

Current knowledge of interactions between *Drosophila suzukii* and microbes, and their potential utility for pest management

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Abstract Insects exhibit complex symbiotic interactions with microorganisms, which provide an opportunity for developing novel pest management strategies. Closely related to *Drosophila melanogaster*, which is commonly used as a model to explore insect–microbe interactions, *Drosophila suzukii* is an important invasive insect pest of fruit crops in the Americas and Europe. We provide an overview of *Drosophila*–microbe interactions and review current research with *D. suzukii*. Recent studies revealed yeast and bacterial species associated with *D. suzukii* flies, fly guts and infested fruit. The ecological importance of these insect–microbe interactions is under investigation. Microbes have a strong impact on insect physiology and *D. suzukii* responds both positively and aversively to microbial volatiles. We highlight potential pest management strategies that take advantage of *D. suzukii*–microbe ecology, including improved monitoring as well as management using behavioural manipulation, phagostimulants and biotechnology.

Keywords Spotted wing drosophila · Yeast · Bacteria · Attractant · Repellent · Behavioural manipulation

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Key message

- Symbiotic microorganisms play important roles in insects' life cycles, and yeasts and bacteria impact *Drosophila* food quality, development time and reproductive output.
- Despite an affinity for ripening or ripe fresh fruit, *D. suzukii* shows associations with bacteria and yeasts, similar to other drosophilids.
- We review recent work describing *D. suzukii*–microbe ecology and areas where these relationships can potentially be used to improve *D. suzukii* pest management.

Introduction

Microbes are found in insect habitats, on their food substrates, on and inside the insect body, and within insect cells (Phaff et al. 1956; Begon 1982; Chandler et al. 2011; Douglas 2007). Notably, most of these microbial associations are not pathogenic, but rather beneficial or apparently benign (Douglas 2007). The ecological status of insect-associated microorganisms vary from taxa that maintain substantial free-living populations outside their associates to taxa that are insect species specific and generally do not develop outside the insect host (Douglas 2015). Insects disperse free-living microorganisms between external environmental habitats (Douglas 2015) and in special cases even “farm” mutualistic microbes on plant substrates such as leaves or fruit (Mueller et al. 2005; Stamps et al. 2012). Insect-associated microbes comprise a significant portion of the known microbial flora, as has been impressively demonstrated for yeasts by the hundreds of species isolated from beetles (Suh et al. 2005).

Insect–microbe associations have historically been studied using culture-dependent approaches; however, advances in high-throughput sequencing have provided new tools to supplement these approaches. Targeted rRNA gene sequencing of 16S for bacteria, 18S for eukaryotes, and the internal transcribed spacer region for fungi has been used to profile microbial communities (Bokulich and Mills 2013; Segata et al. 2013). Genome-wide sequencing approaches, including metagenomics, metatranscriptomics, metametabolomics and metaproteomics are becoming increasingly popular as technology advances and the cost of high-throughput sequencing decreases (Knief 2014). These approaches detect both culturable and unculturable microbes from within the community, and can provide information not only at a phylogenetic or taxonomic level, but also can provide information on gene function. Indeed, the whole meta-genome shotgun sequencing technique has been validated and bioinformatic procedures have been developed to answer taxonomic and metabolic profiling questions (Segata et al. 2013; Escobar-Zepeda et al. 2015). As more studies are performed and technology improves, these techniques will continue to improve our understanding of microbial community systems biology, including insect–microbe interactions.

