Bulletin of Entomological Research

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Tephritidae fruit fly gut microbiome diversity, function and potential for applications

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Review

Cite this article: Raza MF, Yao Z, Bai S, Cai Z, Zhang H (2020). Tephritidae fruit fly gut microbiome diversity, function and potential for applications. *Bulletin of Entomological Research* **110**, 423–437. https://doi.org/10.1017/S0007485319000853

Received: 9 February 2019
Revised: 1 November 2019
Accepted: 3 December 2019
First published online: 11 February 2020

Keywords:
Cue-lure; Enterobacteriaceae; gut bacteria; host fitness; probiotics; tephritidae

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Abstract

The family Tephritidae (order: Diptera), commonly known as fruit flies, comprises a widely distributed group of agricultural pests. The tephritid pests infest multiple species of fruits and vegetables, resulting in huge crop losses. Here, we summarize the composition and diversity of tephritid gut-associated bacteria communities and host intrinsic and environmental factors that influence the microbiome structures. Diverse members of Enterobacteriaceae, most commonly *Klebsiella* and *Enterobacter* bacteria, are prevalent in fruit flies guts. Roles played by gut bacteria in host nutrition, development, physiology and resistance to insecticides and pathogens are also addressed. This review provides an overview of fruit fly microbiome structure and points to diverse roles that it can play in fly physiology and survival. It also considers potential use of this knowledge for the control of economically important fruit flies, including the sterile insect technique and cue-lure baiting.

Introduction

The order Diptera comprises numerous families, such as Tephritidae, which includes economically important insect pests. Insects of the family Tephritidae are also known as fruit flies and include 4300 defined species from approximately 500 genera worldwide (White, 2006). The damage caused by fruit flies is exacerbated by two major factors: wide host range and high fecundity rate (Clarke *et al.*, 2005; Rwomushana *et al.*, 2008; Yee and Goughnour, 2008; Schutze *et al.*, 2015*a*). However, insect performance is influenced by a number of ecological factors, i.e., which plants are present in the environment, their accessibility and a plant's intrinsic value for insect development and survival (Fahrig and Paloheimo, 1988; Kuussaari *et al.*, 2000). The polyphagous species of tephritidae family offer different case histories of successful invasions; for example, *Ceratitis catoirii*, *C. rosa* and *C. capitata*, *Bactrocera zonata* and *B. dorsalis* can survive on a longer range of host plants than that of the oligophagous species, e.g., *Zeugodacus cucurbitae*, *Dacus demmerezi* and *Neoceratitis cyanescens* (Clarke *et al.*, 2005; Hafsi *et al.*, 2016).

Tephritids span various continents, including South-East Asia, Indian subcontinent, China, southern Thailand (Aketarawong *et al.*, 2007; Drew and Romig, 2013), Nicobar and Andaman Islands (David and Ramani, 2011), Philippines (Drew and Hancock, 1994; Schutze *et al.*, 2012), South Pacific Islands and Hawaii (Stephens *et al.*, 2007), America (Papadopoulos *et al.*, 2013; Suckling *et al.*, 2016), New Guinea Island (Nair *et al.*, 2017) and Africa (Khamis *et al.*, 2009). This broad geographic distribution complicates the application of different control methods, quarantine, international trade and food security (Schutze *et al.*, 2015*b*). In the past few decades, various pest-control tactics, such as insecticide spraying (Wang *et al.*, 2013), methyl eugenol and cue-lure traps, protein baiting (Vargas *et al.*, 2000), essential oils (Ling-Chang *et al.*, 2009), biological control exploiting entomopathogens (Douglas, 2007), predators (Cao *et al.*, 2012), parasitoids (Bokonon-Ganta *et al.*, 2013) and sterile insect techniques (SITs) (Hendrichs *et al.*, 2002), have been used to control fruit flies. However, high adaptability, fecundity and resurgence can limit the effectiveness of such approaches, thus improvement of these techniques is needed.

SIT, an environmentally-friendly approach, is one of the most promising strategies for management of fruit flies (Hendrichs *et al.*, 2002). In this approach, mass-reared and radiation sterilized male fruit flies are released in the field where they compete with wild males for mating with wild females. When a sterile male mates with a wild female, no offspring is produced; thus, the population is significantly reduced (Ben-Ami *et al.*, 2010). However, gamma-radiation can reduce male mating competitiveness, which is a limiting factor of this approach (McInnis *et al.*, 1996; Lance *et al.*, 2000; Lux *et al.*, 2002). Moreover, gamma-radiation damages the intestinal epithelium and other tissues that results in the reduction of gut

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microbial community (Lauzon and Potter, 2012; Hamden *et al.*, 2013). Several issues are being faced for the implication of successful SIT strategy, including inappropriate cage design, oviposition substrates and contamination from human caregivers or damage caused during handling of eggs, mature larvae, pupation and adults (Estes *et al.*, 2011). Additionally, the difference between microbiota of wild and laboratory reared fruit flies is also concerning. For example, lower bacterial diversity in laboratory flies is most likely the result of laboratory environments and artificial diets that may contain antibiotics and antimicrobials (as described in Estes *et al.*, 2011) or opportunistic pathogens, e.g., *Morganella morganii* (Estes, 2009*a*; Salas *et al.*, 2017), which could harm beneficial gut microbes. Hence, there is a need to enhance the competitiveness of mass reared sterile males to increase the efficiency of the SIT. Previous studies have suggested that for the maintenance of symbiotic microbiota, inoculation of gut bacteria prior to sterile male release may improve the effectiveness of SIT (Niyazi *et al.*, 2004; Ben-Ami *et al.*, 2010; Hamden *et al.*, 2013).

The gut of Metazoans harbours a complex microbial community that may include beneficial symbionts, non-symbionts and life-threatening pathogens (Dillon and Dillon, 2004; Yao *et al.*, 2015). The evolutionary success and diversification of insects are dependent in part on their association with beneficial microbes. Different beneficial gut–microbe interactions influencing the survival, nutrition, protection, communication, reproduction and various fitness aspects of insects have been reported (Petri, 1909; Stammer, 1929; Lemaitre and Hoffmann, 2007; Brune, 2014). In addition, symbiotic microorganisms of insects contribute to intra- and inter-specific communication (Dillon *et al.*, 2002), influence developmental time (Chouaia *et al.*, 2012) and affect reproductive and mating systems, such as improved sterile male performance in copulation (Ben-Ami *et al.*, 2010).

Knowledge about the structure of these gut communities is just beginning to develop. Earlier studies of the gut microbiota of various insects were summarized by Dillon and Dillon (2004) and Engel and Moran (2013). In this review, we consider what is known about the gut bacterial community of tephritids. We review new approaches to analyse the structure of the tephritid microbiome, consider the prospects of discovering additional microbiome functions and discuss the knowledge gaps for the use of gut symbionts as biocontrol agents.

