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Review

Insects and microbes: best friends from the nursery

Estelle Chabanol and Mathilde Gendrin



Insects host microbes and interact with them throughout their life cycle. This microbiota is an important, if not essential, partner participating in many aspects of insect physiology. Recent omics studies have contributed to considerable advances in the current understanding of the molecular implications of microbiota during insect development. In this review, we present an overview of the current knowledge about the mechanisms underlying interactions between developing insects and their microbial companions. The microbiota is implicated in nutrition, both via compensating for metabolic pathways lacking in the host and via regulating host metabolism. Furthermore, the microbiota plays a protective role, enhancing the insect's tolerance to, or resistance against, various environmental stresses.

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Introduction

Like most animals, insects associate with some micro-organisms — bacteria, fungi, viruses, protists, and archaea [1]. The association with micro-organisms is essential for the development and survival of several insects. Without any microbiota, *Aedes aegypti*, *Anopheles gambiae*, or *Toxorhynchites amboinensis* mosquito larvae cannot develop past the first instar [2,3], and without its symbiotic fungus *Pichia anomala*, the beetle *Doubledaya bucculenta* does not go beyond the second larval stage [4]. In both beetles and mosquitoes, growth is restored when introducing into the rearing environment the key symbiont or a nonspecific bacterium, respectively. The

microbiota is nonessential for other insects, such as *Periplaneta americana* cockroaches or *Apis mellifera* honeybees, but their germ-free larval development is not optimal. Rearing these insects in sterile conditions can delay development, reduce larval growth, alter morphology, and affect female fecundity [5,6].

Micro-organisms colonize the cuticle and the digestive tract, and settle in different organs or even inside cells [1]. Microbial colonization generally starts when eggs hatch into larvae and interact with their environment, and sometimes already during embryogenesis. Symbionts can be vertically transmitted to offspring, either directly, through the ovaries during egg development, or indirectly, by microbes deposited on eggs that are later ingested by larvae [7]. Horizontal transmission between individuals also occurs via ingestion of conspecific feces, mouth-to-anus or mouth-to-mouth contacts, mating, or contamination of a shared environment [8,9]. Finally, insects can also acquire their microbiota from their environment, including water, soil, plants, and food substrates [10,11].

Recent advances in the role of the microbiota throughout the insect life cycle were facilitated thanks to the development of the omics approaches. Sequencing allowed metagenomic and metatranscriptomic studies, and analytical technologies, such as mass spectrometry, enabled precise proteomic and metabolomic investigations. Here, we review the importance of microbes during insect postembryonic development, focusing particularly on recent progress based on omics studies. The microbiota has been shown to contribute to larval nutrition, often complementing insect auxotrophies. It also protects insects against biotic and abiotic stresses, allowing larvae to develop in various ecological niches.

Main text

Nutrition

Micro-organisms sometimes simply serve as food for insects, providing nutritional value as a protein source. Heat-killed micro-organisms were shown to support the development of axenic *Ae. aegypti* mosquitoes [12] and to improve the lifespan of *Drosophila melanogaster* [13] in a quantity-dependent manner. Here, we will focus on the active roles that micro-organisms play in the digestion and transformation of nutrients essential for insect development [14,15]. Particularly, micro-organisms participate in the recovery and production of essential elements, activate different metabolic pathways, and send signals to promote larval development.

