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REVIEW

Midgut microbial diversity and their role in insect pest management

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ABSTRACT. Insects, with over a million species, exhibit intricate associations with microorganisms, particularly in their gut microbiota. The insect gut microbiota, comprising bacteria, fungi, viruses, and protozoa, significantly influences nutrient digestion, metabolism and immune system modulation. From harmful parasites to beneficial mutualists, symbiotic associations impact insect development and adaptability, with specific microbial communities highlighted across various species. The composition of insect gut microbiomes, shaped by factors like insect development and ecological conditions. Additionally, insect gut microbes serve as taxonomic markers, aiding accurate species identification, even in challenging taxonomic groups. The potential of gut microbes in pest management is explored, spanning biopesticides, symbiotic relationships for pest suppression and microbial endophytes in plant defense. Advances in microbial genomics enable precision targeting within the insect gut microbiome, offering tailored interventions and emphasizing ecological considerations for sustainable deployment. In summary, this detailed understanding of insect-microbe interactions holds promise for innovative and sustainable pest management strategies, revolutionizing approaches to agriculture and ecological management. This review explores the diverse roles of midgut bacterial diversity in insect pest management, covering physiological aspects within the insect host and ecological implications for pest populations.

Keywords: insects; bactéria; gut microbiota; sustainable agriculture; pest management.

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Introduction

In the realm of biodiversity, insects stand out as the most numerous group, boasting a staggering array of over a million species that thrive in nearly every conceivable habitat. Given their global ubiquity, insects engage in diverse associations with microorganisms such as bacteria, archaea, viruses, fungi, protozoa, nematodes and multicellular parasites (Kaltenpoth & Florez, 2020). These microbe-insect interactions can take on various forms, ranging from symbiotic and pathogenic to vectorial relationships. Notably, insects have established a crucial and intricate symbiotic bond with their gut microbiota, a relationship that has proven to be a pivotal evolutionary adaptation for their survival in challenging environments (Gupta & Nair, 2020). The insect gut microbiota demonstrates a diverse spectrum of microbial associations, ranging from potentially harmful to obligatory mutualistic relationships (Mondal et al., 2023). A study displayed that the gut of *Apis mellifera* L. diverse group of bacteria among the most dominant species are, two different species of *Lactobacillus,* one species of *Bifidobacterium, Snodgrassella alvi* and *Gilliamella apicola* (Douglas, 2018). Further the gut bacteria of *Antheraea assamensis* Helfer, *Bombyx mori* L., *Dendroctonus rhizophagus* Thomas & Bright*, Helicoverpa armigera* Hübner, *Plutella xylostella* L. are associated with various enzymatic activities like hydrolase of cellulose, esters, lipids, pectin, starch and xylan (Jing et al., 2020). Similarly, the mosquitoes (*Anopheles stephensi* Liston*, A. gambiae* Giles and *A. albimanus* Wiedemann) gut contains the bacterial species such as *Enterobacter agglomerans, Flavobacterium* spp. *Pseudomonas cepacian* in abundant number (Pumpuni, DeMaio, Kent, Davis, & Beier, 1996). But, the ecologically or geographical location wise the most dominant bacteria species in *A. gambiae* and *A. funestus* Giles are *Enterobacter agglomerans* and *Escherichia coli* (Straif et al., 1998). Further, by using bacterial 16s RNA the midgut microbiota of *Dactylispa xanthospila* Gestro were isolated using high-throughput platform, Illumina MiSeq. The results displayed that, the gut microbiota belongs to 30 phyla, 64 classes, 135 orders, 207 families and 369 genera. Among all the phyla, the most dominant one is Proteobacteria (91.95%), Bacteroidetes (3. 44%) and Firmicutes (2.53%). Families such as Enterobacteriaceae, Caulobacteraceae, Rhizobiaceae, Sphingomonadaceae and Comamonadaceae, representing rich species composition 69.51, 5.24, 4.61, 4.23 and 2.67%, respectively (Cui, Guo, Wang, Duffy, & Dai, 2021).

Symbiotic microorganisms within the insect gut play various vital roles (Figure 1), such as aiding in food digestion, produce essential nutrients that may be deficient in the diet, boosting the host immune system to fend off pathogens, breaking down phytotoxins and pesticides, producing antibiotics, and participating in nutrient competition (Table 1) (Gupta & Nair, 2020). Further, they act as natural defense system, resist the heat stress, make availability of the nutrition and resistance to pathogens and toxins (Figure 1) (Mogren & Shikano, 2021; Pons et al., 2022). Importantly the microbes evolve faster than insects mutualistically, that results in pesticides adaption by the insects (Siddiqui et al., 2022). The bacteria displayed the breakdown of organophosphate compound chlorpyrifos, dimethoate and ethoprophos (Gunstone, Cornelisse, Klein, Dubey, & Donley, 2021), these bacteria may be present in the environment and that will be absorbed by insect during the feeding activities (Kikuchi, Hosokawa, & Fukatsu, 2007). Multiple studies highlighted that the secondary metabolites synthesised by the gut microbiota play a major role in insect interaction (Shang et al., 2021). Symbiotic relation of microbes helped in adoption of insects to unbalanced food sources namely blood or plant sap and new or altered ecological niche (Sudakaran, Kost, & Kaltenpoth, 2017). Sometimes these symbiotic bacteria disturb the disease-causing vector that act notable target for disease management (Ricci et al., 2012). Most of the insects associated with symbiotic bacteria feed on the nutritionally poor and hard to digest food source (Salem & Kaltenpoth, 2022) and the most studied symbiotic bacteria is *Buchneria aphidicola* in aphids those having their association from 200 million years (Baumann, 2005).

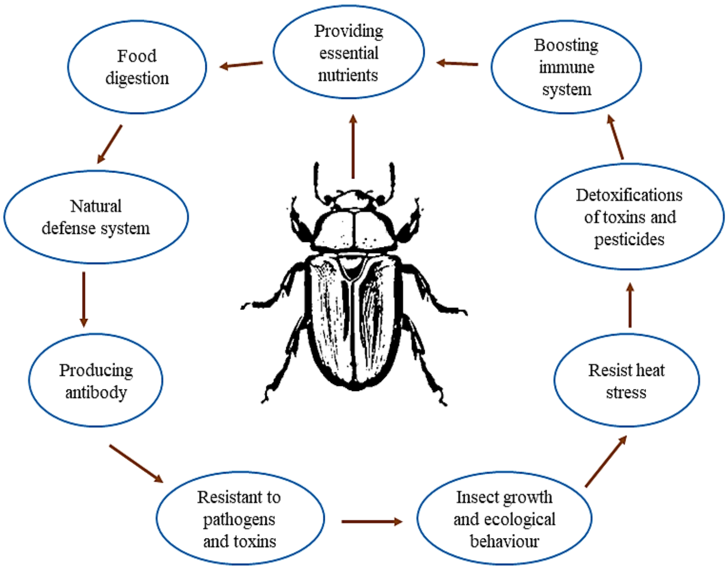

Figure 1. Important role played by gut-microbiota in insect physiology Microbial Diversity in insect gut.

