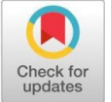


Review Article

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Microbial Masters: Endosymbionts' Influence on Insect Nutrition and Ecological Balance



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ABSTRACT

Endosymbiosis, a specific form of symbiosis, involves one organism residing inside another and has a pivotal role in the evolution of eukaryotic organisms. Insects, thriving globally due to their adaptable diets, harbor endosymbionts in various body regions, notably near the digestive tracts. Endosymbionts play a vital role in insect nutrition, nitrogen recycling, amino acid provisioning, manipulation of plant phenotypes, detoxification of plant secondary metabolites, and pest management strategies, such as reproductive manipulation and pathogen interference. Microbial associations of insects can impact ecological communities by altering the dynamics of plant interactions with both competitors and natural adversaries of their insect hosts. The study of endosymbiosis in insects faces challenges such as the complexity of symbiotic relationships and the specificity of host interactions, requiring advanced techniques and interdisciplinary approaches. Despite these challenges, it elucidates the crucial roles of endosymbionts in insect nutrition, plant-insect interactions, and pest management, offering insights for sustainable agriculture and effective pest control strategies. An attempt is made to explain the role of endosymbionts and insect-plant interactions with promising literature. This review focuses on the significance of endosymbionts in insect biology, their functions, pest management strategies, challenges, and prospects.

Keywords: Endosymbionts, insect-plant interactions, pest management, insect nutrition, insect adaptations, insect-microbe interactions, symbiotic relationships, nutrient provisioning, ecological impact, sustainable agriculture

1. Introduction

"Symbiosis," is derived from the Greek word "simbios" or "living together," was initially coined by Anton de Bary in 1879. De Bary defined symbiosis as "the permanent association between two or more specifically distinct organisms, at least during a part of their life cycle." Interestingly, DeBary included parasitism as a type of symbiosis in this definition [1]. Endosymbiosis is a specific type of symbiotic relationship where one organism lives inside the body of another [2]. This phenomenon has been particularly significant in the evolution of eukaryotic cells. One popular explanation suggests that certain organelles seen in eukaryotic cells, such as mitochondria and chloroplasts, were formerly free-living bacteria that were swallowed by ancestral eukaryotic cells. This is known as the endosymbiotic theory. Over time, these engulfed bacteria developed a mutually beneficial relationship with their hosts, leading to the formation of the complex cells we see today [3]. In contrast to endosymbiosis, some symbiotic bacteria may reside on the surface of hosts or in specific tissues, establishing more localized interactions [4, 5, 6]. The balance between mutualistic and parasitic interactions can vary, and in some cases,

the relationship may shift depending on environmental conditions [7].

Insects thrive globally due to their highly successful lifestyle, with their adaptability to diverse diets being a key factor. The flexibility in their feeding habits is, in part, attributed to the presence of endosymbionts. The distribution of endosymbionts within insects can vary significantly based on factors such as the insect species, the specific endosymbiont involved, and the nature of their symbiotic relationship. Endosymbionts, for example, are located in various places in insects such as midgut, reproductive organs, haemolymphs, and bacteriocytes [8]. These microscopic companions are frequently seen close to an insect's digestive system, and it is generally acknowledged that endosymbionts are essential to the host insect's ability to feed [9].

Endosymbionts play a role in both nitrogen fixation and recycling. Nitrogen recycling is the process by which bacteria or fungi preserve nitrogenous waste products from insect diets or metabolism and transform them into forms that insects can consume. Alternatively, nitrogen fixation by bacteria produces accessible nitrogen forms but is energy-intensive. In amino acid provisioning, symbionts synthesize essential amino acids or precursors, addressing amino acid imbalance without necessarily resolving the overall nitrogen shortage in host diets. N-fixers and N-recyclers often contribute to this, while some intracellular symbionts in hemipteran insects play a significant role in amino acid biosynthesis without explicit nitrogen fixation or recycling [10].

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Microbial symbionts can protect pests from toxins through detoxifying symbioses, creating a defensive partnership between the insect and various microorganisms [11]. Numerous insects' biology is impacted by mutualistic connections with optional, non-essential heritable microorganisms, which can also, in some situations, have a major impact on the fitness of insect hosts. A prime example may be found in aphids, where the bacteria *Hamiltonella defensa*, a facultative endosymbiotic relationship, offers defense against parasitoids that are part of the Hymenoptera order [12]. Some endosymbionts are also involved in pest management strategies such as reproductive manipulation, sterility induction, pathogen interference, nutritional mutualism, RNA interference enhancement, and population monitoring [13]. Despite of these, there are some challenges pertaining to the use of endosymbionts like ethical considerations, ecological impact, host specificity, regulatory framework, resistance management, and technological advancements. These points to be considered carefully while deploying endosymbionts as a pest management tool. This review mainly focuses on the importance of endosymbionts, their types, and functions like their role in nutrition, detoxication of pesticides, pest management strategies, challenges, and its future directions.

2. Types of Insect Endosymbionts

2.1. Primary, secondary (Facultative), mutualistic and Parasitic endosymbionts

Primary endosymbionts have formed obligatory associations with their insect hosts for extensive periods, ranging from 10 to several hundred million years in some instances. They exhibit distinct characteristics such as residing within bacteriocytes, being indispensable for the host's fitness, and maternal transmission, and showing precise co-evolutionary patterns with their hosts [14]. The principal symbionts, which are unable to be cultured outside of their host settings, are Aphid-*Buchnera*, *Wigglesworthia* in tsetse flies, *Baumannia* in sharpshooters, *Carsonella* in psyllids, *Tremblaya* in mealybugs, *Blochmannia* in carpenter ants, and *Nardonella* in weevils [15].

