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Integration of mushroom production into circular food chains

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Abstract Edible mushrooms are cultivated mainly on ligno-cellulosic plant materials, thereby turning agricultural wastes to high-quality products. In this review, several ways in which mushroom cultivation could help in the transition towards a circular agricultural economy are discussed, including food, feed, and compost production. The production processes of different mushroom species are also described and an overview of the global mushroom market and its history are given. Resource use efficiency could be maximized by using spent mushroom substrate as feed for invertebrates, such as insects or earthworms, which produce high-quality compost and can serve as food or feed for other livestock. In the context of an increasing world population, as well as limited resources and agricultural land, mushroom cultivation could fulfill the need for protein-rich food and for the recycling of nutrient-poor agricultural wastes.

Keywords Mushrooms · Nutrition · Spent mushroom substrate · Insect feed · Vermicomposting

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Introduction

Population growth, climate change, and the depletion of non-renewable and limited resources like phosphate and fossil fuels are some of the major challenges to the global agricultural system and threaten food security, especially in densely populated and less-developed regions of the world (Rahmann et al. 2017). One of the most promising strategies for tackling these challenges is the improved usage and recycling of non-consumable biomass. Among these wastes are large quantities of nutrient-poor plant residues from cropping, which are of little value as food, feed, or fertilizer and are therefore often burned, disposed off in unsustainable ways (Arai et al. 2015; Feng et al. 2011), or left on the fields as organic matter to keep or improve soil fertility (Rahmann et al. 2017). These materials include straw, various husks, leaves and stems, corncobs and all other parts of plants which are rich in the cell wall components cellulose, hemicellulose and lignin. Fungi are the most efficient decomposers of such materials and especially of lignin (Stamets 1993); a more clever integration of edible mushrooms into the food and biomass chain could be the most sustainable way of utilizing this biomass. To realize this potential, it is however necessary to look at mushroom cultivation in a different way than is the case today: not primarily as a method of food production, but rather as the first step in a value-adding composting process which also provides feed for livestock and nutrients for plants.

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Mushroom production

Mushrooms have been cultivated by humans for more than a millennium (Stamets 1993). However, in recent decades, the scope and methods of cultivation have changed dramatically.

Market

According to Royse et al. (2017), the global consumption of mushrooms, 1993 to 2013, increased from 1 to 4.7 kg (fresh weight) per person and year. The mushroom market was valued at around 63 billion USD in 2013, only 8% of which was accounted for by wild mushrooms. The global production of cultivated edible mushrooms has increased around 30-fold since 1978, to around 34 million tons annually. China is by far the largest mushroom producer in the world, accounting for around 87% of the global production in 2013.

Mushroom production methods

Most cultivated species of mushrooms grow naturally on dead wood, while others are found on compost-like materials and nutrient-rich soils, often in association with manure (Stamets 1993). Virtually all cultivated species of mushrooms have a saprotroph lifestyle, meaning they are decomposers of organic matter. Some wild edible mushrooms, like truffles (*Tuber melanosporum*), porcini (*Belotus edulis*), and chanterelles (*Cantharellus cibarius*), are mycorrhizal fungi which require a symbiotic tree partner to grow and can therefore not easily be mass-produced. The world's leading cultivated mushroom is shiitake (*Lentinus edodes*), followed by oyster (*Pleurotus* spp.) and wood ear mushrooms (*Auricularia* spp.) and button mushrooms (*Agaricus bisporus*), which are the most popular mushroom species in western countries.

