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REVIEW

Insect Gut Microbiota as a Reservoir of Industrially Relevant Enzymes: A Comprehensive Review

Aswin Viswan[1] · **Neenu Augustine**[2]

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Abstract

The insect gut microbiome constitutes a substantial yet underexplored reservoir of microbial diversity with important implications for entomology and biotechnology. Gut-associated microbes are crucial for maintaining host physiology, encompassing digestion, nutrient absorption, immune function, and resistance to environmental stress. In addition to these biological functions, the insect gut contains metabolically versatile bacteria that can synthesise a variety of bioactive substances, including amino acids, vitamins, antimicrobial agents and a wide range of industrially important enzymes. Enzymes such as cellulases, amylases, proteases, lipases etc., isolated from insect gut microbes have attracted increasing attention owing to their stability, versatility and facilitation of optimisation for large-scale production. Insects, being able to thrive in extreme environments, possess gut-derived enzymes that demonstrate exceptional stability and catalytic effectiveness, rendering them suitable for industrial and biotechnological applications. The current review compiles contemporary findings on enzyme-producing gut bacteria from various insect orders, emphasising the main enzyme classes identified, potential microbial species, traditional as well as advanced screening methodologies for important enzymes reported, viz., cellulases, proteases, amylases and their multifaceted applications in bioconversion, bioremediation and other industrial domains.

Keywords Insect gut microbiome · Industrial enzymes · Cellulase · Screening techniques

Introduction

The gut microbiome refers to the consortia of microbial communities residing in the gastrointestinal system. This includes bacteria, archaea, fungi, protists, etc. This microbial diversity creates intricate, dynamic communities that engage in mutualistic, commensal or occasionally pathogenic interactions with their hosts [1]. In many animals, the gut microbiome is known as a vital second genome. Recent studies exploring the gut microbiome explain their primary functions in nutrition uptake and metabolism. Microbes play a vital role in enzymatic systems to degrade complex dietary polymers, including cellulose, hemicellulose, lignin and resistant starches, which are otherwise indigestible to the host [2]. Fermentation activities yield short-chain fatty acids (SCFAs) and other metabolites that play a crucial role in host energy equilibrium and nutrient absorption [3]. In addition, gut microbes produce vital vitamins such as B and K, as well as amino acids, thereby favouring host nutrition [4]. The gut microbiota significantly impacts the host immunity and disease resistance by producing antimicrobial substances and promoting the development of the host immune system [5].

Insects account for almost 50 per cent of all identified living species that exhibit a wide array of behaviours and diets that are closely associated with their gut microbiota [6]. The insect gut is divided into foregut, midgut and hindgut, each exhibiting unique physicochemical conditions like pH, oxygen gradients, redox potential, etc. that favour specific microbial populations (Fig. 1a) [6, 7]. The midgut generally exhibits an alkaline environment, which is mostly detrimental to several bacteria, whereas the hindgut offers an anoxic, fermentation-supportive environment conducive to robust

✉ Neenu Augustine
neenu.augustine@vit.ac.in

[1] School of Bio Sciences and Technology, Vellore Institute of Technology, Vellore, Tamil Nadu 632014, India

[2] VIT School of Agricultural Innovations and Advanced Learning, Vellore Institute of Technology, Vellore, Tamil Nadu 632014, India

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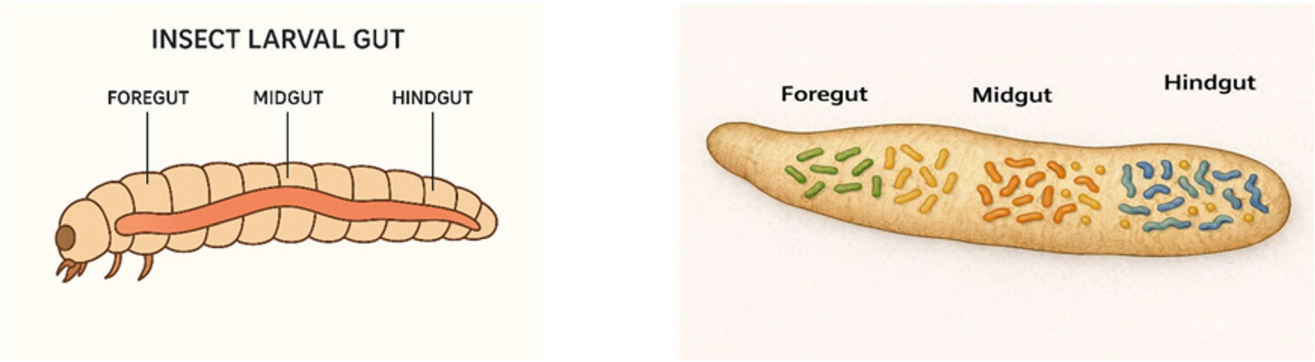

Fig. 1 (**a**) & (**b**) Larval gut compartments illustrating differential microbial diversity- foregut (microbial diversity is less), midgut (consist of diverse microbial diversity) and hindgut (having rich microbial diversity)

microbial communities [8]. Figure 1 (b) shows the difference in microbial communities across the three different gut compartments, wherein the hindgut possesses diverse microbial communities along with the midgut, suitable for isolating and harnessing beneficial microbiota for isolating enzymes and bioactive compounds. The predominant bacterial phyla in insects are Proteobacteria, Firmicutes, Bacteroidetes and Actinobacteria, although their relative abundances exhibit considerable variation [9, 10]. Studies have been done exploring the microbiome of termites and cockroaches, which are reported to possess complex hindgut communities predominantly composed of anaerobic microorganisms proficient in lignocellulose breakdown [11, 12]. Lepidopteran and Coleopteran larvae were also reported to harbour beneficial microorganisms in their gut [13, 14].

The gut microbiome of insects produces several types of enzymes and metabolites that are important for the host's nutrition and ability to adapt. A plethora of these compounds exhibits significant biotechnological potential [15]. These metabolites also have important antibacterial, antifungal, and medicinal properties that can be used in industries [16, 17]. Microbial enzymes such as cellulases, proteases, and amylases have garnered significant attention and application due to their stability, ease of production, and optimisation strategies at an industrial level, in contrast to other sources [15, 18]. Likewise, substances such as siderophores, iturin, surfactins, and others, extracted from the gut microbiota of beetles and wasps, exhibit potential antimicrobial and antifungal characteristics, respectively [19]. In a context where industries prioritise profit and effective scaling, microbial enzymes are significantly important, particularly in the exploration of a relatively under-researched area, the insect microbiome. Nonetheless, a restricted amount of research has examined microbiome patterns across ecologically diverse insect taxa, highlighting the importance of beneficial microorganisms on host physiology and behaviour. Recent recognition of the importance of insect-microbe interactions has led to various studies investigating the bioprospecting of commercial applications for gut microorganisms.

The current review mainly focuses on the various enzymes reported from different insect orders and their screening, as well as prominent applications, for focusing more on the exploration of the insect gut microbiome and identification of several bioactive compounds for industrial production.

Collection of Literature for Review

The literature source for the current review was searched using several prominent online databases, such as Scopus, Google Scholar, Web of Science, PubMed, etc. We have done an extensive literature search to understand different insect orders and their gut microbiome studies. The former studies started way back in 1980, understanding the cellulolytic potential of the Eri silkworm, *Philosamia ricini* [20], a lepidopteran insect, studying only the host enzyme, but with several years forward, studies have begun on the gut microbiome and the biotechnological applications of enzyme-positive strains. Major works have been started from the year 2015, with breakthrough studies during the 2020s. We used specific keywords like insect gut microbiome, cellulase, lepidopteran gut microbiome, protease, coleopteran, etc. Around 200 articles appeared, and after scrutinising almost 100 papers were relevant to our focus. This includes mainly research articles and a few review articles. The number of review articles focusing on the current perspective is rare, and this highlights the importance of exploring the reported gut microbiome in each insect order and the techniques involved in screening several enzymes.

Insect Gut Microbiome and Bioactive Compounds – Beneficial Roles and Applications

The gut microbiota of insects is a dynamic environment that is habitant to many different groups of microbes that are important for the host's nutrition, immune system, and ability to adapt to new environments [21]. These gut inhabitants act as a bioreactor to make enzymes and bioactive compounds that can be used in several biotechnological industries. The gut microbiome of insects facilitates various aspects of their life and metabolism. It provides nutritional support through the synthesis of essential amino acids and vitamins such as B-complex and Vit-K, the fermentation of plant-derived polysaccharides into short-chain fatty acids and nitrogen fixation by diazotrophic bacteria, including *Enterobacter* and *Klebsiella* [22, 23]. In addition to providing food, they help break down tough polymers like cellulose, hemicellulose, lignin, pectin and chitin [24]. Figure 2 shows the main functions that the gut microbiome of insects performs.

