microbial biotechnology

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Microbial food: microorganisms repurposed for our food

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Summary

Sustainable food production is a key to solve complicated and intertwined issues of overpopulation, climate change, environment and sustainability. Microorganisms, which have been routinely consumed as a part of fermented foods and more recently as probiotic dietary supplements, can be repurposed for our food to present a sustainable solution to current food production system. This paper begins with three snapshots of our future life with microbial foods. Next, the importance, possible forms, and raw materials (i.e. microorganisms and their carbon and energy sources) of microbial foods are discussed. In addition, the production strategies, further applications and current limitations of microbial foods are discussed.

Snapshots from the future

#1

1 March 2031. Sunny, Seoul, Republic of Korea.—This is my first anniversary of starting a vegan diet. Why did I become a vegan? Two reasons. First, I support animal rights, yet the current system of farming livestock and preparing meat is still unethical. Second, more practically, the price of meat is sky-rocketing. Livestock industries have been pointed out for decades as one of the major contributors of climate and food crises, and most countries around the world started charging unbelievably high taxes on livestock products. So, I changed my lifestyle to participate in making a better world and save money for living. What about my health? I consume more fermented foods – including cheonggukjang (Korean fermented soya beans) and kimchi (Korean fermented vegetables) – than before, and also supplement 'Microbe Powder' to my vegan meals to enrich the nutrition in my diet. Actually, I am a big fan of Microbe Powder, which not only improves the nutritional balance but also enriches the taste of foods! Many of my athletic friends often praise Microbe Powder as the best protein supplement with such a great taste.

#2

25 July 2036. Steaming hot, Boston, MA, U.S.A..—Global warming was not a lie after all. Today's highest temperature is 45°C, and most plants on farmlands withered up. Thankfully, people do not worry about food shortage thanks to food microbes – microorganisms of which biomass is consumed as food. In most countries, governments started distributing 'lyophilized microbial inoculum' to individuals, which can be cultured and consumed as food at home. Many food companies also culture such microbes in large quantities and produce various types of foods for sale at local supermarkets and through the Internet. Diverse recipes to cook the food microbes are actively shared through social networks worldwide. Hey, wait, here is a new food microbe recipe just being released on my favourite YouTube cooking channel. Ingredients of 'Wonder Pancake': 1 cup flour, 2 tablespoon sugar, 1/2 teaspoon salt, 2 teaspoon baking powder, 2 tablespoon canola oil, and 5 tablespoon 'Wonder Microbes'. . ..

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#3

15 September 2046. Dark but starry, Spaceship to Mars.—Tomorrow is the 100th Earth day of this voyage to Mars. The crews in this spaceship will have a small celebration party tomorrow, and I need to prepare some party foods. One secret of this spaceship: there is no meat nor vegetable in this ship but only food microbes. Engineers had to minimize cargos on the spaceship to send a dozen of crews to Mars, but freeze-dried foods comprising meats and vegetables to support the crews during the mission were too heavy for loading. Instead, we brought cell stocks of food microbes that enable recycling of materials inside the spaceship. The food microbes can transform carbon dioxide and pre-treated organic/inorganic materials exhaled and excreted by the crews into edible biomass, consuming energies derived from sunlight. In addition, they double their biomass very rapidly compared with animals and plants, allowing fast recycling of the materials. Taste? Gorgeous! Carbohydrate-rich microbes substitute flour and rice; protein-rich strains are cooked like egg white, milk, and meats; oil-rich strains can be used to extract some oil for cooking. We also have tens of spice/flavouring microbes giving the flavours of black pepper, red pepper, mustard, garlic, clove, coriander, cinnamon, cacao, vanilla, truffle, saffron, peppermint, strawberry, etc. My favourite dish in this spaceship is truffle-oiled beef-flavoured lasagna with a cup of non-alcoholic mojito. A piece of microbe cinnamon roll with strawberry cream is perfect for dessert...

Why do we need microbial food?