Stamets (1993) describes the production of shiitake, oyster, and wood ear mushrooms. They are categorized as primary decomposers, all of them inhabiting wood in the wild. The traditional cultivation method of these fungi is simply to transfer mushroom mycelium onto logs of wood. These are kept outside, in a sufficiently moist and temperate environment (or in some cases buried) until mushrooms can be harvested. Nowadays, they are usually cultivated in plastic bags, filled with sterilized sawdust or other ligno-cellulosic materials, like straw. To optimize yields, it is important to keep these bags at the right temperature and moisture conditions for the chosen species of fungus. Fruiting will often occur by itself but can be induced through changes in the temperature or light condition, depending on the mushroom species (most of them do not require any light). Usually two to three flushes can be harvested at intervals of around a week before the substrate has been depleted. To increase yields, nitrogen-rich supplements are often added to the substrates. However, even without supplements high yields can be achieved. The common measure for efficiency in mushroom cultivation is biological efficiency (BE). A BE of 100% means that the mass of fresh mushrooms harvested is equal to the dry weight of the substrate. Given the water content of mushrooms of around 90%, the conversion ratio in this example would be 10:1. Skilled cultivators produce mushrooms with a BE of between 75% and 125%.

The button mushroom is usually categorized as a secondary decomposer (Stamets 1993). Such organisms depend on the prior activity of other microorganism and their metabolites to grow. However, it has been demonstrated that the button mushroom can also be cultivated on non-fermented substrates (Till 1962). The basis for substrate formulation depends on local availability of substrates but most often a combination of straw and animal manure is used (Royse and Beelman 2007). The most common substrates are compost-like materials, which are prepared in a two-phase fermentation process. A complete production cycle for button mushroom production takes roughly 14 weeks, according to Royse and Beelman (2007) from whom the information of the following short summary was taken.

- Phase 1: The composting takes about 6 to 14 days, depending on materials and facilities, such as the availability of forced aeration. The substrate materials are gathered in a large heap and mixed to achieve homogeneity. Water is added, as well as gypsum to stabilize pH. During this phase, very high temperatures are reached due to microbial activity. Since temperatures should not rise above (but also not fall substantially below) 80 °C in the center of the pile, it is necessary to turn and water the compost at intervals of about 2 to 3 days. The metabolic activity of the thermophilic microflora helps to create a more selective substrate for *A. bisporus*. When the compost has a chocolate brown color, a strong smell of ammonia, soft, pliable straws, and a water content between 68 and 74%, it is ready for phase 2.
- Phase 2: The purposes of this phase are to assimilate ammonium, to stimulate the growth of beneficial

thermophilic microflora and to kill nematodes, insects, molds, and other possible pathogens of the button mushroom. The thermophilic microorganisms, which thrive in this phase and help to metabolize the ammonium, will not be competitive at the lower temperatures during cultivation and will serve as a food and nitrogen source to the mushroom. The optimal temperature range of the substrate during phase 2 is between 50 and 55 °C. Unlike in phase 1, it is very common for cultivators to use a climate-controlled chamber during this phase, instead of relying purely on self-heating of the substrate and on turning and watering to decrease substrate temperatures. Once the phase is completed, after roughly 5 days (Gerrits 1988), it is necessary to let the substrate cool down to room temperature (ca. 23 °C) before mixing the substrate with mushroom spawn.

A typical spawning rate for button mushrooms (as for many other species) is about 2% (spawn to substrate, dry weight). The mushroom will colonize the substrate in 13 to 20 days and is then filled into trays and covered with casing soil (although it is also possible to cover the substrate with casing soil directly after spawning). Although hygienic conditions are important in button mushroom cultivation, the "semi-sterile" process described above is sufficient for very effective cultivation. The activity of some bacteria in the casing soil even seems to be beneficial, as it removes volatiles from the button mushroom which suppress fruiting (Noble et al. 2009). In general, the button mushroom prefers temperate over hot climates. China has therefore set up most of its button mushroom production in the northern parts of the country (Royse et al. 2017). In tropical countries, heat-resistant oyster mushroom species, or paddy straw mushrooms (*Volvariella volvacea*) are particularly suited for cultivation (Stamets 1993).

