWD) is a major invasive pest of soft fruits in the Americas and Europe.
- We review the current global distribution and economic impacts of SWD, develop models for predicting its further spread, and discuss the prospects for biological control of this pest.
- The following research areas into SWD biology appear particularly promising: its biology at low temperatures, the dispersal and migratory abilities of adults, and exploration in Asian regions for potential classical biological control agents.

Introduction

Spotted wing *Drosophila*, *Drosophila suzukii* (Matsumura) or SWD, is a newly significant worldwide pest of berries and stone fruits, with adverse economic effects having been

reported in its native continent of Asia, the Americas, and Europe (Fig. 1) (Lee et al. 2011a; Calabria et al. 2012; Deprá et al. 2014; Kinjo et al. 2014). Of particular concern is the rate of SWD's global spread. Despite isolated early reports of SWD-related damage in Asia (Kanzawa 1939; Tan et al. 1949), first reports of the pest in North America and Europe date back only to the late 2000s (see below), followed by rapid range expansion within these continents. This leaves many unanswered questions related to putative invasion corridors and dispersal modes, thermal constraints on SWD biology, and the absence of effective levels of natural biological control in the invaded regions (Cini et al. 2014; Wiman et al. 2014).

Following a brief review of SWD biology, we examine its recent invasion into North America and Europe, and its pest status from a global perspective to assess biological similarities and differences among regions near its native range, and those newly invaded by the pest. Recent demographic modeling research is reviewed with the aim of providing a better understanding of the future geographic spread of SWD, and new directions for research. After updating the geographic component of SWD invasion, current management practices in the US are reviewed as a case study for applied research and extension efforts. Finally, given the strong ties between invasion biology and biological control (Fagan et al. 2002), we close with a review of the current prospects for natural and classical (=importation) biological control of SWD by hymenopteran parasitoids.

Pest biology

Taxonomy and identification

SWD is a member of the *D. suzukii* subgroup within the *D. melanogaster* species group of the subgenus *Sophophora* (Diptera: Drosophilidae). The *D. suzukii* species subgroup is not traditionally considered monophyletic; however, this interpretation hinges on the exclusion of a single species (*D. lucipennis*) (Yang et al. 2011a). Recent molecular phylogenetic analyses suggest a sister group relationship between SWD and *D. biarmipes* (Yang et al. 2011a; Chiu et al. 2013).

Two key morphological characters are commonly used to differentiate SWD from other drosophilids (Kikkawa and Peng 1938; Walsh et al. 2011; Cini et al. 2012): (1) a dark spot on the leading wing edge of males, and (2) a large serrated ovipositor in females (Fig. 2a). While these traits are readily observable with appropriate magnification, they may not be completely diagnostic. This is because (1) wing spots require up to 2 days to be fully formed, and (2) these traits are similar to those found in some closely related species (e.g., *D. subpulchrella* possessing a serrated

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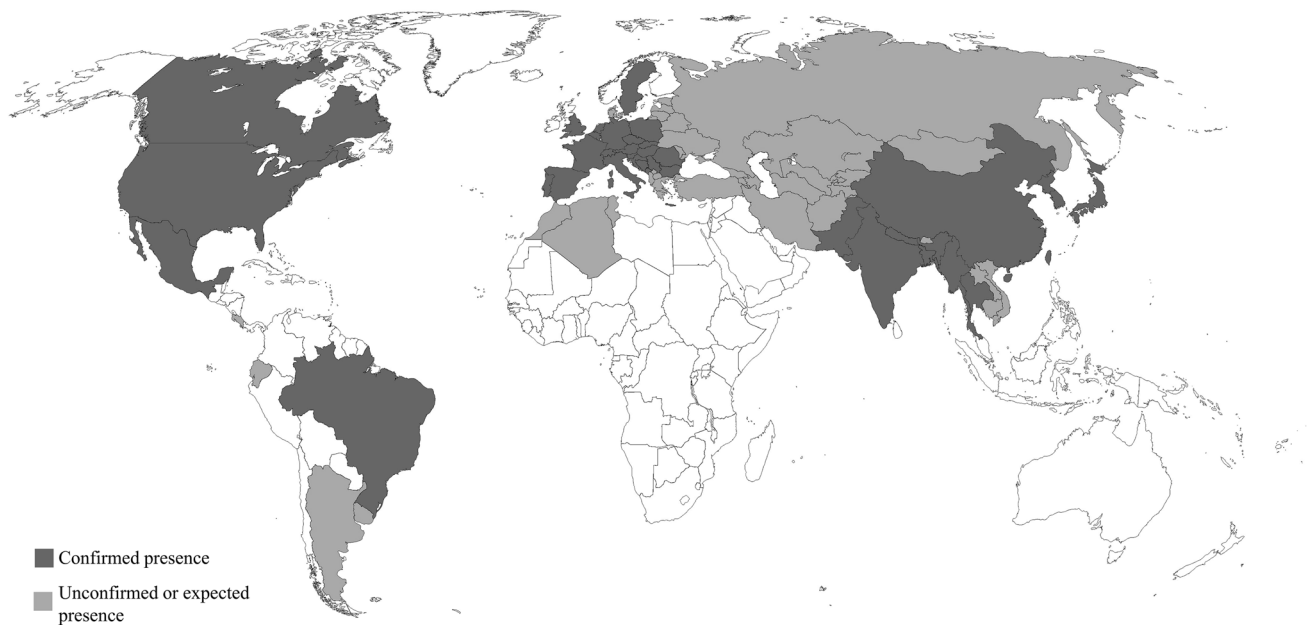


Fig. 1 Current worldwide SWD distribution map (as of May 2015). Countries are indicated as follows: (1) SWD presence has been confirmed (*dark gray*), and (2) SWD is considered present because of geographic proximity, or because the presence has been not confirmed after an initial record (*light gray*). Hawaiian Islands are not

ovipositor and similar dark wing spots; see Hauser (2011) for a more detailed discussion of SWD identification). More accurate identification may require molecular diagnostic methods, which have been developed for this species (e.g., Kim et al. 2014).

Life history, damage, and host range

Most *Drosophila* species associated with humans are considered nuisance, household and fermentation industry pests. For example, *D. melanogaster* is often attracted to overripe or spoiled stored fruits. SWD, on the other hand, shows a preference for ripening or ripe fruit, the skin of which is penetrated by its serrated ovipositor (Lee et al. 2011b). Eggs are deposited under the oviposition scar, with larval development progressing through three instars feeding on internal fruit tissues (Fig. 2b). Pupariation and pupation typically occur partially or fully outside of infested fruit (Fig. 2c). As in other insects, development rates are temperature dependent, with total time from egg to adult ranging from 10 to 79 days (Kanzawa 1939; Lee et al. 2011a; Tochen et al. 2014). Depending on the weather conditions, up to 13 generations can be found per year (Kanzawa 1939; Tochen et al. 2014), and the short generation time coupled with high reproductive potential causes rapid population growth and increasing pest pressure through the crop-ripening season (Wiman et al. 2014). The pre-oviposition period is ca. 1–3 days and oviposition

represented although SWD presence has been known since 1980 (Hauser 2011 and references herein). The information provided is based on a compilation of reports from plant protection services and extension specialists, and on published scientific articles

rates can exceed 25 eggs per day, depending on temperature (Kinjo et al. 2014). The highest net reproductive rate and intrinsic rate of population increase was recorded at 22 °C on cherry (Tochen et al. 2014). During summer months, SWD adults are most active at temperatures ranging between 15 and 20 °C, and activity decreases at temperatures above and below this range (Hamby et al. 2013).

SWD-related damage to fruit can be both direct and indirect in nature. Internal larval feeding constitutes the main source of direct damage, leading to fruit tissue collapse (Fig. 2d). In addition, the process of oviposition by SWD exposes fruit to secondary pathogens (e.g., bacteria and yeasts) (Cini et al. 2012; Hamby et al. 2012; Ioriatti et al. 2015). Finally, deterioration of fruit by SWD can increase its susceptibility to attack by other drosophilid species (Walsh et al. 2011).

SWD possesses a broad host range, with thin-skinned berries (e.g., caneberries, blueberries, strawberries) and stone fruits (e.g., cherries, peaches, apricots, plums) being particularly susceptible to infestation (Bellamy et al. 2013). In Japan, where SWD biology has been studied since the 1930s, Kanzawa (1939) reported SWD-related damage on various fruit crops with subsequent authors reporting its occurrence on various wild fruits as well (Kimura et al. 1977; Nishiharu 1980; Mitsui et al. 2010).

In the US, raspberries and strawberries appear to be particularly preferred hosts for SWD (Bellamy et al. 2013;

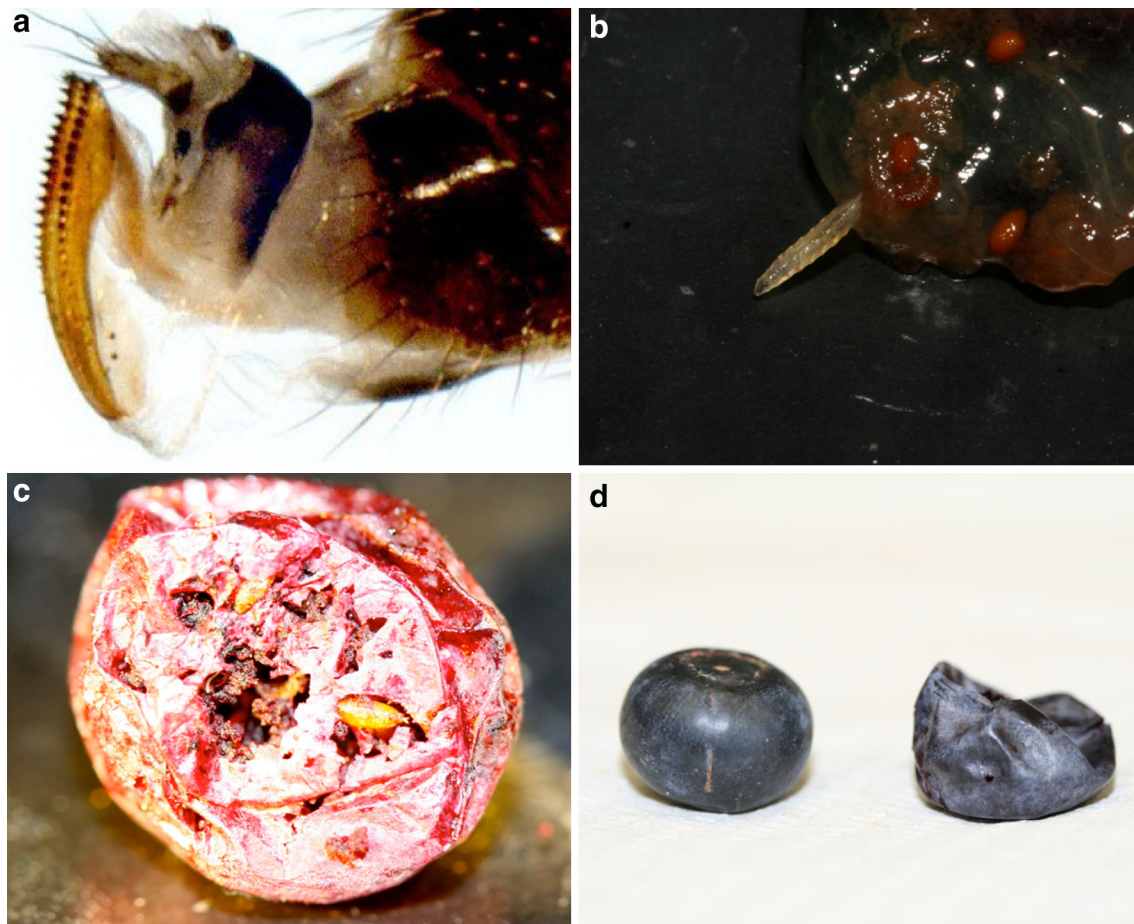


Fig. 2 **a** Magnified view of the SWD ovipositor, **b** SWD larva infesting blueberry tissue, **c** SWD pupae infesting fruit. **d** Comparison of blueberry fruit morphology when undamaged (*left*) or after 1 week

of SWD infestation (*right*). Photographs in (**a**) by Martin Hauser, those in (**b**), (**c**), and (**d**) by Vaughn Walton

Burrack et al. 2013), while some other small fruits, such as cranberries, are unsuitable unless damaged (Steffan et al. 2013). Certain fruits (e.g., apples, pears, tomatoes) can also be infested if split or previously damaged (Lee et al. 2011a), but SWD is not a significant pest of these crops. In addition to cultivated fruits, many wild plants can serve as potentially important hosts (Mitsui et al. 2010; Cini et al. 2012; Poyet et al. 2014; Lee et al. 2015). Important SWD host associations are mentioned for specific countries in the following section.

