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EDITED BY
John Abraham,
University of Cape Coast, Ghana

REVIEWED BY
Claire Dumenil,
University of Padua, Italy
Flavia Cerasti,
Centro Ricerche Casaccia, Italy

*CORRESPONDENCE
Samuel Cruz-Esteban
cruzestebansam@gmail.com

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Advances in the management of *Drosophila suzukii* population: from olfactory and visual stimuli to development of push–pull systems

Samuel Cruz-Esteban*

Independent Researcher, Tapachula, Chiapas, Mexico

Drosophila suzukii (Matsumura) is an invasive pest of major concern because of its ability to lay eggs in immature or thin-skinned ripening fruits, leading to substantial economic losses in berry production. This review examines recent advances in ethological control strategies—those that exploit pest behavior—including olfactory attractants, visual stimuli, trap density and spacing for mass trapping, and push–pull systems incorporating oviposition deterrents. Original data from Mexico and other countries are included, along with a discussion of current limitations, knowledge gaps, and future research directions aimed at improving practical effectiveness.

KEYWORDS

***Drosophila suzukii*, ethological control, fermentative attractant, integrated management, mass trapping, oviposition deterrent, visual stimulus**

1 Introduction

The spotted wing drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), is an invasive pest affecting berries and other soft-skinned fruits and has become established in various regions worldwide. This species is native to Southeast Asia and was first described from infested cherries in Japan by Kanzawa in 1916 (Kanzawa, 1935; Walsh et al., 2011). The species is now established across multiple regions worldwide, including Europe (Cini et al., 2012), Oceania (Garcia, 2021), North Africa (Ouantar et al., 2020), North America (Hauser, 2011), Central America (Chacón-Cerdas et al., 2024), and South America (Andreazza et al., 2017). In North America, it was first collected specifically in California (USA), in 2008 and has rapidly spread through several states of the USA, reaching parts of Canada by 2010 (Lee et al., 2011; Asplen et al., 2015; Funes et al., 2018). In Mexico, the pest was first reported in 2011 in Los Reyes, Michoacán, and its current distribution includes the states where cherries (*Prunus* spp.: Rosaceae) (Walsh et al., 2011), blackberry (*Rubus ulmifolius* Schott: Rosaceae), raspberry (*Rubus idaeus* L., Rosaceae), strawberry (*Fragaria* spp.: *Rosaceae*), blueberries (*Vaccinium corymbosum* L.: Ericaceae) (Cruz-Esteban et al., 2021a, 2021b; Cruz-Esteban, 2021; Cruz-Esteban et al., 2024a, 2024b), guava (*Psidium guajava* L.: Myrtaceae) (De los Santos Ramos et al., 2014; Lasa and Tadeo, 2015), and fig (*Ficus carica* L.) are cultivated (Bautista-Martínez et al., 2017). In addition, it is also associated with wild or non-cultivated soft-skinned fruits such as *Rubus adenotrichos* Schltdl. (tropical blackberry), *Spondias mombin* L. (yellow mombin), *Prunus serotina* subsp. *capuli* (capulín cherry), *Muntingia calabura* L. (tropical capulín), and *Psidium guajava* (guava) (Lasa and Tadeo, 2015; Bautista-Martínez et al., 2017; Castro-Sosa et al., 2017; SENASICA (Servicio Nacional de Sanidad, Inocuidad y Calidad Agroalimentaria), 2019; Garcia et al., 2022; Franco-Valbuena et al., 2025). Its broad geographic spread is linked to its strong dispersal capacity (Hauser, 2011), its ability to tolerate a wide range of climatic conditions (Cini et al., 2012), and its extensive host range. Asplen et al. (2015) and Morales-Abeijon et al. (2025), along with several subsequent reviews, reported that *D. suzukii* exploits more than 50 plant species belonging to diverse botanical clades. The family Rosaceae is the most heavily represented and includes many of its main cultivated hosts; however, the fly also infests species within Ericaceae, Myrtaceae, Grossulariaceae, Actinidiaceae, and Vitaceae, among others. This broad host range underscores the species' high ecological plasticity and its capacity to exploit both cultivated and wild fruits throughout the season. Ecological distribution models and recent sampling confirm its expansion into the central and southeastern regions of the country, including Guanajuato, Querétaro, Chiapas, and Oaxaca, where its presence has been documented across various tropical and temperate agroecosystems (Tait et al., 2018; Cruz-Esteban et al., 2022; Franco-Valbuena et al., 2025). Niche modelling predicts that suitable habitats for this species in Mexico include the temperate and subtropical highlands of the Trans-Mexican Volcanic Belt and the humid regions of the southeast (Calabria et al., 2012; Asplen et al., 2015; Castro-Sosa et al., 2017; Little et al., 2020a; Franco-Valbuena et al., 2025).

Unlike most *Drosophila* species, female *D. suzukii* possess a serrated ovipositor that enables them to puncture the skin of healthy fruit, and once the larvae emerge, they feed on the fruit's mesocarp, causing substantial economic damage (Walsh et al., 2011; Atallah et al., 2014; Asplen et al., 2015; Lee et al., 2015; Kirschbaum et al., 2021; Dreves et al., 2023; De Ros, 2024). Its rapid reproduction and spread pose challenges for pest management, particularly as chemical control faces limitations related to insecticide resistance (Rossi-Stacconi et al., 2020; Liburd and Rhodes, 2021; Shawer, 2021), concerns regarding residues, and environmental impact (Asplen et al., 2015; Kirschbaum et al., 2021; Shawer, 2021; Tait et al., 2021). However, Morales-Abeijon et al. (2025) highlight an even more alarming scenario compared with earlier studies, summarizing substantial economic losses attributed to this pest and the high expenses associated with its management. For instance, in California, Oregon, and Washington (USA), estimated losses for strawberries, blueberries, raspberries, blackberries, and cherries could reach USD 511.3 million (Bolda et al., 2010). Reported impacts also include yield reductions of up to 20% in raspberry production in Minnesota (USA) (DiGiacomo et al., 2019), losses of approximately €3.3 million in Trento (Italy) (De Ros et al., 2013), between USD 5,000 and 17,550 per hectare for cherries and around USD 4,000 for blueberries in Ñuble (Chile) (Buzzetti Morales, 2020), and up to USD 21.4 million for peaches and USD 7.8 million for figs in Brazil (Benito et al., 2016). Beyond yield losses, pest management costs have risen sharply; for example, raspberry revenues in California (USA) decreased by 37% and strawberry revenues by 20% due to increased expenditures on insecticides (Goodhue et al., 2011). Therefore, in recent years, there has been increased interest in behavioral control strategies—based on the insect's behavior—that include the use of attractants as homemade ferments and fermentation products (Cha et al., 2014, 2018; Tonina et al., 2018; Cruz-Esteban et al., 2024b), microorganisms such as yeast (Becher et al., 2012; Cha et al., 2017; Spitaler et al., 2020), optimized traps commercial and home-made (Renkema et al., 2017; Cha et al., 2018; Cruz-Esteban et al., 2021a; Cruz-Esteban, 2021), visual stimuli as colored traps and cards placed inside traps (Kirkpatrick et al., 2016; Little et al., 2018, 2019, 2020b; Cruz-Esteban, 2021, 2024a; Lasa et al., 2024), repellents, and oviposition inhibitors that manipulate the orientation and reproductive activity of the species (Revadi et al., 2015; Renkema et al., 2016, 2017; Tonina et al., 2020; Tait et al., 2021; Roh et al., 2023). These studies have been conducted by evaluating individual variables as well as the synergistic effects or combinations among them.

This review aims to synthesize recent advances (2015–2025) in behavioral strategies for managing *D. suzukii*, with an emphasis on their practical application in berry production systems in Mexico and other regions worldwide, and to propose applied research directions for the development of sustainable monitoring and control tools.

2 Methods of literature search

A comprehensive literature review was conducted using the Web of Science, Scopus, and Google Scholar databases, covering the period from 2015 to 2025. Combinations of keywords in both English and Spanish were utilized, including *D. suzukii*, attractant, bait, trap design, visual cues, oviposition deterrent, repellent, mass trapping, push-pull, ethological control, and behavioral manipulation.