Mushrooms as food and feed

While the quality of mushrooms as food has received increased recognition and is reflected in rapidly increasing consumer demand, the potential of mushrooms as feed is largely unknown and unexploited. Mushrooms can be marketed fresh for roughly 5 days after harvest. If they are to be sold afterwards, they have to be conserved, for example by drying them. Dried mushrooms are very popular in Asia, while in western countries mainly fresh mushrooms are in demand (Stamets 1993). Due to spoilage, overproduction or simply "low visual quality," many mushrooms never reach the market for human consumption. While it would make little economic sense to cultivate mushrooms primarily for livestock feed, usage of "unmarketable" mushrooms in such a way would be a sustainable solution.

Mushrooms as human food

Edible mushrooms are calorie-poor but rich in protein, minerals, and vitamins. Due to the high water content (ca. 90%) of fresh mushrooms (FM), their energy density is relatively low, with only ca. 30 kcal per 100 g FM (Mattila et al. 2002). Leaving aside the water content, the most common cultivated mushrooms—shiitake, various oyster mushrooms and button mushroom—have a protein-content of approximately 20% and are a good source of all essential amino acids for human diets (Mattila et al. 2002). Mushrooms consist of around 50% carbohydrates, around a third to a half of which is dietary fiber, while the fat-content is usually low, with around 3–4% of the dry weight (Mattila et al. 2002). Mushrooms are a good source of the vitamins B2, B3, B9, and contain vitamins D, C, and trace elements of vitamin B12 (Mattila et al. 2001), which is often lacking in vegetarian and vegan diets. Additionally, many mushrooms contain macromolecules with anti-carcinogenic, immuno-stimulating or other medical effects, such as enhanced neurogenesis (Rop et al. 2009; Ryu et al. 2018; Stamets 1993).

Mushrooms are often equated to vegetables, even in the scientific literature, although they are more closely related and more similar to animals in their metabolism and nutrient composition. Supplementing mushrooms for meat can have significant health benefits for obese people, including weight loss, improved systolic and diastolic pressure, improved lipid profile, and a decrease of inflammatory markers in their blood (Poddar et al. 2013). Studies such as this, as well as their dietary profile, show that mushrooms are a healthy food and especially suitable as meat substitutes. In sensoric tests, meat analogues made from fungi were found to taste better than those made from vegetables. Additionally, the concentration of proteins and essential amino acids was found to be higher (Kumar et al. 2017). These meat analogues are most commonly produced from the mycelium of fungi such as *Fusarium graminearu*, which do not form mushrooms and are cultivated in liquid medium rather than on solid substrates. Given the increasing worldwide need for protein, mushrooms, and fungal meat analogues could play an important role in the future of the agricultural system, where high animal numbers might not be supportable.

Mushrooms as livestock feed

Very few studies have been carried out on mushroom as feed. Slightly more literature is available on the use of spent mushroom substrate as feed.

Supplementation of 2% shiitake mushroom extract in the diet of the rainbow trout *Oncorhynchus mykiss* significantly improved their immunological parameters and survival rate during exposure to the bacterial pathogen *Lactococcus garvieae* (Baba et al. 2015). A positive impact of mushrooms on weight gain of fish was found in a study where the feed of the fingerlings *Labeo rohita* and *Hemigrammus caudovittatus* was partly replaced with mushrooms. This study looked at the effect of replacing half of the fish meal with shiitake or earthworm meal in a regular feed composed of 18% fish meal, 32% ground nut oil cake, 28% tapioca, and 22% rice bran. The diet with earthworm meal showed an approximately 2-fold higher growth rate compared to the fish meal diet, while the diet with mushrooms showed a 1.2- to 1.7-fold increase, depending on species of fish (Paripuranam et al. 2011). Similarly, shiitake extracts had positive effects on health parameters of chicken (Willis et al. 2007). Feeding button mushrooms to chicken at the rate of 20 g per kg of feed led to significant growth promotion and improved antioxidant-protective activity (Giannenas et al. 2010).