Worldwide pest status and geographic spread

The known worldwide distribution of SWD is based on a review of CABI (2014) as well as the most recent current literature (Fig. 1). We expect this distribution to expand further with additional monitoring for this pest. The purpose of our review is to not provide a complete list of all countries with documented SWD infestations; rather, our

aim is to contrast the historical context of SWD in Asia with a perspective on what is being learned from the most recent invasions in North America, South America, and Europe.

Asia

Japan

SWD was first reported from mainland Japan in 1916 (Kanzawa 1939). The highest SWD population levels in Japan occur on the three main islands (Honshu, Kyushu, and Shikoku: 30–41.5°N in latitude); however, it occurs with lower frequency in the northernmost main island (Hokkaido: 41.5–45.5°N), and is least frequently observed in the southernmost islands (Ryukyu archipelago: 24–27°N) (Momma 1954, 1965; Nishiharu 1980; Beppu 2000; Hirai et al. 2000; Kimura 2004; Kondo and Kimura 2008). In central Japan, it reproduces from mid-April to late October and overwinters as an adult (Sasaki and Sato

1995b, c; Mitsui et al. 2010). It is not clear whether this species is able to overwinter successfully in Hokkaido (Kimura 2004).

Economic losses due to SWD in Japan are concentrated on cherries (Kanzawa 1939; Yamakawa and Watanabe 1991; Sasaki and Sato 1995a), although considerable losses have been reported recently on blueberries (Shimizu 2004; Kawase et al. 2008). Wax-myrtle fruit (*Myrica rubra*) is also attacked by SWD, but this crop is not economically important (Yukinari 1988). Control in cherry (*Prunus avium*) and blueberry (*Vaccinium* spp.) crops is typically achieved through insecticides or covering with nets (Yamakawa and Watanabe 1991; Kawase et al. 2008).

Resource conditions for SWD in Japan vary both seasonally and regionally. In central Japan, for example, putative wild hosts are abundant in late spring and autumn at low altitudes. This changes in mid-summer, however, where they are far more abundant at high altitudes (Mitsui et al. 2010). To cope with these changing conditions, it is hypothesized that SWD seasonally migrates between low and high altitudes (Mitsui et al. 2010).

Korea

SWD is widely distributed in cities, towns, crop production areas, and natural environments throughout Korea, including Jeju Island (Fig. 3a). Nagayama and Okamoto (1940) described damage to Korean-type cherries (*Prunus tomentosa*), grapes, and Autumn olive (*Elaeagnus umbellata*). Since no reports of SWD-related damage have been made, this species has not been considered a pest in Korea, and no studies have been conducted outside of faunistic surveys.

More in-depth research on SWD in Korea was stimulated following the export of Korean table grapes (*Vitis vinifera*) to Australia. The QIA (Animal and Plant Quarantine Agency) installed clear plastic bottle traps containing apple cider vinegar (ACV) and wine in 20 sites (including montane habitats, vineyards, table grape packing houses, blueberry orchards, cherry orchards, and strawberry [*Fragaria* × *ananassa*] farms) in order to track SWD population levels from September 2011 onward (Choi 2012). The results suggest that this species begins to emerge in May, with population numbers increasing rapidly in autumn (Fig. 3b). In addition, QIA and Chonnam University researchers are currently analyzing mitochondrial COI genes from several Korean SWD populations, as well as two from China. The goal of this study is to accumulate sequence information for examining genetic diversity, which is necessary both for molecular species identification and determining geographic genetic variation (Kim 2013; see below).

China

Tan et al. (1949) first reported SWD in China. The country houses a rich fauna in the *D. melanogaster* species group, comprising at least 67 species. Among them, six (*D. auraria*, *D. kikkawai*, *D. melanogaster*, *D. simulans*, *D. suzukii*, and *D. takahashii*) are geographically widespread, with SWD having been detected in at least 22 Chinese provinces (Fig. 4; Xue and Zhao 1996; Qian et al. 2006).

During the past decade, *Drosophila* spp. have been among the most important fruit pests in China, especially in the production of cherries, Chinese cherries, blueberries, and wax-myrtle fruit (Guo 2007). Increased damage levels

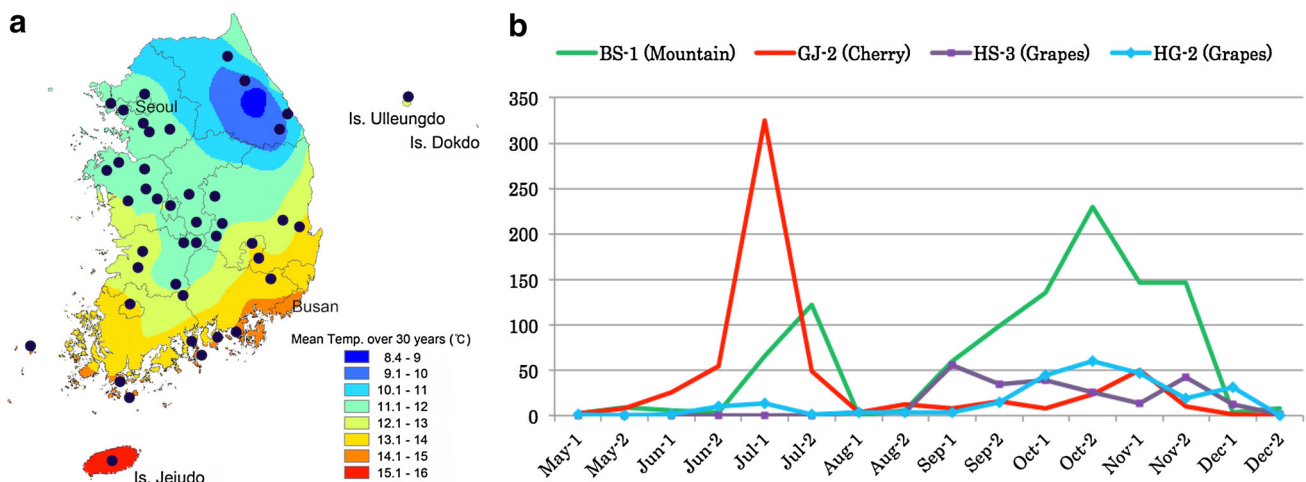


Fig. 3 SWD demography and phenology in South Korea. (a) Geographic distribution of SWD in South Korea. From Kim et al. (2012). (b) Seasonal captures from a trapping network in South Korea (see

text for details). Trapping locations are as follows: *BS* Busan, *GJ* Gyeongju-si, *HS* Hwaseong-si, *HG* Hwanggan-myeon

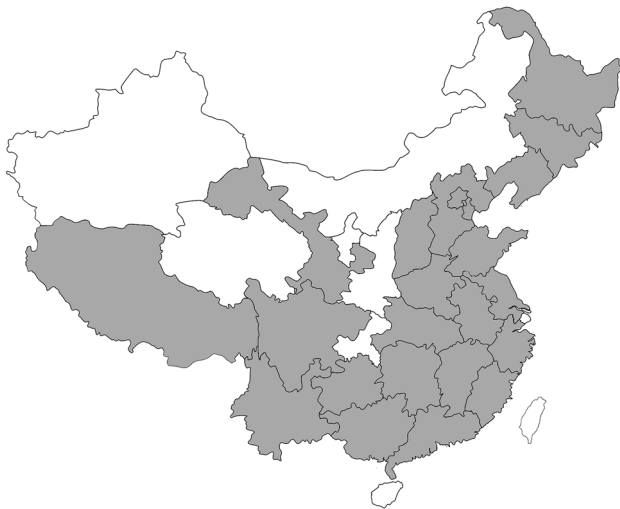


Fig. 4 Current geographic distribution of SWD in China. Provinces colored in light gray are those with confirmed presence of the pest

are likely linked with rising levels of fruit production (Zhang et al. 2012). In cherries, three species dominate: *D. melanogaster*, *D. suzukii*, and *D. hydei*. Interestingly, previous records (Guo 2007) suggest that SWD is not the dominant *Drosophila* species in Chinese fruit production; as such, it appears that the relative damage from SWD is not as severe as that found in North America and Europe.

While SWD has not been considered a problematic pest in China, there is still potential for it to cause significant damage in cherries and wax-myrtle fruit in certain provinces. For example, field infestation rates of cherry fruit by SWD in Wenchuan (Sichuan province) have reached 21.5–42.3 % (Zhang et al. 2011), and significant damage of cherries has also been reported in Gansu, Henan, Shandong, Shanxi, and Sichuan (Guo 2007; Hui et al. 2010; Yang et al. 2011b). In addition, as levels of commercial production of wax-myrtle fruit have increased in southern China (Wang et al. 2003; Wang and Xu 2004), considerable SWD-related damage to this fruit has been reported (Wang et al. 2003; Jiang et al. unpublished data). Wax-myrtle fruit ripens during the early summer in southern Chinese growing regions, when climatic conditions are most suitable for SWD survival, growth, and reproduction. The most remarkable example of wax-myrtle damage occurred in Honghe (Yunnan province) where SWD populations peaked between 15 and 30 May and infestation rates reached 80 % (Wu et al. 2007).

Several factors may explain the different levels of SWD-related damage observed in China versus the North American and European invasions. First, more efficient top-down regulation of SWD populations by natural enemies (especially specialist parasitoids) may be occurring in China (see below). Furthermore, the high abundance of *D. melanogaster* and *D. hydei* may impose higher levels of

interspecific resource competition. Finally, at least in the population introduced to the US, elimination of a genetic load may have occurred through a severe bottleneck; this is supported by the observation of fewer mitochondrial haplotypes in this population when compared with those from China or Korea (D. Chu, unpublished data). This bottleneck appeared not to be as severe in nuclear genes compared to Japan (Adrion et al. 2014), however, indicating the importance of a wider population genetic analysis for a correct understanding of its invasion and damage behavior.

North America

Pacific coast and western US

SWD was first recorded on berry crops in the coastal production regions of California in 2008. In May of the following year, some cherry producers recorded losses due to SWD (Goodhue et al. 2011). In August 2009, after positive identification of SWD on blueberries in Oregon, a website and pictorial guides (www.spottedwing.com, Dreves et al. 2009; Walton et al. 2011) were created to help growers identify and report potential infestations. Within the remainder of the 2009 growing season, SWD was reported in all major small and stone fruit production areas of this region, ranging from southern California to British Columbia, Canada. The primary economically affected crops in these regions include blueberries, raspberries, blackberries, and cherries (Lee et al. 2011b; Bellamy et al. 2013). Without adequate control measures, SWD-related damage can result in up to \$500 million in annual losses in Western US production areas (Goodhue et al. 2011).

Current infestation patterns differ substantially among Pacific production regions of the US (Fig. 5). In mild coastal California regions, SWD can be found year round with pest pressure adequate to warrant control action as soon as fruit starts to ripen and until the last harvests of the season. In the central San Joaquin Valley regions, however, populations develop during the early portion of the season and then decrease to virtually undetected numbers during the middle of the season when air temperatures exceed 30 °C (Dalton et al. 2011; Tochen et al. 2014). When temperatures become more suitable during the latter portion of the season in this region, populations can increase to a peak in late November after which they decrease to virtually undetectable numbers during colder December conditions.