Tephritidae microbiota structure

Classical and molecular methods have been used to determine the composition of symbiotic microbes associated with the gut (White, 1988; Murphy *et al.*, 1994; Marchini *et al.*, 2002; Thaochan *et al.*, 2010) and oesophageal bulb (Marchini *et al.*, 2002). The oesophageal bulb (or diverticulum) is a unique organ found in the fly heads of many Tephritids, with some morphological differences (Girolami, 1973). From this organ, the obligate endosymbionts are multiplied and discharged into the oesophagus and intestine where they are eventually digested (Petri, 1909; Mazzon *et al.*, 2008). Significant diverse bacterial components across the different life stages, such as eggs, larvae, pupae and adult fruit flies, have also been reported using classical and molecular methods (Fitt and O'Brien, 1985; Daser and Brandl, 1992; Zhao *et al.*, 2018; Yao *et al.*, 2019). Initially, classical microbiological approaches, such as culture-dependent isolation (Marchini *et al.*, 2002), physiological and morphological characterization and analytical profile index (API) systems, were widely used to isolate and identify microbes associated with fruit flies (Fitt and O'Brien, 1985). However, these approaches can only account for a small proportion of the gut flora, i.e., 10–40% by some estimates (Macfarlane and Gibson, 1994; Langendijk *et al.*, 1995; Wilson and Blitchington, 1996). Currently, molecular approaches have been utilized to categorize both culturable and non-culturable bacteria (Mazzon *et al.*, 2008) mainly by polymerase chain reaction (PCR) amplification of the bacterial 16S rDNA and sequencing (Capuzzo *et al.*, 2005; Thaochan *et al.*, 2010; Wang *et al.*, 2011; Aharon *et al.*, 2013; Wang *et al.*, 2014*a*,*b*; Andongma *et al.*, 2015; Ventura *et al.*, 2018). Major components of different genera microbiome associated with laboratory and wild tephritid populations are summarized in Table 1. Additional (major and minor) bacteria components according to the host species, locality and type of diet are listed in Table S1. Enterobacteriaceae (most common genera *Klebsiella* and *Enterobacter*) have been repeatedly shown to be the dominant gut bacteria family among fruit flies, including *Bactrocera tryoni* and *B. cacuminata* (Thaochan *et al.*, 2010), *B. jarvisi*, *B. neohumerali* (Fitt and O'Brien, 1985), *B. tau* (Prabhakar *et al.*, 2009, 2013; Khan *et al.*, 2014), *B. zonata* (Naaz *et al.*, 2016), *Z. cucurbitae* (Hadapad *et al.*, 2016), *B. oleae* (Sacchetti *et al.*, 2008; Kounatidis *et al.*, 2009; Ben-Yosef *et al.*, 2015; Blow *et al.*, 2016), *B. dorsalis* (Wang *et al.*, 2014*a*,*b*; Cai *et al.*, 2018), *C. capitata* (Behar *et al.*, 2005, 2008*a*,*b*,*c*, 2009), *Anastrepha ludens* (Kuzina *et al.*, 2001; Ventura *et al.*, 2018), *A. serpentina*, *A. obliqua*, *A. striata* (Ventura *et al.*, 2018), *Rhagoletis pomonella* (Lauzon *et al.*, 1998) and *Dacus* (Drew and Lloyd, 1991) (Table 1). These studies have reported the most common gut bacterial genera associated with many tephritids, viz., *Klebsiella*, *Citrobacter*, *Enterobacter*, *Providencia*, *Erwinia*, *Proteus* and *Bacillus*. However, the gastrointestinal tract of some fruit flies also harbours *Morganella* (Salas *et al.*, 2017), *Pseudomonas* and *Serratia* spp., which are generally benign but can be opportunistic pathogens.

The latest calculation based on scaling law describes that a trillion microbe species are yet to be discovered (Locey and Lennon, 2016). There are many pros and cons of genomic analysis of gut microbial communities. Many recent studies document that gut communities are based on 16S rRNA gene profiles, but some of these do not provide sufficient information on bacterial cell numbers. For example, next-generation sequencing (NGS) only accounts for the relative abundance and composition of gut bacteria. Quantitative PCR is another quantitative molecular technique generally used to enumerate individual species as well as total bacteria using species-specific probes and can detect a broad linear range from 10 to more than 10^8 cells (Heid *et al.*, 1996; Corless *et al.*, 2000; Guiver *et al.*, 2000; Higgins *et al.*, 2000). In the near future, some novel tools, such as metatranscriptomics, gut microbiotassay (Hermann-Bank *et al.*, 2013), metagenomics and functional genomic assessment, could be addressed to develop our awareness about gut microbial communities of unreported genera of fruit flies.

Factors influencing gut microbial diversity

Gut bacterial communities may be influenced by host factors (transmission modes, species, tissue environment, developmental stage and genetics), environmental factors, sterilizing radiation, diet and immunity. Below, we document the reported evidence that may demonstrate a link with each aspect that influences gut microbial diversity.

A key parameter defining symbiosis is the transmission efficiency of microbial symbionts between host individuals and

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Table 1. Major gut bacterial composition of Tephritid fruit flies.

Tephritids	Major gut bacteria				Methods	Citations
	Phylum (Class)	Order	Family	Genus		
Oriental fruit fly (*B. dorsalis*)	Proteobacteria *(γ-proteobacteria)	Enterobacteriales	Enterobacteriaceae	*Klebsiella* *Enterobacter* *Cirtrobacter* *Pectobacterium* *Serratia*	PCR-DGGE fingerprinting	Wang *et al.* (2011)
	Actinobacteria (Actinobacteria)	Actinomycetales	Mycobacteriaceae	*Microbacterium* *Agromyces* *Leucobacter*		
	Firmicutes (Bacilli)	Lactobacillales Bacillales	Streptococcaceae Bacillaceae Paenibacillaceae			
Pumpkin fly (*B. tau*)	Proteobacteria (γ-proteobacteria) Firmicutes (Bacilli)	Enterobacteriales Bacillales	Enterobacteriaceae Staphylococcaceae	*Klebsiella* *Pantoea* *Proteus* *Streptobacillus* *Staphylococcus*	Morphological, biochemical and 16sDNA Identification	Prabhakar *et al.* (2009) Khan *et al.* (2014)
	Proteobacteria **(α-Proteobacteria) Bacteroidetes (Flavo-bacteria)	Rhizobiales Flavobacteriales	Phyllobacteriaceae Brucellaceae Flavobacteriaceae	*Defluvibacter* *Delftia* *Ochrobactrum* *Flavobacterium*	Morphological, biochemical and 16sDNA Identification	Prabhakar *et al.* (2013)
Melon fly (*Z. cucurbitae*)	Proteobacteria (γ-proteobacteria) Firmicutes (Bacilli)	Enterobacteriales Bacillales	Enterobacteriaceae Bacillaceae	*Enterobacter* *Klebsiella* *Citrobacter* *Providencia* *Bacillus*	16s DNA molecular identification	Hadapad *et al.* (2016)
Chinese citrus fly (*B. minax*)	Proteobacteria (γ-proteobacteria)	Enterobacteriales	Enterobacteriaceae	*Klebsiella* *Enterobacter* *Citrobacter* *Serratia*	454 pyrosequencing	Wang et al. (2014a) Yao et al. (2019)
Queensland fruit fly (*B tryoni*)	Proteobacteria (γ-proteobacteria)	Enterobacteriales	Enterobacteriaceae	*Klebsiella* *Enterobacter* *Citrobacter* *Hafnia* *Providencia* *Serratia* *Pantoea*	API-20E method and 16sDNA Identification	Thaochan *et al.* (2010)
Wild tobacco fruit fly (*B. cacuminata*)	Proteobacteria (γ-proteobacteria)	Enterobacteriales	Enterobacteriaceae	*Klebsiella* *Enterobacter* *Citrobacter* *Escherichia* *Pseudomonas* *Pantoea*	API-20E method And 16sDNA Identification	Thaochan *et al.* (2010)
Olive fly (*B. oleae*)	Proteobacteria (γ-proteobacteria)	Enterobacteriales	Enterobacteriaceae	*Klebsiella* *Enterobacter* *Pantoea* *Erwinia* (*Candidatus Erwinia dacicola*) *Escherichia*	Morphological and 16sDNA molecular identification	Capuzzo *et al.* (2005)
Peach fruit fly (*B. zonata*)	Proteobacteria (γ-proteobacteria) Actinobacteria (Actinobacteria)	Enterobacteriales Actinomycetales	Enterobacteriaceae Microbacteriacea Nocardiaceae	*Klebsiella* *Microbacterium* *Rhodococcus*	Morphological, biochemical and 16S rDNA sequence analysis	Naaz *et al.* (2016)
Jarvis fruit fly (*B. jarvisi*)	Proteobacteria (γ-proteobacteria)	Enterobacteriales Neisseriales	Enterobacteriaceae Neisseraceae	*Proteus* *Enterobacter* *Serratia* *Acinetobacter*	API-20E method	Fitt & O'Brien (1985)
Lesser Queensland Fruit fly (*B. neohumerali*)	Proteobacteria (γ-proteobacteria)	Enterobacteriales Pseudomonadales	Enterobacteriaceae Pseudomonadaceae	*Proteus* *Serratia* *Enterobacter* *Pseudomonas*	API-20E method	Fitt & O'Brien (1985)