On the other hand, **secondary symbionts** have developed more recently and typically form facultative associations. They may undergo horizontal transfer between hosts, reside in the hemolymph or gut (as opposed to specialized bacteriocytes), and play crucial roles in providing protection, enhancing stress tolerance, manipulating reproduction, and contributing to defense mechanisms [14]. Unlike primary symbionts, Cultures of secondary endosymbionts are easily obtained, including *Wolbachia*, *Spiroplasma*, *Hamiltonella defensa*, and *Sodalis glossinidius* [16]. In addition to main bacteriocyte endosymbionts, secondary endosymbionts are frequently present in insects. These endosymbionts can be extra- or intracellular and are connected with bacteriocytes [17]. These bacteria are often cultivable outside of the host environment and can enter host tissues independently, in contrast to primary endosymbionts. *Sodalis glossinidius* is one of the well-studied secondary symbionts; it co-exists with *Wigglesworthia* in tsetse flies and is vertically transferred. When removed selectively, this bacteria has been shown to have a beneficial effect on host biology, as demonstrated by changes in the longevity of tsetse flies [17].

Insects as hosts for mutualistic bacteria: Mutualistic relationships between insect hosts and endosymbionts are characterized by mutual benefits for both parties involved.

Wolbachia is a common endosymbiont found in insects that often exhibit mutualistic relationships. It can provide benefits to the host, such as enhanced reproductive capabilities or protection against certain pathogens. Parasitic relationships involve one party (the parasite) benefiting at the expense of the other (the host), causing harm to the host. *Spiroplasma* bacteria can establish parasitic relationships with insect hosts. They may manipulate host reproduction or cause reproductive abnormalities, negatively impacting the host's fitness [16].

3. Endosymbionts and Insect Nutrition

The bacterial symbionts have involving two interacting processes: **selfish metabolism to cooperative metabolism**; the bacteria synthesize certain nutrients at sufficient rates to meet both their own requirements and those of the animal host. For example, 50% or more of the essential amino acids synthesized by the γ -proteobacterium *Buchnera aphidicola* in aphids is released to the host, supporting aphid growth and reproduction [18]. The second one is, **Coevolutionary changes**, which relates to genome reduction of the bacteria and associated functional compensation by the animal. Obligate vertical transmission leads to genome reduction partly because of the loss of a free-living life stage. The bacteria have different linked metabolic pathways, and in others, they have different reactions within a single pathway [19].

3.1. Role in Nutrient Provision

3.1.1. Amino Acid Production

Aphids and *Buchnera* bacteria collaborate to synthesize essential amino acids within specialized cells called bacteriocytes. While many organisms can produce some amino acids, not all are required for protein synthesis, deficiencies in essential amino acids in food sources, like plant sap, pose a nutritional challenge [18]. In particular, *Buchnera* depends on the aphid for amino acid routes that are not essential and the aphid depends on *Buchnera* for amino acid pathways that are necessary and are encoded by the bacterium [19]. In certain symbiotic systems, multiple obligatory members are crucial to meet the host's metabolic needs. By providing the nutrition, *Serratia symbiotica*—which was previously thought to be facultative—becomes important since *Buchnera* in *Cinara cedri* is unable to manufacture the necessary tryptophan. *Auchenorhynca* indicates metabolic interdependencies in which distinct partner symbionts from different lineages complement the obligatory symbiont *Sulcia*. Whereas *Hodgkinia* supplies the final two amino acids, vitamins, and cofactors, *Sulcia* supplies the eight necessary amino acids found in cicadas. A methionine synthase that is dependent on cobalamin is retained by *Sulcia*, which affects *Hodgkinia*'s genome, which is greatly reduced yet dedicates 7% of its sequence to the cobalamin biosynthesis pathway [20]. As a member of the γ -proteobacteria group, *Carsonellaruddii* is an essential endosymbiont in psyllids. According to Baumann, [17], it plays a crucial function in its psyllid host by encoding pathways necessary for the production of amino acids. According to Skidmore et al. (2017) [20], certain psyllid species obtained these secondary symbionts after *Carsonella*, and they provide genes that complete the gaps in *Carsonella*'s vital amino acid biosynthesis pathways.

3.1.2. Nutrient Recycling

Symbiotic microbes play a crucial role in nitrogen recycling from stored uric acid in shield bugs and termites.

Reticulitermes flavipes hindgut bacteria ferment uric acid transported from fat bodies into ammonia, CO₂, and acetate [21]. Cockroaches, relatives of termites, host *Blattabacterium* sp. near uric acid deposits, participate in nitrogen recycling [22]. Ants are commonly perceived as predators or omnivores, observations, and stable isotope analyses suggest that many arboreal ants feed on nitrogen-poor or inaccessible diets, including extrafloral nectar, hemipteran honeydew, and vertebrate excreta [23]. This has led to the hypothesis that "herbivorous" ants might rely on symbiotic bacteria for nutrition [24]. Carpenter ants in the Camponotini tribe and their *Blochmannia* symbionts, with a co-speciation history of around 40 million years, exemplify this hypothesis [25, 26, 27]. *Blochmannia*'s genome reveals its ability to synthesize essential amino acids (EAAs) and convert urea to ammonia. Functional urease enzymes are present in all sequenced *Blochmannia* genomes. Genome sequencing across *Blochmannia* species highlights their capacity to synthesize most EAAs. Interestingly, glutamine synthetase loss in some *Blochmannia* strains raises questions about their ability to assimilate ammonia from urea catabolism, making them unique among bacteria [28]. Cysteine conjugate beta lyase may offer a novel mechanism for ammonia processing in certain camponotine-*Blochmannia* symbioses. Drawing parallels with the pea aphid-*Buchnera* system, it emphasizes host involvement in providing essential compounds for symbiont functions. Beetles, which harbour fungal mutualists, also consume fungal tissue, providing an additional source of nitrogen and helping overcome dietary nitrogen shortages [29]. The widespread symbiont, *Erwinia dacicola*, found in olive fruit flies, plays a crucial role in nitrogen recycling, allowing the hosts to utilize nitrogen from waste in their diet [28, 30]. These symbionts are also associated with female ovipositors, suggesting transmission from mother to offspring through egg smearing. This partner fidelity explains the presence of a monophyletic lineage of these bacteria in *Bactroceraoleae*, distinct from other *Erwinia* sp. [10].

