

THE EVOLUTIONARY AND FUNCTIONAL SIGNIFICANCE OF GUT MICROBIAL SYMBIOSES IN HONEY BEES, BEETLES, AND APHIDS

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Abstract

Symbiotic associations of insects with microorganisms have great importance in insect ecology and evolution. The digestive systems of insects offer unique habitats for several microbial communities that are able to fulfill a number of biological roles in host organisms, such as nutrient uptake, metabolic control, immunological defense, and detoxification of hazardous chemicals. Therefore, the gut microbiome is considered one of the key factors in insect survival, adaptation, and ecological success in various environments. Gut microbes of insects are important players providing immunological defense, nutrient uptake, metabolic regulation, and detoxification of hazardous compounds. Thus, the gut microbiome is an important factor determining the ability of insects to adapt to and survive in different environments. The diets of many insects consist of foods that are poorly nourishing or have some chemical defenses, including pollen, sap from trees, or wood itself. Many insects cannot degrade complex nutritional substances in food sources by themselves. Insects may generate essential amino acids, degrade carbohydrates, and transform components of their diet into a usable form owing to the enzymatic actions performed by friendly bacteria in the intestines. The metabolic pathways lead to inter-related biological systems which aid the development and reproduction of insects. Insects such as aphids, beetles, and honeybees are used as models to study the interactions between hosts and microbes. Honeybees rely on a specific but simple composition of gut microbes in order to facilitate digestion within their colonies. Aphids maintain bacterial symbionts that provide necessary amino acids not available from their plant-based diet. Beetles are able to adapt to different environments due to the presence of various microbes which assist in digestion and detoxification.

Introduction

Insects can be found in almost every available niche across the globe. Insect success depends heavily on associations with symbiotic microbes residing in different parts of the insect body, especially in the intestine. The bacterial community provides indispensable metabolic abilities lacking in insects. Symbiosis has influence

on host immunity, metabolism, and ecological adaptability, contributing to evolutionary processes in insects (Sabree et al., 2009). Technological progress in sequencing techniques revealed the complexity and functional diversity of insect-associated microbial communities, surpassing earlier expectations (Hammer et al., 2017). All these data have underlined the

importance of microbial association as an integral part of insect lifestyle (Bordenstein & Theis, 2015).

Metabolic versatility is achieved through microbial communities capable of performing different functions due to the variable microenvironment present in the insect gut. They contribute to nutrient absorption and digestion by acting on the substrates and the body cells. As reported in research, microbes facilitate the degradation of complicated components that the insect cannot digest, such as plant polymers (Flint et al., 2012). Metabolites synthesized during fermentation processes in the stomach help the insect receive additional sources of energy (Engel & Moran, 2013). Besides their metabolic functions, gut microbes also influence the immune system of the insect host and protect it from harmful pathogens (Koch & Schmid-Hempel, 2011).

Some insects' species have emerged as useful models for investigating relationships between hosts and microbes. Social insects like honey bees contain stable gut microbiota populations which spread throughout the colony members in order to maintain overall colony health, as explained by Kwong et al. (2017). Insects like aphids make interesting models since they contain beneficial symbionts which supply essential nutrients not found in their food (plant sap), as noted by Hansen & Moran (2011). Additionally, various kinds of microbiomes in beetles have been identified to aid in digestion and breakdown of toxins present in plants, as stated by Ceja-Navarro et al. (2015).

Knowledge about microbiota within the digestive tract of insects is acquiring more relevance in practical applications such as agriculture and ecosystem management. Insect symbiosis with

microbial partners influences insect behavior in interaction with host plants and insecticide resistance or stress tolerance (Douglas, 2015). In addition, evidence has been shown that changes in microbial consortia can lead to novel methods for pest management or for enhancing pollinator fitness (Crotti et al., 2012). Hence, investigation into insect-microbe interaction has great potential significance not only in biological studies but also in practice (Engel et al., 2016).

The Insect Gut Microbiome

The insect gut system is subdivided into three major segments, namely the foregut, midgut, and hindgut. Each segment contains unique environmental components, which dictate microbial colonization and carry out certain physiological activities. As the foregut is mainly involved in feeding and storage of food, the midgut serves as the principal site for digestion and assimilation of nutrients (Nation, 2015). In addition to being a vital organ for waste disposal and water desorption, the hindgut serves as an essential region for microbial fermentation (Engel & Moran, 2013).