Microbial products have long since been used as lures in entomology and pest management (Landolt and Hammond 2001, and references therein). Torula yeast (*Candida utilis*), as a prominent example, has been applied as a food lure to trap adult Tephritid fruit flies (Lopez-D et al. 1971; Daane and Johnson 2010; Leblanc et al. 2010). It has long been noted that torula yeast and other food lures targeting tephritids also capture non-target organisms, many of which are saprophagous flies, such as: calliphorids, ceratopogonids, chloropids, drosophilids, lonchaeids, muscids and sarcophagids (Thomas 2003; Leblanc et al. 2010). The richness of attracted taxa illustrates the potential of yeast as a powerful attractant on the one hand and challenges application aiming at high target specificity on the other. Favourably, insects show clear species-specific responses to different blends of fermentation compounds (Landolt and Alfaro 2001, and references therein). Understanding of mechanisms underlying specific ecological insect–microbe interactions will help us to develop targeted microbe-based pest control techniques. Given that many insects are associated with specific microbes, and these interactions can be critically important for insects' fitness, in particular close interactions like symbioses can be a resource for developing novel, species-specific pest management tactics (Douglas 2007). As a proof of concept, the recognition of insect–microbe interactions has led to a control method exploiting the association between the codling moth *Cydia pomonella* with yeasts, and an insect-pathogenic virus (Witzgall et al. 2012; Knight and Witzgall 2013).

Drosophila species typically develop in decaying plant material like overripe fruit as well as in mushrooms and other fungi (Starmer 1981; Begon 1982; Markow and O'Grady 2005). *Drosophila*–yeast associations are among the best studied of insect–microbe interactions, and are a model system for interactions between free-living microbes and insects. Yeast communities have been collected from *Drosophila* for many years (Phaff et al. 1956; Chandler et al. 2012). Unlike most other drosophilids the spotted wing drosophila, *Drosophila suzukii*, develops in ripening and ripe fruit rather than overripe and rotting fruit (Walsh et al. 2011) but still is closely associated with yeasts (Hamby et al. 2012). Adult females oviposit directly into fruit with their sclerotized and serrated ovipositor, and cause economic damage to susceptible small and stone fruit in North America, Asia and Europe (Cini et al. 2012; Walsh et al. 2011; Asplen et al. 2015). The worldwide economic impacts due to *D. suzukii* are significant, and new management strategies are needed (Asplen et al. 2015).

Here we provide a brief summary of *Drosophila*–microbe ecology including the impacts of microbes on *Drosophila* physiology and behaviour as well as the role *Drosophila* plays in yeast dispersal and ecology. We then review the current literature on *D. suzukii*–microbe interactions, and, finally, we emphasize how insect interactions with free-living microorganisms can be exploited for pest management.

***Drosophila*-microbe ecology, physiology and behaviour**

Many dipterans are saprophagous, feeding upon microbe-rich host substrates. *Drosophila* species often use fermenting plant material where larvae and adult flies feed on the nutritious microbial flora (Starmer 1981; Begon 1982). Microbes live closely associated with drosophilids, and use larval as well as adult flies as their hosts (Ganter 2006; Douglas 2007; Chandler et al. 2011).

***Drosophila* yeast and bacterial associations**

Drosophila species with diverse habits and hosts are characterized by distinct assemblages of associated yeast microbes on which they feed (Phaff et al. 1956, Begon 1982; Chandler et al. 2012; Stamps et al. 2012; Lam and Howell 2015). Yeast proteins and lipids improve the food quality of plant substrates and support fly survival and development (Bos et al. 1976; Begon 1982; Yamada et al. 2015). Moreover, *D. melanogaster* females require a complex diet or yeast for ovarian maturation (Bownes et al. 1988). *Saccharomyces cerevisiae* is sufficient for *D.*

melanogaster development and more flies develop on fermenting grapes that contain yeast, relative to grapes without yeast (Becher et al. 2012).

Fermenting substrates like overripe fruits are not only used as food resource but also as mating site, explaining attraction of virgin females and males to fermentation odours (Fig. 1). Indeed, yeasts are integral elements of *Drosophila* ecology that influence fly physiology and behaviour. Larvae of various *Drosophila* species prefer yeasts that result in high survivorship to adulthood (Lindsay 1958, Anagnostou et al. 2010). Despite potential adaptations for a novel ripening fruit niche, when yeast is removed from standard laboratory *Drosophila* diet, fewer *D. suzukii* survive to adulthood relative to the standard diet at low population density (Hardin et al. 2015). Adult *D. suzukii* flies readily feed on yeast and fruit blossoms in the laboratory, and microbes together with floral nectar or pollen likely are important food resources especially during early spring when fruit may be sparse (Tochen et al. 2016; Mori et al. accepted). Similar to other drosophilids, *D. suzukii* hosts a specific yeast flora, with *Hanseniaspora uvarum* most frequently cultured from field-collected

adults and larvae, followed by *Issatchenkia terricola* (formerly *Pichia*) and *P. kluyveri* (Hamby et al. 2012). *D. suzukii* has shown a preference for *H. uvarum* in a laboratory multiple choice assay when given the choice between six species (Scheidler et al. 2015). Therefore, it is likely that *D. suzukii* has similar relationships with yeasts as other drosophilids.