3.2. Impact on Insect Fitness and Development

According to Ferrari et al. (2012) [31], *Hamiltonella defensa* is widely distributed in populations of *Aphis pisum* and protects pea aphids from hymenopterous parasitoids [32]. *Aphis fabae*, the black bean aphid, is also protected by this function [33]. Furthermore, there is evidence to suggest that *Aphis craccivora*, the cowpea aphid, can be protected by *Hamiltonella defensa*. Among the well-researched secondary symbionts is *Sodalis glossinidius*, which is vertically transmitted and co-resides with *Wigglesworthia* in tsetse flies [34]. This bacterium has been observed to positively influence host biology, as evidenced by alterations in the longevity of tsetse flies when selectively eliminated. *Wolbachia*, a symbiotic bacterium found in various insect hosts, has been observed to impact a range of behaviors, including sleep, learning and memory, mating, feeding, and aggression [35]. Infected flies displayed heightened nocturnal activity, indicating a potential decrease in arousal levels during nighttime, as observed in a study by [36]. Additionally, the presence of *Wolbachia* was found to prolong the time it takes for flies to fall asleep as the night progresses, as documented by the same researchers. Furthermore, *Wolbachia* infection was associated with improved long-term memory consolidation in both *Drosophila melanogaster* and *Drosophila simulans*, as reported by [37]. In terms of mating behaviors, *Wolbachia* was shown to influence mating preferences, timing, and frequency in host species, according to studies by [38] and [39].

For instance, infected males exhibited higher mating rates compared to uninfected males in both *D. melanogaster* and *D. simulans*, as reported by [38]. In *Drosophila paulistorum* semi-species, females displayed a strong preference for mating with males harbouring the same *Wolbachia* variant, with this preference diminishing when *Wolbachia* levels were reduced, resulting in random mating, as observed by [40]. Similarly, reducing *Wolbachia* levels in male *D. paulistorum* led to the rejection of mating by homogamic wild-type females, indicating *Wolbachia*'s involvement in both pre- and post-mating isolation, as noted by [41]. Additionally, [42] found that male *A. vulgare* spent more time in the vicinity of *Wolbachia*-free females, particularly in virgin females. *Wolbachia* infection was also correlated with increased locomotor activity in insect hosts, as reported by [43]. The effects of *Wolbachia* on host fitness traits seem to be complex, involving alterations in host genes, miRNAs, and proteins.

4. Endosymbionts in Plant Feeding Insects

4.1. Aphids and *Buchnera* symbiosis

Aphids commonly harbor intracellular bacteria called *Buchnera*, a symbiotic relationship crucial for both parties. The bacteria are vertically transmitted through the aphid ovary and are indispensable for optimal aphid growth and reproduction. Aphids without these bacteria exhibit poor growth and limited offspring production. While *Buchnera* remains unculturable outside aphids, it plays a pivotal nutritional role by supplying essential amino acids. Despite its minimal contribution to nitrogen recycling, there is no significant evidence supporting bacterial involvement in aphid lipid and sterol nutrition [44]. Beyond nutrition, *Buchnera* is thought to have non-nutritional functions, with the most supported role being the facilitation of aphid transmission of circulative viruses. This suggests parallels between the nutritional dynamics of the aphid-*Buchnera* association and other insect symbioses involving intracellular microorganisms [45].

4.2. Whiteflies and *Portiera* symbiosis

The key endosymbiont found in all whitefly species, referred to as *Portiera* (officially named "*Candidatus Portiera aleyrodidarum*"), plays a vital role in providing essential amino acids, carotenoids, and other vital metabolites to its host, as highlighted by [46]. These nutrients are essential for whiteflies, as they cannot internally synthesize them or acquire them from their diet or other symbiotic partners. *Portiera*, categorized within the gamma-proteobacteria group, exhibits a significantly reduced genome size. This reduction in genome size is a characteristic feature of the genomic degeneration observed during the co-evolution of obligate intracellular symbiotic bacteria with their hosts, as elucidated by [47].

4.3. Leafhoppers and *Sulcia-Muller* symbiosis

"*Candidatus Sulcia muelleri*," commonly known as *Sulcia*, is a primary endosymbiotic bacterium found in various sap-feeding hemipteran insects, including planthoppers, cicadas, spittle bugs, leafhoppers, and treehoppers [48, 49]. These bacteria, along with other primary endosymbionts, inhabit specialized clusters of cells called bacteriomes located in the abdomen of the insects, where they participate in nutrient exchange with the host. Vertical transmission, passed from parent to offspring, is the primary mode of transmission for these endosymbionts, with no observed instances of horizontal transmission. Consequently, these bacteria function as specialized organelles

within their host insects, and their evolutionary history is expected to closely parallel that of their hosts. *Sulcia*, classified within the Phylum Bacteroidetes, shares a close affiliation with Flavobacteriales, as described by [49, 50, 51]. Currently, *Sulcia* has been definitively identified only in the hemipteran suborder Auchenorrhyncha, although there have been tentative reports from a moss bug and a true bug.

5. Endosymbionts-Mediated Adaptations to Plant Defense Mechanisms

5.1. Counteracting Plant Toxins

In the ongoing interaction between insects and plants, a series of co-evolutionary events have transpired, leading to the development of mechanisms by both parties to surpass each other's defense responses [52]. The complexities of these interactions surpass initial observations, as emphasized by research on the microbiomes of plants and insects [53, 54, 55]. Various insects have developed distinct tactics to cope with plant secondary metabolites or toxins, including terpenes, caffeine, nicotine, cocaine, isothiocyanates, as well as phosphorus- or sulfur-containing insecticides, as documented by [56, 57, 58, 59, 60, 61, 62, 63]. These tactics involve strategies such as storing toxins in fat bodies and employing insect-produced enzymes like cytochrome P450 enzymes, glutathione S-transferases, or esterases, as outlined by [64]. Insects may also sequester toxins for self-defense or metabolize them into non-toxic products that are subsequently excreted [65, 66].