Winter survival studies (Dalton et al. 2011) indicate that some non-cold hardy individuals will persist in cool winter temperatures, as found in coastal production areas in this region. In contrast, inland areas are subjected to more prolonged cold periods of higher intensity. For this reason, lower survival rates in these areas are likely. In

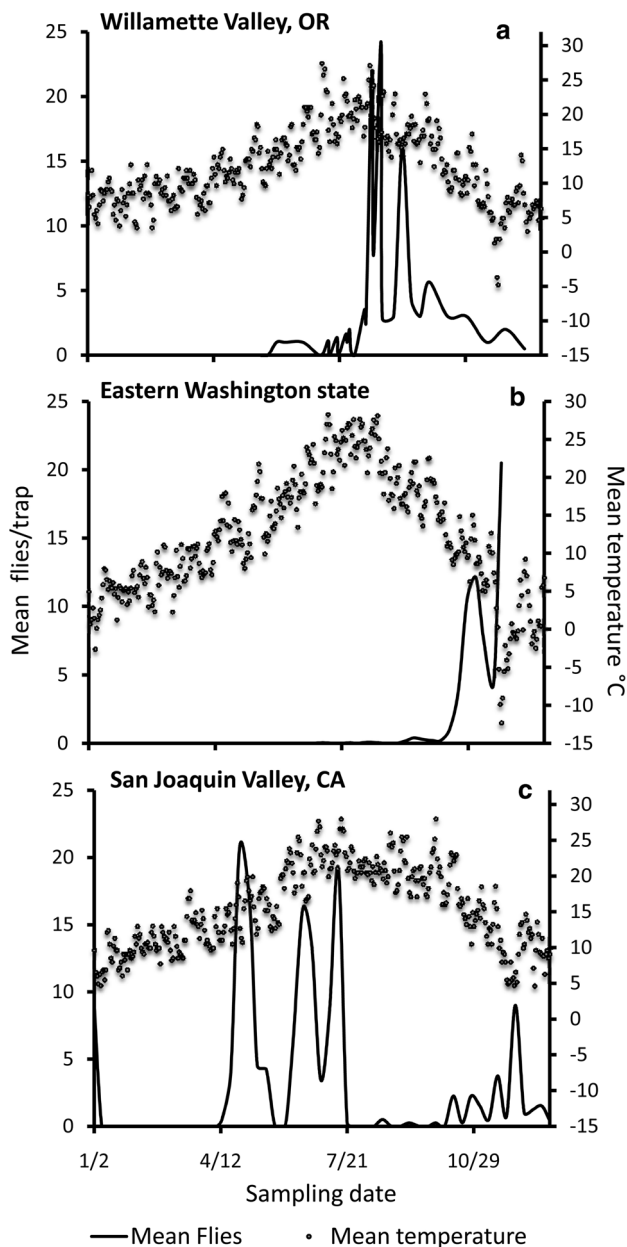


Fig. 5 Adult SWD counts as a function of trapping date in representative Pacific regions of the US: (a) the Willamette Valley in Oregon, (b) Eastern Washington state (e.g., Columbia Gorge, Columbia Basin), and (c) the San Joaquin Valley in California. Adapted from Dalton et al. (2011)

progressively colder regions, the first SWD captures in traps were found later during the season (Dalton et al. 2011). Seasonal counts of SWD increase during April in California, suggesting higher winter survival rates compared to the Pacific Northwest. Winter survival in areas of extreme cold likely relies on the ability of SWD to adapt to colder climates or overwinter in man-made habitats or other sheltered sites, while seasonal migration may allow populations to build to high numbers throughout the summer and fall.

Eastern US

States east of the Rocky Mountains have locally significant areas of berry crops and stone fruit production, with many plantings set within small (0.1–5 acre) fields. Additionally, the customers of many of these producers expect that the fruit will be sustainably or organically managed, and farmers have invested in these practices accordingly. While this situation is common across the whole of the eastern US, there are also local concentrations of larger-scale commercial plantings of susceptible berry and cherry crops (e.g., strawberries in Florida and North Carolina; blueberries in Michigan, New Jersey, North Carolina, Georgia and Florida; caneberrries (*Rubus* spp.) in North Carolina and New York; and tart cherries in Michigan).

Early reports of SWD detection and its related economic damage on the Pacific Coast (Goodhue et al. 2011; Bolda et al. 2010) led to an initial awareness of this pest within the eastern US in 2008. The 2009 detection of SWD in Florida (Price et al. 2012) created significant alarm in some eastern states with large areas of susceptible crops; as a result, monitoring programs were initiated (e.g., Isaacs 2011). During 2010, SWD was also found through similar monitoring efforts in North and South Carolina, Mississippi, and Utah. In 2011, sixteen additional states east of the Rocky Mountains reported first detection of SWD, but for some this was made evident only once the pest had already reached high populations and fruit damage caused growers to report infested fruit. In subsequent seasons, SWD has been detected through most of the temperate regions of the US.

The early detections of SWD in eastern states occurred because extension entomology programmes quickly put monitoring programmes in place for susceptible crops. In addition, the early detections in the eastern US highlighted the importance of preparation of agricultural stakeholder groups for the possible arrival of a new pest. The SWD situation also demonstrated that grower responses to a new, widely distributed pest are often delayed until the problem is experienced first-hand. Despite considerable extension efforts, many potentially affected producers with susceptible crops did not monitor or prepare for SWD. Unfortunately, it took the economic hardship of lost sales due to infestation detection or downgraded fruit to elicit a significant response.

In North Carolina, a volunteer network was organized for coordinating the weekly sampling and reporting of SWD captures (Burrack et al. 2012), while extension educators and researchers monitored a similar trapping network in Michigan starting in 2010. Data are compiled into SWD-specific reports for growers and crop consultants, and are increasingly being integrated into regular extension scouting reports provided for a range of crops.

This reflects that SWD is now a component of the pest complex that growers must manage annually.

The arrival of SWD in the eastern region of the United States has caused shifts in management tactics used for berry pest management, particularly in fall red raspberries and later ripening varieties of blueberry. The combined effects of the economic impacts of this pest are challenging to quantify, but a recent survey of growers in the eastern United States indicates an impact of \$27.5 million in 2013 (Burrack 2014). The majority of SWD-susceptible fruit grown in the eastern US is still being harvested and marketed, despite the arrival of this pest. In some cases, this is because the fruit's harvest season is early enough to avoid periods of high SWD population size (e.g., strawberries, tart cherries, summer raspberries), while for crops with later ripening times it is because growers have used the information available from cooperative extension services to select and implement effective pest management programs.

Range expansion in north central and interior US

The first confirmation of SWD in Wisconsin came from trapping in Racine County in 2010, with 12 counties reporting the pest by 2012 (Hamilton 2010). In Minnesota, grower reports from adult trapping and/or larval infestation of fruit confirmed SWD presence in August 2012. By October, a standardized volunteer trapping network of master gardeners, organized by the University of Minnesota, demonstrated the presence of SWD in 29 counties. As of 2012, SWD was also confirmed in an additional 8 states (Arkansas, Colorado, Idaho, Illinois, Indiana, Iowa, and Texas). In 2013, first reports of SWD were made in the following interior states: Kansas, Missouri, Nebraska, Oklahoma, South Dakota, and Wyoming. Interestingly, SWD was first reported in Montana in 2011, despite the fact that positive reports from states bordering it did not come until a year or two later (although the pest was reported in the neighboring province of Alberta, Canada in 2010; Alberta Agriculture and Rural Development 2013).

As a case study for the more recently invaded North Central region states, growers in Minnesota have suffered considerable negative impacts from the arrival of SWD. Minnesota small fruit production is strongly focused in smaller farms, as discussed above for several eastern states, with the use of organic practices being commonplace. This agricultural practice has been effective largely due to relatively low insect pest pressures in these high-value crops, which have historically required limited numbers of insecticide applications. With the emergence of SWD as a statewide pest, Minnesota growers are now suffering economic losses both from decreased yields and substantially increased production costs. Moreover, many of the

Minnesota farms rely on “pick-your-own” harvesting and marketing practices with the general public; unfortunately, the lack of consistent fruit removal and “clean harvests” enhances SWD survival and hinders maintaining effective pest management programs.

Europe

A chronological summary of the SWD invasion of Europe, by country, can be found in Fig. 6. Here, we discuss the major trends of SWD timing and economic impact on a regional basis.

Southern and western Europe

SWD was first reported in Europe during the autumn of 2008 in Spain (Rasquera, Tarragona Province) (Calabria et al. 2012); however, traps deployed in Tuscany (San Giuliano Terme, Pisa, Italy) in 2008 also caught SWD (Cini et al. 2012). In 2009, SWD adults were recorded in traps in other regions of Spain (Bellaterra, near Barcelona), in France (Montpellier and Maritimes Alpes), and in Italy (Trentino) (Grassi et al. 2009; Calabria et al. 2012). The first known damage to commercial small fruit in southern Europe was found in Italy (Trento Province) during 2009 (Grassi et al. 2009). From these regions came the first Spanish records of (1) oviposition on wild hosts (*Vaccinium*, *Fragaria* and *Rubus* spp.) and (2) economically important damage on several species of cultivated berries (Sarto and Sorribas 2011).

By 2010–2011, the range of SWD broadened further. In Italy, it was reported in several other regions along the whole peninsula, including the two major islands Sardinia and Sicily. SWD adult surveys conducted in various fruit orchards of Northwest and Southeast Italy in 2012 and 2013 confirmed that the pest is well established in these regions, and that adult populations decrease considerably in the summer (peaking in late summer/early fall; Baser et al. 2015; Mazzetto et al. 2015). In France, SWD was found in additional locations in 2010 (Rhones-Alpes) and 2011 (Lorraine, Ile de France, Pays de la Loire, Poitou-Charentes, and Corse) (Withers and Allemand 2012). Subsequently, other Mediterranean European countries made their first records, such as Slovenia, Croatia, and Portugal (Seljak 2011; Milek et al. 2011; Rota-Stabelli et al. 2013; see also EPPO Website and references therein).

In the Iberian Peninsula, after its first detection in a pine forest 170 km south of Barcelona in autumn 2008, SWD was detected in autumn 2009 in Barcelona within a natural forest (Calabria et al. 2012), and later (2010) in Girona from traps in fruit crops (Sarto and Sorribas 2011). In the summer of 2011, it was detected more westerly in Spain, more precisely from a wholesale fruit market in Navarra

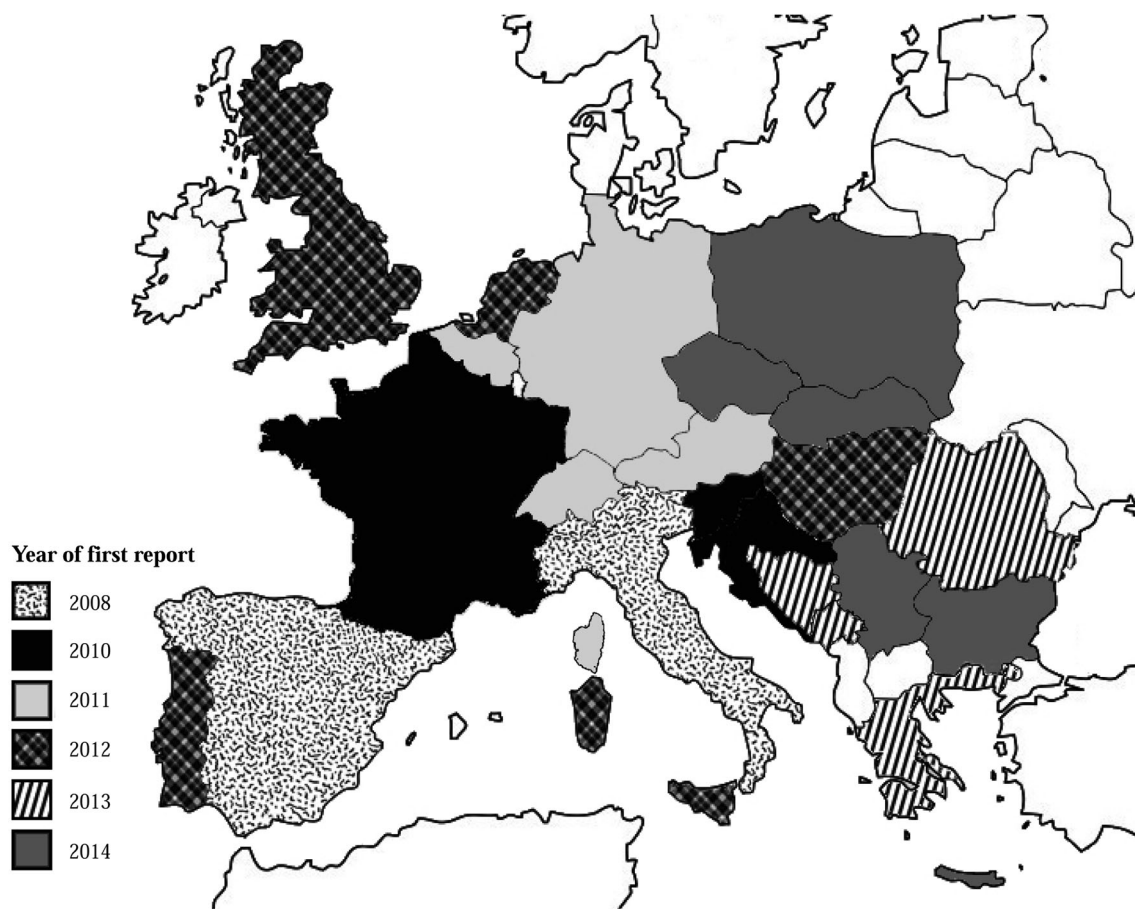


Fig. 6 Current European SWD distribution map (as of May 2015). Countries are indicated accordingly to the year of the first SWD report

(Biurrun et al. 2013). In 2012, SWD was detected in several provinces of southern Spain. Also in 2012, it was first identified in the westernmost part of the Iberian Peninsula, in the regions of Odemira and Algarve (Portugal) (Franco 2013). By the spring of 2013, it was found in cherry orchards of Galicia (the northwestern-most part of Spain) in areas where sampling had been carried out since 2010 (Pérez-Otero et al. 2013). The genetic bottleneck in Europe seems greater than that reported in the US with smaller allele numbers (Adrion et al. 2014). These data are based on only one population (Barcelona, Spain), however, which prevents assessing whether multiple independent introductions have occurred in Europe, thus potentially not depicting the real European scenario.