Although fly genotype, diet, and host bacterial community impact the gut bacterial community associated with *Drosophila*, the bacterial microbiome of different populations and species are dominated by few bacterial groups such as Enterobacteriales, Rhodospirillales and Lactobacillales (Chandler et al. 2011; Broderick and Lemaitre 2012; Chandler et al. 2012; Wong et al. 2011). Interestingly, bacterial communities of *D. suzukii* were reported to be dominated by *Tatumella*, a genus of enterobacteria previously not considered a common associate of drosophilids (Chandler et al. 2014). Moreover, Acetobacteraceae were abundantly associated with *D. suzukii* (Chandler et al. 2014) with different species differing in their odour profiles and attractiveness to the flies (Mazetto et al. 2016). Similar to yeasts, bacteria ingested with

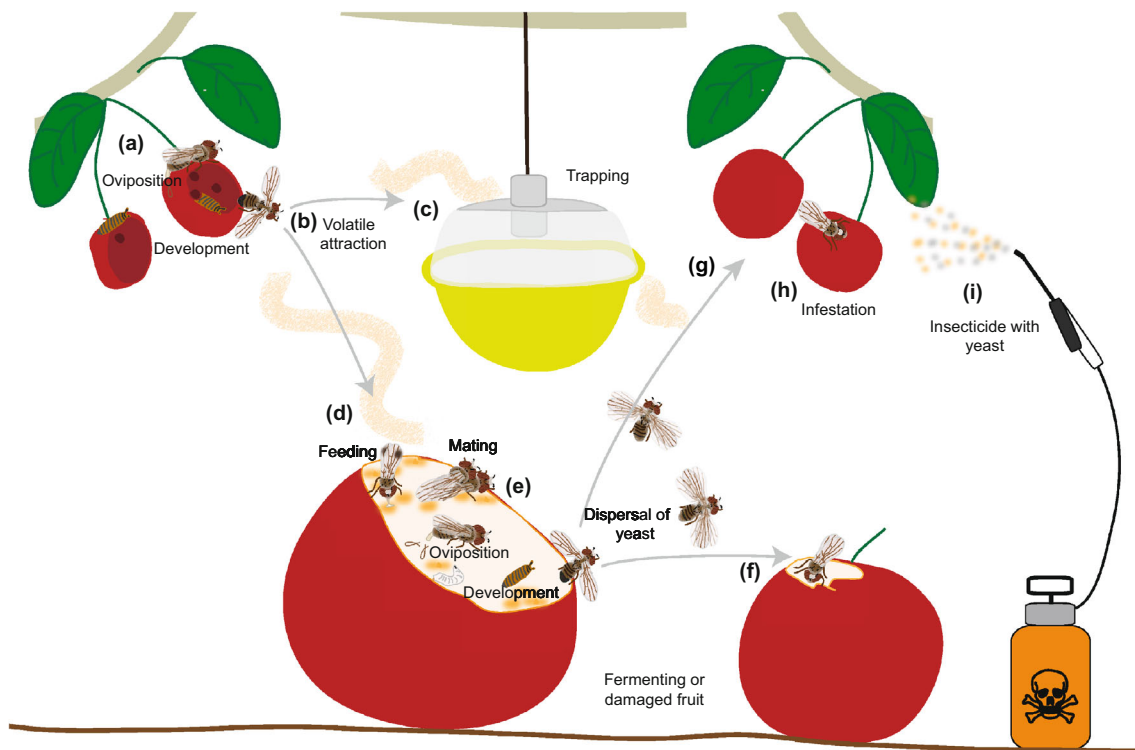


Fig. 1 Illustration of interactions between *Drosophila* and microbes and their utility for pest management. *a* Infestation of ripening fruit by *Drosophila suzukii*. Larvae develop inside the fruit, pupate and emerge as adult flies. *b* *Drosophila* females of various species require food for ovarian maturation and are attracted to food odours like yeast volatiles. *c* Such volatiles lead female as well as male drosophilids to traps used for monitoring or attract-and-kill strategies, or *d* guide the

