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Black soldier fly larvae for organic manure recycling and its potential for a circular bioeconomy: A review

Tao Liu [a], Thomas Klammsteiner [b], Andrei Mikhailovich Dregulo [c], Vinay Kumar [d], Yuwen Zhou [a], Zengqiang Zhang [a], Mukesh Kumar Awasthi [a,*]

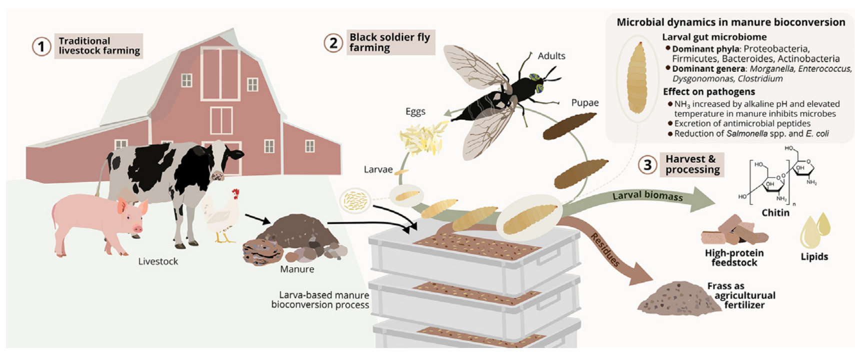
[a] College of Natural Resources and Environment, Northwest A&F University, Yangling, Shaanxi Province 712100, PR China
[b] Department of Microbiology, University of Innsbruck, Technikerstrasse 25d, 6020 Innsbruck, Austria
[c] Federal State Budgetary Educational Institution of Higher Education "Saint-Petersburg State University" 7-9 Universitetskaya emb., 199034, Saint- Petersburg, Russia
[d] Department of Biotechnology, Indian Institute of Technology (IIT) Roorkee, Roorkee 247667, Uttarakhand, India

HIGHLIGHTS

- Black soldier fly larvae (BSFL) were reviewed as an efficient tool for resource recovery from organic wastes.
- Discussion of the potential of BSFL for organic manure recycling
- Economic feasibility, lifecycle assessment, and circular bio economy related to the application of BSFL.
- Future perspectives associated with BSFL application were evaluated.

GRAPHICAL ABSTRACT

Illustration of how black soldier fly larvae can be used to convert livestock manure into various value-added products. 1. Typical livestock species and their manure accumulating at farms. 2. Black soldier fly life cycle and treatment of animal manure in typical rearing containers, and 3. Harvest and processing of larvae and residues into value-added products.



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ABSTRACT

Livestock farming and its products provide a diverse range of benefits for our day-to-day life. However, the ever-increasing demand for farmed animals has raised concerns about waste management and its impact on the environment. Worldwide, cattle produce enormous amounts of manure, which is detrimental to soil properties if poorly managed. Waste management with insect larvae is considered one of the most efficient techniques for resource recovery from manure. In recent years, the use of black soldier fly larvae (BSFL) for resource recovery has emerged as an effective method. Using BSFL has several advantages over traditional methods, as the larvae produce a safe compost and extract trace elements like Cu and Zn. This paper is a comprehensive review of the potential of BSFL for recycling organic wastes from livestock farming, manure bioconversion, parameters affecting the BSFL application on organic farming, and process performance of biomolecule degradation. The last part discusses the economic feasibility, lifecycle assessment, and circular bioeconomy of the BSFL in manure recycling. Moreover, it discusses the future perspectives associated with the application of BSFL. Specifically, this review discusses BSFL cultivation and its impact on the larvae's physiology, gut biochemical physiology, gut microbes and metabolic pathways, nutrient conservation and global warming potential, microbial decomposition of organic nutrients, total and pathogenic microbial dynamics, and recycling of rearing residues as fertilizer.

* Corresponding author.
E-mail addresses: a.dregulo@spbu.ru (A.M. Dregulo), mukeshawasthi85@nwafu.edu.cn; mukesh_awasthi45@yahoo.com (M.K. Awasthi).

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1. Introduction

Livestock wastes have a significant impact on our environment. The ever-growing demand for animal products creates serious problems in managing the increasing volumes of manure (Åkerman et al., 2020; Awasthi et al., 2022a) and in eliminating the negative environmental consequences of abandoned livestock farms (Dregulo and Rodionov, 2020). Manure has valuable fertilizing properties, but the excessive introduction of manure into the soil leads to the pollution of natural environments (He et al., 2016; Khanal et al., 2020). Proper exploitation of manure allows the generation of biogas (Esteves et al., 2019; European Commission, 2021), compost for restoration of disturbed lands (Duan et al., 2019a; Pandey et al., 2022), and briquettes as an alternative fuel source (Bonelli et al., 2019; Hamid et al., 2021). However, most processing technologies are focused on the solid fraction of manure (Awasthi et al., 2022b; Khoshnevisan et al., 2021). Today it is recognized that treating organic waste with insect larvae is more efficient than conventional composting since it reduces the processing time and residual substrates have better-fertilizing properties (Awasthi et al., 2019a; Das et al., 2020; Ddiba et al., 2021; Kumar et al., 2022).

Ecosystem services provided by the natural environment as part of national economic activities are not properly priced by the market, leading to an inhibition of the market for products based on sustainable technologies and, thus, reducing the development of a closed-cycle economy (Awasthi et al., 2019; Cong and Thomsen, 2021; Wainaina et al., 2020). Despite the difficulties and efforts of transitioning to a "green economy", optimizing the utilization of organic waste (manure) is inevitable, ultimately meeting the requirements of closed-cycle bioeconomics. This is especially important for countries with suitable climatic conditions and (Awasthi et al., 2022d; da Silva and Hesselberg, 2020; Duan et al., 2021a) socioeconomic prerequisites (high cost of livestock feed, suitable legislative framework for waste management, and low income of the population etc.) (Duan et al., 2021b; Hamid et al., 2021; Lohri et al., 2017). In this article, we focused on summarizing the potential of black soldier fly larvae (BSFL) for processing organic manure as a means to manage agricultural wastes within the system of a circular bioeconomy.

2. Potential of black soldier fly larvae for organic manure recycling

The global prevalence of the black soldier fly (BSF; *Hermetia illucens* L.) is attributed to its domestication, and at the same time, there is an increasing introgression between domesticated strains as has been confirmed by individual samples from 57 countries (Awasthi et al., 2022c; Kaya et al., 2021). Consequently, the potential for producing BSFL as a regenerative resource of biomolecules within the prospects of a circular economy continues to grow. Converting organic waste with larvae of the BSF represents a potential benefit for countries striving for the transition to a more sustainable exploitation of their resources, and for developing countries in which waste is disposed of by primitive and unsustainable methods – e.g., in open landfills, etc. Moreover, the nutritional value of organic waste can be exploited by the BSFL as a response to the increase in prices for ecological raw materials and animal feed (Awasthi et al., 2019b; Awasthi et al., 2020a; Lakshmi et al., 2021).

Using BSFL to turn manure and other organic wastes into valuable products has several beneficial aspects: manure can be converted into safe compost, larval fat and rearing residues can be used to generate biofuels, and furthermore larval biomass can serve as a valuable protein source for livestock (Chia et al., 2021; Duan et al., 2019b; Wang et al., 2021) and aquaculture feed (Čengić-Džomba et al., 2020; Jiang et al., 2019; Awashti et al., 2022e). BSF females can lay several hundred eggs. The growth and reproduction of BSFL is similar to other insects and depends on a complex interaction of abiotic and biotic factors such as ambient temperature, humidity, lighting, nutritional value (caloric content) of the substrate consumed, and microbial colonization, etc. Moreover, the availability of nutrients in organic waste is not always the same (Matheson, 2019; Nguyen et al., 2013; Sideris and Tsagkarakis, 2017; Yuvaraj et al., 2021). Therefore, carefully studying the balance between larval growth and the amount of consumed substrate is required to assess the efficiency of waste processing. Organic manure also contains microorganisms of different trophic levels, which in turn are potential food competitors of BSFL, metabolizing available nutrients vital for larval thriving (Duan et al., 2019c; Leow et al., 2018; Pan et al., 2012).