In phytophagous and xylophagous insects, the microbiota is involved in the digestion of lignocellulose — the main component of plant wall and wood — composed of cellulose, hemicellulose, and lignin. Lignin is an aromatic polymer, while hemicellulose and cellulose are carbohydrate polymers. Lignocellulose is the principal source of carbon for plant-feeding insects — including some Diptera, Lepidoptera, Hymenoptera, and Coleoptera — that nonetheless lack the cellobiohydrolases and ligninases necessary to fully digest these materials and rely on their microbiota to do so [16]. In the wood-feeding beetle *Odontotaenius disjunctus*, depolymerization of lignocellulose compounds and fermentation of sugar monomers are supported by aerobic and anaerobic bacteria throughout the digestive tract [17]. This process allows adults to predigest wood, transforming a low-nutrient diet into a high-nutrient, energy-rich food, containing acetate, formate, lactate, sugar monomers such as glucose and xylose, and aromatic monomers such as benzoate and phenylpropionate. Larvae then ingest the enriched frass, which provides the nutrients required for their survival and development. *Protaetia brevitarsis* beetle larvae digest wood compounds thanks to their microbiota, mainly Firmicutes and Bacteroidetes bacteria, that allow degradation and fermentation in the hindgut via producing cellulases, hemicellulases, and ligninases [18].

In addition, a herbivorous diet is generally low in nitrogen, and the insect requirements usually exceed the available resources. Nitrogen is however an essential element required to biosynthesize nucleotides, amino acids, and other metabolites. Some symbionts can compensate for this scarcity by fixing atmospheric dinitrogen or by recycling nitrogen-rich compounds, such as urea or uric acid. This type of microbiota is an important partner for the growth of arboreal ant colonies, including *Azteca alfari*, *Azteca constructor*, and *Azteca xanthochroa*. The queens scrape their host plant parenchyma, creating a pile of waste where bacteria and fungi grow, and lay their eggs nearby, allowing larvae to feed on it and develop [19]. These waste patches contain diverse bacteria predicted to be diazotroph, that is, bacteria with various genes encoding dinitrogenase reductases, that transform dinitrogen into ammonia [20]. *Cephalotes* turtle ants source nitrogen from other animal wastes [21]. Bacteria, notably Enterobacterales, possess all genes necessary for a complete uricolytic pathway required to transform purines, such as adenine, guanine, xanthine, and hypoxanthine, into uric acid and to recycle uric acid into urea and then ammonia [22]. Ammonia can be assimilated into the reactions for essential and nonessential amino acid biosynthesis.

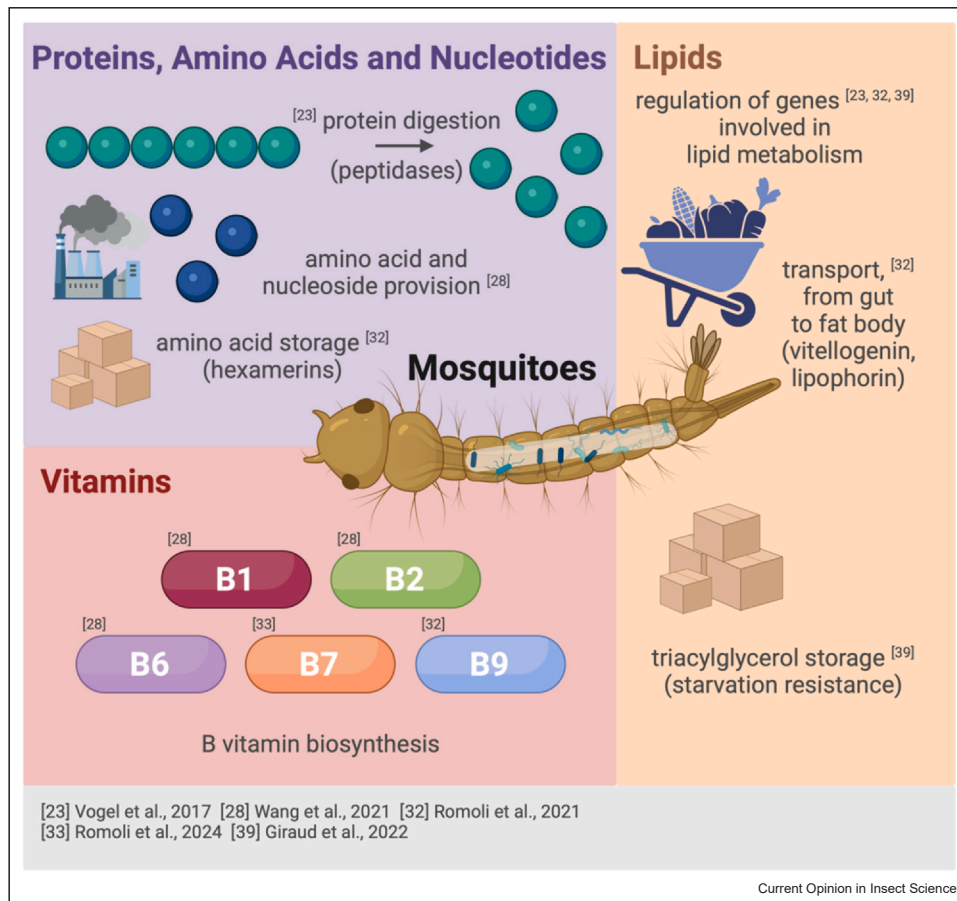
Beyond nitrogen provision, micro-organisms are also involved in other mechanisms to supply amino acids to insects, whether via protein digestion or *de novo* amino