flies to natural resources. *e* Overripe fruit is a food resource and habitat for many *Drosophila* species, and *D. suzukii* also visits fermenting fruit. *Drosophila* vector yeasts and bacteria to *f* damaged and *g* fresh fruit. *h* Sexually mature females can infest fresh fruit. *i* As male and female *D. suzukii* are attracted to fermentation odours, yeast can be applied as attractant and phagostimulant in combination with killing agents

food or inhabiting the gut influence *Drosophila* larval growth and development (Shin et al. 2011; Ridley et al. 2012; Newell and Douglas 2014), and may even be capable of influencing *Drosophila* mating behaviour (Sharon et al. 2010). Additionally, *Wolbachia* bacteria, maternally transmitted intracellular endosymbionts that are widespread in *Drosophila* species, can have a diversity of effects on *Drosophila* physiology such as reproductive manipulation or increased longevity (Zug and Hammerstein 2015). In *D. suzukii*, *Wolbachia* infections have been suggested to be mutualistic but our understanding of mechanisms underlying such interactions and effects on fecundity need further investigation (Hamm et al. 2014; Mazzetto et al. 2015).

Odour-mediated responses to microbial volatiles

Considering the value of yeasts and bacteria as food resources and potential indicators of habitat quality, it is not surprising that microbial odours induce strong attraction in *Drosophila* larvae and flies (Fishilevich et al. 2005; Becher et al. 2010, 2012; Venu et al. 2014; Dweck et al. 2015; Scheidler et al. 2015). Like most drosophilids, *D. suzukii* is strongly attracted to yeast (Iglesias et al. 2014; Scheidler et al. 2015) and specific fermentation compounds (Landolt et al. 2011; Cha et al. 2012; Kleiber et al. 2014). Such behaviours are the output of chemosensory processes and various microbial volatiles have been shown to induce responses in *D. suzukii* antennae (Cha et al. 2012; Abraham et al. 2015; Keeseey et al. 2015; Revadi et al. 2015; Scheidler et al. 2015).

Evidently, *Drosophila* chemosensory receptors are sensitive to microbial metabolites. For example, fermentation products like esters, alcohols, acids or carbon dioxide are ligands of *Drosophila* olfactory (Stensmyr et al. 2003), ionotropic (Ai et al. 2013) and gustatory receptors (Kwon et al. 2007; Wisotsky et al. 2011; Charlu et al. 2013). Microbial metabolites both positively and aversively affect feeding, mating and oviposition behaviours. Glycerol provides a sensory cue for fermentation processes, which influences adult *D. melanogaster* feeding responses towards yeast (Wisotsky et al. 2011). Additionally, fermentation products enhance *Drosophila* responses to the male pheromone during courtship (Bartelt et al. 1985; Lebreton et al. 2012, 2015), increase female sexual receptivity (Gorter et al. 2016) and mediate oviposition behaviour (Joseph et al. 2009; Becher et al. 2012). In contrast, microbial odours also induce aversive behaviours as demonstrated for geosmin, which negatively affects attraction, feeding and oviposition in *D. melanogaster* (Becher et al. 2010; Stensmyr et al. 2012). In *D. suzukii*, geosmin as well as 1-octen-3-ol induce aversion as described further below (Wallingford et al. 2015).

