



GUARDIANS OF THE INSECT REALM: SYMBIOTIC MEDIATION FOR HOST PROTECTION

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Symbiosis involves the coexistence of dissimilar organisms, with the symbiont referring to the organism residing in this mutually beneficial relationship. Insects consistently harbor microorganisms, typically non-pathogenic, that prove beneficial or even essential for the insect host's well-being. These microorganisms in the insect gut are commonly referred to as microbiota, acting as symbionts in the symbiotic relationship and constituting a significant portion of the insect's biomass, ranging from 1–10 per cent. Symbionts within insects can be categorized as ectosymbionts or endosymbionts based on their developmental site within the host. Additionally, they may be classified as primary or secondary symbionts depending on the host. In the intricate web of life, insects rely directly and indirectly on their microbiota throughout their life cycle.

ABSTRACT

The symbiont plays a crucial role in safeguarding its host from microorganisms, predators, parasites, and even conferring resistance against insecticides. Through the production of toxic compounds such as antibiotics or bacteriocins, symbionts can eliminate or impede the growth of parasites, while also competing with them for host resources. Furthermore, symbionts induce alterations in the host's immune responses, enhancing resistance to parasites or predators. Symbionts can also be used as a source of paratransgenesis. In honey bee, genetically engineered symbiotic bacteria have been used to combat the varroa mite. These paratransgenic symbionts can interfere with the ability of pathogens to infect bees by enhance the immune response. Importantly, symbionts contribute to the fitness of their host during infection without diminishing the fitness of the parasites. This is achieved by boosting host tolerance, thus highlighting the intricate and often advantageous dynamics of symbiotic relationships in the insect world.

Key words : Endosymbiont, Paratransgenesis, Protection, Symbiont, Xenobiotics.

Introduction

Symbiont refers to an organism living in symbiosis, while symbiosis means 'The living together of unlike organism'. The term symbiosis invented by Albert Frank in 1877 described "all the cases where two different species live on or in one another". Examples of symbiosis can be found in all kingdoms of life. The association between pollinating insects and plants is well known example of symbiosis. Commonly, the symbiont is smaller than its host. Insects consistently harbour microorganisms that are generally non-pathogenic, often proving to be beneficial or even essential for the well-being of the insect

host. Microorganisms present in the insect gut are usually called microbiota. It acts as a symbiont in a symbiosis relationship and accounts for up to 1–10 per cent of the insect's biomass. The relationship between insects and microbiota is significant for evaluating ecological features and feeding habits in insects. It plays important roles in insect physiology and behaviour, such as food digestion (Warnecke *et al.*, 2007), host nutrition (Engel *et al.*, 2012), immune response (Ryu *et al.*, 2008), pathogen defence (Dillon *et al.*, 2005), plant specialization (McLean *et al.*, 2011), mating preference (Sharon *et al.*, 2010), degradation of xenobiotics or confer resistance to

insecticides (Kikuchi *et al.*, 2012; Almeida *et al.*, 2017; Blanton and Peterson, 2020). Plant sap-sucking aphids (Baumann *et al.*, 1995) or blood-feeding tsetse flies (Rio *et al.*, 2003) diet having low protein, amino acid and vitamins (Moran *et al.*, 2008). These insects can use these minerals through symbiotic associations with microorganisms. The most common micro-organisms are the bacteria found in Dictyoptera, Isoptera, Hemiptera, Anoplura, Mallophaga, Coleoptera, Hymenoptera and Diptera. Among protozoans, flagellates are widely occurring in wood-eating cockroaches and termites (Honigberg, 1970; Yamin, 1979; Brune, 1998; Brune and Friedrich, 2000; Brune, 2006; Brugerolle and Radek, 2006). The yeast is found in some Homoptera, Coleoptera and actinomycetes in *Rhodnius*. Insects are directly and indirectly depending on symbionts. *Wolbachia* is the most common bacteria present in most of all insects (Hilgenboecker *et al.*, 2008; Weinert *et al.*, 2015). These are cytoplasmically inherited rickettsiae that are found in reproductive tissues (ovaries and testes) of a wide range of arthropods (Hertig and Wolbach, 1924). *Wolbachia* induced parthenogenesis, feminization, male killing and cytoplasmic incompatibility in various host (Stouthamer *et al.*, 1999; Werren *et al.*, 2008) and also inhibit apoptosis in parasitic wasp (Pannebakker *et al.*, 2007). Symbiosis is a broad term, it may be a Mutualism (+, +), Mutualistic interactions benefit both partners (positive effect on each) and therefore represent cooperative or mutually exploitative relationships. Commensalism (+, 0), is a relationship between different species where one organism gains benefits from the relationship and the other is unaffected. e.g., Sexton beetle (genus *Nicrophorus*) covered with mites. Parasitism (+, -), is a symbiont relationship between two organisms. Where one organism (the parasite) gets benefits from the other organism (Host) e.g., the varroa mite parasite on the honey bee. Competition (-, -), Many species compete for the same resources in an ecosystem. If one species has an abundance of resources and another doesn't both species could suffer and possibly die out. Amensalism (0, -), One organism is inhibited or damaged by the presence of the others, who do not benefit.