This knowledge, in turn, holds promise for the formulation of innovative strategies such as biotechnologically driven product in the realm of insect pest management (Arora & Douglas, 2017; Yongqi, Xie, Lan, & Sun, 2019). For instance, the *Bacillus thuringiensis* (Bt), a gram-positive soil bacterium, synthesise insecticidal proteins that have been harnessed for the devising the environmental friendly pest control strategies (Crickmore et al., 1998). These proteins, when ingested by susceptible insect larvae, exert their toxic effects primarily in the midgut, disrupting cellular integrity and leading to the death of the insect (Bravo et al., 2013). Further, the mutualistic symbiosis act as promising mechanism where bioactive compound and novel enzymes can use potentially in the area of industry, medicine and environment (Yongqi et al., 2019).

This review explores the multifaceted roles of midgut bacterial diversity in insect pest management, encompassing both the physiological aspects within the insect host and the ecological implications for pest populations. By synthesizing current knowledge and delving into the potential applications for sustainable pest control strategies, this review aims to throw a light on the intricate relationships between midgut bacteria and their insect hosts.

Table 1. Role of different bacteria and functions.

S. No.	Bacteria	Role
1	*Enterococcus faecalis*	Digestion and nutrient metabolism
2	*Lactobacillus plantarum*	synthesis of essential vitamins and supports insect development
3	*Wolbachia* spp.	insect reproduction
4	*Spiroplasma*	insect physiology and development
5	Bifidobacterium	carbohydrate metabolism and nutrient utilization
6	*Serratia marcescens*	nitrogen recycling and may influence the host's susceptibility to pathogens
7	*Pantoea agglomerans*	Modulates the insect immune response and affects susceptibility to microbial insecticides
8	*Enterobacter* spp.	cellulose digestion and contributes to the breakdown of complex plant materials
9	Bacteroides	degradation of complex polysaccharides
10	*Acetobacter tropicalis*	Impacts insect metabolism and contributes to the breakdown of organic acids
11	*Xenorhabdus nematophila*	symbiotic associations with nematodes, influencing insect-pathogen interactions
12	*Yersinia pestis*	Associated with fleas and plays a role in the transmission of plague
13	*Streptococcus* spp.	Contributes to the digestion of complex carbohydrates in the insect midgut
14	*Clostridium* spp.	Involved in cellulose degradation and contributes to the insect's ability to utilize plant materials
15	*Micrococcus* spp.	May influence insect immune responses and gut homeostasis

References: Goodrich-Blair and Clarke (2007); Hinnebusch et al. (2017); Engel and Moran (2013).

Insect midgut microbiota

The insect midgut is a dynamic ecosystem that hosts a diverse and complex community of microbes, contributing significantly to the overall health and physiology of the host insect. This intricate assembly of microorganisms plays pivotal roles in nutrient digestion, metabolism and immune system modulation, shaping the complete fitness of the insect.

The diversity of insect midgut microbes varies with taxonomic groups, including bacteria, fungi, viruses and protozoa. These microorganisms have adapted to the unique physiological and biochemical conditions of the insect digestive system, forming intricate symbiotic relationships with their hosts. High-throughput sequencing technologies have unveiled the vast diversity within the insect midgut, revealing many unknown microbial species and functional capacities (Engel & Moran, 2013). For instance, honey bees (*Apis mellifera* L.) harbor a complex microbial community in their midgut, including *Gilliamella*, *Snodgrassella* and *Frischella*, which play roles in nutrient metabolism and immune system development (Kwong & Moran, 2016). Termites possess a highly specialized hindgut with microbial symbionts like *Trichonympha*, *Fibrobacter* and *Ruminococcus*, crucial for cellulose digestion. Similarly, *Drosophila* fruit flies have a diverse midgut microbiota, featuring genera like *Acetobacter* and *Lactobacillus* that contribute to nutrient metabolism (Broderick et al., 2014). Mosquitoes, exemplified by *Aedes aegypti*, may carry *Wolbachia* in their midguts, influencing pathogen transmission (Hughes et al., 2014). Cockroaches, including *Blattella germanica* L. host bacteria like *Blattabacterium*, essential for cellulose digestion (Sabree et al., 2009). Even butterflies, such as *Heliconius* species, exhibit specific gut microbial communities implicated in plant metabolite detoxification (Hammer et al., 2014). A study using 218 insect species from 21 taxonomic order adopting 16S pyrosequencing revealed that the most dominant group of gut microbiota in insect was Proteobacteria (62.1 %) that includes Wolbachia (14.1 %) and Formicutes (20.7%) (Yun et al., 2014). This indicates that the insect gut contains one or more microbiota to enhance their digestion activities.

Bacterial dominance

Bacteria are often the predominant members of the insect midgut microbial community. Families such as Enterobacteriaceae, Lactobacillaceae and Bacteroidaceae are frequently encountered across various insect species (Table 2) (Hadapad, Shettigar, & Hire, 2019). These bacteria contribute to critical functions, including nutrient processing, digestion of complex polysaccharides, pathogen resistance, physiology, detoxification and the synthesis of essential vitamins (Table 1) (Dillon & Dillon, 2004). However, the functionalities vary with cultivable bacteria and free leaving or midgut-colonising bacteria (Jing et al., 2020). The cultivable bacteria from *Antheraea assamensis*, *Bombyx mori, Dendroctonus rhizophagus, H. armigera* and *P. Xylostella* displayed the enzymatic hydrolyzation of lipids, startch, cellulose, pectin, esters and xylans. All these were identified based on the invitro studies using the cultivable bacteria and it may differ with free leaving or midgut colonizing bacteria (Ohbayashi et al., 2019; Jing et al., 2020b). The insect orders *viz.,* Coleoptera, Diptera, Hemiptera and Lepidoptera consist of several diverse microbiotas namely *Wolbachia, Symbiotaphrina, Staphylococcus, Pseudomonas, Microbacterium, Lysinibacillus, Lactobacillus, Lachnospiracease, Enterococcus,* *Clostridium, Citrobacter, Exiguobacterium, Burkholderia, Arsenphonus, Aeromonas, Actinobacteria* and *Acetobacter*, play a vital role in insect metabolism and very importantly detoxification of the different insecticides (Siddiqui et al., 2022). The termites gut contains nearly 90% of bacteria and archaea populations which help the various physiological activities (Hongoh, 2010).

