



Review

Insect-based agri-food waste valorization: Agricultural applications and roles of insect gut microbiota



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ABSTRACT

Meeting the demands of the growing population requires increased food and feed production, leading to higher levels of agri-food waste. As this type of waste seriously threatens public health and the environment, novel approaches to waste management should be developed. Insects have been proposed as efficient agents for biorefining waste, producing biomass that can be used for commercial products. However, challenges in achieving optimal outcomes and maximizing beneficial results remain. Microbial symbionts associated with insects are known to have a critical role in the development, fitness, and versatility of insects, and as such, they can be utilized as targets for the optimization of agri-food waste insect-based biorefinery systems. This review discusses insect-based biorefineries, focusing on the agricultural applications of edible insects, mainly as animal feed and organic fertilizers. We also describe the interplay between agri-food waste-utilizing insects and associated microbiota and the microbial contribution in enhancing insect growth, development, and involvement in organic waste bioconversion processes. The potential contribution of insect gut microbiota in eliminating pathogens, toxins, and pollutants and microbe-mediated approaches for enhancing insect growth and the bioconversion of organic waste are also discussed. The present review outlines the benefits of using insects in agri-food and organic waste biorefinery systems, describes the roles of insect-associated microbial symbionts in waste bioconversion processes, and highlights the potential of such biorefinery systems in addressing the current agri-food waste-related challenges.

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1. Introduction

Bioconversion of waste into high-value products is necessary for effective waste management and establishing a circular economy [1]. Insects have gained attention for the bio-conversion of low-value substrates into affordable, high-quality animal feed and organic fertilizers [2,3]. Insects have many advantages over plants and livestock animals, such as a short life cycle, growing on cheap feedstock (organic waste), limited land and water requirements, high conversion rate, low gas emissions, and high sustainability [4].

Certain bioconverter insects can be used as feed and food. Insect meals or edible insects, such as the yellow mealworm (YMW), *Tenebrio molitor* L., and the black soldier fly (BSF), *Hermetia illucens*, can be used as efficient and sustainable high-quality protein sources for humans and animals, with low environmental impact [4,5]. Several other insect species have been studied for their potential to utilize biowaste in their diets. The insect species mentioned in this review are listed in Table 1.

Insects fed organic residual streams, such as food byproducts and waste, generated within the current food systems can produce biomass rich in valuable proteins, fats, vitamins, and minerals, potentially replacing conventional feed ingredients, such as soybean and fishmeal, that negatively impact the climate and biodiversity [6]. Farmed insects can be used as feed for sustainable and

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Table 1

List of insects mentioned in this study that were investigated for potential waste-utilization and use as animal feed or frass fertilizers.

English name	Scientific name
Black soldier fly (BSF)	<i>Hermetia illucens</i>
Yellow mealworm (YMW)	<i>Tenebrio molitor</i>
House fly (HF)	<i>Musca domestica</i>
Lesser mealworm (LMW)	<i>Alphitobius diaperinus</i>
Superworm (SW)	<i>Zophobas morio</i>
Chafer flower beetle	<i>Protaetia brevitarsis</i>
House cricket	<i>Acheta domestica</i>
Two-spotted cricket	<i>Gryllus bimaculatus</i>
Kenya new cricket	<i>Scapsipedus icipe</i>
Silkworm	<i>Bombyx mori</i>
Desert locust	<i>Schistocerca gregaria</i>
Garden fruit chafer	<i>Pachnoda sinuata</i>
Coconut rhinoceros beetle	<i>Oryctes rhinoceros</i>
African golden emperor moth	<i>Gonimbrasia krucki</i>

circular livestock production and improved livestock welfare by supporting their natural foraging behavior and health [7]. Organic waste bioconversion into organic fertilizers by insects can reduce landfilling and return the nutrients to agricultural lands. Insect frass fertilizers are promising alternatives to existing commercial fertilizers, such as mineral and organic fertilizers. Frass fertilizers derived from edible insects play important roles in improving the fertility, yield, and nutritional quality of various crops [8-10].

Studies on insect and associated microbiota interactions provide insights into the impact of microbes on insect physiology and biological functions. They also provide evidence for microbial involvement in insect development and survival on diverse organic substrates. Along with the agri-food waste (agri-FW) biorefinery insects, microbes have been found to play key roles in the bioconversion process and can be targeted for optimizing the efficiency of industrial rearing [11].

The advantages of insect-based bioconversion in developing marketable agricultural products and the involvement of insect-associated microbial symbionts necessitate further investigations to understand the underlying mechanisms and microbial roles in insect-based bioconversion of agri-FW. Therefore, this review aims to present the findings of recent studies on the utilization of insects for agri-FW valorization to obtain value-added agricultural products, particularly animal feed and frass fertilizers, which may improve the role of edible insects in the circular bioeconomy. In addition, the roles played by insect-associated microbiota in insect development and organic waste bioconversion processes are discussed, highlighting some methods to enhance the bioconversion process using microbe-based approaches.

2. Insect-based biorefinery of agri-food waste

Agri-FW is considered a resource of valuable products, such as nutraceuticals, antioxidants, bio-polymers, biopeptides, antibiotics, industrial enzymes, polysaccharides, chitosan, and pigments [12,13]. Traditional food waste disposal methods, such as landfilling and combustion, cause economic and environmental problems. The annual global cost of food waste is estimated to be \$1 billion, and when considering environmental costs, this actual number can rise to \$2600 billion [14]. Food waste is estimated to contribute to 3.3 billion tons of CO₂ accumulation in the atmosphere per year as greenhouse gas emissions, negatively affecting climate change [15,16]. Food waste can also cause other environmental issues as it is dumped without pretreatment by landfilling or combustion [17]. The combustion of food waste also causes environmental concerns, such as breathing difficulties for living organisms and air pollution due to dioxin, ash, and flue gas emitted into the atmosphere [16,17].

Toxic byproducts of food combustion, such as methane and hydrogen sulfide, produced by food waste landfilling, contaminate groundwater and generate corrosive gases [17]. Food waste energy content is reduced when disposed of in landfills.

Efforts are currently being undertaken to find sustainable and eco-friendly approaches to managing food waste. A range of research scientists, government, and non-governmental organizations have proposed and implemented innovative strategies to address food waste. These strategies are largely centered around the waste management hierarchy, which prioritizes the three R's of waste management: reduce, reuse, and recycle. Insect-based waste bioconversion strategies are considered a component of both the reuse and recycle strategies and have attracted growing global attention [18,19]. Many insect species are highly versatile and adaptable to a wide range of organic wastes, including agri-FW, with high conversion rates (Fig. 1). A summary of the bioconversion parameters of the main insect species that can convert agri-FW and be mass-reared for use as a potential source of food, feed, and fertilizer, as well as their larval composition based on some example substrates, is provided in Table 2.