The gut microbiome of termites, particularly *Spirochetes* and *Clostridia*, is vital for the degradation of lignocellulose, enabling these insects to utilize indigestible plant materials and thrive in various ecological conditions [25]. These microbial communities are also very important for detoxification and defence, in addition to digestion. They break down harmful plant allelochemicals, insecticides and other xenobiotics while also making antimicrobial molecules that protect the host pathogens [26]. Additionally, gut microbiota enhances host immunity by modulating immunological responses [27]. Beetles, ants and wasps have symbiotic

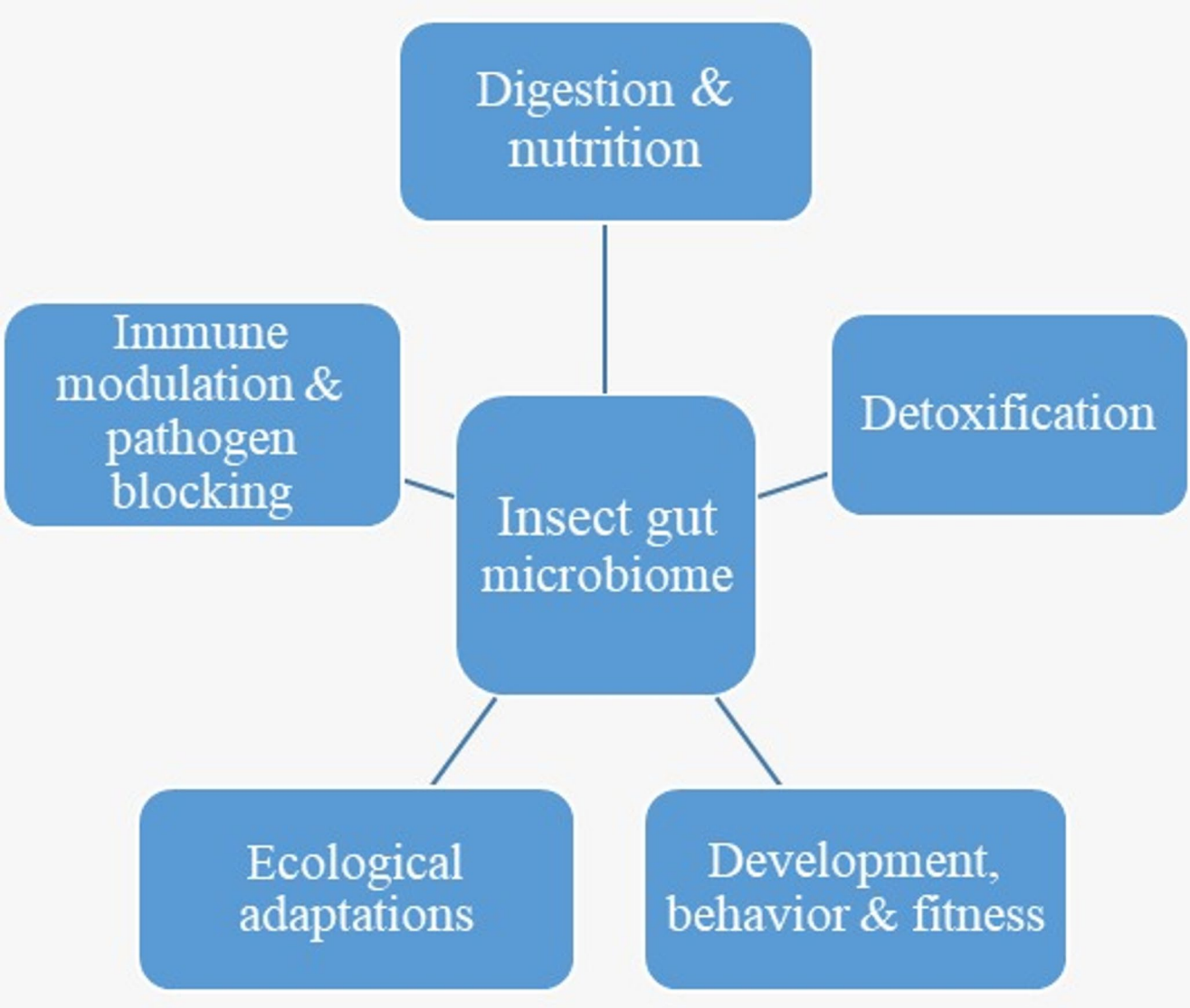

Fig. 2 Functions of the gut microbiota of insects

bacteria that make antifungal and antibacterial substances that protect their eggs and larvae [28]. This makes the host's natural defences stronger.

The gut microbiota of insects are important sources of bioactive compounds that can be used in numerous applications. Enzymes like cellulases, xylanases, and ligninases are necessary for the conversion of biomass into biofuels, while chitinases are used as biocontrol agents, mainly as antifungal compounds [29, 30]. Proteases and lipases from gut bacteria are used in the pharmaceutical industry and in industrial processing [31]. Furthermore, cellulase enzymes are primarily utilised in saccharification, food processing, and biofuel production [32]. Additionally, compounds such as iturin, surfactin, and fengycin, derived from *Bacillus* and *Pseudomonas* isolated from insect guts, possess extensive applications as antibacterial and antifungal agents [33, 34]. Table 1 below lists different bioactive compounds that have been found in the gut microbiomes of different insects.

Ecological and Host-Driven Determinants of Gut Microbiome Assembly

The composition and functional ability of insect gut microbiota are significantly influenced by ecological factors, including nutrition, environment and gut morphology, which impose selective pressures affecting microbial colonisation and enzymatic capabilities [10]. The diet serves as the primary determinant for insects that consume cellulose-rich plant materials like termites, Lepidopterans, Coleopterans and Orthopterans. Here, the host microbial communities are predominantly composed of cellulolytic Bacteroidetes, Fibrobacteres, Clostridia and Actinobacteria, indicating significant enrichment for cellulases, xylanases and lignin-modifying enzymes [24, 41, 42]. Sap feeders, which include the Hemiptera, obligate symbionts such as *Buchnera* and *Sulciato*, provide essential amino acids absent in phloem diets, whereas carnivorous or detrivorous insects like Dipterans possess microbiomes rich in proteases and lipases, suitable for proteinaceous or decomposing materials [43]. The social Hymenopterans maintain highly stable and host-specific microbiota primarily dominated by *Gilliamella*, *Snodgrasella* and *Lactobacillaceae*, where enzymes are oriented towards pollen digestion (pectinases and glycosidases) as well as antimicrobial defence rather than lignocellulose degradation [44, 45].

Habitat influences gut community composition, as insects residing in the soil, aquatic ecosystems or decomposing organic matter assimilate ambient bacteria that enhance hydrolytic or detoxifying functions. Black soldier fly larvae acquire a variety of lignocellulose and pollutant-degrading bacteria from organic waste environments, hence augmenting their collection of hydrolases and oxidoreductases [46, 47].

Gut morphology and physiology have further limitations on microbial assembly, as differences in gut length, compartmentalisation, pH, oxygen gradients, and redox conditions influence the diversity of microorganisms that may colonise and the enzymes that can be produced [20]. In addition to gut morphology, the larval instars also influence the microbial diversity and the enzyme quantity [48]. Termite hindgut sustains strict anaerobes, microoxic microbial communities, while hydrogen rich microenvironment that facilitates spirochetes and fibrolytic symbionts specialised in lignocellulose degradation [49]. Lepidopteran midgut, characterised by a highly alkaline environment (pH 10–12), promotes bacteria capable of enduring extreme pH while generating detoxifying or chitinolytic enzymes [50]. These ecological filters collectively provide unique and predictable patterns in the microbial and enzymatic composition of the insect gut, fostering functional specialisation that closely corresponds with host feeding strategies, environmental exposure and physiology.