The use of BSFL for composting chicken and pig manure increases the rate of humification (humic acid / fulvic acid) of compost threefold compared to untreated samples, and also contributes to better extraction of trace elements such as Cu and Zn (Liu et al., 2020a; Awasthi et al., 2021a). On an industrial-scale production, it is necessary to adjust the BSFL's daily diet in accordance with the fly's life cycle development in order to determine the optimal amount of substrate that enables both rapid waste bioconversion and high biomass yield (Duan et al., 2019d; Gobbi et al., 2013; Norgren et al., 2021). The feed amount may have a lesser effect on the survival of larvae, but at the same time it can strongly affect the biomass gain of larvae and the treatment of the manure during continuous feeding (Dzepe et al., 2021; Awasthi, 2022). For BSFL, fresh waste is more preferable than waste from advanced stages of decomposition (Rehman et al., 2017; Nana et al., 2019), which partially explains the better consumption of a mixture of organic waste and manure. However, this study showed that applying a feeding substrate once in three days was more effective compared to daily feeding, both in terms of larval biomass gain and conversion rate of the waste substrate. Despite the fact that manure or other organic wastes quickly rot and oxidize due to the high amount of protein and fat, BSFL can consume organic wastes with high differences in pH (4–9.5) with almost the same success (Meneguz et al., 2018a; Awasthi et al., 2019a; Romano et al., 2021). Among equally nutrient-rich substrates, there is variability in both the biomass yield from larvae and the rate of substrate consumption. BSFL have a high potential for organic waste consumption; on average, 17 g of 5 day-old-larvae are able to process up to 0.7 kg of organic waste per day (Pintowantoro et al., 2021). Other data from a large scale trial with 45,000 larvae showed a reduction of pig manure from approx. 68 kg to 41 kg dry weight, producing an insect biomass of approx. 26 kg (Newton et al., 2005; Duan et al., 2020a; Awasthi et al., 2021b). An important aspect is adjusting the number of larvae for a certain amount of waste and rearing scale, i.e. the larval density (Klammsteiner et al., 2021a). This is necessary because an excessive number of larvae (or perhaps their feeding behavior) creates obstacles around food, reducing the rate of its consumption. A mathematical model of the rational arrangement of BSFL on the waste surface showed that in order to overcome these limitations, it is necessary to form a cone-shaped flow of larvae, optimizing the surface of their contact with the waste substrate and thereby increasing the rate of its consumption (Shishkov et al., 2019; Awasthi et al., 2021c).

The dynamics of processing organic waste can be optimized by introducing additional organic waste or specific enzymes into the "larvae – waste" system. For example, a substrate consisting of bread dough improved larval growth and bioconversion but showed lower amino acid contents, while a substrate based on sweet potato increased the amount of fatty acids and amino acids in the biomass of BSFL (Sommer et al., 2013; Awasthi et al., 2020a; Romano et al., 2021). Ex situ fermentation using *Rhizopus oligosporus* fungi can increase the growth of BSFL by about 50% (Liu et al., 2022; Wong et al., 2021). This indicates that it is necessary to combine methods to further enhance the larvae's conversion of waste. For example, the addition of straw to cow manure during vermicomposting with earthworms (*Eisenia fetida*) increased the number of cocoons of worms, and the addition of biochar and nano-carbon made it possible to obtain bio-humus of higher quality in terms of C:N ratio (Awasthi et al., 2020b; Cao et al., 2021). Vermicomposting of a mixture of goat manure and food waste made it possible to increase the proportion of released phosphorus (Duan et al., 2020b; Katakula et al., 2021). Another important aspect is the reduction of fecal bacteria and xenobiotics in manure processed by larvae (Lalander et al., 2015; Awasthi et al., 2020c).

The bioconversion of chicken manure by BSFL changed the substrate's microbial diversity, increasing the proportion of dominant *Firmicutes* bacteria in chicken manure from 56% before treatment to 98% after treatment within 15 days (Liu et al., 2021a; Zhang et al., 2020). At the same time, the observed number of *Bacteroidetes* and *Proteobacteria* decreased, but the diversity of metabolic functions in bacteria isolated from the intestines of BSFL was significantly higher. A study by Wynants et al. (Wynants et al., 2018) showed that the composition of the microbial community isolated from BSFL may not depend on the substrate's microbial composition alone, but is also affected by the physiological characteristics of the larvae. Both the abundance and composition of bacterial communities may vary depending on the place of cultivation and the properties of the organic waste. This indicates that microbial communities might not only influence the efficiency of bioconversion processes, but they also offer an option to discover novel metabolic pathways useful to understand the biochemical dynamics during organic waste and animal manure processing Fig. 1.

The use of fecal sludge as feeding substrate for BSFL supplemented with 30% organic waste at a feeding rate of 200 mg larva^{-1} day^{-1} makes it possible to achieve higher processing efficiency of organic waste (Liu et al., 2021b; Nyakeri et al., 2019). During the conversion of sewage sludge, BSFL accumulate heavy metals, however, the concentrations of these metals in the extracted larval oil were low. This still allows the use of larval oil as technical oils, while heavy metals remain in the larval body as in an isolated container (Cai et al., 2018a; Awasthi et al., 2020d; Liu et al., 2021c). It is noted that the accumulation of heavy metals (Cd and Cr) in the body depends on the age of the larvae and can be transferred along the entire path of development from the larva to the pupa (Gao et al., 2017; Liu et al., 2020a; Zhou et al., 2021a). Mixing of rice husk-based sheep litter with dairy manure, while increasing the ratio of manure to sheep litter, decreased the treatment time proportionally (Cestonaro et al., 2017; Awasthi et al., 2020e). After the manure-based substrate was digested by BSFL, the amount of volatile organic compounds in the manure was almost completely reduced, and, accordingly, also the release of fecal (including greenhouse) gases declined. This especially plays an important role when using larvae for manure processing on an industrial scale (Beskin et al., 2018; Awasthi et al., 2020f; Zhou et al., 2021b). A study by Pang et al. (Pang et al., 2020a) showed that the consumption of a mixture of pig manure and corn cobs reduced total greenhouse gas emissions by >90%. The C:N ratio was identified as an important parameter in this process which affected the growth of larvae and, consequently, the conversion of organic waste biomass. In a study by Matos et al. (Matos et al., 2021), methane reduction reached 86% when cattle manure was processed by BSFL. A rich variety of digestive enzymes within the gut of BSFL (including high amylase activity (Kim et al., 2011b; Liu et al., 2021d) and other antimicrobial peptides) allows larvae to transform the ingested nutrients and convert them into their own biomass.

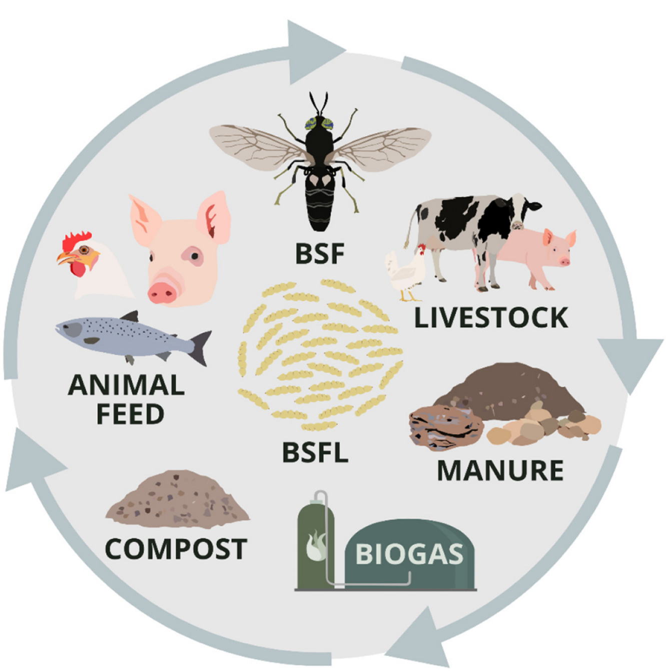

Fig. 1. Network of potential products and processes resulting from using black soldier fly larvae for organic manure recycling.

The omnivorous nature of BSFL opens new ways for profitable production and cultivation of larvae. Norgren et al. (Norgren et al., 2021) have shown that after fermentation, pulp and paper bio-sludge dissolved in fermentation fluid are easily absorbed by BSFL. The larvae were able to exploit these nutrients, whereas the conversion rate of these substances was higher compared to bottom sediments and unfermented pulp and paper waste. However, earlier data obtained by these researchers suggested that processing of pulp and paper bio-sludge by BSFL may be inefficient, even with the addition of a liquid nutrient substrate as an aid for its processing (Norgren et al., 2020). This indicates that the parameters affecting the growth and bioconversion dynamics of BSFL may lay within a fairly narrow range of their physiological aptitudes and, therefore, require additional research.