acid biosynthesis. In the absence of a microbiota, peptidase genes are downregulated in *Ae. aegypti* mosquito larvae [23] (Figure 1) and peptidase activities, mainly trypsin, drop in *Hermetia illucens* black soldier fly larvae [24]. Similarly, in *D. melanogaster*, larvae fed on a low-nutrient diet, a mono-association with *Lactobacillus plantarum* bacterium is sufficient to enhance host protease expression, allowing a better digestion of proteins and a higher level of free amino acids throughout development, and therefore promoting growth [25]. *Lactobacillus plantarum* together with *Acetobacter pomorum* also plays an important role in complementing fly auxotrophies by synthesizing several amino acids [26]. In the stinkbug *Megacopta punctatissima*, the bacterium *Ishikawaella* compensates for the phloem sap deficiencies by converting nonessential amino acids, mainly glutamine, into essential and aromatic ones, notably tyrosine that is needed for nymph cuticle melanization [27]. Microbiota is also required for host amino acid provision in numerous other insects [28–31] (Figure 1). Finally, transcriptomic data in *Ae. aegypti* larvae suggest that the microbiota induces the production of hexamerins, that is, large proteins serving as amino acid reserve for metamorphosis [32] (Figure 1).

In addition to proteins and amino acids, the microbiota can also contribute to the synthesis of other essential nutrients, such as vitamins. In *Ae. aegypti* larvae, the microbiota contributes to B vitamin supply, in particular thiamine (B1), riboflavin (B2), pyridoxine (B6), biotin (B7), and folate (B9) [28,32,33] (Figure 1). As several B vitamins (particularly B2) quickly degrade when exposed to light, their steady provisioning by the microbiota is important for larval development [28]. Likewise, the *Wolbachia* endosymbiont of the *Cimex lectularius* bedbug larvae possesses a complete pathway for B7 biosynthesis — likely acquired through horizontal gene transfer from unrelated bacteria — as well as a complete pathway for B2 biosynthesis and partial pathways for B1, B6, and B9 biosynthesis [34]. Without its symbiont (and associated B vitamin production), bedbug growth rate is reduced, and adult female fitness, fertility, and fecundity is impacted [35]. The bean beetle *Callosobruchus maculatus* harbors a simple microbiota, mainly composed of *Staphylococcus gallinarum*. This bacterium is conserved between larvae and adults and its genome retains complete pathways to synthesize five B vitamins (B1, B2, B5, B7, and B9) and an incomplete pathway for nicotinic acid production (B3) [36]. Similarly, *Drosophila* and other fruit flies, ants, cotton stainers, and kissing bugs depend on their microbiota for vitamin biosynthesis [22,26,37,38].

