



Review article

Application of microbial resources in biorefineries: Current trend and future prospects

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ABSTRACT

The recent growing interest in sustainable and alternative sources of energy and bio-based products has driven the paradigm shift to an integrated model termed “biorefinery.” Biorefinery framework implements the concepts of novel eco-technologies and eco-efficient processes for the sustainable production of energy and value-added biomolecules. The utilization of microbial resources for the production of various value-added products has been documented in the literatures. However, the appointment of these microbial resources in integrated resource management requires a better understanding of their status. The main aim of this review is to provide an overview on the defined positioning and overall contribution of the microbial resources, i.e., algae, fungi and bacteria, for various bioprocesses and generation of multiple products from a single biorefinery. By utilizing waste material as a feedstock, biofuels can be generated by microalgae while sequestering environmental carbon and producing value added compounds as by-products. In parallel, fungal biorefineries are prolific producers of lignocellulose degrading enzymes along with pharmaceutically important novel products. Conversely, bacterial biorefineries emerge as a preferred platform for the transformation of standard cells into proficient bio-factories, developing chassis and turbo cells for enhanced target compound production. This comprehensive review is poised to offer an intricate exploration of the current trends, obstacles, and prospective pathways of microbial biorefineries, for the development of future biorefineries.

Abbreviations: PUFA, Polyunsaturated fatty acid; ARA, Arachidonic acid; GLA, Gamma linolenic acid; IEA, International Energy Agency; TAGs, Triacylglycerides; PHAs, Polyhydroxyalkanoates; HPB, Hydrogen producing bacteria; VFAs, Volatile fatty acids; FAME, Fatty acid methyl ester; LAB, Lactic acid bacteria; CO₂, Carbon dioxide; CO, Carbon monoxide; BBE, Blue bioeconomy; EPA, eicosapentanoic acids; DHA, docosahexaenoic acid; EPS, Extracellular polymeric substances; PHB, polyhydroxybutyrate; COD, Chemical oxygen demand; HVAC, High-value added compounds; HRAP, High-rate algal ponds; AOX, Adsorbable organic halogens; IREP, Integrated renewable energy park; MFC, Microbial fuel cells; PAMFC, Photosynthetic alga microbial fuel cell; ACS, Acetyl CoA synthetase; TAN, total ammonia; ABE, Acetone-butanol-ethanol; GC-MS, Gas chromatography-mass spectrometry.

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1. Introduction

The overreliance of humans on conventional non-renewable sources of energy and day-to-day products has affected their existing supplies globally while deteriorating and polluting the environment [1]. The conversion of the renewable resources and production of green technologies under the “biorefinery” concept, however, will open the gates for a new paradigm of environmental sustainability. The International Energy Association (IEA) Bioenergy Task 42 has defined biorefinery as an upstream, midstream and downstream processing facility or a plant for the conversion of biomass into a spectrum of marketable products and energy in an economically, socially acceptable and environmentally sustainable manner [2]. The main driver for the establishment of biorefineries is the holistic environmental sustainability which could be achieved by employing the microbes as large volumes of biomass is required to generate commodities for the global demand. The exploitation of multifaceted microorganisms for their diversity and plasticity may empower the production of various bio-products in a sustainable manner. The feedstock, substrate or media required to harbor such large and diverse amount of microbes can be availed through vastly available and negatively assessed waste, a value generating feedstock. Such biorefineries have attracted attention of the researchers as the microbes offer biomass cultivation on a non-agricultural land, climate and time independent cultivation, short harvesting cycle, less environmental load and complete biodegradable nature [3–5]. Moreover, microbial biorefinery put forward a holistic model for economic, environmental and social growth by sequestering carbon from renewable carbons sources such as environment (in case of autotrophic microbes), lignocellulosic waste, industrial waste and municipal waste as described in Fig. 1. Inclusion of circular cascading approach for self-sustainable biorefinery and aligning with consolidated sequential bioprocessing approach for generating multiple products from a single biorefinery are the major traction points of microbial biorefineries. Roughly 1.3 billion tons of lignocellulosic biomass is produced annually on a global scale, however, a mere 3 % of this vast resource finds its utilization [6]. Microorganisms can be employed for the hydrolysis of the leftover lignocellulosic materials for biofuel production along with by-products such as carotenoids, essential lipids arachidonic acid (ARA) and γ -linolenic acid (GLA) or protein rich animal feed.