Table 1 Bioactive compounds from insect gut microbiota and their applications

Category	Compounds	Insects	Applications	References
Industrial enzymes	Cellulases, xylanases, proteases, lipases	Termites, cotton ball worm, beetles, etc.	Biofuel, paper, detergents, textiles, food processing	[32, 35]
Bio-control agents	Chitinases, lipopeptides, antifungals	Caterpillars, beetles, etc.	Eco-friendly pest management, crop protection	[36]
Pharmaceuticals	Antibiotics, polyketides, siderophores	Beetles, termites, ants	Antimicrobial drugs, anticancer, anti-inflammatory	[37, 38]
Probiotics & Nutraceuticals	Vitamins, short-chain fatty acids, amino acids	Fruit flies, fruit pests	Animal feed, gut health products	[22, 39]
Bioremediation	Ligninases, detox enzymes	Beetles, termites	Degradation of pollutants, pesticide residues	[40]

Gut Microbiome of Different Insect Orders and Different Enzymes

The main insect orders studied for exploring the gut microbiome are in the orders like Coleoptera, Orthoptera and Lepidoptera. Several enzymes have been reported in these insect orders, with major studies on cellulase and protease, with literature also on amylase, lipase, and tannase. These enzymes allow insects to utilise a variety of diets from lignocellulosic plant matter in termites and beetles to nutrient-deficient phloem sap in aphids [51]. Cellulases

and xylanases break down cellulose and hemicellulose into fermentable sugars, thereby providing energy to the host. Ligninases, on the other hand, help wood-feeding insects in breaking down lignin polymers [45]. Chitinases produced by gut bacteria can break down the cell walls of fungi or the exoskeletons of insects, which helps recycle nutrients and protects against infections [52]. Proteases and lipases enhance the host's ability to utilise proteins and lipids [53]. These enzymes are widely utilised in many different industries. Because they come from bacteria, they provide multiple advantages such as ease in production and being able to be optimised for enhanced production. Also, the raw materials for the media are cheaper, thereby increasing profits. Figure 3 shows a summary of the different enzymes that have been reported from different insect orders.

Coleoptera (Beetles and Weevils)

Beetles are one of the most diverse families of insects, consuming wood, foliage, grains and decomposing organic material. Their gut microbiota is predominantly composed of Enterobacteriaceae, Clostridia and Actinobacteria [54]. These microorganisms produce cellulase, xylanases and lignases that facilitate the degradation of lignocellulosic substances in wood-feeding organisms. In grain-feeding beetles, microbial lipases aid in lipid digestion [55].

The industrial potential of a protease from *Bacillus subtilis* AU-2, isolated from the gut of the red flour beetle, *Tribolium castaneum*, was demonstrated by its effective hydrolysis of several protein substrates such as casein and soy protein, indicating its utility in protein hydrolysate manufacturing, meat tenderisation and dairy processing. The optimized extracellular protease exhibited maximum protease activity at pH 8.0 and 37 °C, with substantial stability between pH 7–9 and temperatures up to 50 °C. This strain was further evaluated for food utility by Raut et al. (2025), confirming sustained activity under mildly alkaline conditions (optimum pH 8.0–8.5) and thermal tolerance up to 55 °C, supporting its industrial suitability [56, 57].

Yadav et al. (2022) and Yang et al. (2021) examined lignocellulose-degrading bacterial populations within wood-feeding beetle larvae. The former isolated cellulolytic and hemicellulolytic bacteria from kulsi teak borer, *Stromatium barbatum* larvae, identifying major taxa like *Bacillus*, *Staphylococcus*, *Enterobacter*, *Pseudomonas*, *Enterococcus*, *Ochrobactrum*, *Brachybacterium*, and *Microbacterium*. Similarly, the later study isolated cellulolytic strains from white-striped long-horned beetle, *Batocera lineolata* larvae, predominantly within Proteobacteria and optimised the fermentation conditions to enhance cellulase production. The optimum enzyme production was found at pH 7.0 and 35 °C, while maintaining stability across pH 6–9 [58, 59]. The gut microbiota of white grub larvae, *Anamola dimidiata*, was investigated, identifying bacteria exhibiting cellulolytic, lipolytic and nitrate reductase potential. The predominant genera comprised *Bacillus*, *Pseudomonas*, *and Enterobacter*, signifying their essential function in digestion and potential for biotechnological applications. 207 cellulolytic strains from the gut microbiome of dark black chafer, *Holotrichia parallela* larvae, including novel species such as *Siphonobacter aquaeclarae*, *Paracoccus sulfuroxidans*, and *Pseudomonas nitroreducens*. The predominant genera were *Pseudomonas*, *Ochrobactrum*, *Rhizobium*, *Cellulosimicrobium*, and *Microbacterium*, highlighting the diversity and uniqueness of cellulolytic bacteria in the gut of scarab beetles [60, 61].

The digestive enzymes like amylase, lipase and protease in cowpea weevil, *Callosobruchus maculatus*, fed with *Vigna unguiculata* grains fluctuated with diazotrophic bacterium treatment, indicating that plant-microbe interactions affect insect digestive physiology [62]. Two α-amylases

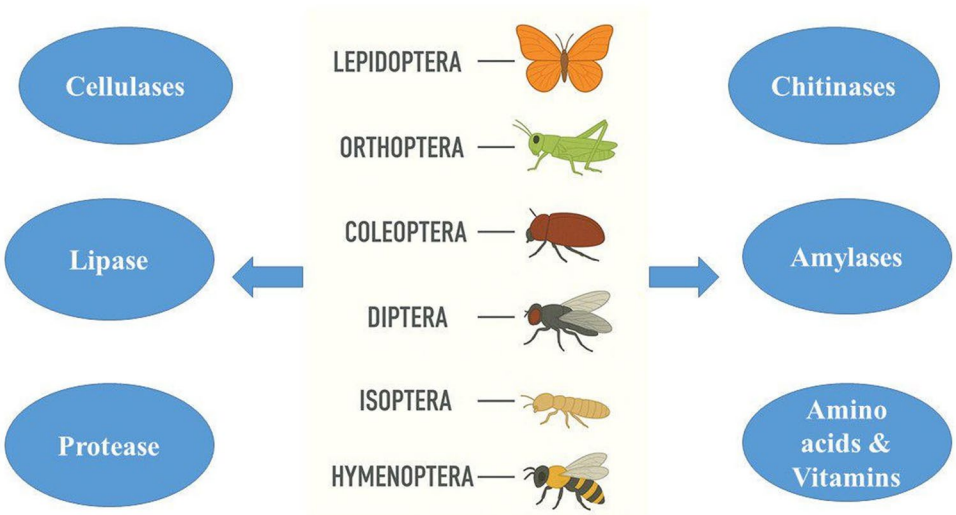

Fig. 3 Enzymes and bioactive compounds reported from different insect orders

were characterised from coleopteran insects, demonstrating variations in kinetic and structural features along with differing reactions to the inhibitor acarbose. The findings elucidated enzyme-inhibitor relationships pertaining to pest management [63]. Gaikwad & Bhavane (2015) similarly reported substantial lipase and protease activity in the dung beetle, *Chironitis arrowi*, highlighting their significance in organic matter degradation and potential waste bioconversion [64]. Coconut rhinoceros beetle, *Oryctes rhinoceros*, was also explored for several enzyme-producing bacteria mainly belonging to *Bacillus*, *Pseudomonas*, and *Enterobacter*, producing enzymes like amylase, cellulase, protease and lipase. Among these, *Bacillus* spp. had the greatest overall hydrolytic capacity. In addition, a thermostable chitinase enzyme-producing *Bacillus* species was also isolated, demonstrating optimal activity at 60 °C, with notable thermal stability up to 70 °C and pH 7.5, which signifies exceptional thermostability and efficacy in chitin degradation. The purified chitinase demonstrated significant activity against colloidal chitin [65, 66]. The findings underscored the crucial function of gut-associated microorganisms in organic matter decomposition and nutrient reclamation. Chitinase-producing bacteria from the gut of pleurostict scarab beetle larvae showed multiple bacterial strains, including *Bacillus*, *Enterobacter*, and *Serratia* families, exhibited notable chitinolytic activity on colloidal chitin substrates. Among all, *Bacillus cereus* and *Serratia marcescens* demonstrated the greatest enzyme activity. The pure chitinase was identified as extracellular, alkaline and moderately thermostable [67].

Lepidoptera (Butterflies and Moths)

The larval stages of Lepidoptera, especially caterpillars, are avid consumers of leaves and other plant materials. Their gut microbiota is abundant in *Enterococcus*, *Bacillus*, *Lactococcus*, and *Pseudomonas* [68]. Moreover, detoxifying enzymes produced by gut microbiota decompose plant secondary compounds like alkaloids and terpenes, allowing caterpillars to consume chemically protected host plants [69]. A recent review by Basit et al. (2025) highlighted the nutritional importance of gut microbiota in Lepidoptera, specifically in fall armyworm, *Spodoptera frugiperda*, where symbionts, including *Enterococcus*, *Acinetobacter*, *Enterobacter*, *Sphingobacterium*, and *Pseudomonas*, were associated with digestion, amino acid biosynthesis and immune regulation [70]. At the same time, 21 gut bacteria isolates were identified from the same organism by Winssy et al. (2024) and evaluated for chitinase and protease activity. Five genera were reported by 16 S rRNA sequencing. *Enterobacter*, *Enterococcus*, *Bacillus*, *Pantoea*, and *Kocuria* were identified. Among them, two isolates, *Bacillus licheniformis* FGE4 and *Enterobacter cloacae* FGE18, exhibited the highest chitinase production. When administered topically or by feed supplementation, these isolates diminished the larvae's consumption index, relative growth rate and food efficiencies, consequently adversely affecting survivorship [71].