Table 2. Bacterial species in different insects gut.

Bacterial Family	Examples of Genera/Species	Insect Hosts
Enterobacteriaceae	*Escherichia, Klebsiella, Enterobacter*	Honey bees, Fruit flies, Mosquitoes
Lactobacillaceae	*Lactobacillus, Enterococcus*	Honey bees, Fruit flies, Termites
Bacteroidaceae	*Bacteroides, Prevotella*	Honey bees, Fruit flies
Spirochaetaceae	*Treponema, Spirochaeta*	Termites, Cockroaches
Firmicutes	*Clostridium, Bacillus*	Honey bees, Fruit flies, Butterflies
Bifidobacteriaceae	*Bifidobacterium*	Honey bees, Beetles
Wolbachia	*Wolbachia*	Mosquitoes, Butterflies
Flavobacteriaceae	*Flavobacterium*	Fruit flies, Mosquitoes
Rickettsiaceae	*Rickettsia*	Ticks, Lice, Fleas

References: Kwong and Moran, (2016); Douglas (2015).

Classification of Insects–Bacterial interaction

There are several mechanisms involved in insect bacterial interaction, the primary one is commensalism, for examples the galleries of bark beetle provide nutrients and shelter for various insects and microbial commensals without significantly impacting the fitness of the bark beetles themselves (Stephen, Berisford, Dahlsten, Fenn, & Moser, 1993). Similarly, parasitic interactions in the insect-microorganism realm, often involve bacteria that exploit their hosts for nutrients and resources, potentially causing harm to the host organism (Drew, Stevens, & King, 2021). The parasite is completely dependent on the host for metabolic activities, without host parasite has zero fitness but it is more in host without the parasite (Combes, 2001; Goater, Goater, & Esch, 2014). Some well-known examples of parasitic bacterial interactions in insects are *Wolbachia* in insects that infect a wide range of arthropods, including insects. It is known for altering the reproduction of its host to enhance its own transmission (Werren, Baldo, & Clark, 2008). Similarly, Spiroplasma in *Drosophila* influences the host's reproduction and physiology (Jaenike, Unckless, Cockburn, Boelio, & Perlman, 2010). Further, the pathogenic interaction like how microorganisms survive and interact within their host organisms, requires a high degree of adaptation (Pandey, Deka, Varshney, Cheramgoi, & Babu, 2021).

The next is mutualism, a cooperative relationship where both partners benefit. In the case of termites, they have evolved mutualistic associations with both protozoa and bacteria in their gut to aid in cellulose digestion (Nalepa, 2020). Unlike the parasitism, reciprocal advantages observed in the mutualism from each associated partner (Combes, 2005). For instance, presence of protozoa in termite gut, aiding in the digestion of cellulose. These protozoa break down complex plant materials into simpler compounds (Brune & Ohkuma, 2011). Similarly, bacterial genus *Treponema*, are important for nitrogen fixation and assist in the breakdown of complex polysaccharides in termites (Hongoh, 2010).

Final important one is the endosymbiotic relationships of the gut microbes with the insects that divided into two important sections. First one is obligate or primary endosymbionts, that is long-evolved symbionts crucial for host fertility and survival, transmitted vertically and enclosed in specialized cells (Simpson et al., 2015). Second one is facultative secondary symbionts which are more of latest associations, retaining the capacity to return to a free-living state. Usually transmitted vertically and occasional horizontal manner, for instance *Rickettsia* sp. in whiteflies and *Hamiltonella defensa* in sap-sucking insects (Caspi-Fluger et al., 2012). Several reports documented that, the plant toxin *viz.,* glycoside, alkaloid (caffeine), phenols and terpenoids, encountered by insect while feeding and those could be detoxified by gut symbionts (Itoh, Tago, Hayatsu, & Kikuchi, 2018). The identified saxA gene of *Delia radicum* (L.) could degrade the insecticidal toxin, isothiocyanate produced from cabbage (Welte et al., 2016).

Symbiotic associations

The diversity and association of insect midgut microbes observed beyond simple commensalism, with many species forming symbiotic associations with their hosts. These symbiotic relationships often confer adaptive advantages to both the microbe and the insect (Mondal, Somani, Roy, Babu, & Pandey, 2023). The

Candidatus, Erwinia dacicola is the first reported symbionts from the Tephritid fruit fly, *Bactrocerea oleae* (Rossi), provide the congenial environment for the midgut caeca (Petri, 1910; Ben-Yosef, Pasternak, Jurkevitch, & Yuval, 2014). Within the realm of symbiotic interactions, some bacteria function as pathogens or parasites, causing harm to their host, whereas others, termed mutualists, confer benefits (Wiesmann, Wang, Zhang, Liu, & Haney, 2023). The mutualistic interactions are prevalent in many insects, fostering a broad array of associations with microorganisms. The symbiotic bacteria play a vital role in enhancing resistance to parasitoids, high-temperature tolerance, defense against toxin synthesis and harmful viruses (van den Bosch & Welte, 2017; Mondal et al., 2023). These microorganisms significantly contribute to insect development by bolstering adaptability to diverse environments (Itoh et al., 2018). For example, *Rickettsia* sp. has been shown to enhance basic host fitness (Himler et al., 2011), aiding the host in surviving challenges from *Pseudomonas syringae* Van Hall, an entomopathogen in whiteflies (Hendry, Hunter, & Baltrus, 2014). Additionally, the bacterium *Hamiltonella defensa* influences host sex ratios by providing nutrients to whiteflies (Oliver, Russel, Moran, & Hunter, 2003). In various insect species, such as psyllids, tsetse flies and aphids the primary symbiont assumes a protective role and is responsible for synthesizing essential nutrients (Crotti et al., 2012). In case of whiteflies, specifically *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae), the *Candidatus Portieraaley rodidarum*

Costa serves as their principal symbiont, supplying vital carotenoids and amino acids, akin to other primary symbionts found in phloem-feeding insects (Sloan & Moran, 2012). *Buchnera aphidicola* Munson is another noteworthy example of a major symbiont, residing within bacteriocytes in the abdominal body cavity of almost all aphids. This symbiont contributes essential amino acids which are absent in the phloem sap diet of insects (Table 3) (Shigenobu, Watanabe, Hattori, Sakaki, & Ishikawa, 2000).

