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RESEARCH ARTICLE

Valorization of soybean-processing wastewater sludge via black soldier fly larvae: insights into the performance and bacterial community dynamics

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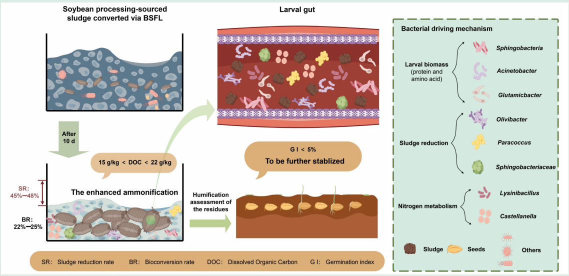
HIGHLIGHTS

- Feasibility of high-value conversion of soybean-processing-sourced sludge by BSFL.
- The larval gut exhibited higher bacterial diversity versus the residues.
- Diverse bacterial community could cause larval biomass and waste reduction.



ABSTRACT: Efficient and environmentally sound treatment of soybean processing wastewater sludge is importance for industrial sustainability. Bioconversion by black soldier fly larvae (BSFL) has been extensively applied in biowaste recycling because of its efficacy and production of high-value outputs. However, the performance and underlying bacterial drivers of the BSFL-mediated sludge bioconversion require further investigation. This study investigated the larval bioconversion of the sludge, emphasizing waste reduction, larval quality, and the relationship between these aspects and bacterial communities. The inoculation with BSFL remarkably enhanced the reduction in the initial substrate (i.e., sludge plus wheat bran as the bulking material). This intervention also yielded a high larval bioconversion rate of approximately 22% along with a higher larval crude protein content ranging from 45%–48% and a 17 amino acid to protein ratio of 86%–92%. Higher dissolved organic carbon concentrations (15–22 g/kg), coupled with lower germination indices (< 5%), indicated that the residues retained biological instability after the bioconversion and required further composting. The potential risk of heavy metal pollution from mature larvae may not be a concern when used as aquaculture feed. The larval gut exhibited a higher bacterial diversity than the residues. Ammonium concentration increased with wheat bran and was positively correlated with the genera *Lysinibacillus* and *Castellanella*. Diverse gut bacteria (*Olivibacter*, *Paracoccus*) primarily facilitated notable sludge reduction. *Sphingobacteria, Acinetobacter* and *Glutamicbacter* played key roles in larval growth traits (biomass, protein, and amino acids). This

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study indicated that the valorization of soybean-processing-sourced sludge was achieved via functionally important BSFL intestinal microbiota, providing an efficient recycling approach for similar waste streams.

KEYWORDS: Black soldier fly, Bio-stabilization, Gut microbes, Excess sludge, Valorization

1 Introduction

The soybean processing industry generates over 20 million tons of wastewater annually in China (Wang et al., 2021), and the resulting byproduct, known as sludge (referred to as SS), poses challenges in terms of treatment and disposal. This type of sludge is considered a valuable resource owing its high organic content. Currently, the common methods for treating sludge are incineration and anaerobic digestion, which have drawbacks such as high energy consumption, high investment costs, and incomplete resource utilization (Wang and Lee, 2021; Liu et al., 2023). Unlike sludge from municipal sewage treatment plants, SS is less contaminated with toxins such as antibiotics and microplastics, because the input wastewater has relatively simple components (protein and sugar) (Shi et al., 2014; Canaan et al., 2022). Given its advantages in resource utilization, there is an urgent need to explore efficient and environmentally friendly recycling approaches.

Owing to its many advantages, including significant waste reduction and lower carbon emissions compared to anaerobic digestion (Bohm et al., 2022; Siddiqui et al., 2022), the biotechnology using black soldier fly larvae (BSFL), which convert organic waste into high-quality products has received increasing attention (Bohm et al., 2022; Rossi et al., 2023; Du et al., 2025). BSFL can quickly utilize easily degradable organic matter with the aid of intestinal microorganisms and enzymes (Quan et al., 2023). This allows for rapid waste reduction and the production of high-valued larval proteins and frass, which can be used as biofertilizers. The treatment targets of BSFL mainly include perishable organic wastes such as animal manure and food waste (Mishra and Suthar, 2023; Deng et al., 2024; Wu et al., 2024; Du et al., 2025). Although previous studies have explored the bioconversion of excess municipal sludge via BSFL (Arnone et al., 2022; Bohm et al., 2022; Rossi et al., 2023), a risk of heavy metal (HM) pollution in the final residues remains. In addition, external materials such as food waste, are typically added to adjust the water content and nutrient composition of municipal sludge (Mishra and Suthar, 2023; Tian et al., 2024), thus posing challenges for the application and promotion of BSFL biotechnology. It is reasonable to infer that SS with a high organic biowaste content is a suitable feed for BSFL growth. Therefore, investigating its feasibility is of great significance for the valorization of this type of sludge and the sustainable development of related fields.

The BSFL-based bioconversion of biowastes is essentially driven by larval intestinal microorganisms, although the effects of factors such as substrate composition, external materials and feeding approaches are important (Jiang et al., 2019; Mannaa et al., 2023; Rossi et al., 2023; Wang et al., 2024). The degree of waste reduction, the occurrence of nitrogen, and humification level, which were considered critical parameters for the bioconversion system (Mannaa et al., 2023; Mishra and Suthar, 2023; Deng et al., 2024; Tian et al., 2024), can be used to evaluate the performance of sludge degradation and the application potential of residues obtained in agriculture. Nevertheless, studies on the correlation between these material transformations for the BSFL-based bioconversion system and the associated microbial communities are still relatively scarce. The particle size of the substate is as a key parameter for BSFL bioconversion and the relationship between chemical properties and bacterial community has been investigated (Wang et al., 2024). BSFL inoculation decreased the emission of odor components during the bioconversion of food waste through changing the abundance of several bacteria (*Lactobacillus* and *Enterococcus*) (Michishita et al., 2023). In addition, high-quality larval biomass (bioconversion rate, the content of protein and amino acids), regarded as an important parameter for the BSFL-based system is primarily attributed to the digestion and absorption of organic matter by specific gut microorganisms (Jeon et al., 2011; Mannaa et al., 2023; Wang et al., 2024). In other words, the changes in microbial community impact larval growth, particularly under different water contents conditions that are sensitive factors for a BSFL system. Consequently, unraveling the above mechanisms related to the microbial community is essential for achieving the valorization of SS by BSFL.

In short, the purpose of this study was to investigate the bioconversion performance of soybean -processing-sourced sludge with the aid of BSFL and elucidate the potential bacterial driving mechanism for sludge valorization. The target sludge, mixed with different ratios of additives (wheat bran) to regulate water content, ensuring it complies with the specific feeding requirements of BSFL (Lalander et al., 2020; Ganesan et al., 2024), was prepared as the feedstock for the BSFL. Sludge reduction and evaluation of the biochemical properties (dissolved organic carbon (DOC), ammonium/nitrate, and germination index (GI)) of the final residues were conducted to understand the performance of sludge decomposition. Larval biomass and quality were examined by analyzing the weight and crude protein/amino acid content of the mature larvae after bioconversion. A correlation between these indicators and the bacterial community was established through bioinformatic analysis to attempt to gain insight into the possible mechanism of sludge valorization by BSFL. This study is expected to provide a novel and feasible approach for the high-value utilization of sludge generated in a similar field.

