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REVIEW PAPER

Insect gut bacteria: a promising tool for enhanced biogas production

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Abstract Utilization of unexplored lignocellulolytic microbial resources is in demand due to its ability to degrade the waste-plant biomasses like water-hyacinth or noxious weeds for alternative second-generation biofuel production, i.e., biogas. One such "biotechnological treasure-box" is the herbivorous insect gut-system, as its' symbionts produce key hydrolytic enzymes like lignocellulases, cellulases, xylanases, and pectinases responsible for degradation of their host's diet plant-biomasses. In this context, this review revealed such lignocellulolytic gut bacterial populations inhabiting the gut-system of only eight orders viz., Blattodea, Lepidoptera, Isoptera, Coleoptera, Orthoptera, Hemiptera, Hymenoptera, and Diptera among 31 insect orders. Proteobacteria is the most predominant group found in every case. Regarding enhanced biogas production, gut bacteria from only three insect orders i.e., Blattodea, Coleoptera, and Diptera were explored so far. Therefore, deployment of such gut bacteria with immense lignocellulolytic potentialities can be harnessed as the sustainable bioresource technology for augmented biogas production utilizing waste-plant biomasses.

Binoy Kumar Show and Sandipan Banerjee these authors contributed equally to this work.

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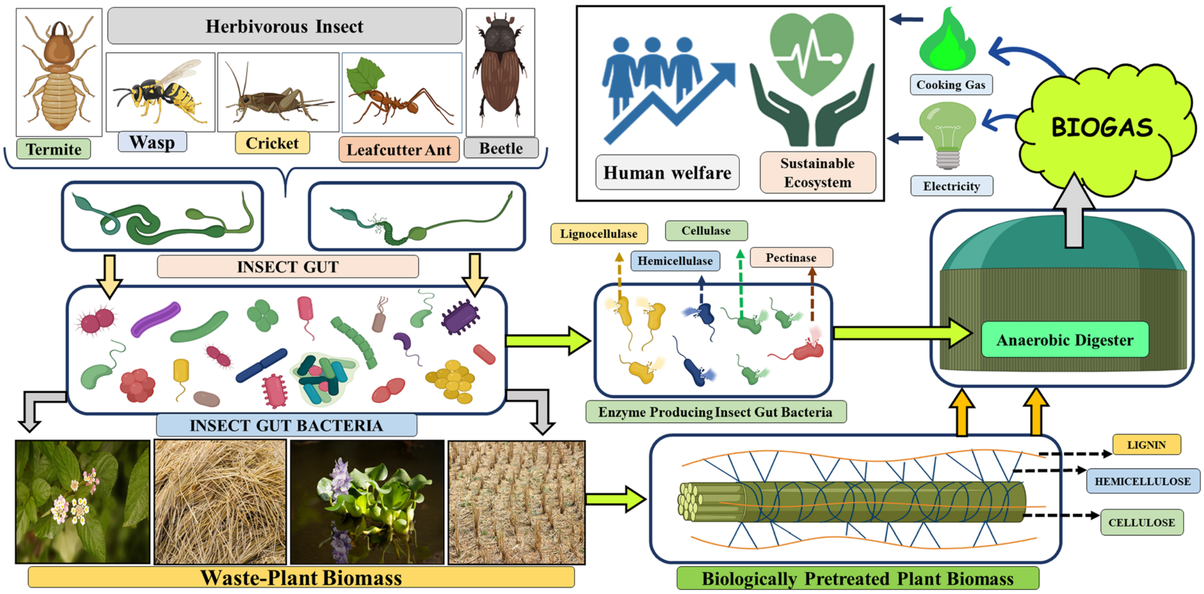
Graphical abstract



Keywords Renewable energy · Gut microbes · Plant-biomass · Cellulase · Hemicellulase · Lignocellulase

1 Introduction

The development of second-generation fuel for replacing fossil fuel usage extends to a higher magnitude, like upgrading biogas production as renewable energy. Day by day, renewable energy systems are becoming more efficient, functional and cheaper, and sharing the total energy consumption cumulatively (LaBelle 2018). Currently, more than two-thirds of all newly installed global power generating capacities are renewable (Mohammed et al. 2019). The increasingly fast rate of renewable energy as biogas production with 85% of energy requirements is projected to be met by renewables 2050 (Abraham et al. 2020). The scarcity of petroleum and coal is one of the significant threats of the contemporary world as well as their combustion leads to various environmental pollution. Biogas' energy holds promise among these renewable energy sources because it is economical, non-hazardous, and eco-sustainable. Alternative energy production as biogas can reduce greenhouse gas emissions and reduce the usage of fossil fuels (Cheng et al. 2017). The thrust area of biogas from other kinds of renewable energy is its characteristics of using organic waste matters and at the same time produces fertiliser, slurry and clean water for use in agricultural irrigation (Mwirigi et al. 2014). Despite the advantages of the anaerobic digestion (AD) process, the technology has suffered drawbacks in low methane yields, incomplete bioconversion, process instability, and low calorific values. So, to overcome these constraints, a sustainable approach like bioaugmentation with lignocellulolytic bacterial activity appeared as a biotechnological treasure box for human welfare.

Biogas production using AD with different microorganisms such as bacteria, fungi, and archaea with the substrate like cow dung, sewage sludge, etc., is a typical bioaugmentation phenomenon. In the AD process, for the digestion of plant biomass, proficient amount of active inoculum and multifaceted population of microbes catalyse a sequence of inter-reliant

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biochemical reactions (hydrolysis, acidogenesis, acetogenesis, methanogenesis), is obligatory. Different enzyme-producing microbes, especially bacteria, play a pivotal role in bioaugmented biogas production at each stage of conversion. Like the other conventional processes (physical and chemical pretreatments) for biogas enhancement, biological pretreatment and bioaugmentation get much more attention due to their cleaner and eco-sustainable approaches (Sinha et al. 2021).

Plant biomasses used as substrate in bioenergy production consist of complex compounds, i.e., lignin, cellulose and hemicelluloses. Among these biomass ingredients, lignin is the most complex structure and rigid to degrade. Lignin resists the complete microbial degradation of fermentable organic matters (cellulose and hemicelluloses), and the simpler sugars from the microbial digestion promote bacterial growth and activity by using these sugars as substrates in the fermentation process, leading to the formation of volatile fatty acids and subsequently converted to methane (Sinha et al. 2021). In the bioaugmented plant biomass digestion coordination, the microbial system plays an indispensable role as it recovers the required energy from biomass degradation. Unlike the other microorganisms, different groups of bacteria are more productive in degrading the plant constituents in this system. The bacterial communities with their key hydrolytic enzymatic activities, i.e., lignin peroxidases (LIP), manganese peroxidases (MNP), and laccases (LAC), cellulases (endoglucanases, cellobiohydrolases, and β-glucosidases), and hemicellulases (endo-1,4-β-xylanes, β-xylosidase, α-arabinofuranosidase, and esterases) can accelerate the digestion process to enhance biogas production (Sindhu et al. 2016; de Gonzalo et al. 2016; Sinha et al. 2021).

Delignification of plant biomass using bacteria is biotechnologically significant due to several advantages over fungi because bacteria are an attractive source of commercially operated metabolites having large-scale growth efficiency, product versatility, the limited space requirement for cultivation, conveniences in genetic makeup, and susceptibility towards genetic manipulation (Banerjee et al. 2017). Nowadays, researchers focus more on bacteria and their hydrolytic enzymes in "waste-to-bioenergy" production (Bhatt and Tao 2020). Research has largely been performed on bacteria isolated from soil, litter soil, and vegetable waste, but bacteria from lignocellulosic and cellulosic food consuming insect gut systems are less explored in this arena (Banerjee et al. 2021). Among the diverse sources of bacteria, the role of insect gut bacteria on biogas production is studied very little. Insects are well-diversified, and represent the largest species groups with availability in all ecological niches, with more or less one million species in number (Lysenko 1985) having an arthropod lineage (Moran and Telang 1998). Earlier studies have mainly focused on classical techniques to describe the gut microbial community, information regarding their sustainable biotechnological prospects is lacking (Fox-Dobbs et al. 2010). Most insect species are the host to many kinds of microorganisms, especially bacteria, those are adapted as the gut symbionts (Xie et al. 2019), play an indispensable role in the host's digestion, nutrition, immunogenic responses and life cycle development (Douglas 1992; Tanada and Kaya 1993; Engel et al. 2012; Kudo et al. 2019). During the host metabolic activities, insect gut bacteria produce different hydrolytic enzymes, i.e., lignocellulases, cellulases, hemicellulases, xylanases, pectinases, chitinases, and esterases etc. (Appel 2017). With the help of these enzymatic proficiencies, the microbes can be harnessed for other sustainable purposes, i.e., energy production, bioremediation (Yang et al. 2014; Yang et al. 2015), pest control (Fukui et al. 2015), production of antimicrobial compounds, vitamins, amino acids and lactic acids (Salem et al. 2014; Wang et al. 2015; Liang et al. 2018). Still, there is ample scope of the enzyme-producing insect gut bacteria on bioenergy production as this perspective is rarely explored. This review encompasses the bacterial diversity and potentialities of the lignocellulolytic enzyme-producing insect gut symbionts and their possibilities in bioenergy production via plant biomass utilisation as a "green seedling" as well as "welfare economics".

2 Review methodology

Here, a total of 695 articles, with the keywords of biogas, anaerobic digestion, insect gut bacteria, and enzyme, were carried out on the Web of Science. By using the VOSviewer software, keywords were analysed. Here the keyword occurrences results were outlined to be 12, and a network map was produced using the most used keywords, and the results are listed in Fig. 1. The cluster and the occurrence frequency of the individual keyword were specified by colour and size, and the line between the circles represents links. By the network mapping of the keywords, it can be found that these articles mainly focus on the following four aspects: (1) biogas production by anaerobic digestion with the help of pretreatment (yellow cluster); (2) methane production using lignocellulosic plant biomass via biological pretreatment (green cluster); (3) biofuel generation via cellulosic plant materials (blue cluster); (4) role of insect gut microbiota in the lignocellulose digestion (red cluster). These keywords covered biogas production with the help of AD, various waste biomass and lignocellulase enzyme-producing insect gut bacteria, etc., which helps in the direction of this review article.

3 Plant biomass as a bio-resource for biogas production

Plant biomasses such as agricultural residues and water hyacinth, and other noxious weeds with immense biogas producing credibility were not appropriately exploited during the AD process due to their lignocellulosic complexity, recalcitrant rigidity and hydrophobic impermeability with various biologically stable linkages (Patinvoh et al. 2017). Lignocellulosic biomass is composed of polymeric substances such as cellulose, hemicellulose (fermentable organic matter), and lignin. Cellulose shapes the principal portion of lignocellulose, surrounded by a hemicellulose matrix and the exterior by the lignin layer (Saini et al. 2015). Cellulose consists of more than 100-140,000 D-glucose units and is condensed by β-1,4-glycosidic bonds or linkages and forms a straight-chain polymer. The occurrence of multiple hydroxyl groups on the glucose forms hydrogen bonds that hold the chain and make it steadier. Cellulose is hydrophilic, but its large polymeric structure render it less soluble in water (Karimi and Taherzadeh 2016). The other polymeric constituent of the lignocellulosic biomass is hemicelluloses, which is a heteropolysaccharide with side chains, i.e., major structural unit pentoses (xylans), followed by arrangements of hexoses like mannose, glucose and galactose and sugar acids (D-glucuronic and D-galacturonic acids) (Somerville et al. 2004). Unlike cellulose, hemicelluloses have an amorphous structural integrity and a random degree of polymerisation, making them more prone to physical, chemical, and biological degradation sensitive. Therefore, the digestibility of the plant biomass more or less depends upon the hemicellulose content of the biomass (Li et al. 2015).

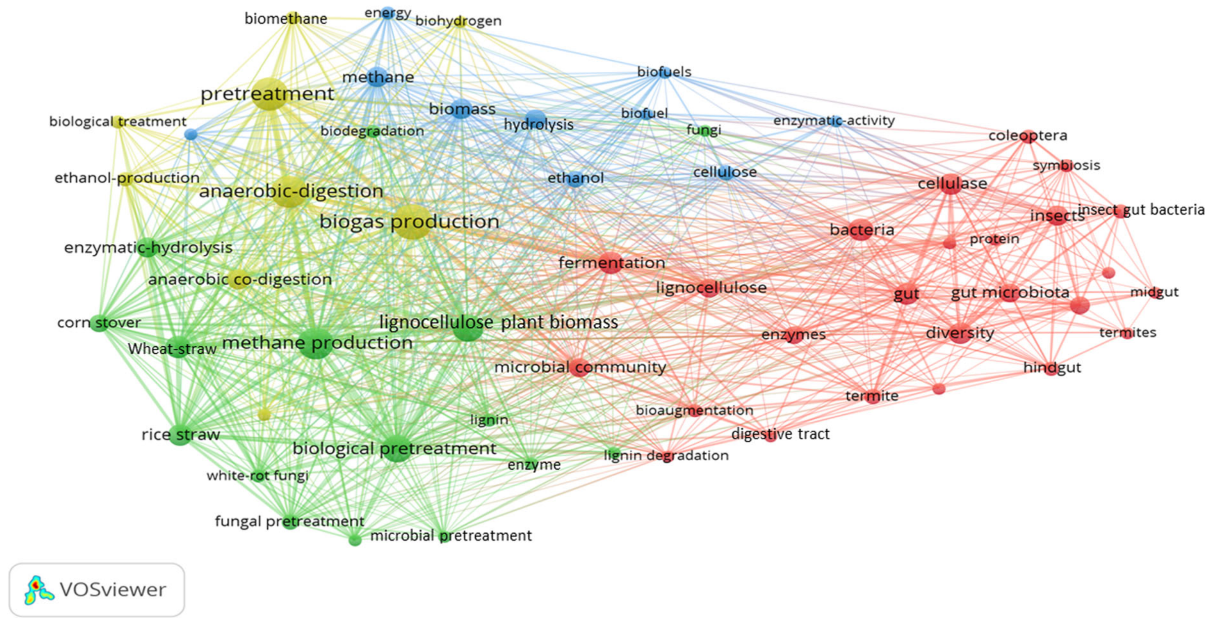

Fig. 1 Keywords co-occurrence network analysis using VOSviewer software

Moreover, the fermentable organic layers (cellulose and hemicelluloses) are protected by the hydrophobic lignin heteropolymer and stand as a physical barricade against biological and oxidative digestion, which is the main constrain for the utilisation of lignocellulosic biomass in the AD practices. The spaces between the cellulose and hemicellulose structures are occupied by this lignin constituent of the plant biomass and consist of phenylpropane units (coniferyl, sinapyl, and coumaryl alcohols) and are generally linked by ether bonds (Woiciechowski 2020) (Fig. 2). Due to its hydrophobic characteristics with impermeability and rigidity, high molecular weight and active recalcitrant compound with various biologically stable types' linkages, lignin rich compounds in the AD process needs potential lignocellulase producing microorganisms with unexplored microbial resources like insect gut system etc. In the AD practices, poor methanogenic activity is often observed when single substrates are used due to little organic matter content, imbalanced nutritional inputs in feedstock, rapid acidification, higher nitrogen and heavy metals contents, and long-chain fatty acid generation (Mata-Alvarez et al. 2014). To overcome this problem, using multiple substrates such as agricultural residues (stubbles), noxious weeds, cattle manure, and other organic wastes can be used for co-digestion with potent lignocellulolytic bacteria (Haider et al. 2015). One of the crucial characteristics for optimum bacterial performances (nutrient requirements) for significant energy production during the AD process is the C/N ratio of the substrates. The ideal proportion is ranged between 10 and 35 (Naik et al. 2014), and in the case of stubbles, noxious weeds, water hyacinth, animal food waste, that ratio varied between 50 and 150 (Divya et al. 2015). Therefore, in future, it will be a vital criterion to select the substrates depending upon their C/N ratio for enhanced bioaugmented biogas production systems.