The human population in the world has grown to over 78 billion and is estimated to exceed 80, 90 and 100 billion by 2023, 2037 and 2057 respectively (Worldometer, 2021). People looking for more food are destroying forests to secure more farmlands and unintentionally affect the productivity of agriculture and food supply through the aggravation of climate change (Grossi *et al*., 2019). In particular, the world's increasing demand for meats accelerates the grain consumption and the greenhouse gas release (e.g. methane and carbon dioxide) by livestock, further exacerbating global food and climate crises. To break up this vicious cycle, securing alternative and sustainable sources of nutritious food is required.

Microorganisms are sustainable food resource of the future. Compared with animals and plants, microorganisms double their biomass very rapidly with doubling time as short as tens of minutes (Xu *et al*., 2011) – for example, about 20–30 min for *Escherichia coli* and *Bacillus subtilis*, and 90 min for *Saccharomyces cerevisiae*. In addition, cultivation of microorganisms requires less water/land and leaves less carbon footprints (e.g. carbon dioxide) to produce a unit amount of biomass than crop/livestock farming (Table 1). Moreover, the biomass of many microorganisms, which is rich in protein (as high as 70% of the dry cell weight), vitamins, antioxidants and bioactive compounds (Delgado *et al*., 2013; USDA, 2021), is nutritionally comparable to or even better than meats (Fig. 1). Less, if not absent, ethical issues compared with contemporary livestock farming is another attractive point of producing foods from microorganisms. Taken together, microorganisms can be a promising food resource toward making our food system more sustainable.

What will microbial food look like?

The most traditional and familiar forms of microbial food are fermented foods, which will continue to be so in the future. Famine food plants (e.g. potato, sweet potato, cassava and yam) can grow in relatively harsh conditions and would still be important source of food in future. Unfortunately, they are mostly rich in carbohydrates and nutritionally unbalanced (Fig. 1). So are most other major grains and vegetables, such as rice, wheat, and corn (Fig. 1). Fermentation mediated by microorganisms can upgrade the nutritional value of such carbohydrate-rich food resources. During fermentation, microorganisms transform carbohydrates into their protein- and other nutrient-rich biomass, thus rebalancing the nutritional composition of the food. In the near future, the world's traditional fermented foods and their recipes will rapidly evolve and diverge into various forms of nutritionally balanced microbial foods.

Nutrient powders extracted from microbial fermentation would be another valuable form of microbial foods. Similar to single-cell proteins that have been studied over decades (Ritala *et al*., 2017), carbohydrates, proteins, fatty acids, vitamins and other functional nutrients from microbial culture can be enriched through extraction and purification processes and used for various purposes (e.g. breads, alternative meats, fries, food additives). In addition, the purification steps enable eliminating undesired compounds in the final product and provide broader choices of the microbial species and substrates employed for the microbial food production. However, one should bear in mind that the additional purification steps might increase the production cost and have more chances of polluting the environment.

The most explicit and sustainable form of microbial food would be the biomass of cultured microorganisms or the culture broth itself. Unlike chlorella and spirulina that are mostly consumed as tablets for dietary supplement, such microbial biomass would be used as ingredients for cooking and consumed in the forms of typical, contemporary foods cooked with diverse recipes. Such 'whole-cell foods' would provide well-balanced nutrition

Table 1. Modes of biomass production and their environmental impacts.[a]

	Products	Water footprint[b] (m^3 water kg^{-1})	Carbon footprint[c] (kg CO_2-eq kg^{-1})	Land use[d] (m^2 kg^{-1})
Animal	Beef	15 400	99.5	326.2
	Pork	6000	12.3	17.4
	Chicken	4325	3.5	9
	Egg	3300	4.5	6.3
Fish	Salmon	1400	5.8	3.7
Plant	Soya bean	2145	3.2	3.5
	Wheat	1827	1.6	3.9
Microorganism	*Fusarium venenatum* (Quorn[e])	500	5.5	2
	Methylococcus capsulatus (FeedKind[f])	20–58	2.2	0.034
	Arthrospira plantesis (Spirulina[g])	104	0	0.086

a. Environmental impacts from the production of 1 kg of edible biomass.
b. Water Footprint Network (2021).
c. Carbon Trust (2021), Matassa *et al*. (2016).
d. Poore and Nemecek (2018).
e. Quorn (2021).
f. Calysta (2021), Carbon Trust (2021).
g. We Are The New Farmers (2021).