In this context, BSF larvae (BSFL), for example, showed a significant bioconversion rate of 6.9%, dry mass reduction of 49.0%, and fat content of 26.1% [20]. An efficient conversion was observed when larvae grew on okra and brewer grains [21]. House fly larvae (HFL), *Musca domestica*, can degrade and transform various agricultural wastes (including corn, wheat, and rice straw) into feed sources [22]. One kilogram of larvae can be produced from fermented cornstalks weighing 18.75 kg [23,24]. Corn straw and sawdust dissection by *Protaetia brevitarsis* larvae were noted at 24.37% and 14.46% digestion rates, respectively [25]. Crop residues (rice and corn straw) affect both the growth and performance of YMW, with 90% waste consumption. The bioconversion rate of YMW fed on wheat straw was 8.13%, and 78.43% resulted in frass [26]. Feeding on mushroom residues has also been observed [27]. The mushroom *Lentinus edodes* is used as an alternative substrate to the traditional YMW feeding source, and the residual waste can be used for insect feeding after recycling [28].

Not all waste substrates are equally available or suitable for every type of bioconversion insect due to differences in composition, nutritional needs, and rearing conditions. The optimization of food waste's chemical and physical characteristics, such as moisture content and nutritional load, in combination with the functional attributes of the insects, such as feeding behavior, mouth parts, morphological features, and disease resistance, is the reason

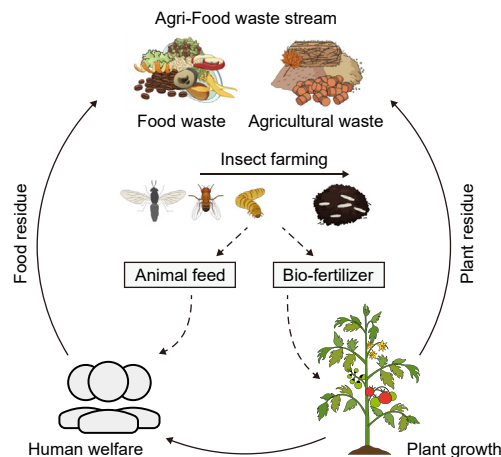


Fig. 1. Insect-mediated waste bioconversion to value-added products (i.e., animal feed and biofertilizer) within the concept of sustainable agriculture.

Table 2
The nutritional composition and bioconversion parameters of the main bioconverter insects fed on agri-food waste substrates.

Insect	Feed substrate	Larva composition		Bioconversion parameters				Reference
		Protein (%)	Lipid (%)	Ash (%)	ECD ^a (%)	FCR ^b (%)	Degradation ^c (%)	
<i>Hermetia illucens</i>	Palm kernel expeller (PKE)	38	18	NM	17.6	NM	NM	[29]
	Fungi fermented-PKE	38.2–44.5	18.6–24.7	NM	24–30	NM	38.8–62.4	[29]
	Food waste	39.2	30–40	8.13	NM ^d	NM	55.3	[30,31]
	Soybean curd Residues (SCR)	52.9	26.1	NM	10.2	9.8	49	[20]
	Bacteria inoculated-SCR	55.3	30	NM	12.5	8	55.7	[20]
	Fermented maize straw	42	31	9	NM	NM	48.4	[32]
	Wheat bran	43	35	9.1	NM	NM	55	[32]
<i>Tenebrio molitor</i>	Agricultural waste	53.4	30	5.2	50	3.2	NM	[33]
	Agricultural by-products	46.4	32.7	2.9	9.87	7.9	NM	[34–36]
<i>Musca domestica</i>	Wheat bran	63.6	15.6	7.6	NM	NM	NM	[22]
	Food waste	55	22	NM	NM	NM	NM	[37]
<i>Alphitobius diaperinus</i>	Agri-food waste	37–49	14–28	NM	NM	15.2	NM	[35,38]
<i>Zophobas morio</i>	Agricultural feed	46.8	43.6	8.2	NM	NM	NM	[39]

^a ECD (The efficiency of conversion of digested feed, %) = Biomass gained (g)/Total feed consumed (g) × 100.

^b FCR (Feed conversion rate, %) = Feed intake (g DM)/Weight gained (g DM) × 100.

^c Degradation (%) = (Initial feed dry weight (g) – Final feed dry weight (g))/(Initial feed dry weight (g)) × 100.

^d NM: Not mentioned.

why certain insects may thrive on particular substrates while others may not [40]. For example, vegetative food waste that is low in protein may not be appropriate for rearing HFL, but may be suitable for rearing BSFL and MWL, whereas waste containing meat, such as restaurant and kitchen waste, is suitable for both BSFL and HFL [41,42].

The rate of insects' growth and their role in bioconversion varies depending on the type of organic waste. Some organic waste types may not support satisfactory growth rates, impairing bioconversion. To enhance bioconversion efficiency, several studies have investigated the influence of different types of waste and tested various waste mixtures on the BSF as the main insect species considered for bioconversion of organic wastes. High fiber wastes, in particular, may pose challenges for conversion. However, in the case of dairy manure, which is known for its high fiber content, mixing it with soybean curd residue resulted in enhanced conversion by BSFL, as evidenced by increased survival rate, conversion rate, waste mass reduction, nutrient utilization, and fiber content reduction [43]. Similarly, Li et al. [44] found that corncob, a problematic waste type due to its high lignocellulose content, could be highly converted by BSFL when pretreated with restaurant wastewater. The restaurant wastewater improved the biochemical characteristics of the corncob, and the soaking residue was converted by BSFL for ten days, yielding a 24% insect grease yield. These findings suggest that tailoring substrate mixtures and pretreatment methods can enhance the bioconversion of challenging waste types, contributing to more sustainable waste management practices.

Another type of organic waste that is challenging for conversion and utilization is human feces which poses a significant burden in waste management. A recent study by Purkayastha and Sarkar [45] demonstrated that BSFL could consume human feces, albeit resulting in significantly lower body weight compared to larvae fed on food waste. Interestingly, the degradation and bioconversion process of human feces were significantly improved when mixed with food waste, compared to larvae reared on human feces or food waste alone. These findings suggest that optimizing rearing conditions, especially substrate mixtures, could enhance the bioconversion and degradation, even for difficult waste types, such as human feces, representing food residues with limited nutritional value after human gut nutrient absorption. Extracting marketable products from human excreta and recognizing it as a resource is crucial from the sustainability perspective.

In contrast to previous studies that utilized benchtop laboratory

scale experiments, Scala et al. [46] conducted experiments at an industrial scale to test the efficacy of various waste substrates derived from agricultural by-products and their mixtures for rearing BSFL. It was confirmed that the bioconversion efficiency and nutrient composition of the larvae were influenced by the specific waste substrate utilized for rearing and the associated rearing conditions. These findings demonstrate the importance of considering the scale and complexity of waste management systems when evaluating the efficacy of bioconversion technologies.