2 Materials and methods

2.1 Soybean-processing-sourced sewage sludge and BSFL

The target sludge used in the BSFL bio-conversion experiment was collected from a soybean- processing-sourced wastewater treatment facility with a spiral extruder in Shandong Province, China. This facility adopts an anaerobic biological treatment process with a hydraulic retention time of 20 h, followed by aerobic biological treatment with a hydraulic retention time of 10 h, resulting in the daily generation of approximately 200 t of wet sludge. Wheat bran was added to the sludge to improve the BSFL bioconversion system because its fibrous structure provides an ideal environment for the survival and feeding of BSFL (Bohm et al., 2022; Siddiqui et al., 2022). Four treatments with different water contents were established, and the initial biochemical properties of the substrates are presented in Table 1. The BSFL eggs used in the BSFL bioconversion experiment were purchased from a BSFL breeding company in Huizhou, Guangdong Province, China. The eggs were incubated for 2 d under dark conditions at a temperature of 27 °C and a humidity of 70%. They were then fed with wheat bran for 3 d before being inoculated into the target sludge. 50 randomly selected larvae were weighed to determine the initial average weight per larva (0.23 mg/larva).

2.2 BSFL bioconversion process

Different wheat bran addition ratios were used to adjust the moisture content of the SS, ensuring it complies with the specific feeding requirements of BSFL (Lalander et al., 2020; Ganesan et al., 2024), as shown in Table 1. The BSFL experiment was conducted in plastic boxes measuring 17 cm × 11 cm × 5 cm (length × width × height). Due to the limited feeding capacity of larvae in the initial stages of treatment, the feed was incrementally added multiple times throughout the bioconversion process. This feeding approach was referred to the Chinese National Standard for Resource utilization of agricultural wastes—Comprehensive utilization of biomass resources (GB/T 42697–2023), minimizing variations in larvae across different groups. In detail, three-day-old larvae (0.092 g in total) were inoculated into 50 g of the mixed substrates for each reactor on day 0 according to the larval stocking density of 2.1 larvae/cm^2 (Sideris et al., 2021). Then, 70 and 80 g of the mixed substrates were respectively added on day 5 and day 7. The specific addition amounts were detailed in Table 1. Each treatment was replicated three times and each reactor was covered with a nylon mesh to prevent the larvae from escaping. The bioconversion experiments were conducted in an incubator at a temperature of 30 ± 1 °C and humidity of approximately 70% (Tian et al., 2024). When the body of the larvae darkened slightly, signaling its nearing pupation, the bioconversion of the substrate was terminated, typically taking a total of 10 d. Mature larvae were separated from the final mixture using a 5 mm sieve and weighed in terms of

Table 1 Experimental design of BSFL bioconversion and the properties of initial mixed substrates

Ratio of sludge to wheat bran	Wet weight of initial mixed substrate (g)	Water content (%)	OM (%)	pH	EC (mS/cm)	C/N	NH_4^+ (g/kg)	NO_3^- (g/kg)
10:1	220	82.42 ± 1.73	79.44 ± 2.48	6.63 ± 0.05	4.46 ± 0.05	7.83 ± 0.27	3.40 ± 0.00	0.38 ± 0.00
10:1.5	230	80.18 ± 0.24	80.17 ± 1.06	6.59 ± 0.00	4.04 ± 0.05	8.54 ± 0.15	3.23 ± 0.01	0.39 ± 0.00
10:2	240	76.81 ± 0.70	82.65 ± 0.40	6.70 ± 0.00	3.66 ± 0.08	9.49 ± 0.53	2.84 ± 0.00	0.38 ± 0.00
10:2.5	250	75.09 ± 0.12	83.20 ± 0.51	6.79 ± 0.03	3.27 ± 0.10	10.66 ± 0.24	2.87 ± 0.00	0.39 ± 0.00

Note: values are represented in mean ± deviation; OM, organic matter; EC, electrical conductivity; C/N, the ratio of carbon to nitrogen.

total and individual weight. For subsequent bacterial analysis, 10 larvae were randomly selected from each treatment group. To extract the gut contents of the larvae, the surface debris was first washed with sterile water, then the remaining moisture was absorbed using sterile paper. Finally, the larvae were allowed to defecate in a sterile culture dish for three hours. The collected residues and larvae were freeze-dried for physical and chemical analyses.

2.2.1 Substrate reduction and bioconversion efficiency

To evaluate the overall performance of the BSFL bioconversion system, the residual waste and the obtained larvae were used to calculate the sludge reduction rate (SR) and bioconversion rate (BR) using the following equations:

$$SR = \frac{WI - WF}{WI} \times 100\%, \tag{1}$$

$$BR = \frac{LF - LI}{WI - WF} \times 100\%, \tag{2}$$

where SR and BR are calculated based on the dry weight (Diener et al., 2009; Gold et al., 2020), LI is the weight of initial larvae, LF is the weight of final larvae, WI is the weight of the initial substrate, and WF is the weight of the final substrate.

2.2.2 Biochemical properties of the residues

The prepared samples were extracted using Milli Q water in a 1:10 (dry weight: volume) ratio. The resulting mixtures were divided into two parts. One part was used to determine the pH and electrical conductivity (Cui et al., 2023), and the other part was measured for DOC, ammonia and nitrate using a TOC analyzer (TOC-L CSN, Shimadzu, Kyoto, Japan) and an ion chromatograph analyzer (Dionex Aquion, Thermo Fisher, MA, USA) after filtration through a 0.22 μm pore size membrane (Cui et al., 2023). The HM concentrations in the residues were determined using an ICP-MS analyzer (ICAP RQ, Thermo Fisher) (Wang et al., 2023). The humification extent of the residues after BSFL bioconversion was assessed by examining the GI of the residues for different treatments, following the method from a previous study (Cui et al., 2023).

2.3 Larval quality

The amounts of crude protein and amino acids were measured to determine larval quality. Dried larvae were prepared using a vacuum freeze-dryer (5810 R, Eppendorf, Hamburg, Germany). The detailed methods for measuring crude protein and amino acids followed the Chinese national standards of GB/T 6432–2018 and GB/T 18246–2019. In detail, the determination of crude protein content in dried larvae involves digesting the sample with sulfuric acid in the presence of a catalyst, distilling the resulting mixture with alkali to release ammonia, absorbing the ammonia using boric acid, and titrating the absorbed ammonia with a standard hydrochloric acid solution, after which the measured nitrogen content is multiplied by 6.25 to estimate the crude protein content. Moreover, the proteins in the larvae were hydrolyzed into amino acids using a 6 mol/L hydrochloric acid solution, followed by separation via ion exchange chromatography and derivatization using an indenone column, with proline quantified at a wavelength of 440 nm and other amino acids measured at 570 nm. Eighteen amino acids were analyzed to gain further insight into the quality of larvae under different conditions. The HM concentrations in both BSFL and sludge were investigated to assess the environmental risk of HMs in relation to the application of larvae. To determine HM concentration, the obtained larvae were fully digested in a microwave digestion machine at 165 °C for 20 min, and measured by using an ICP-MS analyzer (ICAP RQ, Thermo Fisher) (Wang et al., 2023). The bioaccumulation factor (BAF) can reflect the ability of the BSFL to accumulate a specific HM, and its calculation equation is as follows:

$$BAF = \frac{Concentrations\ of\ HM\ in\ the\ BSFL}{Concentrations\ of\ HM\ in\ the\ residues}, \tag{3}$$

where BAF stands for bioaccumulation factor, and HM refers to the heavy metal.