The microbes in the insect's digestive tract are usually found in the hindgut due to the availability of constant conditions that facilitate microbial growth. The lack of oxygen and the availability of food fragments make this site suitable for microbial growth and fermentation (Brune, 2014). Most bacteria attach themselves to the surface of the gut or produce biofilms to ensure prolonged symbiotic relationships with their hosts (Engel et al., 2012). These microorganisms play a critical role in the digestion of foods and nutrient metabolism, which cannot be performed independently by the insects (Douglas, 2015).

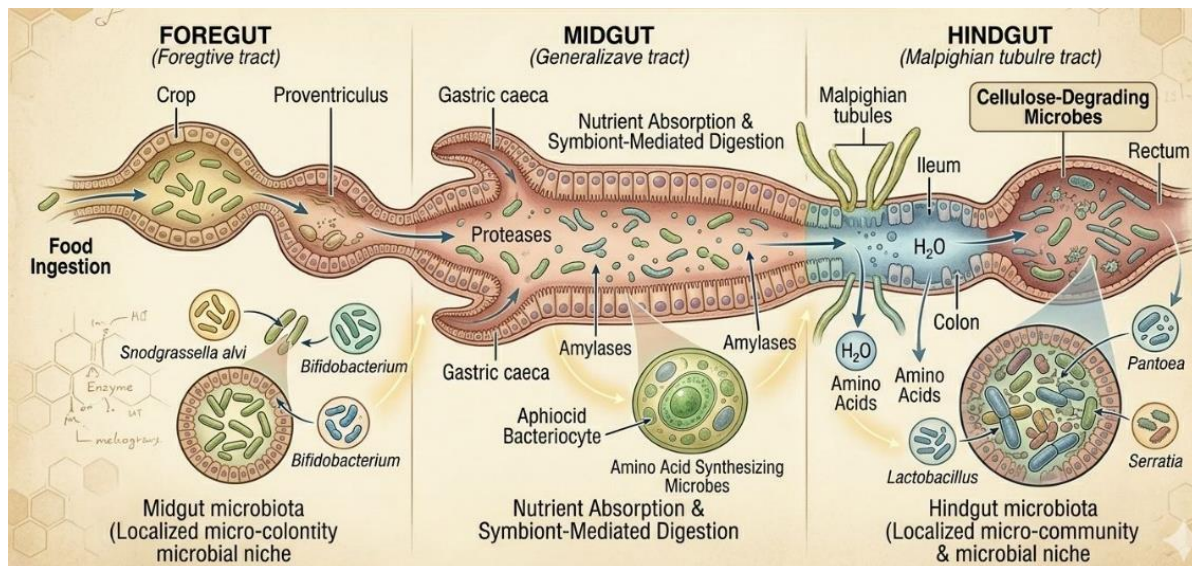


Figure.1: General structure and micro biota regions of insects gut

Based on the impact they have on the host organism, there can be three forms of symbiotic relationship between insects and microbes: mutualism, commensalism, and parasitism. Interactions that provide benefits for both the microbial entity and the insect host are called mutualistic interactions. Many gut bacteria are helpful for insects because they degrade complex food substrates and synthesize nutrients which are not present in the diet of the host (Douglas, 2015). As their contribution to symbiosis, the insect host provides the microorganisms with stable conditions and constant nutrition (Crotti et al., 2012). Coevolution of hosts and symbiotic microorganisms usually results in mutualistic interactions (Bordenstein & Theis, 2015).

Commensalism refers to a situation where bacteria gain from interactions with their hosts without causing any significant decrease in host fitness. Bacteria present in the environment may interact with the insect and temporarily colonize it due to the ingestion of contaminated food or contact with other organisms, Hammer et al. (2017). Although they may not be benefiting the host, they contribute towards the diversity of microbes and can affect ecological interactions inside the gut microbiome (Engel et al., 2016). Metabolic and competitive interactions among different microbial species may be influenced by the

presence of a variety of microbial species (Flint et al., 2012).