Although a great deal has been written on the many insect-microbe symbioses, one area that still needs more research is symbiont-mediated detoxification, in which microbes connected to insects are essential for the detoxification of plant toxins [67, 68]. Growing research in the area indicates that gut-associated microorganisms play a role in detoxifying synthetic pesticides as well as naturally occurring plant metabolites [69, 70, 71, 72, 73]. An example of a symbiont that helps detoxify calcium oxalate from legumes is the *Candidatus ishikawaella* capsulate, which is found in stinkbugs. It has a plasmid that encodes oxalate decarboxylase [74]. According to [75], endosymbiotic bacteria that detoxify isothiocyanates from cruciferous plants, such as *Serratia*, *Providencia*, *Pectobacterium*, and *Acinetobacter*, are harbored by the larvae of the cabbage root fly. Using 2-phenylethyl isothiocyanate as a source of nitrogen, *Pectobacterium* breaks it down with the help of its enzyme, Sax A [75]. Furthermore, the gut bacterium *Pseudomonas fulva* helps the coffee berry borer *Hypothenemus hampei* overcome the protective alkaloid caffeine in coffee plants by breaking down the toxin [74, 75].

According to [75, 76, 77, 78], insect endosymbionts influence plant defense pathway modification and insect gene expression through their involvement in salivary secretion, elicitor chemicals, proteins, and insect defense enzymes. Salivary protein composition differs dramatically between endosymbiont-carrying and non-carrying insects, and microorganisms in insect regurgitant can suppress essential plant defense enzymes to provide defense while eating [79, 80].

5.2. Modulation of Plant Hormone Signaling

Plants respond to insect attacks by activating induced responses, which are primarily controlled by phytohormones such as cytokinin (CK), salicylic acid (SA), ethylene (ET), jasmonic acid (JA), and ethylene (ET) [81, 82]. Due to their distinct elicitor and effector molecules, herbivores and microbial pathogens initiate particular signaling pathways that

result in different patterns of response [83]. When subjected to herbivory by chewing insects, plants initiate responses through the JA/ET signaling pathway. Endosymbionts present in the oral secretions of these chewers not only activate herbivory defense in the plant but also modulate hormonal interactions. According to [84], symbionts connected to insect salivary glands generate inhibitors that block JA-mediated reactions. One prominent example is the Colorado potato beetle (*Leptinotarsa decemlineata*), a major pest of potatoes that feeds on the host plant while transferring its salivary endosymbiont, *Pseudomonas*. According to [85], these symbionts release flagellin, which triggers an SA-dependent pathway in the plant. This pathway suppresses JA signaling, weakening the plant's defenses against the pest. Another example is the aster yellow phytoplasma, which infects plants by way of *Macrostelus quadrilineatus*, a leafhopper, and its salivary glands. The leafhopper's fertility increases when this phytoplasma prevents JA synthesis at its feeding site [86].

6. Evolutionary Dynamics of Endosymbiont-Plant-Insect Interactions

6.1. Co-evolutionary pattern

Within natural ecosystems, a complex interplay occurs among various living organisms, with plants and insects being key contributors. The intimate association between these two organisms is marked by insects providing essential services such as defense and pollination, while plants offer shelter, oviposition sites, and food – crucial elements for insect proliferation [87]. However, depending on the severity of insect attacks, herbivores can pose a significant threat to plants, potentially leading to their demise.

The relationship that exists between plants and insects is dynamic and constantly evolving. Plants have evolved a variety of defense systems, including chemical and physical barriers, to lessen the impact of insect attacks. These mechanisms include producing secondary metabolites [88, 89]; modulating trichome density [90]; inducing defensive proteins [91]; and emitting volatiles that draw insect predators [92]. As a result, insects have evolved defense mechanisms against these plant barriers. These include sequestering toxins [91], detoxifying poisonous chemicals [93], and changing gene expression patterns [94].

Illustrating the coevolutionary dynamics between animals and symbionts under controlled laboratory conditions poses challenges due to the typically lengthy timeframes involved. Nonetheless, researchers can infer insect-symbiont coevolution through phylogenetic and genomic analyses, as noted by [95] and [96]. Insects that rely on phloem sap as their primary food sources, such as species within the Hemiptera, harbour symbionts capable of supplementing nutrients to compensate for deficiencies in their diet, as highlighted by [97] and [98]. Many hemipteran taxa and their bacterial endosymbionts exhibit complementary biosynthetic and metabolic processes, fostering close associations, as observed in studies by [99, 100, 101]. For instance, the primary endosymbiont *Buchnera aphidicola* has coadapted and evolved alongside aphids over millions of years, as demonstrated by [102, 103, 104]. Similar instances of coevolution have been documented with extracellular gut symbionts that facilitate nutrient provisioning, such as *Ishikawaella capsulata* in plataspid stinkbugs, as researched by [105], and *Rosenkranzia clausaccus* in acanthosomatid stinkbugs, as observed by [106].

6.2. Horizontal transmission

The transmission of germs horizontally may have been a major factor in detoxification processes, in addition to the direct involvement of detoxification. Here, we provide data suggesting that *Cardinium* can spread interspecifically and horizontally in leafhoppers. This spread happens when the insect host punctures plant tissue. We show that the salivary glands of the cicadellid *Scaphoideus titanus*, a grapevine-feeding insect that carries *Cardinium*, release the metal into the plant tissues, where it is then horizontally absorbed by other insects that feed on grapevine and those that feed on other plants [107].

A free-living life stage and horizontal transmission through environmental acquisition are likely possessed by many toxin-degrading microorganisms, as they are commonly found in the gut and are easily cultured outside of their hosts [108].

The *Burkholderia* that breaks down MEP, for example, is found in the surrounding soil in the case of the bean bug *Riptortus pedestris*. There is evidence of a mixed mode of symbiont transmission in the chinchbug *Cavelerius saccharivorus*. In this case, the *Burkholderia* symbiont is mainly obtained from environmental soil, but it is also partially transferred from mother to offspring via contamination of the egg surface [109, 110].

6.3. Impact on Insect-Plant Coevolution

In the intricate relationships between insects and plants, microorganisms are essential but frequently disregarded "hidden players" [54, 111, 112]. The impact of insects is multifaceted and includes things like the range of host plants that they can infect [113, 114], how well they can feed [115], how insects metabolize [67], how well they can manipulate plant physiology to their advantage [116, 117] and more broadly, how diverse and speciation are among insects [118].

