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Future perspectives in the study of mutualistic interactions between insects and their microorganisms

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Abstract. The impact of climate change and habitat destruction on insect diversity and survival is a critical area of study. These disruptions could severely affect the symbiotic relationships between insects and their microorganisms. Understanding how these interactions respond to such changes is essential for mitigating the decline of insect populations, which are already alarmingly decreasing worldwide. Mutualistic interactions between insects and microorganisms present vast opportunities in ecology, agriculture, and biotechnology. These associations are crucial for insect nutrition, defense, and adaptation and hold great potential for developing antimicrobial compounds with promising applications in the pharmaceutical industry. In agriculture, insect-associated microorganisms could play a key role in biological pest control, offering sustainable alternatives to chemical pesticides. This would not only protect beneficial insects but also enhance agricultural efficiency. The conservation of mutualism must be integrated into biodiversity preservation efforts, as protecting these relationships will be critical in addressing future ecological challenges. The following sections describe the main mutualistic interactions between insects and their associated microorganisms, with a prospective approach to the directions that future research should consider.

1 Introduction

Insects are the group of organisms with the greatest species diversity in the world, with approximately 1 million species described; however, it is believed that this number represents only about 20 % of the species that currently exist (Li and Wiens, 2023). Insects play a fundamental role in ecosystems, as they participate in various key functions such as nutrient recycling, organic matter decomposition, seed dispersal, and pollination (Wagner, 2020; Li and Wiens, 2023). Some insects act as predators, meaning they feed on other insects. Moreover, certain groups considered parasitoids oviposit within the bodies of pest insects, allowing their larvae to hatch in the hemocoel where they feed and develop while avoiding the immediate death of their host, until the larvae are able to emerge (Wagner, 2020; Toro-Delgado et al., 2022; Li and Wiens, 2023). These pests can feed on plants (phytophagous) or act as vectors of diseases that affect both plants and animals, including humans.

Insects play a crucial role in the stability of ecosystems worldwide and in human survival. It is estimated that approximately 75 % of agricultural crops depend on insect pollination, which directly links them to global food security (Wagner, 2020). Some experts suggest that most terrestrial vertebrates are directly or indirectly connected to insects, and their disappearance would accelerate the sixth mass extinction (Wagner, 2020; Wagner et al., 2021).

Currently, there is growing concern due to estimates indicating a reduction of up to 70 % in flying insect populations in some regions of the world. This phenomenon is evident in everyday situations, such as the decrease in the number of insects splattered on car windshields, which was common in the past. Nevertheless, in the present day, this phenomenon occurs less frequently due to the considerable reduction in insect populations, leading to a marked decline in their sightings (Wagner, 2020; Wagner et al., 2021). The decline in insect populations has been linked to factors such as global warming and climate change, as well as various human activities, including habitat destruction, intensive agriculture, and the excessive use of pesticides. These factors impact not only pest insects but also beneficial ones (Wagner, 2020; Wagner et al., 2021; Maurice-Lira et al., 2024).

As previously mentioned, various studies have focused their efforts on designing strategies for the management and protection of beneficial insects. A promising alternative is the study of microorganisms associated with these insects. Recent research has demonstrated that microbiota play a fundamental role in the health and development of organisms. Therefore, understanding the ecophysiology of the interactions between insects and their microorganisms will enable future studies to develop strategies based on the microbiome (Mondal et al., 2023; Maurice-Lira et al., 2024). These strategies could enhance the resilience and survival potential of these important organisms.

The objective of this work was to describe the primary mutualistic interactions between insects and their associated microorganisms while providing a forward-looking perspective on potential directions for future research. To do so, we conducted a narrative literature review of scientific publications. The search for relevant materials was performed using Google Scholar, Scopus, and PubMed. On these platforms, we focused on peer-reviewed research articles, review articles, and books published in English.

2 How do microorganisms enhance the survival capacity of insects?

There is no doubt that insects are among the most successful organisms, dispersed across all continents and latitudes. Their abundance is so great that it is estimated there are approximately 200 million insects for every human being (Li and Wiens, 2023). The success of insect survival is believed to be partly due to their ability to establish symbiotic interactions with various organisms, including plants, other animals, and microorganisms (primarily fungi and bacteria). The latter are crucial to insect survival (Mondal et al., 2023).