Profit for microbes

Microbes also benefit from their association with drosophilids, suggesting that for some interacting species the relations are mutualistic. As in other insects, microbes generally profit from drosophilids as hosts (Janson et al. 2008) exploiting in particular the insect gut as a habitat (Engel and Moran 2013). In addition, microbes benefit from transportation and dispersal to new substrates (Gilbert 1980; Buser et al. 2014), particularly yeasts which generally are only poorly dispersed by wind. On the host substrate, *Drosophila* larval feeding positively affects yeast density, and decreases the development of mould fungi (Wertheim et al. 2002; Stamps et al. 2012; Caballero Ortiz et al. 2013). Yeast spores were found to survive the passage through the *D. melanogaster* gut facilitating dispersal and outcrossing between different yeast strains (Pulvirenti et al. 2002; Reuter et al. 2007).

Volatile signals emitted by microbes possibly coevolve together with insect sensory systems (Scheidler et al. 2015). There is increasing support that attraction of insect vectors is a prime function of yeast volatiles. Indeed the aroma gene ATF1, which encodes an acetate ester synthase promotes dispersal of yeast while deletion of ATF1 shows no other negative effect than decreased vectoring by *D. melanogaster* when tested in the lab (Christiaens et al. 2014).

Implications of *Drosophila*-microbe ecology for pest management

Current *D. suzukii* management relies on repeated applications of broad-spectrum insecticides (Beers et al. 2011; Bruck et al. 2011; Van Timmeren and Isaacs 2013). Alternative pest management strategies are required to develop successful Integrated Pest Management (IPM) programs. Symbioses with microorganisms represent an untapped resource for pest management (Douglas 2007, 2015). While obligate symbionts are particularly promising, facultative symbionts that have significant impacts on the pest's life history can also be exploited (Douglas 2007). We describe pest management tactics where *Drosophila*-microbe ecology may be leveraged for improved *D. suzukii* management.

Monitoring pest populations

Monitoring insect populations to evaluate their phenology, population dynamics and the risk of crop damage is an important component of IPM. For many insects, monitoring is achieved using traps baited with attractive semiochemicals. Sweet baits and fermentation products have traditionally been used as attractants for a broad range of insects (Ditman and Cory 1933; Landolt and Hammond

2001). Indeed, fermentation-based attractants have been developed for *D. suzukii* (Cha et al. 2012; Landolt et al. 2012; Burrack et al. 2015). Actively fermenting baker's yeast (*S. cerevisiae*) baits are often among the highest capturing attractants when compared to other fermentation products such as apple cider vinegar and wine (Hamby et al. 2014; Iglesias et al. 2014). However, despite efforts to improve both trap designs and attractants (Lee et al. 2012; Landolt et al. 2012; Lee et al. 2013), *D. suzukii* monitoring remains difficult for growers to implement (Burrack et al. 2015). Current monitoring systems suffer from inconsistent efficacy, and they exhibit variability in trap captures depending on crop type, crop phenology and *D. suzukii* phenology. It is difficult to relate trap captures to infestation. Therefore, it is difficult to use trap captures to schedule time-sensitive IPM actions. Perhaps the largest constraint to widespread adoption of *D. suzukii* monitoring by stakeholders is the lack of selectivity. Because non-target drosophilids are also captured, users of the current monitoring system must identify trap captures under magnification which is time consuming and cumbersome. Additionally, separating *D. suzukii* from other drosophilids can be challenging for nonexperts (Burrack et al. 2015). Therefore, developing trapping systems with increased selectivity is an important research priority.

One avenue for attractant development is microbial volatile emissions. Microbial volatiles are used by many insect species to locate resources, and play an important role in insect behavioural ecology (Davis et al. 2013). In a survey of insects that are attracted to fungal headspace odours from *Aureobasidium pullulans* in spearmint fields, 65 % of trapped insects were dipterans (Davis and Landolt 2013). Moreover, drosophilids and other dipterans were among the insects significantly attracted to traps baited with live yeasts in an apple orchard (Andreadis et al. 2015). Recent work suggests that *Drosophila* species can distinguish between the volatile emissions produced by different yeast species and strains, and that closely related *Drosophila* (*D. melanogaster* compared to *D. suzukii*) differentially respond to specific microbial volatile constituents (Arguello et al. 2013; Scheidler et al. 2015). Therefore, microbial volatile emissions may be useful for improving attractant selectivity. A successful monitoring system for *D. suzukii* would selectively attract *D. suzukii* adults prior to commercial infestation, effectively track population activity throughout the season and accurately relate to larval densities in the fruit.