Apart from biofuels (including biodiesel, bio-hydrogen, bioethanol, and biogas), the microbial resources, algae, fungi and bacteria, have also been explored for the production of high-valued metabolites, such as carotenoids, lipids, pigments, amino acids, and proteins from agricultural, dairy and industrial feedstocks [7]. Biopolymers, platform chemicals, and bio-electricity, have also been generated while remediating natural resources. Production of biopolymers such as polyhydroxyalkanoates (PHA) or acetate from microbial source can be a significant approach in reducing the production cost of biopolymers while proving a great competency to synthetic ones. It was reported that microbes are capable of 15–300 times increased oil production than per unit area of conventional terrestrial crop and can be used for the production of biodiesel instead of traditional vegetable oil [1]. Thus, there is an alarming need to harness the potential of these microorganisms to valorize the abundantly available renewable resources.

Fig. 2 summarizes the overview of the biorefinery concept focusing on the sustainable generation of the bio-products. Microbes

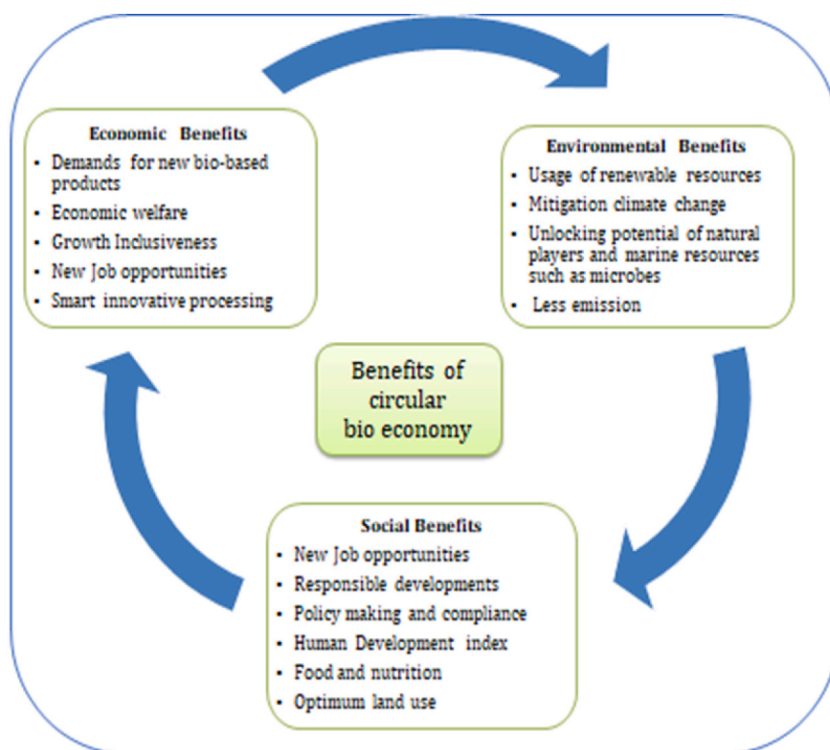


Fig. 1. Schematic showing the benefits of circular economy.

