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MINI-REVIEW

Biotechnological utilization of animal gut microbiota for valorization of lignocellulosic biomass

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Abstract

The aim of this review is to give a summary of natural lignocellulose-degrading systems focusing mainly on animal digestive tracts of wood-feeding insects and ruminants in order to find effective strategies that can be applied to improve anaerobic digestion processes in engineered systems. Wood-feeding animals co-evolved with symbiotic microorganisms to digest lignocellulose-rich biomass in a very successful way. Considering the similarities between these animal gut systems and the lignocellulose-based biotechnological processes, the gut with its microbial consortium can be a perfect model for an advanced lignocellulose-degrading biorefinery. The physicochemical properties and structure of the gut may provide a scheme for the process design, and the microbial consortium may be applied as genetic resource for the up-scaled bioreactor communities. Manipulation of the gut microbiota is also discussed in relation to the management of the reactor communities.

Keywords Biomimicry · Anaerobic digestion · Biorefinery · Gut · Microbiota · Lignocellulose · Bioaugmentation

Introduction

In order to mitigate global climate issues caused by increasing anthropogenic greenhouse gas (GHG) emissions, fossil energy carrier consumptions must be drastically reduced and organic municipal, agricultural, and agro-industrial wastes should be properly treated (Aguirre-Villegas and Larson 2017; Aneja et al. 2009; Bogner et al. 2008). Utilization of plant biomass for both material and energetic use can be considered an important strategy to contribute to these aims, but further improvements of the current state of technology are necessary (Sawatdeenarunat et al. 2015). The major structural component of plant cells is lignocellulose, a complex matrix composed of cellulose (D-glucose homo-polysaccharide), hemicellulose (hetero-polysaccharide containing both C6 and C5 sugars, such as arabinose, galactose, glucose, mannose, and xylose, as well as their uronic acids), lignin (hetero-polymer of mainly aromatic compounds, such as *p*-coumaryl alcohol, coniferyl alcohol, and sinapyl alcohol), pectin (hetero-polysaccharide rich in galacturonic acid) and various minor components (proteins, terpenic oils, fatty acids, fatty acid esters, and inorganic components). For more details about the composition of lignocellulose, see the following references (Rubin 2008; Scharf and Tartar 2008). Annually, approximately 200 billion tons of lignocellulosic biomass is produced (da Silva et al. 2012) and a considerable part of it is treated as waste, such as agricultural wastes or green cuts from parks and gardens. Despite the energy potential conserved in the polysaccharide structure, the cost-effective utilization of lignocellulose is hampered by its recalcitrant nature. The plant cell-wall material has evolved complex structural and chemical mechanisms to withstand external digestion by microbes and animals, which makes the hydrolysis of these main biopolymers the rate-limiting step of biochemical conversion processes. Nature offers already successful and established systems that decompose dead plant material relatively fast, as a result of complex interactions of numerous bacteria, fungi, protists, and a variety of wood-feeding animals (Cragg et al. 2015). Compared to conventional anaerobic digesters, lignocellulosic biomass breakdown in rumen of cow is estimated to be three times more effective (Bayane and Guiot 2011). In the digestion system of wood-feeding termites, the rate of biomass biodegradation is even higher (Okwakol 1980). Therefore, more detailed knowledge on the digestion mechanisms of specific herbivores and the contribution of co-evolved microorganisms in their gut

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might be applied in the design of novel biorefinery concepts. Biomimicry or biomimetics is an emerging strategy studying the principles in biological systems that have been evolved over geological times to apply this knowledge to create novel technologies for the purpose of solving complex challenges (Dicks 2017; Vincent et al. 2006). The aim of this review is to give an overview of effective natural lignocellulose-degrading systems with high biotechnological application potentials in biorefineries focusing mainly on animal digestive tracts of wood-feeding insects and ruminants with a major focus on their symbiotic microbial partners. The potential utilization of such microbiota in engineered systems for biomass conversion will also be discussed. Besides biological treatment and enhancement options, the structure and physiology of the digestive tract of effective herbivorous animals may provide a better design for future lignocellulose-utilizing biorefinery systems. Due to the important role of the microbiota in nutrition and health of the host, potential manipulation of the microbial community has attracted lots of research in case of livestock animals. Management of bioreactor microbiota is similar in many aspects; therefore, the review will give also an overview on these topics.

Structural and functional differences between animal gut systems and biogas reactors

During evolution, animals developed highly sophisticated digestive systems to get maximum benefit from various food sources to gain energy, to sustain their lives, and to be successful in reproduction. These "ecosystem engineers" have completed the optimization period of the digestion process for all kinds of feedstock (Godon et al. 2013). Compared to the digestion systems in animals, human-engineered anaerobic digestion (AD) is a relatively new technology, which still deals with challenges especially regarding limited hydrolysis rates of lignocellulosic biomass.

In nature, there are many invertebrate (e.g., termites or some beetle larvae) and vertebrate animals (e.g., ruminants) that evolved digestive tracts having the ability to effectively degrade lignocellulosic substrates thanks to the specific structure and the symbiotic interactions with a wide variety of microorganisms colonizing the digestion tract (Auer et al. 2017; Bayane and Guiot 2011; Ozbayram et al. 2018d). The gut systems of these animals are considered as efficient bioreactors (Brune 2007). Furthermore, it is assumed that the smaller body size of the animals enables higher concentrations of cellulolytic enzymes contributing to faster degradation of these substrates.

Biomass digestion in insects highly depends on the symbiotic relationships with microorganisms, whereas the microorganisms provide various compounds, such as digestive enzymes and nutrients (amino acids, vitamins, etc.) (Andert et al. 2010; Berasategui et al. 2016). Members of the family *Scarabaeidae* (order *Coleoptera*) are abundant in grassland environments, and larvae of this family are mostly herbivorous and digest plant material very effectively (Huang et al. 2010). They have unique digestive tracts with three compartments: the first part is a foregut, the second part is a long midgut with alkaline conditions, and the third part is an expanded hindgut, also called paunch or fermentation chamber (Fig. 1a) (Engel and Moran 2013; Huang et al. 2010).

A considerable amount of energy is spent on chewing and grinding the food particles to smaller pieces to improve their digestibility. As part of the foregut, strong mandibles as well as a proventriculus region (also called gizzard) with teeth-like cuticle structures and a strongly developed muscle layer around it have been evolved for the more effective mechanical treatment/grinding of the plant biomass. The so-called crop is a flexible part of the foregut between the esophagus and the proventriculus, with the function of temporary storage. Another typical characteristic of the scarab larvae is a long midgut with high pH conditions and an expanded hindgut with lower pH environment. Such pH gradients play a role in the digestive process for effective decomposition and absorption of nutrients. The high pH in the midgut is a key driver for enhancing the solubility of various polymers, such as hemicellulose and lignin (Huang et al. 2010). Alkaline conditions of the midgut enable dissolution of lignin and de-esterification of intermolecular ester bonds, increase the surface area and porosity, and decrease crystallinity of the biomass (Kim et al. 2016). Rows of caeca circle the midgut tract with hypothesized functions related to digestion, nutrient and fluid reabsorption, and ion homeostasis. The entry of Malpighian tubes, which are involved in excretion and osmoregulation, marks the transition from midgut to hindgut. A highly muscular pyloric sphincter separates these two sections and enables the food transfer from midgut to hindgut (Huang et al. 2010). The dilated hindgut has lobe-like structures and is considered the main region for digestion of (hemi)celluloses. The pH of the lumen content is closer to neutral, but the redox potential is more negative compared to the midgut (Cazemier et al. 2003; Lemke et al. 2003) providing appropriate conditions even for methanogenesis. However, only the central part of the paunch is completely anoxic due to the oxygen diffusion through the epithelial tissue.