On the other hand, secondary symbionts are usually more diverse and show less host-specificity (van den Bosch & Welte, 2017). For examples *B. aphidicola*, bacteria not help in survival and reproduction of the aphids but helps in other services for the host insects (Liu et al., 2023). In aphids total nine secondary symbionts were identified till date *viz., Fukatsuia symbiotica, Serratia symbiotica, Regiella insecticola, Arsenophonus, Rickettsia, Hamiltonella defensa, Spiroplasma, Rickettsiella* and *Wolbachia* (Patel et al., 2019). Beyond their sheer diversity, the functional significance of insect midgut microbes is profound. These microorganisms contribute to nutrient acquisition by aiding in the digestion of complex dietary materials, such as cellulose and hemicellulose (Table 3) (Liu et al., 2023). Additionally, some microbes play essential roles in detoxifying harmful compounds and modulating the insects immune responses (Engel & Moran, 2013), highlighting their multifaceted contributions to host fitness.

Table 3. Functions of the midgut microbiota in insects gut.

Sl. No.	Insect species	Midgut microbiota function	Reference
		Primary symbionts	
1	Aphids, tsetse flies, and psyllids	Synthesising the vital nutrients and acts as protective agents	Crotti et al. (2012)
2	Whiteflies, *Bemisia tabaci*	Provide the essential amino acids and carotenoids in phloem-feeding insects	Sloan and Moran (2012)
3	Aphids	Provide essential protiens that are absent in the phloem sap	Shigenobu et al. (2000)
		Secondary symbionts	
1	Whiteflies	*Host fitness improved due to the presence of Rickettsia* sp. against *Pseudomonas syringae* Van Hall	Himler et al. (2011)
2.	Whiteflies	Sex ratio altered, by supplying the *Hamiltonella defensa* with nutrients	Shan, Luan, Liu, Douglas, and Liu (2019)

Composition of microbiome in insect gut

The insect gut consists of various bacterial phyla *viz.,* Actinobacteria, Alphaproteobacteria, Spirochetes, Bacterioidetes, Clostridia, Firmicutes, Gammaproteobacteria, Proteobacteria and Verrucomicrobia, which are having significant influence on the insect ecology (Colman et al., 2012; Gomes, Omoto, & Cônsoli, 2020). *Apis* and *Bombus* gut microbiota influence on the bees health and nutrient supply (Zheng et al., 2016). The species composition of the gut-microbiota affected by biochemical changes, available nutrient, insect development and intestinal region (Crotti et al., 2012). The bacterial composition in the insect body distributed in different part of the alimentary canal. In case of the *Cyclocephalla signaticollis* Burmeister (Coleoptera: Scarabaeidae) gut having various microbes having function of fermentation of the food materials present in the modified hind gut called fermentation chamber (Huang, Zhang, Marshall, & Jackson, 2010). In honey bees and termites, the bacterial species *viz., Bifidobacterium bifidum*, *Lactobacillus*, *Gilliamella apicola*, *Snodgrassella alvi*, harbour in digestive tracts (Hongoh, 2010; Douglas, 2015) and similarly, in sac-like structure in posterior midgut of *Murgantia cribraria* Fab. and *Riptortus pedestris* Fab. (Itoh et al., 2018), midgut crypts in plataspid stinkbug (Hosokawa, Kikuchi, Nikoh, & Fukatsu, 2012).

The diversity of bacteria, archaea, protozoa and fungi are more in the endoperitrophic space of insect midgut (Engel & Moran, 2013). The reason behind the difference in the composition of microbiota in gut due to the extension of the body cavity for collecting the left-over waste and providing optimum feeding space for ease activity of the microbes to increase their diversity and proliferation (Siddiqui et al., 2022). The culture dependent technique provides biased results, but the culture independent techniques uses the important techniques based on omics and molecular approach such as 16S rRNA and BLAST technique that provide more precise evidence on the species diversity in the insect gut (Erb & Kliebenstein, 2020). A study using 16S rRNA gene primer in the gut of *Rhodnius prolixus* Stål and *Melanoplus sanguinipes* Fab. revealed 109 and 106 bacterial densities were observed in their gut respectively (Eichler & Schaub, 2002). Further the density of bacteria in gut of *Drosophila melanogaster* Meigen was 105 (Ryu, Ha, & Lee, 2010) and in case of honey bees 109 was observed (Martinson, Moy, & Moran, 2012). An investigation on the microbial diversity in the gut of *Adelphocoris suturalis* across the different stages of insect life revealed that the first and second instar insect associated with diverse bacterial species. The phyla Firmicutes contains 9.43% and Proteobacteria of 87.06% was the most diverse group. Further the genus, *Erwinia, Staphylococcus* and *Acinerobacter* were dominant with ratio about 28.98, 5.69, and 4.54%, respectively (Xue et al., 2021). The results displayed that the, composition of the gut microbes differs with insect species, their feeding environment and acquiring capacity (Ren et al., 2023). In addition, application of the next generation high throughput sequencing provides new avenue to study the microbial diversity and ecology (Harishankar, Sasikala, & Ramya, 2013). Further it also helps in identifying the boon or bane of the acquired bacteria from the environment by insect, that can be device for developing the novel pest management tool for biological insect control.

Role of gut microbes in insect development and evolutions gut microbes in insect reproduction

Some gut microbes influence the reproductive biology of insect pests. Targeting these microbial interactions can lead to innovative approaches for population control. For example, manipulating the gut microbiota to induce sterility or disrupt reproductive processes in pests could offer a sustainable and species-specific method for pest management (Pérez-Brocal et al., 2006).

Microbiota-mediated nutrient regulation

Insect gut microbiota plays a pivotal role in nutrient acquisition and metabolism (Engel & Moran, 2013). Microbes aid in the digestion of complex polymers like lignin or cellulose, which are often indigestible by the insects own enzymes (Pal & Karmakar, 2018). By breaking down these compounds into simpler forms, gut microbes contribute to the nutritional content of the insects diet, influencing its growth, development, and reproduction (Engel & Moran, 2013). Insects cannot digest the metabolic complex created by gut-microbes except microbes themselves (Rosengaus et al., 2014). Gut microbe of *Buchnera* sp. present in the aphids gut helps in synthesis of amino acids intern provide good stand for the nutritional physiology of insects (Russell & Moran, 2006). Similarly, in the coprophagous and xylophagous insects, cellulose breakdown into simpler molecule for there nutrition and physiology (Singh et al., 2022). The microbial communities in the beetles gut break down the lignocellulose compound and extract the essential nutrients to the insect (Ceja-Navarro et al., 2019).