Based on the above background, insect-based bioconversion is an efficient approach for utilizing food waste. It can convert waste into high-nutrition and value-added products. For instance, BSFL transformed food waste and sawdust to reduce the composting time to a short period and decrease organic matter [47]. HFL plays a significant role in food waste utilization owing to its scavenging behavior and high reproductive rate. Reportedly, 1 kg culture diets were used to produce 53.08 g of dried larvae with high content of both protein (57.06%) and oil (15.07%) [37]. Another study by Yin et al. [48] revealed that the crude protein and fat contents of fly larvae (insect biomass) fed on kitchen waste were 45.1% and 48.1%, respectively.

3. Agricultural applications of agri-food waste-utilizing insects

3.1. Insect-based livestock animal feed

Animal feed is a significant driver of land use, contributing to land acidification, energy use, climate change, and water consumption [49]. Two major protein sources for animal feed, fish meal and soybean meal, are widely used particularly for monogastric animal diets. However, overreliance on these feeds can have negative environmental impacts. Soybean meal production, for example, requires intensive cultivation, which can increase water consumption and reliance on pesticides and fertilizers, among other environmental burdens. Fish meal is heavily dependent on fish catch stocks, which can contribute to marine ecosystem degradation and result in variable quality and quantity of the feed [50]. To address these environmental concerns, using renewable protein sources in animal feed is increasingly important. Insects represent a particularly sustainable option, especially when they are fed on organic waste. Insect-based feed has the potential to reduce pressure on fish stocks and soy cultivation, while also diverting organic waste from landfills and reducing greenhouse gas

emissions associated with waste disposal. A shift towards more sustainable and efficient animal feed production is critical to mitigating the negative environmental impacts of current feed practices [51].

Several factors should be considered when choosing insect species as animal feed. Among them, the feeding habits of the species play a significant role. Insects that efficiently convert waste into high-quality protein are particularly desirable, as they can replace increasingly expensive compound feed ingredients. Insects are known to be highly efficient food converters due to their ability to maintain high growth rates without the need for energy-intensive temperature regulation [52]. Another important factor to consider is the sustainability of using insects as animal feed. Compared to traditional livestock feed, insects require significantly less land and water to rear, making them a more sustainable option. In addition to waste recycling, insect rearing has shown a low score on carbon footprint [53].

Therefore, by utilizing insects as a feed source for animals, the environmental impact of animal agriculture could be significantly reduced while still providing high-quality nutrition for the animals, which requires a comprehensive evaluation of the nutritional composition and safety of the insects and their acceptability. Furthermore, research is needed to optimize the rearing, processing, and storage of insects for animal feed, minimizing costs, and maximizing benefits [54].

The impact of insect-based feed on farmed animals has recently drawn researchers' attention. For instance, literature reviews have focused on the use of insects in aquaculture [55], poultry [56], and pig farms [57], presenting large and diverse research on the benefits and applications of insects as animal feed. In comparison to the aquaculture industry, there are fewer data on the use of these insects as feed for other animals. Insects can be used as poultry feed for various reasons, including improved animal health and high conversion rates in various industries (e.g., layers and broilers) [56]. Furthermore, replacing part of the pig diet with insect meal instead of traditional row crops represents a valuable approach for promoting sustainability, as the inclusion of insects in the pig diet has no negative impact on associated growth; however, it was not confirmed whether the variations between results are due to insect meal or some other factors, as reviewed by Veldkamp and Vernooij [57]. Presenting insects to farm animals as feed does not promote animal welfare or production sustainability by default [7]. Understanding and optimizing all the factors involved and the potential of insect-based diets are necessary. Therefore, food waste should be decreased, and reared insects should be optimally fed with waste substrates that are completely safe and suitable for use as animal feed. All processes must be observed under strict regulatory frameworks, and a balance must be maintained between environmental sustainability, the welfare of livestock and insects, and livestock productivity. In addition, academic organizations, regulatory agencies, waste management sections, insect and livestock producers, and consumers should collaborate to achieve sustainable food systems.

3.2. Utilization of insect frass as agricultural fertilizers

Waste management deficiency and soil degradation are major environmental issues and negatively affect food security worldwide [58,59]. Moreover, micronutrient inadequacy, low organic matter, and high acidity in soil hinder the mineral fertilizers' efficiency [60,61]. Using organic fertilizer as a soil amendment is an affordable and acceptable option for farmers [62]. However, it has low uptake due to long production times, low quality, and inadequate organic material sources on the farm [63]. Therefore, alternative sources of fertilizers that are affordable, easily obtained, and

of adequate quality need to be explored [64,65].

Several studies have been performed to utilize insect frass, e.g., BSF and YMW, as potential organic fertilizer sources, providing plants with nutrients and beneficial microbes (Fig. 2) [66–69]. In this context, BSFL converts organic waste into stable, mature, and nutrient-rich frass fertilizer within five weeks, whereas conventional composting requires 8–24 weeks [69]. The yield and nutritional quality of maize, barley, cowpeas, French beans, tomatoes, and chili pepper is grown using BSF or YMW frass fertilizers were higher than those grown using conventional fertilizers [70,71]. Moreover, when BSF and YMW frass fertilizers were used as soil amendments, nutrient availability, mineralization of nitrogen, and soil microbial activity were improved, whereas the number of soil-borne pathogens and soil salinity and acidity considered as indicators of enhanced soil quality for crop production, were reduced [72–74].

To provide specific recommendations for their efficient use in enhancing soil fertility and crop yield, a comparative study was conducted to report the characteristics of frass fertilizer produced by nine edible insect species, including BSF, YMW, *Schistocerca gregaria*, *Gryllus bimaculatus*, *Scapsipedus icipe*, *Pachnoda sinuata*, *Oryctes rhinoceros*, *Bombyx mori*, and *Gonimbrasia krucki* [10]. All of the insect species' frass fertilizers had acceptable quality and quantity of macronutrients, secondary nutrients, and micronutrients. The fertilizing indices of the frass fertilizers were >3 (Table 3). The frass fertilizer from BSF had notably higher nitrogen (N) and potassium (K) concentrations than other fertilizers. While phosphorus (P) concentration was higher in *G. bimaculatus* fertilizer than in other insect species fertilizers. Seeds treated with BSF frass fertilizer had the highest seed germination rate and germination index. The phytotoxicity of the frass fertilizer obtained from the other eight insect species ranged from medium to high. The higher N–P–K concentrations in BSF, YMW, *G. bimaculatus*, and *S. icipe* frass fertilizers may be because of the high nutritional values in the diet substrates, such as wheat bran, brewery spent grain, soybean, and potato peels, used to rear these insects [75,76]. Nutritional element concentrations in frass fertilizers produced by all nine insect species were within the Kenya Bureau of Standards guidelines for optimal commercial organic fertilizer [77] and