Despite its relatively recent detection, SWD has already caused severe yield losses in several small fruit crops grown across southern Europe, such as sweet cherries, strawberries, raspberries, blackberries, and blueberries. Extreme damage has been reported for locations in Northern Italy (Trentino) and in France, with up to 100 % damage reported on caneberries, strawberries, and sweet cherries (Cini et al. 2012; Weydert and Mandrin 2013). In

France, it has also been reported on apples and peaches, although without economically significant damage (Weydert and Mandrin 2013).

In most Mediterranean areas, relatively low populations are observed in spring but numbers increase rapidly during the summer months, peaking in late autumn (Weydert and Mandrin 2013). Although cherry is considered to be a favored host for SWD, population densities in early summer (during the cherry ripening period) are much lower than those faced by crops maturing later in the summer (e.g., strawberries and other berries), following the dynamics described for other regions. On the other hand, although grapes are not considered a primary host for SWD (Bellamy et al. 2013), some soft-skinned varieties may suffer “spill-over damage” from the extremely high population densities in autumn.

While assessments of the economic impacts of SWD in Southwestern Europe are relatively scarce, it appears to be emerging as a major threat for the fruit industry of affected countries. De Ros et al. (2013) present the first evaluation of the economic impact in Europe, although the study only focused on Trento Province, Italy. There, it was estimated

that the 400-ha soft fruit production areas faced losses of around 500,000 € in 2010, and 3 million € in 2011. While the magnitude of these economic impacts in Trentino can be ascribed to high levels of blueberry production, this estimate is also somewhat conservative in that it did not consider costs of control strategies and other societal consequences of increased chemical inputs.

Northwestern Europe

SWD was detected for the first time in Germany in 2011 (Vogt et al. 2012 a, b; Table S1), following a preliminary monitoring effort in the autumn of 2010 that resulted in no catches. From 2011 onward, monitoring efforts for SWD were organized in most Federal States of Germany, but with limited fly catches (Vogt and Baufeld 2011). Adult SWD presence was verified in March 2012 near the Northwest coast of Lake Constance (KOB Bavendorf, personal communication) and in Northern Baden (data from JKI Dossenheim). In the following fall, the number of localities and SWD captured increased steadily (Fig. 7a); fruit infestation by SWD larvae was found in late tart cherries, raspberries, blackberries, elderberries, and grapes (Vogt 2014). High post-harvest adult capture rates were found both in orchards (cherry or apple [*Malus domestica*])

and in wild areas (Briem et al. 2015). In autumn, increased SWD captures could relate to decreasing temperatures serving as a stimulus to search for suitable overwintering habitats. Although these could include fruits of privet (*Ligustrum* spp.) and blackthorn (*Prunus spinosa*), where SWD eggs have been found (W. Breuer and W.B.I. Freiburg, personal communication), an absence of further development on these plants suggests a need for further research.

In 2013, higher population densities of SWD were found in many regions of Germany, especially in the Upper Rhine Valley (Fig. 7b, c). Correlated with these adult trap counts, larval infestation in fruit was mainly recorded in late raspberries and blackberries (Fig. 7d). Infestation in grapes was also documented, with levels dependent on the variety: red varieties (e.g., Roter, Gutedel, Dunkelfelder, Acolon, Spätburgunder) were most susceptible to oviposition by SWD, but successful development to adults was limited ($\leq 20\%$; Bleyer and Breuer 2013). Despite this poor developmental performance, grape infestations in Germany may still pose a concern, as (1) grape berries are highly abundant, leading to population increases in spite of low per fruit developmental success rates; and (2) they offer a potential late-season resource for SWD due to incomplete harvests and/or the late development of bunches. In 2014,

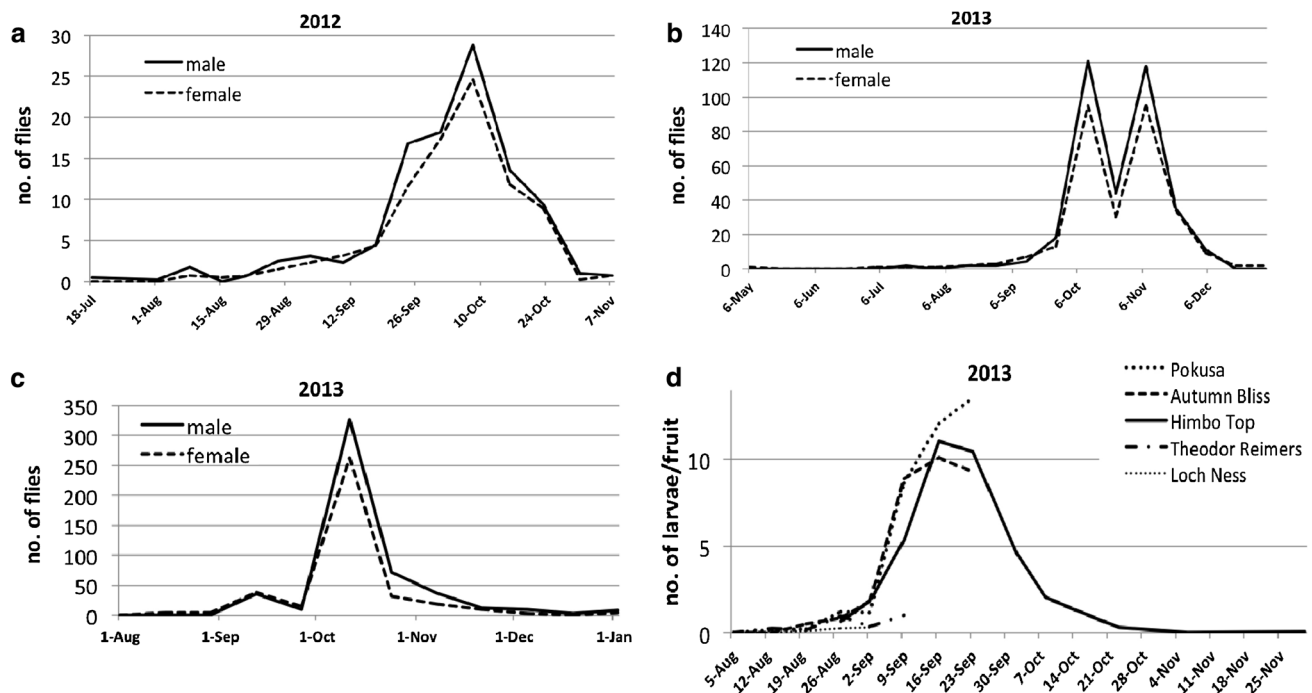


Fig. 7 SWD phenology and infestation data from JKI Dossenheim, Germany in 2012 and 2013. **(a)** Average number of adult SWD captures per trap in a mixed berry plot (raspberry, blackberry, red/black currants). **(b)** Total adult SWD trap captures in an experimental sweet cherry orchard. **(c)** Total adult SWD trap captures in a wild blackberry hedge. **(d)** Larval infestation data for raspberries and

blackberries from an experimental plot. For **(b)** and **(c)**, traps were baited with apple cider vinegar and water at a 2:3 ratio, compared to the ratios used in 2012 (1:1 or 1:3). For **(d)**, fruit samples were taken until the end of fruiting, with only ‘Himbo Top’ producing fruits until November

presumably due to a relatively mild winter, re-immigration to fruit orchards took place about 3 months earlier than in 2013, and SWD presence was confirmed throughout the country.

SWD was first reported in Belgium in September 2011, with a single male captured in Ostend near the harbor in Zerbrugge (Mortelmans et al. 2012). In 2012, the first SWD was caught relatively late in the growing season, i.e., during the second half of July in Gembloux, and in the first half of August in Zoutleeuw (Beliën 2013). The largest numbers of the pest in Flanders were found in sweet cherries, but SWD was also present in plums, strawberries, raspberries, and blueberries. In Wallonia, the largest numbers of flies were captured within a sheltered culture of raspberries at Gembloux. The results of the 2012 monitoring campaign showed that SWD is present throughout Belgium, from Knokke-Heist in the north to Malmedy in the south (a total of 14 locations). Most SWD in 2012 were caught late in the growing season in September and October, with a large number also caught in November. The first detections in 2013 were also late in the season (August 2013), with highest catches recorded in November. Despite the spread of SWD throughout the country, there have been limited reports of damage in Belgian fruit production; no record of damage was made in 2012 and, aside from some grower reports in the field, no serious reports of damage were noted as of 2013.

The first report of SWD in Austria dates from September 2011, where SWD was found in the Federal States of Tirol (East Tirol), Steiermark and Kärnten. Infestations were observed in raspberries, elderberries, and hardy kiwi. In 2012 and 2013, a nationwide monitoring effort was carried out under the direction of AGES (Austrian Agency for Health and Food Safety). In 2012, SWD detections were concentrated in the western and southern regions of Austria, with damage reported in the Federal States of Vorarlberg, Tirol (North and East Tirol), Kärnten and Steiermark. Relatively few SWD individuals were caught in late summer and autumn in the Federal States of Wien and Niederösterreich. The monitoring results of 2013 showed, however, that SWD is distributed throughout the country. In Austria, the main hosts appear to be elderberries, late raspberries, and blackberries; unlike in Germany, however, neither captures nor fruit infestations have been reported from grapes (Lethmayer 2012; Lethmayer and Egartner 2014).

SWD was first confirmed in Switzerland in 2011 (Baroffio and Fischer 2011; Baroffio et al. 2014). Extensive monitoring via apple cider vinegar bait (50 % water, 40 % apple vinegar, 10 % red wine) was used to quantify the seasonal buildup of adult SWD populations. SWD was found throughout the country, from low elevation fruit production areas to the timberline. As noted in several

temperate countries, a similar pattern of increasing pest pressure through the season, from May to November, was observed.

In the Netherlands, an SWD-specific survey using traps baited with ACV and red wine traps was initiated in late September 2012. The pest was detected at 8 survey locations out of 12, including both sets of traps placed in forest habitats. A later monitoring network in 2013 covered 80 locations in the Netherlands, with no SWD captured until the second half of August. Captures increased in September and October, but remained below 20 individuals per trap during the peak season. SWD was caught at half of the monitoring sites. The first and highest trap catches occurred in cherry orchards, near where imported fruit was sold. Elderberries (*Sambucus* spp.) may also be of particular concern in this country, as examination of this crop from 90 locations revealed infestation by SWD at 26 locations (Helsen et al. 2013).