Parasitism is characterized by the fact that microorganisms cause harm to the host by exploiting the host's resources. Bacterial and fungal pathogens can infect various parts of insects and interfere with their biological functions (Koch & Schmid-Hempel, 2011). Nevertheless, positive microbial communities in the gut can protect the host from being infected by pathogens since they can compete with them for nutrients and produce antibiotics (Kwong et al., 2017).

Microbial Symbionts of Insects Are Either Transmitted Vertically or Horizontally

According to Moran et al. (2008), vertical transfer refers to the direct transfer of microbes from the parents to their offspring, either through eggs or certain reproductive parts. Crucial symbionts that are necessary for the development and persistence of the hosts usually employ this transfer mechanism (Hansen & Moran, 2011). Vertical transmission between insect hosts and their microbial counterparts leads to the development of specialized interactions because of long-term coevolution (Sabree et al., 2009).

Horizontal transmission involves the acquisition of microbes by insects in their surroundings. Environmental bacteria may be ingested via food, soil, and plants (Hammer et al., 2017). Insects can

obtain novel microbial species that can improve their metabolism or offer protection against environmental hazards (Ceja-Navarro et al., 2015). Horizontal transmission also has an identical effect on the variety and abundance of microbial communities within insect populations (Sudakaran et al., 2017). Table 1: Beetles, aphids, and honey bees exhibit distinct gut microbiota composition, transfer, and stability based on their unique ecological and evolutionary adaptations (Kwong & Moran, 2016; Douglas, 1998; Engel & Moran, 2013).

Transmission of microbes typically occurs via social behaviors among colony members in the case of social insects such as honey bees. Transmission of beneficial microbes among humans can be achieved through social behaviors such as trophallaxis, grooming, and eating together (Kwong et al., 2017). As per Engel et al. (2016), such interactions ensure that any new recruits into the colony receive the essential microbes necessary for their physiological development.

Functions of Gut Microbes in Insects

It is essential that the roles of microbial gut symbionts in insects are understood to be able to understand how symbiotic microorganisms help their hosts in metabolism, adaptation, and evolution. Insects cannot undertake many metabolic, behavioral, and immunological tasks on their own due to genetic and nutritional constraints. However, the insect gut microflora does these tasks. These tasks include protection from invading microbes, regulation of the immune system, degradation of pesticides and phytochemicals, breakdown of complex carbohydrates, and even manipulation of host physiology and behavior. These tasks illustrate how important insect gut microbiomes are for the host (Douglas, 2018; Engel & Moran, 2013; Hammer et al., 2017).

Insects increase their capacity for ingesting various types of foods through gut microorganisms with enzymes that help in degrading complex polysaccharides, proteins, and lipids that do not have corresponding genes in insects. Termites depend on the presence of symbionts in the gut to

help hydrolyze lignocellulose using cellulases and hemicellulases so that they can derive nutrients from wood-based foods (Brune & Dietrich, 2015). Also, *Popillia japonica* beetles that feed on plants depend on gut microbiomes that produce genes associated with carbohydrate metabolism to digest the food items (Coleman et al., 2019). Besides, gut bacteria in lepidopteran larvae are also likely to be involved in breaking down plant cell wall elements to obtain energy in the form of fatty acids (Paniagua Voirol et al., 2018).

Moreover, the gut flora enhances the dietary habits of insects by producing important chemicals that are not found in the insects' source of food. The sap-sucking insects including the planthoppers depend on the synthesis of B vitamins by the microbes since phloem sap lacks sufficient nutrients (Hansen & Moran, 2011). This also applies to stinkbugs whose symbionts synthesize the necessary amino acids for the development of the host insects (Kaiwa et al., 2014). Apart from helping in the production of important nutrients, the gut microbes cycle nitrogen by turning waste products such as uric acid into important nitrogen-containing chemicals (Sabree et al., 2009).