Symbionts may be ectosymbionts (e.g., *Pseudonocardia* sp. and *Streptomyces* on the body surface of fungus-growing ants) or endosymbionts (e.g., *Buchnera* present in the gut of aphids) according to the developmental site in the host and according to the host; they may be primary and secondary symbiont (Nation, 2009). Primary symbionts are obligate and obligatory symbionts that often are intracellular and may exist in specialized structures (mycetocytes, pouches, cavities)

and vertically transmitted by transovarial transmission and it is necessary for the development and reproduction of insects (Baumann, 2005) e.g., *Wolbachia* present in mosquitoes. Secondary symbionts are facultative, either horizontally or vertically transmitted, confer fitness and also increase survival or reproduction (Morrow *et al.*, 2014; Chrostek *et al.*, 2017) e.g., *Serratia symbiotica* present in aphids. Some symbionts are transmitted by both the ways, known as a mixed-mode transmission (Ebert, 2013).

The flagellates live in the hindguts of wood-eating cockroaches and termites and the bacteria live in the gastric caecae of the last segment of the midgut in plant-sucking Heteroptera. In *Rhodnius*, Actinomycetes live in crypts between the cells of the anterior midgut. The cell-housing symbionts are known as mycetocytes and these may aggregate together to form organs known as mycetomes and if bacterial symbionts then it is known as bacteriocytes (Tembhare, 1997; Maire *et al.*, 2020). According to the presence and colonization of symbionts in the insect gut, variation is observed in the various parts of the insect digestive system (Buchner, 1965; Chapman, 1998; Fukatsu and Hosokawa, 2002; Brune, 2010).

Effect of Symbionts on Insects

Directly and indirectly, insects depend on the microbiota in their life cycle. The overall functions of microbiota in insect life are presented in Table 1. Insects' diets are deficient in one or another of the nutrients and minerals to fulfill their requirements insect depends on the microbes present in their body. Insects that are sap-sucking and feed on xylem and phloem, are generally deficient in vitamins and amino acids and are rich in sugars (Redak *et al.*, 2004). Blood-feeding insects like *Glossina*, *Rhodnius*, bed bugs and ticks have a Vitamin B deficient diet and therefore depends on endosymbionts like *Wiggles worthia*, *Rhodococcus rhodnii* other symbionts to obtain sufficient B vitamins (Baines, 1956; Aksoy, 1995; Pachebat *et al.*, 2013; Duron and Gottlieb, 2020; Bonnet *et al.*, 2017; Hosokawa *et al.*, 2010; Michalkova *et al.*, 2014). Symbionts can also protect insects against pathogens, natural enemies, plant metabolites, insecticides and also from the harsh environments (Fig. 1) (Miller *et al.*, 2021; Frago *et al.*, 2012; Ceja-Navarro *et al.*, 2015; Barcoto *et al.*, 2020; Brumin *et al.*, 2011; Trivedi *et al.*, 2024; Phugare *et al.*, 2013).