SWD was reported for the first time in the United Kingdom in 2012 (EPPO 2012). In 2013, a national monitoring effort was initiated on 14 soft and stone fruit farms in the principal fruit-growing areas of England and Scotland. Two traps were deployed in each crop (one at the edge and one inside the crop), with an additional two traps in a nearby woodland or wild place on the farm. This network first detected SWD in August and then, after a lag time of a couple of weeks, captures increased steadily throughout the late autumn and winter. Interestingly, trapped SWD numbers were greater in the traps in woodlands than in crops, as has been reported elsewhere. SWD was not a commercial problem in the UK in 2013; however, the country experienced a cold winter and very late spring (J. Cross, personal communication).

Eastern Europe (including Serbia)

SWD was first recorded in Hungary in 2012 (Kiss et al. 2013). As part of a complex survey of invasive pests and their natural enemies along highway margins in Hungary, the authors placed plastic bottle traps containing ACV (100 mL) at 33 sites along highways throughout the country in mid-September 2012. The first SWD specimens were found at one location, near the village of Táská (Somogy county) at the beginning of October. Following this first record, the countrywide monitoring program was continued (Kiss et al. 2014a, b, 2015), and others have also been launched. During a survey coordinated by the Department of Entomology at Corvinus University of Budapest (CUB), carried out in October and November of 2014, SWD adults were captured in plastic bottle traps (containing 150 mL ACV) placed randomly at 13 locations in Hungary (Table S2). Based on these latter data, and those of Kiss et al. (2014a, 2015), SWD seems to have

become widely distributed throughout the country by the end of 2014. From an economic perspective, damage caused by the pest has also been observed in raspberry (*Rubus idaeus*, cv. Sugana), plum, and nectarine orchards in 2014 (Kiss et al. 2015).

In Poland, the Research Institute of Horticulture (RIH) carried out SWD monitoring during 2012–2014. In 2012, studies were conducted on blueberry plantations in central Poland (Skierniewice region). In 2013, the research expanded to the Grójec, Machnówka, and Piskórka regions of central Poland, and to Września in western Poland; in 2014, research was conducted at Brzezina, in raspberry plantations in the south. In addition, between 2013 and 2014, observations were also carried out at the wholesale market in Bronisze near Warsaw, where imported and domestic fruits are stored and traded, and held for subsequent shipment to other countries. No SWD was detected in 2012 and 2013, but adults were captured at the end of 2014 in western blueberries and southern raspberries (*R. idaeus*). To date, however, there have been no reports of fruit damage by SWD in Poland (Łabanowska and Piotrowski 2015; W. Piotrowski, personal communication).

In 2013, SWD was first reported in the Ioannina region of Greece (Papachristos et al. 2013). This initial report has been not yet confirmed and consisted of an adult male captured in an ACV/wine-baited trap in a mixed berry orchard (blackberry and raspberry). Five SWD specimens were also caught through a beer trap placed in a shrub growing in the garrigue in the island of Crete during March 2014 (Máca 2014). The first detection of SWD in Romania also occurred in 2013; here, adults were found in Tephri traps set in wild blackberry bushes in Bucharest as part of a national fruit fly trapping program (Chireceanu and Chiriloaie 2014). In 2014, SWD adults were caught for the first time in the Southwestern part of Bulgaria using an unspecified trap placed close to cherry trees (EPPO 2015).

SWD was first reported from Serbia in 2014 by Toševski et al. (2014). Further occurrence of the species in the country was confirmed by the study by CUB (Table S2). In Bosnia and Herzegovina, SWD was recorded at several locations as early as 2013 (Ostojić et al. 2014). During October and November of 2013, SWD was found in Montenegro using Tephri traps in localities along the sea-coast and in the area of and surrounding Podgorica (Radonjić and Hrnčić 2014).

SWD was recently confirmed in late 2014 in many of the fruit production areas of the Czech Republic. SWD adults were collected using apple cider vinegar traps, but some beer-baited traps were also effective, as was sweeping in wooded areas (Březíková et al. 2014). The pest was first found in a trap at a farm at Malé Ludince, Slovakia, on 9 October 2014. While grapes are processed at this site, and apple and plum trees are present, no damage was observed

(NPPO of Slovakia 2014). The trapping study by CUB (see above) also resulted in SWD catches in Slovakia in October 2014 (Table S2).

Central and South America

While unpublished and unconfirmed records suggested SWD presence in Costa Rica and Ecuador (Hauser 2011), SWD presence was first confirmed in the Neotropics in 2013. Deprá et al. (2014) recovered 156 SWD specimens exposing banana-baited traps in five locations of southern Brazil, specifically in the states of Rio Grande do Sul and Santa Catarina. In January 2014, SWD was also documented in São Paulo in a unique way; here, researchers based their detections on purchased fruit at a local grocery in Sao Paulo and SWD were reared from blueberry (Vileia and Mori 2014).

Prospects for predicting geographic expansion

While the regional reports provided in this review are useful for documenting the recent and rapid spread of SWD worldwide, they lack predictive power regarding the demography and phenology of this pest in the future. As with many arthropod species that have short generation times, there are challenges in using traditional degree-day models to forecast the seasonal phenology, or key life-stage events for SWD. In this section, we review two demographic models for SWD: a stage-specific Leslie-matrix model (Wiman et al. 2014), and a distributed maturation time, physiologically based demographic model (PBDM) in a GIS context (Gutierrez, Plantamp, and Ponti, see Supplemental Material).

Wiman et al. (2014) used a degree-day approach for time and age within a Leslie-matrix modeling structure. The model is based on temperature-dependent developmental, survival, and fecundity data from Tochen et al. (2014). Using mean daily temperature data from several US and European locations, they assessed phenology trends and subsequent impacts on SWD stage structure at each location. Although SWD generational dynamics varied considerably across locations, the prediction of a generally low proportion of adults within a given population (e.g., often <20 %) was relatively consistent (i.e., a stable age distribution). The goal of their modeling for SWD pest management programs is to forecast the timing of oviposition activity to allow better timed insecticidal sprays. Mean ambient daily temperatures should be used to initialize the model to project initiation of pest pressure in fruit production areas within a given country. The best application by pest managers in the different regions, however, may be to compare model forecasts to the timing of early season trap catches.

The PBDM for SWD (Gutierrez and Ponti; see Supplemental Material) uses the same data from the literature, but has the added advantages of (a) being process oriented and (b) including non-linear submodels that capture temperature-dependent developmental rates, survivorship, and fecundity in an age–time–space varying manner (e.g., Gutierrez and Baumgärtner 1984; Gutierrez 1996; Gutierrez and Ponti 2013). An additional goal of the PBDM in a GIS context is to capture prospectively the geographic range and relative abundance of SWD across North America, Europe, and the Mediterranean Basin. Here, we review data on SWD (a) development rate, (b) temperature-dependent mortality, and (c) age-specific oviposition in order to highlight research needs that will increase our ability to forecast SWD range expansion and to better

understand the SWD response to cold temperatures (see Supplemental Material).

Development rate

A temperature-dependent developmental rate model ($R_{e-a}(T)$) for the egg to adult stages of SWD on temperature (T) can be developed based on models similar to that of Brière and Pracros (1999) (Fig. 8a). This model is parameterized based on analysis of empirical data generated for these stages (see Supplemental Material), yielding the following function (Eq. 1):

$$R_{e-a}(T) = \frac{0.0044 \cdot (T - 5.975)}{1 + 4.5^{(T-31.5)}} \tag{1}$$

Fig. 8 Biological parameters of SWD as a function of temperature. (a) Development time in days (dashed line) and developmental rate (solid line). (b) Mortality rate, fitted with both a simple convex function (solid line) and a polynomial function (dashed line). (c) Mortality rate, after exclusion of low temperature data (square symbols in b), fitted with a simple convex function. Sources for data points are labeled as appropriate. See text for details

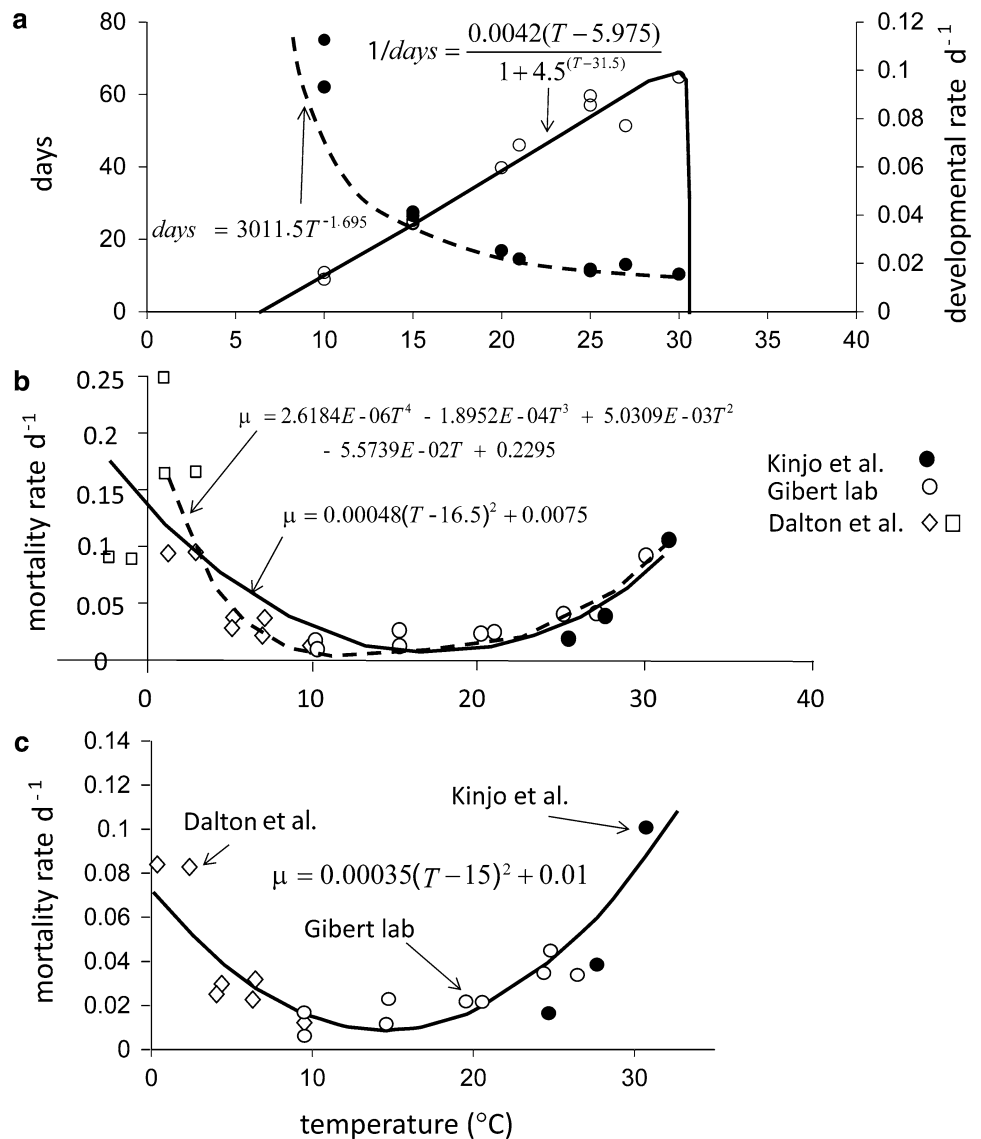


Table 1 Developmental times in degree days (dd) for SWD, assuming a lower developmental threshold of 5.975 °C (see text)

Stage	Developmental time (dd)
Egg	19.025
Larva	121.76
Pupa	93.22
Adult	1050

Parameters based on developmental data for the egg, larval, pupal stages (Kinjo et al. 2014), and data on adult longevity generated for this study (see Supplemental Material)

SWD has an estimated lower thermal threshold of 5.98 °C, peaking at about 29 °C, then declining to zero at approximately 31.5 °C. Using this lower developmental threshold, as well as data on egg development at 25 °C from Kinjo et al. (2014), stage-specific development times (in degree days [dd]) were calculated for SWD in the mid-range of favorable temperatures using the formula: $dd = \text{days} \times (T - 20)$ (Table 1). We note, however, that daily changes in physiological time and age follow Eq. 1. Average adult developmental time is 1050 dd, which translates into ca. 70 days at 21 °C. In the PBDM, the developmental times of population cohorts would have a characteristic mean and distribution (see Supplemental Material).