Finally, insect symbiotic micro-organisms are sometimes involved in sugar and lipid metabolism. In *Ae. aegypti* larvae, the microbiota stimulates lipid uptake from the gut to the fat body by upregulating the genes encoding vitellogenin and lipophorin transporters, while in contrast,

Figure 1



Mosquito larvae microbiota contributes to nutrition by participating in protein, amino acid, and nucleotide supply (purple), vitamin biosynthesis (red), and lipid metabolism (orange). The microbiota stimulates protein digestion via peptidase expression and is also implicated in amino acid and nucleoside provision. In addition, it induces hexamerin production, which constitutes amino acid reserve for the insect metamorphosis. The microbiota contributes to B vitamin biosynthesis, notably thiamine (B1), riboflavin (B2), pyridoxine (B6), biotin (B7), and folate (B9). The microbiota also regulates genes involved in lipid metabolism, thereby favoring lipid transport from the gut to the fat body, and enhances lipid storage, increasing starvation resistance. (Figure created using BioRender.com).

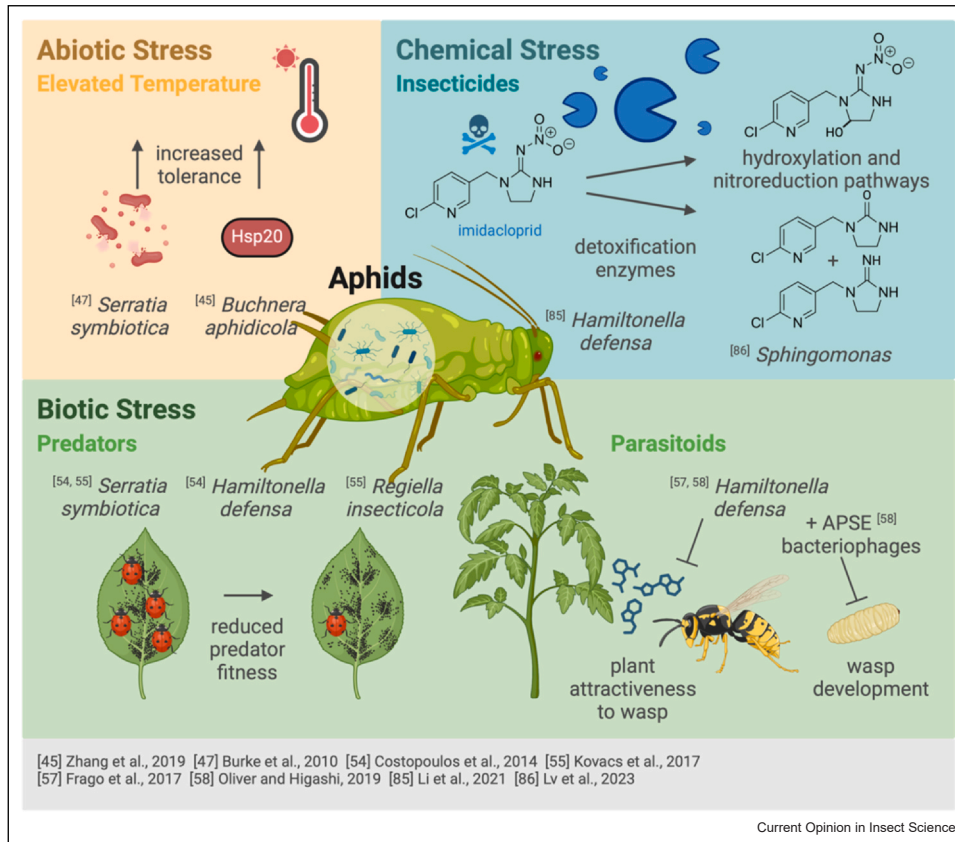
lipids accumulate in the gut of germ-free larvae [32] (Figure 1). Giraud et al. have demonstrated that adult lipid storage, specifically triacylglycerol levels, and starvation resistance are influenced by the larval bacterial environment [39] (Figure 1). *Serratia symbiotica* promotes fatty acid biosynthesis, fatty acid metabolism, lipogenesis, and adipogenesis in the pea aphid *Acyrtosiphon pisum* [40]. Likewise, the microbiota of *D. melanogaster* larvae fosters distribution of lipidic resources, ensuring optimal development, while germ-free conditions result in intestinal lipid accumulation [41]. Regulation of lipid metabolism is mediated by microbial production of acetic acid, which activates the immune-deficiency (IMD) pathway and insulin signaling [41,42]. Notably, the acetic acid produced by *Acetobacter pomorum* modulates host insulin/insulin-like growth factor signaling (IIS), accelerating development and enhancing adult body size and weight [42]. Another symbiotic bacterium, *Lactobacillus*