(*Continued*)

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Table 1. (*Continued.*)

Tephritids	Major gut bacteria				Methods	Citations
	Phylum (Class)	Order	Family	Genus		
Mediterranean fruit fly (*C. capitata*)	Proteobacteria (γ-proteobacteria)	Enterobacteriales	Enterobacteriaceae	*Pseudomonas* *Klebsiella* *Pectobacterium* *Enterobacter* *Pantoea* *Citrobacter* *Serratia*	SuPER-PCR PCR-DGGE API	Behar et al. (2005, 2008*b*,*c*) Ben-Ami *et al.* (2010) Marchini *et al.* (2002)
Mexican fruit fly (*A. ludens*) West Indian fruit fly, (*A. obliqua*) Guava fruit fly, (*A. striata*) Sapodilla fruit fly, (*A. serpentina*)	Proteobacteria (γ-proteobacteria) Firmicutes (Bacilli) Proteobacteria (γ-proteobacteria) Proteobacteria (γ-proteobacteria) Proteobacteria (γ-proteobacteria)	Enterobacteriales Eubacteriales Pseudomonadales Bacillales Enterobacteriales Enterobacteriales Enterobacteriales	Enterobacteriaceae Micrococcaceae Pseudomonadaceae Bacillaceae Enterobacteriaceae Enterobacteriaceae Enterobacteriaceae	*Enterobacter* *Providencia* *Serratia* *Klebsiella* *Raoultella* *Staphylococcus* *Aeromonas* *Listeria* *Escherichia* *Citrobacter* *Leclercia* *Raoultella* *Klebsiella* *Erwinia* *Leclercia* *Pseudomonas* *Citrobacter* *Escherichia* *Raoultella* *Enterobacter* *Leclercia* *Citrobacter* *Escherichia* *Raoultella* *Pseudomonas* *Tatumella* *Kluyvera*	API system 454 pyrosequencing 454 pyrosequencing 454 pyrosequencing 454 pyrosequencing	Kuzina *et al.* (2001) Ventura *et al.* (2018) Ventura *et al.* (2018) Ventura *et al.* (2018) Ventura *et al.* (2018)
Rose hip fly (*Rhagoletis alternata*)	Proteobacteria (γ-proteobacteria)	Enterobacteriales	Enterobacteriaceae	*Enterobacter* *Erwinia*	Morphological and Physiological properties	Daser and Brandl (1992)
Apple maggot (*R. pomonella*)	Proteobacteria (γ-proteobacteria)	Enterobacteriales	Enterobacteriaceae	*Enterobacter* *Klebsiella* *Escherichia*	API-20E method	Lauzon *et al.* (1998) Rossiter *et al.* (1983)
Tephritis conura *Urophora cuspidate* Nodding Thistle Gall Fly (*Urophora solstitialis*) *Tephritis dilacerata*	Proteobacteria (γ-proteobacteria)	Enterobacteriales	Enterobacteriaceae	*Stammerula* (*Candidatus Stammerula tephritidis*)	16S rDNA sequence analysis	Mazzon *et al.* (2008)

*γ, gamma, **α, alpha.

generations (Bateman, 1972). The mode of bacteria transmission from one generation to the next varies with the host. Mammals have an established social communication that enables the direct transmission of microorganisms in the form of parent–child contact. Conversely, insects in general lack consistent mechanisms for direct transmission of gut bacteria to the next progeny. However, social insects, such as ants, bees and termites, are exceptions; they transfer bacteria from one individual to another via social interactions (Benemann, 1973; Ohkuma *et al.*, 1999). Most tephritids have developed mechanisms for vertical transmission of bacteria to progeny via smearing the egg surface with bacteria during oviposition, which is subsequently consumed by offspring (Marchini *et al.*, 2002; Mazzon *et al.*, 2008; Estes *et al.*, 2009b; Hamden *et al.*, 2013; Wang *et al.*, 2013). Another example of maternal transmission in adult female *B. oleae* has been demonstrated by Petri (1909). He found that the dorsal wall of the rectum is thrown up into a complex series of tubules or rectal crypts, which are filled with bacteria. Eggs passing down the oviduct are pressed against the open mouths of these crypts and smeared with bacteria immediately before they are injected into the fruit. Subsequently, bacteria enter the egg through the micropile and multiply in the developing larvae in gastric caeca. A few bacteria remain throughout pupal development and induce infestation in the adult oesophageal bulb, and these symbionts spread through the alimentary canal of the adult (Petri, 1909). Later, Capuzzo and his colleagues

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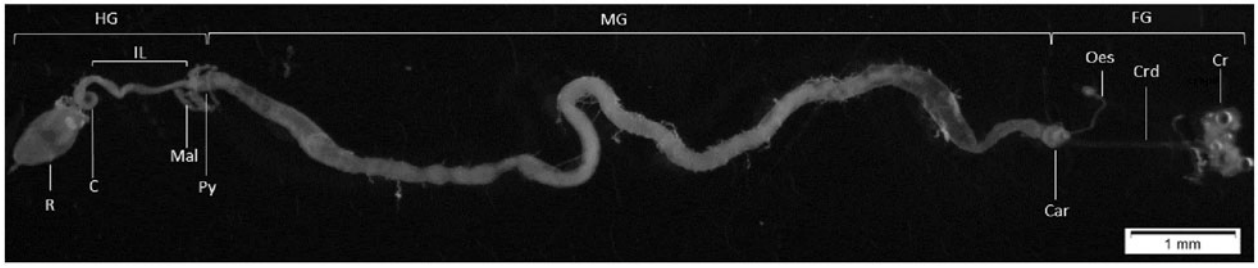


Figure 1. Dissected gut structure of *B. dorsalis*. FG, foregut; Car, cardia; Crd, cardial duct; Oes, oesophagus; Cr, crop; MG, midgut; HG, hindgut; py, pylorus, Mal, malpighian tubules; IL, ileum; C, colon; R, rectum.

(2005) confirmed that once *B. oleae* embryo development is completed in the egg, the unhatched larva already contain the bacterial symbiont within its blind sacs even before it has a chance to start feeding on the olive pulp (Capuzzo *et al*., 2005). However, decaying fruit also plays a vital role in the transmission of bacterial symbionts to fruit fly offspring and as a source of nutrition for developing larvae (Behar *et al*., 2008*c*).

Gut structure plays a vital role for the development of bacterial community, and insect gut structure (Fig. 1) is simpler and offers less ecological niches than that of the mammalian gut. As mentioned by Colman *et al*. (2012), the complexity of the insect microbiome is considerably reduced compared with mammals (tens to hundreds vs. thousands bacterial species) (Dethlefsen *et al*., 2008; Ley *et al*., 2008; Robinson *et al*., 2010; Broderick and Lemaitre, 2012). Moreover, the average retention time of gut bacterial communities is shorter in insects than that of the gut of higher organisms (Chapman *et al*., 2013). Another reason for reduced microbial niches could be that foregut and hindgut regions are shed during moulting. In addition, during metamorphosis, the whole larval gut is substituted by a new adult gut. Hence, the transitory gut nature of tephritid flies may be incompatible with the development of a diverse bacterial community (Robinson *et al*., 2010).