Plant biomass (non-edible) sources such as energy crops, agricultural and forest residues, stubbles, noxious weeds, animal food waste, municipal organic wastes, etc., are commonly utilised for renewable energy production (Sepehri et al. 2020). According to the Indian Agricultural Research Institute (IARI), India generates approximately 2.2 × 10^6 tons of rice stubble per year (Abdurrahman et al. 2020). In contrast, *Lantana camara*, a notorious invasive weed, has occupied over 13.2 million hectares of grasslands in India (Negi et al. 2019). In many countries like in

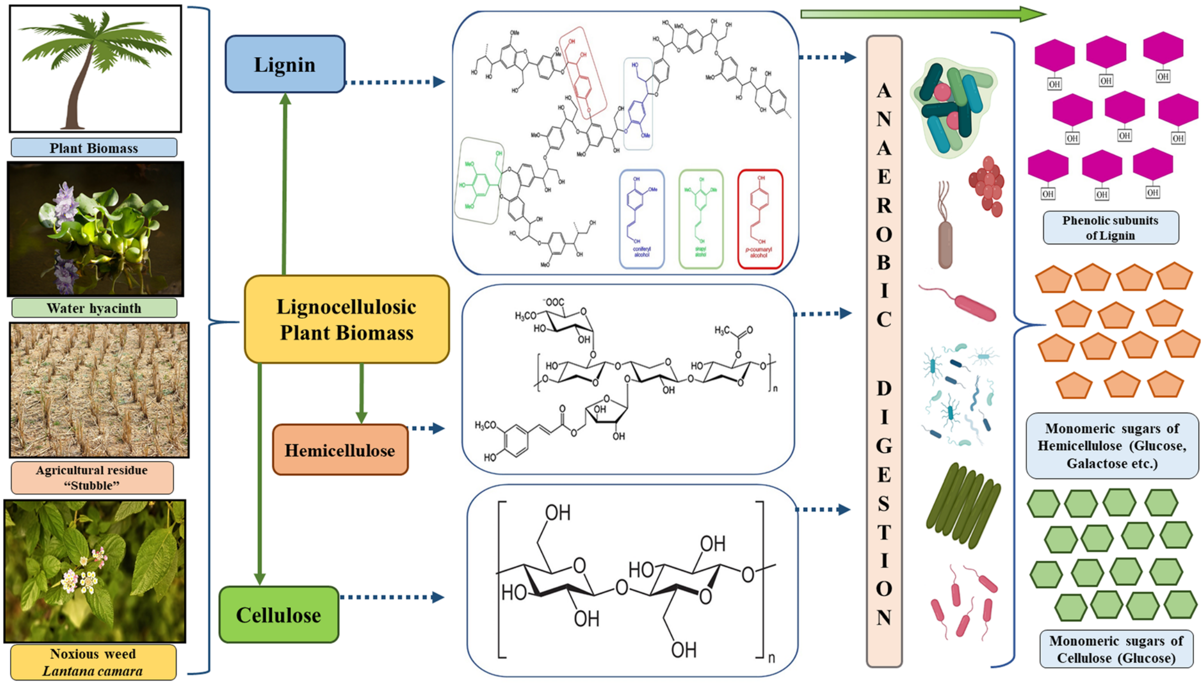

Fig. 2 Illustration of microbes mediated anaerobic digestion of lignocellulosic plant biomass

India, non-functional crop residues, i.e., stubbles and the noxious weeds abandoned in the field, are burned openly, causes serious air pollutions with the generation of greenhouse gasses such as CO_2 (1.5 × 10^7 tons), CO (9 × 10^5 tons), SO_X (2.5 × 10^4 tons), particulate matter (1 × 10^5 tons) and black carbon (5 × 10^4 tons), as per reported in the year 2020 (Porichha et al. 2021). To transform this pollution into sustainable energy production, such lignocellulosic biomass resources are considered an utmost substrate for bioenergy production in several perspectives like biogas, biohydrogen, bioethanol, etc. Globally, the lignocellulosic biomass production is approximately 120 × 10^9 tons per annum, equivalent to 2.2 × 10^{21} Joule, 300 folds more than the current global energy needs (Guo et al. 2015). Crop residues that remained after agricultural practices like stubbles and the noxious weeds like *Lantana camara* are reflected as a greater foundation of lignocellulosic biomass, and these do not have additional applications (Pandey et al. 2009; Sinha et al. 2021). The resistance that protects the plant biomass from various microbial utilisation is commonly known as the "biomass recalcitrance", consists of carbohydrate (50% of cellulose and 20% of hemicelluloses) and non-carbohydrate fractions (mainly 25% of lignin and rest of proteins) (Nanda 2013, 2015) that varies from plant to plant (Table 1).

4 Pretreatment strategies for enhanced biogas production

To achieve greater biogas yields from the lignocellulosic biomass, pretreatment is an obligatory approach during AD practice due to the rigid lignocellulosic complexity of the plant biomass. The factors that lead to the confrontation in the biodigestibility of the lignocellulosic biomasses consist of cellulosic crystallinity and degree of polymerisation, porosity and availability of surface area, lignin mediated fortification and hemicellulosic casing to the cellulose matrix etc. (Mosier et al. 2005). In that scenario, the application of pretreatment techniques can accelerate the removal of lignin and digestion of hemicelluloses, followed by the altered crystalline structure of cellulose (Agbor et al. 2011). Additionally, in the AD process, pretreatment helps in increasing the substrate surface area, which escalates more microbial adherence to the lignocellulosic biomass, promotes the substrate-enzyme interactions, and improves the hydrolytic process (Chandra et al. 2015). In this context, several pretreatments based approaches, i.e., physical (mechanical, comminution and irradiation), chemical (acidic, neutral and alkaline hydrolysis, oxidative treatment, organic solvent facilitated, ionic liquids, and alkaline hydrogen peroxide treatment), physicochemical (steam explosion, extrusion, hydrothermal and ammonia fiber expansion) and biological (microbial, i.e., bacterial and enzymatic) techniques are well recognised globally (Kumar et al. 2019). Among these pretreatment practices, biological pretreatment strategies are receiving more acceptance over the other pretreatments owing to their sustainability, less corrosiveness, safe chemical usage, maximum specificity, minimum energy consumption and by-product formation, accessibilities in genetic makeup and susceptibility towards genetic manipulation (Banerjee and Mandal 2020; Sindhu et al. 2016). Pretreatment in AD practice is crucial for the biotransformation of lignocellulosic biomass into fermentable sugar, preferable for microbial growth, nutrition, and optimised hydrolytic enzyme production (Atelge et al. 2020).

On the other hand, the main constraints in physical treatments are high energy requirements (Veluchamy and Kalamdhad 2017), insignificant productivity of methane due to too much size deduction of lignocellulosic biomass (Kumari and Singh 2018), etc. In chemical treatment practice, the major limitations are excess maintenance costs due to the high concentration of acid that leads to corrosion problems (Chen et al. 2017), therefore escalating the purification expenses. Additionally, in this process, some methane inhibitors are formed as byproducts like furfural and 5-hydroxymethyl furfural (5-HMF) which in turn severely reduce the methane yield. Greater alkaline concentrations usage causes degradation and decomposition of polysaccharides, which induce poor methane yield, sodium discharge from sodium hydroxide treatment influences soil salinization, which has serious negative impacts on the environment (Hernández-Beltrán et al. 2019). Moreover, organosolv pretreatment strategy with a chemical catalyst like acids generates acid-catalyzed deterioration of the monosaccharides into furfural and 5-HMF, which subsequently accelerates condensation reactions among lignin and the reactive aldehydes, successively develop low methane production as in

Table 1 Lignocellulosic ingredients in different plant biomass

Plant Biomass	Family	Plant group	Cellulose (%)	Hemicellulose (%)	Lignin (%)	References
Pineapple leaf waste	Bromeliaceae	Tree	31–31	17–22	17–20	Mund et al. (2021)
Water lettuce (*Pistia stratiotes*)	Araceae	Aquatic herb	16.47	16.91	15.70	da Silva Paulo et al. (2021)
Lantana camara	Verbenaceae	Shrub	34.9	17	–	Kumar et al. (2019)
Fruit and vegetable waste	Umbelliferae Lamiaceae Solanaceae Asteraceae Brassicaceae Liliaceae Rosaceae	Herb and shrub	26.9	15.3	12	Edwiges et al. (2018)
Duckweeds (*Lemna minor*)	Araceae	Herb	23.5	26.2	3.5	Kaur et al. (2019)
Rice husk	Poaceae	Herb	35	17	26	Heng et al. (2017)
Switchgrass	Poaceae	Herb	45.9 ± 1.5	24.0 ± 1.0	22.3 ± 0.9	de Lima Brossi et al. (2016)
Palm kernel shell	Arecaceae	Tree	24.5	22.9	33.5	Chan et al. (2015)
Sugar cane bagasse	Poaceae	Herb	42	25	20	Kim et al. (2011)
Energy cane	Poaceae	Herb	43	24	22	
Sweet sorghum	Poaceae	Herb	45	27	21	
Water hyacinth	Pontederiaceae	Herb	19.5	33.4	9.27	Gunnarsson and Petersen (2007)
Nutshells	Fagaceae	Herb	25–30	25–30	30–40	Howard et al. (2003)
Corn cobs	Poaceae	Herb	45	35	15	
Grasses	Poaceae	Herb	25–40	35–50	10–30	
Wheat straw	Poaceae	Herb	30	50	15	
Cottonseed hairs	Malvaceae	Shrub	80–95	5–20	0	
Coastal Bermuda grass	Poaceae	Herb	25	35.7	6.4	Reshamwala et al. (1995)

acid pretreatment practice (Chaturvedi et al. 2013). Similarly, the main drawback of the ionic liquid application is its high cost. Physicochemical pretreatments also comprised with several limitations like hemicelluloses are partially removed in steam explosion process, and in the case of ammonia fiber expansion practice, recycling of ammonia is necessary, which is also an additional costlier process (Brodeur et al. 2011; Chaturvedi and Verma 2013; Chen et al. 2017; Zhang et al. 2017; Hernández-Beltrán et al. 2019). Overall, the main challenges regarding physical, chemical and physicochemical practices are the formation of methane inhibitors (Atelge et al. 2020) and toxic chemical by-products that can cause severe environmental pollution (Yang et al. 2015). Furthermore, some advanced strategies in the AD techniques have evolved in response to the degradation of lignocellulosic biomass, such as the rumen derived anaerobic digestion (RUDAD) practice and the rumen simulating technique (RUSITEC), where utilisation of digestion mechanisms by the rumen microbial consortia might be better exploited in the design and operation of anaerobic digesters (Bayané et al. 2011).

5 Biological pretreatment

Plant biomass is symbolised for renewable carbon feedstock, which can substitute a substantial level of petroleum-derived fuels. Production of second-generation biofuel from the plant biomasses is a snowballing concept "plant-waste to fuel" where the substrates used in the form of sugarcane bagasse, rice straw, corn straw, corn stover, aquatic macrophytes (water hyacinth) and noxious weed (*L. camara*) etc. (Table 2). The key challenge in its exploitation is the mainstream of this carbon is entombed in between the recalcitrant polymers like i.e., lignin, cellulose and hemicellulose of the plant cell wall. The deconstruction of lignin is the crucial and challenging footstep in processing lignocellulosic biomass to renewable energy like biogas, biofuel, etc. To conquer this challenge, microbial appliances, as a "biological pretreatment" strategy, performed some molecular tools on lignin depolymerisation as they have developed several deep-seated pathways (Brown and Chang 2014). Biological pretreatment is an eco-sustainable practice that leads to improvised utilization of lignocellulosic biomass and ameliorates the convenience to the enzyme producing microbes, heightening hydrolysis proficiency for greater biogas production (Sindhu et al. 2016). Such pretreatment is commonly associated with applying microbes like bacterial and fungal species, which produces enzymes, i.e., lignin peroxidases, polyphenol oxidases, manganese dependent peroxidases, and laccases etc. capable for digestion of plant biomass substrates like lignin, hemicelluloses and cellulose (Fig. 3).