It is interesting to note that there are no published feeding trials with animals that are known to be fungivores. Insects and other invertebrates have so far received very little attention from scientists, even though they are the largest group of fungivores in nature, and often depend on wood-inhabiting fungi to complete their life cycle (Vega and Blackwell 2005; Boddy and Jones 2008). Some mammals, such as squirrels and chipmunks, also have a strong reliance on fungi as a primary food (Fogel and Trappe 1978) and wild boars are known to consume truffles and other types of mushrooms. Nevertheless, the only feeding trials with mushrooms found for this review were conducted on chicken and fish.

Mushroom compost

On average, roughly 5 kg of spent mushroom substrate are produced per kg of mushrooms (Finney et al. 2009). Therefore, since 34 million tons of mushrooms are produced globally per year (Royse et al. 2017), the amount of spent substrate might be roughly 170 million tons. However, Stamets (1993) speaks of a 2:1 ratio of spent substrate to (oyster) mushrooms, without specifying if this is on a dry weight or fresh weight basis (just as Finney et al. fail to specify this). The lack of clarity on this subject in the mushroom literature is altogether surprising.

The amount and quality of spent mushroom substrate as compost is dependent on the substrate ingredients, species of cultivated mushroom and method of cultivation. The cultivation of a single mushroom species will not result in complete decomposition of the materials. The cultivation of several species of mushroom in succession on the same substrate or further composting of spent mushroom substrate will however result in the production of rich topsoil (Stamets 1993). It is also possible to use spent mushroom substrate as livestock feed—and use the manure as fertilizer. In the following paragraphs, both recycling pathways are discussed.

Mushroom compost as feed

As with mushrooms themselves, spent mushroom substrates have mainly been investigated as feed for common production animals—cows and pigs—rather than as feed for animals that naturally rely on fungal biomass as a primary food, which are mostly invertebrates.

Spent mushroom substrates as feed for pigs and cows have produced mixed results. Song et al. (2007) measured a negative effect on body weight gain of pigs with addition of 5% fermented spent oyster mushroom substrate, while 3% had no effect. Chu et al. (2012) also found negative to neutral effect of spent mushrooms substrate on growth. However, they describe an improvement in meat quality. Also, spent mushroom substrate could be a good bedding material for pigs. Durrell et al. (1997) found that enriching sow pens with spent (button) mushroom compost reduced aggressive behavior, injuries, floor sniffing, and lying down with open eyes.

Even though chemical analyses have shown that the cultivation of mushrooms should increase the digestibility of straw by reducing the amount of lignin and cellulose (Nasehi et al. 2017), feeding trials showed that cows refuse eating more than 17% of straw-based spent oyster mushroom substrate in a maize and hay based diet (Adamovic et al. 1998). The same study showed that supplementation above 10% had negative effects on weight gain. However, in another study, the growth performance of postweaning calves was improved by 8% by supplementing their feed with 10% fermented, sawdust-based spent oyster mushroom substrate (Kim et al. 2011).

Only one study (Lee et al. 2018) which examined the use of spent mushroom substrate as insect feed was found when writing this review. The paper is written in Korean (except for the abstract and tables in English) and was therefore analyzed using Google Translate (https://translate.google.com/) for this review. The study looked at a beetle (*Protaetia brevitarsis seulensis*), reared for medicinal purposes, fed with either fermented oak saw dust (control) or spent oyster mushroom and shiitake substrates. The results suggest that the beetle larvae grew fastest and gained most weight when reared on spent oyster mushroom (*P. eryngii*) substrate. Spent shiitake substrate on the other hand seems not to have fared better than the control. Aside from this source, only anecdotal evidence, as well as related studies, which looked at the use of straw fermented by fungi, rather than spent mushroom substrate, can serve as evidence that mushroom cultivation could produce insect feed as a side product. Gao et al. (2019) showed that black soldier fly larvae can be fed with maize straw fermented with *Aspergillus oryzae* (a mold, which is usually used to produce soy sauce, sake or vinegar). In the most successful treatment, where straw was fermented for 24 h, the success was similar (slightly but not significantly lower) than in the control treatment, where the insects were fed wheat bran. Qi et al. (2019) showed that fermentation of corn and wheat straw by the mold *Trichoderma viride* and the yeast *Saccharomyces cerevisiae* increased the bioconversion of these substrates by house fly larvae.