The search included experimental articles, reviews, and field reports focused on ethological management strategies, which encompass olfactory attractants (Renkema et al., 2017; Cha et al., 2018a; Tonina et al., 2020; Beers et al., 2022; Cruz-Esteban et al., 2024b; Brilinger, 2024), visual cues and traps design (Kirkpatrick et al., 2018a; Cruz-Esteban, 2021; Little et al., 2021; Cruz-Esteban et al., 2024a), mass trapping: density, spacing, and trap interference (Hamby et al., 2016) push-pull oviposition deterrents, and repellents (Hamby et al., 2016; Iglesias and Liburd, 2017). Additionally, studies examining interactions with parasitoids and natural enemies were reviewed (Wang et al., 2016; Girod et al., 2018; Renkema et al., 2020). Some studies published prior to the period defined for the systematic search were incorporated in order to strengthen the contextualization of certain topics, particularly within the conceptual framework of the review.

The selected articles were filtered based on their relevance to the ethological control of *D. suzukii*, experimental validity, demonstration in field or semi-field conditions, and their contribution to the development of sustainable management methods (Cha et al., 2018; Alkema et al., 2019; Morales-Abeijon et al., 2025).

3 Results

3.1 Olfactory attractants

Olfactory attractants constitute the foundation of monitoring and control strategies for *D. suzukii*. However, this section focuses exclusively on the odors emitted by fruits at different developmental stages—ripening, mature, and decaying—and by the microorganisms associated with them. The underlying premise is that flies seek host fruits at various stages for feeding, mating, and oviposition (Tochen et al., 2016; Cloonan et al., 2018; Young et al., 2018; Clymans et al., 2019; Galland et al., 2020; Piñero et al., 2022; Elsensohn and Burrack, 2023; Kim et al., 2023). Traditional attractants, including apple cider vinegar (ACV), rice vinegar, wine vinegar, acetoin, octanoate, acetic acid, ethanol, and isoamyl acetate compounds alone or in mixtures, have long been used as reference or control (Cloonan et al., 2018; Renkema et al., 2018; Lasa et al., 2020; Cruz-Esteban et al., 2021a, 2024a, 2024b). However, their efficacy varies depending on the composition and ratio of volatile compounds (Abraham et al., 2015; Cha et al., 2015; Mazzetto et al., 2015, 2016a; Akasaka et al., 2017; Cloonan et al., 2018; Feng et al., 2018; Jaffe et al., 2018; Kirkpatrick et al., 2018a; Lasa et al., 2019; Willbrand and Pfeiffer, 2019; Lasa et al., 2020; Toledo-Hernández et al., 2021a, 2021b; Urbaneja-Bernat et al., 2021; Keene-Snickers et al., 2025). In Mexico, several commercial products are available that are based on the four most attractive compounds—acetoin, methionol, acetic acid, and ethanol—previously reported by Cha et al. (2014, 2015, 2017, 2018). One such product is Z-Kinol® (Squid Biological and Pheromones S.A. de C.V., Texcoco, Mexico) (Cruz-Esteban et al., 2021a), which uses water with 5% soap as the retention solution. Another commercially available product manufactured outside Mexico is Pherocon® SWD (Trécé Inc., Adair, OK, USA) (Burrack et al., 2015; Frewin et al., 2017; Tonina et al., 2018), as well as Scentry® (Scentry Biologicals Inc., USA), which uses ACV as the retention solution (Kirkpatrick et al., 2017; Lethmayer and Egartner, 2017; Briem et al., 2018; Whitener et al., 2022). These four volatile organic compounds (VOCs), identified as highly attractive and incorporated into the formulation of these commercial attractants, have also been detected and confirmed in homemade fermentations evaluated in Mexico (Cruz-Esteban et al., 2024b; Alavez-Rosas et al., 2024). Other food-based attractants, such as SuzukiiTrap® (Bioibérica, Barcelona, Spain) (Tonina et al., 2018; Cruz-Esteban et al., 2021a), Fruit Fly Attractant (Koppert), and SuzukiiLURE-Max (Dinusa, Oaxaca, Mexico), also employ these components as retention solutions and claim to be effective for monitoring *D. suzukii*. However, these products should be evaluated under local conditions, as not all of them were specifically developed for Mexican populations. Furthermore, some products are described as scientifically developed, yet the supporting references demonstrating their efficacy are often not available, possibly due to geographical variation in *D. suzukii* populations (Jaffe et al., 2018; Wollmann et al., 2019; Larson et al., 2021; Whitener et al., 2022). Another important factor is their relatively high cost, which highlights the need to identify and develop formulations that are more effective, affordable, long-lasting, and environmentally friendly—safe for pollinators and, above all, for farmers—and that can be readily adapted to local populations.

When discussing fermented products, it is essential to consider another group of VOCs produced and emitted by microorganisms, such as bacteria, fungi, and yeasts, that are associated with fruits (Hamby and Becher, 2016). These organisms participate directly or indirectly in the fermentation process. Among symbiotic bacteria, the most common species found in microbial communities associated with *Drosophila suzukii* are *Tatumella* spp. (Enterobacteriaceae) (Chandler et al., 2014), *Gluconobacter* spp (Chandler et al., 2014; Mazzetto et al., 2016a; Bueno et al., 2020), *Komagataeibacter* spp (Mazzetto et al., 2016a), and *Acetobacter* spp. (Acetobacteraceae) (Chandler et al., 2014; Mazzetto et al., 2016a; Bueno et al., 2020). Other bacteria, such as *Oenococcus oeni*, commonly involved in malolactic fermentation during wine production (Alawamleh, 2021; Đurović et al., 2021; Maddalena, 2016, 2021), and *Lactobacillus kunkeei* and other lactic acid bacteria strains (Alawamleh, 2021; Alawamleh et al., 2021), have also been associated with *D. suzukii*. Yeasts are particularly important because they play a key role in the attraction of *D. suzukii* (Barata et al., 2012; Scheidler et al., 2015). The most studied species include *Saccharomyces cerevisiae*, a yeast widely used in baking (Batista et al., 2017; Lasa et al., 2017; Spitaler et al., 2020); *Saccharomycopsis vini* (Spitaler et al., 2020; Castellan et al., 2024); *Hanseniaspora uvarum* (Scheidler et al., 2015; Batista et al., 2017; Mori et al., 2017; Noble et al., 2019; Bianchi et al., 2020; Bueno et al., 2020; Spitaler et al., 2020; Huang and Gut, 2021; Kleman et al., 2022; Rehermann et al., 2022; Castellan et al., 2024); *H. opuntiae* (Bueno et al., 2020); *Issatchenkia terricola; Metschnikowia; Metschnikowia pulcherrima* (Spitaler et al., 2020; Jones et al., 2021); *Candida zemplinina* (Scheidler et al., 2015; Spitaler et al., 2020; Jones et al., 2021); *Clavispora santaluciae*; *Saccharomycopsis vini*; *Issatchenkia terricola*; *Metschnikowia pulcherrima* (Castellan et al., 2024), and *Pichia pijperi* (Jones et al., 2021), a yeast frequently found in the alimentary canals of flies and in larval excreta (Hamby et al., 2012; Solomon et al., 2019; Bellutti et al., 2018). These species are highly attractive to *D. suzukii*, enhance fecundity, and often exhibit positive synergistic effects when combined (Jones et al., 2025), as well as with commercial or homemade attractants, and with bioinsecticides or conventional insecticides (Jones et al., 2022; Barone and Hartbauer, 2024; Duménil et al., 2025; Molokwu et al., 2025). Gas chromatography–electroantennographic detection (GC-EAD) analyses have identified isobutyl acetate and isoamyl acetate emitted by *H. uvarum* as key volatiles perceived by *D. suzukii* antennae (Scheidler et al., 2015). Isoamyl acetate is also found in several attractive fruits, including strawberries and blueberries (Dekker et al., 2015). Studies have shown that mated females are more strongly attracted to *H. uvarum* and fruit odors but may reduce oviposition when feeding on yeast, suggesting a trade-off between feeding and reproduction (Mori et al., 2017). Yeast-associated volatiles can also enhance oviposition in other fruits, such as cherries (Bellutti et al., 2018), although their effects appear to depend on the background fruit odors (Cloonan et al., 2019). Furthermore, acetic acid bacteria such as *Gluconobacter* spp. emit volatiles including ethanol, acetic acid, and aldehydes, which also elicit antennal responses in *D. suzukii* (Mazzetto et al., 2016a). More recently, Castellan et al. (2024) and Duménil et al. (2025) reported that in electrophysiological assays, antennae of *D. suzukii* responded to ethyl acetate, propanoate, isoamyl acetate, β-myrcene, benzaldehyde, and linalool, compounds that may underlie the strong attractiveness of *S. vini* and *H. uvarum* to this species.