There is evidence that gut microbiota has an essential role in influencing the immune competence of the host (the fence). If immune pathways of the host become activated due to symbiotic bacteria present in their gut microbiome, these bacteria will produce additional antimicrobial compounds or peptides that will limit pathogen proliferation. For example, according to Kwong et al. (2009), *Drosophila melanogaster* larvae colonized by gut bacteria display an enhanced level of immune gene expression and increased resistance to pathogen attack compared to the germ-free larvae of the same species. Honey bees possessing healthy gut bacteria have been found to have high gene expression levels and enhanced resistance as well. Plant secondary compounds include alkaloids, phenolics, and terpenoids. Such compounds are toxic in high concentrations or inhibit feeding. For hosts, it is easier to use plants that have such chemicals if these substances are decomposed or converted into metabolites that are not harmful

anymore by gut bacteria. Resin acid terpenoids are decomposed in the stomach of pine weevil *Hylobius abietis*, increasing the insect's ability to survive (Adams et al., 2013). Likewise, gut microorganisms within *Helicoverpa armigera* larvae produce genes encoding enzymes used in the detoxification of phytochemicals (Priya et al., 2012). Detoxification processes increase the use of hosts by insect symbionts.

In addition, the intestinal flora of insects affects their ability to cope with artificial poisons. Gut bacteria in the Colorado potato beetle *Leptinotarsa decemlineata* are responsible for the decomposition of chemical compounds of some types of insecticides; thus, these microorganisms participate in the process of developing insecticide resistance (Kumar et al., 2019). As seen from this information, gut symbionts affect both natural and artificial toxins. Thus, detoxification mediated by gut bacteria is essential for adaptation due to the symbiont-host relationship.

In addition to the immune system and metabolism, the gut microbiota has an effect on the development and behavior of insects. Gut microorganism imbalance leads to decreased body size and development delay in insects like *Drosophila*, implying that the presence of the symbionts is vital for proper growth in the organism (Shin et al., 2011). The possible effects of the microbiome on development are seen in the relationship between the gut microbiome structure and the rate of maturation and endocrine signaling in worker bees (Rubin et al., 2017).

The microbiota could potentially have effects on insect behavior through metabolites. Some gut bacteria in fruit flies produce compounds that influence social behaviors and mate choice decisions, linking the microbiome to the ecology of the host organisms (Begon et al., 2006; Sharon et al., 2010). Gut bacteria in social insects like ants and termites could influence nestmate recognition and cohesion within colonies through chemical signals (Stoll et al., 2007). The results above demonstrate that gut. Besides the physiological effects, the microbiomes play a role in the ecology and social interactions of the hosts.

Gut Microbiome in Honey Bees (*Apis mellifera*)

There is a very limited and highly specialized microbiome made up of only a few key bacterial strains found in the gut of honey bees. These include species from *Lactobacillus*, *Bifidobacterium*, *Gilliamella apicola*, and *Snodgrassella alvi* (Moran et al., 2012). Each bacterium occupies a specific location in the gut and plays a role in the breakdown of nutrients. For example, *Gilliamella* primarily exists in the lumen and plays an important role in carbohydrate digestion, whereas *Snodgrassella* is associated with the ileum epithelial lining (Powell et al., 2014). Furthermore, other non-core bacteria such as *Frischella perrara*, which exist intermittently but may influence the immune system, have been discovered through recent metagenomic research (Martinson et al., 2012).

Based on geographic studies, there is remarkable consistency among the microbiome compositions across colonies, although differences might arise based on age, nutrition, and habitat conditions (Kwong et al., 2014). The microbial communities inside honey bees demonstrate a distinct distribution in their habitats, with specific members occupying either the crop, the midgut, or the hindgut of the bees. (Engel et al. 2016) The most abundant and actively working microbial populations live inside the hindgut, where they contribute significantly to pollen fermentation and digestion. (Lee et al., 2015) Additionally, the bacteria form biofilms protecting against pathogens and stabilizing the microbiome in general. (Emery et al., 2017) As recent studies show, even individual bacteria with relatively lower numbers might influence colony health through producing antimicrobial substances and impacting gene expression. (Raymann et al., 2017) The microorganisms inhabiting honey bees' guts participate in important physiological processes such as nutrition, detoxification, and immunological functions.