Several studies on vermicomposting of spent mushroom substrates have been carried out. However, while the quality of vermicompost from spent mushroom substrates was analyzed, there has been no investigation of the feed conversion ratios. Nevertheless, there is good reason to assume that conversion ratios are high. Edwards et al. (2010) writes that earthworms convert cow dung with an efficiency of 10%. In an experiment in which cow dung and spent oyster mushroom substrate were vermicomposted together, the treatment where earthworms grew fastest consisted of 60% spent mushroom substrate and 40% cow dung (Nik Nor Izyan et al. 2009). Therefore, the feed conversion ratio for spent mushroom substrate might also be 10% or higher. This assumption is supported by another experiment: in a vermicompost consisting of 25% sewage sludge and 75% spent oyster mushroom substrate the earthworm biomass increased by 896% in only 70 days (Bakar et al. 2011).

Mushroom compost as fertilizer

Many studies have found mushroom composts to be of excellent quality and rich in nitrogen (N), phosphorous (P), and potassium (K). Nevertheless, the production of great amounts of spent mushroom substrate can lead to similar disposal problems as other kinds of organic wastes (Grimm and Wösten 2018). This is especially the case for substrates which contain animal manure, such as used for the button mushroom. Spent button mushroom substrate is used for crop production in horticulture and agriculture. However, some authors recommend that, to convert this spent substrate to high-quality compost, it should be subjected to a weathering period of at least 6 months, during which it is spread in heaps of roughly 1.5 m height and subjected to the elements. In this way, salts and minerals, which reduce the quality of the compost (Courtney and Mullen 2008), are washed away and the decomposition of the material continues. In a comparison of spent button mushroom substrate, forced aeration compost and mineral "NPK" fertilizer, it was shown that of all treatments, a 100 t per ha application of spent substrate had the strongest positive effect on grain yield (59% increase compared to no-fertilizer control), and that even 50 t/ha came close to producing the same yields as the mineral fertilizer treatment. Also, the amount of soil phosphorous, potassium and nitrogen, as well as soil organic matter were greatly increased. The authors of this study remark that salinity problems are unlikely to occur "as the P content of soil and compost would limit further large applications" (Courtney and Mullen 2008). The application of mushroom compost, as for any other compost or fertilizer, should nevertheless be case-depended. For example, magnesium-deficiency could arise at high application rates due to antagonism with potassium, which is abundant in mushroom compost (Uzun 2004).

Spent substrates of oyster or shiitake mushrooms have been shown to not only improve plant growth but also their health status and to be able to suppress plant pathogens in soils. In a bio-essay experiment with cucumbers and the fungal pathogen *Colletotrichum lagenarium*, it was shown that spent shiitake substrate greatly reduced anthracnose symptoms (Di Piero et al. 2006). The effect was largest in unsterilized spent substrate. Fresh (unused) shiitake substrate showed a much slighter reduction in these symptoms. Therefore, metabolites from shiitake mushroom cultivation must be responsible for the positive effect. Spent oyster mushroom substrate, as well as extracts and live mycelium from the oyster mushroom were shown to suppress the sugar beet nematode *Heterodera schatii*: the addition of 100 g and 200 g of spent substrate per 3 kg of soil reduced the numbers of nematode cysts by 85% (Palizi et al. 2009). In another study, spent oyster mushroom substrate suppressed root-knot nematodes in field conditions, though not as effectively as other organic wastes (El-Sherbiny and Awd Allah 2014).