Termites and their evolutionary sister group, the cockroach family *Cryptocercidae*, have similar digestive systems and can digest wood effectively in their hindgut by cooperating with microbial symbionts (Bauer et al. 2015; Watanabe and Tokuda 2010). Generally, the digestive systems are composed of the mouth, esophagus, salivary glands, foregut, midgut, and hindgut. The mandibles are used to grind solid particles, and, according to the size of the animal, the mandible's size gets smaller from cockroaches to termites. Whereas lower termites and cockroaches have a large anterior part in the form of a

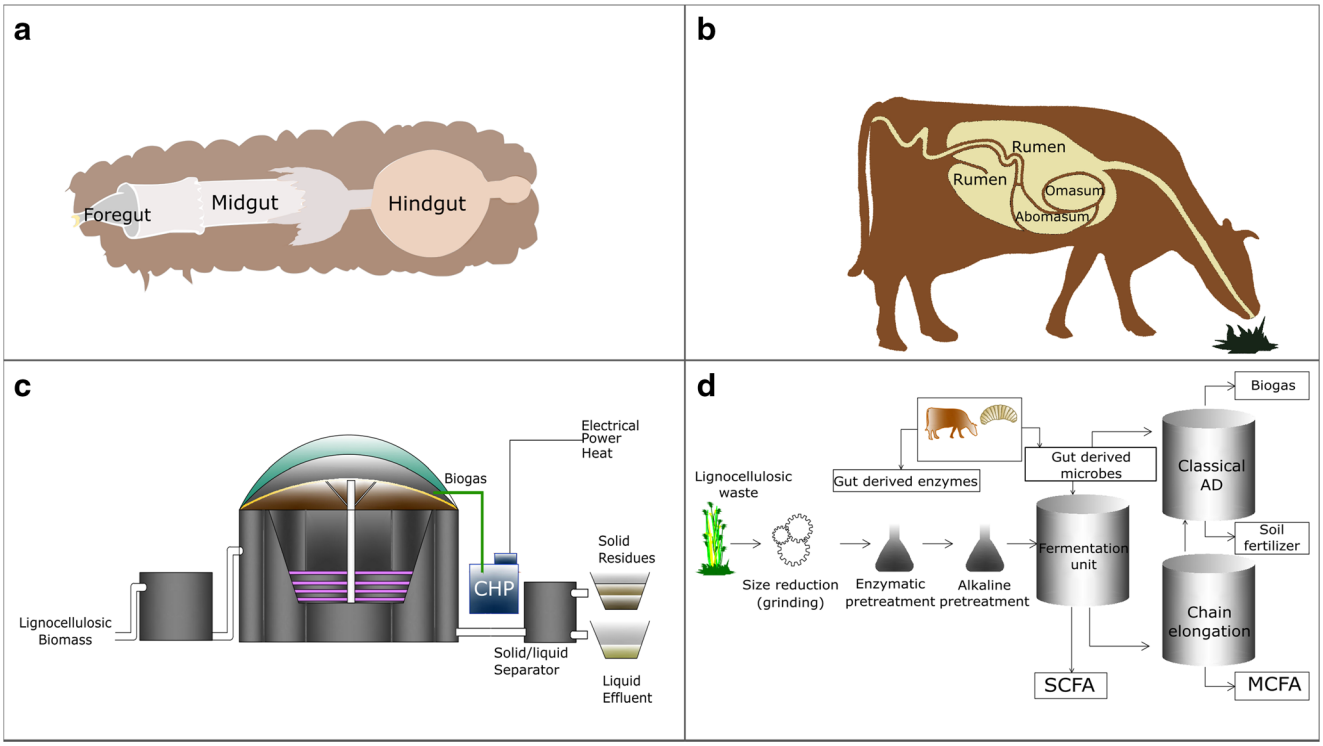

Fig. 1 Simplified schemes of (**a**) the gut of the sun beetle larva, (**b**) the gut of a ruminant represented by a cow, (**c**) a current biogas reactor digesting plant biomass, and (**d**) a future biorefinery based on the gut system of herbivorous animals. CHP, combined heat and power system; SCFAs, short-chain fatty acids; MCFAs, medium-chain fatty acids

crop in their foreguts, higher termites have a reduced crop. The volume of the midgut in termites is smaller compared to that of cockroaches. Moreover, cockroaches have bigger gastric ceca in the anterior midgut than lower termites. In cockroaches, the hindgut is divided into two compartments, namely ileum and rectum. However, termites have more specialized hindguts composed of ileum, enteric valve, paunch, colon, and rectum (Watanabe and Tokuda 2010). Termites are very efficient in cellulolytic biomass degradation with estimated degradation rates of 74–99% for cellulose and 65–87% for hemicellulose carried out mainly by microbial symbionts (Watanabe and Tokuda 2010).

The ruminants are considered the most important foregut fermenters having a special four-chamber stomach (reticulum, rumen, omasum, and abomasum) (Fig. 1b). The feed fermentation and the absorption of the resulting volatile fatty acids (VFAs) take place in the first three chambers, including rumen, reticulum, and omasum, collectively named forestomach. The fourth part is called a true stomach (abomasum) regarding its acidic conditions. The rumen microbiota is responsible to convert ingested biomass to VFAs, providing 70–85% of the nutrients absorbed by ruminants (Noel et al. 2017). The produced VFAs are continuously absorbed by the rumen epithelial cells, thus maintaining stable conditions for microbial activities (Bayane and Guiot 2011). The most distinct feature of the ruminants is a mechanism called rumination, which means that the animals regurgitate the large particles of the semi-digested substrate and chew again for long periods to enhance the surface of the feed for enzymatic attacks (Welch 1982).

AD is a good example of a biotechnological application in the field of renewable energies as well as in waste management (De Vrieze and Verstraete 2016). The conversion of biomass into methane-rich biogas is a complex biochemical process occurring in four steps, namely hydrolysis, acidogenesis, acetogenesis, and methanogenesis. It is completely carried out by synergistic interactions among the members of a diverse microbial community (Wei 2016). The process occurs in a controlled engineered system, in which operational parameters, such as temperature, mixing, hydraulic retention time, and solid retention time, are maintained in the reactor (Fig. 1c).

There are two major types of ideal continuous reactors, the plug flow reactor (PFR) and the continuous stirred tank reactor (CSTR). The PFR has usually a cylindrical geometry where the reactor content progresses from the inlet in the axial direction to the outlet as a series of infinitely thin coherent "plugs." A key assumption is that the reactor content is perfectly mixed in the radial but not in the axial direction and each plug is considered a separate small batch reactor. CSTRs consist of a well-stirred tank, which is fed (semi)continuously and at the same time the digestate stream is removed. If all four AD steps take place in a single reactor, the system is called as one-stage digestion. In contrast, two-stage digestion systems consist of two sequential reactors to separate hydrolysis and acidogenesis in the first stage from acetogenesis and methanogenesis in the second stage

(Nkemka et al. 2015). The main functional difference between the animal gut and the current AD systems is that the process in the gut is optimized toward production of VFAs that are utilized by the animal, while methane is just a side product of hydrogenotrophic or methylotrophic methanogenesis (Breznak 1982; Brune and Dietrich 2015; Mason and Stuckey 2016). In current engineered AD systems, a high degree of biomass degradation is only achieved because methanogenesis is a major sink of VFAs and acetoclastic methanogenesis is involved in addition to hydrogenotrophic methanogenesis. Besides hydrogenotrophic methanogenesis, homoacetogenesis, in which hydrogen is used to reduce carbon dioxide to acetate, is another hydrogen sink in the gut of wood-feeding termites (Tholen and Brune 1999; Tholen and Brune 2000) and ruminants (Gagen et al. 2015; Henderson et al. 2010). Although homoacetogenic bacteria are also found in biogas reactors treating biomass (Demirel and Scherer 2008), due to thermodynamic reasons, they do not play a major role in reductive acetogenesis but rather in the reverse process of syntrophic acetate oxidation, which is coupled to hydrogenotrophic methanogenesis (Schnürer et al. 1999; Westerholm et al. 2019). Nevertheless, Siriwongrungson and co-workers found that under altered conditions these bacteria can indeed perform homoacetogenesis (Siriwongrungson et al. 2007). In biomethanation systems utilizing extra hydrogen generated from excess electricity of other renewables, this process is supposed to play an important role (Omar et al. 2018; Wahid et al. 2019; Zabranska and Pokorna 2018).