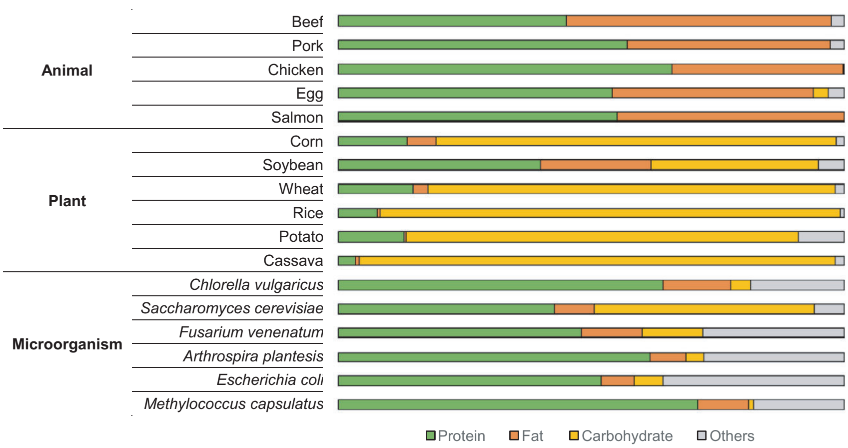

Fig. 1. Nutritional facts of various biomasses. The contents of protein, fat and carbohydrate in animal-, plant- and microorganism-derived biomass. The content of each nutrient is calculated based on dry weight (Lee *et al*., 2008; USDA, 2021).

to consumers with valuable micronutrients (e.g. vitamins). In addition, some microorganisms would be consumed alive to maximize their probiotic effects, while most microbial cells in the microbial foods would be sterilized before or during cooking.

Which microorganisms will be used?

Microorganisms that have been consumed as (a part of) food in human history (Table 2) would be most attractive candidates for the production of microbial foods. Such microorganisms have been demonstrated to be harmless and even health-promoting throughout the long history of consumption. Their nutritional values and benefits on health have been empirically, clinically, and scientifically demonstrated as well (Yoon *et al*., 2000; Feng *et al*., 2005; Chang *et al*., 2010). However, auxotrophic traits frequently observed in such microorganisms (Teusink and Molenaar, 2017) necessitate supplementation of the corresponding growth medium components during cultivation, which increases the cost of microbial food production. In addition, the bad flavour and odour of some microorganisms are critical hurdles for their use as food resources.

The state-of-the-art strategies and technologies of system metabolic engineering and synthetic biology (Chae *et al*., 2017; Choi *et al*., 2019) can help upgrading the properties and characteristics of microorganism to allow sustainable and economical production of microbial foods and also to improve nutritional value, flavour, and odour. For example, a microbial strain can be engineered to be prototrophic and to rapidly grow on a low-cost substrate while using more renewable energy (e.g. consuming

Table 2. Examples of microorganisms historically consumed by humans.

	Microorganisms	Source	Ref.
Fungi/yeast	*Penicillium camemberti*	Cheese	Button and Dutton (2012)
	Penicillium candidum		
	Penicillium roqueforti		
	Rhizopus oligosporus	Tempeh (fermented soya bean)	Feng *et al.* (2005)
	Saccharomyces cerevisiae	Bread, beer, wine	Gorter de Vries *et al.* (2019), Heitmann *et al.* (2018)
	Saccharomyces pastorianus		
Symbiotic culture of bacteria and yeast	*Saccharomyces cerevisiae* along with *Gluconacetobacter xylinus*	Kombucha	May *et al.* (2019)
Bacteria	*Bacillus subtilis*	Cheonggukjang (fermented soya bean)	Jung *et al.* (2014)
	Bacillus licheniformis		
	Leuconostoc spp.	Kimchi	Jung *et al.* (2011)
	Lactobacillus spp.		
	Salinicoccus jeotgali	Jeotgal (salted, fermented seafood)	Guan *et al.* (2011)
	Staphylococcus spp.		
	Lactobacillus bulgaricus	Yoghurt	Aryana and Olson (2017)
	Streptococcus thermophilus		
	Brevibacterium linens	Cheese	Button and Dutton (2012)
	Lactococcus lactis		
	Propionibacterium freudenreichii		