By obstructing signal transduction pathways, suppressing or opposing the expression of genes related to plant defense, or altering plant primary and secondary metabolisms, insect symbionts can have an impact on plants either directly or indirectly [119, 120, 121]. Through direct or indirect impacts on their insect hosts, these symbionts also affect the relationships between plants and insects. They could alter insect immunity and reproduction [122, 123] or introduce new metabolic pathways [67, 96], which would impact plant exploitation [124].

7. Manipulation of Plant Phenotypes by Insect Endosymbionts

7.1. Gall Formation and Plant Structure Modification

Numerous of invertebrates have formed close partnerships with bacterial symbionts, with certain genes responsible for cytokinin synthesis potentially originating from bacteria. This is exemplified by *Agrobacterium* inducing distinctive galls through cytokinin production, as discussed by [125]. Many herbivorous insects, which harbour these symbiotic microbes, employ cytokinins to establish 'green islands,' redirecting plant nutrients to these infection sites and thus delaying the death of the host tissue. A notable example is observed in the apple leaf miner *Phyllonorycter blancardella*, which depends on cytokinins produced by its endosymbiotic bacteria *Wolbachia* to maintain a green island on the plant leaf, as described by [117]. Within the genomes of *Wolbachia*, a key gene involved in cytokinin biosynthesis is tRNA-IPT. Various *Wolbachia* species are associated with a wide range of insects and are known for their ability to suppress induced plant responses, thereby aiding the feeding and/or reproduction of their hosts, as highlighted by

[85, 113, 126].

8. Applications in pest management

Due to the effects of global climate change and growing human populations, insect symbionts offer a possible solution to the growing demand for creative pest management techniques [127, 128]. The use of heterologous microorganisms, paratransgenesis, the insect incompatibility technique (IIT), and the destruction of microbial symbionts critical for insect pests are four major strategies that have a great deal of promise [72]. These tactics are presently being developed, with an emphasis on battling disease pathogens that are transported by insect vectors. Here, we'll talk about notable instances and developments in the application of these approaches to the management of vector-borne illnesses, in the larger framework of the growing need for sustainable, efficient methods of controlling insect pests and environmentally friendly.

8.1. Heterologous associations

Wolbachia trans-infection has emerged as a promising avenue in controlling insect-borne diseases, including malaria, dengue, yellow fever, and Chagas. This strategy involves transferring *Wolbachia* strains from one species to another, particularly into major disease vectors like *Aedes aegypti* and *Anopheles* mosquitoes, which do not naturally harbour *Wolbachia* [129]. The presence of *Wolbachia* in transinfected mosquitoes has been found to interfere with pathogen transmission, impacting a wide range of pathogens. Studies suggest that *Wolbachia*, particularly strains like wMelPop, which shorten the mosquito's life span, can significantly reduce disease transmission by removing older individuals, critical for pathogen dissemination. Moreover, the antiviral effects of *Wolbachia* in heterologous associations are attributed to a combination of metabolic and immunological processes, including the priming of the immune system and the production of reactive oxygen species. These findings emphasize the potential of *Wolbachia*-based strategies in controlling vector-borne diseases by exploiting heterologous associations in various mosquito species, thus offering a promising approach to disease management [130, 131, 132, 133, 134, 135]. The utilization of *Wolbachia* in insect pest management, particularly through the trans-infection of *Aedes aegypti* mosquitoes, has emerged as a promising strategy. Initially introduced through a careful two-step process involving adaptation in mosquito cell culture and subsequent microinjection into *Ae. aegypti* embryos, strains such as wMelPop-CLA have displayed significant potential in reducing the vector competence of these mosquitoes for pathogens like dengue virus. Notably, field trials in regions such as Australia, Indonesia, Malaysia, Vietnam, and Brazil have shown promising reductions in dengue incidence following the release of *Wolbachia*-transinfected *Ae. aegypti* populations [136, 137, 138, 139].

Furthermore, the application of *Wolbachia* extends beyond *Ae. aegypti* to other mosquito vectors such as *Anopheles* spp. The introduction of *Wolbachia* into *Anopheles* mosquitoes, traditionally vectors for malaria, has shown potential in reducing the transmission of *Plasmodium* parasites. Studies have indicated that *Wolbachia* strains like wMelPop and wAlbB can significantly inhibit the development of *Plasmodium* spp. in *Anopheles* mosquitoes, presenting a novel avenue for malaria control strategies [132, 134, 140]. However, challenges such as the induction of cytoplasmic incompatibility and stable vertical transmission in wild mosquito populations remain crucial

factors to address for the successful implementation of *Wolbachia*-based control measures [133]. These advancements highlight the potential of *Wolbachia* trans-infection as a versatile tool in combating mosquito-borne diseases, both in human health and agricultural contexts. Moreover, recent endeavors have extended the application of heterologous associations to agricultural pest management, as evidenced by the successful introduction of *Wolbachia* strain wStri into the brown planthopper, *Nilaparvata lugens* [141]. This intervention not only induced high levels of cytoplasmic incompatibility but also inhibited the transmission of Rice ragged stunt virus, signaling a novel strategy for controlling major agricultural pests and their associated pathogens [142].

Regarding agricultural pests and human disease vectors in particular, paratransgenesis—which modifies insect features by genetically altering related microorganisms—has become a viable strategy in insect pest management [143]. In contrast to direct genetic manipulation of insects, paratransgenesis addresses issues like lower transgene fitness outside of the laboratory and inefficiency in introducing transgenes into natural vector populations by engineering gut bacteria to produce proteins that hinder pathogen development and insect fitness. Key requirements for successful paratransgenesis include the ability to culture, transform, and reintroduce microbial partners into insect hosts, with gut bacteria like *Sodalis glossinidius*, *Asaia sp.*, and *Pantoea agglomerans* being suitable candidates due to their genetic amenability and specificity to target insects. This strategy has been applied across various disease vectors, including the triatomine *Rhodnius prolixus* for Chagas disease, anopheline mosquitoes for malaria, tsetse flies for sleeping sickness, and the glassy-winged sharpshooter *Homalodisca vitripennis* for Pierce's disease of grapes, showcasing its potential for integrated pest management in both human health and agriculture [77, 144, 145, 146].