2.4 DNA extraction and bacterial 16S rRNA sequencing

DNA extraction and subsequent sequencing were performed using samples from the initial sludge, final residues, and gut contents. The procedures were performed by Shanghai Majorbio Bio-Pharm Technology Co., Ltd., China. The main processes, including DNA extraction, PCR amplification, cDNA library construction, and Illumina sequencing, were conducted according to our previous study (Lei et al., 2024). Bioinformatics analysis, such as principal component analysis (PCA), cluster analysis, network analysis, and difference analysis of phenotype, were performed on the company's platform.

2.5 Statistical analysis

Differences between treatments, with a significance level set at $p < 0.05$, were analyzed using SPSS software (IBM SPSS Statistics 27, IL, USA). A histogram of the parameters was generated using Origin Pro software. A diagram illustrating the potential mechanism of SS treatment using BSFL was created on the online platform FigDraw.

3 Results and discussion

3.1 Performance in the reduction and decomposition of sludge by BSFL

As shown in Fig. 1(a), all treatments exhibited a notable reduction with an SR of 45%–48%. Specifically, the systems with 20% and 25% wheat bran exhibited the highest SR of approximately 48%. Treatments with 10% and 15% wheat bran showed similar SR, implying that the larvae could survive and grow under the corresponding water content of the SS. A previous study showed that BSFL reduced the amount of municipal sludge by 29.5%–40.7% after the bioconversion of 20 d, which is lower than the reduction rate observed in the present study (Bohm et al., 2022). These findings demonstrate that BSFL can efficiently promote significant reduction of the SS, mainly due to the digestion and assimilation of BSFL leading to remarkable organic degradation (as confirmed by DOC) of the SS (Mannaa et al., 2023). Consequently, a significant increase in larval biomass (i.e., BR) was also observed after BSFL bioconversion.

As a carbon source, DOC is easily utilized by microorganisms (Chen et al., 2023). The different treatments displayed significant discrepancies in DOC content. The treatments with the addition of 10% and 25% wheat bran had the lowest (15 g/kg) and highest (22 g/kg) DOC contents, respectively (Fig. 1(c)). The treatment with a high wheat bran supplementation amount, known for its capacity to offer enhanced nutritional provisions (Siddiqui et al., 2022), stands as the predominant factor driving the augmented biomass of BSFL. However, regardless of the added amount of wheat bran, the residues did still not meet the requirement (DOC < 4 g/kg) for sludge maturity (Zmora-Nahum et al., 2005). The humification extent of biowaste and its biotreated residues (i.e., compost) is typically assessed using the GI (Kong et al., 2024). The GI values for all treatments were < 5% (Fig. 1(e)), indicating that the obtained products were biologically unstable according to the Chinese agricultural standard (GI ⩾ 70%, NY/T 525–2021) and contained toxic substances for plant growth, such as polyphenols and organic acids (Aiello et al., 2020; Chen et al., 2021). It is associated with the preference of BSFL for ingesting and digesting easily utilizable carbon compounds by microorganisms (Luo et al., 2018; Lopes et al., 2022). These results also validate that further biodegradation/

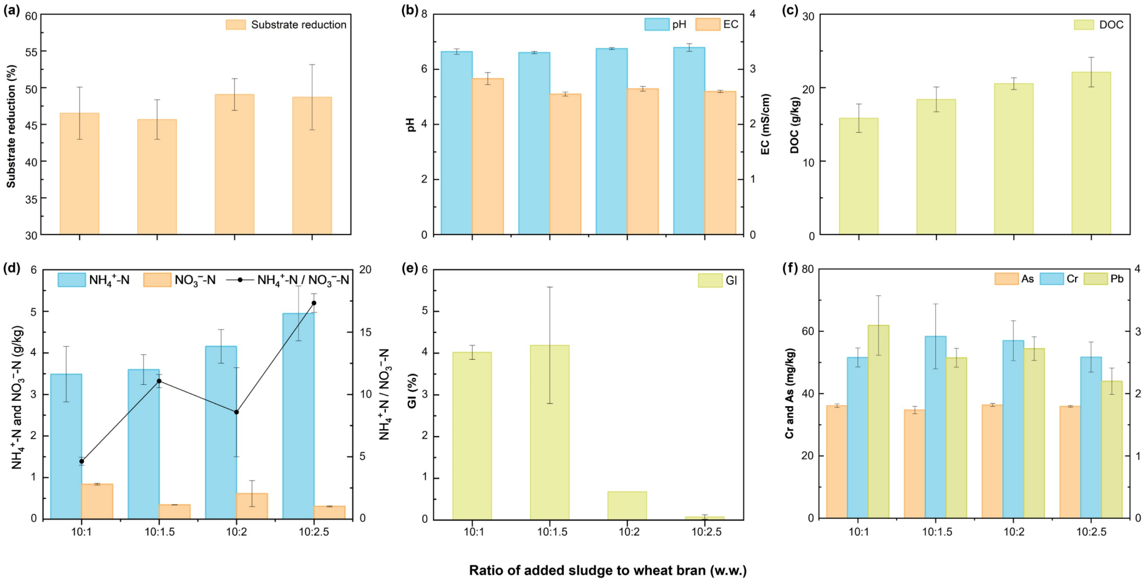


Fig. 1 Assessment of substrate properties in the BSFL bioconversion system under different conditions. (a) substrate reduction; (b) pH and electrical conduction (EC); (c) dissolved organic carbon (DOC); (d) NH_4^+-N and NO_3^--N; (e) germination index (GI); (f) heavy metals (HMs).

bio-stabilization processes are required before application as a soil amendment or biofertilizer (Song et al., 2021; Cui et al., 2023), which is a common feature of this technology (Ma et al., 2021; Song et al., 2021; Lopes et al., 2022).

The presence of residual HMs is not only related to the agricultural feasibility of the final product and to the safety of larvae as feed. Except for cadmium, which was not detected, other HMs (chromium, arsenic, and lead) were detected (Fig. 1(f)). However, their concentrations did not exceed the thresholds of the Chinese National Agricultural Standard for Organic Fertilizers (NY/T 525–2021) and the Chinese Standard for Organic-inorganic Compound Fertilizers (GB/T 18877–2020). This indicates that the final residues obtained from the BSFL bioconversion of sludge can be used as feedstock for the preparation of both fertilizers. These results differ from the occurrence of HMs in the conversion of municipal sludge by BSFL. In the latter case, the concentration of the target HMs after bioconversion often exceeds the environmental risk threshold, probably because of an HM-polluted wastewater source. Notably, the chlorine ion (Fig. S1) contained in the final residues did not exceed the limitation (5%) of the Chinese National Standard for ‘Compound fertilizer’ (GB/T 15063-2020). This finding indicates that there is no chloride ion toxicity when used as an organic fertilizer or soil amendment in agriculture.