The high efficiency of lignocellulose degradation by specialized animals is also due to their unique characteristics of the digestive systems. Different mechanisms in the digestive systems, such as enzymatic attacks (e.g., by cellulases, xylanases, esterases, ligninases), mechanical grinding, and chemical conditions (e.g., alkaline or acidic conditions), contribute to the successful solubilization of lignocellulosic compounds. The fermentation products are removed continuously by different mechanisms to promote degradation, for instance VFAs by absorption on epithelial surface and hydrogen by methanogenesis or homoacetogenesis. The compartmentalization in biomass-feeding animals, such as ruminants, enables both homogenization and stratification of digestate during fermentation. Rumination is the main characteristic of these vertebrate animals, a process creating new surface areas for microorganisms to degrade polymers. Moreover, radial and/or axial oxygen gradients along the digestive system may contribute to delignification of these compounds. Some microorganisms are located on the epithelium or trapped in the mucus retaining them in the digestive tract, and adhesion on the lignocellulosic particles facilitates the contact with the feed (Bayane and Guiot 2011; Mason and Stuckey 2016). Since hydrolysis rate in these animals is faster than in a typical anaerobic digester, biomimicry is an important approach for successful innovations (Mason and Stuckey 2016). Thus, in order to enhance the digestion performance, some additional approaches, such as pre-treatment (chemical, physical, enzymatic), bioaugmentation, and co-digestion strategies, should be integrated in future sophisticated AD systems. Moreover, the biorefinery concept can be incorporated in such AD systems by including compartmentalization and utilization of carboxylic acids as additional products besides biogas (Fig. 1d).

Major differences in microbial communities from gut and current engineered AD systems

Recent trends in high-throughput amplicon sequencing and metagenome analysis of microbial communities and decreasing sequencing costs have led to proliferation of studies investigating lignocellulose-degrading communities in various natural and engineered environments.

The gut microorganisms with direct or indirect roles in lignocellulose degradation belong to *Bacteria*, *Archaea*, and *Eukarya*, such as protists and fungi. Figure 2 shows key families of the three domains of life found as abundant members of the microbiota of termite gut, beetle larvae gut, rumen, and AD systems. There is a strong link between the phylogenetic classification of the host and the microbial community of arthropods (Ley et al. 2008). The gut of scarab beetle larvae, *Pachnoda* spp. (*Coleoptera*: *Scarabaeidae*), harbors diverse bacterial communities involved in the degradation of plant materials. Previous studies pointed out that *Bacteroidetes*, *Proteobacteria*, and *Firmicutes* are the predominant phyla in the hindgut compartment, while *Actinobacteria* members are most abundant in the midgut (Andert et al. 2010; Egert et al. 2003). Due to the alkaline conditions in the midgut of beetle larvae, the bacterial richness is much lower than that of the hindgut, where diverse microbial processes and high concentrations of fermentation products occur (Andert et al. 2010). A new species, *Promicromonospora pachnodae*, excreting xylanases and endoglucanases, was also isolated from the hindgut of *Pachnoda marginata* larvae (Cazemier et al. 2003).

The digestive tract of beetle larvae, termites, and ruminants harbors also archaeal communities dominated by methanogens (Brune 2014; Cunha et al. 2011; Hook et al. 2010; Paul et al. 2017; Shi et al. 2015). There are two main pathways to produce methane. During acetoclastic methanogenesis, methane is produced by conversion of acetic acid to methane by *Methanosarcinales* comprising the families *Methansarcinaceae* and *Methanotrichaceae* (formerly *Methanosaetaceae*). The members of the genus *Methanothrix* are strictly acetoclastic methanogens and use only acetate as a substrate for methanogenesis (Oren 2014). The members of *Methansarcinaceae* are usually not predominant but frequently found in the gut of insects and ruminants, and the presence of the strict acetotroph *Methanothrix* has not yet been reported (Janssen and Kirs 2008).

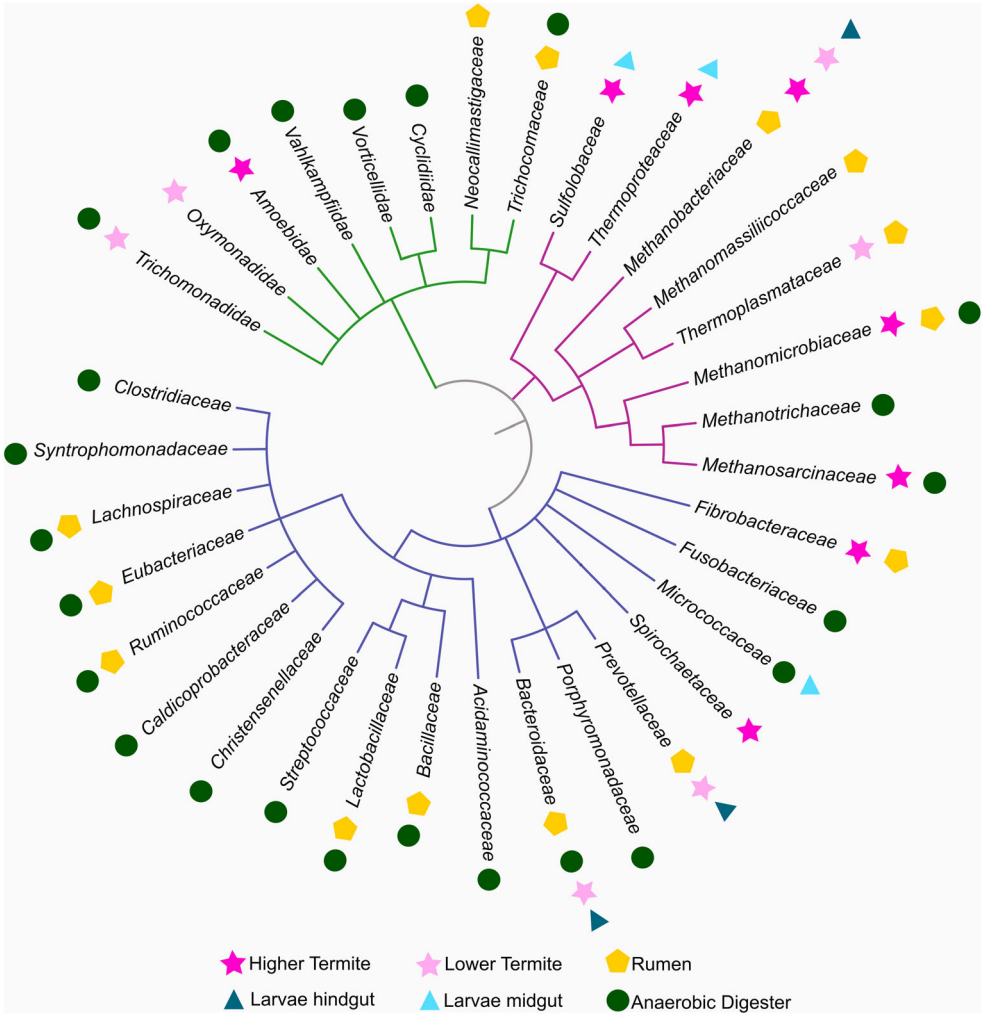

Fig. 2 Potential key families found as abundant members of the microbiota of termite gut, beetle larvae gut, rumen, and AD systems. The data for the tree was derived from the Taxonomy database in NCBI using common tree option (https://www.ncbi.nlm.nih.gov/Taxonomy/CommonTree/wwwcmt.cgi). All the families mentioned in the review were added manually and saved as phylip tree format. Then, the tree was drawn using iTOL v4 software (Letunic and Bork 2019). The colors represent the three domains as follows: purple for *Bacteria*, pink for *Archaea*, and green for *Eukarya*

In contrast, hydrogenotrophic methanogens, such as *Methanococcales*, *Methanobacteriales*, *Methanomicrobiales*, and *Methanocellales*, produce methane by reduction of carbon dioxide with hydrogen (Bayane and Guiot 2011; Buan 2018; Christy et al. 2014). Methane formation can also be carried out through the methylotrophic pathway, in which methylated compounds, such as methanol, methylamines or methylated thiols, are converted into methane by *Methanomassiliicoccales*, *Methanobacteriales*, or *Methanosarcinales* (Enzmann et al. 2018). Methylotrophic methanogens are classified into two groups based on the way the reducing equivalents are provided. In case of *Methanosarcina*, one methyl-CoM is oxidized to CO_2 via the reverse hydrogenotrophic pathway to generate the reducing equivalents for three methyl-CoM to methane (Enzmann et al. 2018). Hydrogen-dependent methylotrophs, such as members of the *Methanomassiliicoccales*, cannot oxidize the methyl groups to CO_2; therefore, they require hydrogen as electron donor for methanogenesis (Lang et al. 2015). In the beetle larvae, *Crenarchaeota* is the most abundant archaeal phylum in the midgut, while species belonging to the *Euryarchaeota* (mostly *Methanobacteriaceae*) are dominant in the hindgut (Egert et al. 2003).