When considering the relationship between microorganisms and insects, the first association that often comes to mind is that of entomopathogenic fungi that infect and feed on them. However, numerous associations between insects and microorganisms are highly beneficial for the insects, which provide key advantages for their survival and adaptation (Chevrette et al., 2019; Cusumano and Lievens, 2023; Maurice-Lira et al., 2024). First, it is important to understand that the relationship between insects and entomopathogenic microorganisms is classified as "parasitism", in which one organism (the entomopathogen) benefits while the other (the insect) is harmed; however, this article will focus on "mutualism symbiosis", in which both symbionts, microorganisms and insects, obtain mutual benefits.

2.1 Microorganisms as food for insects

One of the most iconic mutualistic interactions between insects and microorganisms occurs between fungus-farming ants of the tribe Attini. Approximately 60 million years ago, these ants developed the ability to cultivate their own food. Their sole nutritional source is an edible fungus of the species *Leucoagaricus gongylophorus* (Möller) Singer, 1986 (Basidiomycota: Agaricales: Agaricaceae), which has become incapable of surviving outside of this symbiosis, making it an obligate mutualist. This fungus depends on the ants to cultivate and protect it in fungal gardens built by them. In return, the fungus produces microscopic, globular structures called gongylidia, which contain specialized vacuoles that store lipids, amino acids, and carbohydrates, all easily assimilated by the ants (Schultz, 2020, 2022).

Another fascinating case of mycophagous insects involves the larvae of *Scaptotrigona depilis* (Moure, 1942) (Hymenoptera: Apidae: Meliponini), which develop in a liquid culture medium primarily composed of honey, propolis, and fermented pollen, prepared by adult stingless bees. It was discovered that the larval food harbors two symbiotic fungi: a filamentous fungus of the genus *Monascus* Tiegh., 1884 (Ascomycota: Eurotiales: Aspergillaceae), and a yeast of the genus *Zygosaccharomyces* Barker, 1901 (Ascomycota: Saccharomycetales: Saccharomycetaceae). Both fungi were consumed by the stingless bee larvae. In the case of the filamentous fungus, the larvae ingested the mycelium during the early stages of their development, while the yeast provided an additional benefit by producing ergosterol, a precursor molecule in the synthesis of metamorphosis-promoting compounds, facilitating the transformation of larvae into adult insects. When the yeast was removed, a significant reduction in metamorphosis success was observed. Similarly, scientists found that removing the filamentous fungus resulted in larval mortality or defective development, underscoring the importance of these microorganisms in the successful development of stingless bees (Menezes et al., 2015; Paludo et al., 2018; Maurice-Lira et al., 2024).

As in the previously mentioned cases, other mycophagous insects, such as flies and beetles, have been identified as feeding on the mycelium of saprobic fungi that grow on decaying organic matter (Pollierer et al., 2020; Six and Klepzig, 2021). Some collembolans from the order Poduromorpha also play a notable role as fungal spore dispersers; these arthropods consume mushrooms but are unable to digest the spores, which remain viable when expelled in fecal pellets (Hernández-Santiago et al., 2020). Similarly, termites of the genus *Macrotermes* Holmgren, 1913 (Blattodea: Termitidae), from the family *Termitidae* feed on a fungus of the genus *Termitomyces* Heim, 1942 (Basidiomycota: Agaricales: Lyophyllaceae), that grows within their nests (Um et al., 2013; Darlington, 2021).

The previously described interactions demonstrate that insects benefit from fungi, which utilize nutrients from fresh or decaying plant matter, acting as intermediaries that facilitate the flow of nutrients from plant tissues to the insects. This occurs because insects lack the necessary enzymes to break down plant biomass on their own, as detailed below (Tsegaye et al., 2019; Khadempour et al., 2020; Six and Klepzig, 2021; Schultz, 2022; Huerta-García and Álvarez-Cervantes, 2024).

2.2 Microorganisms as an extension of insect metabolism

Due to their often specific and restricted feeding habits, insects frequently have limited nutrient acquisition; consequently, some microorganisms present in their digestive system perform specific metabolic functions to enhance the nutrition of their insect hosts (Khadempour et al., 2020). These microorganisms assist in insect nutrition by carrying out enzymatic processes that insects cannot perform on their own, enabling them to access nutrients from their food that would otherwise be unavailable (Huerta-García and Álvarez-Cervantes, 2024).

Most wood-feeding insects (xylophagous) lack the physiological capacity to assimilate the carbon sources present in lignin. However, these insects harbor specialized microorganisms that can break down complex molecules like lignin, generating simpler compounds that the insects can assimilate (Singh et al., 2019; Six and Klepzig, 2021).