Various physicochemical conditions, such as pH and the redox potential of different gut compartments, determine the composition of the bacterial community along the gut. Most bacteria prefer pH ranging from 6 to 7 (Dillon and Dillon, 2004). Bacteria may also populate gut compartments displaying extreme pH; for example, the midgut of *Dacus* (*Bactrocera*) larvae has a strong acidic pH ranging from 1.4 to 2.0 that supports the growth of lactic acid bacteria (Fitt and O'Brien, 1985; Dillon and Dillon, 2004). Acid-metabolizing bacteria of the genera *Leuconostoc* and *Lactobacillus* were also found in the crop of adult tephritids. An acidic pH in the crop of some *Bactrocera* spp. has been reported by Drew *et al*. (1983) and can hold acid-metabolizing bacteria (Thaochan *et al*., 2015). However, it is possible that the acidity of crop in insects gut is partly related to the characteristics of the ingested diet (Thaochan *et al*., 2015). For example, a substantial difference of bacterial representation between gut and crop of both *B. tryoni* and *B. cacuminata* was observed and was attributed to dissimilar pH values of these parts, which is possibly due to the different types of diets (Thaochan *et al*., 2010). However, lactic acid bacteria can produce their own low pH environment in the gut by secreting acids (Kodama and Nakasuji, 1971). Similarly, Acetobacteraceae likely can create acidic micro-niches in an otherwise alkaline or neutral gut (Kounatidis *et al*., 2009). This may explain why Acetobacteraceae bacteria are found in two members of Acalyptratae, *Bactrocera* and *Drosophila*.

A diet also plays a key role in structuring gut microbial diversity. Effects on the microbiome structure have been observed in comparisons between artificial and natural diets (Table S1), as well as between diets in which main nutritional classes (protein and sugar) are different (Capuzzo *et al*., 2005). Previously, Wang *et al*. (2011) explored whether different types of diets could significantly influence the gut bacteria community of *B. dorsalis* (Wang *et al*., 2011). The field-collected flies have more diverse gut flora compared with laboratory-reared flies. A possible reason for the gut community variations could be that the field-collected flies had more opportunities to feed on uncontrolled natural diets, while laboratory reared flies were fed with sterile sucrose solution under sanitary and controlled conditions (Wang *et al*., 2011).

Sterilizing irradiation procedures used for SIT affects the gut microbiome structure of mass-rearing strains of tephritids. The level of dominant gut bacteria (e.g., *Klebsiella* spp.) decreases after sterilization, whereas potentially pathogenic species, such as *Pseudomonas*, which is known to harm insects, increase in industrial strains (Ben-Ami *et al*., 2010). Optimization of mass-rearing conditions is an important goal in SIT programmes. For example, irradiation used in mass rearing of tephritids can also have substantial negative effects on insect performance, e.g., reduced flight capacity, female attraction, mating competitiveness and longevity (Ben-Ami *et al*., 2010; Cai *et al*., 2018).

The dysbiosis of physiological processes and chronic inflammation in the intestinal tract of insects are resulted by the deregulation alterations of the gut microbiota (Round and Mazmanian, 2009; Nyholm and Graf, 2012). Therefore, the host maintains suitable microbiota homoeostasis for beneficial host–microbe interactions. The gut epithelium is commonly exposed to harmful pathogens; therefore, an efficient immune system is required for protection (Kuraishi *et al*., 2013). The roles of antimicrobial peptides and reactive oxygen species in the gut immune response are well documented in *B. dorsalis*, *Aedes aegypti* and *Drosophila melanogaster* (Fig. S1), but the molecular mechanisms underlying the associations between insect gut immunity and its resident micro-organisms is still poorly understood. Future studies are needed to explore how the host distinguishes beneficial bacteria from pathogens and whether the host determines gut homoeostasis or pathogenesis through bacterial metabolites or other factors. Besides providing immunity, gut microbiota might also be useful for efficient parasitoid rearing, i.e., high quality and cost-effective. Host *C. capitata* larvae are commonly subjected to irradiation before exposing them to parasitoids (Cancino *et al*., 2012; Yokoyama *et al*., 2012). Both X-ray and gamma irradiation do not seem to have negative influences on *C. capitata* (Cancino *et al*.,

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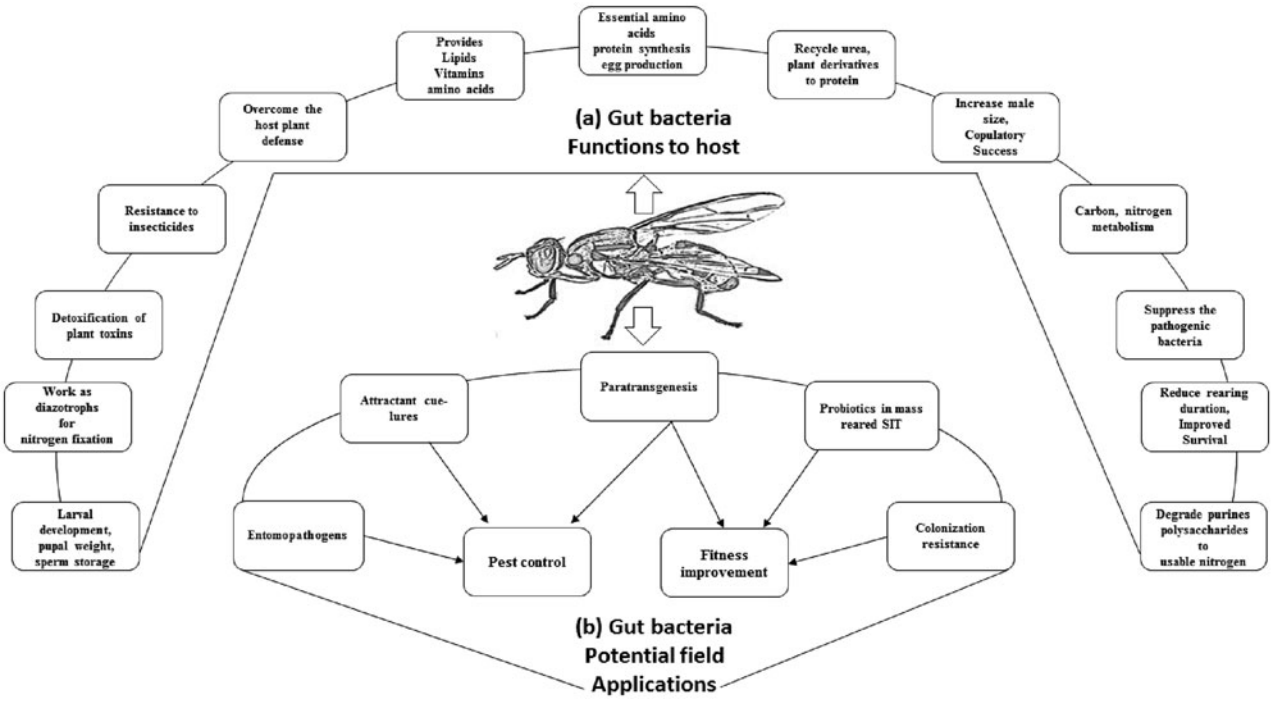


Figure 2. Different roles of gut bacteria in Tephritidae fruit flies. (a) Functions contributing to host nutrition, development, physiology and resistance to pathogens and insecticides. (b) Potential for field applications, viz., insecticidal potential of entomopathogenic gut bacteria can be used to control pests. In paratransgenesis, bacteria can be used as sources to express molecules in the gut that positively or negatively affect the health of the host. In colonization resistance, gut bacteria that inhibit parasite colonization naturally could be dispersed in insect populations to promote host fitness, gut bacteria can be used as cue-lure-kill strategies of pests, probiotics used in SIT could enhance the fitness of mass reared flies.