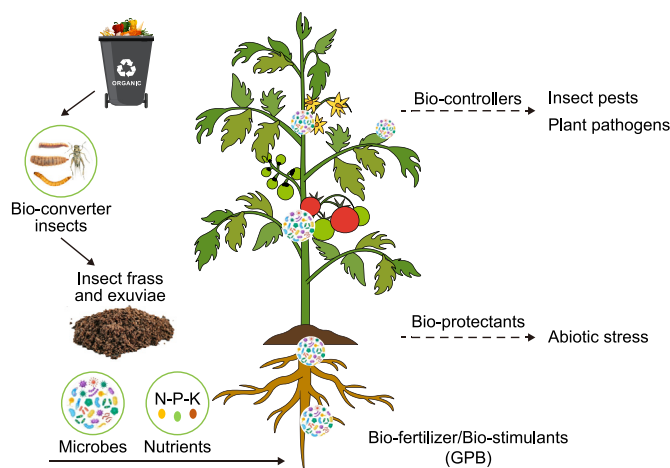


Fig. 2. The benefits of using insect frass and exuviae as a bio-fertilizer for plant growth and protection. The frass of insects, particularly those that feed on biowaste substrates, has been demonstrated to be a rich source of nutrients and beneficial microbiota. When used as fertilizer for plants, it has been shown to promote plant growth. The microbiota present in insect frass includes plant-beneficial microbes that can act as biocontrol agents against plant pathogens. They can also function as bioprotectants that enhance plant tolerance under stress and biostimulants that induce plant resistance.

Table 3
Characteristics and fertilization efficiency of frass fertilizer obtained from edible insects feeding on different waste substrates.

Insect species	Waste type	Feeding duration	Fertilizing index	C/N ratio	N–P–K values (kg ha ⁻¹)	Germination rate (%)	Reference
<i>Hermetia illucens</i>	Mixture of Irish potato peels + brewery spent grain	2 weeks	~5	13.2	N: 147.5 P: 63.2 K: 203.7	93.3	[10]
	Brewery spent grains	-	-	10.7	N:180.5 P: 25 K: 14.5	86	[79]
<i>Tenebrio molitor</i>	Wheat bran + chayote (<i>Sechium edule</i>)	5 weeks	~4.5	20.0	N: 124.3 P: 69.8 K: 104.8	56.7	[10]
<i>Musca domestica</i>	Food waste	4–6 days	-	-	N:148.5 P: 11.5 K: 15	-	[80]
<i>Schistocerca gregaria</i>	Wheat & barley seedlings + wheat bran	-	~4.5	19.5	N: 103.3 P: 36.5 K: 175.3	23.3	[10]
<i>Gryllus bimaculatus</i>	Wheat bran + soybean + sweet potato vines + weeds	2 months	~4.5	18.6	N: 114.5 P: 76.7 K: 103.7	76.7	[10]
<i>Scapsipedus icipe</i>	Wheat bran + soybean + sweet potato vines + weeds	3 months	~4.5	17.4	N: 120.7 P: 74.2 K: 122.7	63.3	[10]
<i>Pachnoda sinuata</i>	Fresh cattle dung from a dairy farm	4–5 weeks	~4.5	14.6	N: 106.8 P: 52.2 K: 151.2	96.7	[10]
<i>Oryctes rhinoceros</i>	Fresh cattle dung from a dairy farm	-	~4.5	14.6	N: 82.8 P: 21.5 K: 82	93.3	[10]
<i>Bombyx mori</i>	Leaves of mulberry tree (<i>Morus</i> spp.)	6 weeks	~4	19.1	N: 117.2 P: 8.5 K: 86.5	60	[10]
<i>Gonimbrasia krucki</i>	Brazilian pepper tree leaves (<i>Schinus terebinthifolia</i> Raddi)	5 weeks	~4	22.9	N: 107 P: 9.8 K: 70.3	86.7	[10]

meeting international standards [78] for organic fertilizer quality in the United States, the European Union, and Canada.

Notably, different insect species exhibit different rates of waste degradation and composting, which affect the amount of available frass fertilizer. For example, BSFL have a high waste degradation efficiency (55–80%) and require a short bioconversion time, allowing them to produce more organic fertilizer than other insect species [81,82]. The YMW, *O. rhinoceros*, and *P. sinuata* converted waste substrate into fertilizer within 4–6 weeks, while BSF spent only two weeks [69]. Frass fertilizer could be produced daily from *S. gregaria* and crickets but in smaller amounts than those from BSFL. The high germination rate (>90%) achieved with BSF-based fertilizer indicates the absence of phytotoxicity (Table 3) and, thus, the ability to promote plant growth [83]. In addition to the aforementioned species, *P. brevitarsis* was found to feed on maize straw and mushroom residues, and the resulting fertilizer after larval feeding had a rich nutritional content, high humic acid, and low phytotoxicity [25,27].

The application of insect frass as fertilizer has also been shown to improve plant tolerance to stress and enhance plant quality. In comparison to cattle manure, BSF frass was determined to be more effective in promoting basil plant growth and mitigating the effects of drought, leading to an improvement in plant quality [84]. Similarly, using BSF frass as an organic fertilizer has been demonstrated to reduce salinity stress and enhance lettuce quality. Specifically, it was found to reduce the nitrate concentration in the leaves, indicating a potential role for insect frass in activating nitrogen assimilation in plant cells. Additionally, the application of BSF frass improved soil biological fertility, as evidenced by increased active carbon levels and

enzyme activity involved in nutrient cycling [85].

Regarding the YMW, recent research has demonstrated the potential of YMW frass to enhance the growth of multiple crops. Compared to hen manure, YMW frass exhibited similar growth-promoting effects across different crops. The application of YMW frass was found to increase edible biomass by up to 16-fold and produce larger and more abundant flowers. These promising results suggest that YMW frass could be a sustainable alternative to traditional fertilizers in various crop systems [86].

4. Agri-food waste utilizing insects and gut symbiotic microbiota

The insect gut harbors an array of microbial symbionts that affect health and fitness [87]. Some of these symbionts play diverse roles in their relationship with insects, ranging from egg production to insect development, survival, and fitness [88,89]. The digestive process in insect guts is attributed, at least in part, to gut microbial activity, with enzymes produced by gut microbes playing a significant role in the biodegradation of biomass [90]. Therefore, understanding the complexity of gut microbes, including their assembly determinants and functions, is essential to promote effective bioconversion.