3. Current challenges for BSF organic manure processing

The transition from outdated linear models of economy to a more sustainable circular bioeconomy is one of the most promising ways to develop a modern society with high awareness of its responsibility to nature and future generations. Today, this transition is being studied and slowly implemented in different countries. However, even in developed countries, the transition to a circular waste economy is quite difficult. As an example, in the city of Brussels no >1% of the 1.5 million tons of collected waste are treated in a way that contributes to the closure of material cycles. Especially the separation (detailing) of waste for recycling can lead to an increase in prices for waste disposal services and a number of other problems (Liu et al., 2020b; Zeller et al., 2019). Focusing only on manure processing will obviously not be easy either. Studies conducted in the USA on the development of agriculture without animals showed that the reduction in greenhouse gas emissions would amount to 28% of livestock emissions, but only 2.6% of total emissions (White and Hall, 2017; Awasthi et al., 2020e). However, no matter how contradictory it may sound, the problem of livestock waste mostly affects regions where the population has relatively low incomes, which affects household management and the quality of services consumed. Ddiba et al. (Ddiba et al., 2021) conducted studies in a low-income region (Kampala, Uganda) and showed that the use of BSFL for the treatment of sewage sludge, fecal sludge, and household waste can produce 135,000 tons of solid fuel, 108,000 tons of compost, or 39.6 million Nm^3 of biogas per year. The revenues from the sale of these products can reach 5.1 to 47 million US dollars. However, to use the potential of BSF in low-income regions, initial capital will be required for the construction of BSF farms, waste collection and disposal sites, electricity fees, and labor fees, etc. Based on observations on the implementation of the Ento-Prize Project in Ghana, Chaalala et al. (Chaalala et al., 2018) concluded that for a small farm it is enough to spend an hour a day preparing a feed mixture and collecting and distributing fly eggs in incubators. This could allow an employee to receive an annual income three times the national average.

The processing of organic waste by BSFL is recognized as one of the most promising solutions for low-income countries (Joly and Nikiema, 2019; Liu et al., 2020c). The high increase in prices for animal feed, as well as the requirements for reducing greenhouse gases (Chen et al., 2020a; Kataria, 2016) are likely to become the dominant factors in the use of balanced feeds or feeds with lower nutritional value (Ouatahar et al., 2021). Therefore, there is still a significant need to study and improve the effectiveness of growing larvae on manure substrates with low nutritional value. Observations by Tittonell et al. (Tittonell et al., 2010), who studied the storage conditions of manure for 6 months, showed that the retention of nutrients during storage varied depending on whether the manure was stored under the roof or in the open air. While the manure under the roof contained high concentrations of N and K, precipitation-induced leaching may have caused the loss of nutrients from manure stored in the open air.

Of high relevance is also the use of the BSF protein in poorer countries. This is especially important for regions in Africa and Asia, as the predicted population growth over the next years may be accompanied by food shortages. Several hundred species of insects are consumed in African countries (Chen et al., 2018; Kelemu et al., 2015). Therefore, the solution of the food issue in these countries for the near future will be in some way connected with the development of an insect protein industry for the production of insect-based food and feed (Babarinde et al., 2021; Stull and Patz, 2020). However, when using livestock wastes as feeding substrate it is important to take into account 1) the nutritional potential of manure and 2) the storage time and conditions for manure. The nutritional potential of manure depends on the nutritional value of the feed that the animals receive. The characteristics of the composition of nutrients in various types of manure are shown in Table 1. As some researchers have noted (Joosten et al., 2020), BSF is not a vector for disease transmission. However, the use of substrates containing the fecal microbiome of livestock (e.g., manure) for BSFL farming does not reduce the risk of parasitic infection (helminths entering the body of animals and humans) because larval digestion does not affect the viability of helminth eggs (oocysts) (Müller et al., 2019). Along with hygienic aspects, another problem arises - the attitude of consumers towards the choice of food of animal origin. Despite the widespread traditions of eating insects in the world, eating pork, chicken, or fish fed with BSFL protein is not accepted by many people (Liu et al., 2020d; Verbeke et al., 2015). From an economic point of view, the switch to BSF protein by farmers is explained by the high price of feed and various aspects of feed losses (Carr and Howells, 2021). It is also economically justified based on the risks associated with raising young piglets and their habituation to other foods after a period of feeding on their mother's milk. The introduction of live BSFL into piglets' feed reduced food neophobia and had a positive effect on their behavior (Ipema et al., 2021).

As pointed out by Pinotti and Ottoboni (Pinotti and Ottoboni, 2021), the most important obstacle of using insects for the processing of organic waste is not related so much to the technology as to the lack of reasonable criteria (coefficients) to evaluate the conversion of organic substrate by insects, often expressed in mass by dry matter. A study by Gold et al. (Gold et al., 2018) showed that different researchers obtained inconsistent values: the processing time of animal and bird manure by BSFL ranged from 24 to 31 days, the efficiency of manure reduction varied between 26 and 63%, and the bioconversion rate ranged between 3.7 and 6.3% (Awasthi et al., 2022d; Liu et al., 2020a). These parameters will determine further interest and commercial success in establishing the use of BSF in the waste recycling industry. As an abstract discussion, it can be assumed that in the near future insect farmers will need to provide the history of cultivation (passport) of e.g., BSFL (information on applied substrates, duration of feeding, method of sanitization, content of essential micronutrients, etc.). A comparative overview on the nutritional value of insects for protein production as an additive in offal for humans, animals, and fish is presented in Table 2. When evaluating the insect's nutritional properties for feed applications, the digestibility of essential amino acids needs to be considered as a key factor for obtaining high quality protein raw materials. Feeding larvae with various organic wastes resulted in a similar protein content in BSF pre-pupae, ranging from 399 to 431 g kg^{-1} dry matter depending on the type of treatment. However, the ether extract and ash content varied significantly depending on the type of waste consumed by BSFL (Spranghers et al., 2017; Liu et al., 2020).

Table 1
Comparative characteristics for the nutrient composition in various types of manure.

Type of manure	Calories/ 100 g	Fat g/ 100 g	K, %	N, %	P, %	References
Pig	295.23	1.4	–	–	–	(Nguyen et al., 2015)
Cattle	–	–	24–38	34–38	18–34	(Tittonell et al., 2010)
Chicken	–	–	2.24	5.96	1.38	(Beskin et al., 2018)

Other studies showed that microwave drying (as a method of processing insects to obtain protein) of larvae, compared with conventional drying, polymerizes protein particles extracted from black soldier fly larvae and makes them less digestible (Chen et al., 2020b; Huang et al., 2019). This indicates that we do not yet know much about how to exploit the nutritional potential of insect biomass properly and effectively. As can be seen from the presented data, the potential of BSFL is sufficient to consider it as an economically important aspect in the development of the food industry. However, along with competing insect species, additional research aimed at efficiently replacing unsustainable protein sources for fish and animal rearing, as well as changing the psychological barriers associated with eating insect products is required. Several advantages of insect farming could help to overcome these hurdles. Firstly, under appropriate climatic conditions, simple technology and primitive infrastructure are sufficient to grow BSFL (Fig. 2). After hatching from the eggs, the neonate larvae are nursed to the required age to introduce them into the process of processing organic waste. Adult and well-fed larvae can then serve as a source of protein raw materials. Secondly, due to accelerating climatic changes that increasingly affect the productivity of the agricultural sector necessitates us to rethink our farming strategies. These environmental challenges frequently lead to food shortages in the most affected regions of the world and, consequently, cause a high rise in prices for food and feed. This will lead to the fact that for the population of poor countries, the use of insect protein will become a highly important alternative to animal feed, with a great potential to fight hunger and improve self-sufficiency. And thirdly, global disruptions in the food sector caused by the spread of coronavirus and other infections may intensify price and supply fluctuations (Doi et al., 2021; Rzymski et al., 2021).

All this raises a difficult question for us: will we be able to come to terms with the fact that in the near future, products containing insect protein might displace livestock farming as the main source of animal protein; especially if we take into account that the insects that became our food were reared on feces (manure)?. Today, we can only rely on profitability indicators of the insect products market to forecast the development of the sector. But in any case, the question concerns not only what to eat, but also how to grow insects, and how to address competitive advantages. However, these issues should also be considered from the point of view of religious restrictions in certain types of food. It is widely known that several insect species relevant for insect farming feed on organic waste substrates, which is why they are a marker of sanitary problems in areas with problematic waste disposal practices. There are studies that also question the halal compliance of meat produced with BSFL grown on feces and allowed for consumption in Islamic communities (Chen et al., 2020c; Jamaludin et al., 2021).