Cellulose-degrading bacteria from cotton ballworm, *Helicoverpa armigera*, specifically *Bacillus subtilis*, *B. methylotrophicus*, *B. tequilensis*, *Klebsiella pneumoniae*, and *K. variicola*, all demonstrated significant cellulase activity with potential use in biomass conversion and biofuel production. Cellulolytic bacteria from sugarcane borer, *Diatraea saccharalis* larvae, were isolated and identified, which can degrade sugarcane biomass, showcasing their lignocellulose-degrading efficacy [32, 72]. Similarly, organisms like *Enterobacter cloacae*, *Enterococcus faecalis*, and *Bacillus subtilis* were isolated from *H. armigera*, which were characterised for their proteolytic activity concerning the pathogenicity of *Bacillus thuringiensis* (*Bt*) toxin. The isolates produce alkaline serine protease, inhibited by Phenylmethane Sulfonyl Fluoride (PMSF), which promoted the activation of *Bt* cry toxins and augmented their insecticidal effectiveness. This also highlights the coordinated function of gut bacterial protease in influencing Bt toxicity and prospective applications [73]. Msango Soko et al. (2020) previously identified lipase-producing bacteria from the gut of eri silkworm, *Samia ricini*, emphasising their potential use in the food, detergent and pharmaceutical industries [74]. Significant cellulolytic and proteolytic enzyme activity in the midgut and hindgut of horse chestnut leaf miner, *Cameraria ohridella* larvae, was explored, validating both microbial and host roles in plant digestion [75]. Similarly, in 2018, Gandotra et al. studied the gut microbiota of *Antheraea assamensis*, *Helicoverpa armigera*, and *Plutella xylostella*, documenting the bacterial synthesis of cellulase, protease, amylase and lipase, highlighting their significance in digestion and biotechnology [76].

Zibaee (2012) examined digestive enzymes in *Pieris brassicae*, uncovering site-specific activity of protease, amylase and cellulase, which suggests a coordinated function in larval nutrition [77]. Bacterial enzymatic activity in the saturniid caterpillars, *Automeris zugana* and *Rothschildia lebeau*, revealed several strains that produce cellulase, protease, lipase and amylase, thereby offering preliminary evidence of diverse enzymatic symbionts in the Lepidopteran gut [78].

Orthoptera (Grasshoppers and Crickets)

Grasshoppers and crickets mostly consume fibrous plant matter, which is digested with the assistance of gut bacteria like *Enterobacter*, *Klebsiella*, and *Serratia*. These microorganisms produce cellulase and amylase that hydrolyse cellulose and starch, while protease facilitates protein digestion [79, 80].

Recent studies have highlighted the enzymatic diversity of Orthopteran gut microbiota and their significance in

biomass degradation and commercial enzyme synthesis. The gut microbiome of mole cricket, *Gryllotalpa orientalis*, contributes to protease-producing bacteria, including strains like *Priestia aryabhattai* (DBM-1, DX-4), *P. megaterium* (DX-3), and *Serratia surfactantfaciens* (DBM-5), with DBM-5 found to be the highest protease-producing strain [81]. Cellulolytic bacteria were isolated from the rice grasshopper, *Oxya chinensis*, with *Bacillus*, *Pseudomonas* and *Enterobacter* species exhibiting significant cellulose-degrading activity. Similarly, *Bacillus* species like *B. subtilis* and *B. cereus* were isolated from desert locust, *Schistocerca gregaria*, indicating their ecological function in the digestion of fibrous plant material and prospective application in industrial cellulose hydrolysis. In addition, a potential cellulase-producing strain, *Acinetobacter junii* GAC 16.2, was isolated from African mole cricket, *Gryllotalpa africana*, which can degrade cellulose and lignocellulosic substrates such as sawdust, demonstrating its potential for biomass conversion and waste valorisation. The optimisation study revealed an optimum activity for the cellulase at pH 6.8 and 38 °C, with over 80% residual activity retained between pH 6–8 and temperatures up to 45 °C [82–84]. Previously, Banerjee et al. (2016) found the amylase-producing bacterium *Rhodococcus opacus* GAA 31.1 from the same insect, with improved culture conditions to enhance enzyme production [85]. Tannase-producing *Bacillus* species from *Gryllotalpa krishnani*, emphasising their potential applications in food processing, feed detoxification and bioremediation [86]. A variety of gut bacteria, including *Bacillus subtilis*, *Staphylococcus aureus*, *Klebsiella pneumoniae*, *Proteus vulgaris*, and *Escherichia coli* from the variegated grasshopper, *Zonocerus variegatus*, were reported, which were capable of producing several enzymes like amylase, cellulase, lipase and protease, which collectively facilitate the digestion of plant-derived macromolecules in this polyphagous pest [87].

Diptera (Flies and Mosquitoes)

Flies and mosquitoes inhabit various environments, subsisting on decomposing organic material, nectar or blood. Their gut microbiota frequently comprises *Acetobacter*, *Asaia*, *Enterobacter* and *Pseudomonas* [88]. Enzymatic contributions comprise lipases, proteases and chitinases. In mosquitoes, gut symbionts facilitate blood meal digestion via proteolytic enzymes, but in saprophagous flies, microbial enzymes enhance the decomposition of organic materials [89, 90].

Recent studies emphasise the exceptional biodegradation and therapeutic potential of Dipteran larval microbiota. Klüber et al. [91] investigated the microbiome of black soldier fly, *Hermetia illucens*, in the context of industrial waste biodegradation, identifying significant bacterial genera, including *Klebsiella*, *Enterococcus*, and *Sphingobacterium*, that facilitate the degradation of resistant compounds and promote sustainable bioprocessing and bioremediation [91]. Metatranscriptomic analysis was done to identify lignocellulolytic enzymes like cellulases, hemicellulases, and ligninases in *H. illucens* larvae consuming fibre-rich diets, thereby illustrating their function in plant polymer degradation and waste valorisation [92]. Exploration of the gut microbiome of black soldier fly larvae showed cellulose-degrading bacteria that enhanced the co-digestion of dairy and poultry manure, highlighting the role of gut microbiota in waste-to-value conversion [93].

In addition to waste bioconversion, some Dipteran species exhibit significant biological promise. Antiparasitic efficacy of excretory-secretory (ES) products derived from green bottle fly, *Lucilia sericata* larvae against *Leishmania major*, markedly suppressing parasite multiplication and regulating immune responses in infected murine models [94]. A new serine protease was characterised from *L. sericata* that increased plasminogen-mediated fibrinolysis, thereby affirming its therapeutic significance in wound healing and thrombosis [95].

Reports are also there from the gut microbiome of housefly, *Musca domestica* larvae, for producing industrial enzymes. Species from *Enterobacter*, *Klebsiella*, *Providencia*, *Proteus*, and *Bacillus* have been isolated, indicating considerable potential for enzyme-based biotechnological applications and microbial transfer via feeding behaviour [96].

Isoptera (Termites)

Termites exhibit one of the most complex gut microbiomes among insects, consisting of a varied diversity. Symbiotic taxa such as *Treponema*, *Clostridium* and *Fibrobacter* are pivotal in lignocellulose degradation, with their enzymes promoting the effective decomposition of wood and plant waste. Metagenomic analyses indicated that their gut communities are predominantly composed of *Fibrobacter*, *Spirochaetes* and *Firmicutes*, which possess genes that encode cellulases, xylanases and lignin-modifying enzymes. This complex metabolic collaboration renders termites an important model for investigating lignocellulose conversion and its implications for biofuel production [97, 98].

The microbial community in the termite gut, primarily composed of *Clostridia* and *Bacteroidetes*, promoted lignocellulose breakdown in anaerobic environments, resulting in the release of sugars and volatile fatty acids [99]. Numerous studies have emphasised the enzymatic diversity among termite gut microbiota. Chitinolytic strains, including *Bacillus cereus*, *Serratia marcescens*, and *Stenotrophomonas maltophilia*, isolated from *Microcerotermes* sp., demonstrated significant antifungal efficacy against *Fusarium oxysporum* and *Rhizoctonia solani*, suggesting their potential as biocontrol agents in agriculture [100].