Paratransgenesis, initially employed in the triatomine bug *Rhodnius prolixus*, a vector for *Trypanosoma cruzi* causing Chagas disease, involves manipulation of the insect gut microbiota. The symbiont *Rodhococcus rhodnii*, which co-localizes with *T. cruzi* in the midgut, plays a pivotal role in the bug's growth and development, as indicated by [147, 148, 149]. *Rhodnius rhodnii* has been genetically engineered to produce anti-trypanosomal molecules, such as cecropin A, which demonstrate significant inhibitory activity against *T. cruzi*, as outlined by [150, 151, 152]. The introduction of these modified bacteria into insects has resulted in the reduction or elimination of *T. cruzi*, often reducing levels to undetectable levels, according to [147]. Additionally, transformation with an anti-trypanosome single-chain antibody has shown a substantial decrease in parasite load, as reported by [147]. Subsequent field trials have assessed the dispersal efficiency of modified symbionts. *R. prolixus* nymphs naturally acquire the symbiont from adult feces, and field trials introduced engineered symbionts via synthetic faecal materials known as CRUZIGARD, leading to successful infection of insect progeny, as documented by [147, 153].

Incompatible Insect Technique (IIT) offers a promising approach to controlling insect pests by exploiting the mechanism of *Wolbachia*-induced cytoplasmic incompatibility (CI) to manipulate natural populations of arthropod pests through embryonic lethality. This technique involves either unidirectional or bidirectional CI, where incompatible matings lead to embryonic lethality, ultimately suppressing target

populations. While traditional IIT methods resemble the sterile insect technique (SIT), involving mass-rearing and inundative releases of sterile males, *Wolbachia*-based IIT provides a species-specific and environmentally friendly alternative. However, before field applications, critical assessments of IIT insects' genotype, *Wolbachia*'s impact on host fitness, and the stability of the association are necessary. Extensive research has explored the application of IIT against various mosquito species, such as *Culex pipiens* and *Aedes albopictus*, demonstrating successful suppression of target populations and the feasibility of combined SIT/IIT protocols. Feasibility studies have shown promising results for controlling mosquito populations by integrating SIT with *Wolbachia*-infected strains, which exhibit strong CI effects, requiring lower irradiation doses for achieving female sterility. Additionally, IIT has shown success against agricultural pests like *Ephesia cautella* and *Ceratitis capitata*, where mass production and release of incompatible males effectively reduced insect populations, suggesting the potential of *Wolbachia*-induced CI as an environmentally friendly tool for pest control. These findings highlight the versatility and potential of IIT in both vector and agricultural pest management [154, 155, 156, 157, 158, 159].

Manipulating insect-associated symbionts involves eliminating or disrupting the microorganisms essential for the insects' growth, reproduction, and survival, as well as interfering with symbiont transmission to the next host generation [17, 72, 160]. This can be achieved through methods such as heat treatment and the use of specific symbiostats [45, 146]. Heat treatment indirectly affects insects by manipulating their microbial partners, as discussed in previous sections [45, 161]. Another method involves using symbiostats to perturb or eliminate symbionts, particularly effective for insects reliant on obligate bacteria transmitted vertically [45, 161]. Antibiotics have been routinely used to eliminate prokaryotic microorganisms from various insect species, but their toxicity to the host insect and environmental concerns limit their applicability [131]. Antimicrobial peptides (AMPs) have also been explored to manipulate insect symbionts, with the potential for heterologous expression in crops [72, 152]. However, toxicity to other organisms remains a concern. The focus now is on developing cost-effective and specific methods to disrupt insect-symbiont associations, particularly nutrient translocation between the insect and microbial partners [64, 162].

Surface sterilizing eggs can be a useful method of stopping symbiont transmission to the following generation. To stop newly hatched nymphs from obtaining symbiotic bacteria, sterilizing treatments such as formaldehyde or bleach can be used to eliminate the bacteria from the egg surface [163, 164]. Many stinkbug species have been targeted with this technology as a pest management approach [128, 163, 166].

9. Challenges and future directions

9.1. Unravelling Complexity in endosymbiont- plant-insect networks:

Nutrition plays a vital role in the interactions between organisms, with insects, displaying over 4 million species, standing out as evolutionary successes. Among their diverse feeding strategies, herbivory predominates, although plant tissues often provide suboptimal nutrition. Phytophagous arthropods employ various behavioral and physiological adaptations, including symbiotic associations with microorganisms to bridge this gap. These symbionts, often

overlooked but significant, influence insect host plant range, feeding efficiency, metabolism, and even their ability to manipulate plant physiology. Moreover, they can indirectly impact plant-insect interactions by altering insect reproduction, immunity, and interactions with natural enemies. Recent studies highlight the complex ecological dynamics of insect-microbe interactions and their profound effects on plant-insect interactions, promising insights into the broader understanding of these ecological relationships [54, 111, 112].

9.1.1. Direct Effects of Symbionts in Plant-Insect Interactions

9.1.1.1. Influence on Insect Nutrition and Metabolism:

Insects, particularly those feeding on nutritionally imbalanced diets like plant sap, often form symbiotic relationships with microorganisms to acquire essential nutrients and vitamins they cannot produce independently. For instance, obligate symbioses with intracellular bacteria like *Buchnera aphidicola* in aphids or *Sulcia* in sap-feeding Auchenorrhyncha insects provide vital amino acids and vitamins. These symbionts, despite having reduced genomes, complement the insect's metabolic deficiencies, showcasing metabolic interdependency and compensatory mechanisms [17, 96, 167, 168, 169].

9.1.1.2. Influence on Insect Immunity and Plant Exploitation

Insect symbionts can modulate the host's immune responses, affecting interactions with host plants. For example, symbionts in aphids influence immune gene expression, potentially altering their ability to exploit plant hosts [124, 170, 171, 172]. Additionally, they can secrete proteins like macrophage migration inhibitory factors, interfering with plant immune systems and aiding in plant exploitation [172]. This illustrates how symbionts can manipulate insect immune responses to benefit the insect's interaction with host plants.