In 2020, Persistence Market Research predicted an unprecedented growth of the world market of edible insects for the production of animal feed by 39%.By 2030, the market volume will reach 72 billion US dollars, with the greatest demand associated with the BSF (Persistence Market Research, 2020). For example, Alexander et al. (Alexander et al., 2017) believe that farming will soon undergo changes due to the observed transition of consumers from cattle meat to chicken, imitation of meat, and insect protein. Within this trend, they find major positive aspects: a reduction in the area of land for livestock grazing and a reduction in greenhouse gas emissions. Studies in Spain (Khalil et al., 2021) showed that during the spread of COVID 19, the use of products (yogurt and jam) that included insect protein varied across gender and age. The majority of the population prone to the use of such products was in the group of 18–39 years, while the proportion of the male population was more than three times greater than for women. At the same time, people living on 1000 euros or less were two times more likely to buy products with insect protein. In some cases, it may be ignorance of the existence of such products (Chen et al., 2020d; Wilkinson et al., 2018).

There is no doubt that the African and Asian continents are dominant in the consumption of insects as food compared to Europe. However, in some areas of China (a region where eating insects is an element of traditional cuisine), age-related and economic aspects are the main factors influencing decisions on the purchase of these products (Liu et al., 2019a).

Table 2
Comparative overview of the potential use of insect food products.

Insect species	Product	Volume	Types	Problems/prospects	References
For food purposes					
Crickets *(Acheta domesticus)*	For the production of bread	10 to 30% from the volume of flour (in the form of flour)	Human	The presence of spore-forming bacteria in bread after adding protein from crickets / approval by taste indicators	(Osimani et al., 2018)
Striped Cricket *(Gryllodes sigillatus)* and Yellow mealworm *(Tenebrio molitor)*	For the production of cupcakes	2%, 6%, 10% in the form of flour		total phenolic content and antioxidant capacity against ABTS·+ and DPPH· increased	(Zielińska et al., 2021)
For feed purposes					
Black soldier fly larvae *(Hermetia illucens)*	Live larvae age 1–2 weeks	40%	Ruminants	Replacement of soybean meal with larvae shows lower nutritional efficiency / however, there is a decrease in the formation of methane during digestion	(Jayanegara et al., 2017)
	Pet food	37%	Cats and dogs	High digestibility of protein and calcium, compared to flour feed containing a protein substrate of venison (as an alternative food source) / fiber digestibility was lower	(Penazzi et al., 2021)
	Flour from larvae	50% 75% 100%	Pigs	The weight of the carcass of pigs was higher than that of pigs receiving a control diet with 100% fish meal.The protein content reached 65–93% in terms of dry matter	(Chia et al., 2021)
Yellow mealworm (*Tenebrio molitor*) and Field cricket (*Gryllus assimilis*)	Partially skimmed flour	20%	Chicken	Digestibility 65–70% / high calorie content (5000–6000 kcal/kg)	(Dourado et al., 2020)
For fish					
Yellow mealworm *(Tenebrio molitor)*	Partially skimmed flour	5–25%	Rainbow trout *(Oncorhynchus mykiss Walbaum)*	Increase in growth rate, feed conversion rate and protein efficiency ratio	(Rema et al., 2019)
Black soldier fly larvae *(Hermetia illucens)*		40%		Caused a decrease in polyunsaturated fatty acids in the back muscles / can be used in feed	(Renna et al., 2017)
	Live larvae	50–250 гр/кг	Tilapia *(Oreochromis niloticus L.)*	Weight gain by 15% compared to fish/ similar costs for aquaculture from other substrates	(Wachira et al., 2021)

Nevertheless, global changes in recent years have begun to influence the perception of entomophagy as an element of normal nutrition in European countries with a high level of socio-economic development (Germany, and Poland) (Orkusz et al., 2020; Orsi et al., 2019). However, for Italy, the most compelling factor in the rejection of products with insect protein is food neophobia, which is quite understandable in the light of strong cultural and culinary traditions (Moruzzo et al., 2021; Toti et al., 2020). Similar motives in behavior regarding the use of BSFL were also among the American population. Many Americans had a negative attitude towards the use of BSFL, at the same time, some of them were willing to try products containing BSF protein, but all tended to believe that the use of products that include insects is more acceptable than direct consumption of insects (Higa et al., 2021). According to the World Bank, the density of livestock per square kilometer can vary five to nine times across different countries (China, Europe, and USA) (World Bank Group, 2018). These listed countries are leaders in the consumption of pork, beef, and poultry, which is likely to cause the greatest development of the BSF market in these countries.

4. Bioconversion of manure to BSFL biomass

4.1. BSFL cultivation on manure and impact on larval growth

The larvae of the BSF are known for their versatility in degrading a broad variety of decomposing organic matter ranging from agro-industrial by-products to human excrements. These dietary preferences also include manures originating from traditional livestock such as dairy, swine, and poultry, which have previously been considered suitable substrates for BSFL bioconversion (Lalander et al., 2019; Miranda et al., 2020; Newton et al., 2005; Sheppard et al., 1994). Larvae hatch from eggs with an average biomass of approx. 0.028 mg per egg (Booth and Sheppard, 1984). Under optimized artificial conditions, these neonate larvae can reach a harvest-ready peak biomass of around 160 to 200 mg per larva (fresh weight) within eleven to 14 days when fed with manure (Lalander et al., 2019; Miranda et al., 2020). Larval biomass yields from manure bioconversion are comparable to trials conducted under controlled conditions with other organic waste substrates (Nguyen et al., 2015), but can be slightly lower than the yields of approx. 220 mg per larva when using wild populations of the BSF to convert manure (Sheppard et al., 1994).

Although generally suitable for bioconversion, not all types of manure perform equally well as nutrient source. A direct comparison of dairy, swine, and poultry manure in an industrial-scale set-up showed that BSFL fed with dairy manure were delayed in their growth and exhibited lower survival (approx. 45%) than larvae on a diet of swine and poultry manure (>73%) (Miranda et al., 2020). Higher survival of >70% on dairy manure was observed by Myers et al. (Myers et al., 2008) in a lab-scale trial. Such contrasting findings often originate from differences in the scale of the experiment (lab- vs. industrial scale (Kooienga et al., 2020)), substrate quality (e.g. nutrient availability (Meneguz et al., 2018b), water content (Fatchurochim et al., 1989), pH (Meneguz et al., 2018a), and salinity (Cho et al., 2020), or BSF-strain-related variations (Zhou et al., 2013). For example, Fatchurochim et al. (Fatchurochim et al., 1989) found moisture levels in poultry manure between 40 and 60% to improve BSFL survival, while largest larvae were obtained at 70%; however, at the price of significantly higher mortality. Although the use of dairy manure with moisture levels above 80% as used by Miranda et al. (Miranda et al., 2020) is thought to work in well-ventilated settings, the risk of drastically increasing BSFL

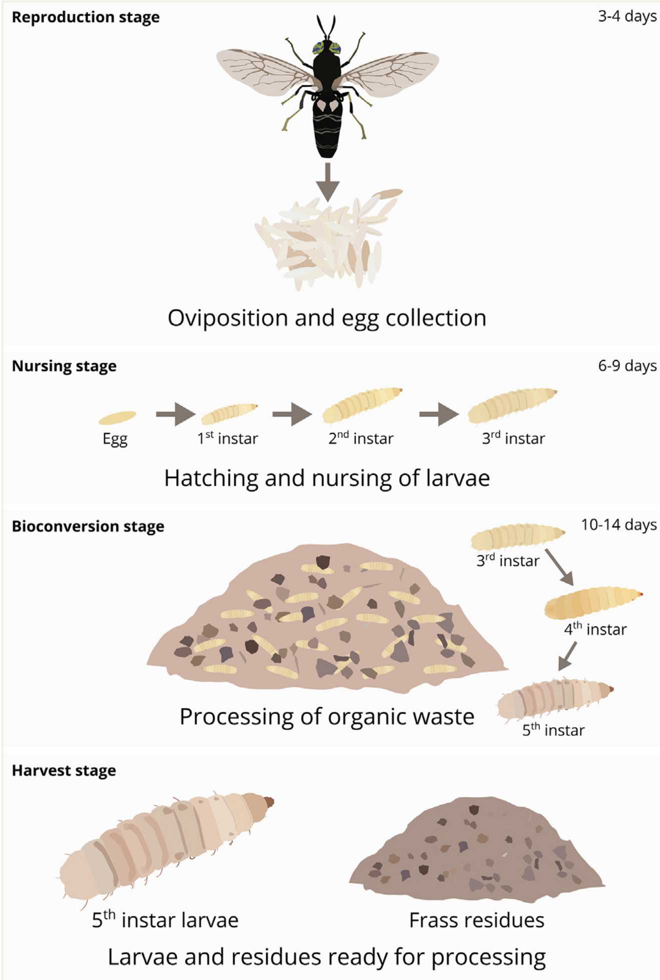

Fig. 2. Black soldier fly larvae production.

mortality and potentially impeding process stability in large scale operations should not be neglected (Fatchurochim et al., 1989; Lalander et al., 2020).