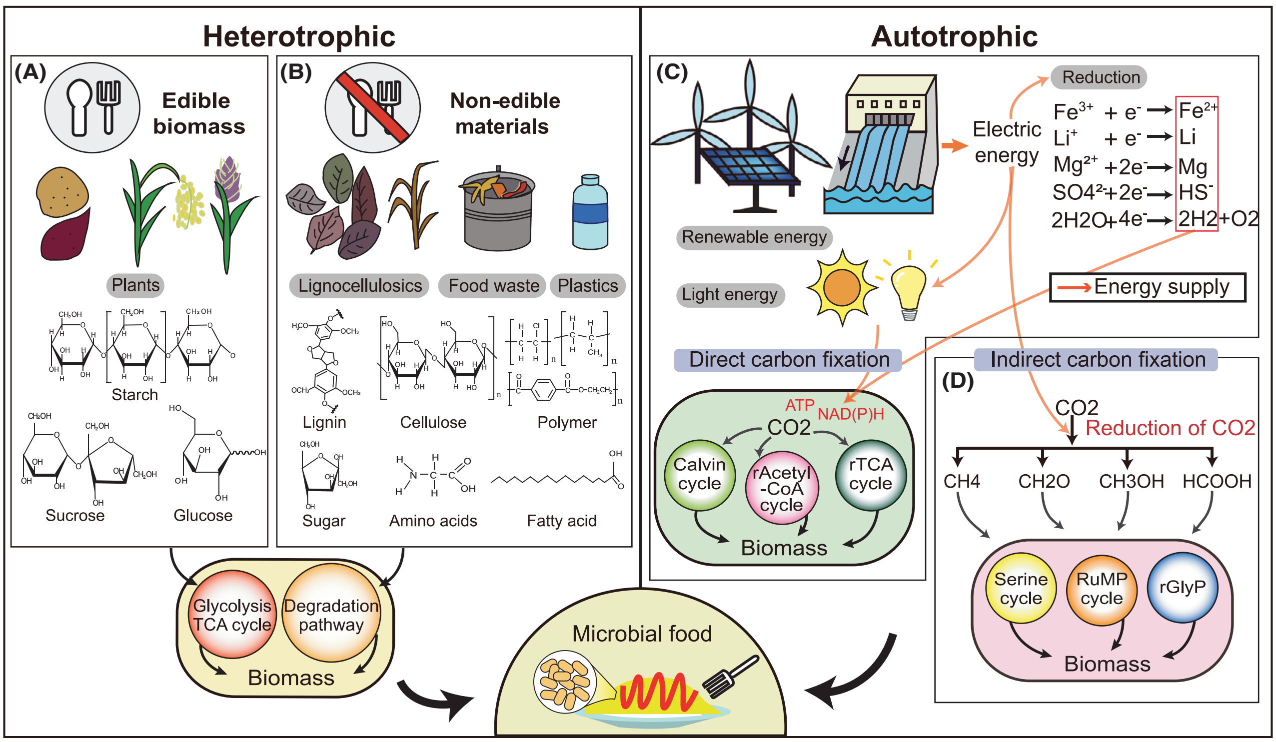

Fig. 2. Possible sources of carbon and energy for microbial food production.
A. Carbohydrates derived from edible biomass can serve as carbon and energy source of food microbes.
B. Non-edible materials, including lignocellulosic biomass, food waste and plastic, can be consumed by food microorganisms for sustainable production of microbial foods.
C. Light energy derived from sunlight or other forms of renewable energy can directly drive fixation of CO_2 to biomass through photosynthesis. In addition, renewable energy can be converted to chemical energies (e.g. H_2, reduced metal ions, reduced sulfur compounds) and provide reducing power to food microorganisms for CO_2 fixation.
D. Renewable energy can be used to reduce CO_2 into organic compounds, such as methane (CH_4), formaldehyde (CH_2O), methanol (CH_3OH) and formic acid (HCOOH), that are easier to be consumed by microorganisms. The resulting products can serve as both carbon source and reducing power, enabling indirect fixation of CO_2 into biomass. rAcetyl-CoA cycle, reductive acetyl-CoA cycle; rTCA cycle, reductive TCA cycle; RuMP cycle, ribulose monophosphate cycle; rGlyP, reductive glycine pathway.