Mechanism of Defensive Symbionts

Symbionts produce toxic compounds, such as antibiotics or bacteriocins, which may either kill the parasite or reduce its growth rate and it also, competes with parasites for host resources (Gerardo and Parker,

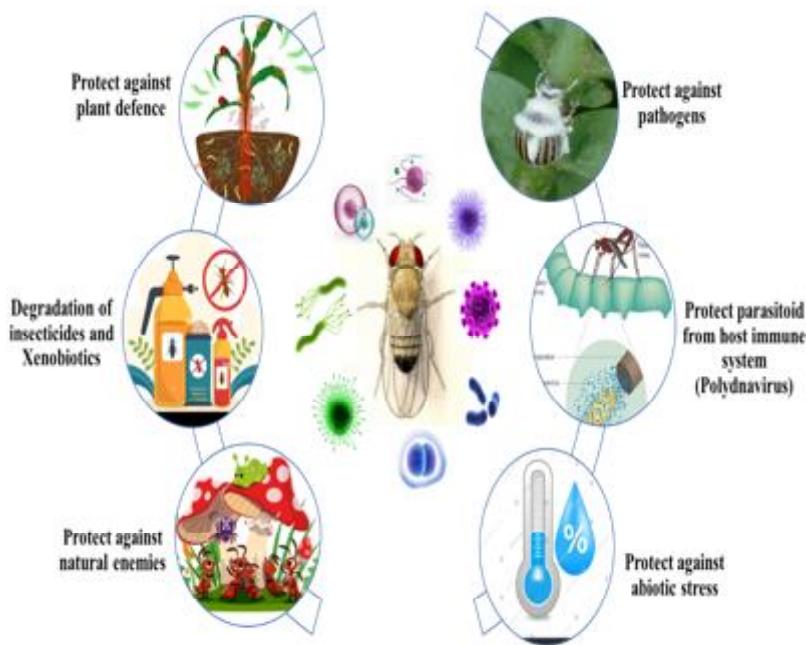


Fig. 1: Symbionts protect the insect host from different biotic and abiotic stress.

2014; Lombogia *et al.*, 2020). It induces changes in their hosts' immune responses that increase resistance to parasites or predators. e.g., in the tsetse fly, *Wiggles worthia* bacteria alter host immune responses such that they suppress trypanosome survival (Gerardo and Parker, 2014). *Wolbachia* activate toll immune pathway in mosquitoes, *Aedes aegypti* to inhibit dengue virus (Bian *et al.*, 2010; Moreira, *et al.*, 2009; Pimentel *et al.*, 2021). Symbionts increase the fitness of their host during infection without reducing the fitness of the parasites by enhancing host tolerance (Raberg, 2014; Rafaluk-Mohr *et al.*, 2022).

Protective Benefit Rendered to insect host by symbionts

Defence Towards Microorganisms

In the year 2009, Yoshiyama and Kimura isolated 35 bacteria from the gut of a Japanese honey bee, *Apis cerana japonica* and they found that out of 35 isolates, seven showed strong inhibitory activity against *Paenibacillus larvae* the causal agent of American foulbrood disease. Most of the symbiont bacteria belonged to *Bacillus* species and also, they reported that symbiont bacteria are absent in first instar larva while present in fourth instar larvae and Forager honey bees. An endosymbiont, *Walbachia* protected fruit flies from *Drosophila C* virus, *Nora* and flock house virus (Hedges *et al.*, 2008; Teixeira *et al.*, 2008; Brownlie *et al.*, 2009; Schissel *et al.*, 2021) and mosquitoes from filarial *Brugia pahangi* infection (Kambris *et al.*, 2009). Koch and Schmid-Hempel (2011) reported that a symbiont bacteria, *Gilliamella apicola* in honey bee and bumble bee gut