Termites (order *Blattodea*) comprise diverse species and are divided into lower and higher termites (Inward et al. 2007). Lower termites contain symbiotic protists in their hindguts, such as *Trichomonadida*, *Hypermastigida* (class *Parabasalea*), and *Oxymonadida* (class *Oxymonadea*), which excrete cellulases for plant biomass degradation (Ohkuma 2003). These symbionts can be horizontally transferred between the individuals in a colony (Kitade 2004; Ohkuma 2003). Moreover, each colony of termites may have different microbial communities due to the diet and/or living environment (Minkley et al. 2006). Whereas the microbiota of lower termites comprise flagellated protist symbionts, the hindgut in higher termites (family *Termitidae*), which constitute the major part of all termite species, has different physicochemical conditions not suitable for these protozoan symbionts (He et al. 2013; Warnecke et al. 2007). Generally, the hindgut microbial community is dominated by bacteria. Besides, in some higher termites, amoebae were detected in the gut system playing a role in cellulose digestion (Brune and Ohkuma 2010).

The bacterial hindgut community of higher termites is considered a great source for motile bacteria. Species belonging to the *Spirochaetes* and *Fibrobacteres* are dominant in this environment. *Treponema* has been described to be the most abundant genus in the hindgut of higher termites (Warnecke et al. 2007). In the lower termites, the hindgut community is dominated by species belonging to the *Spirochaetes*, *Bacteroidetes*, and *Proteobacteria*. It was found that termites contribute substantially to global methane emissions, which is estimated around 3–15 Tg CH_4 yr^{-1} (Saunois et al. 2016). The methane is mostly produced by the hydrogenotrophic pathway, whereas acetoclastic methanogenesis was not yet detected in termites. The methane production rate in lower termites is dependent on the activity of hydrogen-producing gut flagellates, while hydrogen in higher termites is mostly produced by fermenting bacteria. *Methanobrevibacter* is the most abundant archaeal genus in the hindgut of lower termites. In higher termites, members of the *Methanosarcinales* (genus *Methanimicrococcus*) and the *Methanomicrobiales* in addition to *Methanobacteriales* (genus *Methanobrevibacter*) were also detected (Hongoh et al. 2003; Ohkuma 2003). Furthermore, *Thermoplasmatales* and *Crenoarchaeota* were also found in some termites (Ohkuma 2003). More information about the gut microbiota of the termites can be found in detailed reviews by Brune (2014) and Brune and Dietrich (2015).

As in the beetle larvae, termites, and wood roaches, a diverse microbial community in ruminants carries out the plant material degradation. In the rumen, protozoa comprise almost 50% of the total rumen microbial biomass and produce similar fermentation products as bacteria (Choudhury et al. 2015). A total of 30–40% of fiber degradation in the rumen is accomplished by ciliates (Bayane and Guiot 2011). The bacteria associated with protozoa can accomplish various functions, such as serving electron sinks through nitrogen fixation, acetogenesis, or methanogenesis, and can provide nutrients for the protozoan host organisms. This relationship can be ecto- or endosymbiotic having benefits both to the protozoan host and symbiotic prokaryotes (Levy and Jami 2018). Furthermore, nearly 20% of the rumen microbial biomass is composed of anaerobic fungi, mostly of the phylum *Neocallimastigomycota*, that play an active role in the degradation of lignified plant biomass (Choudhury et al. 2015). There are numerous studies that investigated the microbial community structure, dynamics, and functions of rumen microbiota (Ozbayram et al. 2018b; Pitta et al. 2014; Söllinger et al. 2018; Zened et al. 2013). The bacterial community of the rumen fluid is dominated by the phyla *Bacteroidetes*, *Firmicutes*, and *Proteobacteria* in different proportions depending on the animal (Ozbayram et al. 2018b; Pitta et al. 2014; Söllinger et al. 2018; Zened et al. 2013). Additionally, the phylum *Fibrobacteres* includes several important rumen bacteria, such as *Fibrobacter succinogenes* and *Fibrobacter intestinalis*, which contribute to the degradation of plant material in the rumen environment (Ozbayram et al. 2018b; Ransom-Jones et al. 2012). Moreover, some members of this phylum were recently found in termites (Rahman et al. 2016). As a significant feature, *Prevotella* (order *Bacteroidales*, phylum *Bacteroidetes*) is the most abundant genus in the rumen, playing a key role in the breakdown of proteins and carbohydrates and excreting cellulolytic enzymes like carboxymethylcellulase and xylanase (Nyonyo et al. 2014). Henderson et al. (2015) described *Butyrivibrio* and *Ruminococcus* as well as unclassified *Lachnospiraceae*, *Ruminococcaceae*, *Bacteroidales*, and *Clostridiales* belonging to the core rumen bacterial community. Methane production in the rumen is a secondary microbial activity while the major function of rumen fermentation is to produce VFAs (Bayane and Guiot 2011). However, ruminants are considered one of the major contributors to methane emissions. The emissions vary according to the ruminant species. Whereas 26–497 g methane per day is emitted from a dairy cattle, the daily values in beef cattle and Suffolk sheep were found as 161–396 and 22–25 g, respectively (Broucek 2014). The genera *Methanobrevibacter*, *Methanobacterium*, and *Methanomicrobium* are dominant methanogens in the rumen environment and thus have been defined as characteristic hydrogenotrophic rumen methanogens (Bayane and Guiot 2011). In a recent study, the order *Methanomassiliicoccales*, which comprises hydrogen-dependent methylotrophic methanogens, was found to be abundant in the rumen fluid (Jin et al. 2017; Ozbayram et al. 2018b; Söllinger et al. 2018).

According to the hologenome concept, multicellular organisms should be considered holobionts (host plus symbionts) with their hologenome (host genome plus metagenome of the symbionts) rather than individuals as a level of selection in evolution (Rosenberg and Zilber-Rosenberg 2011, 2016; Zilber-Rosenberg and Rosenberg 2008). The gut microbiota as part of the holobiont co-evolved with their hosts over millions of years, while engineered AD systems are typically *ad hoc* inoculated without much consideration of selecting the most effective microbiota (Godon et al. 2013). The co-evolution of gut symbionts with their host requires specific transfer mechanisms from parents to offspring, which will be discussed later in this review. The bacterial communities of biogas systems are mostly dominated by *Firmicutes* and *Bacteroidetes* members (Kröber et al. 2009; Lucas et al. 2015; Lv et al. 2019), and a diverse microbial community takes a part in each step of biogas production. Hydrolytic and fermenting bacteria, namely *Clostridia*, *Micrococcus*, *Bacteroides*, *Butyrivibrio*, *Fusobacterium*, *Selenomonas*, and *Streptococcus* excrete various enzymes, such as cellulases, cellobiases, xylanases, amylases, proteases, and lipases, for hydrolyzing the insoluble biomass polymers into smaller units. Moreover, anaerobic microorganisms can excrete extracellular enzyme complexes, so-called cellulosomes, to degrade plant cell walls and form various fermentation products, such as ethanol and organic acids (Doi and Kosugi 2004). Right after hydrolysis, sugars, long-chain fatty acids, and amino acids are converted into VFAs, such as acetic, propionic, butyric, and other short-chain

carboxylic acids, alcohols, H_2, and CO_2 by fermentative bacteria, such as *Streptococcus*, *Lactobacillus*, and *Bacillus*, during acidogenesis, which is considered the fastest step during AD (Christy et al. 2014). VFAs longer than two carbon atoms and alcohols longer than one carbon atom are further converted to acetate, hydrogen, and carbon dioxide in the acetogenesis step (Schink 1997) involving, e.g., the genera *Smithella*, *Pelotomaculum*, *Syntrophobacter*, and *Syntrophomonas* (Mathai et al. 2015). This syntrophic oxidation process should be distinguished from homoacetogenesis, which is acetate formation by using hydrogen to reduce carbon dioxide to acetate. Acetate is a central metabolite of the AD process that is either converted directly to CH_4 and CO_2 by acetoclastic methanogens or is oxidized to H_2 and CO_2 or formate by syntrophic acetate-oxidizing bacteria (SAOB). However, the latter process is only possible if the hydrogen partial pressure is kept low by hydrogenotrophic methanogens (Westerholm et al. 2016).