Enzyme mediated performances are expeditiously attaining attention because of the short catalytic reaction period, low energy consumption, cost-effective, non-hazardous, and environment-sustainable capabilities (Li et al. 2012; Choi et al. 2015). Enzymes of microbial origin are proficiently employed in various industries for greater superiority as well as with an augmented production rate with low cost management and in a non-hazardous approach (Thapa et al. 2020). In the 21st century, the consequences of industrial usage of microbial enzymes have been intensified remarkably and significantly meet the call of a fast-growing population to manage the fatigue of natural resources. Globally, the evaluated value of the industrially potential enzymes is about USD 5.9 billion in 2020 and is predicted to extend USD 8.7 billion by 2026 (Lugani et al. 2021). Microbial enzymatic breakdown of lignocellulosic biomass is essential in mitigating the wastes and generating biofuel (Shah et al. 2015). Microbial pretreatment has several advantages with higher impacts, such as the recovery of the plant biomass's total energy, greater functional diversity, improves productivity, expansion of the enzymatic saccharification, low energy requirement, advanced adaptability (tolerance to several environmental factors like temperature, pH, etc.), as well as its controls the pH during sugar and substrate utilisation (Kalyani et al. 2013; Shrestha et al. 2017; Sharma et al. 2019).

On the other hand, biological pretreatment is also considered a green technology because it has no-chemical usage and curtails the adverse effects of physical and chemical pretreatments (release of toxic chemical by-products) (Sindhu et al. 2016). Among the microbial pretreatment agents, bacteria-mediated pretreatment strategies are more advanced as they shorten the treatment duration due to their fast growth rate and high metabolic activity, vast availability, thermal and chemical stability, and genetic flexibility compared to the fungal system. Moreover, prolonged retention time is required (10–14 days) for coherent fungal growth. Also, fungi consume a significant fraction of carbohydrates used as a raw material for methanogenesis (Hatakka 1994). Therefore, in this type of bacterial pretreatment practice, up to 15% of electricity can be saved, required for ethanolysis in beech wood under bioorganosolv pretreatment (Palmowski and Müller 2000).

Biological pretreatment with bacterial inoculation can assist in sugar recovery up to 75% than the untreated one where *Sphingomonas paucimobilis* and *Bacillus circulans* were employed for pretreatment of office paper (Kurakake et al. 2007). Bioconversion of lignocellulosic biomass into fermentable sugar was also documented by *Cellulomonas cartae, C. uda, B. maceran*, and *Zymomonas mobilis* in the case of sugar cane bagasse pretreatment (Singh et al. 2008). Banu et al. (2018) reported that *B. jerish* used in waste activated sludge pretreatment for biomethane production yields 0.279 g COD/ g COD methane. Microbial agents as consortium [0.01% (w/w) for 15 days] can also amplify the digestibility of lignocellulosic biomass (60.9% of lignin and 43% of hemicelluloses) by reducing 34.6% technical digestion time as well as 96.33% higher methane yield (Zhong et al. 2011). In

Table 2 Bacteria mediated pretreatment of waste-plant biomass

Bacteria as inoculum	Phylum	Isolated from	Substrate used	Media used	References
Bacillus circulans	Firmicutes	Henan Agricultural University	Corn straw	Peptone broth (PB)	Li et al. (2020a)
Pseudomonas aeruginosa	Proteobacteria			Luria–Bertanibroth (LB)	
Streptomyces badius	Actinobacteria			Yeast powder and Starch broth	
Citrobacter werkmanii	Proteobacteria	Silverfish Gut and soil	Water hyacinth	Carboxymethylcellulose agar (CMC)	Barua et al. (2018)
Paenibacillus sp.	Bacteroidetes				
Pandoraea sp.	Proteobacteria	NM	Corn stover	Luria Bertani broth (LB)	Zhuo et al. (2018)
Pseudobutyrivibrio xylanivorans	Firmicutes	Biogas plant, Koto, Slovenia	Microalgae	DSMZ medium	Vidmar et al. (2017)
Cupriavidus basilensis	Proteobacteria	Forest soil	Rice straw	Mineral medium	Yan et al. (2017)
Bacillus sp.	Firmicutes	Forest soil	Rice straw	BSGYP medium	Chang et al. (2014)
Paenibacillus sp.	Firmicutes	Sludge reeds pond	News paper	Basic media: alkaline lignin	Wang et al. (2013)
Pseudomonas sp.	Proteobacteria				
Pseudomonas stutzeri	Proteobacteria				
Microbacterium pumilum	Actinobacteria				
Acinetobacter sp.	Proteobacteria				
Bacillus sp.	Firmicutes	Soil with Rotten lignocellulosic materials (decaying straw, cow manure, silt in paddy field)	Cassava residues	Peptone–cellulose medium	Zhang et al. (2011)
Clostridium sp.	Firmicutes				
Thermanaerovibrio acidaminovorans	Synergistetes				
Thermoanaerobacterium sp.	Synergistetes				
T. thermosaccharolyticum	Synergistetes				
Bacillus licheniformis	Firmicutes	Soil	Corn straw	Dry ground corn straw powder	Zhong et al. (2011)
B. subtilis	Firmicutes				
Pseudomonas sp.	Proteobacteria				
Cellulomonas cartae	Actinobacteria	National Chemical Laboratory, Pune, India	Sugarcane trash	1/2 strength nutrient agar + filter paper strips in broth + 2% glucose	Singh et al. (2008)
C. uda	Actinobacteria				
Bacillus macerans	Firmicutes				
Zymomonas mobilis	Proteobacteria				
Sphingomonas paucimobilis	Proteobacteria	Soil	Office paper	Cellulose medium (0.5% crystal.line cellulose + 1.5% agar)	Kurakake et al. (2007)
Bacillus circulans	Firmicutes				
Bacillus stearothermophilus	Firmicutes	Thermophilic aerobic digestion reactor	Organic sludge	NM	Hasegawa et al. (2000)

[#] NM = Not Mentioned

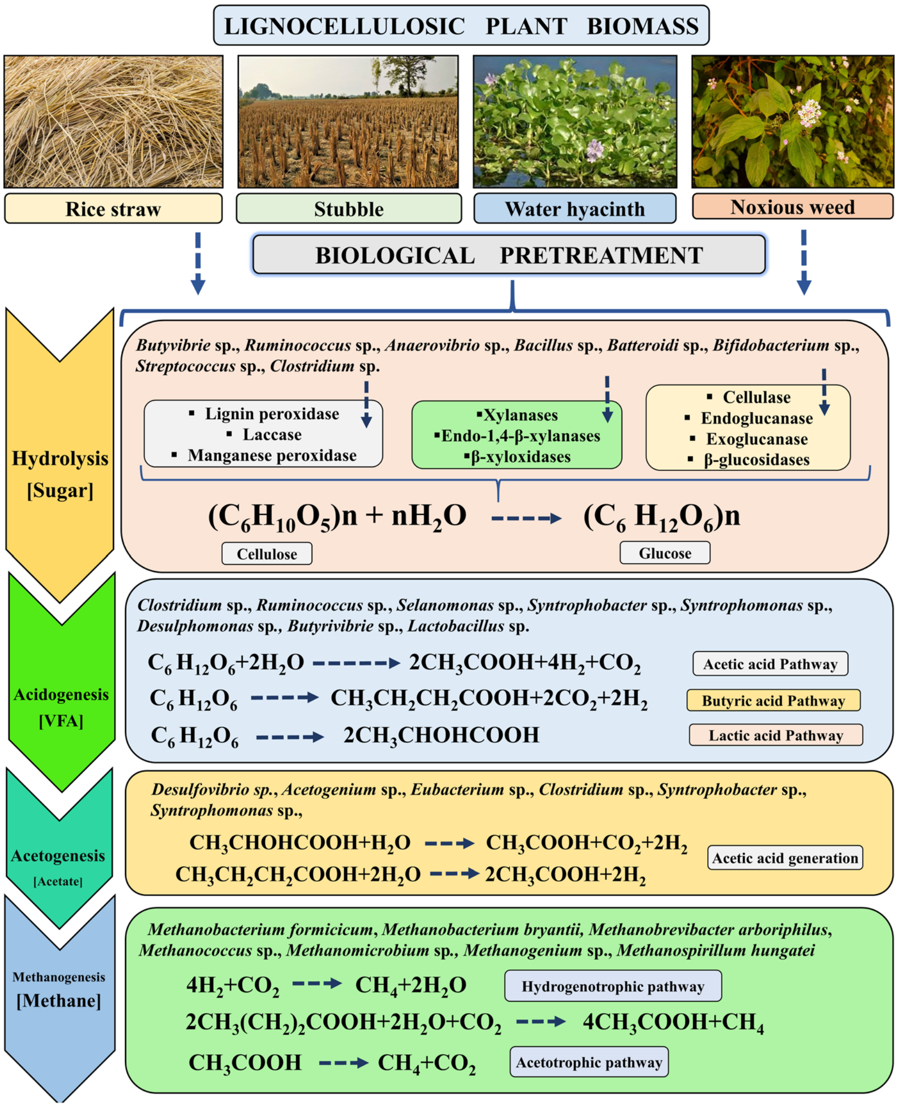

Fig. 3 Elucidation of Biological pretreatment processes of plant biomass

the case of bacterial pretreatment of corn straw, *Pseudomonas aeruginosa, Streptomyces badius,* and *B. circulans* can reduce hemicellulose, cellulose, and lignin content by 44.4%, 34.9%, and 39.2%, as well as increases yields of methane up to 14.85 mL/h (Li et al. 2020a) (Table 2). Methane production from microalgae as a substrate can upsurge by 13% when *Pseudobutyrivibrio xylanivorans* is used as a pretreatment agent (Vidmar et al. 2017).

Currently, the sources of prospective biomolecules with microbial origin have remarkable demand in relation to biotechnological aspects. In this circumstance, exploration of unmapped microbial resources having promising enzymatic potential will be a key way in modern-day's industrial biotechnology. Among such unexplored natural resources, herbivorous insect gut symbionts, specifically lignocellulolytic bacteria are the true pathfinders as their host diet system are depends on plant biomasses. As per the phenomenon fact that in accordance with the host's food materials composition, the gut microbes play a pivotal role in host digestion by enzymatic breakdown, therefore, it can be assumed that these endosymbionts may be the good manufacturer of plant biomass digestive enzymes, particularly lignocellulases, cellulases and hemicellulases (Banerjee et al. 2021).

Nonetheless, only a few insects orders among the one million insect species with 31 orders have been reported regarding their lignocellulolytic gut microbiota (see supplementary S1-S3). Therefore, insect gut symbionts are full of prospects with a source of biotechnologically potential bio molecules as these microorganisms have to undergo various selection pressures in their host gut system. So there are plenty of possibilities to explore these "biotechnological warhorses" for biological pretreatment.

Both fungi and bacteria have opted for different biochemical processes for lignin disintegration. In this review, the bacterial approaches towards plant biomass utilisation for renewable energy production will be elucidated with modern advances. The bacterial representatives which are involved in the transformation of plant biomass to biogas generation have been reported from different gut environments, such as animal rumen (mainly cow dung), native Australian marsupials, herbivorous insects (termite, caterpillar, cricket, beetle, chafer, cockroach, locust, and agronomic plant pests), and other obligate herbivorous gut systems (Morrison et al. 2009; Banerjee et al. 2016; Gales et al. 2018; Sinha et al. 2021; Zhang et al. 2021). Several research laboratories have documented the digestion of lignocellulosic plant biomasses by the potential insect gut bacteria. Anukam et al. (2020) reported that *Morganella morganii*, a ligninolytic symbiont from the gut system of *Cryptotermes brevis*, a wood-feeding termite, can reduce the lignin component up to 53.27% in the case of rice straw digestion. On the other hand, in wheat straw treatment by the gut symbionts of *Potosia cuprea*, degradation of plant waste biomass extends up to 20% (Gales et al. 2018). Significant plant biomass (saw dust) digestion was also observed by *Acinetobacter junii* GAC 16.2, a cellulolytic gut bacteria from *Gryllotalpa africana* (Banerjee et al. 2020). Moreover, *Enterobacter hormaechei*, a gut isolate of *Hypomeces squamosus* can digest lignin ingredients of corn straw as high as 32.05% (Zhang et al. 2021). The most promising and studied plant biomass degrading gut symbionts are reported from termites gut system, which can digest up to 74–99% of the cellulose of lignocellulosic biomass (Breznak and Brune 1994).

6 Plant biomass consuming insect gut system: a bioreactor

Insects are among the most diversified and species-rich groups that have transformed to establish themselves in several ecological niches. The steady diversification of this arthropod lineage stands on the plant biomass consumption as these plant biomasses are ubiquitous in nature and the plant cell walls are the major resources for organic carbons on the earth (Banerjee et al. 2021). Insects are well known for ingesting living or dead plant substances as they can consume up to 20% of a crop plant due to their herbivorous food habit, and their choices are ranged from algae to angiosperms (Khan et al. 2010). Sometimes they consume single or multiple plant species or families. On the other side, it is often different plant parts specific to seed or leaves, developing leaf tissues, reproductive or senescing tissues, cell sap, etc. (Bernays and Chapman 2007). Due to their versatile ecological fitness, their requirements are diverse plant ingredients, i.e., starch, cellulose, hemicellulose, lignocellulose, pectin, xylan, tannins, terpenes, esters, glucosinolates, pyrrolizidine alkaloids, and essential amino acids from phloem sap as in the case of Lepidoptera, Diptera, Coleoptera, Isoptera, Orthoptera, Blattodea, and Hemiptera (Banerjee et al. 2021).