produces a biofilm on the ileum wall and provides a barrier to attachment or entry of gut parasite, *Crithidia bombi*. Actinobacteria produce secondary metabolites with antifungal activities (Oh *et al.*, 2009; Currie *et al.*, 1999; Van Arna *et al.*, 2016). Ant-associated *Pseudonocardia* inhibits *Escovopsis* more strongly than it inhibits other fungi (Cafaro *et al.*, 2011). According to Hendry *et al.* (2014), *Rickettsia* infection caused a significant decrease in the death rate related to exposure to the two *Pseudomonas syringe* (B728a and DC3000) strains. A bacterial strain, *Serratia Y1* infected *Anopheles stephensi* renders the mosquito resistant to *Plasmodium berghei* infection by activation of the toll immune pathway (Bai *et al.*, 2019). Symbiont bacteria, *Bombella apis* present in honey bee gut suppress the fungal pathogen, *Beauveria bassiana* and *Aspergillus flavus* by secretion of antifungal metabolites like 1 polyketide, terpene and aryl polyene (Miller *et al.*, 2021). A pellet-like structure is present on the legs of mealybugs, which harbours the fungus, *Penicillium citrinum*, protect against other fungal pathogens (Li *et al.*, 2024).

Effect on Predation and Parasitisation

A secondary symbiont inoculated aphids (*Acyrthosiphon pisum*) conferred resistance to parasitism by *Aphidius ervi* (Oliver *et al.*, 2003; 2005; Oliver and Perlman, 2020; Russell and Moran, 2006). Secondary endosymbiont, *Rickettsiella* increased the amounts of blue-green polycyclic quinines in pea aphids, causing a change in the body color of the host from red to green therefore ladybird beetles tend to consume red aphids on green plants and aphids escape from the predator (Tsukuda, *et al.*, 2010, 2014; Polin *et al.*, 2015; Nikoh *et al.*, 2018). Ladybird beetle, *Hippodamia convergens* larvae fed a diet of aphids (*A. pisum*) with facultative symbionts (*Serratia symbiotica* and *Hamiltonella defensa*) had significantly reduced survival from egg hatching to pupation and therefore had reduced survival to adult emergence (Costopoulos *et al.*, 2014; Bennett *et al.*, 2016).

Protect against Plant Defense

Insect symbionts degrade secondary metabolites of plants by interfering in the signal transduction pathway (Body *et al.*, 2013; Sugio *et al.*, 2015). Olive flies (*Bactrocera oleae*) larvae require bacteria (*Candidatus Erwinia dacicola*: Enterobacteriaceae) to develop in

Table 1 : Overall functions of Symbionts in insects.

Insect host species	Transmission route	Symbiont	Proposed roles in hosts	References
Plataspid bug (<i>Megacopta punctatissima</i>)	Maternal (egg capsule)	<i>Ishikawaella capsulatus</i> (Proteobacterium)	Nutrient provisioning (amino acids)	Fukatsu and Hosokawa (2002), Hosokawa <i>et al.</i> (2006)
Grasshopper (<i>Schistocerca gregaria</i>)	Acquisition from food	<i>Enterococcus, Serratia,</i> <i>Klebsiella, Acinetobacter</i>	Produce components of aggregation pheromone	Dillon <i>et al.</i> (2008, 2010)
Fruit fly (<i>Drosophila melanogaster</i>)	Acquisition from food	<i>Lactobacillus</i> spp., <i>Acetobacteraceae, Orbaceae</i>	Prime immune system, affect metabolism and mating preferences	Broderick and Lemaire (2012)
Gypsy moth caterpillar (<i>Lymantria dispar</i>)	Acquisition from food	<i>Pseudomonas, Enterobacter,</i> <i>Pantoea, Serratia,</i> <i>Staphylococcus, Bacillus</i>	Unknown, may increase susceptibility to toxin by affecting midgut epithelial permeability	Broderick <i>et al.</i> (2004, 2006)
Pea aphid (<i>Acyrtosiphon pisum</i>)	Environment	<i>Staphylococcus, Pseudomonas,</i> <i>Acinetobacter, Pantoea</i>	Mostly pathogenic, produce signaling compounds that attract aphid predators	Harada <i>et al.</i> (1997)
Honey bee (<i>Apis</i> spp. and bumble bees (<i>Bombus</i> spp.)	Social transmission	<i>Snodgrassella alvi, Gillianella</i> <i>apicola, Lactobacillus</i> spp.	Digestion, protection against parasites	Koch and Schmid-Hempel (2011), Engel <i>et al.</i> (2012), Martinson <i>et al.</i> (2011)
Lower termite (<i>Reticulitermes speratus</i>)	Social transmission	<i>Flagellates, Bacteroidetes,</i> <i>Spirochetes, Proteobacteria,</i> <i>Firmicutes</i>	Nutrient provisioning, N recycling, fixation, lignocellulose digestion, fermentation	Nakajima <i>et al.</i> (2005), Hongoh <i>et al.</i> (2005), Desai and Brune (2012)
Higher termite (<i>Nasutitermes</i> sp.)	Social transmission	<i>Spirochetes, Fibrobacteres,</i> <i>Bacteroidetes, Firmicutes,</i> <i>Acidobacteria, Proteobacteria</i>	Nutrient provisioning, N recycling, fixation, cellulose digestion, fermentation	Warncke <i>et al.</i> (2007), Kohler <i>et al.</i> (2012)