2012) and Anastrepha *fraterculus* (Bachmann *et al.*, 2015) quality for use in rearing of *Diachasmimorpha longicaudata*; however, the effect of larval irradiation on the immune response remains poorly understood. Numerous other functions of gut microbiota may affect parasitoid biology. For example, it would be interesting to explore whether bacteria help developing parasitoids by avoiding or overcoming the host immune system in the same way as viruses (Lawrence, 2004). Additionally, successful development of endoparasitoid wasps in the larval bodies of *A. obliqua* depends on the ability to avoid encapsulation by the host immune system (Silva *et al.*, 2002). Haemocytes are responsible for making the cellular components of the capsules that surrounds the parasitoids in larval hosts (Ratcliffe, 1993). As the haemocytes are involved in defence reactions in insects, they could be very useful to understand host–parasite interactions in the future. The immune system is an important feature that regulates microbiota homoeostasis in the insect gut, but we will not discuss the details of immunity in this review.

Gut microbe functions for the fitness improvement of host fruit flies

The gut microbial community of tephritid flies govern a massive array of functions contributing to host nutrition, development, physiological resistance to pathogens and insecticides and insect immune system modulation. However, our recent information about microbiota functions in host flies remains inadequate. In the following section, we review some important findings (Fig. 2) that emphasize the practical roles of gut microbiota to economically important tephritid flies.

Gut bacteria provide nutrients to the host

In the early 20th century, Metchnikoff embarked upon a series of experiments to investigate the positive role of gut microbes in the nutrition and development of host. He found that trypsin-producing bacteria were necessary for nutrition and normal development in the *D. melanogaster* maggot, while a lack of microbial flora in axenic flies resulted in stunted growth (Metchnikoff, 1901). More recently, a study investigated the nutritional role of gut microbes on the host revealed that the intestinal bacteria of *C. capitata* provides significantly higher amount of lipids and proteins to the host compared with that of antibiotic-treated flies (Ben-Yosef *et al.*, 2008*a*). This finding may be attributed to the fact that gut bacteria affect lipid and carbohydrate metabolism in an unknown manner (Ben-Yosef *et al.*, 2008*a*). As reported in *B. tryoni*, another reason may be that adult gut acidity is adequate to autolyse the ingested bacteria and release of their cell contents in the form of vitamins, amino acids and other nutrients (Drew *et al.*, 1983). A major role of the acetic acid bacterium *Acetobacter tropicalis* in the nutrition, development and physiology of *R. pomonella* has also been reported (Dean and Chapman, 1973).

Insect food contains numerous polysaccharides that are generally difficult to digest. Many insect endosymbiotic bacterial communities have the potential to digest different polymeric carbohydrate molecules (Prem Anand *et al.*, 2010; Dey *et al.*, 2011). Saha and Ray (2015) demonstrated that *B. dorsalis* gut bacteria might produce enzymes that help in the digestion of polysaccharides, including xylan, pectin, cellulose and starch. Similarly, *R. pomonella* creates a facultative symbiotic relationship with *Enterobacter* and *Klebsiella*, which degrade purines and purine

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derivatives and provide usable nitrogen for the insect (Lauzon *et al*., 2000).

Many tephritid flies rely on poor diet sources that have variable amino acid composition. For instance, adult *B. oleae* feed on nectar, honeydew, fruit and plant exudates, and pollen (Chrlstenson and Foote, 1960; Drew and Yuval, 2000). The nutritional significance of these foodstuffs may fluctuate greatly; for example, plant-derived exudates, nectar and honeydew are typically rich in carbohydrates but poor in amino acids (Wäckers, 2005; Lundgren, 2009). Ben-Yosef *et al*. (2010) demonstrated that the gut microbiota of *B. oleae* flies that survive primarily on a nitrogen-poor diet such, as honeydew, are able to compensate skewed amino acid composition (Ben-Yosef *et al*., 2010). Similarly, *in vitro* studies showed that gut bacteria can recycle uric acid, urea and plant derivatives into protein via mechanisms that contribute to the host nitrogen levels (Hellmuth, 1956; Lauzon *et al*., 2000; Robacker and Lauzon, 2002).

Different authors reported the association of *Candidatus* Erwinia dacicola as the main symbiont of wild *B. oleae*. *Ca.* E. dacicola is maintained extracellularly in both adults and larvae; however, it also resides intracellularly in the gastric caeca of the larval midgut (Estes *et al*., 2009b, 2012; Ben-Yosef *et al*., 2014). This bacterium can utilize urea as a nitrogen source and can use essential amino acids for protein synthesis and egg production. This type of symbiosis enables adult flies to exploit low or imbalanced food substrates and thus to overcome nitrogen limitations in their natural diet (Ben-Yosef *et al*., 2014).

In insects, including tephritids, male and female development and reproductive potential depend on the acquisition of nitrogenous compounds (Drew and Yuval, 2000; Du *et al*., 2012). Termites are the prominent insects that harbour diazotrophic bacterial communities, such as *Citrobacter freundii*, *E*nterobacter *agglomerans* and *Desulfovibrio* spp., as shown by phylogenetic analysis of both dinitrogenase reductase (*nifH*) genes and 16S rRNA (Benemann, 1973; Ohkuma *et al*., 1999). Behar *et al*. (2005) reported that natural populations of *C. capitata* harbour large diazotrophic populations of Enterobacteriaceae that express dinitrogen reductase (*nifH*) genes in the gut (Behar *et al*., 2005). The diazotrophic bacterial species retrieved from the *C. capitata* gut were also reported in other tephritid guts, viz., *R*hagoletis *completa* (Peloquin *et al*., 2000), *B. tryoni* (Murphy *et al*., 1994), *R. pomonella* (Rossiter *et al*., 1983; Lauzon *et al*., 2000) and *A. ludens* (Kuzina *et al*., 2001). On the basis of acetylene reduction assay (ARA), laboratory-reared *B. tryoni* fed dinitrogen-fixing strains of *Klebsiella oxytoca* and *Enterobacter* spp. revealed nitrogenase activity (Murphy *et al*., 1988, 1994). However, it is noteworthy that ARAs were associated with fruit flies, and *nifH* genes were detected in bacteria isolated from their guts. Thus, the nutritional contributions of gut bacteria to the host due to nitrogen fixation must be further explored. Additionally, it is premature to conclude that the availability of atmospheric nitrogen to diazotrophs' gut bacteria favours the activation of nitrogen fixation mechanism. The natural diet of wild flies is poor in organic nitrogen but does contain amino acids, uric acids and proteins. Thus, a contribution of fixed nitrogen to the host may be very small and has minimal fitness consequences (Wackers, 2005; Lundgren, 2009).

Development and reproduction

Primarily, Petri postulated that bacteria are present at every stage of the *B. oleae* life and play a significant role for successful growth and development (Petri, 1906, 1909). Probiotics added to the adult fruit flies diet may provide essential nutrients for fecundity and increase the longevity compared with those fed a conventional diet (Drew *et al*., 1983; Halder *et al*., 2013). Bacterial association significantly increased survival and reproductive success of *C. capitata* males when well-nourished on a sugar diet (Hamden *et al*., 2013). Ben-Yosef *et al*. (2008b) investigated the reproductive potential and longevity of *C. capitata* males and females after removing gut bacteria using antibiotics. They found that intestinal bacteria affect the life span in a diet-dependent fashion (Ben-Yosef *et al*., 2008b). Similarly, the addition of probiotics in the diet increased pupal weight, male matting success, longevity and male size and improved sperm storage in the females' spermathecae (Hamden *et al*., 2013). Damodaram and his colleagues found that male *B. dorsalis* flies are attracted to and ejaculated more sperm into females harbouring the microbiota, but this attraction was eliminated when female flies were fed antibiotics (Damodaram *et al*., 2016), which suggests that the gut microbiota mediates mate selection. Sacchetti *et al*. (2014) isolated *Pseudomonas putida* from the oesophageal bulb of wild *B. oleae*; they found that its probiotics diet increased the egg production and reduced the longevity of *B. oleae*. A possible reason could be that it took longer for colonization in the oesophageal bulb of the *B. oleae* adults (Sacchetti *et al*., 2014). These results provide several important clues about the beneficial role of gut microbiota in reproduction and development of the flies; while these explanations are possible, we feel that a more comprehensive view of these interactions need to be worked out in further experiments, regardless of diet type or gut bacterial strains.