plantarum, activates the target of rapamycin pathway, increasing insulin-like peptide and ecdysone production, additionally promoting growth and metamorphosis [43]. Lastly, the fungus *Zygosaccharomyces*, present in the brood cells of stingless bee larvae *Scaptotrigona depilis*, is an essential source of sterols [44]. It provides ergosterol that allows the insect to produce cholesterol-like sterols, precursors of steroid hormones, particularly ecdysone and 20-hydroxyecdysone, that stimulate pupation.

Protection

Insects are subjected to a wide range of biotic and abiotic stresses from their environment. Their symbionts sometimes protect them from these events, allowing them to develop and survive in otherwise hostile conditions. This protection can be conferred directly, through the symbiont's metabolism, or indirectly, by the symbiont modifying the host's metabolism.

Figure 2



Aphid nymph microbiota contributes to resistance and tolerance to abiotic (yellow), biotic (green), and chemical (blue) stresses. Abiotic examples include aphids' increased ability to endure heat stress, provided by both *Buchnera*'s release of heat shock proteins and *Serratia*'s cell lysis releasing protective metabolites. Biotic examples include predation reduction facilitated by *Serratia*, *Hamiltonella* and *Regiella* via symbionts' reduction of lady beetle fitness. Other biotic examples include parasitism reduction by *Hamiltonella*'s inhibition of volatile emitted by colonized plants to attract parasitoid wasps, and, when infected by APSE bacteriophages, *Hamiltonella*'s inhibition of wasp larvae development in the aphid. Examples of chemical stress reduction include *Hamiltonella*'s detoxifying enzymes, which are effective against several insecticides, and *Sphingomonas*'s detoxification pathways for imidacloprid (Figure created using BioRender.com).

Seasonal variations and changes in meteorological conditions, such as a temperature increase or a drop in humidity level, can be extremely challenging for insects. In *Aphis* and *Acyrtosiphon* aphid nymphs, *Buchnera aphidicola* bacteria increase their host's viable thermal range by producing Hsp20 heat shock proteins that confer tolerance to heat stress [45] (Figure 2). In *A. pisum* nymphs, a second symbiont, *Serratia symbiotica*, also confers resistance to repetitive heat stress [46], likely via lysis of bacterial cells that release protective metabolites during the thermal challenge [47] (Figure 2). Conversely, metabolomic and genetic analyses indicate that the gut microbiota of *Bactrocera dorsalis* flies increases host tolerance to cold by stimulating arginine and proline metabolism, two amino acids with cryopreservation properties [48].

Additionally, other insects are more desiccation resistant due to stronger cuticles (thicker, denser, and more

hydrophobic to avoid water loss) due to their microbiota [49]. This is the case in *Cephalotes varians* turtle ants, whose microbiota contributes to the production of chitin, cuticular proteins, and cross-linkers for cuticle formation [50]. In *Oryzaephilus surinamensis* beetles, the endosymbiont *Shikimatogenerans silvanidophilus* contributes to cuticle melanization and sclerotization that start during metamorphosis, protecting the insect from dry conditions [51]. The symbiont's shikimate pathway synthesizes chorismate and prephenate, which the host then converts into tyrosine, a precursor of phenolic compounds involved in cuticle hardening. Similarly, the obligatory symbiont *Nardonella* of the *Pachyrhynchus infernalis* weevil conserves a small genome essentially directed to tyrosine production for their hosts [52].