Behavioural manipulation for *D. suzukii* management

Behavioural manipulation using insect semiochemicals is an important component of sustainable pest management.

Repellents, attract-and-kill and mass trapping have been used against various insect pests to reduce economic damage (El-Sayed et al. 2006, 2009). Recent work has shown that repellent chemicals can be used to reduce *D. suzukii* oviposition in host fruit. In the laboratory, a significant reduction in *D. suzukii* oviposition in blueberries was achieved when the blueberries were painted with butyl anthranilate, a DEET-substitute compound that is approved for human consumption (Pham and Ray 2015). Wallingford et al. (2015) evaluated two compounds that are commonly associated with bacterial and fungal volatile emissions, 1-octen-3-ol and geosmin. Both compounds repelled adult female *D. suzukii* in laboratory gated-trap choice tests. Field trials were conducted in red raspberries using odorant dispensers affixed to plants and the repellent 1-octen-3-ol. Fruit near the dispensers were sampled for infestation and significantly lower infestation was observed in the fruit near the repellent dispensers versus the solvent controls. Microbial volatiles could be used to develop repellent compounds for *D. suzukii* pest management. However, the compounds must be safe for human consumption and cannot affect fruit quality and taste.

Attract-and-kill and mass trapping are similar approaches that are separated by the method of killing the insect after attraction, typically a toxicant for attract-and-kill compared with a physical killing system such as an adhesive or drowning solution for mass trapping (El-Sayed et al. 2006, 2009). Both strategies are effective for low density insect populations, and would be most useful during the early season before the *D. suzukii* population builds. A very competitive lure that outcompetes the natural odour source or host signal is required for either of these techniques to work (Fig. 1c). These strategies diverge in their formulation and release strategy with attract-and-kill systems requiring sufficient contact with the toxicant that the insect is killed, and these formulations are commonly patented (e.g. GF-120 and SPLAT). Mass trapping systems require experiments on effective trap design and trap density. Indeed, preliminary mass trapping experiments using an apple cider vinegar–yeast–flour bait for management of *D. suzukii* reported that blueberry infestation was significantly higher where traps were deployed, with increased *D. suzukii* activity near the attractant traps (Hampton et al. 2014). Both mass trapping and attract-and-kill systems have been used successfully to manage various Tephritid fruit fly pests (El-Sayed et al. 2006, 2009); therefore, they may have potential as management strategies for *D. suzukii* with an improved attractant and effective deployment technology. Indeed, mass trapping has been integrated with other *D. suzukii* pest management techniques in Italian and Swiss fruit systems (De Ros et al. 2015; Baroffio 2015). Microbial

volatiles are underutilized in behavioural manipulation strategies, and are likely a good resource for such strategies since these volatiles are often chemically distinct from the pervading background of plant volatiles (Witzgall et al. 2012).

Sterile insect technique

Recent work in Tephritid fruit fly sterile insect technique (SIT) has demonstrated the importance of understanding insect–microbe interactions for successfully developing novel pest management strategies. For example, *Bactrocera oleae* sterile insect technique programmes were practically abandoned in the 1980's due to a lack of understanding of the fly's basic biology, including its microbe interactions (Estes et al. 2012). *Bactrocera oleae* possesses gut evaginations that house their bacterial endosymbiont 'Candidatus *Erwinia dacicola*', which is important for adult and larval nutrition and helps larvae to overcome host defence (Ben-Yosef et al. 2010, 2015). Additionally, transiently acquired free-living bacteria are common in wild *B. oleae* and likely benefit *B. oleae* health. Laboratory flies reared on artificial media exhibit declines in endosymbiont populations and significant changes in their transient bacterial microbiome (fewer and different taxa) compared to wild flies. Because one of the biggest challenges for *B. oleae* SIT is mass rearing high-quality flies (necessary for competitiveness in the wild), facilitating these bacterial interactions during rearing (e.g. removing antibiotics from artificial media which has been successful) has been highlighted as important for the success of future SIT programmes (Estes et al. 2012). In *Ceratitis capitata* the irradiation process to produce sterile males affects the gut bacterial community. These males are less competent in attracting and mating with wild females, and providing diets containing bacteria significantly improved the sterile male performance in copulatory tests (Ben Ami et al. 2010). Transgenic genetic technologies are being developed in *D. suzukii* using the *piggyBac* transposon vector (Schetelig and Handler 2013) and CRISPER/Cas9-mediated gene editing (Li and Scott 2016). In the future, these technologies could be used to develop a SIT or a gene drive system for suppression of *D. suzukii* populations (Schetelig and Handler 2013; Li and Scott 2016), and mass rearing high-quality *D. suzukii* would be important.