4.1. Assembly and determinants of gut microbiota composition in agri-food waste-utilizing insects

Recently, a wide range of research using metagenomic analysis has been conducted to study the microbial communities in edible

insects [91,92] and residual frass [93,94]. These metagenomic studies have advanced our understanding of the composition and roles of microbes in nutrient metabolism in insects, frasses, and animals. Based on several recent studies on the taxonomic profiling of insects destined for food or animal feed, the dominant microbial groups are summarized in Table 4. In all observed insect species, the highest abundant phyla of gut bacteria generally belonged to Proteobacteria, Firmicutes, Actinobacteria, and Bacteroidetes [95-103]. Regarding the BSF, considered the most efficient biowaste-converting insect species, Ijdema et al. [104] conducted a meta-analysis of 16S ribosomal RNA gene sequence data sets from 11 studies to gain deeper understanding insights into the gut microbiota of BSFL. The study revealed that the core microbiota of BSFL primarily comprised *Enterococcus*, *Klebsiella*, *Morganella*, *Providencia*, and *Scrofulimicrobium*, as these bacterial genera were found to be prevalent in BSFL gut samples.

The assembly of gut microbial communities in agri-FW bio-refinery insects, mainly BSF, is influenced by several environmental, diet-related, and insect-related factors. Several microbial taxa have been frequently found in association with the fly larvae gut and could be considered the core microbiota composed of a simple microbial group represented in high abundance (e.g., members of *Pseudomonas*, *Providencia*, *Enterococcus*, and *Morganella* genera), regardless of the variations in the diet [106]. This indicates that several basic microbial groups originating from the adult fly are transferred and maintained in the fly larvae, while other microbes are acquired from the substrate they feed on, and the environment represents diverse groups of low-abundance taxa [106,107]. The study by Bruno et al. [108] investigated the impact of different diets and regions within the midgut on microbial load and diversity. Results showed that while different diets affected the microbial composition in the anterior midgut, no such effect was observed in other parts of the midgut. Additionally, distinct differences were observed in microbial composition and load across different parts of the midgut. Specifically, the anterior part displayed higher diversity, gradually decreasing along the midgut, while the posterior part had the highest microbial load. Moreover, Schreven et al. [109] reported that in addition to feed substrate, larval density also significantly impacts the microbial composition of larvae and substrate. The study found that several common bacterial genera exhibited changes in abundance, highlighting the importance of considering larval density as a factor. These findings highlight the importance of considering the specificities of different regions within the midgut as well as the larval density while studying the BSF gut microbiome.

Insects exert significant selective assembly power on the gut microbiota through the unique conditions of their gut environment, such as the oxygen level, pH level, larval antibacterial activity, and competition with core microbiota, which together control the diversity and population of the gut microbiome [11,110]. Variability in the microbial community composition was observed between different gut compartments (foregut, midgut, and hindgut) and even between the different parts within the midgut region based on the distinction in prevailing conditions, such as oxygen level and pH [108,111]. The ability of larvae to suppress specific microbial taxa has been observed to include several feed and food pathogens, although the process is regulated by several factors and is not yet fully understood [112].

This inhibition of specific microbial pathogens could be considered as an immunity filter enabling insect survival even on highly microbially contaminated substrates, as shown in the study by Liu et al. [113], confirming the reduction of *Escherichia coli* in dairy manure. In the same line, the ability of BSFL to inactivate or reduce the population of certain pathogenic microbes from

Table 4 Characterization of bacterial communities in the gut of important food and feed insects (*Hermetia illucens*, *Musca domestica*, *Acheta domestica*, and *Tenebrio molitor*) feeding on different substrates; animal-fed insect species.

Insect	Life Stage(s)	Waste/Feed type	Omics technique	Top 3 phyla	Top 5 genera	Reference
<i>Hermetia illucens</i>	Larvae	Commercial chicken feed	Genotyping (BOX-PCR) + Phylotyping (16S rRNA gene)	Proteobacteria, Firmicutes, and Actinobacteria	<i>Providencia</i> , <i>Proteus</i> , <i>Morganella</i> , <i>Enterococcus</i> , <i>Bacillus</i>	[95,105]
	Larvae	Animal manure	16S rRNA (Illumina MiSeq)	Proteobacteria, Firmicutes, and Bacteroidetes	<i>Enterococcus</i> , <i>Providencia</i> , <i>Morganella</i> , <i>Klebsiella</i>	[96,105]
	Larvae	Food waste	16S rRNA (Illumina MiSeq)	Firmicutes, Proteobacteria, and Bacteroidetes	<i>Dysgonomonas</i> , <i>Actobacillus</i> , <i>Providencia</i> , <i>Dysgonomonas</i> , <i>Leuconostoc</i> , <i>Morganella</i>	[97,105]
<i>Musca domestica</i>	Larvae	Plant-based diet with fish meal	16S rRNA (Illumina MiSeq)	Proteobacteria, Firmicutes, and Bacteroidetes	<i>Lactococcus</i> , <i>Pseudomonas</i> , <i>Kurthia</i> , <i>Myroides</i> , <i>Morganella</i>	[98]
	Eggs, larvae, pupae, and adult	Artificial diet	16S rRNA (Illumina MiSeq)	Proteobacteria, Firmicutes, and Bacteroidetes	<i>Myroides</i> , <i>Providencia</i> , <i>Proteus</i> , <i>Morganella</i> , <i>Pseudomonas</i>	[99]
<i>Tenebrio molitor</i>	Larvae	Wheat bran & Polystyrene	16S rRNA (Illumina MiSeq)	Tenericutes, Proteobacteria, and Firmicutes	<i>Spiroplasma</i> , <i>Cronobacter</i> , <i>Enterococcus</i> , <i>Lactococcus</i> , <i>Lactobacillus</i>	[100]
	Larvae	Agro-industrial byproducts	16s rRNA (Ion Torrent)	Tenericutes, Proteobacteria, and Firmicutes	<i>Spiroplasma</i> , <i>Acinetobacter</i> , <i>Bacillus</i> , <i>Lactococcus</i> , <i>Lactobacillus</i>	[101]
<i>Acheta domestica</i>	Adult	Plant-based diet	16S rRNA (Illumina MiSeq)	Bacteroidetes, Proteobacteria, and Verrucomicrobia	<i>Parabacteroides</i> , <i>Bacteroides</i> , <i>Dysgonomonas</i> , <i>Akkermansia</i> , <i>Enterococcus</i>	[102]
	Adult	Crop residues	16S rRNA (Illumina MiSeq)	Proteobacteria, Firmicutes, and Bacteroidetes	<i>Streptococcus</i> , <i>Citrobacter</i> , <i>Lachnospira</i> , <i>Lactococcus</i> , <i>Serratia</i>	[103]

different substrates has been studied using green fluorescent protein-labeled bacteria. Erickson et al. [114] reported the inactivation and reduction of pathogenic microbes, such as *E. coli* and *Salmonella enterica*, by BSFL in poultry manure. Similar results were observed for dairy cow manure substrate, as BSFL significantly reduced the population of *E. coli*. In both studies, temperature significantly affected the larval antimicrobial activity. BSFL also reduced the concentration of pathogenic *Salmonella* spp. in human feces [82,115]. Thus, BSFL could be potentially applied for the inactivation and inhibition of pathogenic microbes by understanding the factors regulating the antimicrobial process. However, it is important to highlight the safety of humans and animals, as pathogenic microbes might still be detected in fly larvae [116].