Depending on the food habits, especially the plant biomass, the insect gut system produces various lignocellulosic digestive enzymes. In some cases, insects make lignocellulases encoded by their genome (Watanabe 1998) and shatter the food macromolecules into smaller ones. At the same time, insect gut symbionts secrete the majority of the metabolism-specific digestive enzymes such as lignocellulases for the enzymatic digestion of the consumed plant food materials for complete energy mining purposes. Thus, these symbionts execute a pivotal role in aiding host digestion via enhanced digestive proficiency through enzymatic potentiality (Yun et al. 2014; Jing et al. 2020). In the insect gut system, various microbial associations like bacteria, fungi, protozoa, and archaea are present for their beneficial host activities. Insects harbour a rich and diversified microbial community in their gut system (Wiseman 1995). The organisation of the symbiotic association between insects and gut bacteria is deep-rooted and can be exemplified by the Miocene termite *Mastotermes electrodominicus*, a 20 million-year-old amber fossil that has been found to comprise protists, spirochetes, and other microorganisms (Wier et al. 2002). The insect gut system acts as a continuous culture system where microbes, capable of degrading dietary compounds, are retained and made to multiply, otherwise, microbes lacking this aptitude are washed out (Hayashi et al. 2007). This type of gut symbiotic diversity is principally determined by the host diet or ingested food materials and the environmental habitat (Yun et al. 2014; Kudo et al. 2019).

In this scenario, several reports were documented regarding the lignocellulolytic potentialities of insect gut bacteria. Among the current research outputs, potent cellulase producers such as *Acinetobacter junii*, *Klebsiella pneumoniae*, *Bacillus licheniformis*, *B. pumilus*, and *B. velezensis* from the diverse gut system of *G. africana* (Orthoptera), *Diatraea saccharalis* (Lepidoptera), *Heterotermes indicola* (Blattodea), *Eudrilus eugeniae* (Haplotaxida), and *Cyrtotrachelus buqueti* (Coleoptera) with 112.38 ± 0.87 U/ml, 30.13 U/mg, 1156 U/mL, 1.480 IU/mL, and 0.752±0.013 U/ml cellulase production were observed, respectively (Shankar et al. 2021; Banerjee et al. 2020; Barbosa et al. 2020; Li et al. 2020b; Afzal et al. 2019) (Table 3). Moreover, hemicellulase (xylanases) producers like *Bacillus* sp., *Arthrobacter* sp., and *Pseudomonas azotoformans* from the different gut systems, i.e., *Cryptotermes brevis* (Blattodea), *Dendroctonus rhizophagus* (Coleoptera) with the production of 0.21 U/ml, 2.6 ± 0.07 U/ml, and 10.6 ± 0.66 U/ml of xylanase, respectively were also observed (Tsegaye et al. 2019; Roblero et al. 2017) (Table 4). In the case of the lignocellulase producers such as *B. subtilis*, *Ochrobactrum oryzae*, and *Dysgonomonas* sp. from the different gut systems of *Helicoverpa armigera* (Lepidoptera), *C. brevis* (Blattodea), and *Cyrtotrachelus buqueti* (Coleoptera) produces 179.30 IU/ml, 158.78 IU/ml, 14.6 IU/ml, and 10±0.2 U/ml of lignin peroxidases, respectively (Dar et al. 2021; Luo et al. 2019; Tsegaye et al. 2019) was also documented. Additionally, a significant amount of lignin peroxidase (585.2 U/l) production was also observed by the gut symbiont *Enterobacter hormaechei* isolated from *Hypomeces squamosus* (Coleoptera) (Zhang et al. 2021) (Table 5). Pectinase production by the gut symbionts, i.e., *B. circulans*, *P. fluorescens*, and *Erwinia* sp., also experimentally evidenced up to 150±5, 25±5, and 110±5 mU/ml pectiase, respectively, from the gut of *Bombyx mori* (Lepidoptera) (Anand et al. 2010). Additionally, up to 1.08 IU/ml pectinase produced by *Aeromonas hydrophila*, from the Coleopteran gut habitat (*Onitis philemon*) has been reported (Surabhi et al. 2018) (Table 6).

In addition to the lignocellulolytic enzyme producing proficiency of these symbionts, the insect gut system can also act as a bioreactor where these symbionts perform acetogenesis and methanogenesis. One such example is the gut system of *Drosophila melanogaster*, where the symbiont *Acetobactor pomorum* promotes acetic acid production (Crotti et al. 2010). Whereas, in the case of Scarab larval gut system, particularly the hindgut, was characterised by an anaerobic condition with a high concentration of volatile fatty acids (VFA) with fermenting bacteria which especially endorses methanogenesis by utilising the VFA as substrates (Huang 2010). Moreover, Bayon and Etiévant (1980) also reported methanogenic bacteria in the proctodeum of *Oryctes* sp. Zhang et al. (2021) reported biogas production by *Enterobacter hormaechei*, a gut symbiont of *Hypomeces squamosus* can generate 59.19 l/kg-VS biogas with methane yield of 14.76 l/kg-VS utilising corn straw as lignocellulosic plant biomass. Interestingly, a commercial scale based production of up to 950 l/kg VS biogas with 57% methane, using *L. camara* biomass, was also observed from the gut bacteria *Microbacterium* sp. of *Microtermes obesi* (Sinha et al. 2021).

Keeping these points in view, the presence of such immense potential of bacterial population with cellulase, lignocellulase, xylanase, and pectinase production capabilities as well as by the performances like acetogenesis, methanogenesis, and biogas production such diversified insect gut bacterial community can act as a pathfinder for modern-days second-generation renewable energy production as biofuel or biogas by utilising lignocellulosic plant biomass.

7 Diversity and distribution of lignocellulolytic enzyme producing insect gut bacteria

Nowadays, the role of insect gut bacteria in the arena of renewable energy production is receiving attention, but the significant application to translate scientific advances into commercial reality is not getting much recognition. So, there is ample scope to explore these gut bacterial populations as a new horizon for integrating biotechnological tools for biogas or biofuel

Table 3 Cellulase producing insect gut bacteria

Insect	Enzyme	Gut bacteria	Phylum	Enzyme yield	References
Blattodea					
Psammotermes hypostoma	Endoglucanase	*Paenibacillus lactis*	Firmicutes	1.47 ± 0.1 U/l	Ali et al. (2019)
		Lysinibacillus macrolides	Firmicutes	0.22 ± 0.1 U/ml	
		L. fusiformis	Firmicutes	2.28 ± 0.1 U/ml	
		Stenotrophomonas maltophilia	Proteobacteria	1.93 ± 0.1 U/ml	
		Bacillus cereus	Firmicutes	0.23 ± 0.1 U/ml	
Macrotermes gilvus	Cellulase	*Provedencia* sp.	Proteobacteria	15.7 mU/ml	Arfah et al. (2019)
		Bacillus sp.	Firmicutes	2.33 mU/ml	
Anacanthotermes sp.	β-1,4-glucanase	*Bacillus* sp.	Firmicutes	0.28 U/mg	Javaheri-Kermani et al. (2019)
Heterotermes indicola	Cellulase	*Bacillus licheniformis*	Firmicutes	1156 U/ml	Afzal et al. (2019)
Amitermes evuncifer	Endoglucanase	*Bacillus cereus*	Firmicutes	6.38 µmol min^{-1} mg^{-1}	Femi-Ola et al. (2019)
		B. mycoides	Firmicutes	5.96 µmol min^{-1} mg^{-1}	
		Pseudomonas aeruginosa	Proteobacteria	4.89 µmol min^{-1} mg^{-1}	
Cockroach Gut	Cellulase	*Bacillus* sp.	Firmicutes	0.11 U/ml	Sharma et al. (2019)
Cryptotermes brevis	Cellulase	*Bacillus* sp.	Firmicutes	0.25 U/ml	Tsegaye et al. (2019)
Coleoptera					
Cyrtotrachelus buqueti	Cellulase	*Bacillus velezensis*	Firmicutes	0.752 ± 0.013U/ml	Li et al. (2020b)
Hypothenemus hampei	Cellulase	*Brochothrix* sp.	Firmicutes	0.031 U/ml	Azizah et al. (2020)
Sitophilus oryzae	Cellulase	*Bacillus subtilis*	Firmicutes	132.069 ± 0.993 U/ml	Prasad et al. (2019)
	(β-1,4-endoglucanase)	*Staphylococcus* sp.	Firmicutes	103.25 ± 0.842 U/ml	
		Citrobacter sp.	Proteobacteria	93.600 ± 1.244 U/ml	
		Enterobacter ludwigii	Proteobacteria	88.820 ± 1.505 U/ml	
Onitis philemon	Cellulase	*Acinetobacter baumannii*	Proteobacteria	0.52 IU/ml	Surabhi et al. (2018)
		Citrobacter amalonaticus	Proteobacteria	0.46 IU/ml	
Osphranteria coerulescens	Cellulase	*Bacillus safensis*	Firmicutes	5.35 U/ml	Hatefi et al. (2017)
Dendroctonus rhizophagus	Cellulase	*Arthrobacter* sp.	Proteobacteria	3.3 ± 0.36 U/ml	Roblero et al. (2017)
		Pseudomonas azotoformans	Proteobacteria	8.0 ± 0.0 U/ml	
Holotrichia parallela	Endoglucanase	*Pseudomonas* sp.	Proteobacteria	0.825 U/ml	Sheng et al. (2012)

Table 3 continued

Insect	Enzyme	Gut bacteria	Phylum	Enzyme yield	References
Leptinotarsa decemlineata	Cellulase	*Klebsiella* sp.	Proteobacteria	140 ± 2 mU/ml	Vilanova et al. (2012)
		Comamonas sp.	Proteobacteria	160 ± 2 mU/ml	
		Acinetobacter sp.	Proteobacteria	130 ± 2 mU/ml	
		Sphingobacterium sp.	Bacteroidetes	120 ± 2 mU/ml	
Pachnoda marginata	Cellulase	*Cellulomonas* sp.	Actinobacteria	6.1 ± 1.0 U/ml	Cazemier (1999)
Isoptera					
Odontotermes sp.	endoglucanase	*Bacillus* sp.	Firmicutes	0.19 IU/mL	Cibichakravarthy et al. (2017)
Heterotermes sp.	Endoglucanase	*Bacillus cereus*	Firmicutes	5.06 U/mg	Sreena et al. (2015)
Odontotermes sp.	β-glucosidase			6.01 U/mg	
Lepidoptera					
Diatraea saccharalis	Cellulase	*Klebsiella* sp.	Proteobacteria	19.97 U/mg	Barbosa et al. (2020)
		K. pneumoniae	Proteobacteria	30.13 U/mg	
		Bacillus sp.	Firmicutes	5.53 U/mg	
Zeuzera pyrina	Cellulase	*Bacillus subtilis*	Firmicutes	0.42 ± 0.002 U/ml	Dehghanikhah et al. (2020)
Agrotis ipsilon	Cellulase	*Bacillus sp.*	Firmicutes	0.233 IU	Biswas et al. (2019)
Cnaphalocrocis sp.		*Klebsiella* sp.	Proteobacteria	0.378 IU	
Bombyx mori	Cellulase	*Bacillus aryabhattai*	Firmicutes	0.45 U/ml	Pandiarajan et al. (2020)
Antheraea assamensis	Cellulase	*Bacillus pumilus*	Firmicutes	0.262 U/ml	Bhuyan et al. (2018)
Cossus cossus	Cellulase	*Bacillus circulans*	Firmicutes	4.359×10^{-2} U/ml	Baharuddin et al. (2016)
		B. circulans		2.775×10^{-2} U/ml	
Diatraea saccharalis	Cellulase	*B. pumilus*	Firmicutes	0.32 U/ml	Dantur et al. (2015)
		K. oxytoca	Proteobacteria	0.22 U/ml	
Ostrinia nubilalis	Cellulase	*Micrococcus* sp.	Actinobacteria	28–32 mU/ml	Vilanova et al. (2012)
		Microbacterium paraoxydans	Actinobacteria		
Orthoptera					
Gryllotalpa africana	Cellulase	*Acinetobacter junii*	Proteobacteria	112.38 ± 0.87 U/m	Banerjee et al. (2020)
Psocoptera					
Psococerastis albimaculata	1,3–1,4-β-glucanase	*Bacillus methylotrophic*	Firmicutes	2040 U/mL	Niu et al. (2016)

production (Angelidaki et al. 2018). In these circumstances, augmented biogas production via enzymatic degradation (cellulase, lignocellulase, xylanase, and pectinase) potentiality of plant biomasses, exploitation of the insect gut systems has been scrutinised, and so far they belong to only three insect orders, i.e., Blattodea, Coleoptera, and Diptera, among the thirty one insect order (Kavitha et al. 2014; Xiao et al. 2018; Sinha et al. 2021; Zhang et al. 2021). Whereas, in case of the reported insect orders, those are harbouring the gut bacterial community responsible for plant biomass degrading potentialities, with the quantified amount of cellulase, lignocellulase, xylanase and pectinase production, are listed within six orders (Blattodea,

Table 4 Xylanase producing insect gut bacteria

Insect	Gut bacteria	Phylum	Enzyme yield	References
Blattodea				
Cryptotermes brevis	*Bacillus* sp.	Firmicutes	0.21 U/ml	Tsegaye et al. (2019)
Odontotermes hiananensis	*Bacillus licheniformis*	Firmicutes	0.37 μmol/min/ml	Bashir et al. (2013)
	B. subtilis	Firmicutes	0.23 μmol/min/ml	
	Paenibacillus polymyxa	Firmicutes	0.44 μmol/min/ml	
Coleoptera				
Dendroctonus rhizophagus	*Arthrobacter* sp.	Actinobacteria	2.6 ± 0.07 U/ml	Roblero et al. (2017)
	Pseudomonas azotoformans	Proteobacteria	10.6 ± 0.66 U/ml	
Pachnoda marginata	*Cellulomonas* sp.	Actinobacteria	2.1 ± 0.9 U/mg	Cazemier (1999)
Isoptera				
Armadillidium sp.	*Paenibacillus polymyxa*	Firmicutes	0.18 μmol/min/ml	Bashir et al. (2013)
	Bacillus subtilis	Firmicutes	0.38 μmol/min/ml	
	B. tequilensis	Actinobacteria	0.34 μmol/min/ml	
	Cellulosimicrobium sp.	Firmicutes	0.31 μmol/min/ml	
Lepidoptera				
Scirpophaga incertulas	*Bacillus subtilis*	Firmicutes	0.35 μmol/min/ml	Bashir et al. (2013)
	Enterobacter sp.	Proteobacteria	0.06 μmol/min/ml	
Bombyx mori	*Bacillus circulans*	Firmicutes	150 ± 5 mU/ml	Anand et al. (2010)
	Aeromonas sp.	Proteobacteria	130 ± 5 mU/ml	
	Serratia liquefaciens	Proteobacteria	120 ± 5 mU/ml	

Coleoptera, Diptera, Lepidoptera, Isoptera, and Orthoptera) only, among the 31 insect orders. In this case, the highest number of cellulase and pectinase producers belong to the Coleoptera and Lepidopteran gut systems. The xylanase and lignocellulase producers of the bacterial population mainly represents Coleoptera, Blattodea and Lepidopteran gut environment (Fig. 4a). Moreover, the most governing bacterial phylum is the Firmicutes and Proteobacteria, respectively, from the quantified lignocellulolytic enzyme producing insect gut residents (Fig. 4b).