To provide the host with metabolites increasing its energy levels, the microbes decompose complex compounds, such as polysaccharides that exist in pollen and nectar. (Zheng et al., 2017) Through bacterial fermentation, short-chain fatty acids and other organic acids are released, which contribute to improving food digestion and maintaining gut

pH. (Kešnerová et al., 2017) Besides, the gut microbiota produces some amino acids and B vitamins lacking from honey bee diets. (Moran, 2015) Microbes also improve the immune system. For instance, *Nosema ceranae* and *Paenibacillus* larvae are suppressed by substances created by *Snodgrassella* and *Gilliamella*, which stimulate immune pathways (Raymann et al., 2018).

The protective impact of these microbes can be proven by the increased susceptibility to disease when the gut microbiota are experimentally reduced (Kwong et al., 2017). The microbes have an effect on social behaviors and feeding preferences through behavioral changes, suggesting the involvement of microbiota in the collective efficiency of bees (Mattila et al., 2012).

As per Powell et al. (2014), the three major routes for the distribution of microbes in the gut of honey bees are trophallaxis, grooming, and nest material sharing. In the initial weeks after hatching, the adult bees develop their communities by obtaining core bacteria from nurse bees and nest surfaces (Martinson et al., 2012). Vertical transmission by queens or contaminated food can enhance diversity, but it occurs rarely (Engel et al., 2016). It has been proven that both social transmission and environmental exposure are required for microbial stability in colonies (Raymann et al., 2017). The condition of colonies is impaired, and the composition of their microbiota changes due to the absence of social transmission, such as isolation and antibiotic treatment (Kwong et al., 2017).

Honey bees' health is dependent on their gut microbiota. Dysbiosis is associated with increased infection susceptibility and shorter lifespans, caused by antibiotics, pesticides, or poor nutrition (Raymann et al., 2017). The symbiotic microorganisms help with the detoxification of dietary toxins and environmental pollutants, improving the bees' stress resilience (Zheng et al., 2017). In addition, microbial metabolites affect pathogen elimination and the expression of immune genes in the host (Kešnerová et al., 2017). Thus, the health of bee colonies, disease resistance, and pollination efficiency rely on the

stability of their core microbes (Mattila et al., 2012).

Symbiotic Microbes in Aphids (*Acyrtosiphon pisum*)

The symbiosis with primary endosymbionts, mainly obligate intracellular bacteria *Buchnera aphidicola*, is crucial for aphids as they help in the production of necessary vitamins and amino acids that do not present in aphids' diet consisting of phloem sap (Douglas, 1998; Shigenobu et al., 2000). According to recent genome studies, the bacteria have significantly reduced the size of their genomes, retaining only genes that are important for provisioning of the hosts (Moran et al., 2008). Since transmission between generations occurs vertically, the symbiotic association is highly stable (Baumann, 2005).

In addition to *Buchnera*, aphids could have facultative symbionts contributing to stress resistance and nutrient metabolism. In case of suboptimal conditions, bacteria can assist aphids' growth and reproduction alongside with providing them with additional amounts of amino acids provided by *Buchnera* (Russell et al., 2013). Only due to the help from symbionts are aphids able to consume nutrient-depleted phloem sap and thrive in populations on their hosts (Douglas, 2006). The need for symbionts' help in acquiring nutrients demonstrates one of the many ways in which symbiosis makes it possible for animals to use ecological niches.

Also, aphids possess secondary symbionts which give them protection from pathogens, parasitoids, and abiotic stress such as *Hamiltonella defensa*, *Serratia symbiotica*, and *Regiella insecticola* (Oliver et al., 2010). By producing protective compounds or altering the host's immune system, secondary symbionts provide aphids with increased resistance to biotic stress (Guo et al., 2017). Aphid communities vary in terms of prevalence depending on the transmission of secondary symbionts vertically and horizontally (Russell et al., 2013). The complex relationships between aphids and their symbionts is also demonstrated by multiple secondary symbionts' presence.

Gut Microbiota of Beetles (*Tribolium castaneum*)

In their gut microbiota, beetles display a diverse range of microorganisms based on their diets. According to metagenomic analysis, the dominant microorganisms in *T. castaneum* are *Firmicutes*, *Bacteroidetes*, and *Proteobacteria*, with the species distribution being influenced by nutrition and environment. (Navarro and Ceja, 2015). The breakdown of plant cell wall compounds or starches from grains enables beetles to thrive in nutritionally diverse ecosystems. (Hammer et al., 2017). In addition, the metabolic versatility brought about by microbial diversity in the beetle gut aids ecological adaptation.