3.2 Larval bioconversion rate and quality

BR and larval growth are key indicators that directly reflect the status of sludge valorization via the BSFL. From the perspective of larval growth, noticeable increases in bodyweight were observed in the range of 17–23 mg/larva (d.w.), with the highest increase observed in the treatments with 15% and 20% wheat bran (Fig. 2(a)). BR under different conditions ranged from 22% to 25%, with the lowest and highest values observed in the treatments with 10% and 15% wheat bran, respectively (Fig. 2(a)). These findings illustrate that BSFL conversion of the mixed substrate generate large numbers of larvae and the addition of 15% wheat bran is also considered optimal for feeding BSFL. The latter reason may be possibly related to the appropriate moisture content and nutritional ratio of the substrate. By comparison, in the study of BSFL digestion experiment, the food waste had a BR of approximately 23.9%, whereas the municipal excess sludge showed no significant larval growth during the process (Tian et al., 2024). The lower larval biomass for municipal sludge is likely associated with the relatively lower biodegradability and abundant emerging contaminants, leading to an insufficient nutrient environment for larvae survival (Wei et al., 2020). Obviously, applying

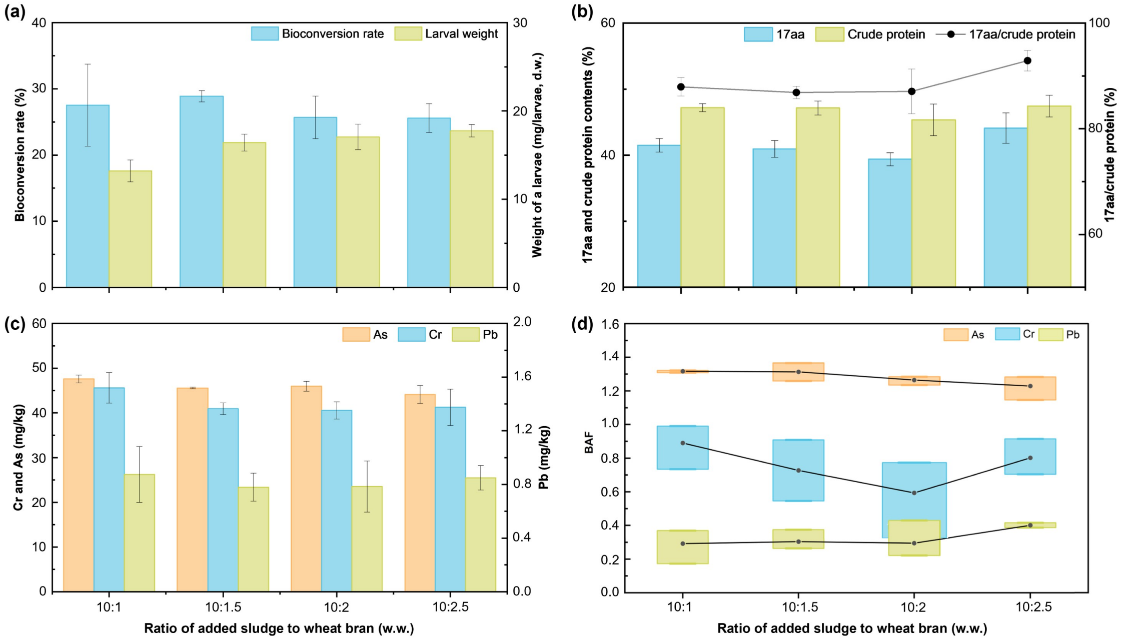


Fig. 2 Assessment for larval biomass and quality after the BSFL bioconversion of sludge. (a) bioconversion rate and larval weight, (b) crude protein, amino acid, and the ratio of 17 amino acid to crude protein, (c) heavy metals (HMs), (d) bioaccumulation factor (BAF).

soybean processing-sourced sludge as the feedstock of BSFL is feasible, which could have expectable larval yield.

Larval quality was assessed based on the percentages of crude protein and amino acids. Herein, the crude protein content was in the range of 45%–47% with no significant difference between the different treatments ($p > 0.05$) (Fig. 2(b)). Eighteen essential and non-essential amino acids were detected in each treatment. Furthermore, the 17 amino acids to crude protein ratio, which is generally used for the characterization of protein quality, reached 86%–92% (Fig. 2(b)), higher than the requirements of the Chinese National Standard for Feed Material-Fish Meal (GB/T 19164–2021). Especially, the treatment with 20% wheat bran presented a higher nutrient content compared to that of the white fish meal, implying that the larvae were more valuable in terms of nutrient content. Notably, the amount of wheat bran added to the sludge did not alter the larval quality. This can possibly be explained by the fact that the sludge used can provide large amounts of available organics (i.e., DOC; Fig. 1(c)) for the growth of larvae and microorganisms in a typical period of 10–14 d. Similarly, the crude protein content of the final larvae obtained from food waste was approximately 37% (Tian et al., 2024). Combining the analysis of larval biomass with quality in the present study shows that the sludge from the soybean processing industry is a high-quality feedstock for the valorization of larvae.

In addition to larval quality, the results based on the bioaccumulation of HMs also confirmed that, except for arsenic with a BAF > 1.0, the BFA values of other HMs (chromium and lead) were all < 1.0 (Fig. 2(d)). This indicates that the BSFL can discharge chromium and lead into the residues because of the specific larval peeling mechanism, specifically for lead (Mireji et al., 2010), which is in accordance with the results for residual HMs (Fig. 1(f)). A previous study found that BSFL did not accumulate HMs in the larval body, but rather in the treated biosolids (Bohm et al., 2022). Therefore, the related risk of HMs pollution from mature larvae may not be a concern when used as feed for aquaculture. The accumulation of arsenic in mature larvae observed in the present study (Fig. 2(c)), may be related to the fact that this element mainly exists in the intestines of BSFL (Van der Fels-Klerx et al., 2016).