The overall distribution of the non-quantified plant biomass degrading lignocellulolytic enzyme (cellulase, lignocellulase, xylanase, and pectinase) producing insect gut bacterial population (Firmicutes, Proteobacteria, Actinobacteria, Bacteroidetes, and Spirochaetes) revealed that Blattodea is the supreme reservoir of lignocellulase and cellulase producing bacterial community and among them, Proteobacteria are the predominant one. Whereas, in terms of xylanase and pectinase producing gut bacterial communities, Proteobacteria are the leading inhabitants of the Lepidoptera gut system (Fig. 5). Proteobacteria and Firmicutes members are primarily liable for the lignocellulase and cellulase producing proficiency within the most reported gut environment, i.e., Blattodea, Isoptera, and Coleoptera in both the cases, respectively (Fig. 6a, b). The Actinobacterial community are principally recognised for their lignocellulase, cellulase, and xylanase activity from the residents of mostly Blattodea, Isoptera, and Coleoptera gut (Fig. 6c). Bacteroidetes are acknowledged for their lignocellulase and cellulase activity from Blattodea, Coleoptera, Isoptera, and Orthoptera gut systems (Fig. 6d). Spirochaetes are only the gut symbionts of the Isoptera and Coleoptera groups and are responsible for lignocellulase and cellulase production only (Fig. 6e).

In other perspective, the abundance of cellulose degraders are mainly documented in the Coleoptera group, and the leading bacterial phyla are Proteobacteria and Firmicutes, with 33 and 16 numbers of reports. In the case of lignocellulase producers, the most documented gut system is the Blattodea, where

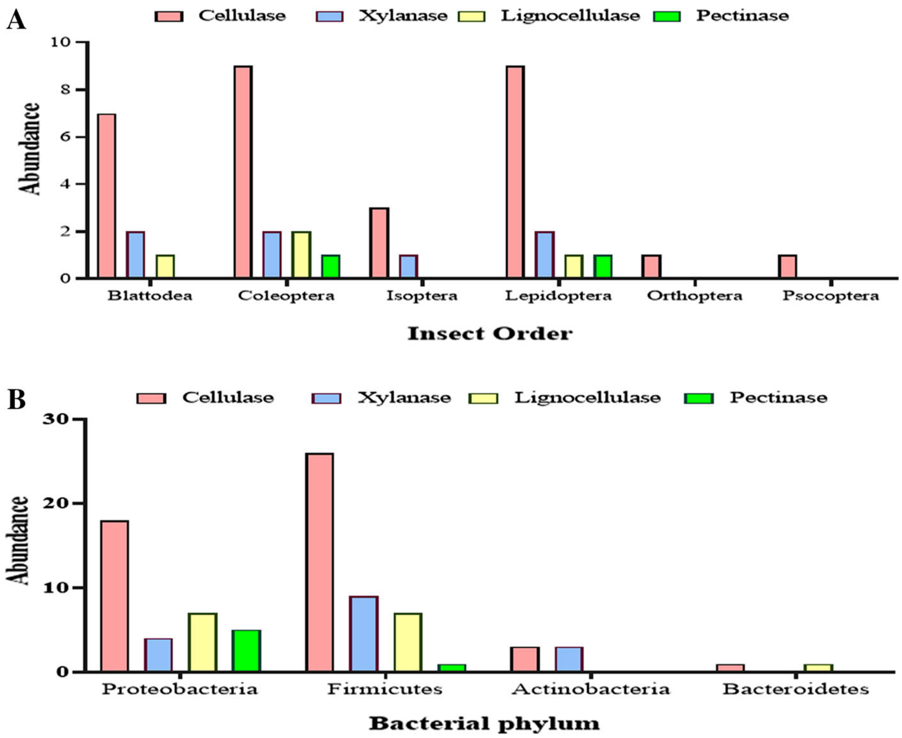

Fig. 4 Abundance of lignocellulolytic enzyme producing bacterial population of insect gut system. **a.** Abundance of bacteria mediated lignocellulolytic enzyme production in different insects gut system. **b.** Diversity of lignocellulolytic enzyme producing insect gut bacterial phyla

the most bacterial representatives are Proteobacteria and Firmicutes with 60 and 28 experimental evidence. Whereas, the xylanase producers are predominantly observed from the gut system of Coleoptera and Lepidoptera with the highest 12 numbers of Proteobacterial evidence. Among the pectinase producers, the leading bacterial member is from the Proteobacteria with four reported studies and mainly residing in the gut of Lepidopterans (Fig. 6a–e).

Therefore, from this review, it can be justified that, in search of unexplored microbial resources for renewable energy production, more exploration of other herbivorous insect gut systems with potent lignocellulolytic symbionts, other than these eight (Blattodea, Coleoptera, Lepidoptera, Isoptera, Diptera, Orthoptera, Hymenoptera, and Hemiptera) reported insect order would be beneficial for fulfilling the next-generation energy demands as well as to achieve sustainable ecosystem also. Lignocellulolytic gut symbionts like Proteobacteria and Firmicutes exhibited their dominancy in plant biomass digestibility, and those can be tied together for greater biogas production.

8 Omics-based projections in the arena of the biogas generating microbial community

Microbiological culture-dependent methods provide only limited knowledge and information, accounting for less than 0.1% of the bacterial community structure, physiological features, and diversity (Stolze et al. 2015). Microbial methane production via the anaerobic digestion process is directly proportional to the microbial community in the anaerobic digester and is a resultant of the various metabolic pathways exercised by the micro-dwellers (Schnürer 2016). This is, in turn, governed by the thermodynamic laws inside the reactor (Schnürer 2016; Campanaro et al. 2018). Microbial biogas generation by converting waste

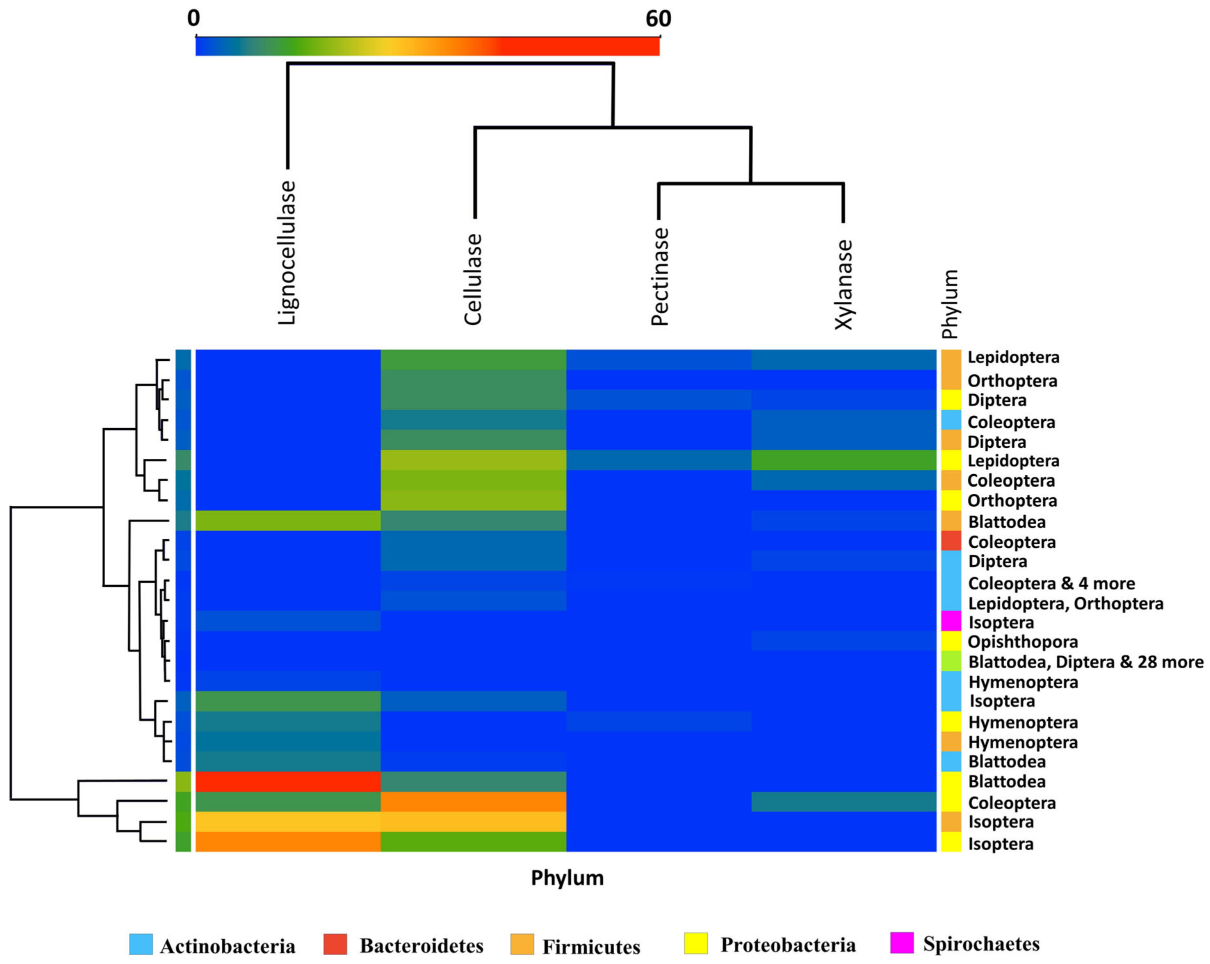

Fig. 5 Distribution of plant biomass degrading insect gut bacterial population

matter yielding methane has been considered a black box setup, and the role of microbiota behind the process has long been unnoticed (Robles et al. 2018). The relation between methane generation and the microbial community composition of the reactor is an inter-linked process, and this paradigm offers to be exploited for improving the efficiency through microbial selection or formulation (Theuerl et al. 2018; Ziels et al. 2018). The complex community of microbes thrives and replaces the various stages of biogas generation; hence, knowledge of the microbial consortia is of utmost importance in augmenting the process.

Metagenome studies of anaerobic digester samples using next-generation sequencing 16S rRNA gene amplicon sequencing empowered researchers with the knowledge of taxonomy outlining biogas generating microbial populations. Profound understanding of microbial communities under laboratory scale (Sträuber et al. 2016; Zhu et al. 2019) and large-scale digesters and biogas plants were carried out recently (Koo et al. 2019; Ma et al. 2021). Metagenome sourced from various anaerobic digesters has helped develop exceptional knowledge about the micro-inhabitants and their characteristic features in biogas generation (see supplementary file). In this regard, metatranscriptome and metaproteome have been the very recent applications of high-throughput sequencing. The first report of metatranscriptome analysis by Zakrzewski et al. (2012) studied the active microbial community of a fabricated biogas plant using the 16S rRNA tags. Analysis of the meta-transcripts revealed encoded enzymes actively carrying out the various methanogenesis processes. A recent investigation in

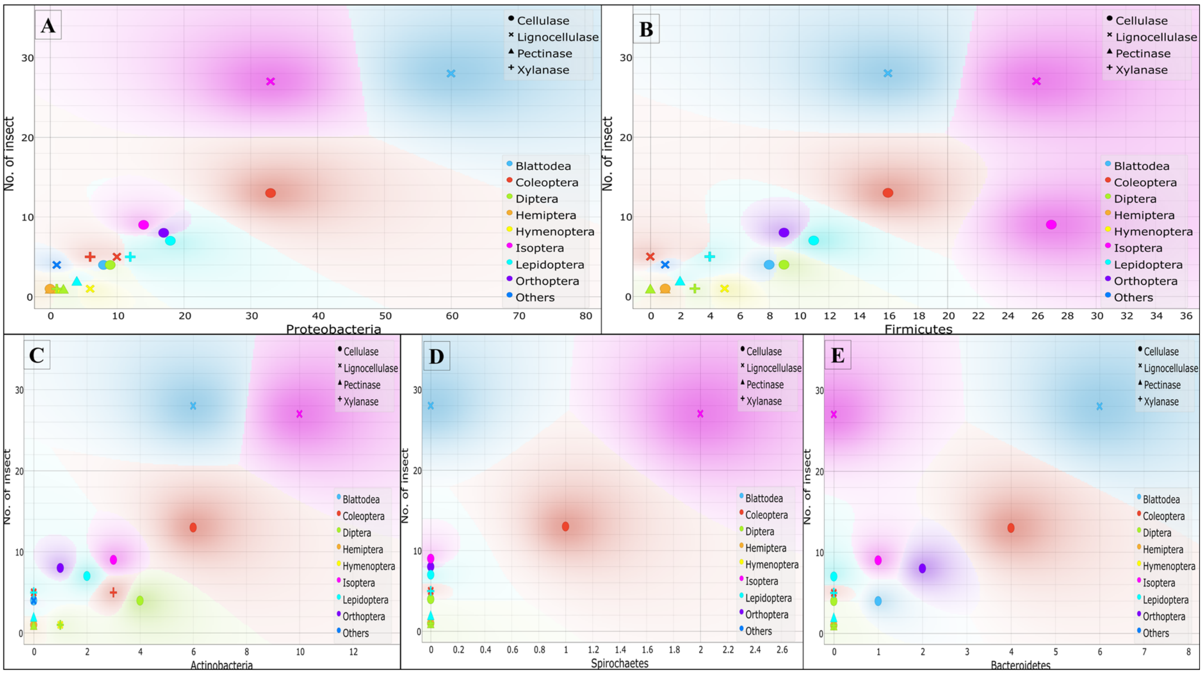

Fig. 6 Distribution of lignocellulolytic enzyme producing insect gut bacterial phyla belongs to different insect orders. **a.** Lignocellulolytic enzyme producing Proteobacteria in reported insect orders. **b.** Lignocellulolytic enzyme producing Firmicutes in reported insect orders. **c.** Lignocellulolytic enzyme producing Actinobacteria in reported insect orders. **d.** Lignocellulolytic enzyme producing Bacteroidetes in reported insect orders. **e.** Lignocellulolytic enzyme producing Spirochaetes in reported insect orders

the metabolism of methanogens inside the anaerobic apparatus using coupled metagenomic and metatranscriptomic approaches unveiled the natural system, and *Methanosarcina thermophila* was shown to be the predominant methanogen (Zhu et al. 2020). Metaproteomic studies targeting the complete protein composition of the diverse microbial anaerobic systems give the perfect image of the multifaceted relationship of microbes with their environment. A metaproteomic study strikingly revealed that microbial communities inside the reactor vessel were shaped by syntrophism and interaction with bacteriophages (Heyer et al. 2019).