Amylase-producing bacteria such as *Bacillus*, *Enterobacter*, and *Pseudomonas* isolated from *Coptotermes*

sp. exhibited effective starch hydrolysis, indicating their potential utility in the food and fermentation sectors [101]. Proteolytic enzymes in Formosan termite, *Coptotermes formosanus*, were derived from both host and microbial origins, with symbiotic bacteria contributing supplementary proteolytic activity to improve protein digestion [102].

Hymenoptera (Ants, Bees, Wasps)

The gut microbiota of Hymenoptera, particularly in social insects such as bees and ants, exhibits relative stability and specialisation. The primary members comprise *Gilliamella*, *Snodgrassella*, *Lactobacillus*, and *Bifidobacterium* [103, 104]. These microorganisms produce pectinases and glycosidases that facilitate the digestion of pollen walls and nectar sugars. Moreover, numerous organisms produce antimicrobial compounds, including bacteriocins and lipopeptides, which bolster colony defence against pathogens. The gut microbiota in honey bees is crucial for the degradation of complex polysaccharides derived from pollen, hence enhancing nutrition and immunity [105].

Hemiptera (Bugs)

Hemipterans frequently consume nutritionally deficient plant sap or phloem, which is devoid of vital amino acids. Their gut microbiota, along with some intracellular symbionts such as *Buchnera* and *Wolbachia*, provide essential metabolic assistance [106]. These microorganisms provide vital amino acids and vitamins lacking in the phloem diet. Furthermore, detoxifying enzymes generated by symbionts neutralise phytochemical defences [107, 108]. The enzyme-positive repertoire of these orders is less documented and studied. The complete overview of reported enzymes and respective enzyme orders discussed is shown in Table 2.

Symbiotic Categories of Insect Gut Microbes and their Relevance to Enzyme Discovery

Insect gut microorganisms encompass a spectrum of commensal, facultative and obligate symbionts, each providing unique benefits for enzyme discovery. Commensals like *Bacillus*, *Pseudomonas*, *Enterobacter* and *Serratia* are environmentally sourced and more prevalent in Coleoptera, Orthoptera, Diptera and Lepidoptera, rendering them highly culturable and scalable sources of cellulases, proteases, amylases and lipases, although their prevalence varies with diet and developmental stages. In contrast, several specialized fibrolytic or detoxifying taxa, including certain *Actinobacteria* and *Proteobacteria*, isolated from wood-feeding beetles, termites or caterpillars often occur as low abundance but high impact members, detectable only under specific diets or gut conditions [35, 82, 109, 110].

Facultative symbionts such as *Enterococcus*, *Acinetobacter*, *Lactococcus* and *Microbacterium* inhibit both the interior and exterior of the host and frequently synthesise resilient, stress-resistant enzymes tailored to diverge gut environments, including the alkaline Lepidopteran midgut and microoxic beetle hindgut, rendering them especially advantageous for industrial applications necessitating stability and reproducibility [111–113]. On the contrary, obligate symbionts like *Buchnera*, *Portiera*, *Sulcia* and the termite-associated *Candidatus Endomicrobium* demonstrate significant genome reduction and strict vertical transmission, providing vital nutrients while remaining unculturable [114, 115]. Despite their limited suitability for direct industrial purposes, their diminished genomes serve as valuable resources for enzyme mining, synthetic biology and heterologous expression.

Phylogenetic Conservation and Evolutionary Dynamics of Gut Symbionts

Host-microbe interactions in insects exhibit significant variability in their evolutionary stability, influencing both the richness and dependability of enzyme repertoires. In several clades, gut symbionts exhibit significant phylogenetic conservation and prolonged co-diversification with their hosts. Notable instances encompass the obligate endosymbionts of Hemiptera like *Buchnera*, *Portiera*, and *Sulcia*, which are characterised by strict vertical transmission, genomic reduction and phylogenetic similarity with their hosts. However, the core gut microbiota of social Hymenopterans like *Gilliamella*, *Snodgrassella*, and *Lactobacillaceae*, maintains stability across bee lineages and delivers essential metabolic functions, including carbohydrate processing and immune modulations [116–118]. These systems show lineage-specific coevolution and generate highly specialised enzymes that are functionally predictable yet challenging to cultivate for commercial applications.

Conversely, numerous digestive and detoxification processes, particularly lignocellulose degradation result from recurrent ecological acquisition of functionally analogous yet taxonomically diverse microorganisms. Termites, beetles and Lepidoptera frequently acquire cellulolytic or toxin-degrading bacteria from their surroundings, resulting in functional convergence and absence of taxonomic conservation. Recent metagenomics and phylogenomic investigations reveal frequent horizontal gene transfers, host-switching and turnover within these communities, suggesting that enzyme activities are predominantly niche-driven rather than lineage specific [22, 119–123]. This indicate that obligatory symbionts offer stable yet unculturable genomic reservoirs, whereas facultative and environmentally acquired taxa represent the most

Table 2 An overview of enzymes reported from different insect orders

S.No	Insect species	Order	Family	Gut bacterial strains/genera	Reported enzymes	Reference
1	*Pachnoda ephippiata*	Coleoptera	Scarabaeidae	*Spirochetes*, *Clostridia*, diverse anaerobes	Cellulases, hemicellulases, ligninases	[6]
2	*Stromatium barbatum*	Coleoptera	Cerambycidae	*Bacillus*, *Enterobacter*, *Microbacterium*	Cellulases, hemicellulases	[58]
3	*Batocera lineolata*	Coleoptera	Cerambycidae	*Bacillus*, *Pseudomonas*, *Enterobacter*	Cellulases	[59]
4	*Anamola dimidiata*	Coleoptera	Scarabaeidae	*Bacillus*, *Enterobacter*, *Klebsiella*	Amylase, protease, cellulase	[60]
5	*Holotrichia parallela*	Coleoptera	Scarabaeidae	*Bacillus*, *Cellulomonas*, *Microbacterium*	Cellulase, hemicellulase	[61]
6	*Oryctes rhinoceros*	Coleoptera	Scarabaeidae	*Bacillus*, *Enterobacter*, *Serratia*	Cellulase, hemicellulase	[65]
7	*Helicoverpa armigera*	Lepidoptera	Noctuidae	*Bacillus*, *Enterobacter*, *Klebsiella*	Cellulase	[32]
8	*Spodoptera frugiperda*	Lepidoptera	Noctuidae	*Enterococcus*, *Klebsiella*, *Bacillus*	Cellulases	[71]
9	*Diatraea saccharalis*	Lepidoptera	Crambidae	*Enterobacter*, *Klebsiella*, *Bacillus*	Cellulases	[72]
10	*Samia ricini*	Lepidoptera	Saturniidae	*Bacillus*, *Staphylococcus*, *Pseudomonas*	Lipases	[74]
11	*Automeris zugana*, *Rothschildia lebeau*	Lepidoptera	Saturniidae	*Bacillus*, *Enterobacteriaceae*, *Pseudomonas*	Cellulases, proteases, lipases, amylases	[78]
12	*Oxya chinensis*	Orthoptera	Acrididae	*Bacillus*, *Pseudomonas*, *Enterobacter*	Cellulase	[82]
13	*Schistocerca gregaria*	Orthoptera	Acrididae	*Bacillus subtilis*, *B. cereus*	Cellulase	[83]
14	*Gryllotalpa africana*	Orthoptera	Gryllotalpidae	*Rhodococcus opacus* GAA 31.1, *Acinetobacter junii* GAC 16.2	Amylase, cellulase	[84, 85]
15	*Gryllotalpa krishnani*	Orthoptera	Gryllotalpidae	*Bacillus* spp.	Tannase	[86]
16	*Zonocerus variegatus*	Orthoptera	Pyrgomorphidae	*Bacillus subtilis*, *Staphylococcus aureus*, *Klebsiella pneumoniae*, *Proteus vulgaris*, *E. coli*	Amylase, cellulase, lipase, protease	[87]
17	*Hermetia illucens*	Diptera	Stratiomyidae	*Enterococcus*, *Klebsiella*, *Dysgonomonas*, *Bacteroides*, *Cellulomonas*	Cellulases, hemicellulases, ligninases, detoxification enzymes	[91–93]
18	*Lucilia sericata*	Diptera	Calliphoridae	*Bacillus subtilis*	Proteases, antimicrobial peptides, bioactive ES products	[94]
19	*Musca domestica*	Diptera	Muscidae	*Enterobacter cloacae*, *Klebsiella pneumoniae*, *Providencia rettgeri*, *Proteus mirabilis*, *Bacillus subtilis*	Proteases, lipases, amylases, cellulases	[96]
20	*Coptotermes* sp.	Isoptera	Rhinotermitidae	*Bacillus*, *Enterobacter*, *Pseudomonas*	Amylase, protease	[101, 102]
21	*Termite species*	Multiple *spp.*		*Fibrobacteres*, *Spirochaetes*, *Firmicutes*, *Clostridia*, *Bacteroidetes*	Cellulases, xylanases, ligninases, proteases, chitinases	[98–100]

scalable sources for enzyme extraction and commercial utilisation. The existing literature indicates that insect enzyme repertoires include an array of coevolved, phylogenetically preserved systems and recurrent ecological recruitment, each providing unique benefits for bioprospecting.