3.3 Response of bacterial community to BSFL digestion

The decomposition of organic matter by BSFL is mainly attributed to the diverse microbial functions in their intestines (Jeon et al., 2011; Mannaa et al., 2023). As shown in Fig. 3(a), the Shannon index of the gut contents in the four treatments is significantly higher than that of the corresponding residues ($p < 0.05$), with the former exhibiting a diversity index between 3.07 and 3.96 and the latter between 2.1 and 2.7 (Table S1). The Ace and Chao indices showed similar trends. These results indicated higher bacterial diversity in the larval gut than in the residues, irrespective of the amount of wheat bran added. The diverse bacterial communities in the larval gut contribute to the rapid decomposition of organics in the sludge, which is consistent with previous studies on the treatment of food waste and cow manure by BSFL (Wang et al., 2024). The PCA results (Fig. 4(a)) showed that the bacterial communities (genus level) of the residues and intestinal contents for all the treatments were divided into two parts (i.e., red and blue zones). Similarly, analysis of the heat map (Fig. 4(b)) with clusters (genus level) further verified the higher bacterial diversity in the larval gut and a comparable bacterial composition, despite the added amount of wheat bran. The stability of the microecological environment in the larval gut, which has evolved over the long-term, may explain this observation (Klammsteiner et al., 2020). Additionally, 15 dominant phyla, including Actinomycetota, Deinococcota, Patescibacteria, Verrucomicrobiota, and Acidobacteriota, showed significantly differences in abundance ($p < 0.05$, Fig. 4(c)). Interestingly, other phyla such as Bacteroidota, Pseudomonadota, and Bacillota, which are commonly prevalent in the larval gut (Fig. 3(b)), did not display remarkable differences. This suggests a relatively stable bacterial community structure in the larval gut and that the decomposition of organics was not affected by substrate characteristics. The phylum Actinomycetota was the most abundant, particularly in the residues. These bacteria are aerobic and commonly present in decaying organics, showing resistance to invasion by pathogenic bacteria. At the genus level (Fig. 4(d)), *Dysgonomonas* was widely present in the intestinal contents and residues, with higher abundance in the residues ($p < 0.05$). Previous studies have found that bacteria inhabiting in the intestinal tract of termites participate in cellulose degradation (Sun et al., 2018). The genus *Dysgonomonas* is a dominant bacterium in the hindgut of termites, possessing multiple lignocellulose-degrading enzyme genes and a complete pathway for the degradation of lignocellulose, producing acetic and lactic acid. This genus also contains genes related to nitrogen metabolism and pathogen resistance, promoting lignocellulose degradation (Sun et al., 2018). Thus, BSFL may also have a promoting effect on lignin

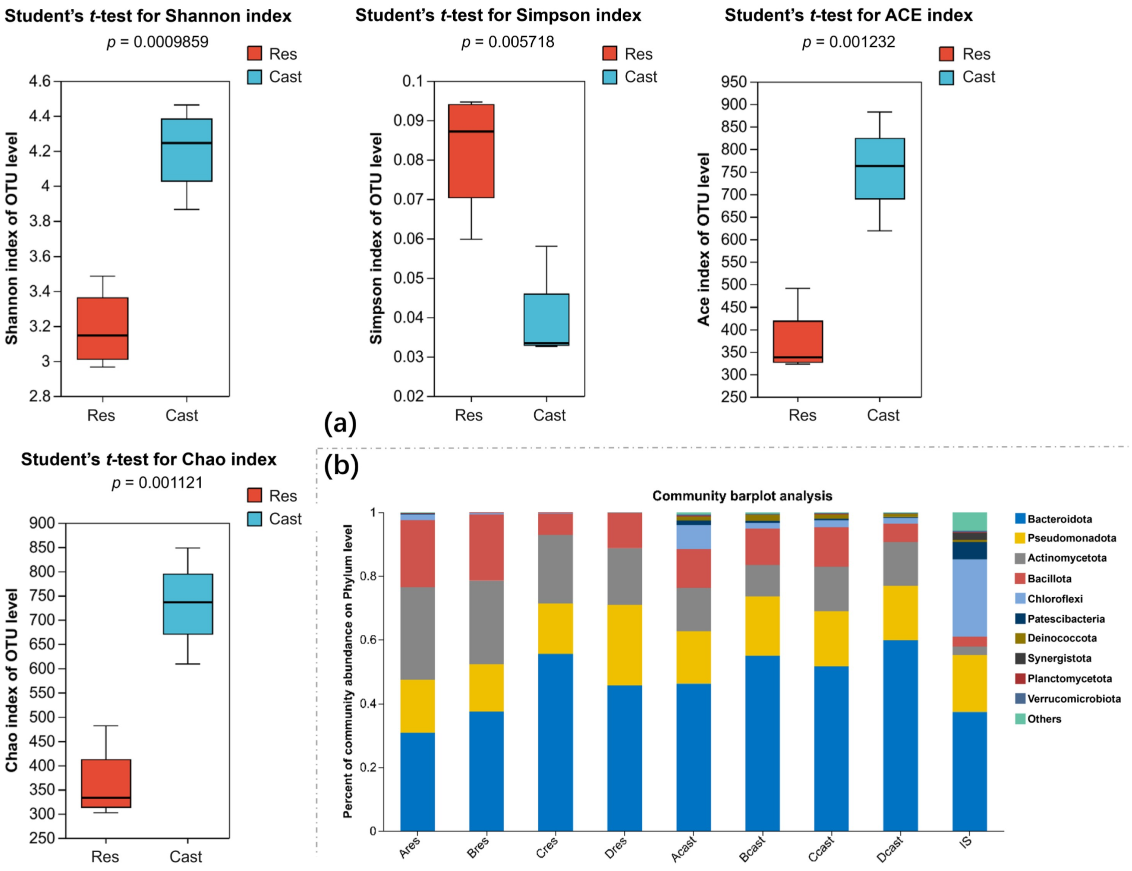


Fig. 3 Difference analysis of diversity index at OTU level (a) and bacterial community structure at phylum level (b) for the residues and larval gut contents. Legends: Res (red chart), the residues; Cast (blue chart), the larval cast.

degradation in sludge, although the underlying mechanism requires further validation. The genus *Thauera* belonging to the phylum Pseudomonadota can degrade aromatic/aliphatic organic compounds as a carbon source and remove nitrogen through denitrification (Mao et al., 2023). Therefore, the larval environment is conducive to the degradation of organics in the sludge. The genus *Chitinophaga* can produce potential antibiotic-resistant substances to inhibit pathogens (Deng et al., 2021a), and its higher abundance in intestinal contents indicates the presence of antibacterial functions, consistent with existing knowledge (Moretta et al., 2020).

3.4 Relationships between sludge reduction, larvae quality, and related bacterial community

3.4.1 Relationships between sludge reduction and bacterial community

Network analysis has been widely applied to elucidate the interactions between bacterial communities and environmental factors. In this study, positive relationships between the SR and dominant bacteria, such as *Olivibacter*, *Paracoccus*, *Alcaligenes*, Sphingobacteriaceae, and *Acinetobacter*, were observed (Fig. 5(a)). This indicates that sludge reduction is the result of a comprehensive regulation by diverse functional bacteria. Among them, *Olivibacter jilunii*, isolated and purified from garden waste composting, has the ability to decompose cellulose (Rao and Xie, 2023). *Paracoccus* exhibits excellent bioremediation potentials, including denitrification of nitrate/nitrite and degradation of various toxic organic compounds (Decewicz et al., 2019). *Alcaligenes*, which are common intestinal parasites in certain animals, participate in the decomposition and mineralization of organic substances, such as butyric acid, fats, and proteins (Shoda, 2020). Sphingobacteriaceae is an excellent degrader of aromatic compounds in the environment (Figueiredo et al., 2022). These bacteria have important contributions to sludge reduction.