Phagostimulants and RNA interference

Phagostimulants can be used to improve the efficacy of insecticides and microbial control agents that require ingestion (Bell and Kanavel 1977; Williams et al. 2004; Knight et al. 2015). In some cases, phagostimulants can

even significantly reduce the amount of active ingredient necessary for successful management. These lower rates increase safety for workers and beneficials (Williams et al. 2004). Sucrose has been evaluated as a phagostimulant for *D. suzukii*, and both contact active and primarily ingestion active insecticides exhibited increased efficacy when used with sucrose (Cowles et al. 2015). Additionally, combinations of sucrose with yeast (*S. cerevisiae*) and yeast-like fungus (*A. pullulans*) have been evaluated as phagostimulants to improve the efficacy of cyantraniliprole and spinosad (Knight et al. 2015). Interestingly, *A. pullulans* is commercially available as Blossom Protect (Westbridge Ag Products, Vista, CA) and registered for control of fireblight *Erwinia amylovora*. In some cases, addition of a yeast-feeding stimulant with sugar improved activity (evaluated by adult mortality, egg and larval infestation) relative to sugar alone; however, the effect varied by insecticide, yeast species and the yeast formulation (Knight et al. 2015). Yeast species that are attractive to *D. suzukii* for feeding could be used as phagostimulants to improve insecticide efficacy (Fig. 1i). Recent findings suggest that this strategy could facilitate attract-and-kill control of *D. suzukii* (Mori et al. accepted).

RNA interference (RNAi) co-opts a cellular mechanism that likely evolved to protect eukaryotes from RNA viruses, introducing exogenous double-stranded RNA (dsRNA) to activate the cellular machinery to degrade or suppress the translation of gene transcripts complementary to the dsRNA (Ding 2010; Burand and Hunter 2013; Gu and Knipple 2013). Recent advancements in RNAi have developed higher throughput and cheaper methods for RNAi target selection, target screening and the synthesis of dsRNA, increasing the feasibility of using RNAi as a tool for pest management (Gu and Knipple 2013; Zotti and Smaghe 2015; Murphy et al. 2016a). Specifically, dsRNA delivery systems involving in vivo expression of dsRNA using vector constructs that contain a target gene sequence (a gene vital to the insect and localized in the insect gut) that use bacteria, host plants or viruses (host plant or insect) to host the vector and express the dsRNA have been successful (Burand and Hunter 2013; Gu and Knipple 2013). However, delivery of intact dsRNA to the target site remains a challenge (Zotti and Smaghe 2015; Taning et al. 2016). Oral application has proven promising to increase gene silencing and *D. suzukii* mortality (Taning et al. 2016). One novel approach to dsRNA delivery takes advantage of *D. suzukii*–yeast interactions (Murphy et al. 2016b). By introducing the vector construct to yeast, this system couples an attractive food source with a readily transformed and cultured in vivo dsRNA expression system (Murphy et al. 2016b). This “yeast biopesticide” was shown to significantly decrease larval survivorship, reduce

adult locomotor activity and reduce reproductive output in a species-specific manner (no significant effects on the closely related *D. melanogaster*). Therefore, *D. suzukii*-yeast ecology may be leveraged to develop new pest management biotechnologies such as RNAi.

Author contribution

K. A. H. and P. G. B. equally contributed to the writing of the manuscript.

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Compliance with ethical standards

Ethical standards This review complies with ethical principles.

Conflict of interest The authors declare that they have no conflict of interest.

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