Transmission Modes of Enzyme-Producing Gut Symbionts

The pathways of insect gut microorganisms significantly influence their stability, evolutionary longevity and potential for industrial enzyme discovery. Vertical transmission is a characteristic feature of several Hemipterans and certain termites, wherein symbionts are transmitted via eggs, ovarian tissues, and trophallaxis. These systems yield highly stable yet host-specific metabolic partners possessing specialized enzymes but exhibiting limited culturability. On the other hand, the majority of enzyme-producing bacteria in Coleoptera, Lepidoptera, Orthoptera and Diptera are acquired from the environment each generation, entering through diet, soil, frass or feeding activity. The cellulolytic bacterial taxa like *Bacillus*, *Pseudomonas*,

Enterobacter and *Klebsiella* demonstrate rapid turnover and exceptional scalability, thereby rendering them ideal candidates for industrial enzyme extraction [9, 20, 124]. Social Hymenopterans demonstrate a hybrid system, wherein primary gut lineages like *Gilliamella* and *Snodgrassella* are sustained through social interactions, while supplementary carbohydrate-degrading or detoxifying microorganisms are sourced from nectar, pollen or the surrounding environment [125–127]. These patterns suggest that vertically transmitted symbionts confer evolutionary stability but exhibit limited cultivability, whereas environmentally acquired and facultatively maintained microbes present the most viable source for industrial enzymes, owing to their accessibility, wider host range and adaptability to laboratory and bioreactor environments.

Screening Techniques Employed for Isolation of Enzyme-Positive Strains

Screening methods are crucial for selecting the right bacteria and enzymes. It helps to focus on the possible superior strains and eliminate other bacterial colonies. The screening technique followed will change depending on the type of enzyme. There are two main types of screening viz.; primary screening, which is a qualitative method and secondary screening, which is mostly about estimating and measuring. The present review focus on the screening methodologies for significant enzymes such as cellulose, protease, amylase, and lipase. An outline of the isolation of microorganism from the insect gut followed by screening is depicted in Fig. 4.

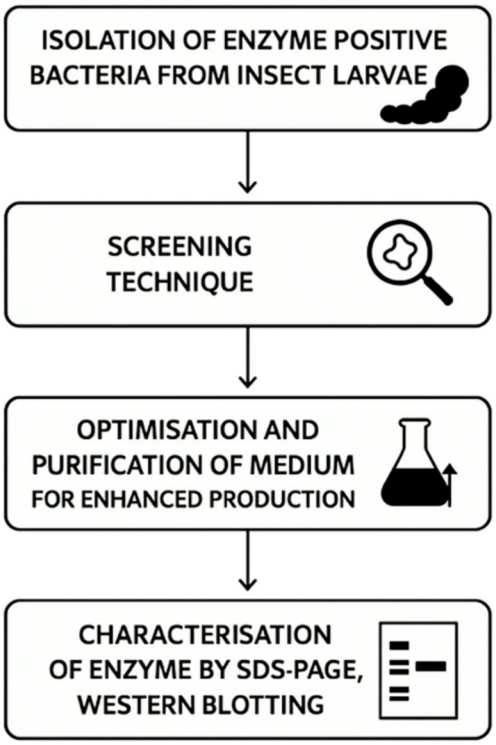

Fig. 4 General overview of the isolation of the gut microbiome from insects

Screening Techniques for Cellulase Enzyme

(a) Primary Screening Techniques

The primary screening techniques mainly include the CMC agar plate technique and the Filter paper method [128, 129].

(i) CMC agar plate technique

The primary screening for cellulase-producing bacteria often focuses on finding possible positive strains by assessing their capacity to hydrolyse cellulose. A prevalent technique entails culturing isolates on agar supplemented with carboxymethyl cellulose (CMC) as the sole carbon source. After incubation, the plates are flooded with congo red dye, which adheres to cellulose and is further rinsed with sodium chloride (NaCl) to elucidate hydrolysis zones. Colonies that produce cellulase create halo zones surrounding themselves, serving as a qualitative indicator of enzymatic activity.

(ii) Filter paper method

Another qualitative method is the filter paper assay, wherein small segments of Whatman filter paper are positioned in contact with microbial cultures; the degradation of the cellulose paper signifies cellulase activity. This is less commonly employed.

(b) Secondary Screening

It is mainly conducted to quantitatively evaluate the cellulolytic capabilities of the strains identified in primary screening. The technique uses the 3,5-dinitrosalicylic acid (DNS) assay, which quantifies the quantity of reducing sugars liberated. Reducing sugars interact with the DNS reagent to form a colored complex, and the absorbance is quantified spectrophotometrically at 540 nm. This test facilitates the quantification of enzyme activity in units per millilitre [130, 131].

Screening Techniques for Protease Enzyme

To screen for protease activity, the skim milk agar, casein agar, or gelatin agar technique is predominantly done, and the azo casein assay is a secondary technique [132–134].

(a) Primary Screening by Skim Milk Agar/Casein Agar
Microbial isolates are introduced into agar plates enriched with a protein substrate, either skim milk, casein or gelatin. Casein or skim milk are widely employed. Protease-producing bacteria degrade the surrounding protein, resulting in a clear halo zone post-incubation. In casein agar, the protease enzyme degrades casein into soluble peptides, resulting in a clear zone contrasting with the opaque white backdrop of agar.
(b) Secondary Screening by Azo casein or Casein Protein
This technique often entails incubating crude enzyme extract with protein substrate like casein or azo casein. The process concludes with the introduction of trichloroacetic acid (TCA), which precipitates unhydrolysed protein and the quantity of soluble peptides released is quantified spectrophotometrically at 660 nm.

Screening Techniques for Amylase Enzyme

The iodine technique and DNS assay are the widely used primary and secondary techniques, respectively, for screening amylase activity [135, 136].

(a) Primary Screening Using Iodine
The common substrate used for primary screening is starch agar plates, onto which microbial isolates are inoculated, followed by the addition of iodine solution post-incubation. The iodine colours unhydrolysed starch in blue-black, whereas hydrolysed starch regions remain transparent, signifying amylase activity.
(b) Secondary Screening Using DNS
The 3,5-dinitrosalicylic acid (DNS) assay is a commonly employed technique that quantifies the reducing sugars liberated during the hydrolysis of starch by amylase, a similar approach to that of cellulose. The DNS reagent interacts with reducing sugars to produce a colored complex, and the absorbance of which is quantified spectrophotometrically at 540 nm.

Screening Techniques for Lipase Enzyme

The primary screening for lipase enzyme can be done mainly by three methods, viz., tributyrin agar method, spirit blue-agar-olive oil method and Rhodomine-B method. The secondary screening technique employs p-nitrophenyl palmitate (pNPP) assay and titrimetric assay [74, 137, 138].

(a) Primary Screening by tributyrin agar method, spirit blue-agar-olive oil method and Rhodomine-B methods
(i) The initial assessment of lipase activity often employs a plate-based experiment using medium enriched with lipid substrates. It uses tributyrin agar, where microbial isolates are plated, and lipase activity is assessed by the formation of a distinct halo surrounding colonies due to the hydrolysis of tributyrin.
(ii) Spirit blue agar infused with olive oil and a dye is employed, where the hydrolysis of triglycerides produces a visible colour change or clear zone signifying lipolytic activity.
(iii) Rhodamine B-olive oil agar facilitates detection under UV light, generating orange fluorescence in areas of lipase activity, hence identifying lipolytic microbes.

(b) Secondary Evaluation for Quantitative Measurement of Lipase

The predominant assay employed for secondary screening of lipase assay is the p-nitrophenyl palmitate (pNPP) assay, wherein lipase catalyses the hydrolysis of pNPP to liberate p-nitrophenol, which is quantified spectrophotometrically at 410 nm. An alternate method is the titrimetric assay, where fatty acids liberated from the breakdown of olive oil are titrated with NaOH, providing a quantitative assessment of activity.