The occurrence of nitrogen in sludge is related to the evolution of microbial communities, the growth and

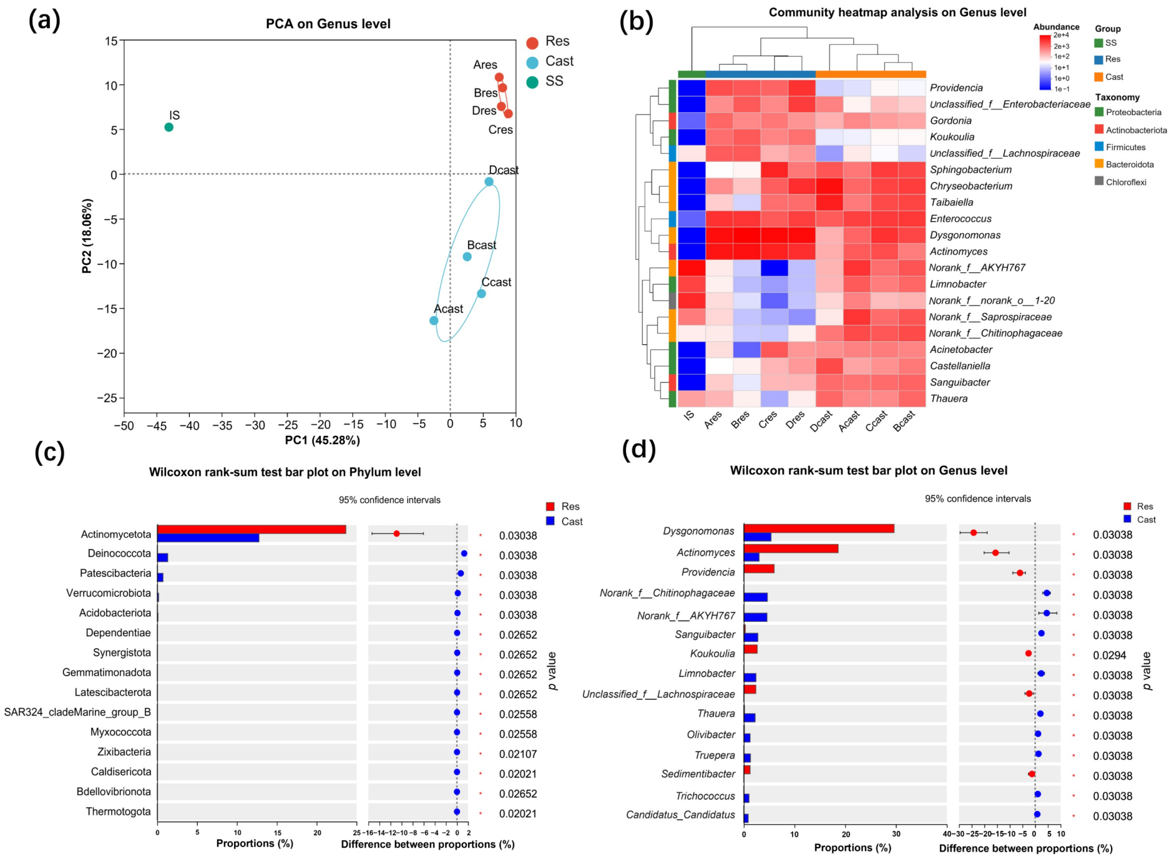


Fig. 4 Comprehensive assessment for difference of bacterial community between the final residues and gut contents. (a) PCA at genus level, (b) heat map, (c) and (d) difference analysis of dominant bacteria community at phylum and genus levels. Legends: Res (red chart), the residues; Cast (blue chart), the larval cast.

development of BSFL, and the nutritional level of the final feces. As shown in Fig. 5(a), NH_4^+ is positively correlated with the genera *Lysinibacillus* and *Castellanella* and negatively correlated with *Bacillus*, *Anaerovorax*, *Phasolarctobacterium*, *Isophaera*, *Mycobacterium*, and *JG30-KF-CM45*. *Lysinibacillus* and *Castellanella* belong to the phyla Bacillota and Pseudomonadota, respectively. The former is often involved in the metabolism of proteins and carbohydrates (Li et al., 2012), whereas the latter is commonly found in anaerobic digestion reactors and has denitrification functions (Deng et al., 2021b). In addition, NO_3^- was positively correlated with the family Atopobiaceae which belongs to the phylum Actinomycetota (Fig. 5(a)), indicating that this bacterium may be involved in the conversion of NH_4^+ to NO_3^- in the sludge. However, direct evidence for this is required. The presence of these bacterial communities was beneficial for the transformation of nitrogen-containing organic matter in the sludge, making the final residues more nutritious. Additionally, the residues for all the treatments with a lower GI were speculated to contain undegraded substances (Cui et al., 2023), which is mainly attributed to the specific metabolic environment in the larval gut. A significant positive correlation was observed between the GI and genus *Actinomyces*, as presented in Fig. 5(a). Furthermore, based on the analysis of the GI under different treatment conditions, the greater the amount of wheat bran added, the lower the GI, indicating that it is difficult for larvae to digest the bran. Considering that wheat bran is rich in cellulose (Xiao et al., 2023), an increase in the abundance of *Actinomyces* is beneficial for the degradation of the aforementioned fibrous substances, resulting in a lower GI by promoting the release of soluble substances (i.e., DOC, Fig. 1(c)).

The change in pH during sludge degradation via the BSFL is mainly controlled by the transformation of nitrogen-containing organics and the production of organic acids. As shown in Fig. 5(a), pH is positively correlated with the genera *Chryseobacterum*, *Glutamicibacter*, *Sanguibacter*, and *Taibaiella*. Among