These observations put special emphasis on the importance of substrate moisture content as a basic parameter for larva rearing and indicate that its adjustment in manure prior to BSFL treatment could benefit the process. In addition, dairy manure contains a high share of fibers such as cellulose, hemicellulose, and lignin that are more difficult to degrade and thus could hamper larval conversion efficiency (Miranda et al., 2020). Mixing manure from livestock species with different nutritional requirements may aid the degradation of complex fibers and thus improve bioconversion rates. A 1:1.5 mixture of dairy and poultry manure was shown to increase consumption of these hardy components and resulted in higher larval biomass yields, feed conversion ratios, and nutrient reduction (Rehman et al., 2017). Especially a meaningful valorization of poultry manure is becoming increasingly important as global meat consumption is shifting towards meat from poultry, leading to an estimated increase in demand of >17% by 2030 (OECD, 2021). Co-digesting dairy manure with other organic wastes, e.g. in a 2:3 blend with residues from soybean curd production (Rehman et al., 2017), may be an alternative whenever manure from other livestock is not available for blending. Future studies will help to identify suitable combinations of livestock wastes and agricultural by-products that allow for an economically and ecologically meaningful insect-based valorization, while at the same time also expanding the knowledge on metabolic and microbiological features of the BSFL.

4.2. BSFL gut physiological and biochemical features

Only recently, physiological characteristics of the BSFL gastro-intestinal tract (GIT) have been more intensively investigated (Bonelli et al., 2020; Bonelli et al., 2019; Gold et al., 2020a). Their generalist polysaprophagous lifestyle is supported by a highly adaptive GIT capable of providing a multifunctional enzymatic toolkit that includes amylases, lipases, and proteases with higher activities than observed in other fly species. High activities of digestive enzymes such as leucine arylamidase, α-galactosidase, β-galactosidase, α-mannosidase and α-fucosidase present in the larval GIT determine the efficient decomposition of complex organic materials such as manures (Kim et al., 2011b). Although its high content of fibers typically curbs BSFL biomass gain compared to food- and cereal-based substrates, animal manure represents a convenient substrate to up-scale insect farming while following principles of circular economy, as manure is readily available in large amounts and at low costs in many rural regions (Gold et al., 2021).

To improve bioconversion, supplementing exogenous bacteria (1% of total waste biomass; 10^8 CFU/ml) such as various *Bacillus* strains (especially MRO_2) has been shown to enhance the metabolic performance of larvae by improving survival rate, biomass gain, development time, conversion of feed, and feed digestion. This approach could offer feasible and efficient means to improve physiological and biochemical processes in larval GITs for large-scale BSFL production, as these exogenous bacteria help to oxidize fibers and, thus, increase digestibility and nutrient of lignocellulose-rich wastes such as manure (Rehman et al., 2019).

The highly efficient larval digestive system can be separated in fore, mid, and posterior gut. The midgut, as the physiologically most important section of the larval GIT, can be divided further into anterior, middle, and posterior midgut (Bonelli et al., 2020). An in-depth transcriptome analysis of the whole midgut found no differential gene expression when exposed to different diets including poultry, swine, and dairy manure, indicating that the larvae rely on a common set of genes for the digestion of various organic wastes (Zhan et al., 2019). Kim et al. (Kim et al., 2011a) found that the midgut not only produces serine proteases specific for larval digestion, but also other proteases with important functions across different BSF life stages.

The three regions of the midgut are capable of maintaining distinct pH levels of pH 6 (anterior), 2 (middle), and 8.5 (posterior), respectively, that play a central role for the activity of digestive enzymes (Bonelli et al., 2019). With a pH of around 8 to 9, fresh manure generally has a higher pH than other organic wastes frequently used for BSFL treatment (Lalander et al., 2019). However, this does not interfere with the larvae's pH preferences (either slightly acidic at pH 6 or slightly alkaline between pH 8 and 10) (Ma et al., 2018). The pH determines the solubility and thus the availability of ingested nutrients, and has a shaping effect on the composition of BSFL gut microbial communities (Bruno et al., 2019; Ma et al., 2018). In addition to pH, the environmental temperature is affecting larval metabolism and associated gut microbial communities (Raimondi et al., 2020; Tomberlin et al., 2009). For artificial BSF rearing, temperature is typically kept between 27 and 30 °C to approximate the natural habitat of this tropic fly and influences the dynamics between nutrient availability and (gut) enzyme activity. The activity of digestive enzymes is tightly coupled to the prevailing temperature as e.g., the proteolytic activity in the midgut juice becomes highest around 45 °C (Bonelli et al., 2019). By densely aggregating during feeding (Shishkov et al., 2019), high larval activity tends to significantly increase the temperature within the substrate to >45 °C depending on the larval density and rearing scale (Klammsteiner et al., 2021a). This may enhance digestive processes but could induce undesired temperature stress in large scale operations if not closely monitored. Moreover, elevated temperatures contribute to increased NH_3 emission from the substrate, which without proper ventilation may negatively affect air quality in the rearing facility.

Although these general physiological features constitute the BSF's overall metabolic versatility, its life history traits, substrate conversion efficiency, and development times are known to vary across strains obtained from different geographical regions (Zhou et al., 2013). These strain-related genetic differences may occur due to the adaptation to distinct environmental conditions as a consequence of global dispersion and are likely to influence the physiological peculiarities of the BSFL gut (Kaya et al., 2021). Thus, careful selection of strains based on metabolic advantages and adaptations is advised when setting up BSF colonies in artificial environments engineered for organic waste management.

4.3. BSFL gut microbes and metabolic pathways

How microbiologically unproblematic organic substrates such as agro-industrial by-products (Galassi et al., 2021), food wastes (Klammsteiner et al., 2021c), and vegetable wastes (Bruno et al., 2019; Klammsteiner et al., 2020b) shape the BSFL gut microbiota has been extensively described. These close-knit interrelationships between the BSF and exogenous microbial communities are predetermined by the larvae's preference for decaying organic matter and are naturally lived out in direct physical contact with nutrient sources that potentially carry a high bioburden. Lately, targeted studies also relevant for understanding and improving manure bioconversion such as the identification of a diet-independent core microbiome or indicator species in BSFL guts acting as biomarkers for e.g. insect health have been addressed (Ao et al., 2020; Klammsteiner et al., 2020b; Klammsteiner et al., 2021c; Zhan et al., 2019). Those taxa with widespread prevalence in BSFL guts (e.g., *Morganella*, *Dysgonomonas*, *Actinomyces*, *Enterococcus*, and *Providencia*) were primarily assigned to the phyla Proteobacteria, Bacteroidetes, Firmicutes, and Actinobacteria and are well-known for their role in degrading complex polysaccharides frequently found in manures such as lignin and cellulose (Klammsteiner et al., 2020b; Zhan et al., 2019). So far, only few studies have investigated the effect of manure digestion on BSFL gut microbial communities (Table 3). Although these studies differed in the type of applied manure, harvest age, and experimental set-up, they reported the prevalence of mainly *Proteobacteria, Bacteroidetes, Firmicutes,* and *Actinobacteria* (Ao et al., 2020; Cai et al., 2018b; Tanga et al., 2021; Zhan et al., 2019; Zhang et al., 2020).