The microbiota can also be involved in insect's defense against predators and parasitoids. Examples in predators include the ascomycete *Fusarium oxysporum*, associated

with the leaf beetle *Chelymorpha alternans*, proliferating early in pupation and reducing predation rates by ants [53]. In the aphid *A. pisum*, the facultative bacterial symbionts *Hamiltonella defensa*, *Regiella insecticola*, and *Serratia symbiotica* do not reduce feeding rates of lady beetles, but reduce their fitness, and thus predator population [54,55] (Figure 2). The acceleration of cuticle formation by the *Shikimatogenerans sikvanidophilus* endosymbiont in *Oryzaephilus surinamensis* beetle is important to protect against wolf spider predation and *Beauveria bassiana* fungus infection during the first hours after pupal eclosion when the imago is still highly vulnerable [56]. Examples of parasitoids include *Hamiltonella defensa* limiting parasitism by *Aphidius ervi* wasps in *A. pisum* nymphs and adults. First, the presence of *Hamiltonella* reduces the emission of chemical signals from the plant that attract parasitoid wasps [57] (Figure 2). Second, *Hamiltonella* also inhibits the development of wasp larvae within the aphid [58] via its APSE bacteriophage (*A. pisum* secondary endosymbiont), whose genome encodes toxins [59,60]. Furthermore, this bacteria's maintenance in the aphid is partly due to the obligate symbiont *Buchnera*'s metabolism – which supplies essential amino acids for which *Hamiltonella* is auxotrophic – highlighting the complexity of mutualistic interactions necessary for the defense of the host [61,62]. In several Lepidoptera, Ascoviridae, Baculoviridae, and Entomopoxvirinae viruses inhibit Microgastriinae parasitoid wasps by releasing parasitoid-killing proteins, which can induce cell apoptosis in wasp larvae. This increases viral fitness while also protecting the host [63]. In *D. melanogaster* larvae, *Spiroplasma poulsonii* bacterium also limits parasitism by *Leptopilina boulardi*, *Leptopilina heterotoma* and *Asobara tabida* wasps. It does this by competing with wasp larvae for available lipids [64] and/or producing ribosome-inactivating proteins, which depurinate wasp ribosomes as soon as wasp larvae hatch [65].

Moreover, the insect microbiota can play a role in defending against other pathogenic micro-organisms. This action can be direct, involving the release of antimicrobial substances or other specific toxins. This is the case for *Burkholderia gladioli* symbionts of *Lagria villosa* beetles, which produce molecules with antibacterial activities, such as lagriene and toxoflavin, and molecules with antifungal activities, such as lagriamide, caryoynencin, and sinapigliadoside [66,67]. The symbiont is thus a crucial partner for eggs, larvae, and pupae, particularly during molting when the insect's cuticle is too soft to provide adequate protection. The microbiota's action can also be indirect by accentuating the insect's immune response against pathogens and by participating in immune priming [68]. For instance, bacterial peptidoglycan activates neuronal signaling in *D. melanogaster* larvae, later triggering adult aversion to food substrates that carry potentially pathogenic bacteria [69]. This

ability is lost in adults reared in a germ-free environment during the first 48 hours of larval development. *Wolbachia* endosymbionts are known to protect their adult host against viruses in multiple systems, but their impact in larvae appears less common or has not been yet investigated [70,71].