Conversely, some authors disagree with the above findings. Bacteria added to the diet of female *B. tryoni* and *B. tau* did not affect fecundity (Meats *et al*., 2009; Khan *et al*., 2014). Another study also showed that gut bacteria did not enhance reproductive success or the nutritional status of poorly fed *C. capitata*. The possible reason of bacteria inefficiencies could be due to the co-existence of mutualistic and pathogenic microorganisms in the fly gut or poor nutritional conditions (Drew *et al*., 1983). Such complications have been revealed in other insect–gut bacteria associations, especially the thrips–*Erwinia* relationship (De Vries *et al*., 2004). Khan *et al*. found that the isolated gut bacterial species *Proteus rettgeri* and *K. oxytoca* supplemented with a protein and sugar diet has no significant influence on egg production and ovariole number compared with an exclusively protein diet (Khan *et al*., 2014). Similarly, Ben-Yosef *et al*. (2010) also examined that gut symbionts supplemented with a protein-rich diet or nutritionally poor sucrose diet did not affect the fecundity of *B. oleae* (Ben-Yosef *et al*., 2010). The results of the above studies showed that gut bacteria did not improve host reproduction quality, which could be due to the nutritionally poor diet used in those studies and/or the co-existence of pathogenic and mutualistic microbes in the fly gut. Additionally, other laboratory environmental conditions, such as housing conditions, sex, age and contamination from human caregivers could also reduce the competitiveness of fruit flies.

Gut symbionts assist to overcome host plant defences

Unripe fruits generally endure less loss from pathogens and herbivores due to less nutritional value and high levels of secondary metabolites with antimicrobial, anti-nutritive and toxic effects (Prokopy and Roitberg, 1984). In contrast to other frugivorous Tephritids, such as *B. dorsalis* and *C. capitata*, which feed upon

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hydrolysed compounds of ripe fruits, *B. oleae* larvae have the unique ability to feed upon olive proteins and other nutrients of unripe olives as well as cope with high levels of phenolic compounds (Ben-Yosef *et al.*, 2015; Pavlidi *et al.*, 2017). A major symbiont '*Ca.* E. dacicola' contributes to larval development by aiding its host *B. oleae* to overcome the unripe fruit chemical defence (Ben-Yosef *et al.*, 2015). It was hypothesized that *B. oleae* gut bacteria might be responsible for disabling the hindrance effect of a bitter taste phenolic glycoside 'oleuropein' in unripe fruits (Ben-Yosef *et al.*, 2015). Recently, Pavlidi *et al.* (2017) reported transcriptomic responses of *B. oleae* and its gut obligate symbiotic bacterium *Ca.* E. dacicola to olive feeding. A number of genes were overexpressed in the *B. oleae* larvae when feeding in green olives that encode digestive and detoxification enzymes, such as uridine-glucuronosyltransferase (Pavlidi *et al.*, 2017). Additionally, a number of biological processes seem to be activated in *Ca. E. dacicola* during larval development in olives, and the most notable is the stimulation of amino-acid metabolism (Pavlidi *et al.*, 2017). These observations indicate a possible host–microbe association in *B. oleae* to cope with green olives. However, it is difficult to say whether degradation of oleuropein occurs with symbiont or insect enzymes or their cooperation; thus, further studies are still required to identify the functional contributions of this unique symbiont to its host.

Resistance to pathogens

It was previously noted that the presence of a dominant bacterial community in the *D. melanogaster* gut is sufficient to suppress the establishment of pathogenic bacteria (Ryu *et al.*, 2008). A minor but stable community of a known pathogen *Pseudomonas* spp. in the *C. capitata* gut was also reported by Behar *et al.* (2008*b*). They found that Enterobacteriaceae added to the *C. capitata* diet not only supports the fly's development, carbon and nitrogen metabolism, copulatory success and longevity, but also may suppress the proliferation of pathogenic bacterium *Pseudomonas* spp. (Behar *et al.*, 2008*b*). The addition of *K. oxytoca* to the post-irradiation diet of *C. capitata* aided in the restoration of beneficial bacteria in the gut and decreased the levels of potential pathogenic *Pseudomonas* species (Ben-Ami *et al.*, 2010). Another study also showed that *C. capitata* fly larvae fed with *K*lebsiella *pneumonia*, *Enterobacter* spp. and *C. freundii* increased Enterobacteriaceae and decreased *Pseudomonas* spp. in the larval stage (Hamden *et al.*, 2013).

Symbiont-mediated insecticide resistance

Recently, research on the largely untapped resource of 'detoxifying-symbionts' has revealed that gut microbial symbionts may have a role in the detoxification of plant toxins and insecticides. The ability of various bacteria to degrade organophosphate pesticides has been described in recent years (Prabhakar *et al.*, 2008; Zhang *et al.*, 2014; Akbar *et al.*, 2015; Siripattanakul-Ratpukdi *et al.*, 2015). Phenol and myo-inositol hexakisphosphate ($InsP_6$) degradation by numerous *Citrobacter* species has been documented, and their degradation pathways are generally well known (Pontoppidan *et al.*, 2012; Ma *et al.*, 2015). A novel insecticide resistance mechanism has been reported by Cheng and his colleagues, in which a bacterium *C. freundii* isolated from *B. dorsalis* gut increases the host resistance against Trichlorphon (Cheng *et al.*, 2017). The inoculation of isolated *Citrobacter* species to *B. dorsalis* resulted in higher trichlorphon resistance, whereas antibiotic-treated flies were less resistant. Comparative genomic analysis with other *Citrobacter* species revealed 55 phosphatase hydrolase (OPH)-like genes and five new genes that were unique to gut symbiont *C. freundii* from *B. dorsalis*. In the presence of trichlorphon, the expression of the five OPH-like genes was activated. Gas chromatography-mass spectrometry showed that *C. freundii* degrades 'trichlorphon' into less toxic products, e.g., chloral hydrate and dimethyl-phosphite (Cheng *et al.*, 2017). Metabolite characteristics of those less toxic products were similar to the results obtained with Citrobacter *braakii* (Pontoppidan *et al.*, 2012), but further evidence is required to determine whether phosphatase is the critical enzyme in degradation pathway used by *C. freundii* and whether this pathway is same as that used by *C. braakii*.

Practical applications of gut microbiota in tephritidae fruit flies

The resident microbiota of tephritids has great potential in promoting practical management of pests, e.g., gut symbiont-based probiotics can be used to improve larval and adult ecological fitness parameters, including morphological properties and mating competitiveness of sterile males used in SIT or using gut bacteria as attractant cue-lures of fruit flies.

Probiotics used in mass-reared SIT

Due to several attractive features, including environmental friendliness and species-specificity, SIT has been used for decades to control tephritids insect pests of agricultural importance (Lance *et al.*, 2000; Hendrichs *et al.*, 2002; Lux *et al.*, 2002). Several studies have addressed the need of defining an optimal dose range of radiations at which reasonable results of both performance and sterility of released males are achieved (Hooper, 1971; Zumreoglu *et al.*, 1979; Rendon *et al.*, 1996). To produce >97% sterility in tephritid males, e.g., *A. obliqua*, sufficient gamma radiation doses ranging from 60 to 70 Gy have been recently reported (Gallardo-Ortiz *et al.*, 2018). Lauzon and Potter compared midgut tissues and microflora from irradiated and non-irradiated mass-reared adult fruit flies through scanning and transmission electron microscopy. They found that cellular damage of midgut tissues included small, distorted nuclei that lacked nuclear material and mitochondria that were dilated or vacuolated (Lauzon and Potter, 2012). In addition, radiation exposure reduced peritrophic matrix (PM) (microorganisms are generally confined in it) formation in the midguts of newly emerged and 2-day-old adult flies of *C. capitata* and *A. ludens*, and bacterial abundance was subsequently decreased (Lauzon and Potter, 2012). However, replenishment of gut symbionts may help restore the impaired gut to a pre-irradiated state. The use of gut symbionts to cope with disruption of morphologic mucosal integrity and normal microbiota populations for human cancer patients receiving radiotherapy treatments has shown potential for developing enteritis and related malnutrition (Demirer *et al.*, 2006). Probiotics for tephritid fruit flies may also exhibit similar effects on the ultrastructure, histology and physiology of sterile insects gut tissues (Lauzon, 2003; Lauzon and Potter, 2012). Thus, harnessing gut microbiota could be an alternative approach to enhance the quality of sterile males used in SIT.