High-Throughput Omics Approaches for Mining Gut Microbiomes

Recent advancements in high-throughput sequencing techniques have transformed the identification of microbial enzymes within insect gut environments. Conventional culture-dependent techniques recover only 1–5% of microbial diversity, thereby missing the vast majority of enzymatic functions possessed by uncultivable or slow-growing microorganisms [139, 140]. Omics-driven methodologies like metagenomics, metatranscriptomics and functional metagenomics facilitate extensive investigation of microbial functional capabilities, uncover novel enzyme families and disclose context-dependent gene expression patterns that classical screening techniques mentioned above fail to capture.

Metagenomics Analysis for Comprehensive Profiling of Microbial Enzymatic Potential

Metagenomics offer a DNA-level overview of the entire genetic composition within the insect gut, facilitating the reconstruction of microbial genomics (MAGs) and the annotation of carbohydrate-active enzymes (CAZymes),

proteases, chitinases, esterases, and detoxification pathways [141–144]. Shotgun sequencing of wood- feeding beetles and termites has identified various putative cellulose, β-glucosidases and xylanases with CAZy families like GH5, GH9, GH45 and GH48, including enzymes exhibiting minimal sequence similarities to existing proteins, suggesting significant innovation potential [145, 146]. Metagenomics addresses culture bias by capturing taxa at all abundance levels, including rare biosphere members that frequently encode stress-tolerant or substrate-specific enzymes, thereby offering insights into the metabolic division of labour between hosts and symbionts [21]. Comparative metagenomics facilitates the identification of ecological determinants influencing the enzymatic repertoire, viz., cellulose-rich versus protein-rich diets, hence enabling the prediction of functional guilds among insect taxa [10]. The notable advantages of metagenomics analysis include access to comprehensive microbial diversity, detailed enzyme annotation utilising Cazy, MEROPS and KEGG databases, as well as facilitating inter-host comparison of metabolic pathways.

Metatranscriptomic Analysis for Identification of Actively Expressed Genes

When metagenomics reveals genomic potential, metatranscriptomics determines which genes are actively expressed in natural dietary conditions. It makes the identification of messenger RNAs (mRNAs) possible, thereby quantifying gene expression levels and active biological pathways. Enzyme expression in insects is critically associated with nutrition, developmental stage, feeding guild and gut redox conditions [147, 148].

Metatranscriptomic analysis of insect gut communities demonstrates active gene expression essential for resource utilisation and detoxification, underscoring the metabolic division of labour between the host and its symbionts. In Black Soldier Fly, *Hermetia illucens*, larval analysis revealed the expression of crucial cellulolytic enzyme families such as GH51 and GH43_16 when larvae ingested lignocellulose-rich diets [148], whereas exposure to chemical stress prompted the expression of deacetylases and other significant detoxification enzymes [149]. Metatranscriptomics in wood-feeding termites such as *Reticulitermes flavipes* revealed unique gene expression profiles for both host and symbionts, with the host actively expressing genes related to lignases and detoxification enzymes like cytochrome P450 and carboxylesterases, thereby affirming their roles in managing complex or chemically defended diet [150].

These datasets demonstrate inducible enzyme systems that activate solely in the presence of certain substrates like flavonoids, cellulose, lignin, etc., providing a more ecologically relevant representation of microbial function than metagenomics. It is considered more reliable for functional analysis because it focuses on functionally active microbes and genes, differentiating live and dead microbiota [151]. The major advantages include discerning enzyme expression specific to food and developmental stages, differentiating between active and inactive microbial community members, disclosing regulatory patterns and environmental stimuli.

Functional Metagenomics for Direct Identification of Novel Biocatalysts

Functional metagenomics connects sequence-based predictions with actual biochemical activity by cloning environmental DNA into heterologous hosts like *E. coli*, *B. subtilis*, etc. and screening for enzymatic function [152]. Libraries obtained from termites, scarab beetles and Lepidopteran larvae have produced thermostable cellulases and xylanases exhibiting activity at 60–70 °C. Alkaline proteases maintaining activity at pH 9–10, chitinases exhibiting elevated catalytic efficiency on colloidal chitin, solvent and surfactant-tolerant lipases, esterases and oxidoreductases that can degrade plant phenolics and contaminants [150, 153–155]. Functional metagenomics screening, which does not depend on sequence similarity, is particularly effective for identifying novel enzyme families and catalytic motifs, especially from evolutionarily diverse or inadequately characterised insect gut microorganisms. The notable applications include acquiring active enzymes despite the absence of known homologs, appropriate for identifying enzymes with industrially significant characteristics, facilitating screening based on phenotype rather than anticipated annotation.

Challenges in Harnessing Insect Gut-Derived Enzymes and Comparison with Traditional Enzyme Sources

The practical application of microorganisms and enzymes produced from insects encounters various limitations that restrict their direct industrial use. A significant challenge is that a substantial fraction of gut symbionts remains unculturable due to their stringent dependence on host-specific factors, including microaerophilic conditions, diet-derived cofactors and gut-specific pH and redox gradients, leading to the recovery of merely 1–5% of the native microbiome via culture-based methods [21]. Many enzymes, even when identified, demonstrate inadequate heterologous expression in traditional hosts such as *E. coli* or *B. subtilis* due to factors like codon bias, misfolding, chaperone dependence or incompatible secretion pathways, which considerably reduce yield and stability outside their native gut environment [156, 157].

Biosafety considerations complicate direct application, as various insect gut-associated genera viz., *Serratia*, *Klebsiella*, and *Enterobacter* contain opportunistic pathogens and may possess antibiotic resistance determinants, necessitating the use of GRAS (Generally Recognised as Safe) hosts for safe enzyme production [150, 158]. The industrial scaling of these enzymes is further impeded by low native expression levels, restricted thermostability and vulnerability to shear stress or chemical inhibitors during fermentation, as numerous gut-derived cellulases exhibit significant activity loss above 50 °C, thus limiting their applicability for high-temperature processing [159, 160]. In addition, metatranscriptomic research reveals that many enzymes are either diet-induced or produced solely in response to particular ecological stimuli within the host, rendering their consistent production outside the insect gut difficult without precise replication of natural cues [161]. These limitations highlight the necessity for integrative solutions, including enzyme engineering, codon optimisation, synthetic biology chassis and bioreactor designs that more accurately simulate gut conditions to facilitate the scalable and safe industrial application of insect gut-derived enzymes.

Conventional industrial enzymes are generally derived from soil bacteria (*Bacillus*, *Streptomyces*), filamentous fungi (*Aspergillus*, *Trichoderma*) and marine microorganisms, which are esteemed for their efficient enzyme production and known fermentation methodologies. Insect gut-derived microorganisms provide a supplementary and frequently superior source of enzymes tailored to highly specialised ecological niches. In contrast to soil or marine microbes that evolve under diverse environmental pressure, insect gut symbionts function within strictly controlled microenvironments having severe pH gradients, significant redox fluctuations, rapid substrate turnover and the presence of resistant polymers such as lignocellulose, chitin and plant allelochemicals. Because of these potential advantages, the insect gut-bacteria-derived enzymes often display inherent characteristics, including improved catalytic effectiveness towards complex plant polymers, resistance to inhibitory compounds and synergistic interactions with other enzymes, attributing to prolonged coevolution with host digestive systems [162–167]. For instance, *Fibrobacter* and *Treponema* from the termite gut produce highly effective lignocellulases that surpass numerous fungal cellulases in low oxygen, high viscosity conditions [150, 168]. Similarly, *Enterococcus* and *Bacillus* from Lepidopteran gut produce chitinases and detoxifying enzymes that effectively digest chemically protected plant tissues, where several fungal enzymes are ineffective [113, 169]. Marine bacteria exhibit exceptional extremophilic adaptations, while insect gut bacterial enzymes have shown comparable stability but pose limited substrate specificity, rendering them appealing for focused biocatalysis [170]. Insect gut microorganisms collectively constitute an underexplored yet functionally diverse alternative to traditional enzyme sources, producing innovative biocatalysis.