Microbiome-mediated induced systemic resistance

Insects with beneficial gut microbes can induce systemic resistance in plants against pest attacks (Figure 2) (Hacquard et al., 2015). The survey conducted in the cotton bollworm, *H. armigera*, gut microbiome revealed that the resistant to *Bt* due to the gut microbiota composition (Visweshwar, Sharma, Akbar, & Sreeramulu, 2015). The colonized gut associated bacteria after treating with the antibiotic in diamondback moth (*P. xylostella*) displayed differential susceptibility against chlorpyrifos (Xia et al., 2018). Similarly, reduced mortality was noticed in the mosquitoes colonized with the different types of commensal gut bacteria (Barnard, Jeanrenaud, Brooke, & Oliver, 2019). Using the 16S rRNA, analysis of gut microbiota of *Spodoptera* *frugiperda* Smith field and laboratory population displayed that, the field population degraded more pesticides and showed resistance to pesticides compared to laboratory individuals (Gomes et al., 2020). In case of *P. xylostella*, the gut symbiont *Enterococcus* sp. produce acetylsalicylic acid and vitamin C resulted in increased regulation of the antimicrobial peptides and that leads to the development of pesticide resistance (Xia et al., 2018). Identifying and altering the induced microbiota-mediated resistant mechanism insect pave the way for novel pest management strategies.

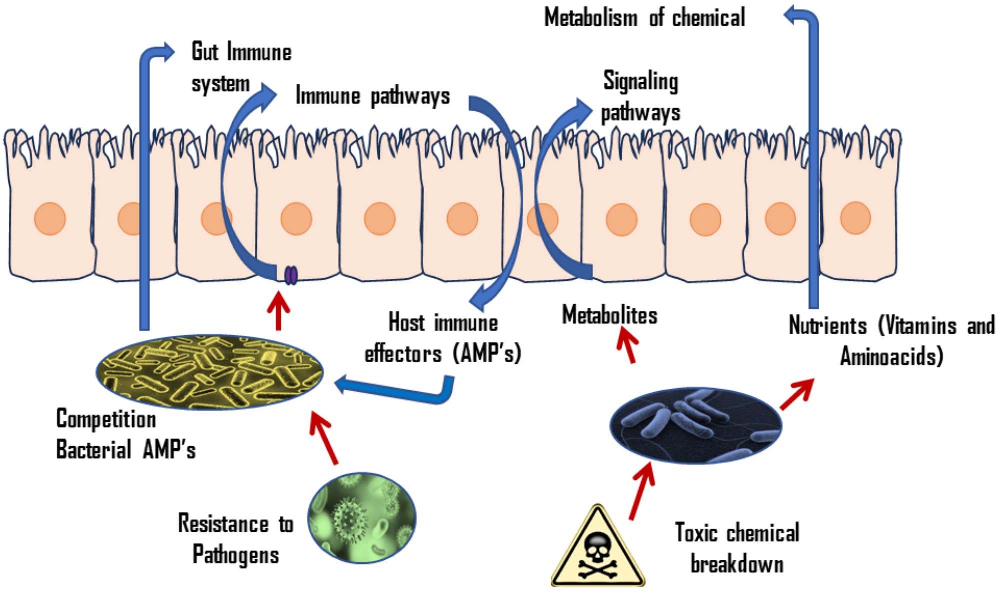

Figure 2. Gut microbiota role in immune and resistance mechanism (Siddiqui et al., 2022).

Host plant interactions and feeding behavior

The presence of specific microbial communities in the gut can enhance the insects ability to tolerate and exploit certain plant defenses, affecting its choice of host plants and potential damage to crops (Hansen & Moran, 2014), because the insect gut microbes contribute to the detoxification of secondary metabolites present in the host plants of insect pests. For instance, the bacterium presents in the gut of *P. xylostella* have capacity to detoxify the plant metabolites from the brassica (Xia et al., 2023). Similarly, the gut microbes of camellia weevils involved in degradation of the tea saponin present in *Camellia oleifera* seeds (Zhang et al., 2020). The host preference primarily governed by gut microbiota present on the plant surface (Zhu et al., 2023), for instance the thrips prefer damaged leaves compared to fresh leaves because prominent microbial on the leaf surface (De Vries, Vos, Jacobs, & Breeuwer, 2006).

Resistance to pathogens and parasitoids

Gut microbes contribute to the immune defense mechanisms of insect pests, influencing their resistance to pathogens and parasitoids by camouflage as well as immune against pathogens by modulating signaling pathways (Figure 2) (Rupawate et al., 2023). The symbiotic relationships between insects and certain microbes can confer protection against infections and potentially affecting the susceptibility of pest populations to biological control agents (Oliver, Smith, & Russell, 2010). For example, the gut microbiota diversity changed from *Enterococcus* to *Pseudomonas* in *S. frugiperda* after parasitized by *Cotesia marginiventris* Cresson (Wang et al., 2021a). In case of aphids, the facultative gut microbes influence the resistance against the parasitoids (Xu, Zheng, Liu, Ye, & Lu, 2009), for instance the *Serratia symbiotica* and *Hamiltonella defensa* defend the parasitic wasp, *Aphidius colemani* Viereckt o colonise (Brandt, Chevignon, Oliver, & Strand, 2017). Artificial inoculation of the *Buchnera aphidicola* in the pea aphids *Acyrthosiphon pisum* Harris reduced the parasitisation of *Aphidius ervi* (Haliday) (Oliver, Moran, & Hunter, 2005). The toxin pederin produce by gut microbes in *Paederus* beetle resist evade predates by wolf spider (Piel, Hofer, & Hui, 2004). The *Wolbachia* transferred from the *Drosophila* to mosquiotoes species reduces the more adoptive capacity against human pathogens like, West Nile virus, Dengue, Chikungunya, Zika virus and plasmodium (Caragata et al., 2019). *Streptomyces* harbor in *Philanthus triangulum* F. gut, reduces the fungal infection in the adults and young once (Ferrari, Darby, Daniell, Godfray, & Douglas, 2004).

Stress tolerance and environmental adaptation

The gut microbiota of insect pests plays an important role in host fitness by enhancing stress tolerance and aiding in environmental adaptation (Kikuchi et al., 2012; Ren et al., 2023). Removal of gut bacteria in oriental fruit fly using antibiotics changed the median survival time compared to conventional flies and the prominent influence was made by *Klebsiella michiganensis* BD177 (Raza et al., 2020). It implies that, the insects exposed to various stressors, such as temperature fluctuations or pesticide, may rely on their gut microbes for physiological support. This microbial contribution to stress resilience can influence the distribution and persistence of pest species in diverse ecological settings (Kikuchi et al., 2012).