The predominant methanogenic pathway for biogas production in anaerobic digesters is dependent on the feedstock and operating conditions (Karakashev et al. 2005; Nettmann et al. 2010). The concentrations of ammonia and VFAs have an effect on the composition of the methanogenic community (Karakashev et al. 2005). Ziganshin et al. (2016) highlighted that the genus *Methanoculleus* was positively correlated with the NH_3 concentration, whereas the prevalence of *Methanocorpusculum*, *Methanobacterium*, and *Methanosaeta* was negatively correlated with the NH_3 level in biogas reactors. In another study, the same group showed that the organic loading rate shapes the methanogenic community in anaerobic digesters treating distillers' grains (Ziganshin et al. 2011). *Methanosarcina* species were abundant in the reactors operated at a high organic loading rate and supplemented with iron hydroxide. However, acetoclastic methanogens of the genus *Methanothrix (*formerly *Methanosaeta*) dominated the well-performing reactors operated at lower organic loading rates. In large-scale agricultural biogas reactors, *Methanobacterium*, *Methanosaeta* and *Methanoculleus* were found as the most abundant genera (Lucas et al. 2015). The methanogenic communities in agricultural biogas plants were dominated by the orders *Methanomicrobiales*, *Methanosarcinales*, and *Methanobacteriales* (Nettmann et al. 2008; Rastogi et al. 2008). Fungi (such as *Ascomycetes* and *Aspergillus*) and protozoa (such as *Amoeboflagellates*, *Cyclidium*, *Naeglaria*, *Rhynchomonas*, *Vorticella*, *Trichomonas*) were detected in anaerobic digesters in lower abundances compared to rumen and termites. However, their role in the substrate degradation remains unknown (Bayane and Guiot 2011; Güllert et al. 2016).

Transfer of gut microbiota between generations

The microorganisms in the gut of herbivorous animals either belong to the core microbiota as obligate endosymbionts or just transient members of the community as non-core, facultative endosymbionts acquired from the environment. According to the hologenome concept, the obligate endosymbionts co-evolved with their hosts (Rosenberg and Zilber-Rosenberg 2011, 2016, 2018). The host is mainly defined at the species level; however, intra-species variations might exist as discussed earlier. Therefore, effective transfer mechanisms of beneficial microbes from the parent to the offspring are important. The way the gut endosymbionts are transmitted from one generation to the next is often related to the importance of the service(s) that they provide for the host (Shapira 2016). It is especially challenging in case of insects with different lifestyles between the larva and the imago stage. In many cases, the effective transfer of these microorganisms requires the bacteria to persist in the environment for a longer period, which might allow their potential transfer and utilization also in engineered systems.

The vertical transfer of beneficial microorganisms is prevailing in case of social insects as was shown in a study assessing the gut microbiota of two social termites (*Mastotermes darwiniensis*, *Heterotermes aureus*), a social wood roach (*Cryptocercus punctulatus*) and a non-social cockroach (*Periplaneta americana*) (Sabree et al. 2012). The gut of social termites harbors a more conserved microbial community similar to that of other termites, whereas cockroaches harbor more variable gut communities that differ among individual hosts and contain more typically environmental microbes. Wood roaches are the sister group to termites and display an early stage of sociality, and their gut community structures are similar among individuals (Sabree et al. 2012). Proctodeal trophallaxis is considered the main transfer mechanism of the microbiota in case of termites (Hongoh et al. 2005; Kohler et al. 2012) and wood-feeding cockroaches of the genus *Cryptocercus* (Nalepa 2015). A recent study showed that rather a "mixed mode" of transmission combining vertical (colony-to-offspring) and horizontal (colony-to-colony) transfer has been the major driving force shaping the gut microbiota of termites (Bourguignon et al. 2018). Another example for strict vertical transmission of symbionts is found in many stinkbug species where the mother lays eggs covered by feces-derived capsules (egg-smearing) containing the endosymbionts. The juveniles ingest the capsules after hatching and inoculate themselves with the symbionts (Fukatsu and Hosokawa 2002; Hosokawa et al. 2006). Reed beetles also use egg-smearing for the vertical transfer of symbionts (Kolsch and Pedersen 2010). An alternative way to acquire gut endosymbionts is via horizontal transmission, in which symbionts are derived from the environment as found in crickets and solitary cockroaches (Engel and Moran 2013). Environmentally acquired symbionts represent higher genetic variation, which could provide more opportunities for adaptation, but also allows the settlement of non-beneficial "cheater" microorganisms (Shapira 2016).

In conclusion, the major mechanisms of endosymbiont transfer of insects include direct strict vertical transmission through producing specific symbiont-containing capsules for the eggs via defecation (egg-smearing), forms of coprophagy or proctodeal trophallaxis, defecating and feeding in the same habitat, and acquiring microorganisms from the environment, or a kind of mixed mode of transmission.

In case of mammals, the major inoculation happens during the transition through the birth canal (vaginal and anal microbiota) and during breast feeding (colostrum, milk, and skin microorganisms) (Fernandez et al. 2013; Rodriguez et al. 2015). The colonization of the rumen of various livestock species (cattle, sheep, and goats) was investigated by many studies because of the prospect of effective manipulation of microbiota to improve the capacity to harvest energy from the feed (better utilization of forage with less methane production) (Hook et al. 2010; Yanez-Ruiz et al. 2015). The whole gastrointestinal tract, including the rumen, was assumed to be sterile at birth but is rapidly colonized by microorganisms within the first day of life (Guzman et al. 2015; Ziolecki and Briggs 1961). All major types of rumen microorganisms are already present during the pre-ruminant period in milk-feeding calves (Li et al. 2012). Jami et al. also detected some rumen bacteria essential for mature rumen function as early as one day after birth (Jami et al. 2013). Rey and co-workers showed that the microbial community establishment is rapid after birth and sequential (Rey et al. 2014). *Proteobacteria* are dominant in the early phase, but, then, they are gradually replaced by *Bacteroidetes* as the main phylum. Later, between days 3 and 12, the bacterial community includes most of the bacteria present in the developed rumen; however, in different relative abundances. Ciliates are detected in the rumen of young ruminants within two weeks after birth and supposed to be transferred by the saliva of the mother (Eadie 1962). This was proved by isolation of infants from their mother, which led to the lack of protozoa establishment in the rumen (Bryant and Small 1960; Eadie 1962). Anaerobic fungi (e.g., *Neocallimastix frontalis*) are also able to develop in the rumen before feeding on solid substrates as shown previously (Fonty et al. 1987). Early establishment (days 2 to 4) of methanogenic archaea long before the first solid feeding was shown in lamb rumen (Fonty et al. 1987). By the application of modern molecular techniques, the detection of methanogens at an even earlier stage (first day or neonatal stage) of dairy calves was possible (Guzman et al. 2015). Transition from liquid (milk) to solid feed has a major impact on the community structure as shown by many studies (Jami et al. 2013; Rey et al. 2014). It can be concluded that the ruminal microbial community establishment happens before intake of solid food, but, then, the arrival of solid substrate shapes the community structure (Rey et al. 2014) and the anatomic development occurring at last (Jiao et al. 2015). Factors influencing early life colonization (presence of mother vs. artificial feeding etc.) of the rumen have been reviewed in detail by Yanez-Ruiz et al. (2015).

Management of the microbiota of various gut and AD systems

Due to the important role of the microbiota in nutrition of various ruminant livestock species, the possibility to influence the microbial community in order to improve the performance of the animals (better utilization of the fodder) has attracted lots of research in the last decades (Chalupa 1977; Hart et al. 2008; Yanez-Ruiz et al. 2015). Some part of knowledge obtained from engineering attempts of animal gut microbiota might be transferred to AD systems.