Temperature-dependent mortality

The temperature-dependent SWD mortality rate ($\mu_T(T(t))$) at temperature T and day t (Eq. 2) can be estimated from survivorship data from three sources: (a) previously unpublished data for the egg to adult stages between 10 and 30 °C (see Supplemental Material), (b) previously published data from Dalton et al. (2011) for adults between –2 and 10 °C, and (c) data from Kinjo et al. (2014). Estimates from Tochen et al. (2014) in the 10–30 °C range were consistently much higher in the upper range and were not used here (see Supplemental Material). Here, two models are fit to the combined dataset: (a) a simple convex function (solid line in Fig. 8b), and (b) a polynomial function (dashed line in Fig. 8b). Due to a lack of consistency in the low temperature data (square symbols in Fig. 8b), a restricted dataset (compare Fig. 8c vs. 8b) was fit using a convex function (Eq. 2; Fig. 8c; see Supplemental Material):

$$\mu_T(T(t)) = 0.00035 \times (T - 15)^2 + 0.01 \quad (2)$$

Given the high level of inconsistency in the available data regarding SWD mortality at different temperatures (Fig. 8b and see Supplemental Material), attempts to model this relationship should best be used as guidance for future efforts.

Age-specific oviposition

An age-specific oviposition model ($f(x) = \text{eggs/female}$) can be fit to data generated for SWD at 21 °C (see Supplemental Material), after Bieri et al. (1983) (Eq. 3):

$$f(x, T = 21^\circ\text{C}) = \frac{0.585 \cdot (x)}{1.0475^{(x)}} \quad (3)$$

After a pre-oviposition period of <1 days, the oviposition rate increases to 4.5 eggs days⁻¹ at age 20 days and then gradually declines (Fig. 9b). These results are similar to those of Tochen et al. (2014). The effects of temperature and RH can also be included (see Supplemental Material). Interestingly, the magnitude and pattern of age-specific fecundity in SWD contrasts sharply with that of *D. melanogaster* at a similar temperature (Fig. 9a). In *D. melanogaster*, oviposition rates are 10 × higher in early adult life (up to ca. 20 days), but fall off dramatically later in life (> 40 days). Early higher fecundity may explain why other *Drosophila* spp. commonly displaces SWD when contaminating colonies of the latter (M.K. Asplen, personal observation). More importantly, it suggests that older SWD populations may be better able to maintain relatively high pest pressures on susceptible fruit than other drosophilids (Tochen et al. 2014; Wiman et al. 2014).

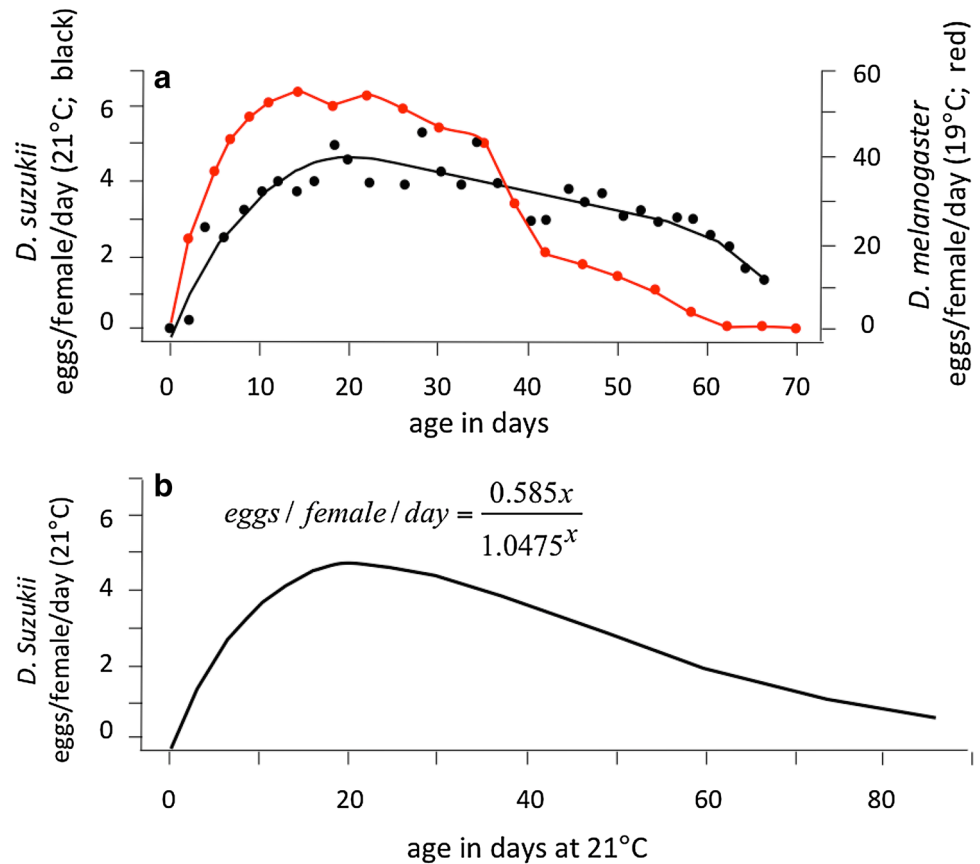
Current state of SWD management—the US as a case study

We highlight research into management strategies (and their challenges) for SWD in the US, which serves as a case study for other invaded regions. Given the constantly expanding literature on SWD management, this section is not intended as an exhaustive review, but rather serves to give a synopsis of major efforts to aid control of SWD within the integrated pest management (IPM) framework. We focus here on research into chemical control, improvements in monitoring/sampling technology, and cultural control, before ending with discussions of the lack of current biological control options in the US.

Chemical control and potential for insecticide resistance development

Insecticide applications are primarily used to manage SWD in US production regions (Beers et al. 2011; Bruck et al. 2011). A key area of research has been the determination of insecticide efficacy and residual activity for various chemical classes. Studies of western SWD populations (Bruck et al. 2011), combined with recent laboratory bioassays using eastern region fly collections, highlight the efficacy of members of the pyrethroid, organophosphate,

Fig. 9 Age-specific oviposition by SWD at 21 °C. The bottom graph (b) reflects the relationship for SWD alone, whereas the top graph (a) compares this relationship to data for *Drosophila melanogaster* at 19 °C. Note the much higher relative oviposition by *D. melanogaster* early in life, and the reverse situation later in life. See text for more details. Data from Chabert et al. (2013)



and spinosyn classes, and of methomyl in the carbamate class. In addition, azadirachtin and organic pyrethrins (either alone or in combination) show poor efficacy, highlighting the challenge for organic growers who must rotate their use of spinosyn with another chemical class to manage insecticide resistance. Laboratory screening of insecticides detected activity of two neonicotinoids dinotefuran and thiamethoxam (R. Isaacs, unpublished), though this class had been initially considered relatively ineffective against SWD (Bruck et al. 2011).

Field research trials have also yielded critical insights for SWD chemical control. For example, recent trials conducted in highbush blueberries in Michigan showed that the duration of fruit protection is variable among insecticides, and that efficacy declines rapidly if the residues are washed off by rain (Van Timmeren and Isaacs 2014). Research into the mechanisms by which effective insecticides are achieving fruit protection have revealed that eggs and larvae can be controlled after penetration of the fruit, highlighting that adult fly control is likely only one component of the mechanisms by which crop protection is achieved (Wise et al. 2014).

In an attempt to synthesize research regarding insecticide performance, data based on various approaches to their evaluation have been integrated into an annual

ranking system that provides nationwide relative scores for the efficacy of insecticides against SWD in the US. Based on research trial data, expert opinion, and field experience, a group of entomologists have contributed to an annual summary of insecticide performance, organized under the auspices of the WERA-1021 Regional Committee on Spotted Wing *Drosophila* (Fig. 10).

While their short generation time and high fecundity make drosophilid flies predisposed to develop resistance to insecticides, our knowledge of this is primarily limited to research on *D. melanogaster*, where genetic variation in resistance-conferring genes has been documented in both field-collected populations (Menozzi et al. 2004) and laboratory-selected colonies (LeGoff et al. 2003). This species has provided a wealth of information on the genetics and molecular basis of insecticide resistance in insects (Bogwitz et al. 2005; Perry et al. 2015), which will be valuable in understanding resistance in SWD, should it develop.

Currently, there is very limited published information regarding the levels or extent of insecticide resistance in SWD, but its global invasion of fruit producing regions and the insecticide-dependent management programs have made this a focus of some research programs. Hamby et al. (2013) found that detoxification gene activity has daily rhythmic patterns in SWD, with the highest activity at

dawn. Surprisingly, this did not correspond to lower susceptibility to malathion so the implications for resistance management are unclear. Also in California and in neighboring Oregon, Shearer et al. (unpublished) have compared the susceptibility of SWD populations from fields managed with synthetic or organic insecticides, finding evidence for reduced susceptibility in some organic fields to spinosad. Research programs in other fruit production regions are conducting baseline monitoring with the most important insecticide classes (e.g., Whitener and Beers 2015), and this will be valuable for detecting resistance if it develops. An international, coordinated effort would be highly beneficial to coordinate testing methods and facilitate data sharing on this issue.

SWD populations on non-crop hosts (Lee et al. 2015) and the fly activity before and after fruit harvest (i.e., when growers are not targeting this pest with insecticide applications) are both expected to reduce the potential for field failures of insecticides in some regions, due to the high likelihood of dilution of resistance genes. However, there are also production systems without adjacent wild hosts and semi-enclosed systems under high tunnels, as well as organic systems with a very limited number of chemical classes. There would be significant implications of a high level of resistance to any of the chemical classes that control this pest, and so susceptibility monitoring should be integrated into SWD management plans. Resistance management is currently an emphasis of grower training, to

ensure rotation of chemical classes to reduce the risk of resistance development; however, there are limited chemical control options in many production regions, making resistance management more challenging and highlighting the need for integrating non-chemical approaches into IPM systems.

Monitoring and sampling

Management activities in the US are based primarily on fruit ripeness levels and adult trap catches. Population estimates derived from adult trapping indicate relative SWD pest pressure (Tochen et al. 2014), and traps baited with ACV or a combination of sugar, water, and baker's yeast are used commonly (Cha et al. 2012; Landolt et al. 2012; Lee et al. 2012). Strong national efforts have been made to evaluate alternative trap designs and baits for SWD (Lee et al. 2012, 2013; Burrack et al. 2015). While permitting a high degree of replication, these studies have highlighted regional and crop-based variation that challenges the development of a unified trapping approach for this pest. In Michigan, for example, initial use of ACV as bait in 2011 and 2012, based on recommendations from other regions, was replaced by the use of a yeast–sugar mix based on data that highlighted the earlier and greater captures achieved with the latter (R. Isaacs et al., unpublished data). It is expected that recent developments in commercial baits by a few companies in the US and E.U. will facilitate transition away from fermenting baits that are messy and require regular replacement.

Although multi-component bait blends may provide a more selective lure to increase the reliability of risk assessments for SWD, additional research is strongly needed to quantify relationships between adult trap catch and egg/larval infestations in susceptible fruit. This information is critical to the development of a formal economic threshold for the pest, as there are currently no reliable metrics linking adult presence with pest damage.