Enhanced pesticide tolerance

Pesticides detoxifying and degrading bacteria present in nature and across the various insect orders such as Coleoptera (Akami et al., 2019), Hemiptera (Kikuchi et al., 2012), Diptera (Cheng et al., 2017) and Lepidoptera (Almeida, Moraes, Trigo, Omoto, & Consoli, 2017). Among the several species some gut microbiomes influence the insect resistance to pesticides. The functional part involved in such resistant may be enzymes and genes that altered the functionality of the applied compound (Bhatt, Ahmad, Joshi, & Bhatt, 2022). The gut bacteria regulate the toxin detoxification in insect by stimulating the NADPH oxidase 1 expression and intern deterring the Nuclear factor E-related factor 2 pathway with the help of reactive oxygen stimulant production (Jones et al., 2013). For instances, the rich gut microbiota composition in German cockroaches, American cockroaches and Oriental cockroaches play a critical role in insect physiology and pesticide resistance (Zhang et al., 2022). The gut Proteobacteria such as Burkholderia, Enterobacteria and Pseudomonada could break the insecticides like acephate, spinosad, chlorpyrifos, trichlorfon and lambda-cyhalothrin (Gomes et al., 2020). Likewise, the Firmicutes and Actinobacteria also can remove the pesticides from the insect system and environment (Ramya, Venkatesan, Srinivasa Murthy, Jalali, &Verghese, 2016). The pesticide like chlorpyrifos degradation and resistance by *P. xylostella* was prominent when the gut contains dominant population of *Enterococcus* sp. and the other hand presence of *Serratia* sp. in the gut increased the susceptibility to chlorpyrifos (Xia et al., 2018). The gut microbiota played a significant role in *Aedes albopictus* for deltamethrin resistance (Wang et al., 2021b). Understanding and identifying the mechanism of microbial induced resistance provide the new way to mitigate resistance problem by insects other than conventional insecticides, that consist of identification of microbiota influencing pesticide resistance and that can be used for improving the pest control measures (Siddiqui et al., 2022).

Gut microbes in biology, behaviour and identification of the insect species gut microbes for identification of cryptic insect species

The gut microbiota of insects often exhibits a unique composition that can serve as a distinctive microbial signature for different insect species. This microbial fingerprint has the potential to complement traditional morphological and molecular methods used in insect identification, providing an additional layer of specificity (Jing et al., 2020). In cases where traditional taxonomic methods face challenges, such as cryptic species complexes or incomplete morphological distinctions, the analysis of gut microbiota can provide a reliable means of species-level discrimination (Rota Stabelli, 2019; Xu et al., 2018; Jing et al., 2020). The gut microbes of *A. mellifera* has been extensively studied, revealing host-specific microbial signatures that can be used to distinguish between closely related honey bee species (Kwong & Moran, 2016). Studies on certain Lepidoptera have demonstrated the potential of gut microbial analysis for distinguishing between closely related species that exhibit minimal morphological differences (Paniagua Voirol et al., 2018). Fall armyworm gut bacteria are unique compared to corn earworm feeding on the same plant in the given time (Jones et al., 2019). Recent studies have demonstrated that the gut microbes of certain beetle species are highly specific, allowing for accurate identification at the species level based on the microbial composition (Xu et al., 2018). Further, insects often exhibit host-specific microbial associations, with certain microbial taxa being consistently associated with particular insect hosts. Analyzing these host-associated microbial patterns can aid in the accurate identification of insect species (Kwong & Moran, 2016), especially when considering cryptic or morphologically similar species.

Geographical and ecological variation

Insect gut microbiomes can show variation based on geographical location and ecological niches. This variation may be influenced by factors such as diet, climate and host plant preferences (Lim et al., 2023). Leveraging this information can contribute to the identification of insects in different habitats or regions (Muturi, Kim, Bara, Bach, & Siddappaji, 2017). The gut microbiota of certain mosquito species has been found to vary based on the geographic location, providing insights into the potential use of microbial profiles for geographical origin identification (Muturi et al., 2017). Notably the insect gut bacteria of the two kin species *Orthetrum lineostigma* Selys and *O. melania* Selys, were different, though they were nourished with same food diet, in contrary same gut microbiota observed in *O. lineostigma* and *Pseudothemis zonata* Burmeister (Lim et al., 2023). Typically, in case of honey bees the gut microbial species are not influence by the dominant gutmicrobes (Ge et al., 2021). *S. frugiperda* feeding on the same host plants having different gut microbiota compared to corn earworm (Jones et al., 2019). Presence of the gut microbiota in the insects resolve the variation based on the geographical and ecological niche.

Forensic entomology applications

Identification of the insect species and microbes associated with the decomposing of the dead carcass is more crucial for postmortem intervention in forensic science (Pechal et al., 2014). Due to the molecular mechanism and gene transfer as well mutation of the traits due to environmental factors in gut-microflora helps insect to degrade smoothly (Xia et al., 2018). The identification of the gut micro-biota helps to solve the various forensic challenges. For instances, with the help of gut-microbiota in blowfly, one could more precisely identify the time of death of an animal (Pechal et al., 2014). The bacterial species identified from the domestic swine carcasses monitored for 14 weeks displayed there were two groups *viz.,* Firmicutes and Gammaproteobacteria were prominent in mouth and rectum of the dipteran larvae (Iancu et al., 2016). This indicates that the presence of insects along with their gut microbiota resolve the most challenging case.

Pheromone production and communication

Gut microbes have been implicated in the synthesis and modification of insect pheromones, which are crucial for communication and mate attraction in many insect species (Brune & Dietrich, 2015). In bark beetle *Dendroctonus valens* LeConte*,* the gut bacteria in the eaten frass produce the some verbenone and multifunctional pheromones, that determine the host suitability and colonization (Lu, Hulcr, & Sun, 2016). There are several semiochemicals available in the market, but all the available products are not derived from insect alone, there are some important compounds which are derived from microbes or plant volatiles (Table 4) (Davis, Davis, Crippen, Hofstetter, & Tomberlin, 2013). Microbial volatile compounds may be produced by several means *viz.,* amino acid catabolism, fermentation, terpenoid biosynthesis and sulfur reduction (Choudoir, Rossabi, Gebert, Helmig, & Fierer, 2019). The compound produced from the gut microbes potential influence the insect chemical signals, that intern alter the population dynamics and mating behaviour (Brune & Dietrich, 2015). It clearly implies that the semiochemcials derived from the microbes have potential impact on the insect attraction and trapping, this study can be taken forward by researcher to identify the novel molecules to trap the insects and adding as a tool in IPM.