Weimer et al. (2010) investigated the stability and host specificity of the ruminal bacterial communities of a cow following a massive exchange of the rumen content including active microbiota derived from another cow. The microbial community structure was altered but returned to a state resembling more to the original structure than the one from the donor. Mitigation of methane emission is an important issue in case of ruminants, not just to reduce the GHG emission from the animal husbandry sector but also to better utilize the carbon in the fodder converting it into meat rather than into methane (Hook et al. 2010). In AD reactors, the enhancement of methane production is usually aimed; however, such reactors can also be utilized to produce carboxylates as value-added products (Agler et al. 2011; Janke et al. 2016; Urban et al. 2017). In such cases, the inhibition of methanogenesis is desired. A review on the potential utilization of plant extracts, such as essential oils, saponins, and organosulfurous compounds, to manipulate rumen fermentation was published previously (Hart et al. 2008). Bromochloromethane (BCM), as a well-known inhibitor of methanogenesis, was applied to young goats to alter their methanogenic community structures (Abecia et al. 2013, 2014). The treatment resulted in a reduction of methane emission but could not completely eliminate it, and 4 months after the treatment the community structure was similar to the ones in non-treated specimens (Abecia et al. 2014). Fonty et al. (2007) inoculated gnotobiotic lambs with a functional rumen microbiota lacking methanogens. Reductive acetogenesis was an effective H_2 sink and sustained a functional rumen; however, H_2 utilization was much lower than in lambs with ruminal methanogens. Additional examples and more details about the potential re-programming of the rumen microbiota can be found in the detailed review by Yanez-Ruiz et al. (2015). A not yet fully confirmed hypothesis of that review is that once the rumen community is more or less constant, there is little room for alteration. Similar difficulties might arise during attempts of microbial community modification of stable (steady state) anaerobic digesters. Application of living microorganisms by addition to the fodder (direct-fed microbes) is applied for ruminants to improve feed utilization (Klieve et al. 2003; Martin and Nisbet 1992) or to mitigate methane emission (Jeyanathan et al. 2014). This approach is similar to the application of probiotics in human medicine.

Probiotics are defined as live microorganisms that, when administered in adequate amounts, confer a health benefit on the host (Hill et al. 2014). The application of probiotics in animal production was previously reviewed (Kmet et al. 1993; Musa et al. 2009).

Bioaugmentation is a well-established biotechnological method to introduce microorganisms to a bioprocess. It is very similar to the application of probiotics used for health improvement via influencing the gut microbiota. There are many requirements for an effective probiotic treatment, and, in an analogous way, similar prerequisites can be listed for strains used for bioaugmentation (Table 1)

There are many studies at laboratory-scale demonstrating positive effects of bioaugmentation (Table 2), but only few strains or complex cultures fulfill the criteria described in Table 1.

Successful recovery and increase of methane production compared to the control was achieved by adding a propionate-degrading enrichment culture to an overloaded reactor (Tale et al. 2011) involved in degradation of propionate or long-chain fatty acids. Remediation of ammonia toxicity of biogas reactors was also possible by adding either a pure culture of the ammonia-tolerant methanogen *Methanoculleus bourgensis* MS2 or a mixed culture containing *M. bourgensis* as a predominant methanogen (Fotidis et al. 2017; Fotidis et al. 2014).

Improving the AD of lignocellulose with microorganisms having excellent degradation properties has been proposed and investigated by many studies (Cater et al. 2015). Adding living microorganisms instead of free enzymes is, in theory, more efficient, because microorganisms can regenerate and produce various useful enzymes at the same time. Bagi and co-workers tested the enhancement potential of two H_2-producing strains, *Enterobacter cloacae* and *Caldicellulosiruptor saccharolyticus*, using a complex substrate in batch experiment. Biogas production increased by 160–170% compared to the control, which was partially due to the cellulolytic activity of the second strain (Bagi et al. 2007). The enhancement potential of these two strains was later also tested in a series of continuous feeding experiments in CSTRs applying various substrates and reactor conditions (Ács et al. 2015; Herbel et al. 2010; Kovacs et al. 2013) (Table 2). Another strain of the genus *Caldicellulosiruptor*, namely *Caldicellulosiruptor bescii*, was successfully used to enhance methane production from steam-explosion treated birch in a batch experiment (Mulat et al. 2018). Another target genus of bioaugmentation is *Clostridium*. The mesophilic *Clostridium cellulolyticum* (Desvaux 2005) and the thermophilic *Clostridium thermocellum* (Akinosho et al. 2014), species well adapted to a cellulolytic lifestyle, were successfully applied to enhance AD of various lignocellulosic biomass (Lü et al. 2013; Öner et al. 2018; Peng et al. 2014; Tsapekos et al. 2017) (Table 2). These strains produce cellulosomes and due to their major fermentation products consisting mainly of formic, acetic, lactic, and succinic acids, and ethanol besides carbon dioxide and hydrogen, they are also perfect candidates for consolidated bioprocessing (CBP). CBP applications combine the enzyme production, hydrolysis, and fermentation stages into a single step, which, in theory, improve the process efficiency by eliminating the need for addition of exogenous hydrolytic enzymes. The enhancement potential of anaerobic fungi was also demonstrated in batch experiments, but less pronounced effects were observed in continuous experiments (Nkemka et al. 2015; Prochazka et al. 2012) (Table 2).

Comparison of such enhancement experiments is not easy, because the control inoculum plays also an important role in the extent of enhancement. The microbiota in an inoculum from a system not treating lignocellulosic substrates is less accommodated to lignocellulose degradation, and, therefore, a more pronounced enhancement is expected via bioaugmentation. A well-operating biogas reactor treating partially or solely lignocellulosic biomass for a long period can be less effectively enhanced further. Although many successful bioaugmentation efforts were demonstrated in small batch scale, the applications of the same strains in continuous experiments were less efficient and the observed methane yield enhancement was lower and often transient. Similar to the human probiotic applications, this is probably due to the fact that the introduced strains do not became stable members of the AD community. Martin-Ryals and co-workers demonstrated that frequent and repeated bioaugmentation can be rather effective (Martin-Ryals et al. 2015). However, such continuous addition of cultivated microorganisms would be extremely expensive at large-scale AD plants. Another approach is to use mixtures of strains or even more complex microbial communities. Ozbayram and co-workers demonstrated the applicability of enrichment cultures derived from the rumen microbial communities of sheep (Ozbayram et al. 2017), goat, and

Table 1 Requirements for probiotics and strains used for effective bioaugmentation of AD systems

Requirements	Probiotic strain	Bioaugmentation strain
Effect	Live microorganism, which is capable of exerting a beneficial effect on the host animal, e.g., increased growth or resistance to disease.	Live microorganism, which is capable of exerting a beneficial effect on the system, e.g., increased gas production or resistance to process inhibition.
Toxicity	The strain must be non-pathogenic and non-toxic.	
Amount	It should be applied as viable cells in large amount.	
Survival	Surviving and metabolizing in the gut environment, e.g., resistance to low pH and organic acids, maintenance of genetic stability in gut microbiota.	Surviving and metabolizing in the reactor environment; maintenance of genetic stability in reactor microbiota.
Stability	Strain should be stable and viable for extended periods under storage and application conditions.	