Detoxification

Certain symbionts can also detoxify a variety of inorganic and organic compounds, including insecticides and plant secondary metabolites. This ability provides a significant advantage for some insects, allowing them to colonize ecological niches with minimal competition. The coffee berry borer *Hypothenemus hampei* can carry out its entire life cycle in coffee beans as a result of its microbiota, which degrades caffeine, a deleterious alkaloid [72]. Several *Pseudomonas* strains' genomes contain a complete set of N-demethylases for the transformation of caffeine into theobromine, 7-methylxanthine, and then xanthine [73]. Guava fruit flies, *Anastrepha striata* and *Anastrepha fraterculus*, colonize guava due to their *Komagataeibacter* symbiont, which degrades fruit tannins and polyphenols, while *Anastrepha ludens*, not associated with this bacterium, cannot [74]. Camellia weevils *Curculio chinensis* grow on trees that produce tea saponin but possess several symbionts, notably *Acetobacter*, that degrade this toxic compound [75]. Many other insects benefit from similar microbial degradation of phytochemicals [76,77].

Finally, micro-organisms contribute to insecticide resistance in various insects [78–81]. The mosquito microbiota has been shown to promote resistance to deltamethrin in *Aedes albopictus* larvae and to propoxur and naled in *Ae. aegypti* larvae [82,83]. This effect is mediated by increased expression and activity of esterases, glutathione-S-transferases, and P450 cytochromes. Similarly, P450 cytochrome transcription, induced by the microbiota in *Apis mellifera* honeybees, improves host survival after exposure to thiacloprid or fluvalinate [84]. The aphid *Sitobion miscanthi* possesses a *Hamiltonella defensa* symbiont producing acetylcholinesterases, glutathione transferases, and carboxylesterases, which detoxify insecticides [85] (Figure 2). In the *Aphis gossypii* aphid, a *Sphingomonas* symbiont specifically degrades the neonicotinoid imidacloprid into nonharmful 5-hydroxy-imidacloprid, imidacloprid-guanidine, and imidacloprid-urea via hydroxylation and nitro-reduction pathways [86].

Conclusion

The microbiota provides a variety of services to its insect host, from facilitating nutrition to adaptation to its environment. This review focuses on positive insect-microbe interactions during insect development, but the spectrum of these relationships is broad and generally

extends into insect adulthood. Recent years have seen significant advancements in understanding the molecular mechanisms underlying microbiota contributions to digestion and nutrient supply [10,87], resilience to biotic stresses [88], production of defense chemicals [89], and breakdown of harmful substances [90,91]. Additionally, researchers have also investigated the microbiota's influence on insect behavior [92] and role in the transmission of human pathogens [93]. These microbial capacities hold promising potential for application in human technology.

Given the diversity of insects affecting the biosphere in many ways, we propose four main categories of potential benefits of insect microbiota. First, probiotics often benefit insect mass production. This is the case in honeybees, black-soldier flies insect-based food production, and mosquitoes released for vector control [94]. Second, some insect–microbe associations can be used as mini-bioconversion factories to recycle natural or artificial substances (wood, plastic), detoxify pollutants (oil, insecticides), or develop new drugs [95,96]. Third, entomopathogens allow humans to fight against agriculture pests and disease vectors [97,98]. If target-specific entomopathogens can be harnessed, these ‘green pesticides’ will certainly be more environmentally friendly than most chemical insecticides. In addition, their insecticidal effect is often linked to a combination of several metabolites, which limits the rise of insecticide resistance. Fourth, knowledge of how the microbiota is influenced by the environment and how it affects host fitness may be integrated into models of the effects of climate change, urbanization, and/or deforestation [99]. Together, these insect microbiota-derived ecological data and corresponding models promise to enable innovative design approaches to protect biodiversity and optimize overall planetary health.

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CRedit authorship contribution statement

Conceptualization: E.C. and M.G. Funding acquisition: M.G. Investigation: E.C. Visualization: E.C. Supervision: M.G. Validation: E.C. and M.G. Writing –

original draft preparation: E.C. and M.G. Writing – review & editing: E.C. and M.G.

All authors have read and agreed to the published version of the manuscript.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors declare no conflict of interest.

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