Symbiont bacteria contribute to host fitness in a systemic manner that is not essentially specific to one of the components of host physiology or behaviour. Niyazi *et al.* (2004) described

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that probiotic post-teneral diets of *E. agglomerans* and *K. pneumoniae* (isolated from wild *C. capitata* gut) have positive effects on the behavioural ecology of sterile *C. capitata* (Niyazi *et al.*, 2004). A significant increase in calling activity or life expectancy and mating performance of probiotic-treated males were observed in laboratory cages (Niyazi *et al.*, 2004). Post-irradiation diet of *K. oxytoca* derived from wild medflies resulted in the restoration of these bacteria in the gut. Moreover, male sexual performance was significantly enhanced, while the mating latency of sterile males was reduced (Ben-Ami *et al.*, 2010). Similarly, larval diets enriched with *Klebsiella*, *Enterobacter* and *Citrobacter* spp. improved morphometric qualities and the mating competitiveness of *C. capitata* males (Hamden *et al.*, 2013). Lauzon *et al.* (2009) demonstrated that vertical transmission of microorganisms from larval to adult stages could be the reason for improved quality and sexual performance of *C. capitata* adults (Lauzon *et al.*, 2009). In the laboratory and field cages, a diet supplemented with *K. oxytoca* improves the survival, mating ability and courtship of mass-reared *C. capitata* sterile males with wild females under starvation (Gavriel *et al.*, 2011). *Enterobacter* spp. used as live or dead probiotic supplemented the larval diet of *Z. cucurbitae* improved morphological properties, including pupal weight and survival compared with the non-probiotic irradiated group (Yao *et al.*, 2017). Interestingly, sterile flies could be used as vectors of virulent fungus, e.g., *Beauveria bassiana* via mating or contact during courtship (Toledo *et al.*, 2007). If mating does not occur, there might be horizontal transmission that could result in the mortality of the wild population, and fungal infection might prevent a wild female from re-mating with a wild male (Toledo *et al.*, 2017). Thus, sterile flies used as fungus vectors in SITs may also represent a new control method for area-wide integrated management of tephritid flies; however, the shortcomings and potential benefits of this technique require further investigation.

Other important issues for the mass-rearing conditions for SIT, i.e., the effects of laboratory-rearing environment on fruit flies symbionts, are also concerning. Laboratory-reared flies maintained on artificial diet have a lower diversity in their gut bacterial community compared with their counterparts, the wild flies (Konstantopoulou *et al.*, 1999; Wang *et al.*, 2011). In *B. oleae* laboratory rearing, antimicrobial agents are used to prevent the growth of pathogenic bacteria or fungi. For example, washing eggs with a 2% Clorox solution may prevent the vertical transmission of the naturally associated bacterial layer that is deposited on the eggs. In addition, the larval medium contains antimicrobial agents, e.g., nipagin, which have been shown to cause changes in the microbiota community structure in *B. oleae* (Konstantopoulou *et al.*, 1999). There are several options to promote symbiont survival in the host, such as modification of larval diet, especially during domestication, which is selective for beneficial bacteria and against pathogens in larvae (Cohen, 2003). Another option is to add symbiotic bacteria to the diet as probiotic supplements, which have been successfully used in other fruit flies, such as *Bactrocera* species (Drew *et al.*, 1983; Meats *et al.*, 2009; Yao *et al.*, 2017; Cai *et al.*, 2018) or *C. capitata* (Niyazi *et al.*, 2004; Ben-Ami *et al.*, 2010; Gavriel *et al.*, 2011; Hamden *et al.*, 2013; Augustinos *et al.*, 2015). Importantly, for effective probiotic supplementations, the target bacterial symbionts should be easy to culture and add to the diet. Generally, transiently associated facultative bacterial species should be considered as probiotics due to their ease of cultivation (Estes *et al.*, 2011).

Attractant cue-lures

Semio-chemically mediated interactions between insects and gut bacteria particularly from the families Enterobacteriaceae, Pseudomonadaceae and Bacillaceae (Leroy *et al.*, 2011) highlight the significance of bacterial cue-lures against tephritids (Robacker and Lauzon, 2002; Drew and Fay, 1988; Robacker and Bartelt, 1997). Despite knowing that fruit flies are attracted to gut bacteria isolates, relatively few studies have been evaluated in this aspect. One possible reason could be that recognition of attractant chemicals produced by bacteria has been nearly as challenging as identifying the nature of associations between bacteria and host fly; it may also attract beneficial insects (Robacker, 2007; Leroy *et al.*, 2011).

However, this finding raised a question as to why tephritid fruit flies searched or are attracted to bacteria. Various possible reasons could include the search for bacteria as food (Drew and Fay, 1988), replenishing gut microbiota, detoxifying allelochemicals in the diet (Lauzon, 2003), or as indicators of food (Robacker and Moreno, 1995). In the last century, it was hypothesized that ammonia produced by bacteria was the reason of attractiveness to fruit flies (Jarvis, 1931; Gow 1954). These studies have provided fruitful information for the development of food-odour *A. ludens* (Robacker and Warfield, 1993) and *C. capitata* lures (Heath *et al.*, 1995). Field trials of bacteria cues prepared from *P. putida* (isolated from foregut of *B. oleae* adults) exhibited more attractive potential to *B. oleae* adults compared with the commercial baits, e.g., Elkofon-type and nitrogen based traps baited with protein compounds and hydrolysed protein (Buminal®), respectively. Both male and female adults were attracted to bacterial cue traps (Sacchetti *et al.*, 2007).

Robacker and Bartelt identified volatile chemicals produced by *K. pneumoniae* and *C. freundii* cultures, which attract *A. ludens* (Robacker and Bartelt, 1997). Wang *et al.* (2014b) described the attraction potential of cultivable gut bacterial communities to *B. dorsalis*. However, autoclaved supernatants revealed more attraction to *B. dorsalis* compared to whole LB broth or filtered supernatants (Wang *et al.*, 2014*a*,*b*). This finding might be attributed to the formation of attractive or heat-stable chemicals during autoclaving, and one or more of the chemicals seemed to be an amine as previously reported (Kai *et al.*, 2009; Robacker and Flath, 1995). Among various bacterial isolates from laboratory and field-collected *B. zonata*, only *Enterobacter cloacae* and *K. pneumoniae* showed the maximum attraction across different age groups of flies (Reddy *et al.*, 2014). Gut microbiota can also be involved in the production of certain signalling compounds, such as cuticle hydrocarbons that work as pheromones; for example, in *D. melanogaster*, gut microbes affect the mate choice and flies are attracted to mates with conspecifics that have a similar gut microbiota (Sharon *et al.*, 2010). The interesting results of above studies however lack definitive evidence and represent a priority for future research or may be implied for the development of biocontrol agents or cue-lure baiting from gut bacterial isolates as proven in economically important tephritid flies (Gow, 1954; Robacker and Bartelt, 1997; Robacker and Lauzon, 2002).

Knowledge gaps

Many of the factors that potentially influence the host–microbiome interactions via antagonistic or synergistic mechanism remain incompletely characterized. Underpinning the knowledge gaps may lead to more sustainable and durable solutions to

https://doi.org/10.1017/S0007485319000853 Published online by Cambridge University Press

tephritid-associated crop damage, worldwide. The high priority knowledge gaps are outlined below.