So far, no clear indication that a certain type of manure promoted the dominance of a certain phylum within the BSFL gut was found. A common flaw of (BSFL) gut microbiome studies is caused by the lack of standardization in sample preparation and processing, thus, it is also not entirely clear whether the observed signals come from the resident or transient gut microbiota (Bosch et al., 2020; Moreno-Indias et al., 2021). *Firmicutes* and *Proteobacteria* alternated in their role as most abundant phylum (up to 99% and 56%, respectively) within studies, while *Bacteroidetes* and *Actinobacteria* were typically present in comparably lesser relative abundances (5–59% and <1–11%, respectively) (Ao et al., 2020; Cai et al., 2018b; Zhan et al., 2019; Zhang et al., 2020). On genus level, genera such as *Morganella*, *Enterococcus*, and *Dysgonomonas,* recently proposed as members of a BSFL core gut microbiome (Klammsteiner et al., 2020b), were detected in high abundances in the majority of experiments employing manures (Table 3). The widespread prevalence of *Enterococcus* is not surprising as it is a typical beneficial colonizer of animal guts and thus natively highly abundant in livestock manure (Soupir et al., 2006). Its occurrence in manure is also not significantly inhibited by larval activity (Lalander et al., 2015). The recurrent presence of *Clostridium*, *Ignatzschineria*, and *Campylobacter* in manure-fed larvae, however, highlights the importance of proper post-harvest sterilization, as these genera are frequently carried also by other Dipteran species associated with infectious diseases (Bahrndorff et al., 2017; Scully et al., 2017). *Providencia*, which was found in rather low abundances across studies is a known insect pathogen in e.g. *Drosophila melanogaster*, but besides being linked to protein and lipid catabolism its role in BSFL guts is not yet entirely clear (Ao et al., 2020; Galac and Lazzaro, 2011).

The functional metabolic potential of gut microbial communities has primarily been investigated for larvae fed food waste (Jiang et al., 2019; Klammsteiner et al., 2021c) or grain-based diets (Liu et al., 2020b). These substrates are considered safer substrates for animal feed production than animal excrements and are thus more likely to find early and widespread application in BSFL rearing facilities. In general, data on BSFL gut metabolic features show that although the composition of microbial communities is affected by changing diets, they still maintain similar metabolic competences primarily associated with energy, carbohydrate, amino acid, and vitamin metabolism (Klammsteiner et al., 2021c). As with other animal species, functional features may be highly redundant across different community profiles in BSFL guts to maintain the ability to metabolize nutritionally diverse and complex diets (Liu et al., 2020b). Many of these functions aiding the digestion of macronutrients were also associated with taxa from phyla predominantly colonizing the gut of BSFL used for manure treatment (e.g. *Firmicutes*, *Proteobacteria*, and *Bacteroidetes*), however, additional studies at the meta-transcriptomic or metagenome level are needed to understand these dynamics in detail (Zhan et al., 2019).

Temporal changes in microbiota composition were also detected when comparing fresh manure with manure residues after exposure to BSFL (Table 4). The microbial communities in larval guts and substrate residues are known to approximate each other the more time larvae spend processing the substrate and excreting metabolic products (Gold et al., 2020b). While in some cases *Firmicutes* dominated the fresh poultry manure during BSFL bioconversion, *Proteobacteria* were most abundant across various types of fresh manure. However, during larval treatment, overall microbial

Table 3
Studies investigating the effect of manure bioconversion on the black soldier fly larval (BSFL) gut microbiome. The dominant phyla refer to those observed in guts of BSFL raised on untreated manure. Possible additional experimental groups focusing on study-specific treatments such as e.g., sterilization or addition of antibiotics were not included.*

Manure type	Harvest age [days]	Temperature [°C]/relative humidity [%]	Dominant phyla in guts of BSFL	Dominant genera in guts of BSFL	References
Poultry	20	27.5/70	35% *Proteobacteria*, 30% *Bacteroidetes*, 29% *Firmicutes*, 3% *Actinobacteria*	23% *Morganella*, 21% *Enterococcus*, 18% *Dysgonomonas*, 7% *Ignatzschineria*, 4% *Providencia*	(Cai et al., 2018b)
Poultry	18	25/35–40	56% *Proteobacteria*, 32% *Firmicutes*, 9% *Bacteroidetes*, 4% *Actinobacteria*	26% *Enterococcus*, 20% *Escherichia-Shigella*, 13% *Citrobacter*, 9% *Ignatzschineria*, 9% *Dysgonomonas*	(Zhan et al., 2019)
Poultry	18	27.5/70	42% *Proteobacteria*, 59% *Firmicutes*, 17% *Bacteroidetes*	<41% *Enterococcus*, <26% *Providencia*	(Ao et al., 2020)
Poultry	20	30/n.a.	99% *Firmicutes*, <1% *Actinobacteria*	47% uncl. *Peptostreptococcaceae*, 30% *Enterococcus*, 10% *Turicibacter*	(Zhang et al., 2020)
Poultry	14	28 ± 1/70 ± 2	59% *Bacteroidetes*, 29% *Proteobacteria*, 8% *Firmicutes*, 1% *Actinobacteria*	41% *Dysgonomonas*, 22% *Campylobacter*, 10% *Parabacteroides*, 6% *Bacteroides*, 3% *Lachnoclostridium*,	(Tanga et al., 2021)
Dairy	18	25/35–40	81% *Firmicutes*, 11% *Actinobacteria*, 5% *Bacteroidetes*, 4% *Proteobacteria*	19% Enterococcus, 17% Romboutsia, 13% *Paeniclostridium*, 8% *Clostridium*. 7% *Leucobacter*	(Zhan et al., 2019)
Swine	18	25/35–40	80% *Firmicutes*, 9% *Actinobacteria*, 9% *Proteobacteria*	24% *Enterococcus*, 23% *Clostridium*, 9% *Terrisporobacter*, 7% *Actinomyces*, 6% *Turicibacter*	(Zhan et al., 2019)
Swine	18	27.5/70	49% *Proteobacteria*, 31% *Firmicutes*, 23% *Bacteroidetes*	<39% *Morganella*, <27% *Campylobacter*, <17% *Dysgonomonas*, <14% *Providencia*	(Ao et al., 2020)

* Missing or incomplete values on relative abundances were derived from figures or supplementary materials provided in the publications.

diversity tends to decrease within the substrate as moisture contents decrease and conditions shift from anaerobic to aerobic (Gold et al., 2020b; Scully et al., 2017). In addition, this constant aeration of the substrate by larval movement promotes the enrichment of aerobic microbial communities (Gold et al., 2018). Changing the substrate microbiota already at early stages was attempted by supplementing probiotic bacteria such as *Bacillus subtilis*, *Bacillus natto*, *Arthrobacter* K19, and *Rhodococcus rhodochrous* that support the bioconversion process by inducing beneficial effects within the host (i.e., the BSFL). This approach has shown promising results also for enhancing the valorisation of manure and could offer an opportunity for the optimization of future treatment facilities (Kooienga et al., 2020; Yu et al., 2011).

5. Influence of BSFL application on organic manure recycling, biomolecule degradation, and process performance

5.1. Global warming potential and nutrient conservation

Inadequately treated animal manure has the potential to severely affect our environment, public health, and wellbeing. Under uncontrolled conditions, microbe-driven decomposition of manure has the capacity to emit large volumes of greenhouse gases including methane (CH_4) and nitrous oxide (N_2O) (Petersen et al., 2013). Odorous volatile organic compounds accompany these gases and potentially create nuisances for close by urban dwellings and threats to human health (Barrett, 2006). BSFL-based bioconversion can significantly reduce odorous compounds frequently associated with the smell of manure such as 2-methylpropanoic acid, phenol, 4-methylphenol, indole, or 3-methylindole without requiring complex infrastructure as it is necessary for e.g. anaerobic digestion (Beskin et al., 2018). During treatment, larvae constantly aerate the substrate, thereby inhibiting fermentative microbiological processes taking place under oxygen exclusion such as methanogenesis (Petersen et al., 2014). Although the elevated larval metabolic activity comes with CO_2 emissions >65% higher than in untreated manure, emissions of CH_4, however, are not decisively changed by BSFL treatment (Parodi et al., 2021). This indicates that mostly microorganisms, i.e. anaerobic archaea, present in stored manure drive methanogenesis and additional CH_4 emissions from larval manure bioconversion are negligible. In terms of global warming potential expressed in CO_2 equivalents, manure incubated with and without BSFL does not significantly differ (43 g CO_2 eq kg^{-1} versus 38 g CO_2 eq kg^{-1} dry matter manure, respectively) (Parodi et al., 2021). Compared to open windrow composting, however, BSFL treatment exhibits only half the global warming potential as life cycle analyses of biowaste treatment have shown (Mertenat et al., 2019).

Due to the continuous excretion of digested material by the larvae and the accumulation of ammonium (NH_4^+) ions within the substrate, the pH becomes more alkaline over time, ultimately reaching a pH above 9 (Erickson et al., 2004; Ma et al., 2018). Higher pH levels typically lead to an increased conversion of NH_4^+ to ammonia (NH_3), which in turn can leak in gaseous form (Parodi et al., 2021). Without appropriate exchange of ambient air, the enrichment of NH_3 may also negatively affect larval metabolism due to poorer air quality and contribute to the corrosion of rearing equipment. This is especially relevant for BSFL manure treatment as the NH_3 emission can turn out up to 50 times higher than for the treatment of food wastes (Parodi et al., 2021). In addition to pH, temperature gradients define these shifts in the NH_3-NH_4^+ equilibrium whereby thermophilic temperatures combined with high pH also enable the conversion of non-volatile NH_3 to volatile NH_3 (Pagans et al., 2006). Overall emissions of nitrous oxide (N_2O) from BSFL treatment have been considered negligible (Ermolaev et al., 2019; Parodi et al., 2020).