In this context, De Smet et al. [117] argued that producers should not rely on the antibacterial activity of BSFL during industrial-scale rearing to eliminate food safety risks. The study found no significant reduction in the presence of *Salmonella*, a food pathogen, on chicken feed substrate due to the larval activity. While the outgrowth of *Salmonella* was slower when lower initial contamination levels with the pathogen were used compared to higher levels, the larvae could not completely eradicate the pathogen or even reduce its count over time.

4.2. Roles of gut-associated microbiota in the development and functions of the agri-food waste biorefinery insects

Like humans, animals, and plants, associated microbial communities play vital roles in sustaining insect growth, fitness, and survivability. Studies involving rearing fly insects under sterilized conditions have confirmed the inevitable roles of associated microbes in sustaining insect growth and development [118,119]. With regard to agri-FW biorefinery insects (mainly BSF), the associated microbiota is an integrated part of the system that contributes to larval development, versatility, and metabolic processes in several ways [120,121].

4.2.1. Decomposition of organic substrates

The larval gut microbiota contributes considerably to the decomposition of agri-FW. Due to the diverse range of microbial and enzymatic activity found in the digestive system of BSFL, it is considered one of the most effective in breaking down food waste and other organic materials [122,123]. Recent metagenomic studies have provided microbiological evidence to support the degradation efficiency of BSFL. The taxonomic composition and potential metabolic analysis of the BSFL gut microbiome in chicken and swine manure conversion systems confirmed the association of several microbial taxa with the functional capacity to degrade various organic substrates [96]. In the latter study, the predicted metabolic functions were dominated by those related to the metabolism of carbohydrates, amino acids, cofactors, and vitamins, indicating the potential contribution of the gut microbiota to the high-efficiency nutrient conversion and nutrition of BSFL. In another study, a wide range of microbial groups (more than 11,000 bacteria) were detected in the BSFL gut, including those belonging to Firmicutes and Bacteroidetes, known for their functional capacity facilitating feed utilization efficiency and degradation of high-molecular-weight organic matter and animal manure [120].

When insects consume high-carbohydrate diets, gut microbes can transform polysaccharides, such as starch and fibers, into short-chain fatty acids and/or simple alcohols [124]. The gut bacteria of BSFL contribute to waste biodegradation by producing enzymes that hydrolyze proteins, lipids, cellulose, and starch [125-127]. In nutrient-poor diets, *Acetobacter pomorum* decomposes carbohydrates and produces metabolites that affect the growth of fruit fly larvae (FFL) by affecting growth signaling pathways [128].

According to Storelli et al. [129], *Lactobacillus plantarum* causes an increase in amino acids generated from FFL reared on poor-protein feed, thus enhancing larval growth.

Because of their adaptable ecological behavior, edible insects digest different plant biomass substrates, including starch, cellulose, lignocellulose, hemicellulose, xylan, pectin, terpenes, tannins, esters, glucosinolates, essential amino acids, and pyrrolizidine alkaloids [130]. The insect gut secretes various lignocellulosic-hydrolyzing enzymes based on its diet, particularly plant biomass. Simultaneously, gut symbionts in insects produce most digestive enzymes for the enzymatic digestion of ingested plant ingredients to achieve energy mining. Therefore, the gut microbiota plays a critical role in assisting host metabolism by improving digestion efficiency through enzymatic activity [131].

As illustrated in Fig. 3, the potent lignocellulase, xylanase, and pectinase producers (e.g., *Bacillus*, *Pseudomonas*, *Staphylococcus*, *Citrobacter*, *Enterobacter*, *Acinetobacter*, *Providencia*, *Klebsiella*, *Lysinibacillus*, *Lactococcus*, *Enterococcus*, *Dysgonomonas*, and *Serratia*) were detected in the gut system of four main edible insects (BSF, HF, YMW, and *A. domesticus*) with minor differences in the detected microbial taxa between insect species as shown in several previous studies [95–99,102,103,132–135]. These findings indicate that the edible insects harbor potential plant biomass-degrading bacteria in their gut, which may help them decompose and convert agri-FW materials to insect biomass. Notably, this suggestion is grounded in the presence of these identified microbial taxa, which are known to produce lignocellulase, xylanase, and pectinase in other insects. The involvement of such activity in biowaste-utilizing insects, such as BSF and YMW, requires experimental confirmation.

Regarding protein degradation and assimilation, a recent study by Yu et al. [123] has provided evidence of the involvement of BSF gut microbial activity in protein digestion and absorption. The study was able to facilitate this evidence by generating germ-free larvae and comparing them with gnotobiotic ones. These findings revealed that certain microbial taxa, namely *Pseudomonas*, *Orbus*, *Campylobacter*, *Dysgonomonas*, *Issatchenia*, *Pediococcus*,

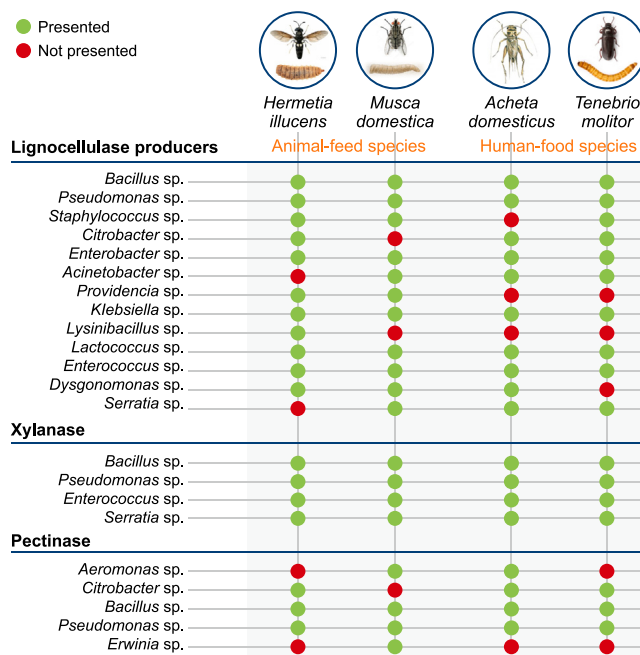


Fig. 3. The presence of plant biomass-degrading bacteria in the gut of edible insects, the animal-feed species (*H. illucens* and *M. domestica*), and the human-food species (*A. domesticus* and *T. molitor*).