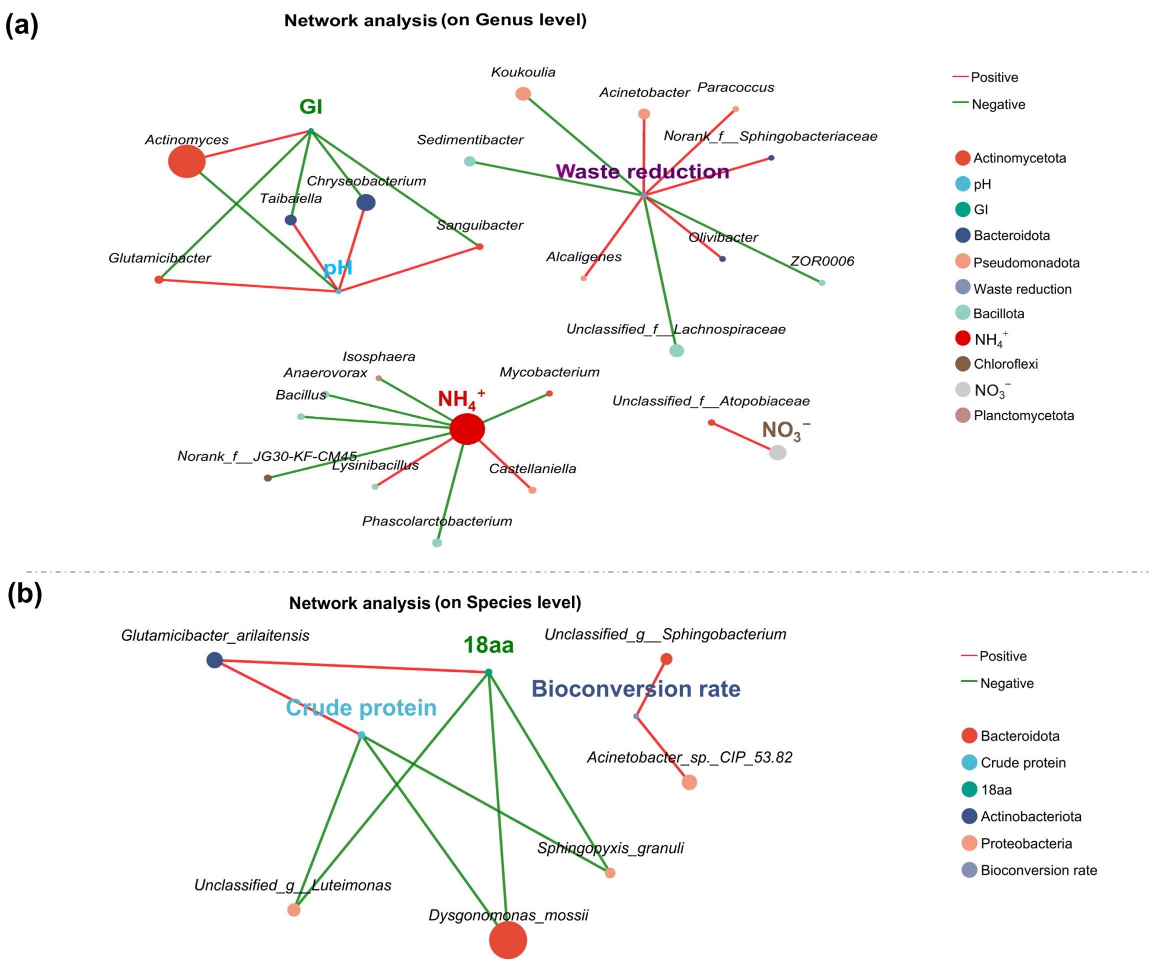


Fig. 5 Network analysis between the biochemical properties (a), larvae quality (b) and bacterial community. Legends ‘negative’ (green line) and ‘positive’ (red line) represent the correlation between the target indicators and bacterial community, respectively.

them, *Chryseobacterum* and *Taibaiella* belong to the phylum Bacteroidota, with *Chryseobacterum* having high enzyme activity to degrade litterfall (Zheng et al., 2021). *Glutamicibacter* and *Sanguibacter* belong to the phylum Actinomycetota, and some *Glutamicibacter* species are considered capable of implementing denitrification in wastewater treatment, contributing to changes in pH. In addition, a negative correlation with *Actinomyces* indicates that these bacteria are involved in the metabolic activities of polysaccharides (cellulose and lignin), leading to changes in the acid-base environment of the sludge (Javed et al., 2021).

3.4.2 Relationships between larvae quality and bacterial community

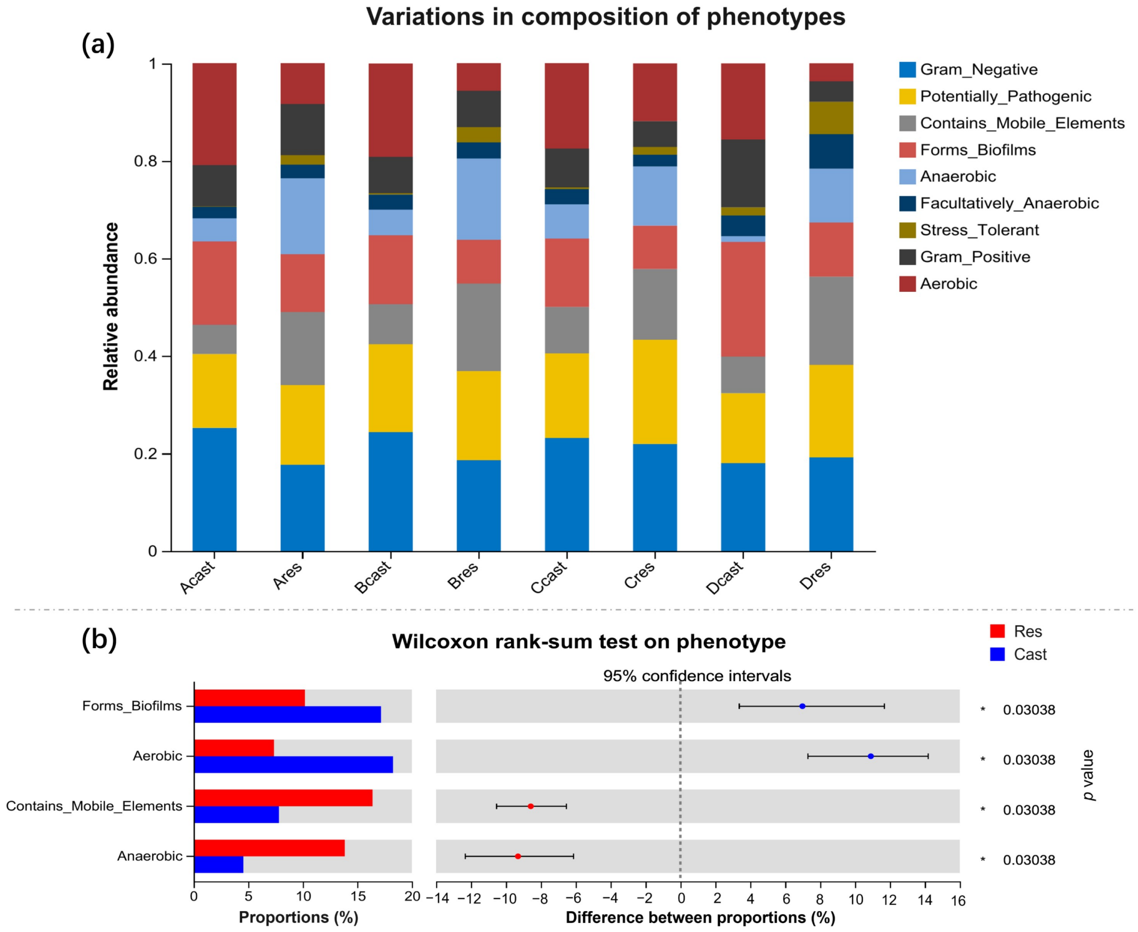
Certain organics in the sludge are metabolized and assimilated into larval biomass, which is closely associated with the gut microbiota (Mannaa et al., 2023). As shown in Fig. 5(b), the BR is positively correlated with the genera *Sphingobacteria* and *Acinetobacter*, which belong to the phyla Bacteroidota and Pseudomonadota, respectively. These genera are mainly responsible for the metabolic conversion of substances such as proteins and sugars (Wang et al., 2022). Therefore, they could promote the conversion of proteins and fatty substances, which are important components of sludge, to the biomass of BSFL. Higher microbial diversity and less complex but more specialized networks are important factors in achieving efficient organic decomposition (Zheng et al., 2021). Additionally, as the main components of the larvae, the formation of crude protein and amino acids was significantly positively correlated with *Glutamicbacter* ($p < 0.05$, Fig. 5(b)). This further verifies the assimilation effect of the BSFL intestinal bacteria on the organics in the sludge. *Dysgonomonas*, *Sphingopyxis*, and *Luteimonas* were negatively correlated with crude proteins and amino acids. It is speculated that these bacteria may negatively regulate assimilation. However, the underlying mechanisms remain to be validated.