Gut bacteria facilitate digestion by degrading difficult-to-digest proteins and polysaccharides in order to increase nutrient absorption by the host (Dillon & Dillon, 2004). Through symbiotic metabolic processes, gut microorganisms generate short-chain fatty acids and vitamins needed for growth and reproduction (Engel & Moran, 2013). The importance of microbial communities within the gut is shown by the experimental elimination of gut bacteria, which results in a decline in the development rate and survival rate of beetles.

The gut bacteria of beetles contribute to the detoxification of pesticides, environmental toxins,

and secondary metabolites produced by plants (Kumar et al., 2019). Due to microbial enzyme activity, the beetles are able to consume plants that have chemical defenses and can survive in various habitats.

Such processes of detoxification lead to an expansion in the food sources available and facilitate adaptation to new environments.

Microbial communities inhabiting the guts of beetles also affect beetle development and reproduction. Hormone signaling and metabolic pathways controlled by symbiotic microbes impact the timing of pupation, growth rate of larvae, and reproductive success of adult individuals (Shukla et al., 2016). The findings presented demonstrate the essential role of gut microorganisms in affecting physiological and ecological characteristics of beetles.

Comparative Analysis of Symbiosis

Comparative studies reveal that honey bees, aphids, and beetles exhibit differences in gut microbial community composition and function, corresponding to differences in their physiology, diets, and ecological niches. The relatively simple core microbiota of honey bees is represented by five to nine bacteria, which are specialized for immune system support and carbohydrates digestion (Engel et al., 2016).