Lactobacillus, and *Bacillus* genera, were correlated with the protein assimilation and digestion process. Additionally, the study found that the presence of gut microbiota significantly increased the level of protein degradation, leading to the substrate protein's conversion into insect body proteins.

4.2.2. Degradation and detoxification of pollutants, pesticides, and toxins

Agri-FW resources contain high levels of hazardous pollutants and contaminants, such as pesticides, veterinary antibiotics, and mycotoxins [116,136]. Insect gut microbiota confers several other beneficial functions for supporting the insect fitness of agri-FW substrates and improving the quality of bioconversion products. Regarding pharmaceuticals and pesticides, Zhang et al. [137] reported the acceleration of biodegradation and enhanced attenuation of antibiotics during vermicomposting of swine manure. Nine antibiotics, including tetracyclines, sulfonamides, and fluoroquinolones, were removed during vermicomposting for six days using fly larvae. In another study, the half-lives of three drugs (carbamazepine, roxithromycin, and trimethoprim) and two pesticides (azoxystrobin and propiconazole) were significantly reduced in fly larvae composting with no bioaccumulation in the larvae, suggesting that the degradation was linked to microbes as the experiments were conducted under conditions favoring microbiological activity [138].

Mycotoxins are also expected hazardous compounds in agri-FW that could be tracked to plant materials or animal feed in the substrates. Agri-FW bioconversion insects have shown remarkable activity in the degradation of mycotoxins, as confirmed in several studies [116]. Mycotoxin degradation is a well-known microbial activity, and several microbes have been isolated and confirmed to efficiently degrade various types of mycotoxins [139]. It appears that insect gut microbes may also be responsible for mycotoxin degradation, although further confirmation and understanding of the degradation and detoxification mechanisms are necessary. The larvae of *T. molitor* were able to feed on *Fusarium*-contaminated wheat grains and exhibited no difference in mortality levels compared to the control, indicating the ability to tolerate or metabolize *Fusarium*-produced toxins [140]. In another study, the growth of BSFL was not affected when larvae were fed on corn substrates contaminated with mycotoxins (aflatoxins, deoxynivalenol, ochratoxin A, and zearalenone) and pesticides (chlorpyrifos, chlorpyrifos-methyl, pirimiphos-methyl), and no accumulation of these hazardous compounds was observed in the larval tissues [141]. Similarly, both BSFL and YMW showed high tolerance and lack of accumulation when fed poultry feed containing specific levels of aflatoxin B1 [142]. Therefore, it is suggested that future research should investigate the mechanisms of detoxification and consider the toxin degradation activity of these insects to enhance the conversion of mycotoxin-contaminated agricultural food waste. This will provide experimental confirmation of the involvement of insect gut microbiota in the process.

An illustration of the different roles carried out by gut-associated microbiota and the black soldier fly model as the most efficient agri-FW bioconverter is shown in Fig. 4.

4.3. Microbe-mediated approaches for enhancing the insect growth and bioconversion of organic waste

4.3.1. Regulation of insect behavior

Starting from oviposition, bacteria isolated from conspecifics on decomposing resources and insect eggs mediate the regulation of

insect behavior by attracting flies for oviposition via their emitted volatile signals [143]. The fact that BSF has co-evolved to thrive on decaying substrates and ephemeral, rapidly vanishing resources, such as vertebrate carrions, could explain the attraction for rapid colonization of such substrates, providing BSF with a competitive advantage over other species utilizing the same type of resources [144,145]. Groups of microbes, not a single species, are responsible for emitting behavioral-regulatory attractant volatiles that are affected by bacterial concentration, strengthening the necessity of studying the role of bacteria in regulating insect behavior within the context of the bacterial community and not a single species [143].

4.3.2. Microbiota as a source of nutrition

Apart from the behavioral regulatory signaling roles of insect-associated microbes, one basic role of acquired microbes in the insect gut is their utilization as a nutrition source, especially when insects are fed on low-protein and substrates lacking essential nutrients, such as methionine [11,146]. Gut microbiota can serve as a source of nutrients for fly larvae, as larval gut acidic conditions, antimicrobial peptides, lysozyme, and pepsin are involved in the lysis of fungi and bacteria in the midgut, releasing nutrients to be absorbed in the posterior midgut and contributing to larval development [11,147,148]. In addition to the larval gut core and other acquired microbes, egg-associated microbes of other fly insects serve as food for hatching insects, although this needs to be confirmed in BSF [149].

Bacteria that selectively survive larval gut metabolism and establish their population carry out several important functions contributing to larval development and waste decomposition processes [121]. Fly insects show a high preference for substrates containing microbes, which might contribute to the synthesis of essential elements for their growth and development. In a unique network, the fly larvae showed a shift in their preference for resources based on the presence of certain microbes capable of producing certain elements lacking in the substrate. A good example of this is the varied behavior of fly larvae in their preference for methionine-amended resources, as more preference was seen when microbes producing methionine were present on methionine-lacking substrates [146]. Methionine, a sulfur-containing amino acid, is essential to cellular metabolism and protein biosynthesis [150]. Insects can compete for methionine resources. Intriguingly, fly larvae preferred resources containing microbes producing methionine, which could be utilized to provide the larvae with this essential amino acid in a methionine-lacking substrate and avoid competition with other species in methionine-rich resources [146].

4.3.3. Microbial intervention to improve insects' biowaste conversion efficiency

As explained above and summarized in Fig. 4, the gut microbiota plays an important role in insect development and contributes significantly to the enhancement of agri-FW bioconversion via several mechanisms. Therefore, the insect gut microbiome could be seen as an opportunity for intervention to improve process efficiency and knowledge about insect-microbe interplay can be utilized to improve the degradation process within the biorefinery framework. This approach has been investigated in previous studies that targeted the exploitation of microbial activity to enhance the process.