Table 2 Bioaugmentation attempts to enhance AD of lignocellulosic substrates

Bioaugmentation strain/community	Substrate	Reactor type (volume)	Temperature	Control inoculum source	Substrate of control inoculum microbiota	Enhancement by bioaugmentation	Reference
Pure cultures used for bioaugmentation							
Caldicellulosiruptor saccharolyticus, *Enterobacter cloacae*	Wastewater sludge, dried plant biomass, and pig manure	Batch (0.5 L)	35 °C and 55 °C	WWTP[a] sludge	Wastewater	160–170% (biogas)	Bagi et al. (2007)
Caldicellulosiruptor saccharolyticus	Pig manure and DDGS[b]	CSTR[c] (5 L)	55 °C	NA[d]	NA[d]	160–170% (biogas), transient	Herbel et al. (2010)
Caldicellulosiruptor saccharolyticus, *Enterobacter cloacae*	Pig slurry and chopped sweet sorghum	CSTR[c] (5 L)	Meso- and thermophilic	Thermophilic sewage sludge digester, mesophilic agricultural biogas plant	NA[d]	30 –50% (biogas), transient	Kovacs et al. (2013)
Enterobacter cloacae	Maize silage	CSTR[c] (5 L)	Mesophilic	Mesophilic agricultural biogas plant	Maize silage, sweet sorghum, and pig manure	20% (biogas)	Ács et al. (2015)
Caldicellulosiruptor bescii	Steam-explosion treated birch	Batch (0.125 L)	62 °C	Thermophilic CSTR[c]	Sewage sludge and food waste	21–44% (methane)	Mulat et al. (2018)
Acetobacteroides hydrogenigenes	Corn straw	Batch (0.12 L)	37 °C	Full-scale mesophilic (35 °C) CSTR[c]	Untreated corn straw	19–23% (methane)	Zhang et al. (2015)
Clostridium cellulolyticum	Wheat straw	Batch (0.5 L)	37 °C	Full-scale mesophilic biogas plant	NA[d]	13% (methane)	Peng et al. (2014)
Clostridium thermocellum	*Chlorella vulgaris* biomass	Batch (0.5 L)	55 °C	Methanogenic granular sludge from a lab-scale (3.5 L) ASBR[f]	Glucose and acetate	17–24% (methane)	Lü et al. (2013)
Clostridium thermocellum	Cow manure and wheat straw	Batch (0.1 L)	55 °C	Full-scale AD plant (41 °C)	Cattle manure	39% (methane)	Öner et al. (2018)
Clostridium thermocellum and *Melioribacter roseus*	Wheat straw	Batch (0.4 L) and CSTR[b]	53 °C	Thermophilic inoculum from biogas plant	Livestock manure and wastes from ethanol industry	10–34% (batch), 0–7.5% (CSTR) (methane)	Tsapekos et al. (2017)
Rumen fungi, best strain: *Anaeromyces* (KF8)	Celluloses, maize, and grass silage	Batch and semi-continuous	39 °C	Mesophilic agricultural biogas plant (41 °C)	Pig slurry	22% (batch) or 4% (semi--continuous)	Prochazka et al. (2012)
Piromyces rhizinflata	Corn silage and cattail	Batch (0.5 L), leach bed reactor (1.3 L) and UASB[e] (1.3 L)	37 °C	Mesophilic pilot UASB[e] plant (40 °C)	Agro-industrial wastes	Transient increase of methane and hydrogen	Nkemka et al. (2015)
Complex microbial community used for bioaugmentation							
Clostridium-dominated proprietary bioculture (continuously added)	Sweet corn-processing residues	Two-phase SBR[e] and two-phase bench-scale continuous reactor systems (0.5 and 0.25 L)	35–40 °C	Mesophilic municipal wastewater treatment sludge	Wastewater	15% (methane)	Martin-Ryals et al. (2015)
Bacteroides-dominated proprietary microbial consortium BYND-5	Rice straw	Batch (1 L)	30 °C	Biogas reactor slurry (30 °C)	Liquid cow manure	49% (methane)	Yan et al. (2012)
Hemicellulolytic bacteria immobilized on zeolite	Xylan	Batch (1 L)	35 °C	Large-scale biogas plant slurry	Maize silage	53% (methane)	Weiss et al. (2011)
Complex community (yeast, cellulolytic bacteria, lactic acid bacteria)	Corn straw	Batch (0.12 L)	20 °C	Mesophilic UASB[e] sludge	NA[c]	76% (methane)	Zhong et al. (2011)
Lignocellulolytic enrichment cultures enriched from soda lake sediments	Wheat straw	Batch (0.5 L), acidogenic leach-bed fermenters (1.65 L)	38 °C	Soda lake sediment	Lake biomass	Transient increase in batch; 61% VFA, 112% fermentation gas	Sträuber et al. (2015)
Thermophilic and cellulolytic consortium enriched from compost	Filter paper	Batch (0.125 L)	55 °C	Sludge from full-scale anaerobic digester	Agro-food organic waste and agricultural waste	12% (methane)	Kinet et al. (2015)
	Wheat straw	Batch (0.5 L)	38 °C	Mesophilic pilot-scale biogas plant slurry	Cow manure and maize silage	27% (methane)	Ozbayram et al. (2017)

Table 2 (continued)

Bioaugmentation strain/community	Substrate	Reactor type (volume)	Temperature	Control inoculum source	Substrate of control inoculum microbiota	Enhancement by bioaugmentation	Reference
Sheep rumen fluid-enrichment cultures							
Cow and goat rumen fluid-enrichment cultures	Wheat straw	Batch (0.5 L)	38 °C	Mesophilic pilot-scale biogas plant slurry	Cow manure and maize silage	6-36% (methane)	Ozbayram et al. (2018c)

[a] WWTP, wastewater treatment plant
[b] DDGS, dried distiller grains with solubles
[c] CSTR, continuous stirred tank reactor
[d] NA, information not available
[e] UASB, upflow anaerobic sludge blanket
[f] (A)SBR, (anaerobic) sequencing batch reactor

cow (Ozbayram et al. 2018c). An important finding was that a considerable amount of bioaugmentation culture compared to the indigenous microbiota is necessary for an effective enhancement, and only a minor fraction of the bioaugmentation culture could establish in the final community at the end of the experiments. De Vrieze and Verstraete suggested in a recent review paper (De Vrieze and Verstraete 2016) that an effective strategy could be the introduction of so-called keystone species, which are not involved in the process itself but are required to be present for structural organization or enhanced proliferation and activity of the community members with the desired (hemi)cellulolytic activity. As a recent example, Ács and co-workers demonstrated that addition of a non-cellulolytic *Enterobacter cloacae* strain successfully enhanced the methane production from maize silage, which was partially achieved by the increased abundance of the polymer-degrading *Clostridiales* derived from the standard inoculum (Ács et al. 2015). Addition of manure with its complex microbiota, including effective fiber-degrading strains or ensiled plant biomass containing lactobacilli, has many beneficial effects observed by biogas plant operators. However, the positive effects of the introduced complex microbiota cannot be clearly separated from the ones originating from the substrate (trace elements, lactate, pre-digested polymers). According to the strict definition of probiotics, foods containing potentially beneficial live and active cultures should not be called probiotics (Hill et al. 2014).

Despite promising laboratory-scale demonstration of bioaugmentation, successful large-scale applications are still missing. This is probably due to the fact that alteration of a stable microbial community by introducing allochthonous microbiota is difficult, similarly as it applies to established gut microbiota. In case of process failure or underperformance, the addition of still a large number of cells would be needed for effective establishment of the bioaugmented microorganisms.

Genome mining for lignocellulose-modifying enzymes appropriate for industrial applications

Although gut symbionts play crucial roles in lignocellulose degradation, many animals can also produce endogenous enzymes that contribute in a complementary way to the overall biomass utilization. The host input was mainly investigated in case of lower termites (Cairo et al. 2011). In several studies, the whole digestome, defined as the pool of host and symbiont genes that collaborate for high efficiency lignocellulose digestion, was investigated by metagenomics or metatranscriptomics (Tartar et al. 2009). While the symbionts play major roles in the hindgut, the host enzymes are produced mainly in the salivary glands and act in the foregut and middle gut. Relatively high levels of oxygen can be detected in these compartments compared to the hindgut,