Another important group of VOCs that influence the attraction of *D. suzukii* are produced and emitted by fruits, particularly across different developmental stages. For instance, it has been reported that virgin or protein-deficient females, as well as males, are attracted to fermented food sources, where females can feed and wait for egg maturation. These same sites also serve as mating grounds, where a possible pheromone and numerous co-occurring compounds are likely involved (Revadi et al., 2015; Tochen et al., 2016; Clymans et al., 2019; Khan et al., 2019). Once mated, females are guided by VOCs emitted from ripening or fully ripe fruits in good condition to locate suitable oviposition sites and ensure offspring survival (Tochen et al., 2016; Cloonan et al., 2018; Young et al., 2018; Clymans et al., 2019). However, this behavior in gravid females has also been shown to vary with seasonal conditions (Clymans et al., 2019). Several studies have demonstrated host preferences for economically important fruits, classifying them according to attraction levels observed in laboratory bioassays. For example, Abraham et al. (2015) found that *D. suzukii* exhibited the strongest preference for raspberry, followed by strawberry, blueberry, and cherry—consistent with the findings of Cai et al. (2019). These results align with field observations by Cruz-Esteban et al. (2021a), who reported higher fly captures in raspberry crops, followed by blackberry, strawberry, and blueberry. However, when cultivated alone, any of these fruits can be highly susceptible to *D. suzukii* infestation (Little et al., 2017; Cruz-Esteban et al., 2021a). Analyses of VOCs from these mature fruits, both intact (healthy) and mechanically damaged, revealed that alcohols, aldehydes, and ketones are the predominant compounds (Abraham et al., 2015; Revadi et al., 2015; Cloonan et al., 2018). Gas chromatography–electroantennographic detection (GC-EAD) analyses have shown that *D. suzukii* antennae respond to several volatiles from raspberry and strawberry, including esters, alcohols, and ketones. An eleven-compound blend identified from raspberry was attractive to both sexes, although less so than the natural fruit extract (Abraham et al., 2015; Keesey et al., 2015). The volatile profile of apples consists mainly of esters, alcohols, and ketones, among which acetoin and octanoate have been identified as the most attractive compounds to *D. suzukii* (Feng et al., 2018). Similarly, four volatile compounds from bayberry—methyl (E)-3-hexenoate, methyl (E)-2-hexenoate, ethyl (E)-2-hexenoate, and α-humulene, in a ratio of 1:1.3:1:6.4—were reported to be attractive under field conditions (Liu et al., 2018). Approximately 33 compounds have been identified from blackberry, with acetaldehyde, hexyl acetate, linalool, and myrtenol being the most attractive (Dewitte et al., 2021). Overall, VOCs emitted by host fruits are highly attractive to this invasive fly species, as confirmed by recent studies comparing natural fruit odors with various commercial attractants (Babu et al., 2022). Therefore, ongoing research efforts remain focused on identifying and developing volatile blends that are more attractive under field conditions.

In Mexico, Cruz-Esteban et al. (2021a) demonstrated that the type of attractant, rather than the trap design, significantly influences the capture efficiency of *D. suzukii* in berry crops. In their study, two commercial attractants—Z-Kinol® and SuzukiiTrap®—as well as apple cider vinegar (ACV) and a previously reported highly attractive blend (ACV + EtOH + CO_2) (Lasa et al., 2017) were compared under a factorial design that included raspberry, blackberry, strawberry, and blueberry crops. Significant differences in capture efficiency were observed among attractants but not between trap designs, highlighting the importance of selecting appropriate baits for effective monitoring and population control. Recent studies conducted outside Mexico support these findings. Larson et al. (2021) evaluated various attractant blends for early detection and monitoring, identifying specific compounds such as acetoin that enhance selectivity and detection sensitivity. The recent work of Cruz-Esteban et al. (2024b) further advanced this field by testing fermented baits formulated from blueberries, raspberries, baker's yeast, and sugar. In field trials, these baits showed superior attractiveness compared to commercial ACV or homemade vinegar blends, resulting in higher capture rates of *D. suzukii* adults in both blueberry and blackberry crops. Notably, these fermentative blends also demonstrated consistent performance across multiple harvests, high attractiveness to *Zaprionus indianus* (Gupta) (Diptera: Drosophilidae)—particularly during seasons when both pests overlap—and low attraction of non-target drosophilids, thereby improving selectivity while maintaining cost-effectiveness and local producibility. Similar findings were reported in Michigan, where a mixture of wine, vinegar, and yeast proved more attractive in the field than each component alone (Huang et al., 2017). Likewise, in the United States, laboratory assays revealed that fruit VOCs became more attractive when combined with β-cyclocitral or a blend of β-cyclocitral, isoamyl acetate, and methyl butyrate (Bolton et al., 2019; Piñero et al., 2019; Bolton et al., 2022). Despite their advantages, fermentative attractants present several challenges, including variable duration of efficacy, sensitivity to environmental conditions, and the potential to attract non-target species. In contrast, synthetic baits with controlled release offer longer persistence, greater selectivity when properly formulated, and reduced maintenance requirements, although they are generally more expensive. Another critical aspect is the capture threshold, as trap detections often occur when populations have already reached levels capable of causing economic damage. For instance, monitoring in Michigan estimated that capturing a single individual in a trap corresponded to approximately 192 flies within a 2.7 ha area, underscoring the need for prompt action upon first detection (Larson et al., 2021).

3.2 Visual cues and trap design

Results regarding the use of visual cues (i.e., attractive colors) and trap designs obtained from laboratory and field studies have been quite contradictory. For instance, Rice et al. (2016) reported that black and red spheres captured significantly more *D. suzukii* than purple, blue, yellow, or white spheres in laboratory assays, and semi-field raspberry trials. Similarly, several studies have concluded that red and black traps are among the most effective for attracting and capturing this invasive fly (Basoalto et al., 2013; Lee et al., 2013; Renkema et al., 2014; Kirkpatrick et al., 2016, 2017; Lasa et al., 2017; Rice et al., 2017). The effectiveness of these visual cues is further enhanced when they act in synergy with food-based attractants (Bolton et al., 2021; Lasa et al., 2024). In contrast, Cahenzli et al. (2018) found that transparent traps fitted with a black lid captured more *D. suzukii* than traps equipped with a red lid. Similarly, other studies have shown that transparent and yellow traps perform comparably to red and black traps (Lee et al., 2013; Iglesias et al., 2014; Briem et al., 2018; Marjanović and Tanasković, 2019). Overall, these differences were primarily numerical and often not statistically significant. In addition, background color contrast has been shown to influence *D. suzukii* attraction (Antignus, 2000; Little et al., 2019). For example, under laboratory conditions, Little et al. (2019) found that black, purple, red, or yellow objects presented against a green background did not differ significantly in attractiveness. However, purple objects against a green background were more attractive than red objects against a black background, black objects against a red background, or blue objects against a yellow background. Similar context-dependent effects of visual cues have been reported by Barone and Hartbauer (2024), who demonstrated that Petri dishes covered with red mesh but containing yellow gels attracted more *D. suzukii* than transparent controls, highlighting the importance of the visual properties of the stimulus itself rather than the external background alone. However, recent studies conducted in Mexico have demonstrated that capture success is not determined by the external color of the trap, but rather by chemical communication and short-range visual stimuli—such as colored cards and reflective surfaces placed inside the trap—which significantly increase the likelihood of fly entry (Cruz-Esteban et al., 2021a, 2021b; Cruz-Esteban, 2021; Figure 1). For example, comparative evaluations of attractants and trap designs showed that chemical cues, particularly fermentation-related compounds, are the primary drivers of *D. suzukii* attraction. No significant differences among trap designs were detected when all were baited with the same chemical stimulus, indicating that capture efficiency was largely independent of trap architecture under these conditions (Cruz-Esteban et al., 2021a; Figure 1a). However, the potential contribution of visual cues at short range could not be excluded. Subsequent experiments incorporating previously untested colors and transparent traps with internal yellow or violet cards—colors reported as attractive in laboratory assays (Little et al., 2019)—revealed a strong effect of internal visual stimuli. Transparent traps equipped with an internal yellow card captured approximately 400% more *D. suzukii* than other designs (Cruz-Esteban, 2021; Figure 1b). Further tests using single colors

FIGURE 1
(A) Trap designs and **(B)** color contrasts evaluated for monitoring *Drosophila suzukii* in berry crops in Michoacán, Mexico (Cruz-Esteban et al., 2021a; Cruz-Esteban, 2021).

and color combinations inside transparent traps, all baited with the same attractant, confirmed this pattern: yellow cards, alone or combined with green, consistently produced the highest captures (≈350% increase) relative to other colors (Cruz-Esteban et al., 2021b; Figure 2). More recently, variation in yellow reflectance was shown to influence trap performance, with a yellow card exhibiting 67% reflectance and a dominant wavelength of 549.74 nm outperforming higher-reflectance yellow cards in apple cider vinegar–baited traps (Cruz-Esteban et al., 2024a, Figure 2).