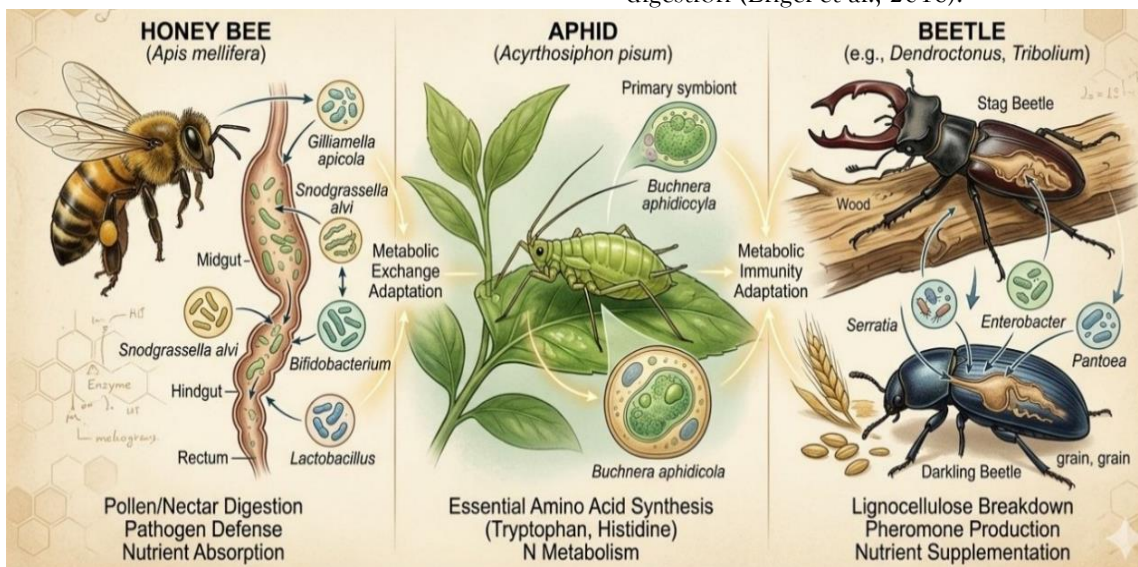


Figure no.2: Gut microbes as symbiotic partners in insects

Beetles have highly diverse gut microbiomes that have evolved to be suitable for consumption of nutritionally complex substrates, including those rich in starch and lignocellulose (Ceja-Navarro et al., 2015). This contrast highlights the connection between adaptation to the environment and diet, host feeding ecology, and microbial diversity (Hammer et al., 2017). Coevolution of the host and symbiotic microbes can be seen from an evolutionary perspective. Phylogenetic analyses reveal co-diversification with their hosts for millions of years, and microorganisms associated with the honey bees are highly host-specific (Kwong et al., 2017). Long-term obligatory mutualism of aphids is evidenced by the reduced genome size of *Buchnera aphidicola* (Moran et al., 2008). Yet, the symbionts of beetles are often flexible enough to adapt quickly to novel environments and new dietary requirements (Kumar et al., 2019). These contrasts demonstrate the balance achieved by insects in symbiotic relationships in terms of specialization and flexibility. Table 2: Insects As partners in maintaining the host's health, gut symbionts play a critical role in nutrition, immunology, detoxification, growth, and ecological fitness (Engel et al., 2012; Moran et al., 2008; Ceja-Navarro et al., 2015). While their respective shares differ, symbiotic microorganisms in different insect groups perform overlapping roles that include detoxification, digestion, nutritional supplementation, and protection against pathogens (Douglas, 2018). Lignocellulose digestion serves as one of the main tasks performed by beetles; in contrast, immunoregulation is typical for honey bees and aphids (Brune & Dietrich, 2015). The comparison allows understanding the driving factors behind the evolution of the relationships between bacteria and insects.

Approaches to Study Gut Microbiota

The current investigation of the microbial communities in the intestines of insects involves both cultural and molecular approaches. Cultural approaches allow conducting experiments and isolating bacteria from the gut.

On the other hand, cultural approaches can only be used for species capable of growing artificially (Dillon & Dillon, 2004). With the advent of molecular approaches, microbiota research has made a leap forward – now researchers can use 16S rRNA sequencing to identify both culturable and unculturable bacteria (Hammer et al., 2017). In this regard, as highlighted by Engel and Moran (2013), the combination of high-throughput sequencing and metagenomics enables comprehensive microbial diversity and functional profiles. Metatranscriptomics and metabolomics provide information about microbial gene expression and metabolism by studying their activity in vivo. For instance, by conducting metabolomics on beetles, it was possible to uncover microbial products that were involved in the detoxification process, whereas metatranscriptomics studies of honey bee stomach revealed active pathways for carbohydrate metabolism (Zheng et al., 2017). Microbes can be mapped within specific regions of the gut by applying FISH and microscopy (Engel et al., 2016), which helps to understand interactions between the host and microbes at a tissue level. Applications of Studies on Insect-Microbe Symbiosis

The fields of agriculture, biotechnology, and environmental management can all make use of the knowledge gained on the topic of interaction between insects and microorganisms. Interventions that target honey bee gut microbiota will contribute to increased bee health and resistance to pathogenic microorganisms, including *Nosema* and *Paenibacillus* (Kwong et al., 2017). Symbionts present in the guts of insect pests may become targets for biocontrol, interfering in their detoxification and nutrition uptake processes (Crotti et al., 2012). In addition, the beetle microbiomes have been explored to develop biofuel and lignocellulose degradation enzymes (Ceja Navarro et al., 2015). Symbiotic insects are also beneficial for the study of nutrient synthesis in bees and aphids.

Future Perspectives and Research Gaps

Despite all scientific advances in insect-microbe symbiosis studies, there are still several unresolved

questions. The importance of viruses, fungi, and archaea in the gut microbiome is not clear yet, as is the case with the low-abundance bacteria whose functions have not been described (Hammer et al., 2017).

There is also a lack of long-term studies, especially those focused on the potential impact of the changing environment on microbial communities (Engel et al., 2016).

Conclusions

The proper functioning of various insects in relation to such essential processes as digestion, detoxification, immunological reactions, and pathogen elimination depends on many types of gut microbes. Comparison studies of honey bees, aphids, and beetles provide an understanding of the effect of the host ecology and physiology as well as evolution on gut microbial diversity and functions. The development of innovative methods in studying the gut microbiota has greatly increased our knowledge concerning gut microbial community structure and functioning, thereby paving the way for applied studies in biotechnologies, agriculture, and environmental sciences

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