In context to the current review of lignocellulose degraders from insect gut, metagenome studies have revealed remarkable populations of microbial degraders with active enzymes for lignin and lignocellulose compound degradation (Joynson et al. 2017). The gut microbiota of insects has been shown to directly decompose the polymeric lignocellulose via its multiple active enzymes at a wide range of temperatures and pH, which suggests that the knowledge and information about these types of consortia can be of much ecological importance (Scully et al. 2013) (see supplementary file). Bio-prospection using the high-end next-generation sequencing tools can be of immense advantage in mitigating the quest for new microbial consortia or enzymes that might one day help curb the energy crisis caused by fossil fuels.

9 Conclusion

To fulfil the global energy demands, enhanced bioenergy production through the unexplored herbivorous insect gut microbial communities, especially Proteobacteria and Firmicutes, and their lignocellulolytic (cellulase, lignocellulase, xylanase, and pectinase) proficiencies can be a “treasure box” with immense biotechnological prospects. The utilisation of waste-plant biomasses like water hyacinth, noxious weeds, and stubbles as substrates can be a true eco-sustainable approach as they cause environmental hazards in other ways. The application of omics-based techniques upon these bacterial symbionts, from the unexplored “Natural Bioreactor”, mainly insect gut system, could be a

Table 5 Lignocellulase producing insect gut bacteria

Insect	Gut bacteria	Phylum	Enzyme produced	Enzyme yield	References
Blattodea					
Cryptotermes brevis	*Bacillus* sp.	Firmicutes	Xylanase	0.21 U/ml	Tsegaye et al. (2019)
			CMCase	0.25 U/ml	
	Ochrobactrum oryzae	Proteobacteria	Lignin peroxidase	14.6 IU/ml	
			Laccase	8 IU/ml	
Coleoptera					
Hypomeces squamosus	*Enterobacter hormaechei*	Proteobacteria	Lignin peroxidase	585.2 U/l	Zhang et al. (2021)
Cyrtotrachelus buqueti	*Lactococcus* sp.	Firmicutes	Endoglucanase	9 ± 0.5 U/ml	Luo et al. (2019)
	Enterococcus sp.	Firmicutes	Exoglucanase	80 ± 2 U/ml	
	Serratia sp.	Proteobacteria	β- glucosidase	7.8 ± 0.2 U/ml	
	Dysgonomonas sp.	Bacteroidetes	Xylanase	140 ± 5 U/ml	
			Laccase	10 ± 0.2 U/ml	
			Lignin peroxidase	2.2 ± 0.2 U/ml	
Lepidoptera					
Helicoverpa armigera	*Bacillus subtilis*	Firmicutes	Endoglucanase	179.30 IU/ml	Dar et al. (2021)
	Klebsiella pneumoniae	Proteobacteria		65.09 IU/ml	
	B. subtilis	Firmicutes	Xylanase	158.78 IU/ml	
	K. pneumoniae	Proteobacteria		43.92 IU/ml	
	B. subtilis	Firmicutes	β-glucosidase	59.99 IU/ml	
	K. pneumoniae	Proteobacteria		35.5 IU/ml	
	B. subtilis	Firmicutes	Exoglucanase	9.89 IU/ml	
	K. pneumonia	Proteobacteria		6.40 IU/ml	

Table 6 Pectinase producing insect gut bacteria

Insect	Gut bacteria	Phylum	Enzyme yield	References
Coleoptera				
Onitis philemon	*Aeromonas hydrophila*	Proteobacteria	0.9 ± .1 IU/ml	Surabhi et al. (2018)
	A. caviae	Proteobacteria	0.8 ± .1 IU/ml	
	Citrobacter freundii	Proteobacteria	1.08 IU/ml	
Lepidoptera				
Bombyx mori	*Bacillus circulans*	Firmicutes	150 ± 5 mU/ml	Anand et al. (2010)
	Pseudomonas fluorescens	Proteobacteria	25 ± 5 mU/ml	
	Erwinia sp.	Proteobacteria	110 ± 5 mU/ml	

budding source for various novel key hydrolytic enzymes that can be harnessed in a “Green Seedlings for Human Welfare”. Additionally, deployment of such reported gut symbionts for augmentation of biogas production is in an infant stage, so there is plenty scope for employment of such untouched insect gut symbionts as a “Biotechnological Game-Changer” in the modern-day alternative renewable energy generating arena.

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Declarations

Conflict of 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.

References

Abdurrahman MI, Chaki S, Saini G (2020) Stubble burning: effects on health & environment, regulations and management practices. Environ Adv 2:100011

Abraham A, Mathew AK, Park H, Choi O, Sindhu R, Parameswaran B, Pandey A, Park JH, Sang BI (2020) Pretreatment strategies for enhanced biogas production from lignocellulosic biomass. Bioresour Technol 301:122725

Afzal M, Qureshi MZ, Khan S, Khan MI, Ikram H, Ashraf A, Iqbal A, Qureshi NA (2019) Production, purification and optimization of cellulase by *Bacillus licheniformis* HI-08 isolated from the hindgut of wood-feeding termite. Int J Agric Biol 21(1):125–134

Agbor VB, Cicek N, Sparling R, Berlin A, Levin DB (2011) Biomass pretreatment: fundamentals toward application. Biotechnol Adv 29(6):675–685

Ali HR, Hemeda NF, Abdelaliem YF (2019) Symbiotic cellulolytic bacteria from the gut of the subterranean termite *Psammotermes hypostoma Desneux* and their role in cellulose digestion. AMB Express 9(1):1–9

Angelidaki I, Treu L, Tsapekos P, Luo G, Campanaro S, Wenzel H, Kougias PG (2018) Biogas upgrading and utilization: Current status and perspectives. Biotechnol Adv 36(2):452–466

Anukam US, Ogbulie JN, Akujuobi C, Braide W (2020) Isolation of high lignolytic bacteria from Termites's gut as potential booster in for enhanced biogas production. Biotechnol J Int 5:19–23

Appel HM (2017) The chewing herbivore gut lumen: physicochemical conditions and their impact on plant nutrients, allelochemicals, and insect pathogens. In: Insect-plant interactions, pp 209–224. CRC Press

Arfah RA, Natsir H, Atifah N, Zarkoni TR, Mahmud M (2019) Isolation and characterization of Soil Termites (*Macrotermes gilvus*) cellulolytic bacteria and activity determination of cellulase enzyme on newsprint substrates. J Phys Conf Ser 1341(3):032037

Atelge MR, Atabani AE, Banu JR, Krisa D, Kaya M, Eskicioglu C, Kumar G, Lee C, Yildiz YŞ, Unalan SEBAHATTİN, Mohanasundaram R (2020) A critical review of pretreatment technologies to enhance anaerobic digestion and energy recovery. Fuel 270:117494

Azizah P, Wiyono HT, Muzakhar K (2020) Morphological and biochemical characteristic of endosymbiont cellulolytic bacteria from gut of *Hypothenemus hampei* Ferr. and its enzyme activity. AIP Conf Proc 2296(1):020013

Baharuddin M, Ahmad A, La Nafie N, Zenta F (2016) Cellulase enzyme activity of *Bacillus circulans* from larvae *Cossus cossus* in lignocellulosic substrate. Am J Biomed Life Sci 4(2):21–25

Banerjee S, Maiti TK, Roy RN (2021) Enzyme producing insect gut microbes: an unexplored biotechnological aspect. Crit Rev Biotechnol. https://doi.org/10.1080/07388551.2021.1942777

Banerjee S, Maiti TK, Roy RN (2016) Identification and product optimization of amylolytic *Rhodococcus opacus* GAA 31.1 isolated from gut of *Gryllotalpa africana*. J Genetic Eng Biotechnol 14(1):133

Banerjee S, Maiti TK, Roy RN (2020) Production, purification, and characterization of cellulase from *Acinetobacter junii* GAC 16.2, a novel cellulolytic gut isolate of *Gryllotalpa africana*, and its effects on cotton fiber and sawdust. Ann Microbiol 70(1):1–16

Banerjee S, Maiti TK, Roy RN (2017) Protease production by thermo-alkaliphilic novel gut isolate *Kitasatospora cheerisanensis* GAP 12.4 from *Gryllotalpa africana*. Biocatal Biotransform 35(3):168–176

Banerjee S, Mandal NC (2020) Fungal Bioagents in the remediation of degraded soils. In: Microbial services in restoration ecology, pp 191–205. Elsevier

Banu JR, Kannah RY, Kavitha S, Gunasekaran M, Yeom IT, Kumar G (2018) Disperser-induced bacterial disintegration of partially digested anaerobic sludge for efficient biomethane recovery. Chem Eng J 347:165–172

Barbosa KL, dos Santos Malta VR, Machado SS, Junior GAL, da Silva APV, Almeida RMRG, da Luz JMR (2020) Bacterial cellulase from the intestinal tract of the sugarcane borer. Int J Biol Macromol 161:441–448

Barua VB, Goud VV, Kalamdhad AS (2018) Microbial pretreatment of water hyacinth for enhanced hydrolysis followed by biogas production. Renew Energy 126:21–29

Bashir Z, Kondapalli VK, Adlakha N, Sharma A, Bhatnagar RK, Chandel G, Yazdani SS (2013) Diversity and functional significance of cellulolytic microbes living in termite, pill-bug and stem-borer guts. Sci Rep 3(1):1–11

Bayané A, Guiot SR (2011) Animal digestive strategies versus anaerobic digestion bioprocesses for biogas production from lignocellulosic biomass. Rev Environ Sci Bio/technol 10(1):43–62

Bayon C, Etiévant P (1980) Methanic fermentation in the digestive tract of a xylophagous insect: *Oryctes nasicornis* L. larva (Coleoptera; Scarabaeidae). Experientia 36(2):154–155

Bernays EA, Chapman RF (2007) Host-plant selection by phytophagous insects, vol 2. Springer, Berlin

Bhatt AH, Tao L (2020) Economic perspectives of biogas production via anaerobic digestion. Bioengineering 7(3):74

Bhuyan PM, Sandilya SP, Nath PK, Gandotra S, Subramanian S, Kardong D, Gogoi DK (2018) Optimization and characterization of extracellular cellulase produced by *Bacillus pumilus* MGB05 isolated from midgut of muga silkworm (*Antheraea assamensis Helfer*). J Asia-Pacific Entomol 21(4):1171–1181

Biswas S, Paul D, Bhattacharjee A (2019) Isolation and identification of cellulose degrading bacteria from gut of two herbivorous pest larvae. The NEHU J 50:1098

Breznak JA, Brune A (1994) Role of microorganisms in the digestion of lignocellulose by termites. Annu Rev Entomol 39(1):453–487

Briones-Roblero CI, Rodríguez-Díaz R, Santiago-Cruz JA, Zúñiga G, Rivera-Orduña FN (2017) Degradation capacities of bacteria and yeasts isolated from the gut of *Dendroctonus rhizophagus* (Curculionidae: Scolytinae). Folia Microbiol 62(1):1–9

Brodeur G, Yau E, Badal K, Collier J, Ramachandran KB, Ramakrishnan S (2011) Chemical and physicochemical pretreatment of lignocellulosic biomass: a review. Enzyme Res 2011:1–17

Brown ME, Chang MC (2014) Exploring bacterial lignin degradation. Curr Opin Chem Biol 19:1–7

Campanaro S, Treu L, Kougias PG, Luo G, Angelidaki I (2018) Metagenomic binning reveals the functional roles of core abundant microorganisms in twelve full-scale biogas plants. Water Res 140:123–134

Cazemier AE (1999) (Hemi) cellulose degradation by microorganisms from the intestinal tract of arthropods. [Sl: sn]

Chan YH, Yusup S, Quitain AT, Tan RR, Sasaki M, Lam HL, Uemura Y (2015) Effect of process parameters on hydrothermal liquefaction of oil palm biomass for bio-oil production and its life cycle assessment. Energy Convers Manag 104:180–188

Chandra RP, Arantes V, Saddler J (2015) Steam pretreatment of agricultural residues facilitates hemicellulose recovery while enhancing enzyme accessibility to cellulose. Biores Technol 185:302–307

Chang YC, Choi D, Takamizawa K, Kikuchi S (2014) Isolation of *Bacillus* sp. strains capable of decomposing alkali lignin and their application in combination with lactic acid bacteria for enhancing cellulase performance. Biores Technol 152:429–436

Chaturvedi V, Verma P (2013) An overview of key pretreatment processes employed for bioconversion of lignocellulosic biomass into biofuels and value added products. 3 Biotech 3(5):415–431