Therefore, advances in trap design now emphasize optimizing internal visual stimuli rather than focusing solely on external color (Little et al., 2018, 2019, 2020b; Cruz-Esteban, 2021; Cruz-Esteban et al., 2024a, Figure 2). These findings underscore the importance of integrating visual cues into trap design as complementary components of ethological control strategies, ensuring that adult flies are efficiently guided into traps even when olfactory plumes have a limited range (Figure 2). Overall, visual stimuli represent a critical factor in the performance of monitoring and mass-trapping programs. Optimizing trap color, internal reflectance, and brightness—when combined with high-quality attractants—can maximize capture efficiency and contribute to the sustainable management of *D. suzukii* in commercial berry systems. When tailored to local crop conditions and fly behavior, these strategies enhance early detection, population suppression, and reduction of crop damage. At the same time, olfactory attractants remain indispensable for both monitoring and population suppression of *D. suzukii*, particularly when integrated with visual stimuli, mass-trapping strategies, and oviposition deterrents. Moreover, these studies have greatly advanced our understanding of the chemical ecology of *D. suzukii*, providing a foundation for targeted research aimed at elucidating behavioral responses under field conditions, including host-seeking activity, oviposition site selection, and multimodal sensory integration (Figure 3). Recent advances in bait formulation, including the evaluation of fermentative blends reported by Cruz-Esteban et al. (2024b), provide evidence that locally formulated baits can function as effective tools within integrated management programs for *D. suzukii* in commercial berry production systems, particularly when cost, accessibility, and sustainability are considered.

FIGURE 2
Transparent multi-hole trap used for the mass capture of *Drosophila suzukii* in berry crops. The trap consists of a transparent plastic container (1 L capacity) perforated with multiple 5-mm holes in the upper half of its wall to allow fly entry. Inside the trap, a yellow card (67% reflectance at a dominant wavelength of 549.74 nm) serves as a visual stimulus to enhance attraction, while the lower section contains a fermented bait composed of blueberries, raspberries, yeast (*Saccharomyces cerevisiae*), and sugar as a nutrient source for yeast fermentation. Optionally, a central wick dispenser can be inserted to release additional volatile compounds and increase bait efficacy. The trap is suspended from the plant canopy, positioned approximately 1.2–1.5 m above the ground, with a spacing of 6 m (equivalent to 289 traps per ha^{-1}) in blueberry and blackberry orchards in Tiripetío, Michoacán, Mexico. This configuration has proven highly effective for population suppression, maintaining infestation levels below 5%, and in some cases, completely eliminating pest presence (Cruz-Esteban et al., 2024b).

3.3 Mass-trapping: Density, spacing, and trap interference

Mass trapping is a key strategy for the suppression of *D. suzukii* populations, going beyond its traditional role in monitoring. This approach relies on deploying attractant-baited traps to capture adults, thereby reducing reproductive output and limiting dispersal. The effectiveness of mass trapping is strongly influenced by trap density and spacing, as closely spaced traps can experience overlapping attraction radii, leading to intra-trap competition and potential saturation of the target area (Clymans et al., 2022). Based on this study, recommended trap densities range from 75 to 200 traps ha^{-1} in spring and 90 to 300 traps ha^{-1} in summer, depending on bait type and environmental conditions. Controlled-release synthetic baits, which maintain attractiveness over longer periods, can allow reductions to approximately 25 traps ha^{-1} without compromising population suppression (Clymans et al., 2022). Trap spacing can range between 3 and 5.5 m (Hampton et al., 2014; Kirkpatrick et al., 2018a; Spies and Liburd, 2019; Clymans et al., 2022).

Field trials in cherry orchards have further demonstrated the utility of mass trapping. The Decis$^{\text{TM}}$ Trap, which combines a persistent attractant with an insecticide-treated interior, was highly effective at reducing *D. suzukii* populations when deployed at 100 traps ha^{-1}, particularly when placed early in the growing season, resulting in significant reductions in fruit damage (De Maeyer et al., 2018). These findings highlight that the timing of trap placement is as critical as trap density in maximizing suppression and preventing early-season infestations.