9.1.1.3. Influence on Plant Nutritional Status and Morphology

Microorganisms associated with insects can influence plant hormonal balances, facilitating insect colonization and exploitation. By secreting or inducing phytohormones, symbionts like *Wolbachia* in leaf-mining insects or biotrophic fungi in gall midges manipulate plant metabolism and morphology, aiding insect development and gall formation [117, 120, 173].

9.1.1.4. Impact on Plant Secondary Metabolism/Plant Immunity:

Symbionts can suppress plant defense mechanisms, facilitating insect feeding. For instance, saliva from symbiont-infected insects can suppress jasmonic acid-related defenses in plants, promoting insect growth [85, 174]. Conversely, symbiont-associated proteins may induce plant defense responses, as seen in the aphid-*Buchnera* system [175]. This indicates the complex interplay between insect symbionts and plant defense signalling pathways.

9.1.1.5. Horizontal Gene Transfers That Influence Plant-Insect Interactions:

Herbivorous insects have adapted to plant diets in part through horizontal gene transfer events from microbes to insects. Enzymes for plant cell wall degradation, detoxification of plant toxins, and metabolism of plant products are encoded by genes

acquired through horizontal transfer, which improves insect fitness and adaptability to particular host plants [176, 177, 178, 179, 180]. Plant-insect interactions can result in indirect impacts of symbionts via both plant-mediated and insect-mediated routes. These consequences cover a wide range of topics, such as effects on insect reproduction, interactions with herbivores' natural enemies, and transfer of plant diseases.

9.1.1.6. Impact on Insect Reproduction

To boost daughter production at the expense of son production, symbionts such as *Wolbachia*, *Arsenophonus*, *Cardinium*, *Rickettsia*, and *Spiroplasma* can control insect reproductive. As to [181], this manipulation encompasses the following: male death, cytoplasmic incompatibility (CI), feminization of genetic males, and induction of thelytokous parthenogenesis. To minimize rivalry with brothers and prevent inbreeding depression, *Spiroplasma*, for example, causes male mortality in pea aphids. This may benefit infected females [182]. According to [136], there is a correlation between the introduction of *Rickettsia* in whiteflies and a rise in prejudice against females in the offspring of infected adults.

9.1.1.7. Interactions with Natural Enemies of Herbivores

Symbionts can confer protection to their host insects against natural enemies such as parasitoids and pathogens. For example, strains of *Hamiltonella defensa* protect aphids against parasitoids [32, 183]. Oliver et al., [32], while *Rickettsiella viridis* protects ladybirds [181]. In *Drosophila*, *Wolbachia* and *Spiroplasma* have been shown to enhance survival against parasitoids and viruses [184]. Mechanisms of protection may involve the production of toxins or other biologically active compounds by symbionts [185].

9.1.1.8. Interactions with Plant Pathogens

Symbionts can influence plant pathogen transmission by insect vectors, either directly or indirectly. In aphids and whiteflies, endosymbiotic bacteria have been implicated in the transmission of plant viruses [186, 187]. For example, GroEL proteins produced by endosymbiotic bacteria may facilitate the circulative transmission of certain viruses [188]. Additionally, *Wolbachia* infection in mosquitoes is utilized to limit the transmission of pathogenic viruses like dengue [189, 208].

9.1.1.9. Variation in Ecological Niches and Specialization among Insects:

Ecological diversification in phytophagous insects often involves symbiotic associations with microorganisms, which can provide crucial adaptations for exploiting new habitats or resources. These symbionts play a significant role in the adaptation of insects to different ecological niches and feeding habits [189]. For instance, the obligate symbioses formed between hemipteran insects and specific bacterial lineages, such as *Buchnera* in aphids, *Carsonella* in psyllids, *Portiera* in whiteflies, and *Tremblaya* in mealybugs, have facilitated the colonization of diverse plant species and contributed to the generation of substantial biodiversity within these insect groups [96].

Furthermore, facultative symbionts acquired by insects can also drive ecological diversification by providing adaptive traits. Horizontal transfer of facultative symbionts, although predominantly maternally inherited, can occur between host species, leading to the rapid acquisition of ecologically significant traits. These symbionts serve as a horizontal gene

pool, endowing the recipient hosts with traits that enhance their ability to exploit new habitats or resources or to thrive in their existing ecological niche [190]. The dynamic nature of symbiotic associations allows for various evolutionary trajectories, such as the replacement of obligate symbionts by facultative ones or the evolution of complementation among multiple symbionts within a host species [100, 191, 192, 193, 194].

Moreover, symbionts can influence the plant specialization of their insect hosts, potentially leading to sympatric speciation events. Changes in the composition of symbiotic communities within insect populations, driven by host plant affiliation or other factors, may indicate symbiont-mediated plant specialization. Experimental studies have shown that symbionts like *Regiella insecticola* and *H. defensa* can enhance the performance of aphids on specific host plants, suggesting a role in plant specialization [174, 195]. These symbiont-mediated effects on host plant specialization can create conditions for divergent selection among plant-adapted populations, contributing to the process of speciation [196].

Additionally, symbiotic associations have been implicated in promoting reproductive isolation and speciation in insects. Symbionts can influence both pre-mating and post-mating isolation mechanisms. Pre-mating isolation can be facilitated by symbiont-mediated habitat specialization or modifications of host behavior, while post-mating isolation can result from symbiont-induced cytoplasmic incompatibility or hybrid inviability/sterility associated with symbiont proliferation [40, 197, 198]. Overall, symbionts can act as "magic traits," promoting ecological speciation by influencing both ecological specialization and reproductive isolation [199].

Understanding the evolutionary dynamics of plant-insect-microbe interactions requires considering the mechanisms facilitating or limiting symbiont acquisition over ecological and evolutionary time scales. Horizontal transmission of symbionts is influenced by factors such as host ecology, phylogenetic relatedness, and interactions with other symbionts or parasitoids [190]. Recent evidence suggests that some symbionts may even exploit host plants for transmission, blurring the line between insect symbionts and plant pathogens [107, 200]. The complex interplay between insects, plants, and microbes underscores the importance of studying symbiotic interactions in shaping the evolutionary trajectories of phytophagous insects.