which promotes lignin modification (Ke and Chen 2013; Ke et al. 2010). Tartar and co-workers identified several genes with potential roles in either lignin degradation or protection from toxic metabolites (e.g., reactive oxygen species) generated during lignin degradation in the lower termite *Reticulitermes flavipes* via metatranscriptomic approach (Tartar et al. 2009). Laccases, catalases, esterases, cytochrome P450, superoxide dismutases, epoxide hydrolases, and glutathione peroxidases are produced by the host, and they are probably involved in the degradation of lignin and its metabolites. In addition, genes encoding endogenous carbohydrate active enzymes associated with cellulose degradation and related to various glycosyl hydrolase families (GHF) were also detected. These enzymes are potential targets of bioprospecting. Especially, addition of lignin-modifying enzymes could be part of pretreatment strategies in gut-inspired biorefinery systems. There are many enzyme preparations commercially available for biorefinery applications, mainly for bioethanol production, but all are similar in composition and have been mostly optimized for acid-pretreated corn stover (Banerjee et al. 2010). However, mimicking gut systems would require other pretreatment chemistry and developed enzyme cocktails should be compatible with mimicked gut conditions (e.g., alkaline conditions in case of insect larvae systems). Besides endogenous enzymes, microbial symbionts are also potential sources of novel enzymes that can be derived by cultivating them. However, obtaining pure cultures is quite complicated in case of many anaerobic microorganisms. Molecular techniques provide an alternative approach, i.e., genes can be obtained by metagenomics and metatranscriptomics and then expressed in heterologous systems. Subsequently, their enzymatic activity can be screened and potential well-performing lignin- or carbohydrate-active candidates can be used for mass production. This approach was demonstrated by Hess and co-workers by sequencing and analyzing 268 Gb of metagenomic DNA from microbes adherent to plant fibers incubated in cow rumen (Hess et al. 2011). From this dataset, 15 metagenome-assembled microbial genomes were reconstructed together with 27,755 genes encoding putative carbohydrate-active enzymes. A selection of 90 candidate genes were expressed, of which the majority produced proteins that were enzymatically active against cellulosic substrates, some of them with low sequence similarity to known enzymes. The general approach presented in this study is applicable to other gut systems and various environmental and engineered systems. A similar metagenomics approach was used for the investigation of camel rumen (Gharechahi and Salekdeh 2018), moose rumen (Svartström et al. 2017), Vietnamese native goat rumen (Do et al. 2018), Indian buffalo rumen (Singh et al. 2014), goat rumen (Lim et al. 2013), and cow rumen (Dai et al. 2015; Stewart et al. 2018) . However, recent studies showed that ruminant feces are probably a poor proxy for the lignocellulolytic potential of the host (Al-Masaudi et al. 2017); therefore, its utilization as inoculum or as target of genome mining is limited. Heterologous expression of the novel genes and testing of enzyme activity were only performed in few cases, including heterologous expression of lignocellulolytic proteins cow rumen (Del Pozo et al. 2012) and buffalo rumen (Shah et al. 2017).

Besides the bottlenecks of finding novel enzymes with good biotechnological potential (Ferrer et al. 2016), the production costs should be drastically reduced for economic application in AD systems. An alternative approach is the production of lignocellulolytic enzymes directly within the plant biomass via the so called *in-planta* expression approach (Abdeev et al. 2003; Borkhardt et al. 2010; Harrison et al. 2011, 2014; Jiang et al. 2011). Enzyme expression can be regulated in a way that they are expressed at a particular stage of development or specifically induced. The potential of *in-planta* lignocellulolytic enzyme production was reviewed elsewhere (Willis et al. 2016).

Potential biomimicry of the gut in advanced reactor engineering

We should be careful when copying the concept of the digestive tract into an engineered system because various gut systems have no uniform features, such as shape, flux, and mixing. The idea to simulate animal digestive tracts in engineered reactors is not new. Many attempts were made to enhance the methane yield in biogas reactors inspired by ruminants. The most well-known systems are the rumen simulation technique (RUSITEC) (Czerkawski and Breckenridge 1977) and the rumen-derived anaerobic digestion system (RUDAD) (Gijzen et al. 1988). Briefly, an anaerobic digester is seeded by rumen-based microbial inoculum in the RUSITEC system, whereas RUDAD is a two-stage system composed of an acidogenic rumen reactor and a high rate methanogenic reactor to sustain optimum conditions for both hydrolysis and methanogenesis. Two-stage anaerobic digester systems are quite similar to RUDAD and show better performance compared to single-stage digesters (Akobi et al. 2016; Lindner et al. 2016). It was reported that a few RUDAD systems were constructed and operated in industrial scale to treat municipal solid wastes (Deublein and Steinhauser 2008).

In a recent study carried out by Bize and co-workers, a biomimetic approach was integrated in anaerobic digesters, which the authors designated as bovid-like engineered digestive system (Bize et al. 2015). They achieved better performance in COD removal in the systems inoculated with cow rumen inoculum. Due to their powerful skills in lignocellulose degradation, a considerable literature has grown up around the theme of termite digestive tract for almost a century (Brune and Dietrich 2015). However, most of the work carried out on industrial application failed to scale-up this cellulolytic system. While termites have mastication, we have pre-treatment steps for size reduction in the engineered systems, which play a vital role for effective degradation rates in the further steps. It

is an energy-consuming step contributing the greatest share to the operational costs (Watanabe and Tokuda 2010).

Lignin has a complex structure resisting biochemical degradation and limits lignocellulose degradation. Oxygen is necessary for lignin degradation/modification, which acts as co-substrate during the oxidative enzymatic breakdown (Breznak and Brune 1994; Scharf and Tartar 2008). Ke and co-workers showed that termites can also modify and/or break down lignin compounds through their gut system. Degradation starts in the foregut and then continues in the midgut of the termites, which is not completely anaerobic (Ke et al. 2011). Oxic treatment steps can be integrated in the biomass utilization systems as a first step, or a biomimicking reactor system might include a pre-digestion reactor that is not strictly anoxic.

Godon and his colleagues suggested some points to be taken into consideration while biomimicking animal digestive tracts (Godon et al. 2016). In summary, adjusting mesophilic temperature, extreme pH hydrolysis (acidic for vertebrates, alkaline for insects), using grinding approach rather than cutting, specific enzyme addition, and including oxidative enzymes could be incorporated into gut-inspired future AD systems. Alkaline pre-treatment was integrated in AD processes, and results revealed significant enhancement on methane yield (Janke et al. 2017; Sambusiti et al. 2013; Sträuber et al. 2015; Zheng et al. 2009). As another approach, size reduction has positive effects on biogas yield in digesters treating lignocellulosic feedstock as it promotes the hydrolysis rate by increasing the surface area (Leite et al. 2015; Silva et al. 2012). Enzyme addition revealed 10–34% enhancement of the methane yield (Bruni et al. 2010; Vervaeren et al. 2010). However, in another study, the biogas yield and methane yield were not affected by enzyme addition (Romano et al. 2009).

Moreover, there are successful applications of co-inoculation of anaerobic digesters with ruminal microbiota. The level on the enhancement of methane yield differed according to the study (Deng et al. 2017; Ozbayram et al. 2018a; Quintero et al. 2012; Wall et al. 2015). Furthermore, our recent studies showed that bioaugmentation with rumen-derived microbial communities also enhanced the methane production in biogas reactors operated in batch mode (Ozbayram et al. 2017, 2018c). However, another attempt to use rumen fluid as co-inoculum was not significantly effective on cellulose degradation compared to sludge from a municipal solid waste digester alone (Chapleur et al. 2014), which means that the enhancement effect is system-dependent.

Perspectives and future challenges

Lignocellulosic biomass has still a great and largely untapped potential for the biorefinery approach producing high-value chemicals and energy carriers. Current engineered systems are underperforming, especially in comparison to the gut systems of few herbivorous animals specialized for lignocellulosic biomass consumption. The new generation of metaomics technologies enable us to better understand the background of this superior performance and hopefully provide us useful information for the significant improvement of our current technological systems.

However, different criteria apply for evolution driven by natural selection and economic considerations for industrial applications. Biomimicry of the gut systems might bring us closer to faster and significantly better lignocellulose to biofuel conversion; however, the invested cost will not necessarily be covered by the higher profit as a result of increased biogas or carboxylate production. Nevertheless, it would be still beneficial to establish and explore such improved engineered systems based on gut biomimicry. Later on, some costly treatment elements of the gut-based engineered system could be omitted and the decrease of the conversion rate could be investigated for further economic optimization. We can expect biotechnological developments in other fields that may contribute to a more economic animal gut mimicking system development. For example, a full implementation of the animal gut strategies might require addition of external enzymes, but current relatively high prizes of (hemi)cellulolytic enzymes prevent such strategies. Alternative solutions could be the implementation of *in-planta* expression of particular enzymes in energy plants as a strategy for accelerated lignocellulose digestion (Mir et al. 2017; Willis et al. 2016). Despite the challenges, the gut structure and inhabiting microbiota, the interaction of the community members, the enzymes and enzyme complexes evolved over millions of years will provide inspirations and valuable resources for process engineers to improve lignocellulose biorefineries.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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