Behavioral responses to environmental cues

Gut-associated bacteria in insects helps in understanding the social interaction, chemical communication, growth and development by altering their odour profiles (Singh et al., 2021). Similarly, they influence on the insect oviposition, mating, long-term dispersal, change in temperature response, host searching and identification (Sharon et al., 2010; Ezenwa et al., 2012). The microbial altered pathways such as sensory and neurotransmitter circuits leads to change in the insect behaviours ranged from migration, diurnal pattern and foraging pattern (Wang & Kasper, 2014). Male killing due to feminization by bacterial symbionts, *Wolbachia* in insects is the more common behaviour changes (Stouthamer, Breeuwer, & Hurst, 1999) and it is the more common phenomenon between insects and microbes (Lewis & Lizé, 2015). The bacterial symbionts also alter the interspecific competitions in insects upon their invasion (Cheng et al., 2019). For instance, the gut-microbiome in *Drosophila melanogaster* influences the odorant-based foraging behaviour while searching the food source (Wong et al., 2017). Identifying the brain and microbiome interaction can act as potential model to study the neurological dysfunction and their possible treatments using the microbes (Liberti & Engel, 2020).

Table 4. Semiochemicals produced by gut-microbiota.

Sl. No.	Compound/process	Microbes produce Semiochemicals	Insects attracted	References
1	Repellent by secondary metabolites (primarily fabclavines)	*Xenorhabdus budapestensis*	*Aedes aegypti*	Kajla, Barrett-Wilt, and Paskewitz (2019)
2	3-methyl-1-butanol, phenol, 2,5-dimethylpyrazine, 2-phenylethanol and 2-methyl-1-propanol from fermented	*Citrobacter freundii*	*Anastrepha ludens*	DeMilo, Lee, Moreno, and Martinez (1996)
3	Increased production of acetoin	Genetically modified the acetic acid bacterium (AAB) *Komagataeibacter europaeus*	*Drosophila*	Ishii, Akasaka, Goda, Sakoda, and Fujiwara (2015)
4	Insect repellents. Geosmin	mold	*Drosophila melanogaster*	Stensmyr et al. (2012)
5	Dimethyl trisulfide and 2-phenylethanol	*Phoma* spp., *Fusarium* spp., or *Rhizopus* spp.) on chicken feces	oviposition by the housefly, *Musca domestica*,	Lam, Tsa, Labrie, Gries, and Gries (2010)
7	Phenolics (act as aggregation pheromone)	*Pantoea agglomerans, Klebsiella pneumoniae, Enterobacter*	*Schistocerca gregaria*	Dillon and Charnley (2002)
8	3-methyl-1-butanol and ammonia	*Enterobacter agglomerans* from infested larvae on fruits	Caribbean fruit fly (*Anastrepha suspensa*) females	Epsky et al. (1998)
9	Fermented compounds *viz.,* alcohols, ketones, pyrazines, phenols and acids	*Klebsiella pneumoniae*	Mexican fruit fly (*Anastrepha ludens)*	Lee, DeMilo, Moreno, and Martinez (1995)
10	Fermenting sugar-yeast mixture plus apple cider vinegar + 10% ethanol combination	Gut microbiota	*D. suzukii*	Lasa et al. (2017)

Advancement of insect gut microbes in insect pest management

The gut microbes play most vital role in the various insects, from their physiology to growth and development. Further, the presence of gut-microbiota pave way to utilize in various aspect of insect pest management, those as follows (Figure 3).

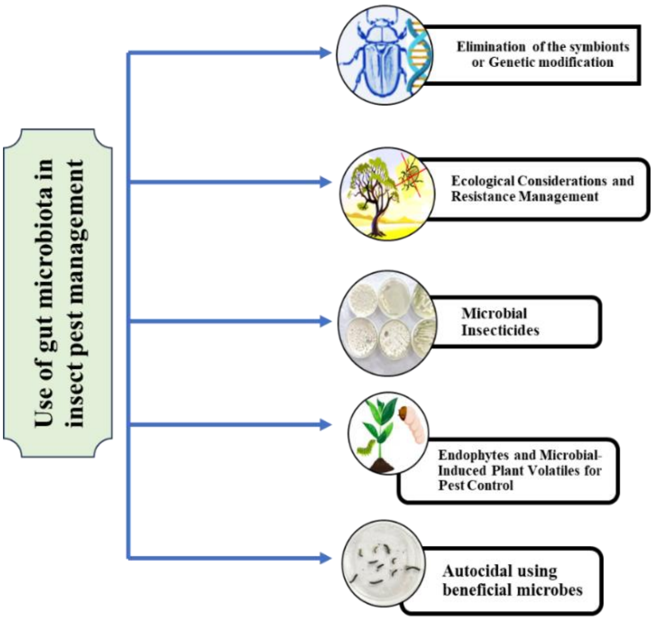

Figure 3. Various use of gut microbiota in insect pest management.

Biological control using gut microbes

The use of gut microbes as biopesticides and microbial insecticides is a promising avenue in pest management. Certain bacteria residing in the insect gut produce toxins harmful to pests, providing a natural means of control (Chalivendra, 2021). Some of the gut microbiota providing nutrient could be targeted and eliminated them, impair the growth and physiological conditions of the insects (Engel & Moran, 2013). Similarly, targeting the amino acid synthesizing microbe *Buchnera* sp. would act as best biopesticide agent (Russell & Moran, 2006), further manipulating the gut microbial community in the gut impair the nutrients availability and affect the mosquito growth (Wang et al., 2011) and disturbing the lignocellulose breaking microbes will affect the beetles physiology (Ben Guerrer et al., 2016). *Wolbachia*, a common intracellular bacterium found in insects, has been investigated for its potential to control mosquito populations by interfering with their reproduction (Hoffmann et al., 2011). Generally, the gut microbiota contributes the immune defense mechanism in the insect system and affecting them will certainly weaken the insect defense (Oliver et al., 2010). *Bacillus thuringiensis* (*Bt*) toxins have been widely employed in biopesticides to target specific insect pests, offering an effective and environmentally sustainable alternative to chemical insecticides (Chalivendra, 2021). Understanding these interactions is crucial for developing sustainable pest management strategies (Oliver et al., 2010). Exploiting the gut microbes of the Ichneumonid and braconid parasitoids while oviposition, they inject the microbes into the caterpillar system that intern reduce its defense and natural immune capacity (Kaltenpoth & Engl, 2014). This evolving field opens avenues for continued research and innovation, fostering a more sustainable and integrated approach to agriculture.