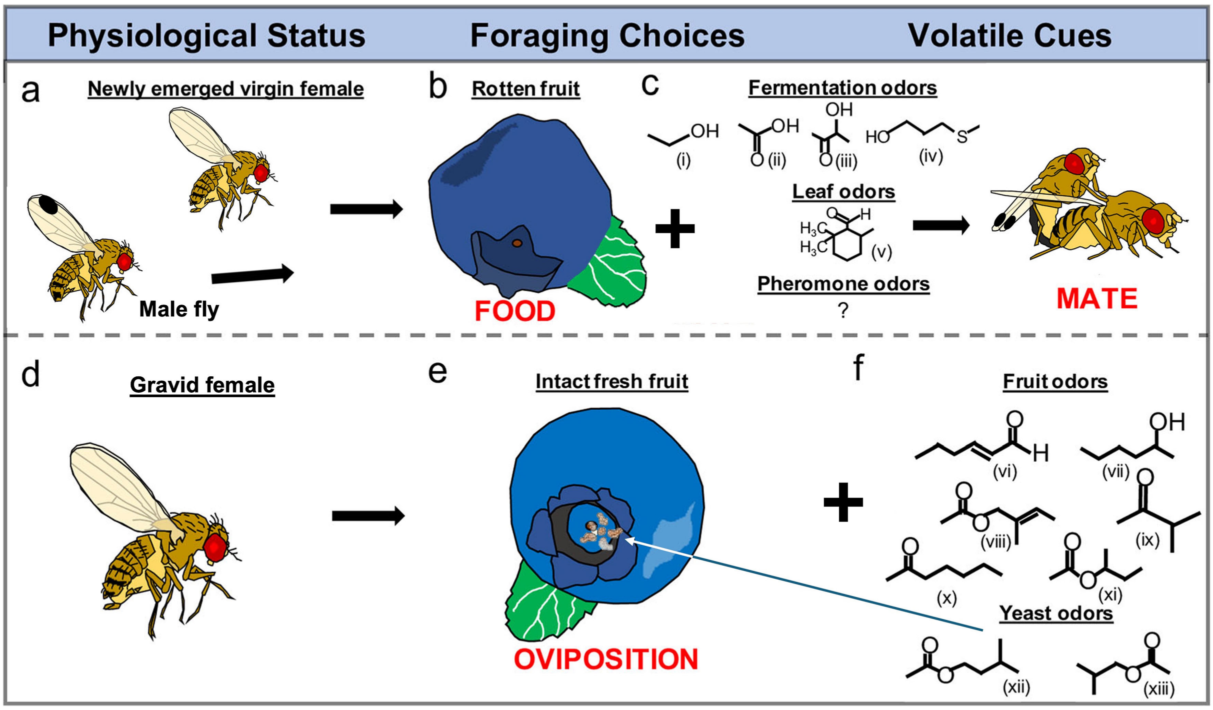

FIGURE 3
Schematic representation of the host-search strategies used by virgin and mated female *Drosophila suzukii* for feeding, mating, and oviposition (adapted from Cha et al., 2018). **(A)** Newly emerged females primarily orient toward decaying fruit as a source of sugars and proteins, relying on long-range olfactory cues and short-range visual and tactile stimuli. **(B)** During this phase, females are likely attracted to fermentation-related volatiles—such as (i) ethanol, (ii) acetic acid, (iii) acetoin, and (iv) methionol—produced and released by fruits and associated microorganisms, including fungi and yeasts, enabling the localization of overripe or decomposing substrates. **(C)** Leaf-emitted odors, such as (v) β-cyclocitral, may further contribute to long-range orientation, whereas tactile cues from foliage may operate at close range. Visual stimuli also play an important role, as *D. suzukii* responds to fruit reflectance and contrast against the surrounding plant canopy. These feeding sites may also function as mating arenas, since males must similarly locate food resources to survive, potentially using comparable sensory mechanisms; however, the involvement of a species-specific sex pheromone has not yet been clearly established. **(D)** In contrast, mated and gravid females shift their search behavior toward fresh, intact fruit suitable for oviposition. **(E)** At this stage, females likely integrate a more specific set of fruit- and microbe-derived volatiles, including those associated with yeasts—**(F)** such as (vi) trans-2-hexenal, (vii) hexanol, (viii) 3-methyl-2-butenyl acetate, (ix) 3-methyl-2-butanone, (x) 2-heptanone, (xi) butyl acetate, (xii) isoamyl acetate, and (xiii) isobutyl acetate—acting at both long and short distances. To locate healthy or ripening fruit, visual and tactile cues become increasingly important, particularly fruit reflectance and contrast against the green background of the crop, as well as physical assessment of the fruit surface, to ensure offspring survival (Bartelt et al., 1985; Lebreton et al., 2017; Kwadha, 2022; Lima et al., 2023).

Mass-trapping strategies have been successfully applied in berry crops. For example, in Tiripetío, municipality of Morelia, Michoacán, Mexico (19°31′55″ N, 101°22′10″ W), transparent multi-hole traps equipped with yellow cards (67% reflectance at 549.74 nm) and baited with a fermented solution containing blueberries, raspberries, baker's yeast, and sugar have been deployed during 2023–2024 in blueberry and blackberry crops (Cruz-Esteban et al., 2024b; Figure 2). Traps were installed 6 m apart, totaling 289 traps ha^{-1}. This approach proved highly effective, maintaining infestation levels below 5% and enabling all harvest lots to meet export standards. It has been observed that when fruits in ripening, mature, and overripe stages are abundant, fly captures decrease, as previously reported by other authors (Harris et al., 2014; Burrack et al., 2015; Joshi et al., 2017). However, we have found a way to stimulate fly activity so that they leave the host fruit and are attracted to and captured by the traps. Applications of garlic extract (an insect repellent, 1 kg/100 L H_2O) have been made every 15 days in the center of each crop row, raising the sprayer half a meter above the ground (Allium, AGROARSA, Mexico). For monitoring purposes, random samples of approximately 100 fruits per hectare per crop are collected, placed in a Ziploc bag, and gently macerated by hand to avoid damaging the larvae. The fruits are then submerged in a sugar-water solution (180–200 g/L) to facilitate larval detection by flotation (SENASICA (Servicio Nacional de Sanidad, Inocuidad y Calidad Agroalimentaria), 2014; Shaw et al., 2019; Babu et al., 2023). This information is complemented with a direct physical inspection of each fruit using a magnifying glass or a stereomicroscope (Van Timmeren et al., 2021).

Several critical factors influence the success of mass-trapping programs. Optimizing trap spacing is essential to avoid intra-trap competition caused by overlapping attraction radii. Bait selection also plays a major role, as controlled-release synthetic baits provide longer-lasting attraction and greater selectivity compared to traditional fermentative baits such as apple cider vinegar. Additionally, environmental factors—including temperature, crop phenology, and pest population density—strongly affect trap performance and must be considered when planning deployment.

The integration of mass trapping with visual stimuli, oviposition deterrents, and complementary biological control can further enhance population suppression, highlighting the importance of multi-tactic approaches for sustainable management of *D. suzukii* in commercial berry production.

3.4 Push–pull and oviposition deterrents

Push–pull strategies and oviposition deterrents are designed to reduce egg laying on host crops while simultaneously attracting adults to traps or non-crop buffer zones (Figure 4). Recent studies have demonstrated the potential of both chemical and biological signals to manipulate *D. suzukii* behavior under field conditions. For instance, the presence of live *Drosophila melanogaster* (Meigen) (Diptera: Drosophilidae) larvae has been shown to reduce oviposition by *D. suzukii* on artificial substrates, with the live larvae acting as deterrent cues, whereas eggs and adults of *D. melanogaster* did not elicit the same response (Tungadi et al., 2022). The mechanism is not fully explained by cuticular hydrocarbon cues, suggesting the involvement of volatile signals, microbial interactions, or physical cues. Chemical deterrents have also been evaluated as key components of push–pull systems. Roh et al. (2023) demonstrated that a two-component deterrent blend—ethyl anthranilate and methyl salicylate—applied to raspberry fruits significantly reduced *D. suzukii* infestation in field trials, confirming its practical potential. Other studies have identified volatile organic compounds (VOCs) such as ethyl anthranilate, methyl salicylate, green leaf volatiles, and monoterpenes as oviposition deterrents that signal unsuitable or previously occupied substrates (Burrack et al., 2015; Iglesias and Liburd, 2017; Tonina et al., 2020). These compounds can be applied via coatings, sprays, or controlled-release dispensers, offering versatility in field applications. Particle films, including kaolin, diatomaceous earth, and mica, have also been tested as oviposition deterrents, particularly in vineyards and berry crops. These films act as physical barriers, reducing ovipositor penetration and altering surface properties such as reflectance, which further discourages egg-laying (Rossi-Stacconi et al., 2016; Tonina et al., 2020). Field evaluations in Austria and other regions demonstrated substantial reductions in oviposition, especially when applied during early fruit developmental stages. Essential oils such as

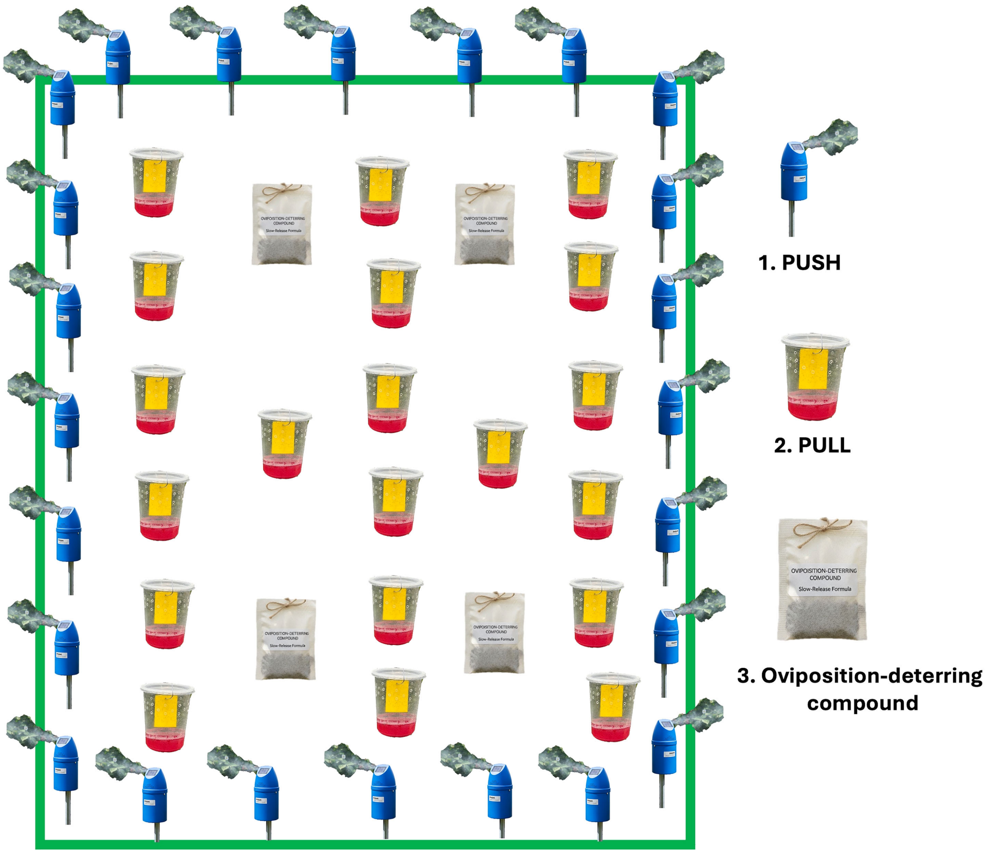

FIGURE 4
Schematic representation of the integrated "push–pull and mass trapping" strategy for the management of *Drosophila suzukii* in blackberry crops (aerial view). The system combines: (1) Repellent volatiles (PUSH) released from blue dispensers placed around the crop perimeter, which deter adult entry into the crop interior and mask volatiles emitted by the fruit and the crop as a whole. (2) Attractant-based mass trapping devices (PULL)—traps baited with a red food attractant and containing a yellow card as a visual stimulus—installed within and around the crop to capture adults. This dual-action approach aims to prevent fruit infestation while simultaneously reducing adult population density in the field, thereby contributing to the sustainable suppression of the pest. (3) Oviposition-deterrent compounds could also be dispersed within the crop interior.