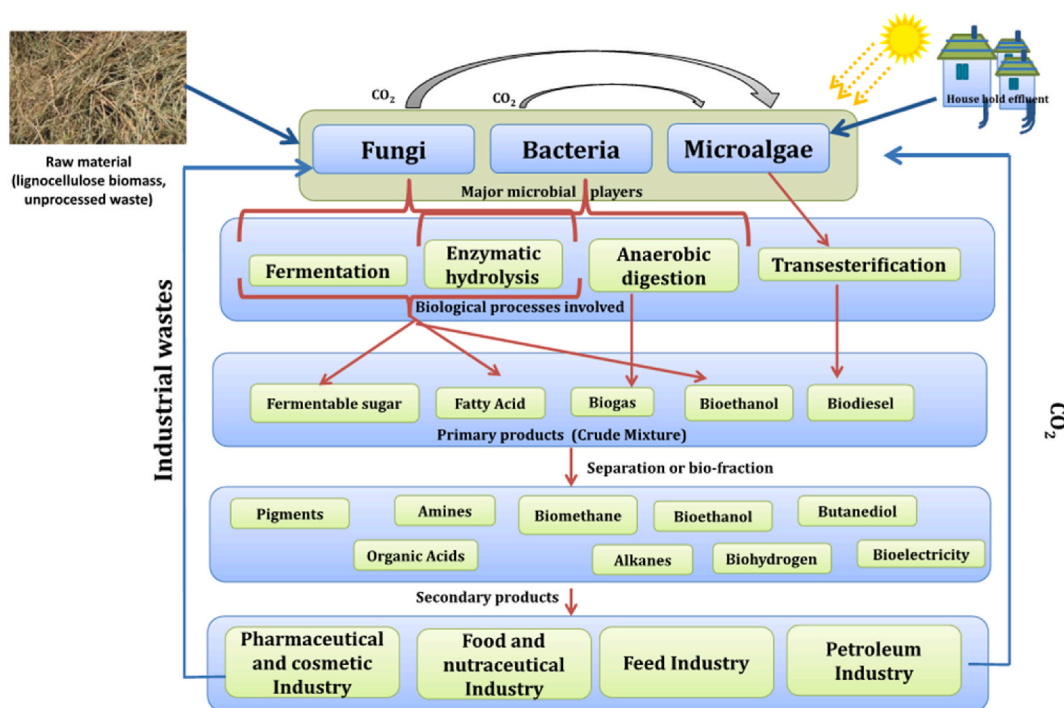


Fig. 2. Illustration showing the major microbial resources with the commodities contributing to the biorefinery concept.

(individually or in consortium) harness the waste raw material and environmental carbon dioxide (CO_2) under meticulously controlled and optimized process conditions to produce products such as fermentable saccharides, fatty acids, and biofuel via fermentation, extracellular enzymatic hydrolysis, aerobic/anaerobic digestion or transesterification pathways. These products are then separated via sequential extraction procedures to obtain the target and by-products separately. These products have profound applications in petroleum, pharmaceutical, nutraceutical, food, feed, biopolymer, cosmetic and other industries.

Taking into consideration the significance of such models for environmental sustainability, there is, however, limited collective information available related to the diverse range of products produced by these microbes. Hitherto, high production cost of these microbial based products has become the key hurdle for the commercialization of these products. However, with integrated approach such as the use of low-cost raw material or waste biomass together with production of value-added bio-products as described in the current review, the mitigation of hurdles in the production of bio-products with bioresources is indeed possible. Moreover, the advancements in the synthetic, systems and chemical biology along with diverse biotechnological interventions have enhanced their role as prolific bio-factories. This review presents a proposition of cohesive microbial biorefinery processes employing fungi, bacteria, and microalgae for the production of biofuel accompanied by industrially relevant value-added products while shedding light on the recent advancements and challenges in the industrialization of these biorefineries with possible overcoming routes. This review aims to equip the reader with a comprehensive understanding encompassing microbial biorefineries from all facets.

2. Microalgal biorefinery

Microalgae are autotrophic cell factories that have an extraordinary potential of converting CO_2 into biomass utilized for high value-added compounds, biofuels, food, feed and others while not competing with the food. The carbon capture rate of algae is approximately four times higher than that of crops along with half of its dry weight being carbon, making it a better option for bio-commodity production at a commercial scale [8]. Microalgae are unicellular photosynthetic organisms, sized in micrometres and typically found in freshwater and marine systems [9]. Their biomass is rich in lipids, proteins, carbohydrates and bio-actives. Along with marine and fresh water, microalgae can also be cultivated in different types of wastewater generated from industries, municipal and agriculture while decreasing the need of land for feedstock generation. Microalgae's utilization for biofuels is also proved to be promising due to their richness in lipid as well as carbohydrates content [10].

Apart from biofuel, microalgae have potential of producing bio-oil, bio-hydrogen, bio-electricity, and compounds for cosmetics, food, feed, nutraceuticals and chemical industries along with other bio commodities, as shown in Fig. 2. In addition, microalgae also serves as a reservoir of biopolymers for food hydrocolloids [11]. Microalgal biorefinery is a promising concept to fully exploit the potential of microalgae while minimizing cost and waste accumulation. Microalgal biorefineries can play a significant role in setting up a platform for sustainable production of biofuels and can supplement in 'Blue Bioeconomy' (BBE), a term used for the activities that are associated with biomass from aquatic origin. It focuses on developing technologies and innovating models to provide with sustainable

solution for the inherited dependency on the fossil fuels for energy [12]. However, to obtain the optimum benefits of the concept, the procedures should not be perceived as merely a series of steps to separate target compounds, but as a sequence of unit operations starting from strain selection and culturing to laboratory-scale research and pilot-scale operations altogether. Out of these, upstream and downstream processing are the two major cost-intensive stages [13]. In the realm of breakthroughs and technological advancements, the key lies in crafting ingenious, sustainably, and economically viable processes that pave the way for enhanced commercialization of microalgal products through the biorefineries.