Symbiotic microbes for pest suppression

The gut symbionts present in hemolymphs and specialized cells provide various essential service in the insect host (Blow & Douglas, 2019). Harnessing naturally occurring symbiotic relationships between insects and specific microbes can contribute to pest suppression. Some insect species harbor symbiotic bacteria that produce antimicrobial compounds or interfere with the reproduction of pests (Frago, Dicke, & Godfray, 2012). Proteobacteria present in the insect gut degrade the secondary metabolites present in the plant *viz.,* alkaloids, glycosides, terpenes and phenolic compounds (Gomes et al., 2020), the elimination of this symbionts helps to suppress the insect. Further, the secondary or facultative gut symbionts in aphids alter the body colour, that prone the insect to predators and parasitoids (Xu et al., 2009). Technique like paratransgensis where modification of the gut microbiota using genome technique instead of insects (Rupawate et al., 2023), for example the gut symbiont *Rhodococcus rhodnii* manipulate genetically and reintroduced in the *Rhodnius prolixus* leads to reduced population of insect due to nutrient shortage (Taracena et al., 2015). Adopting concept like incompatible insect techniques like, use of gut microbiota to make compatible male for reproduction thereby manage the population growth (Rupawate et al., 2023). For instance, use of *Wolbachia* to manipulate the gut microbiota in insect by parthenogenesis or feminization or cytoplasmic incompatibility results in reduction of the male populations (Edenborough, Flores, Simmons, & Fraser, 2021). Adoption of this technique has the potential to reduce the relay on the chemical pesticide and promote the environmentally safe approach.

Microbial endophytes and microbial-induced plant volatiles for pest control

Gut microbes can indirectly contribute to pest management by influencing the plant's defense mechanisms (Berendsen, Pieterse, & Bakker, 2018). The aphids, *Hamiltonella defensa* Moran reduce the release of the volatile compound from the infested plant, that intern reduce the attack of the parasitic wasp to locate (Frago et al., 2017). The microbial endophytes residing within plant tissues can enhance the production of secondary metabolites that deter herbivores (Berendsen et al., 2018). For example, *Muscodor vitigenus* produce naphthalene by staying as an endophyte in tropical liana tree that repel the insects to colonize on the tree (Daisy et al., 2002). In plant system, conversion of compounds such as dihydrojasmone, cis-jasmone to (+) - (R) – 4 - hydroxydihydrojasmone and (-) - 4- hydrojasmone by *Penicllium, Aspergillus* and *Fusarium* act as repellent against aphids and other insect (Gliszczyńska, Gladkowski, Dancewicz, & Gabrys, 2015; Skorbiszewski et al., 2018). Similarly, the gut microbes release the volatile compound that may attract or repel the insect. This technique can be used as potential tool in attract and kill or push and pull strategies in IPM (Qadri, Short, Gast, Hernandez, & Wong, 2020). The volatile organic compound produce from the gut bacteria helps in behavioural attraction of the insect mutualistically for their egg laying and colony multiplication (Zhang, Zhang, & Xu, 2023). Understanding the mechanism of endosymbionts and gut microbiota with insects, can be used in the development of the resistant varieties and engineered insects for devising an environmentally safe pest control strategy.

Precision targeting through microbial genomics

Advances in microbial genomics allow for the identification and manipulation of specific genes within the insect gut microbiome (Harrison et al., 2018). Recently, adoption of the microbes in dsRNA treatment also recorded by several scientists. According to them, the RNAi technology coupled with gut-microbiota will enhance the pest control strategy (Xu et al., 2021). Further, it was identified that the microbiome will act as good medium for delivering the species-specific dsRNA for sustainable RNAi technology (Whitten & Dyson, 2017). This precision targeting enables the development of tailored interventions, such as genetically modified microbes designed to disrupt specific physiological processes in insect pests, providing a highly targeted and environmentally sustainable approach to pest management. CRISPR-Cas9 technology has been employed to modify the microbiota of certain insects, demonstrating the potential for precise control over host-microbe interactions (Harrison et al., 2018). For instance, the genome editing using CRISPR-Cas9 for disabling the expression of ompA gene in *Aedes aegypti* L. leads to reduced the production of biofilm from *Cedecea neteri* in the gut (Rupawate et al., 2023).

Ecological considerations and resistance management

Due to continuous exposure to pesticides by the insect, the gut microbiota develops a peritrophic layer consist of protein-carbohydrate medium and microfibrils, that intern reject or tolerate the toxic compounds under various metabolic process (Rumbos, Dutton, & Athanassiou, 2018). The altered peritrophic medium helps in releasing the nutrients, digestive enzymes and hasten epithelial cell from invaded microbes, all these process results in development of resistance to chemicals (Puri, Singh, & Sohal, 2022; Siddiqui et al., 2022). Regular exposure of the host gut microbes to the insects results in selection pressure, that may also leads to detoxifying or degrading the chemical compounds, that may leads to reduced susceptibility by host (Akami et al., 2019). In case of *Cletus punctiger* Dallas, fenitrothion is degraded by the gut-microbe, *Burkholderia* indicate that the regular exposure can leads to adoption by the insect and gut symbionts (Ishigami, Jang, Itoh, & Kikuchi, 2021). Similarly, the stored pests like, *Sitophilus granaries* L., *Tribolium castaneum* Herbst, *Rhyzopertha dominica* F. and *Trogoderma granarium* Everts showed resistance to phosphine fumigant due to presence of gut-symbiotic microbes that leads to failure in management of stored pests (Wakil, Kavallieratos, Usman, Gulzar, & El-Shafie, 2021). Hence, thorough understanding is required for integrating the microbial-based pest management strategies for effective and sustained control of insect pests. Further, the designed strategy should minimize the unexpected consequences like resistance development, damage to not-target organism and environment (Duron et al., 2008). So, continuous research on identification of gutmicrobiota and their impact on the insect behaviour is pivotal for developing the long-term pest management strategies which may have minimal risk to non-targeted organisms.

Conclusion

Insect physiology governed by various elements to function normally, among them the gut microbes plays a vital role in several insects species. Presence of the gut microbes in several insects helps perform the fundamental duties of the insects such as nutrient supply, host plant interaction, hormonal production, pesticicde resistance, stress tolerance and identification of the complex insect taxon. Positively, gut microbiota acts as biopesticides in the management of insect pest by without harming nature and natural ecosystems. Adopting the various use of midgut microbiota in agricultural practices helps in reduced pesticides usage leads to sustainable crop production.

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