geranium, ginger, peppermint (menthol), thyme (thymol), clove (eugenol), citronella (citronellol, geraniol), lavender, 2-pentylfuran and neem, among others, have shown repellent, oviposition-deterring, and even lethal effects against *D. suzukii* (Renkema et al., 2016, 2017; Gowton, 2019; Galland et al., 2020; Wernicke et al., 2020; Wang Q, et al., 2021; Baleba et al., 2025; Shrestha et al., 2025). Moreover, mixtures of these oils are commercially available under the names KeyPlex Ecotrol® PLUS (rosemary, geraniol, and mint oils) and KeyPlex Sporan® EC2 (rosemary, clove, thyme, and mint oils), which have been evaluated and shown promising results in raspberry and blueberry crops in Forest Lake, MN, USA (Gullickson et al., 2020). Compounds including 1-octen-3-ol (Wallingford et al., 2016, 2017), 2-n-pentylfuran (Cha et al., 2021; Stockton et al., 2021), thymol (Reher et al., 2019), p-menthane-3,8-diol (Wernicke et al., 2020), ethyl butanoate, and ethyl (E)-but-2-enoate (Quadrel et al., 2025), appear to be promising repellents and oviposition deterrents for future field evaluation. One of the promising plants as a repellent, although currently available only commercially, is hop (*Humulus lupulus* L.), which also deserves consideration in future studies (Reher et al., 2019). In contrast, geosmin has shown inconsistent results (Stockton et al., 2021). These active ingredients have been formulated in a slow-release SPLAT® matrix (Specialized Pheromone & Lure Application Technology, ISCA Technologies, Inc.), which does not require water or adjuvants. The SPLAT matrix allows for controlled release of labile semiochemicals (Stelinski et al., 2005) and has been used in formulations for mating disruption, attract-and-kill, and repellency systems targeting both pest insects and pollinators (e.g., Vargas et al., 2008; Rodriguez-Saona et al., 2010; Mafra-Neto et al., 2013). Another formulation, HOOK SWD®, a sprayable attract-and-eliminate (A&E) bait, was evaluated over three growing seasons in raspberry and other small fruit crops in New Jersey and California. Residual activity trials showed adult mortality rates exceeding 78–93% after 35 days of field aging under plastic tunnels (Klick et al., 2019). Under laboratory conditions, lavender oil, Ecotrol®, and Sporan® deterred SWD from diet substrates, while field trials indicated that Ecotrol® reduced infestation in raspberries, though not in blueberries (Gullickson et al., 2020). Recently, a two-component deterrent blend consisting of octanoic and decanoic acids was developed as an alternative to spatial repellents for the behavioral control of *D. suzukii* infestations (Movva et al., 2025). Other promising natural extracts include attract-and-eliminate formulations derived from mandarin (*Citrus reticulata*) and tea tree (*Melaleuca alternifolia*) oils, though fruits treated with the latter were classified as non-edible (Bedini et al., 2020). Integration of push–pull systems with mass trapping and attractant-baited devices enhances overall suppression of *D. suzukii* (Figure 3). By redirecting adult flies away from crops while simultaneously removing them from the population, these tactics reduce both current and future infestations. However, effective deployment requires careful consideration of compound selection, timing, and spatial configuration to maximize deterrent efficacy without reducing trap attractiveness. Future research should focus on identifying synergistic effects among chemical, visual, and biological deterrents to optimize multi-tactic management programs, ensuring sustainable and practical implementation in commercial berry production. For example, in the United States, methyl benzoate was tested as an in-crop repellent in blueberries, while attractant-baited traps were deployed along the field perimeters. However, these compounds alone showed limited synergistic efficiency (Gale et al., 2024). Conversely, mass trapping using RIGA® AG traps (Zürich, Switzerland) baited with 80 mL of RIGA® AG lure (apple cider vinegar, red wine, sugar, and cranberry juice) (Figure 2), combined with perimeter insecticide applications, proved effective for *D. suzukii* control in blueberry fields (Spies and Liburd, 2019; Kehrli et al., 2022).

3.5 Complementary biological control

Although ethological strategies primarily aim to manipulate pest behavior, the integration of complementary biological control has become an essential component for the sustainable management of *D. suzukii*, given the compatibility of both approaches (Daane et al., 2016; Becher et al., 2017; Koźbiał and Lewandowski, 2025).

A recent systematic review found that biological-control research for *D. suzukii* is heavily dominated by parasitoids (64% of publications) compared to entomopathogens (26%) and predators (7%) (Morales-Abeijon et al., 2025). Within parasitoids, the families Figitidae (46%; n = 21), Braconidae (33%; n = 15) and Pteromalidae (13%; n = 6) were most frequently studied (Morales-Abeijon et al., 2025). Among the ten most investigated species are the pupal parasitoids *Trichopria drosophilae* (Perkins) (Kremmer et al., 2017; Rossi-Stacconi et al., 2018, 2019; Gonzalez-Cabrera et al., 2019; Trivellone et al., 2020; Wolf et al., 2020; Collatz and Romeis, 2021; Wang X, et al., 2021; Daane et al., 2025; Morales-Abeijon et al., 2025; Sun et al., 2025), *Trichopria anastrephae* (Lima) (Hymenoptera: Diapriidae) (Krüger et al., 2019; Vieira et al., 2020; da Costa Oliveira et al., 2021; Wang X, et al., 2021; Krüger et al., 2024), *Pachycrepoideus vindemmiae* (Rondani) (Kremmer et al., 2017; Collatz and Romeis, 2021; da Costa Oliveira et al., 2021; Wang X, et al., 2021; Daane et al., 2025; Morales-Abeijon et al., 2025), and *Spalangia erythromera* (Förster) (Hymenoptera: Pteromalidae) (Trivellone et al., 2020), along with the larval parasitoids *Ganaspis kimorum* Buffington formerly also known as *Ganaspis brasiliensis* (Ilhering) (Daane et al., 2016; Girod et al., 2018; Stahl et al., 2024; Morales-Abeijon et al., 2025), *Leptopilina japonica* (Girod et al., 2018; Morales-Abeijon et al., 2025; Rossi-Stacconi et al., 2025), *L. japonica japonica*, *L. j. formosana* (Novković and Kimura), *L. boulardi* (Barbotin) (Hymenoptera: Figitidae) (Daane et al., 2016; Mazzetto et al., 2016b; Daane et al., 2025), *L. heterotoma* (Thomson) (Hymenoptera: Eucoilidae) (Beckwith et al., 2025; Daane et al., 2025; Schöfer et al., 2025), Carton and Keiner-Pillault (Hymenoptera: Figitidae) (Huang et al., 2023), *Asobara japonica* (Belokobylskij) (Girod et al., 2018), *A. rufescens* (Förster), *A. brevicauda* (Guerrieri & van Achterberg), and *A. leveri* (Nixon) (Hymenoptera: Braconidae) (Daane et al., 2016; Mazzetto et al., 2016b). These species have demonstrated significant parasitism potential under laboratory and field conditions, particularly *G. brasiliensis* and *L. japonica*, which have established naturally in several regions of Europe and North America with parasitism rates reaching up to 30% (Girod et al., 2018; Sanchez-Gonzalez et al., 2020; Morales-Abeijon et al., 2025).