Although rearing set-ups, analytic methods, and applied substrates differed largely across the few studies that particularly assessed greenhouse gas emissions, the results agree that BSFL treatment has several advantages over traditional methods and allows for a more climate friendly treatment of organic wastes (Ermolaev et al., 2019; Mertenat et al., 2019; Pang et al., 2020a; Parodi et al., 2021).

5.2. Total bioburden and pathogen dynamics

Abundance and composition of microbial communities in manure are strongly influenced by the applied treatment. During anaerobic digestion, the exclusion of oxygen and a complex food web of syntrophic microorganisms involved in methanogenesis outcompete less specialized microbes and potential pathogens (Sommer et al., 2013). In composting processes, microbiota-induced temperature peaks of up to 70 °C during the thermophilic phase contribute to the hygienization of the organic wastes (Sommer et al., 2013). BSFL treatment requires oxygen and mesophilic temperatures to work properly, however, larvae have been shown to reduce total bioburden and pathogenic bacteria in manure under these conditions. While Erickson et al. (Erickson et al., 2004) observed an efficient reduction of *Salmonella enterica* and *Escherichia coli* by BSFL only in poultry manure (as opposed to dairy and hog manure) and solely under alkaline conditions, Lalander et al. (Lalander et al., 2015) and Liu et al. (Liu et al., 2008) recorded similar effects also for swine and dairy manure, respectively. It is hypothesized that the increased generation of (uncharged) NH_3 due to the alkaline pH in the substrate is a major driver of the antimicrobial effects on both the pathogens and the total bio-burden. An increase in temperatures caused by larval activity might additionally raise NH_3 concentrations

Table 4
Studies investigating the effect of black soldier fly treatment on the manure microbiome. Only treatment groups focusing on black soldier fly treatment were included, other study-specific treatments such as e.g., sterilization or addition of antibiotics were not considered. (n.a. = data not available).*

Manure type	Treatment duration (days)	Substrate moisture [%]	Temperature [°C]/relative humidity [%]	Dominant phyla in fresh manure	Dominant phyla in manure residues	Reference
Poultry	12	73	27.5/70	52% *Firmicutes*, 34% *Bacteroidetes*, 7% *Proteobacteria*, 6% *Actinobacteria*	49% *Bacteroidetes*, 18% *Firmicutes*, 14% *Proteobacteria*, 12% *Actinobacteria*	Cai et al. (2018a)
Poultry	12	n.a.	25/35–40	49% Proteobacteria, 45% *Firmicutes*, 3% *Actinobacteria*, 3% *Bacteroidetes*	n.a.	(Zhan et al., 2019)
Poultry	9	79	29/52	72% *Proteobacteria*, 16% *Actinobacteria*, 12% *Firmicutes*	72% *Proteobacteria*, 22% *Actinobacteria*, 6% *Firmicutes*, <1% *Bacteroidetes*	Awasthi et al. (2020e)
Poultry	15	n.a.	30/n.a.	56% *Firmicutes*, 25% *Bacteroidetes*, 12% *Proteobacteria*, 3% *Actinobacteria*	98% *Firmicutes*, 1.9% *Actinobacteria*, <1% *Proteobacteria*, <1% *Bacteroidetes*	(Zhang et al., 2020)
Dairy	12	n.a.	25/35–40	70% *Proteobacteria*, 16% *Bacteroidetes*, 11% *Firmicutes*, 2% *Actinobacteria*	n.a.	(Zhan et al., 2019)
Dairy	9	83	29/52	85% *Proteobacteria*, 11% *Actinobacteria*, 3% *Firmicutes*	64% *Proteobacteria*, 21% *Actinobacteria*, 14% *Firmicutes*, <1% *Bacteroidetes*	Awasthi et al. (2020e)
Swine	12	n.a.	25/35–40	76% *Firmicutes*, 15% *Bacteroidetes*, 4% *Spirochaetes*, 2% *Proteobacteria*, 1% *Actinobacteria*	n.a.	(Zhan et al., 2019)
Swine	9	82	29/52	85% *Proteobacteria*, 14% *Actinobacteria*, 1% *Firmicutes*, <1% *Bacteroidetes*	43% *Actinobacteria*, 30% *Proteobacteria*, 24% *Firmicutes*, 3% *Bacteroidetes*	Awasthi et al. (2020e)

* Missing or incomplete values on relative abundances were derived from figures provided in the publications.

and thus further inhibit growth of susceptible microbes (Erickson et al., 2004; Lalander et al., 2015; Pagans et al., 2006).

In addition to physicochemical factors contributing to hygienization, several studies have shown that larvae are capable of producing and excreting antimicrobial peptides. Choi et al. (Choi et al., 2012) found that methanol extracts from BSFL exhibited antibacterial effects towards several bacterial species including *Klebsiella pneumoniae*, *Neisseria gonnorhoeae*, and *Shigella sonnei*, and successfully inhibited their proliferation. An artificially induced immune response caused by septically injuring BSFL with a needle inoculated with *Staphylococcus aureus* as done by Park et al. (Park et al., 2014) led to an even broader antimicrobial activity also against methicillin resistant *S. aureus*. The ability of expressing diet-dependent antimicrobial peptides against many different microorganisms may also act as adjustment mechanism to changing diets. This mechanism could support the larvae not only in fighting off exogenous pathogens, but also in adapting to new nutrient sources with high microbial colonization (Vogel et al., 2018). Another indirect effect from BSFL treatment beneficial for reducing the spread of pathogens is the inhibition of house fly (*Musca domestica*) colonization of manure (Furman et al., 1959). In contrast to the BSF, this dipteran species is known for its ability to carry and transmit various pathogens harmful to humans and animals such as *Pseudomonas aeruginosa* (Fotedar et al., 1992), *Enterococcus faecalis* (Fotedar et al., 1992), *Staphylococcus aureus* (Fotedar et al., *1992*), and *Campylobacter* spp. (Bahrndorff et al., 2013).

5.3. Potential applications for bioconversion side-streams

Making use of the BSFL's ability to shape their microbiological surrounding is especially important for of the safety of the substrate residues coming out of the process. Even after determining a well-balanced tradeoff between larval biomass gain and waste reduction efficiency, rearing residues will inevitably accumulate during manure bioconversion. Depending on the type and composition of the organic wastes, residual biomass after larval bioconversion can add up to >57% of the initial input biomass depending on the optimization of feeding rates (Diener et al., 2009). These residues, commonly summarized as frass, are the main by-product of insect farming and consist of undigested substrate wastes, excretions, shed larval skins, and to a defined degree also dead insects (European Commission, 2021). Although there has not yet been established a standardization for insect frass, recent industrial and scientific efforts promote it as alternative organic fertilizer by highlighting its positive effects on soil and plant health (European Commission, 2021; Klammsteiner et al., 2020a; Quilliam et al., 2020). According to the European Commission (European Commission, 2021), the processing methods of insect frass should be aligned with the regulations applying to manure, suggesting a treatment of 70 °C for 60 min to guarantee a high level of safety.

The moisture content not only affects the dynamics of the bioconversion process but is also a highly relevant parameter for these post-conversion residues and determines how efficient harvest-ready larvae can be separated from the substrate (Lalander et al., 2020). Achieving a higher dryness level is preferred, as it allows the use of e.g., sieves (Cheng et al., 2017) and improves the storability of frass for subsequent use as fertilizer. The initial moisture content in different types of manure ranging between 77 and 84% was shown to be reduced by up to 87% by BSFL treatment (Beskin et al., 2018). For frass that cannot be efficiently reduced in moisture content or which was not found suitable for soil application, anaerobic digestion could offer alternative means for treatment (Bulak et al., 2020; Klammsteiner et al., 2021b). Manure has long been used for biogas production, thus, frass obtained from the BSFL-based bioconversion of swine, poultry, or dairy manure could offer promising features for this application and add value to this circular process.