Chen H, Liu J, Chang X, Chen D, Xue Y, Liu P, Lin H, Han S (2017) A review on the pretreatment of lignocellulose for high-value chemicals. Fuel Process Technol 160:196–206

Choi JM, Han SS, Kim HS (2015) Industrial applications of enzyme biocatalysis: current status and future aspects. Biotechnol Adv 33(7):1443–1454

Cibichakravarthy B, Abinaya S, Prabagaran SR (2017) Syntrophic association of termite gut bacterial symbionts with bifunctional characteristics of cellulose degrading and polyhydroxyalkanoate producing bacteria. Int J Biol Macromol 103:613–620

Crotti E, Rizzi A, Chouaia B, Ricci I, Favia G, Alma A, Sacchi L, Bourtzis K, Mandrioli M, Cherif A, Bandi C (2010) Acetic acid bacteria, newly emerging symbionts of insects. Appl Environ Microbiol 76(21):6963–6970

Dantur KI, Enrique R, Welin B, Castagnaro AP (2015) Isolation of cellulolytic bacteria from the intestine of *Diatraea saccharalis* larvae and evaluation of their capacity to degrade sugarcane biomass. AMB Express 5(1):1–11

da Silva Paulo RN, Vieira AVG, Rodrigues P (2021) Evaluation of biogas production through anaerobic digestion of aquatic macrophytes in a Brazilian reservoir. J Energy Res Rev 18:1–14

Dar MA, Shaikh AF, Pawar KD, Xie R, Sun J, Kandasamy S, Pandit RS (2021) Evaluation of cellulose degrading bacteria isolated from the gut-system of cotton bollworm, *Helicoverpa armigera* and their potential values in biomass conversion. Peer J 9:e11254

de Gonzalo G, Colpa DI, Habib MH, Fraaije MW (2016) Bacterial enzymes involved in lignin degradation. J Biotechnol 236:110–119

de Lima Brossi MJ, Jiménez DJ, Cortes-Tolalpa L, van Elsas JD (2016) Soil-derived microbial consortia enriched with different plant biomass reveal distinct players acting in lignocellulose degradation. Microb Ecol 71(3):616–627

Dehghanikhah F, Shakarami J, Asoodeh A (2020) Purification and biochemical characterization of alkalophilic cellulase from the symbiotic *Bacillus subtilis* BC1 of the leopard Moth, *Zeuzera pyrina* (L) (Lepidoptera: Cossidae). Curr Microbiol 77(7):1254–1261

Divya D, Gopinath LR, Christy PM (2015) A review on current aspects and diverse prospects for enhancing biogas production in sustainable means. Renew Sustain Energy Rev 42:690–699

Douglas AE (1992) Microbial brokers of insect-plant interactions. In: Proceedings of the 8th international symposium on insect-plant relationships, pp 329–336. Springer, Dordrecht

Edwiges T, Frare L, Mayer B, Lins L, Triolo JM, Flotats X, de Mendonça Costa MSS (2018) Influence of chemical composition on biochemical methane potential of fruit and vegetable waste. Waste Manag 71:618–625

Engel P, Martinson VG, Moran NA (2012) Functional diversity within the simple gut microbiota of the honey bee. Proc Natl Acad Sci 109(27):11002–11007

Femi-Ola TO, Oyebamiji BA (2019) Molecular characterization and cellulolytic activities of bacterial isolates from the hindgut of wood-feeding termites *Amitermes evuncifer Silvestri*. J Adv Microbiol 22:1–10

Fox-Dobbs K, Doak DF, Brody AK, Palmer TM (2010) Termites create spatial structure and govern ecosystem function by affecting N2 fixation in an East African savanna. Ecology 91(5):1296–1307

Fukui T, Kawamoto M, Shoji K, Kiuchi T, Sugano S, Shimada T, Suzuki Y, Katsuma S (2015) The endosymbiotic bacterium *Wolbachia* selectively kills male hosts by targeting the masculinizing gene. PLoS Pathogens 11(7):e1005048

Gales A, Chatellard L, Abadie M, Bonnafous A, Auer L, Carrère H, Godon JJ, Hernandez-Raquet G, Dumas C (2018) Screening of phytophagous and xylophagous insects guts microbiota abilities to degrade lignocellulose in bioreactor. Front Microbiol 9:2222

Gunnarsson CC, Petersen CM (2007) Water hyacinths as a resource in agriculture and energy production: a literature review. Waste Manage 27(1):117–129

Guo M, Song W, Buhain J (2015) Bioenergy and biofuels: history, status, and perspective. Renew Sustain Energy Rev 42:712–725

Haider MR, Yousaf S, Malik RN, Visvanathan C (2015) Effect of mixing ratio of food waste and rice husk co-digestion and substrate to inoculum ratio on biogas production. Biores Technol 190:451–457

Hasegawa S, Shiota N, Katsura K, Akashi A (2000) Solubilization of organic sludge by thermophilic aerobic bacteria as a pretreatment for anaerobic digestion. Water Sci Echnol 41(3):163–169

Hatakka A (1994) Lignin-modifying enzymes from selected white-rot fungi: production and role from in lignin degradation. FEMS Microbiol Rev 13(2–3):125–135

Hatefi A, Makhdoumi A, Asoodeh A, Mirshamsi O (2017) Characterization of a bi-functional cellulase produced by a gut bacterial resident of Rosaceae branch borer beetle, *Osphranteria coerulescens* (Coleoptera: Cerambycidae). Int J Biol Macromol 103:158–164

Hayashi A, Aoyagi H, Yoshimura T, Tanaka H (2007) Development of novel method for screening microorganisms using symbiotic association between insect (*Coptotermes formosanus Shiraki*) and intestinal microorganisms. J Biosci Bioeng 103(4):358–367

Heng KS, Hatti-Kaul R, Adam F, Fukui T, Sudesh K (2017) Conversion of rice husks to polyhydroxyalkanoates (PHA) via a three-step process: optimized alkaline pretreatment, enzymatic hydrolysis, and biosynthesis by *Burkholderia cepacia* USM (JCM 15050). J Chem Technol Biotechnol 92(1):100–108

Hernández-Beltrán JU, Lira HD, Omar I, Cruz-Santos MM, Saucedo-Luevanos A, Hernández-Terán F, Balagurusamy N (2019) Insight into pretreatment methods of lignocellulosic biomass to increase biogas yield: current state, challenges, and opportunities. Appl Sci 9(18):3721

Heyer R, Schallert K, Siewert C, Kohrs F, Greve J, Maus I, Klang J, Klocke M, Heiermann M, Hoffmann M, Püttker S (2019) Metaproteome analysis reveals that syntrophy, competition, and phage-host interaction shape microbial communities in biogas plants. Microbiome 7(1):1–17

Howard RL, Abotsi ELJR, Van Rensburg EJ, Howard S (2003) Lignocellulose biotechnology: issues of bioconversion and enzyme production. Afr J Biotech 2(12):602–619

Huang SW, Zhang HY, Marshall S, Jackson TA (2010) The scarab gut: a potential bioreactor for bio-fuel production. Insect Science 17(3):175–183

Industrial enzymes market by type (carbohydrases, proteases, non-starch polysaccharides & others), application (food &beverage, cleaning agents, animal feed & others), brands & by region global trends and forecasts to 2026. https://www.marketsandmarkets.com/Market-Reports/industrial-enzymes-market-237327836.html. Accessed 02 Dec 2021

Javaheri-Kermani M, Asoodeh A (2019) A novel beta-1, 4 glucanase produced by symbiotic *Bacillus* sp. CF96 isolated from termite (*Anacanthotermes* sp.). Int J Biol Macromol 131:752–759

Jing TZ, Qi FH, Wang ZY (2020) Most dominant roles of insect gut bacteria: digestion, detoxification, or essential nutrient provision? Microbiome 8(1):1–20

Joynson R, Pritchard L, Osemwekha E, Ferry N (2017) Metagenomic analysis of the gut microbiome of the common black slug *Arion ater* in search of novel lignocellulose degrading enzymes. Front Microbiol 8:2181

Kalyani D, Lee KM, Kim TS, Li J, Dhiman SS, Kang YC, Lee JK (2013) Microbial consortia for saccharification of woody biomass and ethanol fermentation. Fuel 107:815–822

Karimi K, Taherzadeh MJ (2016) A critical review of analytical methods in pretreatment of lignocelluloses: composition, imaging, and crystallinity. Biores Technol 200:1008–1018

Kaur M, Srikanth S, Kumar M, Sachdeva S, Puri SK (2019) An integrated approach for efficient conversion of *Lemna minor* to biogas. Energy Convers Manag 180:25–35

Kavitha S, Gopinath LR, Christy PM (2014) Isolation of methanogens from termite gut and its role in biogas production by using poultry waste. Int J Plant Anim Environ Sci 4(4):281–286

Khan FA, Anis SB, Badruddin SMA (2010) Plant defenses against insect herbivory. Integr Manag Arthropod Pests Insect Borne Dis 9:189–208

Kim M, Day DF (2011) Composition of sugar cane, energy cane, and sweet sorghum suitable for ethanol production at Louisiana sugar mills. J Ind Microbiol Biotechnol 38(7):803–807

Koo T, Yulisa A, Hwang S (2019) Microbial community structure in full scale anaerobic mono-and co-digesters treating food waste and animal waste. Biores Technol 282:439–446

Kudo R, Masuya H, Endoh R, Kikuchi T, Ikeda H (2019) Gut bacterial and fungal communities in ground-dwelling beetles are associated with host food habit and habitat. ISME J 13(3):676–685

Kumar G, Dharmaraja J, Arvindnarayan S, Shoban S, Bakonyi P, Saratale GD, Nemestóthy N, Bélafi-Bakó K, Yoon JJ, Kim SH (2019) A comprehensive review on thermochemical, biological, biochemical and hybrid conversion methods of bio-derived lignocellulosic molecules into renewable fuels. Fuel 251:352–367

Kumari D, Singh R (2018) Pretreatment of lignocellulosic wastes for biofuel production: a critical review. Renew Sustain Energy Rev 90:877–891

Kurakake M, Ide N, Komaki T (2007) Biological pretreatment with two bacterial strains for enzymatic hydrolysis of office paper. Curr Microbiol 54(6):424–428

LaBelle C (2018) Therapeutic play workshops christine LaBelle and Korinna Locke Lasell College April 10

Li S, Yang X, Yang S, Zhu M, Wang X (2012) Technology prospecting on enzymes: application, marketing and engineering. Comput Struct Biotechnol J 2(3):e201209017

Li F, Zhang M, Guo K, Hu Z, Zhang R, Feng Y, Yi X, Zou W, Wang L, Wu C, Tian J (2015) High-level hemicellulosic arabinose predominately affects lignocellulose crystallinity for genetically enhancing both plant lodging resistance and biomass enzymatic digestibility in rice mutants. Plant Biotechnol J 13(4):514–525

Li P, He C, Li G, Ding P, Lan M, Gao Z, Jiao Y (2020) Biological pretreatment of corn straw for enhancing degradation efficiency and biogas production. Bioengineered 11(1):251–260

Li Y, Lei L, Zheng L, Xiao X, Tang H, Luo C (2020) Genome sequencing of gut symbiotic *Bacillus velezensis* LC1 for bioethanol production from bamboo shoots. Biotechnol Biofuels 13(1):1–12

Liang X, Sun C, Chen B, Du K, Yu T, Luang-In V, Lu X, Shao Y (2018) Insect symbionts as valuable grist for the biotechnological mill: an alkaliphilic silkworm gut bacterium for efficient lactic acid production. Appl Microbiol Biotechnol 102(11):4951–4962

Lugani Y, Singh J, Sooch BS (2021) Scale-up process for xylose reductase production using rice straw hydrolysate. Biomass Convers Biorefinery 29:1–2

Luo C, Li Y, Chen Y, Fu C, Long W, Xiao X, Liao H, Yang Y (2019) Bamboo lignocellulose degradation by gut symbiotic microbiota of the bamboo snout beetle *Cyrtotrachelus buqueti*. Biotechnol Biofuels 12(1):1–16

Lysenko O (1985) Non-sporeforming bacteria pathogenic to insects: incidence and mechanisms. Annu Rev Microbiol 39(1):673–695

Ma S, Jiang F, Huang Y, Zhang Y, Wang S, Fan H, Liu B, Li Q, Yin L, Wang H, Liu H (2021) A microbial gene catalog of anaerobic digestion from full-scale biogas plants. GigaScience 10(1):giaa164

Mata-Alvarez J, Dosta J, Romero-Güiza MS, Fonoll X, Peces M, Astals S (2014) A critical review on anaerobic co-digestion achievements between 2010 and 2013. Renew Sustain Energy Rev 36:412–427

Mohammed D, Abdelaziz M, Sidi A, Mohammed E, Elmostapha E (2019) Wind speed data and wind energy potential using Weibull distribution in Zagora, Morocco. Int J Renew Energy Dev 8(3):267–273

Moran NA, Telang A (1998) Bacteriocyte-associated symbionts of insects. Bioscience 48(4):295–304

Morrison M, Pope PB, Denman SE, McSweeney CS (2009) Plant biomass degradation by gut microbiomes: more of the same or something new? Curr Opin Biotechnol 20(3):358–363

Mosier N, Wyman C, Dale B, Elander R, Lee YY, Holtzapple M, Ladisch M (2005) Features of promising technologies for pretreatment of lignocellulosic biomass. Biores Technol 96(6):673–686

Mund NK, Dash D, Mishra P, Nayak NR (2021) Cellulose solvent–based pretreatment and enzymatic hydrolysis of pineapple leaf waste biomass for efficient release of glucose towards biofuel production. Biomass Convers Biorefinery 3:1–10

Mwirigi J, Balana BB, Mugisha J, Walekhwa P, Melamu R, Nakami S, Makenzi P (2014) Socio-economic hurdles to widespread adoption of small-scale biogas digesters in Sub-Saharan Africa: a review. Biomass Bioenerg 70:17–25