Cultural control

Research on cultural control tactics is in the early phases of development in the US, although testing of these strategies is occurring at increasingly larger scales. Research related to the efficacy of the following cultural practices is ongoing: tillage to bury infested fruit, physical exclusion with netting, fruit cooling, irradiation, and post-harvest sorting. Growers of susceptible crops are already adopting these alternative tactics to varying levels, with some having greater potential for use in specific farming contexts. For example, there is increasing production of fruit crops in high tunnels for manipulating harvest date and reducing disease incidence, and these structures provide a basis for

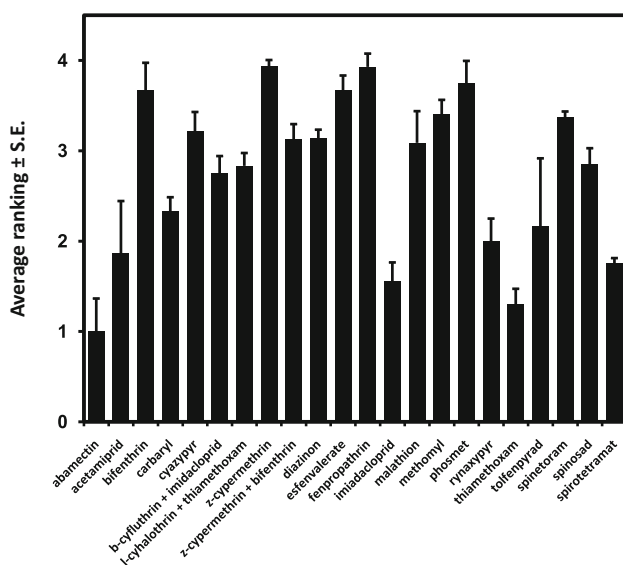


Fig. 10 Relative ranking of insecticides (*active ingredients shown*) for their performance against SWD under field conditions, across all crops and regions in the US. Rankings were provided by applied entomologists in 2013 based on their results from replicated trials, from expert opinion in their regions, and from their field experiences. The scoring system used was 0 ineffective, 1 weak, 2 fair, 3 good, 4 excellent

the application of netting (recommended mesh size of 1×1 mm) to physically exclude SWD (Caprile et al. 2013). This approach has been highly successful on a small scale in recent Canadian studies (Cormier et al. 2015). The linking of smaller high tunnel growing operations with netting may overcome important logistical challenges for netting in larger plantings, and thus better facilitate adoption of the practice.

Biological control in the US

Evidence for successful levels of natural biological control of SWD in the US is lacking. Native parasitoid wasps appear to have limited population level impacts in Pacific production regions; for example, the effects of the generalist ectoparasitoid *Pachycrepoideus vindemmia* (Hymenoptera: Pteromalidae) on SWD appears negligible (Brown et al. 2011; Rossi Stacconi et al. 2013, 2015). Potential native predators of SWD include several species of *Orius* (Hemiptera: Anthocoridae), which were observed feeding on SWD larvae (Walsh et al. 2011). Preliminary laboratory studies with *O. insidiosus* (Walsh et al. 2011) indicated that they could feed on SWD larvae infesting blueberries, although the effects of this predation on population levels are currently unknown.

Despite the lack of successful biological control programs against SWD, the importance of this control tactic within the IPM framework is well recognized by researchers. For example, there has been wide participation in national natural enemy collections (e.g., Rossi Stacconi et al. 2013), and assessment of candidates for augmentative releases is ongoing (e.g., Woltz et al. 2015). We now turn to a broader discussion of biological control prospects for SWD, with particular emphasis on research related to foreign exploration for specialist parasitoid wasps.

Prospects for biological control

Although predators and pathogens may play important roles in regulating SWD populations (see above and the preliminary surveys by Gabarra et al. (2015) and Woltz et al. (2015)), most efforts in examining biological control options for invaded regions have focused on hymenopteran parasitoids. We begin our discussion of the prospects for SWD biological control with a brief review of the taxonomy and biology of larval and pupal parasitoids of *Drosophila*. Next, while active parasitoid surveys have been ongoing in North America (see above), we will focus on the situation in Europe as a case study of natural biological control in newly colonized regions. Finally, we will discuss the prospects for importation of candidate Asian *Drosophila* parasitoids that may show promise as classical

biological control agents of SWD in North America and Europe.

Review of *Drosophila* parasitoid bionomics

Approximately 50 parasitoid wasp species, belonging to four families and at least 16 genera, are known to develop on *Drosophila* spp. (Carton et al. 1986). Parasitoids that attack frugivorous *Drosophila* are diverse, but the most important genera are the larval parasitoids *Leptopilina* (Figitidae) and *Asobara* (Braconidae), and the pupal parasitoids *Pachycrepoideus* (see above) and *Trichopria* (Dipriidae) (Allemand et al. 1999; Carton et al. 1991; Rohlf and Hoffmeister 2004; Wertheim et al. 2006).

Drosophila parasitoids induce high mortality rates in host populations, despite the fact that parasitism levels vary depending on the local breeding site and seasonal conditions. The natural average parasitism rate of non-SWD *Drosophila* larvae can reach 90 % at some sites in Southern France, indicating that parasitoids may be a primary mortality factor in fly populations (Fleury et al. 2004). Pioneering work on the biology of larval *Drosophila* parasitoids comes from Jenni (1951) and Nöstvik (1954) on *Leptopilina* and is well reviewed by Carton et al. (1986) and Fleury et al. (2009). *Asobara* species are all solitary, koinobiont endoparasitoids that attack first and second larval instars. After parasitoid oviposition in the host hemocoel, the *Drosophila* host tissues are consumed by second and third instar parasitoid larvae. Third instar parasitoid larvae then become ectoparasitic, eventually consuming the host pupa, with metamorphosis occurring within the *Drosophila* puparium.

Since the late 1990s, extensive research has focused on the immune response of *Drosophila* against larval parasitoids. The main mechanism of internal host defense is encapsulation, i.e., the formation of a multi-layered capsule that causes the death of the parasitoid through asphyxiation (Rizki 1957; Salt 1970). In addition to physiological defenses, some *Drosophila* species (*D. melanogaster*, *D. simulans*, *D. hydei*, *D. virilis*) can modify their oviposition behaviors in response to parasitoid presence (Kacsoh et al. 2013). Specifically, when in the presence of female *L. bouvardi* wasps (and other larval endoparasitoid species in the case of *D. melanogaster*), female flies increase their preference for substrates high in ethanol content, which in turn medicates developing larvae against development endoparasitoids (Milan et al. 2012). Given the habit for SWD to oviposit in ripening or ripe fruit, when compared to the decomposing (and thus higher in ethanol content) substrates used by nearly all other *Drosophila*, it may be that self-medication is a less viable defensive option for SWD when compared to other species.

Larval parasitoids of *Drosophila* have evolved a variety of mechanisms for overcoming host resistance, both passively (e.g., in *A. tabida*, Prévost et al. 2005) and actively (e.g., *L. boulandi*, Colinet et al. 2013). Interestingly, Kacsoh and Schlenke (2012) showed that among 24 parasitoid strains/species tested, only *A. japonica* is able to successfully overcome SWD defenses (with ~ 80 % successful eclosion rate) and it occurs in sympatry with SWD in its native range. The increased parasitism ability of this species appears to be associated with depression of circulating host hemocyte loads involved in encapsulation (Poyet et al. 2013). This finding suggests the potential for parasitoid virulence to co-evolve with *Drosophila* resistance, and implies that classical biological control may yield more promise than natural biological control in areas recently invaded by SWD (see below).

Pupal parasitoids of the genus *Trichopria* lay their eggs directly into the host hemocoel, whereas *Pachycrepoideus* spp. lay their eggs in the space between the *Drosophila* pupal case and the pupa, thus acting as ectoparasitoids (Carton et al. 1986). It is currently unclear whether or not *Drosophila* pupae can mount an effective immune response or otherwise defend themselves once infected by pupal parasitoids, but this could explain, in part, why *Drosophila* pupal parasitoids are generally thought to have wider host ranges than larval parasitoid wasps (Godfray 1994).

Natural biological control of SWD in Europe

Under laboratory conditions, French and Spanish populations of two generalist pupal parasitoids have shown effectiveness against SWD (Chabert et al. 2012; Kacsoh and Schlenke 2012; Gabarra et al. 2015). Of these, *P. vindemmiae* has the widest host range, having been reported to attack over 60 fly species worldwide (Carton et al. 1986; Wang and Messing 2004). *P. vindemmiae* was recently collected using SWD-baited sentinel traps in commercial soft fruits and natural habitats of northern Italy and Spain. In the lab, its parasitization efficacy was confirmed with parasitism up to 80 % on infested raspberries (Chabert et al. 2012; Rossi Stacconi et al. 2013; Gabarra et al. 2015). The most promising development with respect to this putative biological control agent occurred recently with the demonstration of its development in SWD under standard laboratory conditions (Rossi Stacconi et al. 2015).

Trichopria c.f. *drosophilae* is a more specialized species on frugivorous *Drosophila*, occupying a worldwide geographic range including Europe, Africa, North America, and Australia (Carton et al. 1986). Despite the more attractive (from a biological control perspective) feature of a narrower host range, very little is known about the capacity of these pupal parasitoids to control natural populations of *Drosophila*. Recently, *T. c.f. drosophilae* was

found occurring, with up to 10.7 % SWD parasitism, in two heavily infested commercial strawberry fields of Northeastern Spain, and its basic biology was preliminarily described in the laboratory (Gabarra et al. 2015). As with *P. vindemmiae*, Rossi Stacconi et al. (2015) confirmed the ability of this species to develop in SWD under laboratory conditions. A greater understanding of the host–parasitoid interactions between these two generalist parasitoids and SWD is now both warranted and needed.

With respect to *Drosophila* larval parasitoids, until recently neither *L. heterotoma* nor *L. boulandi* (the two main species in Europe) appeared able to develop on SWD under laboratory conditions (Chabert et al. 2012; Kacsoh and Schlenke 2012). A similar result has been found for two other species of this genus, *L. victoriae* and *L. clavipes* (Kacsoh and Schlenke 2012). A new report (Rossi Stacconi et al. 2015) demonstrates geographic variation in the ability of *L. heterotoma* to develop within SWD between Italian (capable of development) and North American (Oregon; incapable of development) strains; however, this result was found using laboratory assays that may not accurately reflect field conditions. Furthermore, contrary to the fact that *A. tabida* emergence has been reported from field sampled Japanese SWD populations (Mitsui et al. 2007), laboratory studies using European populations failed to observe successful parasitism of SWD by this species (Chabert et al. 2012; Kacsoh and Schlenke 2012).

Foreign exploration for potential classical biological control agents

Classical biological control is a potentially useful management strategy for an invasive pest species whenever effective indigenous or resident natural enemies are lacking in the new distribution range. While there is a large literature on the biology and ecology of *Drosophila* parasitoids (see above), little published literature is available on the natural enemies of SWD and their impact on populations of this species. It is especially concerning that virtually no information on this topic is available from China or Korea, despite SWD being widespread in eastern China, Korea, and Japan. Many *Drosophila* species in Japan, including SWD, are attacked by several larval (*Asobara*, *Ganaspis*, and *Leptopilina* spp.) and pupal parasitoids (*Trichopria* spp.) (Mitsui et al. 2007; Kasuya et al. 2013). Larval *Drosophila* parasitoids include species that are host generalists and others that are apparently quite species specific (e.g., Kasuya et al. 2013; Nomano et al. 2014), whereas pupal parasitoids tend to be host generalists (see above). Increasingly, government regulatory agencies that issue permits for new biological control agents require that potential agents exhibit a high degree of host specificity. Thus, the search for candidate classical biocontrol agents of

SWD is likely to focus on those larval parasitoid species with higher degrees of host specificity.

Within the native range of SWD, its interactions with parasitoids have been best studied in Japan. A field survey of frugivorous *Drosophila* reported a mean level of only 4 % of SWD individuals that were attacked on traps baited with cut fruit by the parasitoids *A. japonica*, *A. tabida*, and *Ganaspis xanthopoda* (Figitidae) (Mitsui et al. 2007). Although this kind of sampling may be not representative due to the use of cut fruits (potentially less attractive than ripening fruits to SWD), these results are in contrast to those obtained in no-choice laboratory studies, in which high levels of *A. japonica* parasitism of SWD were demonstrated (Ideo et al. 2008). Recently, published survey data from Japan record eight *Asobara* species (Nomano et al. 2014): *A. japonica*, *A. pleuralis*, *A. rossica*, *A. rufescens*, *A. tabida*, and three potentially undescribed species (*Asobara* sp. KG1 aff. *leverii*, *Asobara* sp. TS1, and *Asobara* sp. TK1). Subsequent laboratory parasitism assays on SWD larvae revealed that, while five species (in addition to *A. japonica*, which was not tested due to prior knowledge of its use of SWD) could successfully oviposit in SWD larvae, three species (*A. rossica*, *A. rufescens*, and *A. tabida*) could not successfully develop. In addition, *Asobara* sp. TS1 showed low (ca. 13 %) levels of successful parasitism, and *A. pleuralis* did not oviposit in SWD at all. On the other hand, as *Asobara* sp. TK1 has only been recorded from SWD to this point, it is possible that this species is a specialist (Nomano et al. 2014). Successful establishment of a laboratory colony is now needed to assess the efficacy and host range of *Asobara* sp. TK1, in order to evaluate its candidacy as a classical biological control agent for SWD. Note that a similar issue concerns the ‘*suzukii*-associated’ type of *G. xanthopoda*, a dominant parasitoid of SWD based on surveys in central Japan for which no laboratory colony has yet been established (Kasuya et al. 2013; Nomano et al. 2014).