Combination of incompatible insect technique (IIT) and SIT

Gamma-radiation damages the host intestinal floral community and reduces the efficiency of mass-reared sterile males used in SIT. To overcome this problem, the combination of IIT with SIT in addition to more favourable lower radiation doses could be used in the future (Bourtzis and Robinson, 2006). In IIT, the outcome achieved is the crossing sterility between infected males with females that are either infected or uninfected with a different and incompatible *Wolbachia* strain (candidate bacterium for IIT) (Riegler and Stauffer, 2002). This facultative symbiont *Wolbachia* strain, which is commonly known to influence the host reproduction by cytoplasmic incompatibility (CI), has captivated the attention of many researchers. CI is a phenomenon of reproductive incompatibility that results in eggs and sperm being unable to form viable offspring caused by intracellular bacteria, such as *Wolbachia*, that resides in the cytoplasm (Yen and Barr, 1971). The first implication of IIT for naturally infected *R*hagoletis *cerasi* in the field was tested as a substitute to radiation-based SIT (Riegler and Stauffer, 2002). A study reported that trans-infection of *Aedes albopictus* with *Wolbachia* strains wPip generated from *Culex pipiens* resulted in the significant reduction of hatching rates (Fu *et al.*, 2010; Atyame *et al.*, 2011). Similarly, CI was associated with the spread of *Wolbachia* variant *w*Ri in *D*rosophila *simulans* in California via a bistable wave, in which infection tend to increase only once the infection becomes sufficiently common to offset defective maternal transmission and infection costs (Kriesner *et al.*, 2013). Currently, *Wolbachia* infections have been introduced into populations of mosquitoes and other insects for disease suppression (Kriesner *et al.*, 2013). Depending on the rapidity with which *Wolbachia* adapt to novel hosts, its spread after artificial introduction to target tephritid species may be greatly enhanced in future.

Harnessing gut bacteria to promote the efficiency of mass-reared flies

Previous studies have reported that sterilized males are less competitive in mating with wild females and thus have disadvantages compared with natural wild male population. To date, limited research has suggested that probiotics or bacterial inoculations at the larval or adult stage could enhance the mass-rearing efficiency of sterile males (Niyazi *et al.*, 2004; Ben-Ami *et al.*, 2010). We have summarized some interesting examples of fitness improvement of irradiated sterile males achieved by feeding gut-symbionts enriched diet (for details see 'Probiotics used in mass-reared SIT' section). Future strategies based on harnessing commensal gut bacteria inoculations to sterilized insects should be considered to sustain and promote the effectiveness of tephritids pest control.

Symbiont-mediated stress resistance

Although we have reviewed some important findings of gut microbiota functions to their host fitness and performance, our recent information in this regard remain inadequate. For instance, stress affects various biochemical regulatory systems and is considered as the non-specific response of organism to varying environmental demands. Insects are regularly exposed to unfavourable environments, including cold, heat, ultra-violet stress, lack of food resources, insecticides exposure, parasites and infectious diseases or pathogens. In particular, gut microbiota could provide a wide range of beneficial effects on many systems of the host, including survival, development, reproduction, energy metabolism and immune function. It has been previously reported that the gut bacterial association can improve the different fitness parameters of host via providing essential nutrients and/or by maintaining the host energy metabolism under normal environmental conditions (Ben-Yosef *et al.*, 2010; Du *et al.*, 2012; Hamden *et al.*, 2013). However, we pose some questions. Do gut symbionts have the potential to improve host fitness under environmental stress conditions? What is the impact of gut microbes on the cellular mechanisms and biosynthetic pathways of host? Are gut microbes capable of producing major metabolites/essential nutrients in stressed environments in the presence of gut microbes to improve host fitness? Combining some novel tools, including NGS, transcriptomics and/or metabolomics analysis, future experimental work is needed to explore the mechanisms underlying the symbiont-mediated resistance to environmental stress conditions.

Possible applications of gut bacteria for the management of fruit flies

Paratransgenesis

Gut symbionts could help to overcome some of the transgenesis limitations. The vast diversity of gut bacteria associated with tephritids represents a valuable source to recognize activities that could be harnessed for pest control strategy. Genetically modified symbionts can be used as vehicles to specifically express foreign traits, which interfere with pathogen development and attempts to eliminate it from vector populations. This type of pest control technique is termed as paratransgenesis. For example, midgut bacterial species, e.g., *Sodalis glossinidius*, *Asaia* sp. and *P*antoea *agglomerans* in mosquitoes and tsetse flies, have been considered as suitable *in vivo* drug delivery vehicles to control vector borne diseases (Favia *et al.*, 2007; Aksoy *et al.*, 2008; Bisi and Lampe, 2011).

Despite this limited progress in other insects, no transformed symbionts have yet been implied in tephritid pest control, and the efficiency of paratransgenic methods in the environment also remains questionable. However, evaluation of environmental effects and risk assessment are intrinsic challenges associated with the release of genetically modified organisms. To date, it is uncertain whether transformed symbionts can substitute non-transformed symbionts in natural field populations; however, no fitness deficits due to genetically modified symbionts have been reported in the literature. Other demanding challenges include species-specific approaches to ensure the compatibility between bacterial delivery vehicles and host insect.

Entomopathogenic gut bacteria

Entomopathogenic gut bacteria have insecticidal potential and thus can be used to control pest species. Currently, the release of entomopathogenic bacteria producing insecticidal toxins is a common method in various agricultural pest control systems (excluding tephritid flies), such as *Bacillus thuringiensis*, *Photorhabdus luminescens* and *Xenorhabdus nematophilus* (Becker, 2000; Christou *et al.*, 2006). An interesting example is *Pseudomonas* spp. isolated from the gut of *C. capitata* and

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reported as potential pathogenic species for the host (Ben-Ami *et al*., 2010). We have summarized earlier work of spore-forming gut bacterial entomopathogens, such as *Bacillus* spp. and *Paenibacillus* spp., and non-spore forming bacteria that belong to the genera *Pseudomonas* and *Serratia* sp. reported from different tephritids guts (Table S1). However, future research is needed to explore the pathogenic roles or insecticidal toxin complexes produced by these entomopathogenic gut bacteria in their hosts. Using entomopathogens as biopesticides could play a critical role in IPM against several tephritid pests.

Conclusions

The microbiome is ubiquitous in tephritid fly guts and has pervasive impacts on multiple characteristics of host biology. Consequently, gut bacteria should be included as candidate factors affecting many aspects of host fly biology. Luckily, the tools to study these associations are gradually becoming accessible, including methods to quantify and identify gut microbiome, their functions and their interactions with physiological systems of host. A few aspects of fly–microbe association have stable experimental foundations, but others are still contentious. Of particular interest for future research are the mechanisms by which gut bacteria influence the insect resistance to environmental stress, pathogens, phytotoxins and insecticides. New developments in symbiont-based pest control techniques are on-going, such as paratransgenesis (Wang and Jacobs-Lorena 2017), which requires genetic modifications. Applied motivations are required for the manipulations of gut microbes to improve higher quality production of mass-reared sterile insects for SIT applications in an economical manner and the development of attractants for baiting or lure-and-kill strategies.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0007485319000853

Data. All data included in this study are publicly available because it is a review paper, in which data have been published already.

Author contributions. HZ conceived idea of compiling review and MFR and ZY completed first draft. SB and ZC prepared table and helped in writing. Finally, HZ reviewed the manuscript and critically revised it as per the current scenario. All authors read and approved the final manuscript.

Financial support. This work was supported by the National Natural Science Foundation of China (Nos. 31872931 and 31572008), National Key R&D Program of China (No. 2017YFD0202000), the earmarked fund for the China Agricultural Research System (No. CARS-26), International Atomic Energy Agency's Coordinated Research Project (No. D42016) and Fundamental Research Funds for the Central Universities (Nos. 2662019PY055 and 2662015PY129).

Conflict of interest. The authors declare that they have no competing interests.

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