6. Economic feasibility, lifecycle assessment and circular bio economy

The economics of BSFL applications are related to the development of value-added products using a biorefinery approach. This approach includes the production of fuel, feed, and fertilizer that are high in demand (Surendra et al., 2020). The minimization of the environmental footprint associated with BSFL-based technologies and the establishment of material cycles in the interest of a circular economy can lead to a further improvement of the bioconversion of organic residues to BSFL fat and protein biomass (Gao et al., 2019; Lalander et al., 2019; Rehman et al., 2017; Xiao et al., 2018). One of the essential products obtained from BSFL fat could be biodiesel generated by transesterification (Feng et al., 2020; Ishak and Kamari, 2019; Kamarulzaman et al., 2019; Nguyen et al., 2020; Pang et al., 2020b). The residue left after the BSFL biomass harvesting can be used as soil amendment in organic farming as the residues are known to induce plant defense mechanisms and plant growth (Bloukounon-Goubalan et al., 2020; Liu et al., 2019b). BSFL-driven organic waste bioconversion contributes to the degradation of pharmaceuticals and pesticides as well as pathogen inhibition. The introduction of BSFL fertilizer will significantly reduce the use of synthetic fertilizer in hydroponics agriculture (Setti et al., 2019). BSFL improves the quality of the organic fertilizer by removal of heavy metals such as arsenic (Biancarosa et al., 2019), cadmium (Biancarosa et al., 2018), and lead (Van der Fels-Klerx et al., 2016). Biochemical and thermochemical conversion of the residual biomass can produce bioenergy (Bulak et al., 2020). Fig. 3 shows an overview of the processes related to BSFL technologies.

The BSFL-based biorefinery could also produce value-added products such as chitin and its derivatives. Chitin derived from the BSFL can be used in textile, wastewater treatment, and tissue engineering (Purkayastha and Sarkar, 2020). BSFL can be used to produce economically important products such as natural pigments (Ushakova et al., 2019), bioplastic (Barbi et al., 2019), and protein hydrolysates (Firmansyah and Abduh, 2019). They can also serve as a source of industrially important enzymes such as cellulase, trypsin, ligninase, and chymotrypsin (Bonelli et al., 2019; Müller et al., 2017). As a result, the larvae's ability to convert low-value wastes into high-value bioproducts makes them an ideal model to teach new generations about the importance of material recycling and circular economy to ultimately change future consumer habits (Walter et al., 2020; Liu et al., 2019a; Liu et al., 2021d).

Although the number of companies using BSFL to produce value-added products is steadily increasing, the data on economic aspects of BSFL organic waste bioconversion is so far limited. Detailed studies are usually not disclosed by companies and the environmental performance and profitability of the BSFL farming largely depend on the location of the operation, production scale, used substrate, and intended use of the products (Joly and Nikiema, 2019). In many countries including the EU, substrates for insect farming are still strictly regulated due to a lack of information and evidence-based research, thus, necessitating additional studies assessing potential food safety risks. The current legislative constraints limit the use of resources such as human feces, animal manure, and food waste. According to lifecycle assessments, these organic wastes would present the lowest global warming potential, energy use, and land requirements and cause the least financial burden among the substrates suitable for BSFL (Bosch et al., 2019).

Studies on the performance of BSFL biomass as animal feed have also shown that modern technologies cause higher costs than conventional technologies (Ignjatijević, 2010; Pleissner and Smetana, 2020). Estimating the life cycle cost in small-scale production has demonstrated that labor accounts for up to 65% of the total production cost (Joly and Nikiema, 2019). On the other hand, substrate and labor acquisition make up for approx. 90% of BSFL costs (Roffeis et al., 2018). By providing fiscal incentives, governments and authorities can help to decrease the costs of waste management (Matheson, 2019). Onsite production of BSFL biomass can improve the economic feasibility of the technology. To reach a profitable status, appropriate commercial and technological thresholds are necessary to be achieved (Drew and Pieterse, 2015). The development of the insect-based feed industry requires the availability of yet unused or inefficiently exploited organic resources to produce BSFL biomass (Smetana et al., 2019). Exploring novel production pathways and insect-derived resources may further improve profitability and economic efficiency of BSFL-based waste management in the future.

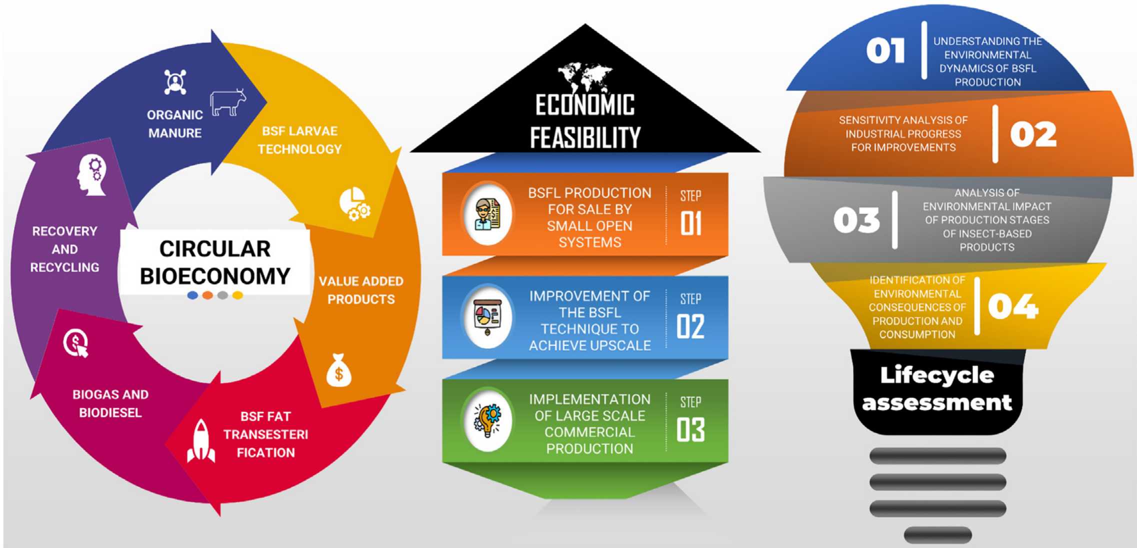

Fig. 3. Economic feasibility, lifecycle assessment, and circular bio economy.

7. Conclusion and future perspectives associated with BSFL application

BSFL farming has emerged as an efficient technology for resource recovery from organic manure. Several benefits including low space requirements, rapid bioconversion, and inhibition of pathogenic bacteria are associated with using fly larvae to manage agricultural wastes. It was demonstrated that larvae not only shape their microbial environment, but they also depend on it to thrive in decomposing organic matter. In addition, the availability of nutrients linked to physicochemical parameters such as the C:N ratio in the larvae's feed affects larval growth and thereby also the efficiency of converting organic waste into their own biomass. BSFL treatment causes significantly less greenhouse gas emissions than conventional methods, partially by impeding anaerobic processes. The larvae produce a broad palette of digestive enzymes to extract nutrients from wastes. The utilization of the technology can be highly effective in developing countries that want to develop advanced waste valorization facilities. However, it can be challenging to implement insect farming in some developing countries where waste production, collection, and separation is low. Another important aspect is the initial capital requirements to start BSFL farming. Financial incentives from governments and development programs could facilitate this process. Moreover, the use of nutrient-poor manure for bioconversion involves more careful process management and monitoring. Transmission of pathogenic microorganisms from manure substrates to BSFL-derived products is considered another challenge. Customer behavior related to the consumption of animal-based products such as protein supplements is debatable, and customer acceptance cannot be guaranteed.

Although a significant expansion in the insect farming sector has been seen recently, various aspects need to be considered for the broad implementation of this technology. These include:

- Up-scaling optimization of BSFL technologies.
- Commercialization of BSFL technology for the production of value-added products.
- Safety concerns related to production, packaging, and storage solutions.
- Environmental impact of BSFL production strategies.
- Improving the quality of BSFL-derived products.
- Use of the nutrient-poor manure as a feed for the BSFL.
- Consumer acceptance of insect-based food as a dietary supplement and awareness-raising.
- Financial support to low-income or developing regions to support BSFL farming.

CRediT authorship contribution statement

Tao Liu: Conceptualization, Methodology, Formal analysis, Data curation. **Thomas Klammsteiner:** Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Andrei Mikhailovich Dregulo:** Writing – original draft, Writing – review & editing, Visualization. **Vinay Kumar:** Writing – review & editing, Formal analysis. **Yuwen Zhou:** Writing – review & editing. **Zengqiang Zhang:** Writing – review & editing, Formal analysis. **Mukesh Kumar Awasthi:** Conceptualization, Writing – original draft, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

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

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