3.5 Metabolic prediction based on bacterial community

Microbial metabolism is a distinct feature of biowaste treatment via BSFL (Yuan et al., 2021). Phenotype analysis of the residues and gut contents, which is expected to reveal the organic dynamics during the bioconversion of soybean-processing-sourced sludge via BSFL, is presented in Fig. 6. Phenotypes such as the biofilm formation and gram-negative bacteria were more frequently observed in the larval gut than in the residues, with $p < 0.05$. This finding indicates significantly different microenvironments in the larval gut, thus facilitating exclusive metabolic properties of organic substances (Mannaa et al., 2023). Furthermore, significantly more aerobic and anaerobic bacteria in the larval gut than in the residues ($p < 0.05$). The presence of more mobile elements related to genetic information transfer (i.e., antibiotic/HM resistant) in the residues suggests that the larval intestinal microenvironments could weaken the communication of these genes. The behaviors of antibiotic- resistant genes during housefly larval conversion of manure have also been documented by a previous study (Wang et al., 2017).

3.6 Possible mechanism of valorization of SS via BSFL

Based on the comprehensive analysis presented above, the potential mechanisms driving the valorization of excess sludge from the soybean-processing industry via BSFL are summarized in Fig. 7. The internal aspects of valorization are mainly reflected in two aspects: a


Variations in composition of phenotypes

Wilcoxon rank-sum test on phenotype

Fig. 6 Phenotype and its difference analysis based on functional prediction of the target samples. Legends: Res (red chart), the residues; Cast (blue chart), the larval cast. Asterisk (*) indicates significant difference at level of $p < 0.05$.

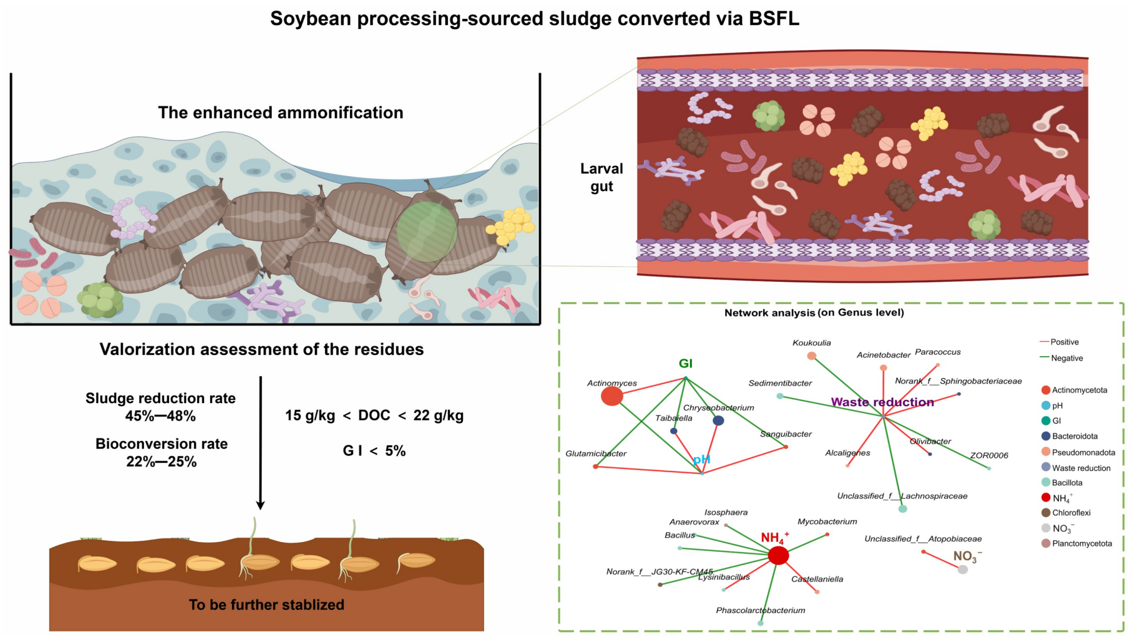


Fig. 7 The potential mechanism of valorization of the SS by BSFL.

significant reduction in sludge and enhanced nutrient quality for larvae. Based on a deeper analysis of the bacterial community, the BSFL gut exhibited exclusive metabolic properties of organic substances, such as increased bacterial diversity. The substantial reduction in sludge mass could be attributed to the active metabolism of the dominant bacteria in the larval gut, including the phyla Bacteroidota, Pseudomonadota, Bacillota, and Actinomycetota. Additionally, certain bacteria, such as the family Atopobiaceae and genus *Lysinibacillus* may contribute to nitrogen transformation during sludge degradation by BSFL. Protein-degrading bacteria (*Glutamicbacter*, *Sphingobacteria* and *Acinetobacter*) play important roles in transforming organics into amino acids, resulting in markedly higher larval biomass and protein nutrient quality. However, the lower GI values and higher DOC levels indicated that the final residues after the BSFL conversion of sludge remained biologically unstable, requiring further biostabilization before use as a soil amendment or biofertilizer. In summary, BSFL-mediated bioconversion can achieve the valorization of sludge sourced from the soybean industry within a relatively short period (10 d) via taxon-specific larval metabolic functions.

4 Conclusions and perspectives

This study investigated the performance and underlying mechanism of recycling soybean-processing-sourced sludge using BSFL. The presence of the larvae significantly enhanced the reduction and degradation of the target sludge. Concurrently, the harvested larvae exhibited large biomass and abundant and diverse amino acid profiles, particularly for the treatments supplemented with higher amounts (i.e., 15% and 20%) of wheat bran. It was concluded that BSFL-mediated bioconversion represents a feasible approach for treating sludge sourced from soybean processing, thereby opening avenues for the effective recovery of resources from similar organic wastes. Furthermore, the distinctive bacterial consortia (high diversity) inhabiting the larval gut largely contribute to sludge metabolic features, including substrate reduction, nitrogen transformation, and the formation of larval proteins and amino acids. Supplementing sludge with approximately 15% wheat bran is considered optimal and capable of simultaneously achieving efficient sludge reduction and the production of high-quality larvae.

Because nutrients may affect the performance (reduction and larval growth) of sludge bioconversion via BSFL under current water-controlling conditions, study through specific dry weight-based experiment setup along with materials balance analysis requires to be carried out to improve the biomass and quality of larvae. Drawing from the findings of our study, there is a clear need to enhance the efficiency of BSFL in converting sludge, particularly when extending their application to other types of sludge. It is crucial to address the adaptability and conversion rates of BSFL in various types of sludge to optimize their effectiveness in bioconversion processes. Although study on the conversion of sludge using BSFL has produced substantial findings, it is essential to critically evaluate the operational models and economic viability (Table S2) during the transition from laboratory studies to industrial applications.

Conflict of Interests The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

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