agricultural plastics and fixing CO_2 using light energy). In addition, the nutritional value of microorganisms can be improved by increasing the content of protein, enhancing the content of valuable nutraceuticals or even customizing the nutritional balance for the specific group of people. Moreover, the palatability of microbial foods can be improved by engineering the corresponding microorganisms through eliminating endogenous metabolic pathways responsible for bad flavour and odour. Also, the heterologous biosynthetic pathways of flavour compounds (e.g. vanillin of vanilla, safranal of saffron, 2,4-dithiapentane of truffle) can be introduced to endow attractive flavours to food microorganisms and microbial foods.

How will microbial food be produced?

It is important to examine which carbon substrates will be employed for the production of microbial food. The most easy-to-use substrates for the production of microbial foods would be carbohydrates derived from plants, such as glucose and sucrose (Fig. 2). Instead of glucose derived from starch and sucrose from sugar cane or sugar beet, however, non-edible lignocellulosic biomass should become the carbon source of choice for the production of microbial foods (Fig. 2). Food microorganisms capable of consuming cellulose, hemicellulose and lignin can produce microbial foods using hay, fallen leaves, wood chips, and other plant-derived biomass and waste as raw materials. Additional introduction of efficient fatty acid degradation pathways will enable efficient upcycling of food wastes (Fig. 2), which can be as much as one-third of all foods produced in the world and are rich in lignocellulosics (17 ~ 33 wt%) and lipids (13 ~ 20 wt%) that can serve as good carbon sources for microorganisms (Banks *et al*., 2018). Moreover, such improved food microorganisms might also be grown on non-edible microbial biomass. Plastic degradation pathway might be introduced as well to convert agricultural or daily plastic wastes to microbial biomass and eventually to microbial foods (Fig. 2).

Autotrophic microorganisms can also be employed for agriculture-independent production of microbial food through direct carbon fixation. The most mundane yet ideal autotrophic system for microbial food production would be photosynthesis, which fixes carbon dioxide (CO_2) using light energy (Fig. 2). Microalgae (e.g. chlorella), cyanobacteria (e.g. spirulina) and other naturally photosynthetic microorganisms are good candidates for this mode of microbial food production. Also, non-photosynthetic microbes can be turned into photosynthetic microorganisms by metabolic engineering (Dogutan and Nocera, 2019; Jin *et al*., 2021), although most of them are not yet appropriate for food due to the combined use of inorganic catalysts. In addition to photosynthetic microbial food production, renewable energies other than light energy can be used for direct/indirect CO_2 fixation. For example, electric energy derived from renewable energy can be used to convert water molecules (H_2O) into molecular hydrogen (H_2) and oxygen (O_2), which are in turn consumed by microorganisms to fix CO_2 (Torella *et al*., 2015) and generate edible biomass (Fig. 2). Alternatively, metal ions or sulfuric compounds can be reduced and provided to lithoautotrophic microorganisms for CO_2 fixation (Fig. 2). Moreover, CO_2 can be directly reduced into easier-to-consume forms of organic compounds (e.g. formic acid) and supplied to microorganisms (Tashiro *et al*., 2018; Bang *et al*., 2020) to produce microbial food through indirect CO_2 fixation (Fig. 2).

When the carbon substrate to be employed is decided, various cultivation technologies including high cell density fermentation technologies (Lee, 1996) can be developed for different food microbes to accomplish their most efficient production. Also, division of labour during microbial food production can be another choice. For example, autotrophic microorganisms with high CO_2 fixation efficiency can be employed to produce nutritionally less-balanced (i.e. mostly carbohydrate- or lipid-rich) biomass and their biomass can be subsequently used to grow heterotrophic microorganisms with higher nutritional values.