Termites *Cryptotermes* spp. (Blattodea: Kalotermitidae) are an extraordinary example of xylophagous insects; their ability to assimilate wood is due to the cohabitation of several bacterial species in their intestines, which are responsible for breaking down the complex carbon molecules that constitute wood, such as lignin, cellulose, hemicellulose, and xylan (Tsegaye et al., 2019). This type of mutualistic association has also been observed in *Acrobasis nuxvorella* Neunzig, 1970 (Lepidoptera: Pyralidae), and beetles such as *Dendroctonus rhizophagus* Thomas and Bright, 1970 (Coleoptera: Curculionidae) (Soto-Robles et al., 2021; Corrales-Maldonado et al., 2024; Huerta-García and Álvarez-Cervantes, 2024).

Intestinal microorganisms in insects can also provide essential nutrients to their hosts. For instance, some strains of *Klebsiella* spp. (Enterobacterales: Enterobacteriaceae) and *Pantoea* spp. (Enterobacterales: Erwiniaceae) are capable of fixing atmospheric nitrogen, converting it into ammonium and nitrate that are stored in the intestine and eventually utilized by the insects (Gouveia et al., 2008; Zhao et al., 2022). Additionally, several strains of *Rhizobium* spp. (Hyphomicrobiales: Rhizobiaceae) have been found in the intestines of hymenopterans. Evidence suggests that these bacteria play a role in the urea cycle by utilizing ammonia compounds to synthesize essential amino acids required for proper insect development (Zhukova et al., 2022).

Unlike fungi-feeding insects, in this type of association, microorganisms are already integrated into the insects' digestive system (Khadempour et al., 2020). These microbial groups are transmitted from parents to their offspring through direct contact or specific behaviors, such as oral or fecal trophallaxis used to feed larvae, a phenomenon observed in termites and ants (Sinotte et al., 2023). During this process, larvae acquire their gut microbiota by ingesting the feces of adults, thereby ensuring the continuity of the mutualism.

2.3 Microorganisms facilitate chemical communication

Insects communicate with each other through volatile chemical signals. These signals, which can be produced by both insects and plants, convey different messages. For example, there are aggregation volatile compounds released by females to indicate their readiness for fertilization; males, in turn, may emit disaggregation volatile compounds to prevent too many competitors from congregating around the same female (Llanderal and Castro, 2021; Ai et al., 2022; Cusumano and Lievens, 2023).

Flowers mimic this mechanism by releasing aggregation volatile compounds to attract their pollinators. It is fascinating that certain microorganisms, such as yeasts and lactic acid bacteria found in flower nectar, are responsible for producing volatile compounds that act as attractants for pollinating insects (Cusumano and Lievens, 2023).

Evidence suggests that certain strains of lactic acid bacteria and yeasts perform fermentative processes that enhance the nutritional quality of flower nectar and pollen by modifying their sugar and amino acid compositions, making them more attractive to specific pollinating insects and pest parasitoids (Yang et al., 2019; Ai et al., 2022). Additionally, during the fermentative process, various volatile compounds are released that stimulate the olfactory receptors of insects, promoting their attraction (Clymans et al., 2019; Cusumano and Lievens, 2023).

In this mutualism, plants benefit by promoting entomophilous pollination while receiving protection against pests from the beneficial insects attracted to them. Furthermore, although flowers possess a stable microbiome, they also harbor occasional microorganisms introduced by visiting insects (de Vega and Herrera, 2012; Cusumano and Lievens, 2023). In this way, fermentative microorganisms capitalize on the presence of insects, which serve as effective dispersers, transferring them to other flowers and facilitating their propagation.

It is important to emphasize that the study of microorganisms as mediators in the communication between plants and insects has significant implications for the biological control of pests in economically important crops. For example, the study by Vannette et al. (2017) observed that coffee flowers with higher microbial diversity were more frequently visited by the ant *Azteca sericeasur* (Hymenoptera: Formicidae), a highly territorial species that defends its mutualistic plants from herbivorous insects. However, this same ant also tends to repel other pollinators, highlighting the need for further investigation into these associations to evaluate the potential of microorganisms as attractants for parasitoids and predators. This approach could serve as an alternative for pest control without negatively impacting other beneficial insects (Ai et al., 2022).