Beyond parasitoids, several other biological control agents (BCAs) have been identified targeting *D. suzukii*, including 23 bacterial species, viruses spanning eight families, nine entomopathogenic nematodes and three major entomopathogenic fungi—*Beauveria bassiana* Bals. (Vuill.), *Metarhizium anisopliae* (Metschn.) Sorokin and *Isaria fumosorosea* Wize (Alnajjar et al., 2017; Hiebert et al., 2020; Bing et al., 2021; Galland et al., 2023; Morales-Abeijon et al., 2025). Among bacterial agents, *Xenorhabdus nematophila* (Poinar and Thomas), *Bacillus thuringiensis* Berliner (Bt) and *Brevibacillus laterosporus* (Laubach) have shown promising pathogenicity, while the La Jolla virus (Iflaviridae) was one of the most frequently reported viral agents (Linscheid et al., 2022; Bruner-Montero et al., 2023; Garriga et al., 2023; Morales-Abeijon et al., 2025). Although these findings demonstrate a rich potential of microbial and entomopathogenic resources for *D. suzukii* control, field efficacy remains variable, often depending on environmental conditions, formulation stability, and the developmental stage of the pest (Sial et al., 2019; Morales-Abeijon et al., 2025). Field evaluations indicate that *B. bassiana* and *M. anisopliae* achieve moderate reductions of adult populations when applied in shaded, humid environments, while *B. thuringiensis* and *B. laterosporus* are more effective against larvae inside fruits or substrates (Cuthbertson and Audsley, 2016; Gutierrez-Palomares et al., 2021; Mastore et al., 2021; Morales-Abeijon et al., 2025). Combining these agents with attractant-based systems—such as bait stations or attract-and-kill traps—enhances exposure and infection rates, thereby increasing overall pest suppression. Furthermore, integrating microbial control with semiochemical-based strategies (e.g., pheromone traps, kairomone lures, or oviposition deterrents) enables more targeted control while reducing reliance on synthetic insecticides (Wallingford et al., 2017; Đurović, 2021; Morales-Abeijon et al., 2025). Such integrated approaches not only improve management efficiency but also promote the long-term sustainability of berry production systems by preserving beneficial organisms and minimizing ecological risks.

In addition to parasitoids and pathogens, predatory arthropods contribute to the natural regulation of *D. suzukii* populations. Fifteen predatory species across eight families have been reported (Morales-Abeijon et al., 2025). The families Anthocoridae (Hemiptera) and Carabidae (Coleoptera) are the most represented, each with four species. Among them, the rove beetle *Dalotia coriaria* (Kraatz) (Coleoptera: Staphylinidae) has been the most extensively studied due to its capacity to prey upon both *D. suzukii* eggs and larvae in the soil or fruit substrate. Other notable predators include the pirate bug *Orius insidiosus* (Say) (Hemiptera: Anthocoridae), the green lacewing *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae), and the European earwig *Forficula auricularia* L. (Dermaptera: Forficulidae), which exhibit opportunistic predation on eggs and early larval stages (Renkema et al., 2015; Englert and Herz, 2019; Morales-Abeijon et al., 2025). Less frequently studied but potentially valuable species include the ground beetles *Bembidion quadrimaculatum* (L.), *Limodromus assimilis* (Paykull), *Poecilus cupreus* (L.), and *Pterostichus melanarius* (Illiger) (Coleoptera: Carabidae); the true bugs *Dicyphus hesperus* Knight, *Macrolophus pygmaeus* (Rambur), and *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae); *Orius laevigatus* (Fieber) and *O. majusculus* (Reuter) (Hemiptera: Anthocoridae); as well as the predatory stink bug *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae) and the field cricket *Gryllus pennsylvanicus* Burmeister (Orthoptera: Gryllidae). Although these species have shown low specificity toward *D. suzukii*, their presence in fruit ecosystems suggests a relevant role within broader functional guilds of natural enemies, contributing indirectly to pest suppression through intraguild interactions and disturbance of oviposition behavior (Ballman et al., 2017; Bonneau et al., 2019; Siffert et al., 2021; Wang X et al., 2021; Morales-Abeijon et al., 2025).

Overall, the synergistic integration of parasitoids, entomopathogens, and generalist predators—combined with behavioral manipulation and habitat management—represents one of the most promising directions for ecologically sustainable suppression of *D. suzukii*. Future research should focus on optimizing the spatiotemporal compatibility among these natural enemies, developing formulations for microclimatic stability, and designing multi-trophic attract-and-kill systems that maximize contact and infection rates in the field.

In Mexico, pupal parasitoids such as *Pachycrepoideus vindemmiae* and *Trichopria drosophilae* have been evaluated, with *T. drosophilae* showing a higher intrinsic rate of increase and a shorter development time, making it a promising agent for natural control, particularly during pupal stages (Garcia-Cancino et al., 2020). Field and semi-field studies in Europe and North America have demonstrated that these pupal parasitoids can significantly reduce adult emergence from infested fruits, especially when integrated with habitat management practices that provide refuges or alternative hosts for parasitoid persistence (Wang et al., 2016; Girod et al., 2018; Renkema et al., 2020; Rehermann et al., 2022; Hogg and Daane, 2025).

The integration of biological control with mass trapping and push–pull systems can enhance suppression by reducing adult emergence while simultaneously disrupting host-seeking and oviposition through the use of attractants, visual cues, and deterrent elements. Furthermore, the combination of parasitoid releases with selective, low-risk insecticides has shown potential to control *D. suzukii* effectively while preserving beneficial arthropod populations (Hamby et al., 2016; Van Timmeren et al., 2025). However, the field efficacy of parasitoids is strongly influenced by environmental conditions, crop structure, and synchronization between parasitoid release and pest population dynamics. Interactions with other drosophilid species, such as *Z. indianus*, may also affect host preference and parasitism success. Consequently, optimizing release strategies, habitat modifications, and compatibility with other tactics remains a priority for improving biological control outcomes within integrated pest management frameworks.

To fully exploit the synergistic potential of behavioral and biological control, further field-scale evaluations under diverse climatic and cropping systems are needed. Future research should focus on refining parasitoid deployment timing, enhancing formulation stability, and assessing multitrophic interactions among parasitoids, entomopathogens, and semiochemical-based tools. Such integration will strengthen eco-efficient management strategies for *D. suzukii*, ensuring sustainable protection of commercial berry crops.

4 Discussion

The integration of ethological and complementary control strategies is fundamental for the effective management of *D. suzukii* in commercial berry crops. Evidence from recent studies consistently indicates that no single tactic can reliably suppress populations or prevent fruit damage. Therefore, the coordinated implementation of mass trapping, attractant optimization, visual stimuli, oviposition deterrents, and biological control is required to achieve meaningful and sustainable reductions in pest pressure.

Crop phenology strongly influences the performance of ethological tactics. Fermentative baits are generally more effective during early crop stages or at lower fly densities, while synthetic or dry attractants maintain efficacy during peak adult activity (Larson et al., 2021; Cruz-Esteban et al., 2024b). Likewise, internal visual cues—such as colored panels and reflective surfaces—enhance captures when combined with olfactory attractants, particularly under conditions where the odor plume disperses weakly (Kirkpatrick et al., 2018a; 2018b).

Trap density and spatial arrangement are critical parameters influencing mass-trapping efficiency, as overlapping attraction radii may generate intra-trap competition and reduce overall capture rates (Clymans et al., 2022). Optimal deployment varies seasonally, with higher densities recommended during spring and early summer, when populations begin to expand. Controlled-release synthetic baits can maintain trap performance while reducing the number of traps needed for effective suppression.

Push–pull strategies and oviposition deterrents complement trapping by discouraging egg laying on fruits and redirecting females toward attractant sources or buffer zones. Compounds such as ethyl anthranilate, methyl salicylate, monoterpenes, and green leaf volatiles have demonstrated deterrent effects under field conditions (Burrack et al., 2015; Roh et al., 2023). Biological cues, including the presence of *D. melanogaster* larvae, may also reduce oviposition through volatile or microbial signaling. Additionally, particle films such as kaolin and diatomaceous earth provide physical barriers and modify surface reflectance, improving the efficacy of deterrent approaches (Rossi-Stacconi et al., 2016).

Complementary biological control using pupal parasitoids, particularly *Trichopria drosophilae*, has proven promising for reducing population growth by targeting pupal stages. This species exhibits a higher intrinsic rate of increase and shorter development time than Pachycrepoideus *vindemmiae*, making it a suitable candidate for integration within ethological control programs (Garcia-Cancino et al., 2020). Combining biological control with attractant-based tactics increases pupal exposure to parasitism and enhances overall suppression efficiency (Wang et al., 2016; Renkema et al., 2020; Rehermann et al., 2022).