Naik L, Gebreegziabher Z, Tumwesige V, Balana BB, Mwirigi J, Austin G (2014) Factors determining the stability and productivity of small scale anaerobic digesters. Biomass Bioenerg 70:51–57

Nanda S, Azargohar R, Dalai AK, Kozinski JA (2015) An assessment on the sustainability of lignocellulosic biomass for biorefining. Renew Sustain Energy Rev 50:925–941

Nanda S, Mohanty P, Pant KK, Naik S, Kozinski JA, Dalai AK (2013) Characterization of North American lignocellulosic biomass and biochars in terms of their candidacy for alternate renewable fuels. Bioenergy Res 6(2):663–677

Negi GC, Sharma S, Vishvakarma SC, Samant SS, Maikhuri RK, Prasad RC, Palni LM (2019) Ecology and use of *Lantana camara* in India. Bot Rev 85(2):109–130

Niu Q, Zhang G, Zhang L, Ma Y, Shi Q, Fu W (2016) Purification and characterization of a thermophilic 1, 3–1, 4-β-glucanase from *Bacillus methylotrophicus* S2 isolated from booklice. J Biosci Bioeng 121(5):503–508

Palmowski LM, Müller JA (2000) Influence of the size reduction of organic waste on their anaerobic digestion. Water Sci Technol 41(3):155–162

Pandey A, Biswas S, Sukumaran RK, Kaushik N (2009) Study on availability of Indian biomass resources for exploitation: a report based on a nation-wise survey. In: TIFAC, New Delhi, vol 105

Pandiarajan J, Revathy K (2020) Cellulolytic potential of gut bacterial biomass in silkworm *Bombyx mori*. L. Ecol Genet Genom 14:100045

Patinvoh RJ, Osadolor OA, Chandolias K, Horváth IS, Taherzadeh MJ (2017) Innovative pretreatment strategies for biogas production. Biores Technol 224:13–24

Porichha GK, Hu Y, Rao KTV, Xu CC (2021) Crop residue management in India: stubble burning vs. other utilizations including. Bioenergy Energies 14(14):4281

Prasad RK, Chatterjee S, Mazumder PB, Sharma S, Datta S, Vairale MG, Dwivedi SK (2019) Study on cellulase (Β-1, 4-endoglucanase) activity of gut bacteria of *Sitophilus oryzae* in cellulosic waste biodegradation. Bioresour Technol Rep 7:100274

Prem Anand AA, Vennison SJ, Sankar SG, Gilwax Prabhu DI, Vasan PT, Raghuraman T, Jerome Geoffrey C, Vendan SE (2010) Isolation and characterization of bacteria from the gut of *Bombyx mori* that degrade cellulose, xylan, pectin and starch and their impact on digestion. J Insect Sci 10(1):107

Reshamwala S, Shawky BT, Dale BE (1995) Ethanol production from enzymatic hydrolysates of AFEX-treated coastal bermudagrass and switchgrass. Appl Biochem Biotechnol 51(1):43–55

Robles G, Nair RB, Kleinsteuber S, Nikolausz M, Horváth IS (2018) Biogas production: microbiological aspects. In: Biogas, pp 163–198. Springer, Cham

Saini JK, Saini R, Tewari L (2015) Lignocellulosic agriculture wastes as biomass feedstocks for second-generation bioethanol production: concepts and recent developments. 3 Biotech 5(4):337–353

Salem H, Bauer E, Strauss AS, Vogel H, Marz M, Kaltenpoth M (2014) Vitamin supplementation by gut symbionts ensures metabolic homeostasis in an insect host. Proc R Soc B Biol Sci 281(1796):20141838

Schnürer A (2016) Biogas production: microbiology and technology. Anaerobes Biotechnol 2:195–234

Scully ED, Geib SM, Hoover K, Tien M, Tringe SG, Barry KW, Glavina del Rio T, Chovatia M, Herr JR, Carlson JE (2013) Metagenomic profiling reveals lignocellulose degrading system in a microbial community associated with a wood-feeding beetle. PloS one 8(9):e73827

Sepehri A, Sarrafzadeh MH, Avateffazeli M (2020) Interaction between *Chlorella vulgaris* and nitrifying-enriched activated sludge in the treatment of wastewater with low C/N ratio. J Clean Prod 247:119164

Shah FA, Mahmood Q, Rashid N, Pervez A, Raja IA, Shah MM (2015) Co-digestion, pretreatment and digester design for enhanced methanogenesis. Renew Sustain Energy Rev 42:627–642

Shankar T, Sankaralingam S, Balachandran C, Chinnathambi A, Nasif O, Alharbi SA, Park S, Baskar K (2021) Purification and characterization of carboxymethylcellulase from *Bacillus pumilus* EWBCM1 isolated from earthworm gut (*Eudrilus eugeniae*). J King Saud Univ Sci 33(1):101261

Sharma S, Prasad RK, Chatterjee S, Sharma A, Vairale MG, Yadav KK (2019) Characterization of *Bacillus* species with keratinase and cellulase properties isolated from feather dumping soil and cockroach gut. Proc Natl Acad Sci India Sect B Biol Sci 89(3):1079–1086

Sheng P, Huang S, Wang Q, Wang A, Zhang H (2012) Isolation, screening, and optimization of the fermentation conditions of highly cellulolytic bacteria from the hindgut of *Holotrichia parallela* larvae (Coleoptera: Scarabaeidae). Appl Biochem Biotechnol 167(2):270–284

Shrestha S, Fonoll X, Khanal SK, Raskin L (2017) Biological strategies for enhanced hydrolysis of lignocellulosic biomass during anaerobic digestion: current status and future perspectives. Biores Technol 245:1245–1257

Sindhu R, Binod P, Pandey A (2016) Biological pretreatment of lignocellulosic biomass–an overview. Biores Technol 199:76–82

Singh P, Suman A, Tiwari P, Arya N, Gaur A, Shrivastava AK (2008) Biological pretreatment of sugarcane trash for its conversion to fermentable sugars. World J Microbiol Biotechnol 24(5):667–673

Sinha D, Banerjee S, Mandal S, Basu A, Banerjee A, Balachandran S, Mandal NC, Chaudhury S (2021) Enhanced biogas production from *Lantana camara* via bioaugmentation of cellulolytic bacteria. Bioresour Technol 340:125652

Somerville C, Bauer S, Brininstool G, Facette M, Hamann T, Milne J, Osborne E, Paredez A, Persson S, Raab T, Vorwerk S (2004) Toward a systems approach to understanding plant cell walls. Science 306(5705):2206–2211

Sreena CP, Resna NK, Sebastian D (2015) Isolation and characterization of cellulase producing bacteria from the gut of termites (*Odontotermes* and *Heterotermes* species). Biotechnol J Int 9:1–10

Stolze Y, Zakrzewski M, Maus I, Eikmeyer F, Jaenicke S, Rottmann N, Siebner C, Pühler A, Schlüter A (2015) Comparative metagenomics of biogas-producing microbial communities from production-scale biogas plants operating under wet or dry fermentation conditions. Biotechnol Biofuels 8(1):1–18

Sträuber H, Lucas R, Kleinsteuber S (2016) Metabolic and microbial community dynamics during the anaerobic digestion of maize silage in a two-phase process. Appl Microbiol Biotechnol 100(1):479–491

Surabhi K, Rangeshwaran R, Frenita ML, Shylesha AN, Jagadeesh P (2018) Isolation and characterization of the culturable microbes associated with gut of adult dung beetle *Onitis philemon* (Fabricius). J Pharmacogn Phytochem 7(2):1609–1614

Tanada Y, Kaya HK (1993) Associations between insects and nonpathogenics microorganisms. Insect Pathol 6:12–51

Thapa S, Mishra J, Arora N, Mishra P, Li H, O'Hair J, Bhatti S, Zhou S (2020) Microbial cellulolytic enzymes: diversity and biotechnology with reference to lignocellulosic biomass degradation. Rev Environ Sci Bio/Technol 19:621–48

Theuerl S, Klang J, Heiermann M, De Vrieze J (2018) Marker microbiome clusters are determined by operational parameters and specific key taxa combinations in anaerobic digestion. Biores Technol 263:128–135

Tsegaye B, Balomajumder C, Roy P (2019) Isolation and characterization of novel lignolytic, cellulolytic, and hemicellulolytic bacteria from wood-feeding termite *Cryptotermes brevis*. Int Microbiol 22(1):29–39

Veluchamy C, Kalamdhad AS (2017) Influence of pretreatment techniques on anaerobic digestion of pulp and paper mill sludge: a review. Biores Technol 245:1206–1219

Vidmar B, Fanedl L, Logar RM, Panjičko M (2017) Influence of thermal and bacterial pretreatment of microalgae on biogas production in mesophilic and thermophilic conditions. Acta Chim Slov 64(1):227–236

Vilanova C, Marco G, Domínguez-Escribà L, Genovés S, Sentandreu V, Bataller E, Ramón D, Porcar M (2012) Bacteria from acidic to strongly alkaline insect midguts: potential sources of extreme cellulolytic enzymes. Biomass Bioenerg 45:288–294

Wang L, Feng Y, Tian J, Xiang M, Sun J, Ding J, Yin WB, Stadler M, Che Y, Liu X (2015) Farming of a defensive fungal mutualist by an attelabid weevil. ISME J 9(8):1793–1801

Wang Y, Liu Q, Yan L, Gao Y, Wang Y, Wang W (2013) A novel lignin degradation bacterial consortium for efficient pulping. Biores Technol 139:113–119

Watanabe H, Noda H, Tokuda G, Lo N (1998) A cellulase gene of termite origin. Nature 394(6691):330–331

Wier A, Dolan M, Grimaldi D, Guerrero R, Wagensberg J, Margulis L (2002) Spirochete and protist symbionts of a termite (*Mastotermes electrodominicus*) in Miocene amber. Proc Natl Acad Sci 99(3):1410–1413

Wiseman A (1995) Introduction to principles. In: Wiseman A (ed) Handbook of enzyme biotechnology. Padstow, New York

Woiciechowski AL, Neto CJD, de Souza Vandenberghe LP, de Carvalho Neto DP, Sydney ACN, Letti LAJ, Karp SG, Torres LAZ, Soccol CR (2020) Lignocellulosic biomass: acid and alkaline pretreatments and their effects on biomass recalcitrance–conventional processing and recent advances. Bioresour Technol 304:122848

Xiao X, Mazza L, Yu Y, Cai M, Zheng L, Tomberlin JK, Yu J, van Huis A, Yu Z, Fasulo S, Zhang J (2018) Efficient co-conversion process of chicken manure into protein feed and organic fertilizer by *Hermetia illucens* L.(Diptera: Stratiomyidae) larvae and functional bacteria. J Environ Manage 217:668–676

Xie S, Lan Y, Sun C, Shao Y (2019) Insect microbial symbionts as a novel source for biotechnology. World J Microbiol Biotechnol 35(2):25

Yan X, Wang Z, Zhang K, Si M, Liu M, Chai L, Liu X, Shi Y (2017) Bacteria-enhanced dilute acid pretreatment of lignocellulosic biomass. Biores Technol 245:419–425

Yang J, Yang Y, Wu WM, Zhao J, Jiang L (2014) Evidence of polyethylene biodegradation by bacterial strains from the guts of plastic-eating waxworms. Environ Sci Technol 48(23):13776–13784

Yang L, Xu F, Ge X, Li Y (2015) Challenges and strategies for solid-state anaerobic digestion of lignocellulosic biomass. Renew Sustain Energy Rev 44:824–834

Yun JH, Roh SW, Whon TW, Jung MJ, Kim MS, Park DS, Yoon C, Nam YD, Kim YJ, Choi JH, Kim JY (2014) Insect gut bacterial diversity determined by environmental habitat, diet, developmental stage, and phylogeny of host. Appl Environ Microbiol 80(17):5254–5264

Zakrzewski M, Goesmann A, Jaenicke S, Jünemann S, Eikmeyer F, Szczepanowski R, Al-Soud WA, Sørensen S, Pühler A, Schlüter A (2012) Profiling of the metabolically active community from a production-scale biogas plant by means of high-throughput metatranscriptome sequencing. J Biotechnol 158(4):248–258

Zhang Q, He J, Tian M, Mao Z, Tang L, Zhang J, Zhang H (2011) Enhancement of methane production from cassava residues by biological pretreatment using a constructed microbial consortium. Biores Technol 102(19):8899–8906

Zhang Q, Hu J, Lee DJ (2017) Pretreatment of biomass using ionic liquids: research updates. Renew Energy 111:77–84

Zhang Q, Zhang J, Zhao S, Song P, Chen Y, Liu P, Mao C, Li X (2021) Enhanced biogas production by ligninolytic strain *Enterobacter hormaechei* KA3 for anaerobic digestion of corn straw. Energies 14(11):2990

Zhong W, Zhang Z, Luo Y, Sun S, Qiao W, Xiao M (2011) Effect of biological pretreatments in enhancing corn straw biogas production. Biores Technol 102(24):11177–11182

Zhu X, Campanaro S, Treu L, Kougias PG, Angelidaki I (2019) Novel ecological insights and functional roles during anaerobic digestion of saccharides unveiled by genome-centric metagenomics. Water Res 151:271–279

Zhu X, Campanaro S, Treu L, Seshadri R, Ivanova N, Kougias PG, Kyrpides N, Angelidaki I (2020) Metabolic dependencies govern microbial syntrophies during methanogenesis in an anaerobic digestion ecosystem. Microbiome 8(1):1–14

Zhuo S, Yan X, Liu D, Si M, Zhang K, Liu M, Peng B, Shi Y (2018) Use of bacteria for improving the lignocellulose biorefinery process: importance of pre-erosion. Biotechnol Biofuels 11(1):1–13

Ziels RM, Svensson BH, Sundberg C, Larsson M, Karlsson A, Yekta SS (2018) Microbial rRNA gene expression and co-occurrence profiles associate with biokinetics and elemental composition in full-scale anaerobic digesters. Microb Biotechnol 11(4):694–709