Applications of Insect Gut-Derived Enzymes

The enzymes found in the gut microbiota of insects can be used in bioenergy, food and drink processing, textiles, agriculture, medicine, and environmental biotechnology (refer to Fig. 5). This wide range of functions shows how insects have adapted to digesting chemically complex foods and reveals how their gut symbionts can be used as a source of enzymes for industry. Cellulases and hemicellulases are two of the most important enzymes. They are especially common in insects that eat wood and fibre, which includes termites, beetles, moths, grasshoppers, and others. These enzymes are very important in the biofuel industry because they help break down lignocellulosic biomass into sugars

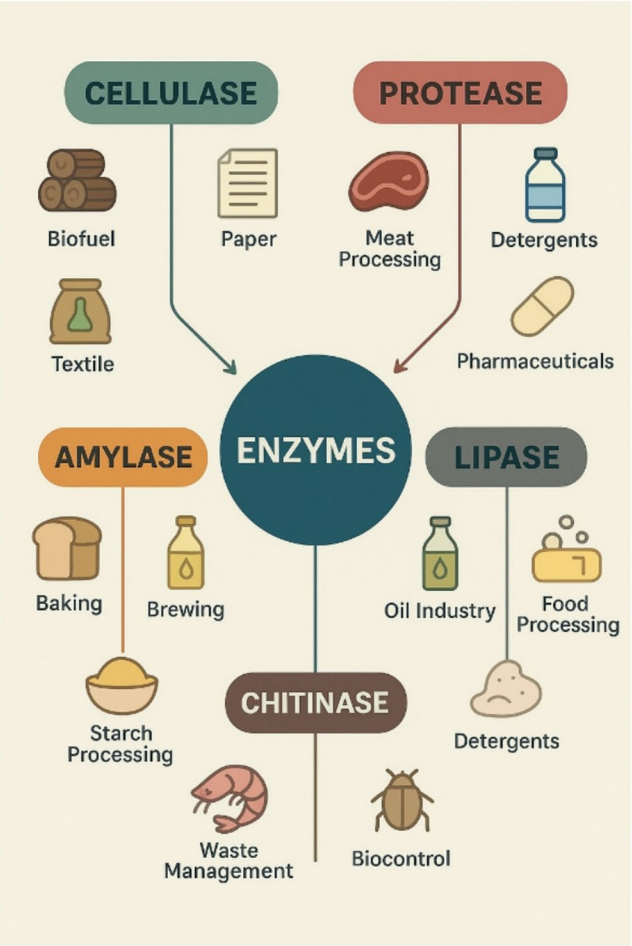

Fig. 5 Applications of different enzymes

that can be fermented. In addition, they are also widely employed in the generation of second-generation bioethanol, biobutanol and biogas plants [171–173]. They are utilised in the pulp and paper sector to reduce chlorine-based chemicals in bleaching effluents and to improve paper softness as well as drainage. Additionally, the breakdown of paper waste enables the production of value-added products, animal feed and supports zero-waste biorefineries for volatile fatty acids, agricultural composting and other environmentally sustainable alternatives to chemical processing [174–176]. Cellulase is an appealing option for disintegrating biofilm. Cellulase can break down the Extracellular Polymeric Substance (EPS) layer, which is made up of cellulose and hemicellulose. This opens up a multitude of possibilities in the pharmaceutical industry. When treated with cellulase, the EPS layer of *E. coli*, *Pseudomonas*, etc., will be degraded so that the resistant structure can be damaged for activation of the action of drugs [177, 178]. Furthermore, cellulases are a major constituent in the detergent industry for removing cellulose-based stains and improving the brightness of fabric material, along with in the textile-based industries for replacing stone washing and removal of microfibrils in cotton fabrics [179, 180].

Gut microbes of Coleoptera, Lepidoptera, Diptera and Orthoptera create proteases that facilitate protein digestion in the host and have several industrial applications. Microbial proteases are extensively utilised in detergents for stain elimination, in the food industry for cheese production, meat tenderisation, protein hydrolysate for nutrient supplements and baking, as well as in medicines as fibrinolytic or anti-inflammatory drugs, and wound debridement enzymes. They can also be used in leather and textile industries for dehairing, bating as well as an alternative for lime-sulphide process [160, 166, 181, 182]. Amylases, identified in the gut microbiota of beetles, caterpillars and crickets, are essentially used in food industries for starch hydrolysis, baking, production of glucose and maltose syrups as well as in clarification of fruit juices and inbioethanol manufacturing [183–185]. Amylase also has significant applications in the detergent industry since it has the activity to remove starch-based stains, and it is active and stable under alkaline conditions. In addition to that, they improve the digestibility of starch in monogastric animals and are hence used in animal feeds [186, 187].

A further extensively researched group is lipase, which is recorded in Coleoptera, Lepidoptera and Diptera. These enzymes derived from insect gut microbiota are utilised in detergent formulations, flavour enhancement in the food sector, biodiesel synthesis and the creation of chiral pharmaceutical intermediates. They can transesterify vegetable oils, waste cooking oils and can be used in biodiesel production. Their potential in modifying fats and oils to improve melting point and texture makes them potential in food industries, as well as they can synthesise flavoured esters [76, 188]. They are applied in the detergent industries as they can remove oil and grease stains, functioning under harsh detergent conditions. This major application directs them in the waste water treatment as well. Furthermore, they can also be used in the pharmaceutical sectors for the production of enantiopure chiral intermediates [189, 190]. Additionally, the enzyme chitinases identified in Coleoptera, Diptera, Orthoptera and Isoptera play a crucial role in biocontrol measures against fungal infections like *Fusarium*, *Rhizoctonia* and insect pests, and are also significant for the recycling of shellfish waste into chitosan, chitin and other derivatives [46, 191, 192]. They can also be used in agriculture as seed coating and soil amendment with chitin derivatives to promote plant immunity. The production of medical-grade chitosan for wound dressing, drug delivery makes them significant candidate in medicine and pharmaceutical industries [193, 194]. Lepidopterans and Hemipterans have symbionts that make tannases and detoxifying enzymes that help insects break down plant secondary metabolites like tannins and alkaloids. Tannases are used in biotechnology to make gallic acid, which is a precursor for antimicrobial drugs, antioxidant formulations, propyl gallate (a food preservative), process tea, coffee, beer and wine, and in the textile and leather industries. They are capable of removing tannins from hides to soften materials [195–197]. Along with these wide applications, they can be essentially used in environmental bioremediation for degrading tannin-rich effluents from tanneries, paper mills and food processing industries as well as in the degradation of anti-nutritional tannins in feed, thereby improving digestibility [198, 199]. Table 3 explains the overall idea about the applications reported for each enzyme discussed above. These works collectively provide a framework from microbe isolation to application testing, a complete translational level approach from lab-scale to application-based results, highlighting insects as an unexplored source of industrially significant enzymes. Future research should expand beyond Coleoptera to include other insect orders such as Lepidoptera, Diptera, Hymenoptera, Hemiptera, and Isoptera, and should explore additional enzyme classes, including proteases and amylases, to fully harness their potential in sustainable bioprocessing, pest management, and green biotechnological applications.

Conclusion

The insect gut opens for the scope of exploring different industrially important enzymes. Their gut microbiota is not much investigated, but the literature suggests a promising idea of the existence of potential industrially important

Table 3 Applications studied for each enzyme isolated from the insect gut microbiome

S. No	Enzyme	Insect	Microbial strain	Application studied	Reference
1.	Cellulase	*Holotrichia parallela* (scarab beetle larva), *Sitophilus oryzae* (rice weevil), *Cyrtotrachelus buqueti* (Bamboo snout beetle)	*Bacillus subtilis*, *Cellulomonas* sp., *Enterobacter cloacae*, *Lactococcus* sp., *Serratia* sp., *Dysgonomonas* and *Enterococcus* spp.	Biomass saccharification for biofuel production, Bioethanol conversion	[61, 200, 201]
2.	Lipase	*Rhantus suturalis* (supertramp beetle)	*Bacillus megaterium* F25	Biodiesel production (transesterification) and food oil hydrolysis	[202]
3.	Chitinase	Soil-associated Coleopteran larvae	*Serratia marcescens*, *Bacillus sp.*	Biocontrol; insecticidal activity against termites and larvae	[203]

strains from the gut of insects. The gut-associated bacteria play a crucial role in vital insect processes, including food absorption, digestion of resistant polymers, detoxification and defence mechanisms. Research spanning various insect orders, including Coleoptera, Lepidoptera, Diptera, Orthoptera and Isoptera, has identified microbial strains that generate cellulases, proteases, lipases, chitinases, amylases, tannases, as well as antimicrobial metabolites and detoxifying enzymes. These microbial products possess significant potential for use in biofuel production, waste valorisation, agriculture, food processing, medicines, etc. Despite increasing research interest, numerous insect-microbe connections remain unexamined, particularly with new enzymes, new bacterial strains, secondary metabolites, etc. The gut microbiome of several insect species from Lepidoptera, Hymenoptera, and Hemiptera is yet to unfold, and the successful exploration of their gut microbiome can open an extensive scope for identifying novel and potential enzyme-producing strains that can be successfully exploited in the industrial sectors. Future research that combines multi-omics methodologies, synthetic biology and large-scale bioprocessing will be essential to fully exploit insect gut microbiomes as sustainable sources of next-generation bioactive compounds and industrial enzymes.

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Declarations

Competing interests The authors declare no competing interests.

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