2.4 Microorganisms protect insects against diseases

One of the mutualism types between insects and microorganisms that has garnered significant interest in recent years, particularly in the context of its ecological and biotechnological implications, involves microorganisms that produce antimicrobial compounds (Chevrette et al., 2019; Van Moll et al., 2021). Various bacteria and fungi capable of producing antibiotics and antifungals have been identified in association with several orders of insects, such as ants, bees, and wasps (Hymenoptera); beetles (Coleoptera); flies (Diptera); and termites (Blattodea) (Van Moll et al., 2021). Evidence suggests that these microorganisms play a crucial role in protecting their associated insects against entomopathogenic pathogens such as *Metarhizium anisopliae* (Metschn.) Sorokin, 1883 (Ascomycota: Hypocreales: Clavicipitaceae), and *Beauveria bassiana* (Bals.-Criv.) Vuill., 1912 (Ascomycota: Hypocreales: Cordycipitaceae), which are the primary agents used in biological pest control. However, it has been demonstrated that certain strains of *Streptomyces* spp. (Kitasatosporales: Streptomycetaceae) associated with hymenopterans can inhibit the growth of these pathogens under in vitro conditions (Bruner-Montero et al., 2021; Pessotti et al., 2021).

Research has primarily focused on Actinobacteria of the genus *Streptomyces*, known for their ability to produce a wide range of bioactive compounds, particularly antimicrobials (Chevrette et al., 2019). This interest in studying the interaction between insects and microorganisms lies in the potential of insects as a source of microbial resources with applications in the pharmaceutical industry (Van Moll et al., 2021). Currently, no drugs derived from these insect symbiotic microorganisms have been developed; however, several promising compounds have been identified, with cyphomycin being particularly noteworthy (Chevrette et al., 2019). This antimicrobial, produced by a strain of *Streptomyces* sp. associated with the ant *Cyphomyrmex* sp. (Hymenoptera: Formicidae), has been shown to inhibit clinically relevant pathogens in laboratory assays, including bacteria that have developed resistance to multiple current commercial antibiotics (Chevrette et al., 2019; Ortega et al., 2021).

3 Prospective analysis

The study of mutualistic interactions between insects and microorganisms represents an emerging field with significant potential in ecology, agriculture, and biotechnology (Qadri et al., 2020). As research on the insect microbiome advances, new microbial species with unexplored functions will likely be discovered. These microorganisms not only play a key role in insect survival but also represent a potential source for the development of new antimicrobial compounds, such as cyphomycin, with applications in the pharmaceutical industry (Van Moll et al., 2021).

In the context of climate change, it is crucial to analyze how environmental alterations affect these symbiotic relationships. Future research should focus on understanding how habitat loss, intensive agriculture, and pesticide use are disrupting these associations. At the same time, studies on microorganism-based biological control are expected to gain relevance, as they may offer sustainable solutions to agricultural pests without negatively impacting beneficial insects (Qadri et al., 2020; Zhao et al., 2022).

In terms of conservation, the need to protect not only insects but also their microbial symbionts becomes evident as an integral component of biodiversity. A deeper understanding of these mutualism types will facilitate the development of more effective strategies to address the current ecological crisis.

Based on the points explained above, several key areas for future scientific work are evident:

a. *Insect microbiomes and their diversity*. Studying the microbial communities present in different insect species, including yet-to-be-described symbionts, will enhance our understanding of their functional diversity and their relationship with the nutrition and adaptation of insects.

b. *Production of antimicrobial biomolecules*. Investigating the biotechnological potential of symbiotic microorganisms, such as *Streptomyces* spp., will develop new antibiotics and antifungals, with applications in human health and pest control.

c. *Impact of climate change on mutualism.* Assessing how global warming and habitat loss affect the symbiotic relationships between insects and their associated microorganisms will provide insights for designing strategies to conserve beneficial insect species and their microbial associates.

d. *Sustainable biological control.* Developing agricultural strategies based on microorganisms that enhance pest control without adversely affecting beneficial insects will play a key role in minimizing the environmental impact of agriculture.

e. *Conservation of mutualism.* Promoting research on the conservation of insect–microorganism interactions will mitigate the decline of insect populations.

4 Conclusions

Interactions between insects and the microorganisms that live in symbiosis with them have significant implications for the environment, agriculture, and medicine. However, this is a relatively new area of study that requires more attention from scientists interested in understanding it. Insects are the most abundant and diverse group of animals on the planet, and part of their success can be attributed to their ability to establish relationships with many types of microorganisms.

In general, these microorganisms act as an extension of the insects' metabolism, helping them acquire nutrients they could not obtain on their own and protecting them from diseases. In return, microorganisms find a favorable environment in insects, rich in nutrients and optimal conditions for growth. Furthermore, insects not only acquire these microorganisms but also disperse them while foraging in different locations.

In line with the previously stated information, there is abundant evidence positioning insects as an innovative source of microbial resources with valuable biotechnological potential. Consequently, future research must focus on deepening the understanding of the biochemical, metabolic, and molecular mechanisms governing insect–microorganism interactions. This approach will not only enable the development of new biotechnological applications but also enhance the sustainable utilization of these resources, as well as the conservation of beneficial insect species.

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