Because of the lack of information on SWD in China and Korea in particular, a multi-year exploration effort is needed to conduct field collections throughout the fly’s range in a variety of locations, habitats, and times of the season to fully document the occurrence and diversity of its natural enemies. Surveys should be planned to accommodate existing knowledge of seasonal fly population changes, altitudinal migrations, and shifts among preferred host plants. Preliminary natural enemy surveys in southeastern China and South Korea by several teams of US explorers and their local cooperators have used banana-baited traps placed in wild habitats of both known and potential fruit hosts, as well as in impacted crops to recover several different species of braconids, eucoilids, and figitids. These are in the process of being identified by a combination of morphological, molecular, and behavioral characteristics

(E. Guerrieri, personal communication). While fruit-baited traps attract parasitoids of other species of *Drosophila* besides SWD, several of these parasitoids successfully attacked and produced progeny when placed in pure SWD cultures (A. Biondi and K.M. Daane, unpublished data). While baited traps provide a quick means of monitoring the presence of adult parasitoids that attack frugivorous *Drosophila*, collections of potentially infested fresh fruits are also needed to identify those species that are likely to be specialized on SWD. Exploratory surveys should therefore include collections of fresh fruits (both from cultivated and wild hosts) for laboratory rearing, in addition to baited field traps. To increase trap specificity for SWD, traps may be baited with fresh fruits rather than cut or damaged fruits. Parasitoid species that are more effective at locating SWD within fruit will perhaps also be more likely to be effective biological control agents than species with broader host and host–habitat ranges.

Despite the low parasitism rates that have been reported for *Ganaspis* species in Japan (Mitsui et al. 2007), parasitism rates may vary widely among different host plants and habitats. It will be important to examine parasitism levels in a variety of natural hosts to obtain an accurate picture of the potential impact of well-adapted parasitoids on fly populations. The ability of parasitoids to develop successfully in SWD may be biologically moderated by the fly’s strong ability to resist attack by at least some species of parasitoids that attack other *Drosophila* species (Kacsoh and Schlenke 2012; see above). Further research will be needed to determine the degree to which parasitoids of SWD are able to escape this immune response.

Recommended research directions for SWD

After reviewing the current state of SWD spread, pest status, and management practices throughout invaded regions of North America and Europe, several pivotal questions remain. In this next section, we briefly highlight research areas that we believe would be particularly fruitful for the improvement of SWD IPM programs.

Population modeling

While the model results discussed above (see Prospects for Predicting Geographic Expansion, and Supplemental Material) provide important first steps in understanding the population dynamics of SWD, we suggest at least three priorities for future work that will improve the accuracy of future efforts:

- (1) *Biology of SWD at lower temperatures* The available data regarding biological parameters of SWD at low

temperatures (i.e., $< 10\text{ }^{\circ}\text{C}$) are both limited (one known published study; Dalton et al. 2011) and inconsistent (see above; Fig. 8b). Higher accuracy in estimating temperature-dependent parameters will require more replicated studies at its lower thermal limits, ideally using insects that have experienced regionally relevant pre-winter environmental conditions. The need to use standardized methods that maximize reproduction and survival cannot be over emphasized.

- (2) *Reproductive diapause* An accurate population dynamics model of SWD requires a better understanding of factors that regulate its reproductive diapause. SWD, like most temperate *Drosophila* species, is presumed to undergo reproductive diapause as adults. While previous data suggest that $10\text{ }^{\circ}\text{C}$ may be a critical threshold for the biology of adults at low temperatures (Dalton et al. 2011), recent observations in Oregon suggest the possibility of an alternative morphological variant associated with cooler temperatures and shorter photoperiod (P.W. Shearer, personal communication). A critical area for future research concerns whether or not this morphological change is indicative of reproductive diapause and, if so, what critical levels of temperature and photoperiod are needed to initiate its formation and influence its mortality rates.
- (3) *Host plant effects* On a final note, given the high degree of polyphagy shown by SWD, a challenge facing researchers concerns the inclusion of plant phenology in population dynamics models (e.g., Gutierrez and Ponti 2013). While simpler models that (a) are parameterized with data from bioassays on artificial diets, and (b) assume constant substrate levels year round can estimate the maximum potential of SWD in a certain habitat, far greater accuracy would be obtained through the inclusion of host plant species phenology and density in target landscapes. Such an effort will, however, require a much better understanding of the relative utilization of local flora by SWD, as well as its relative seasonal abundance; both of which are likely to vary considerably across geographic regions.

Non-crop host plants

Many invaded areas report high trap counts in wild areas (see above), suggesting an important role for non-cultivated host plants in maintaining SWD populations. In European forests, raspberries, blackberries, and other wild plants that can be infested by SWD are common. Of particular note is the strawberry tree (*Arbutus unedo*), which is

abundant in forests in the Iberian Peninsula and other Mediterranean countries and has been shown to be infested by the pest (Gabarra et al. 2012). Another potentially important non-crop host plant in Europe is the invasive American black cherry (*Prunus serotina*), which has showed infestation rates as high as 70 % in one woodland location (Poyet et al. 2014).

In North America, Heimpel et al. (2010) proposed that European buckthorn (*Rhamnus cathartica*) might have facilitated the invasion of a wide variety of species. The potential for a linkage between SWD and *R. cathartica* is of particular concern in the Central US, because (a) it harbors millions of acres of buckthorn-infested woodlands, (b) a congener (*R. frangula*) has been documented as a host for SWD in Europe (Cini et al. 2012), and (c) SWD infestation of *R. cathartica* berries has been recently confirmed in Ontario, Canada (Ontario Ministry of Agriculture and Food 2014). We recommend a region-by-region approach to the investigation of wild host plant associations for SWD, as the relative importance of these associations undoubtedly varies geographically.

Biology of SWD movement

As with many invasive insect pests, there is still much to learn about the movement capabilities of SWD, including the possibility of long-distance migration. The rapid spread of SWD across both North America and Europe (see above) could result from human-assisted movement of produce, long-distance migration, or a combination of the two. A better understanding of SWD movement patterns also has implications for seasonal population dynamics; in parts of North America, for example, it remains unclear if SWD overwinters locally or immigrates from regions with more benign climates. In addition, localized movement between host plants may be important in predicting crop infestation levels (e.g., Klick et al. 2015).

In addition to field-based monitoring and inferences from population genetic and genomics data (e.g., Adrien et al. 2014), laboratory research on flight behaviors could provide important insights on the dynamics of SWD movement. For example, vertical flight chambers can estimate the movement capacity of small insects in two chief ways (Asplen et al. 2009): (1) the duration and speed of an individual's free flight, and (2) the strength of its sustained vertical climb toward skylight, which can increase its likelihood of leaving the flight boundary layer (i.e., the region above which wind speed exceeds an insect's flight speed) under natural conditions. Initial observations suggest that flying, 2-day old SWD exhibits vertical climb toward a skylight cue approximately 40 % of the time (6 out of 16 male flights; $N = 36$ assessed males;

5 out of 12 female flights, $N = 34$ assessed females) (M.K. Asplen, unpublished data). Future studies will examine how different traits (e.g., age, sex, mating status, body size) influence both phototaxis and flight duration/speed in SWD.

Concluding remarks

Insights from historical distributions and new SWD invasions

The rapid spread of SWD across Europe parallels the situation observed in North America (Burrack et al. 2012). Despite their matching time frames, however, the North American and European invasions seem to have arisen from independent demographic events, as inferred by analysis of population genetic data (Adrion et al. 2014). While genetic diversity appears high in North America, it is comparatively reduced in the initial area of description in Europe (Adrion et al. 2014). Low genetic diversity has not appeared to reduce either the invasion potential or adaptive ability of other *Drosophila* species (Gilchrist et al. 2004; Balanyà et al. 2006; Pascual et al. 2007), but in Europe it remains to be tested whether (1) single or multiple introductions have been responsible for its present day distribution, and (2) whether reduced genetic diversity is a common pattern across its present invaded area.

A recent genomic survey linked the invasive success of SWD in specific regions of North America and Europe to an ecological pre-adaptation to temperate climates (Ometto et al. 2013). In addition, to overcome deficiencies in cold tolerance, it is possible that the species may be behaviorally adapted (or pre-adapted) to overwinter in man-made protected habitats (Kimura 2004; Dalton et al. 2011). As a species from temperate ecosystems with seasonal fruit availability, it is likely that SWD has some capacity to migrate either daily or seasonally from lower to higher altitudes to avoid higher temperatures (Mitsui et al. 2010). The presence of winter reproductive diapause in SWD (see above) seems to be a further indication of adaptation to temperate/cool climates. Using relaxed clock studies of both nuclear and mitochondrial genomes, Ometto et al. (2013) suggest that SWD diverged from *D. biarmipes* approximately 9 to 6 million years ago, toward the end of the Miocene (Tortonian). Climate modeling has shown that, during the Tortonian, extended mountainous, temperate forests characterized the ecology of the region between North India, Indochina, and the Chinese coasts. The present endemic distribution of SWD in Asia is relegated to mountain and temperate regions, while *D. biarmipes* is now endemic to equatorial habitats, suggesting that diversification of SWD was accompanied by

adaptation to temperate habitats. It should be noted, however, that niche shifts and/or adaptations to newly invaded areas should not be excluded as explanatory factors for the speed and scale of global SWD invasions (Calabria et al. 2012).

The future of SWD management

A high degree of reliance on chemical control tactics for SWD occurs in all geographic regions impacted by this pest. Given legitimate concerns over resistance issues, possible negative effects on non-target organisms and the environment (e.g., Desneux et al. 2007; Biondi et al. 2012), and the long-term sustainability of such a regime, research groups in affected areas are working to develop improved trapping systems, a wider spectrum of chemical control options, biological and genetic control approaches, and cultural control systems. As these efforts mature, management of SWD is expected to become more integrated and less chemically dependent. This will also reduce the likelihood of insecticide resistance development, which is a significant concern given the short generation times of *Drosophila* pests. Achieving this will also require investment in education programs to transfer information from research programs to end-users.

One of the keys to the development of an IPM program for SWD remains further research into biological control strategies (e.g., see recent works on major invasive alien pests in North America and Europe, Ragsdale et al. 2011; Zappalà et al. 2013). Despite the fly's high reproductive potential and multiple generations per year, biological control of SWD may nevertheless play an important role by reducing populations in natural reservoir habitats, even if not necessarily in cultivated crops. As SWD populations move seasonally among preferred and non-preferred hosts among different habitats and elevations (e.g., Beppu 1984; Mitsui et al. 2010; Choi 2012), significant levels of natural enemy activity in any of the key habitats may reduce numbers of flies that migrate into crop habitats, making it easier and more economical to manage this pest with a combination of other IPM methods.

As has occurred with many other invasive pests, we expect that the proportion of growers experiencing economic loss will decline as grower awareness of and experience with SWD increases. Within invaded habitats, increasing interactions between various biological control agents and SWD are expected to gradually decrease the carrying capacity of wild habitats for this insect, thereby reducing their immigration to agricultural fields. We also see post-harvest management options becoming a greater component of holistic SWD management systems—combining tactics used from initial cultivar selection to the final sale of fruit. This will require greater coordination among

the components of this system, and coordinated management is something that may be needed to effectively manage SWD populations, much like the recent response in Florida, US to the Asian citrus psyllid (Rodríguez-Saona and Stelinski 2009). Whatever the future holds, it is clear that SWD has caused a dramatic and rapid disturbance to well-established IPM programs in susceptible fruit crops, and it will require significant effort and funding to minimize the effects of this invasive pest.

Author contribution statement

MKA, RI, AB, WDH, and ND organized the review based on written contributions from all authors. PG and CP contributed original data, which were analyzed by APG and LP (including the Supplemental Material). All authors reviewed and approved the final manuscript.

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