In addition, food microorganisms might be specialized to produce specific nutrients and used as contemporary food ingredients for cooking. For example, food microorganisms rich in starch would be used to mimic flour and rice, while those rich in proteins would be used to replace meat, egg and fish. Similarly, food microorganisms rich in lipids would be used to extract oils, while special food microorganisms producing flavour and fragrance compounds would be used as spices.

What will be beyond microbial food?

Beyond the applications in food production, some food microorganisms can be repurposed as probiotics or transformed into live-cell medicine (Fig. 3). For example, microorganisms can be engineered to produce desired drug compounds (e.g. diabetes drug and anaemia drug) as well, although they will need to go through drug approval process. In addition to direct consumption by human, the biomass of autotrophic food microorganisms produced independent of plant-derived biomass can be used as pet foods and animal feeds for sustainable livestock farming (Fig. 3). Microbial foods, which are rich in nitrogenous compounds (i.e. proteins and amino acids), can also be used as eco-friendly fertilizer, improving the capacity of the global food production system (Fig. 3).

On the other hand, food microorganisms that are harmless to human, animal and environment can be exploited for environmental remediation to address issues of oil spillage, soil contamination and micro/nanoplastics (Fig. 3).

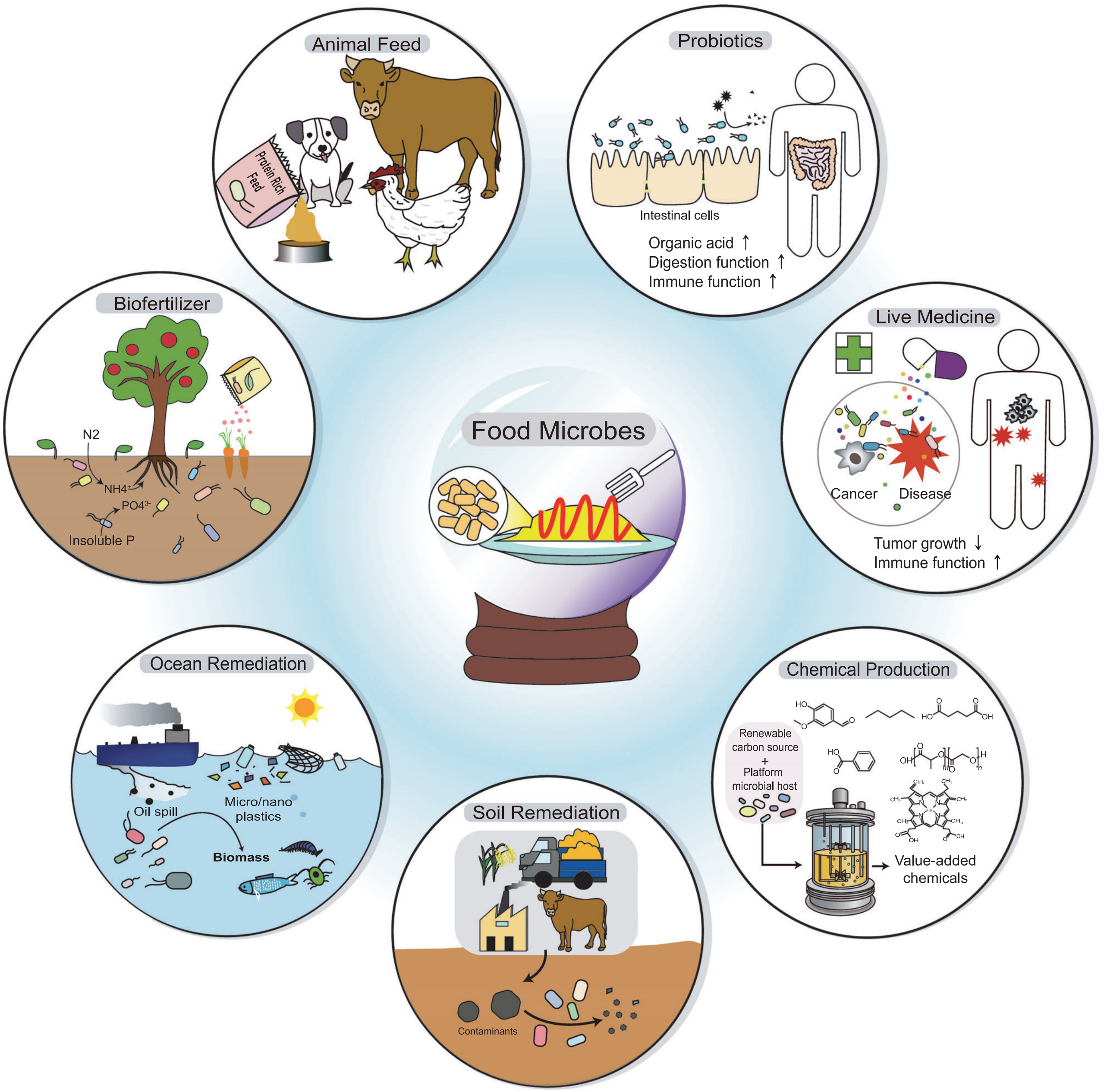

Fig. 3. Further application of food microorganisms beyond microbial food production. Beyond the production of microbial foods, live food microorganisms can be exploited as probiotics and live medicine. In addition, food microorganisms can be designed to be suitable for their use as animal feed and fertilizer. Moreover, food microorganisms that are safe to both human and environment can be further exploited to degrade environmental pollutants and produce valuable chemicals in an environment-friendly manner.

Moreover, such safe microorganisms can be further exploited to produce valuable chemicals to transform the currently unsustainable chemical industries into sustainable bio-based industries (Fig. 3).

Current limitations and perspectives

Securing food-grade microorganisms that are safe for human consumption is one of the most critical requirements for microbial foods to be widely accepted. Currently, 'generally recognized as safe (GRAS)' notices by U.S. Food & Drug Administration (FDA) and 'qualified presumption of safety (QPS)' list from European Food Safety Authority (EFSA) provide the lists of qualified safe-to-eat microorganisms. Since the evaluation processes rely on scientific evidences submitted by notifiers, however, such lists include only a limited number of edible microorganisms, while a much larger number of microbial species and strains have been safely consumed by human throughout the long history. More advanced regulatory system that actively identifies and approves safely edible microorganisms and systematically manages their list is desired to accelerate the development of more diverse microbial foods.