unripe olives. Bacteria counteract the inhibitory effect of oleuropein which is the principal phenolic glycoside in unripe olives (Ben-Yosef *et al.*, 2010, 2015). Elimination of the gut microbiota, *Pseudomonas fulva* had a significant impact on coffee berry borer (*Hypothenemus hampei*) fitness with approximately a 95 per cent decline in eggs and larvae and no progression to pupa or adults' stage. Bacteria were capable of subsisting on caffeine as a sole carbon and nitrogen source using the digestive tracts of insects (Ceja-Navarro *et al.*, 2015).

Detoxification of Insecticides

In the year 1967, the first case of insecticide resistance by bacterial symbiont was reported by Boush and Matsumur in apple maggot, *Rhagoletis pomonella* (Walsh) against dichlorvos, diazinon, parathion, dieldrin and carbaryl. Bacterial symbionts *Pantoea* and *Pectobacterium* present in different insects like cabbage root flies, flea beetles and aphids degrade isothiocyanates (Welte *et al.*, 2016, 2016a; Shukla and Beran, 2020). Kikuchi *et al.* (2012) from Sapporo (Japan) studied the effect of symbiont bacterial strain on the survival of *Riptortus pedestris* after being exposed to fenitrothion insecticide and concluded that the survival rate of the insects infected with the fenitrothion – degrading *Burkholderia* strains was significantly higher than the survival rate of the insects with non-degrading strains. As per the report of Ramya *et al.* (2015), symbiotic bacteria *Enterobacter asburiae* and *B. cereus* present in the gut of diamondback moth

(*Plutella xylostella*) degraded acephate to methamidophos and O-O dimethyl phosphoramidothioate and acephate into O, S-dimethyl phosphoramidothioate, respectively. Almeida *et al.* (2017) isolated several bacteria from the fifth instar larva of the fall armyworm, *Spodoptera frugiperda* which are resistant to lambda-cyhalothrin, deltamethrin, chlorpyrifos ethyl, spinosad and lufenuron. Resistant strain of fruit flies which treated with antibiotics streptomycin significantly increases the mortality of fruit flies as compared to the flies which not treated with antibiotics streptomycin (Cheng *et al.*, 2017). Treating certain insects like cockroaches and *Plutella xylostella* L. with antibiotics significantly increases mortality due to the removal of endosymbionts (Xia *et al.*, 2018; Pietri *et al.*, 2018). Symbiotic relationships with detoxifying bacteria often develop in hosts after exposure to pesticides, as observed in the case of the brown plant hopper, *Nilaparvata lugens* and its gut symbiont, *Arsenophonus* sp. (Pang *et al.*, 2018). Honey bee gut microbiota promoted the expression of P450 detoxification enzymes in the midgut which increase the survivorship of bees treated with a sublethal dose of thiacloprid or fluvalinate (Wu *et al.*, 2020). Symbiotic bacterial strain *Klebsiella pneumoniae* BCH1 isolated from silkworm degrade the imidacloprid insecticides (Phugare *et al.*, 2013). A symbiont, tolerant to pesticides from the genus *Chryseobacterium* within termites demonstrated rapid adaptation to increasing concentrations of imidacloprid insecticides over time (Blanton *et al.* 2023). Bacterial symbionts (*Bacillus* sp., *Klebsiella* sp., *Citrobacter* sp., *Providencia* sp. and *Enterobacter* sp.) present in the hindguts of giant honey bee, *Apis dorsata* degraded the insecticides like Spinosad, fipronil, imidacloprid, cypermethrin and spiromesifen (Trivedi *et al.*, 2024).