Even though these results show that further composting is not strictly necessary for spent shiitake or oyster substrate, it can be very beneficial to do so. Through co-composting, it is also possible to recycle other organic wastes such as pig manure or sewage-sludge. This was shown in the context of vermicomposting, where high-quality composts were produced from sewage sludge and spent mushroom substrate (Bakar et al. 2011).

Discussion

This review showed the potential of mushrooms and spent mushroom substrate for food, feed, and compost preparation from crude fiber and lignin-rich biomass. An improved integration of mushroom production into the food production chain could make important contributions to food security and human health, to soil fertility and carbon sequestration, as well as to animal and plant health, which could even help to reduce the use of antibiotics and pesticides. Other usages of mushrooms and spent mushroom substrates, which were not discussed in this review, include bioremediation and the production of materials and enzymes (Grimm and Wösten 2018). The application of mushroom compost could also be used to increase biodiversity in agricultural landscapes and in forests. However, no studies on this have yet been conducted.

Mushroom cultivation can be integrated into many different agricultural systems, due to the sheer number of different ways in which mushrooms and mushroom compost can be used. Industrial nations could include this in strategies for reaching their self-set climate and sustainable development goals, while the main incentive for developing nations to promote mushroom cultivation in circular food chains, is likely to be food security and public health. Small scale farmers could profit most, as they have all the materials necessary for cultivation and need few materials to get started. Mushroom cultivation would be an additional source of income and food. The limited access to fertilizers in most African nations would be less of a problem if high quality compost was available (Rahmann et al. 2019). Also, the feeding of chicken or fish with mushrooms and earthworms would reduce the need for other, unsustainable feed.

The contribution to food security can best be visualized in an example. We assume that on a field of 1 ha, 4 t of wheat and 4 t of straw are produced (on a dry weight basis). Five percent of the grains are used for the production of oyster mushroom spawn, while all of the straw is used as substrate. Fanadzo et al. (2010) produced oyster mushrooms on un-supplemented wheat straw with a biological efficiency of 71%. If we assume such a low efficiency, the amount of mushrooms produced from the 4 t of straw (dry) would be 2.8 t (fresh)—and therefore 280 kg in dry weight. If we assume a 20% mass reduction from the substrate during colonization, as Nasehi et al. (2017) found with an oyster mushroom, then the amount of spent mushroom substrate would be 3.2 t. If this spent substrate was vermicomposted and if the conversion efficiency of mushroom compost by earthworms is indeed 10%, then 320 kg of earthworms could be produced. If the mass reduction of the compost during vermicomposting is again 20%, and we also subtract the weight of the earthworms themselves, the amount of compost would be roughly 2.2 t. The calculations for the amount of earthworms and compost are by necessity inaccurate, as no literature on this exists. However, it might not be unrealistic, to produce 280 kg of dried mushrooms, 320 kg of earthworms and 2200 kg of compost from 1 h of wheat straw. Given that fungal biomass is one of the main food sources for earthworms (Schönholzer et al. 1999) and that most of the fungal biomass is mycelium, rather than mushrooms, it is possible that the mass of earthworms might exceed that of mushrooms. Nevertheless, it is also possible that the amount of earthworms here is exaggerated. To make a more accurate assessment of the potential of such a mycological recycling pathway, experiments will have to be conducted. These should investigate mushroom cultivation in the context of agricultural systems, rather than as an isolated industry. In this way, a great contribution to the agricultural system could be made.