In this context, strains of *Bacillus subtilis* originally isolated from BSFL were applied to poultry manure to feed conspecific larvae,

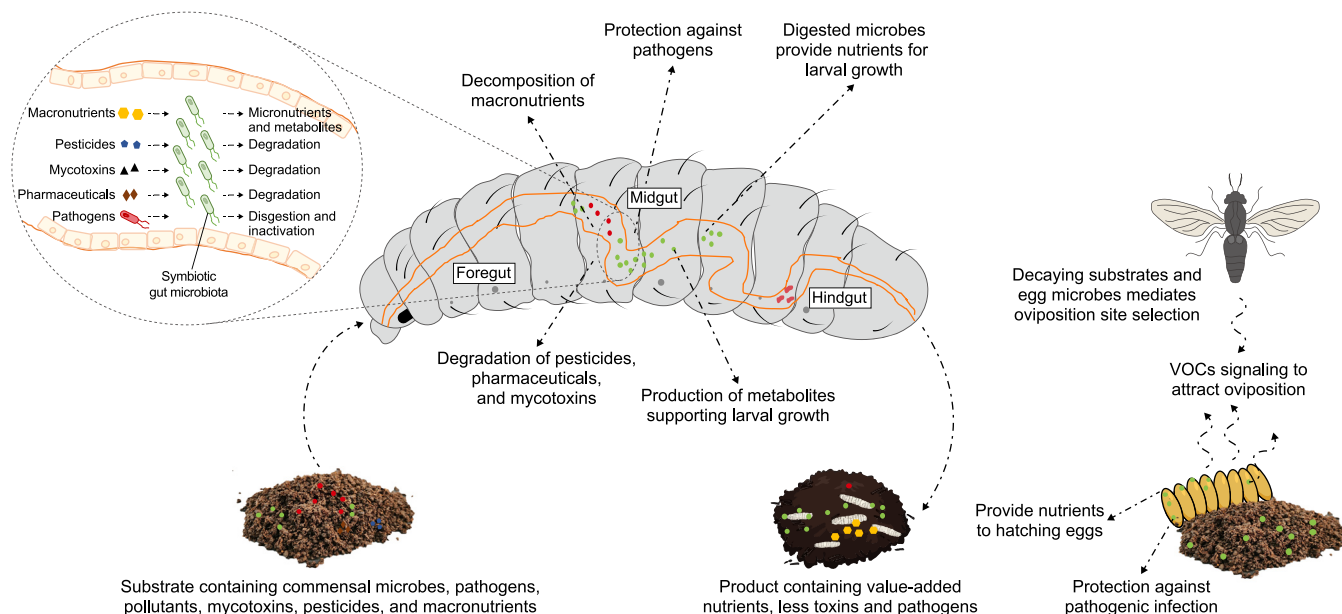


Fig. 4. Illustration of the different roles of the gut-associated microbiota of the black soldier fly within the agri-food waste biorefinery system.

resulting in enhanced larval development and insect growth, as confirmed by the increase in prepupal weight and adult body length [151]. The bioconversion process by BSFL was shown to be enhanced in another study by co-employing *B. subtilis* during poultry manure bioconversion, resulting in rapid harvesting of higher quality biofertilizer and value-added larvae mass [152]. Mazza et al. [153] also isolated several bacterial species from the eggs and larvae of BSFL and reported enhanced growth, nutrient accumulation in BSFL, and manure conversion rates by individual or combined inoculation of chicken manure. Similar results were achieved by Franks et al. [6], as they demonstrated that supplementing the diet of BSFL with *Rhodococcus rhodochrous* resulted in accelerated development, enhanced final body size and protein and fat production, and improved conversion efficiency. Specifically, the conversion rate was nearly doubled in the bacteria-treated larvae, indicating that a reduced amount of food would be necessary to achieve optimal weight gain. This suggests that the supplementation with *R. rhodochrous* facilitated greater metabolism of the diet, resulting in the need for less food to reach optimal weight, which is a crucial consideration for industrial-scale and commercial applications of BSFL larvae.

In another study, an attempt to perform a directional transformation of the BSFL gut microbiota by inoculation with six different bacteria isolated from the BSFL confirmed the colonization and establishment of *Lysinibacillus* in the insect gut [154]. Recent research has highlighted the potential of the probiotic microorganism *Bacillus velezensis* to optimize the conversion of food waste into dry larval biomass in BSFL. This is achieved through the modulation of the gut microbiome, the provision of riboflavin to the host, and the alteration of synthetic and metabolic pathways of amino acids, resulting in an increase in protein content [155]. In this study, a significant change in the diversity and composition of the gut microbiota was observed, primarily by manipulating the relative abundance of *Bacillus*, unclassified members of Caloramatoraceae, and *Gracilibacillus*. These changes were found to improve substrate conversion efficiency and the protein conversion process, indicating that the probiotic effect is not only related to direct

influence on the insect but also through its indirect influence on the composition of the gut microbiome.

In addition to BSFL, the application of *Pediococcus pentosaceus*, a lactic acid-producing bacterium isolated from YMW, was found to inhibit the growth of specific pathogenic bacteria, confer beneficial influence on larval growth and survival, and establish successful colonization in the insect gut, as confirmed from the results of the 16S rRNA gene amplicon sequencing analysis [156]. Altogether, the presented findings highlight the importance of considering the hidden microbial elements in the process to enhance system performance and avoid limitations.

5. Conclusions and future perspectives

Insect-based conversion of agri-FW has been recognized as a promising waste management strategy. Integration of insects into livestock animal feed is promising to maintain the sustainability of animal production systems. However, the incorporation of insects as sustainable protein sources for animal feed requires the support of the academic sector, regulatory agencies, waste management organizations, as well as insect and livestock producers and consumers. Insect frass can be used as an alternative source to obtain affordable and good-quality organic fertilizers. However, all insect frasses, except BSF, require additional composting to promote their stability and maturity. Furthermore, agronomic studies are necessary to determine the optimal soil amendment rates to enhance the nutrient release and improve crop uptake, effective nutrient use, nutritional quality, and crop yield.

Recent studies have focused on determining the biochemical pathways involved in the degradation process to propose new biotechnological alternatives for waste management. However, the industry still lacks a thorough understanding of the benefits of a specific insect species as feedstock for marketable agricultural products. The economics of insect production has received little attention, and more research is required to determine the profitability of insect farms.

Studies on insect gut microbiome composition and function

have acknowledged the significance of insect-associated microbial communities in the agri-FW bioconversion process. Recent studies have proposed strategies to target the insect gut microbiome to enhance the organic waste bioconversion process. However, these studies have only focused on probiotic inoculation with bacteria. Further research should explore the insect gut microbiome to facilitate the use of edible insects in sustainable agricultural practices.

Credit authorship contribution statement

Mohamed Manaa: Investigation, Data Curation, Visualization, Writing - Original draft preparation. **Abdelaziz Mansour:** Investigation, Data Curation, Visualization, Writing - Original draft preparation. **Inmyoung Park:** Investigation, Data Curation, Visualization, Writing - Review & Editing. **Dae-Weon Lee:** Investigation, Data Curation, Visualization, Writing - Review & Editing. **Young-Su Seo:** Conceptualization, Funding acquisition, Project administration, Writing - Review & Editing. All authors read and approved the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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