9.2. Technological Advances in Studying Endosymbiotic Interactions

Advancements in technology are helpful for researchers to study endosymbiotic interactions. Technological advancements in endosymbiont manipulation have emerged as promising strategies for insect pest control. Traditional methods such as transposon mutagenesis have been used to study the role of microbial genes in insect-microbe interactions, but they require mutant libraries and lack precision [201]. Recent approaches utilizing the CRISPR/Cas9 gene editing system offer more targeted manipulation of bacterial genomes within insect guts [202].

According to [203], CRISPR/Cas9 can eliminate particular bacterial genes that are important in host-microbe interactions, which reduces the production of biofilms and colonization in insect guts. Hegde et al, [202] utilized CRISPR/Cas9 to impede the expression of the *ompA* gene in *Cedecea neteri*, a symbiont that causes poor biofilm development in the stomach of *Aedes aegypti* mosquitoes.

This illustrates how CRISPR/Cas9 may be used to modify the genomes of insect symbionts with promising results.

Another innovative approach for insect pest control involves RNA interference (RNAi) mediated by symbionts. RNAi has been established as an effective method for gene knockdown in various organisms, including insects [204]. However, challenges such as high production costs and technical limitations hinder its widespread use [202, 203]. To overcome these challenges, researchers have explored the delivery of dsRNA via microbes. Studies have shown that dsRNA synthesized by bacteria can induce nymphal mortality in beetles and effectively control aphids [205]. Symbiont-mediated RNAi (SMR) involves engineering gut symbionts to synthesize and deliver dsRNA targeting specific genes in the host insect [206]. For instance, symbiont *Candidatus Serratia symbiotica* has been successfully engineered to produce dsRNA, demonstrating the potential of SMR in controlling insect pests.

RNA interference (RNAi) and paratransgenesis have recently been combined in *R. prolixus* through the introduction of genetically modified *Escherichia coli* that express dsRNA for particular proteins. Significant fitness effects for the insect were caused by this strategy, including lower female fertility and poor nymph development [207]. These technological advancements in endosymbiont manipulation offer novel approaches for insect pest management, providing more targeted and environmentally friendly strategies compared to traditional methods. Further research and development in this field should be continued for the promise of future insect pest control.

9.3. Ethical Considerations in Manipulating Endosymbionts for Pest Management

When considering the manipulation of insect endosymbionts for pest management, ethical considerations arise at various levels. It's crucial to conduct comprehensive risk assessments to understand the potential ecological and human health impacts of introducing genetically modified organisms into natural ecosystems [208]. This includes evaluating unintended consequences like the spread of engineered endosymbionts to non-target species or disrupting ecosystem dynamics.

Ethical frameworks stress the importance of prioritizing long-term ecological sustainability, ensuring pest management strategies don't inadvertently harm non-target organisms or disrupt ecosystem functioning [209]. Transparency and stakeholder engagement, including local communities and indigenous groups, are vital to ensure decisions are informed by diverse perspectives and values [210]. Compliance with regulatory frameworks established by government agencies for environmental protection and public health is crucial for risk mitigation and accountability [211]. Additionally, it's essential to address potential disparities in access to pest management technologies, especially in vulnerable communities disproportionately affected by pest-related issues [212]. Integrating these ethical principles into research, policy, and decision-making processes is vital for developing responsible and sustainable approaches to pest management that uphold environmental integrity and ethical stewardship.

10. Conclusions

Endosymbionts play a complex role in shaping the nutritional ecology and fitness of insects, as well as influencing their interactions with plant hosts in various ecological conditions. Endosymbionts play a vital role in mediating adaptations of insects to plant defence mechanisms, facilitating the insects

ability to overcome various challenges posed by their plant hosts. This symbiotic relationship allows insects to thrive on plants that employ chemical defenses as protective mechanisms. Insect endosymbionts have demonstrated remarkable abilities to manipulate plant phenotypes for the benefit of their hosts. The microbiome of agriculturally significant pest insects holds promising potential for advancing current pest management methods. Opportunities include using the host's microbiome to directly target the pest and anticipate host characteristics and the effectiveness of control methods or diminishing vector competence. Rapid microbial evolution overtakes that of insects, enabling swift adaptation of pest insects to plant secondary metabolites through symbiotic relationships. The rising demand for innovative insect pest management, driven by population growth and climate change, made symbiotic microorganisms as a potential solution. Currently, the only method regularly used in symbiont-based pest management is the sterile insect technique; while ongoing developments in paratransgenesis face challenges due to genetic modification requirements. If insect pest status relies on symbiont genotype, this could inform the identification or selection of genotypes aligned with specific pest management goals, ideally using low-tech strategies. Understanding the importance of endosymbionts in these interactions is essential to resolving the complexities of ecological networks and developing strategies for pest management and conservation. In summary, the future implications of endosymbionts in pest management are promising, offering innovative solutions for addressing global challenges in agriculture, public health, and environmental conservation. Continued research and development in this field is needed for effective pest control practices and to promote sustainable approaches to pest management.

11. Future scope of the study

The study of endosymbiosis, particularly its role in insect biology, presents several promising avenues for future research. Investigating the diverse functions of endosymbionts within insects, such as nutrient provisioning, nitrogen recycling, and detoxification, could reveal novel insights into their evolutionary adaptations and ecological significance. Future studies might focus on the genetic and biochemical pathways that facilitate these symbiotic relationships, potentially identifying new targets for pest management and sustainable agriculture practices. Additionally, exploring the manipulation of plant phenotypes by endosymbionts and their influence on ecological communities could uncover innovative strategies for enhancing crop resilience and controlling pest populations. Addressing the challenges in studying these complex interactions, such as the specificity and diversity of endosymbiont-host relationships, will be crucial. Overall, the expanding understanding of endosymbionts holds significant potential for advancements in ecological research, biotechnology, and integrated pest management.

Conflict of interest

All the authors have thoroughly reviewed the review article and have no conflict of interest in submission of the article to "Agriculture Association of Textile Chemical and Critical Reviews Journal"

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