The state-of-the-art technologies of metabolic engineering and synthetic biology are essential to upgrade microorganisms and meet the desired qualities of microbial food. However, public concerns on genetically modified organisms (GMOs) and living modified organisms (LMOs) are discouraging the use of engineered microorganisms as food resources. To drive a positive consensus of the public on consuming engineered microorganisms, a comprehensive and systematic evaluation procedure with scientific criteria to assess the safety of GMOs and LMOs as food resource is requested. In addition, transparent policies and clear communication programmes based on scientific facts should be accompanied.

Recalling that advances in cultivation technologies and tools led to the agricultural revolution, development of efficient fermentation technologies would be critical as well to maximize microbial food production. Although more eco-friendly and energy-efficient than contemporary crop and livestock farming (Papadaki *et al*., 2017; Souza *et al*., 2019), current fermentation technologies still require development of more efficient yet easier cultivation strategies with less energy and fermentation wastes.

The acceptance and popularity of microbial foods will be determined by the public. The most important motivation of developing microbial food is to establish a sustainable food production system and overcome the food crisis. Once the public perceives microbial food as a second class food, there is no future for the microbial foods. To attract people's tongue and mind, it is critical to develop microbial foods having good taste and strong health benefits. Engineering microbial foods to be free of undesired flavour and full of good tastes and health-promoting nutrients would be one solution. In addition, development of diverse recipes that can turn microbial foods into various delicious dishes should be accompanied.

Instead of large-scale food replacement, microbial food will first be employed as a supplementary food that upgrades the traditional food in both nutritional value and taste. Various types of microbial foods will become available to meet the nutritional requirements of particular groups of people for their greater health benefits (e.g. diabetes patients, stomach cancer patients, obese people, men older than 90 years). Such 'precision nutrition' can be achieved best using microbial foods, leading to the emergence of 'precision microbial foods'. It is expected that microbial foods will become an important contributor to accomplish sustainable production and consumption of foods in the Anthropocene, the era of climate change and overpopulation.

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