Protection against Abiotic Stress

Under heat stress, facultative bacterial endosymbionts such as Proteobacteria and Rickettsia confer benefits to pea aphids, *A. pisum* (Montllor *et al.*, 2002). The presence of *Rickettsia* in a whitefly, *Bemisia tabaci* induced the expression of genes (Cytoskeleton) under the high temperature which leads to thermotolerance (Brumin *et al.*, 2011). *Cardinium* endosymbiont bacteria protect *B. tabaci* against heat stress under 31°C (Yang *et al.*, 2021).

Polydnavirus

Insects possess an immune system to defend themselves against foreign materials. When attacked by parasitoids, they mount a defence against the parasitoid offspring. However, parasitoids especially Ichneumonid and Braconid wasp have evolved a unique strategy to overcome the host's immune response. They carry

Polydnaviruses (PDVs) or Virus-Like particles (VLPs), which help protect their offspring from the host's immune defences (Drezen *et al.*, 2017; Herniou *et al.*, 2013). The *Polydnaviridae* family having two genera, *Bracovirus* and *Ichnovirus*, which play a crucial role in suppressing the host's immune system, allowing the parasitoid larvae to develop inside the host without being attacked by its immune defences (Strand and Burke, 2012; Beckage and Drezen, 2012; Stoltz *et al.*, 1979; Espagne *et al.*, 2004; Webb and Summers, 1982). A Ichneumonid parasitic wasp, *Venturia canescens* produce VLPs from the endogenous PDV nudivirus, which are essential for successful parasitism (Cerqueira de Araujo *et al.*, 2022). Polydnavirus (*Toxoneuron nigriceps* BracoVirus; TnBV) present in venom gland and the calyx fluid of endophagous parasitoid wasp, *Toxoneuron nigriceps*, is injected into the *Heliothis virescens* larvae during the injections of eggs and protect parasitoid's eggs from the *H. virescens* immune system by causing loss of haemocyte functionality and inducing cell death (Salvia *et al.*, 2023).

Paratransgenesis

Paratransgenesis is the process of symbiont gut bacteria from vectors are isolated sophisticatedly and then genetically modified *in vitro* to produce compounds that prevent the spread of pathogens. The transformed symbionts are then put back into the host vector, where the expression of designed molecules influences the host's vector competence, or capacity to spread the disease (Durvasula *et al.*, 1997; Ward *et al.*, 2001; Elston *et al.*, 2020). Paratransgenesis can be used to combating the varroa mite, which are a significant threat to bee colonies and also vector for the DWV and *Israeli Acute Paralysis Virus* (IAPV). The Lactic acid Bacterial community, particularly *Lactobacillus* genus having great potential for paratransgenesis in honey bee. Transforming *L. kunkeei* and using it as a vector to promote the health of honey bees and aid in functional genetics research-related activities (Rangberg *et al.*, 2012). In 2020, Leonard *et al.* successfully engineered *Snodgrassella alvi*, a symbiotic bacterium found in honey bees, to induce an RNA interference (RNAi) immune response.

Conclusion

Symbiont-mediated protection is a phenomenon, observed in the natural population of insects. Symbiont enhances the hosts capability to defend against pathogens, predators, parasitoids, insecticides and in some other ways, as an additional immune system. Symbiont mediated protection in insect hosts by employing different protective mechanisms. Protection is mediated as a result of the

production of toxins, antibiotics, degradation, or detoxification of harmful compounds which serve as a newer frontier for insect host physiological study.

Future direction and research challenges

Need to understand the nature of toxins and antibiotics utilized in symbiotic mediated protection, isolate and identify beneficial symbiont enzymes for further amplification, develop methods to tuck symbionts in beneficial organisms to impart protection against pesticides and develop methods to suppress facultative symbionts to increase the survival rate of beneficial organisms.

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