One of the main operational challenges is trap selectivity. Non-target species, including *Z.* indianus, are frequently captured, complicating monitoring and increasing management costs (Cruz-Esteban et al., 2022; Franco-Valbuena et al., 2025). Refining bait composition, trap design, and deployment protocols is therefore necessary to improve specificity and minimize unintended captures. Economic and practical aspects, such as trap maintenance, bait replacement, labor requirements, and grower acceptance, are also crucial for sustainable adoption. Cost-effective options, including homemade traps and locally sourced fermentative baits, have shown promise; however, formal cost-benefit evaluations under commercial conditions remain scarce (Clymans et al., 2022).

Despite these advances, several knowledge gaps persist. Most research has focused on adult captures rather than quantifying actual reductions in fruit damage across different berry crops and management systems (Beers et al., 2022; Tonina et al., 2022; Brilinger, 2024). The mechanisms underlying oviposition deterrence—including chemical, physical, and biological cues—require further elucidation (Roh et al., 2023). Likewise, optimization of visual stimuli such as color, brightness, reflectance, and shape under varying environmental conditions remains necessary to design universally effective or locally adapted traps (Little et al., 2021; Cruz-Esteban et al., 2024a). Understanding the synergistic interactions between ethological tactics, low-risk insecticides, growth regulators, and parasitoids will be essential to improve IPM outcomes while minimizing resistance development (Wang et al., 2016). Moreover, socioeconomic studies addressing grower adoption, maintenance logistics, and operational scalability are vital for achieving long-term implementation in commercial berry systems (Beers et al., 2022; Brilinger, 2024).

Overall, the integration of ethological tools with biological and physical control tactics represents one of the most promising avenues for the sustainable management of *D. suzukii*. Continued interdisciplinary research and validation under field conditions will be essential to bridge the gap between experimental advances and their practical application in commercial production systems.

5 Future perspectives

Despite significant advances in understanding the behavioral ecology of *D. suzukii* and in developing ethological control tools, several critical knowledge gaps and practical challenges remain. Addressing these gaps will require interdisciplinary approaches that integrate entomology, chemical ecology, microbiology, engineering, and agroecology. These include the development of a highly effective attract-and-kill system, which continues to require optimization of trap designs, the use of attractive colors, the identification of more specific and longer-lasting attractants, as well as the search for a potential sex pheromone. Addressing these limitations is essential for the design of effective, economically viable, and environmentally sustainable management strategies.

Although numerous volatile organic compounds (VOCs) have been identified from fruits, microorganisms, and synthetic sources (Abraham et al., 2015; Akasaka et al., 2017; Bolton et al., 2019, 2021), behavioral responses of *D. suzukii* remain highly variable depending on environmental context, geographic population, and physiological state (Asplen et al., 2015). Future studies should focus on standardizing bioassay methodologies and validating candidate compounds under diverse agroecological conditions. Future studies should therefore adopt standardized yet flexible bioassay methodologies that combine chemical, electrophysiological, and behavioral analyses, and validate compound under diverse agroecological conditions. Electrophysiological, chemical, and behavioral analytical techniques have been highly valuable in advancing current knowledge, and their integration will undoubtedly facilitate the identification of key semiochemicals that remain unknown and that mediate attraction, deterrence, and oviposition stimulation. Moreover, further interdisciplinary research is needed to characterize how these responses are modulated by abiotic factors, fruit developmental stages, and host–microbe interactions (Alawamleh et al., 2021).

The optimization of mass-trapping systems continues to be a major research priority. This presents a clear interface between entomology, engineering, and spatial ecology. Future efforts should determine the ideal trap density, spatial distribution, and deployment timing according to pest phenology, crop structure, and landscape heterogeneity (Babu et al., 2023). In this context, the incorporation of smart trap technologies—such as sensors, image recognition, and remote data transmission—illustrates how engineering and data science can enhance biological monitoring, improving accuracy and real-time decision-making within integrated pest management (IPM) programs. These innovations may also enable predictive modeling of pest population dynamics and the early detection of population outbreaks, thereby enhancing management precision.

Push–pull systems represent a promising complementary approach but require further field validation and refinement. This will benefit from collaborative efforts among chemists, entomologists, and formulation specialists. Deterrent compounds such as ethyl anthranilate and methyl salicylate should be incorporated into slow-release formulations that are stable and compatible with local climatic conditions (Babu et al., 2022). The use of attractant-baited traps along crop borders could help prevent oviposition in fruit while simultaneously maintaining population suppression pressure. Moreover, linking behavioral manipulation with biological control—for instance, using olfactory cues to enhance parasitoid host-finding or to protect natural enemies from insecticide exposure—remains an underexplored but potentially transformative direction for sustainable pest suppression (Morales-Abeijon et al., 2025).

Microbial communities associated with fruits and *Drosophila* species play a fundamental role in the emission of attractive or deterrent volatiles. This highlights the importance of microbiology–chemical ecology interactions. The exploration microbial-derived attractants or repellents from yeasts and bacteria has led, and may continue to lead, to the development of new bioformulations for the management of *D. suzukii* (Alawamleh et al., 2021; Alavez-Rosas et al., 2024). Research conducted worldwide should focus on identifying native microbial strains that can be cultured through controlled fermentation processes to produce consistent volatile profiles. Although many microbial species associated with fruits are already known, it remains unclear whether all of them are necessary for attraction, or whether specific strains emit volatile compounds that are particularly relevant to *Drosophila suzukii*. Additionally, interdisciplinary studies are needed to determine whether certain microorganisms interfere with fruit maturation and fermentation processes in ways that promote the production of volatile compounds specifically involved in attracting this species. Understanding microbe–host–insect interactions may also provide insights into the development of low-cost, locally adapted products suitable for smallholder growers.

Environmental heterogeneity and climate change pose additional challenges for behavioral control strategies. These challenges require the integration of climatology, landscape ecology, and pest biology. Variations in temperature, humidity, and host plant availability influence the activity and reproductive behavior of *D. suzukii*, potentially altering the effectiveness of attractant blends (Asplen et al., 2015). Incorporating these variables into predictive models will allow dynamic adjustment of monitoring and control efforts according to local phenology and climatic patterns. This approach could support decision-support systems that integrate weather data, trap captures, and pest thresholds to guide IPM implementation at the landscape scale.

In addition, field experience in Mexico indicates that ethological and biological control tactics are consistently implemented in combination with cultural management practices. These practices are grounded in applied agronomy and grower knowledge. These include orchard sanitation, the removal of overripe or decaying fruits, the destruction of infested material, and the use of physical barriers such as exclusion nets and mulches, as well as protective structures like shade tunnels. Such cultural practices have been shown to significantly reduce *D. suzukii* population pressure by limiting suitable oviposition sites, minimizing larval development, and restricting adult access to host fruits (Rendon et al., 2020; Liburd and Rhodes, 2021; Schöneberg et al., 2021; Tait et al., 2021; Garcia et al., 2022; Parkins et al., 2022). When combined with behavioral tools (e.g., attract-and-kill systems, mass trapping) or biological control agents, these measures contribute to an integrated, robust, and sustainable management framework for *D. suzukii* in small-fruit production systems.

The future of ethological control of *D. suzukii* depends on multidisciplinary collaboration among entomologists, chemists, microbiologists, engineers, and growers. This collaboration should also include data scientists and technology developers. Progress in the coming decade should prioritize the development of standardized and affordable attractant–repellent formulations adapted to regional pest populations, the integration of behavioral manipulation within holistic IPM frameworks that combine cultural, biological, and physical methods, and the validation of field efficacy and cost–

benefit scenarios under commercial production conditions. Additionally, promoting participatory research and technology transfer will be crucial to ensure the practical adoption of these innovations by growers and cooperatives.

In conclusion, future research on the behavioral control of *D. suzukii* should emphasize field-oriented, integrative, and interdisciplinary strategies that combine olfactory and visual cues, microbial interactions, engineering innovations, and environmentally safe deterrents. Such approaches will reinforce the sustainability and resilience of berry production systems against *D. suzukii*and related drosophilid pests while reducing dependence on chemical insecticides.

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