Conclusion

As depicted in Fig. 1, mushroom cultivation could hold a central position in agricultural systems. This is mainly because they can be used to recycle byproducts and biomass from animal husbandry and especially crop production. The integration of mushroom cultivation between these two systems could lead to more productivity and improved resource use efficiency. Mushrooms themselves are "quality" rather than "energy" food. Since they are particularly suited as a meat alternative, they could be used to create more sustainable agricultural ecosystems with relatively low animal densities. In such a system, ligno-cellulosic plant waste would be used for mushroom production instead of ruminant feed. This would not only be more effective but also avoid methane emissions. Since livestock such as fish and chicken have much better feed conversion ratios than most others, and since mushrooms are a healthy feed supplement for them, these species would be the ideal animals in such a "mycological" agricultural system. By vermicomposting spent mushroom substrate, this system could be improved even further by providing earthworms as feed, as well as compost for plant production. If large amounts of spent mushroom substrates are produced, this could be an ideal bulking agent for the composting of sewage sludge, thus also offering a pathway for the recycling of nutrients that would otherwise be lost from the agricultural soil.

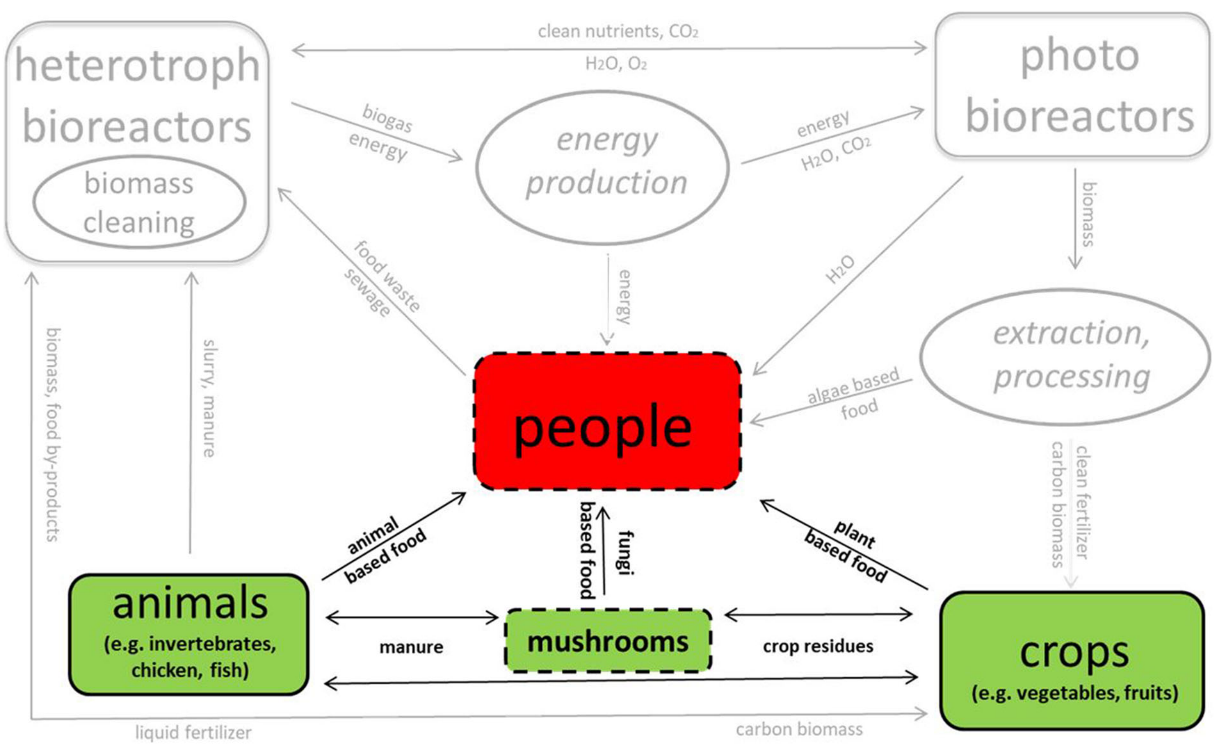

Fig. 1 The position of mushroom cultivation in a circular agricultural system, as proposed in the LandLessFood project (Rahmann et al. 2019)

Availability of data and material Not applicable.

Code availability Not applicable.

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Compliance with ethical standards

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

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Consent to participate I consent.

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