2.1. Production of lipids and bio-fuels using microalgae

The concept of microalgal biorefinery falls under the third-generation of biofuels, one of the most advanced generations as it does not pose the ethical threat of food vs fuel, agricultural land occupation, insufficient feedstock availability and high energy requirements [14]. Microalgae are one of the most promising microorganisms for the production of microbial lipids as they have the potential to store triacylglycerides (TAGs) in their cells in response to the changing growth conditions. Upon optimization of culturing conditions, the lipid content can increase up to 50–70 % of the dry biomass with *Botryococcus braunii* having oil content of 75 % dry weight [15, 16]. Generally, the growth and cultivation of microalgae does not require potential feedstock for commodity production, but it requires optimum conditions and improved technologies for its growth. Temperature, light, illumination pattern, pH, mineral or salinity stress are some essential parameters that enhance lipid accumulation in the microalgal cells by 10–20 %, majorly through modifying the fatty acid metabolism to TAG's synthesis and accumulation [16]. The critical factors influencing microalgal growth and lipid, oil, and fatty acid (FA) production are the presence of essential trace elements and the application of environmental parameters to induce stress conditions [17].

Wet or dry microalgae can either be a source for fermentative biofuel, i.e. algal oil-extracts or whole algae can be biochemically converted into various energy forms such as biogas, bioethanol, and bio-hydrogen through bioconversion by anaerobic digestion, alcoholic fermentation or biophotolysis [18]. The biomass feedstock of aquatic microalgae is a potential reserve for fuels which are renewable and can replace fossil fuels [19]. Thermochemical conversion of biomass can produce syngas through gasification, bio-oil through liquefaction and bio-char, bio-oil and gaseous fuel through pyrolysis. The microbial lipid produced can be turned to bio-diesel through transesterification, converting these TAGs to lipids/fatty acids methyl esters (FAME) and glycerol (by-product). Due to their reduced lignin content, rapid growth rate, high photosynthetic efficiency, more lipid production per hectare and efficient generation of bio-fuels and valuable chemicals, microalgae have emerged as an exceptional microbial feedstock ideally suited for fuel-based industries [20].

Microalgal species reported to contain high levels of lipid content are *B. braunii* (25–75 %), *Chlorella* spp. (28–32 %), *Cryptochloridium cohnii* (20 %), *Dunaliella primolecta* (23 %), *Isochrysis* spp. (25–33 %), *Nannochloropsis* spp. (31–68 %), *Nitzschia* spp. (45–47 %), and *Schizochytrium* spp. (50–77 %) [14]. Microalgal strains used for the production of bio-oil are *Chlorella vulgaris* (29.4 %); *Scenedesmus abundans* (43.4 %); *Dunaliella salina* (2–6 %); *Cyanidioschyzon merolae* (59 %); and *Nannochloropsis* spp. (59 %) of their total biomass [21–23].

2.2. Production of biogas, bio-hydrogen and bioethanol using microalgae

Biogas production individually or along with biodiesel, bio-hydrogen, bio-fuel and various value-added metabolites is a section of microalgal-based biorefinery. A mixture of methane, CO₂ and trace amounts of ammonia, hydrogen sulfide and nitrogen is called biogas. It is generated through four-staged anaerobic digestion, namely, hydrolysis, acidification, acetogenesis and methanogenesis. Biogas production through microalgae depends majorly on strain selection, pretreatment methods, cultivation methods, type of substrate, operational pH and temperature [18]. De-oiled microalgae, when treated with enzymes in the presence of acids, tend to produce methane and sugars through methanogenesis [24]. Many studies accounted the production of bio-methane along with other biofuel products as sustainable source of energy. Methane was generated from post-transesterified *C. vulgaris* biomass, yielding both bio-diesel and bio-methane [25].

Microalgae species such as *Chlamydomonas*, *Chlorella* and *Scenedesmus* are known to contribute in the generation of bio-hydrogen along with biogas because of their high carbohydrate content. Bio-hydrogen can be produced either through bio-photolysis of microalgal cells or from dark/acidogenic fermentation of microalgal biomass [26]. Along with bio-hydrogen, volatile fatty acids (VFAs) are also produced in acidogenic fermentation of microalgal biomass [27]. *Chlamydomonas reinhardtii* was reported to produce bio-hydrogen and the residual biomass of algae was turned into biogas in the form of methane [28]. *C. reinhardtii* is considered as a model organism to produce bio-hydrogen through bio-photolysis and has been modified genetically to produce 300 mL/L of bio-hydrogen [26].

Along with its high carbohydrate content, the absence of lignin is also an added bonus in microalgae for the production of bio-hydrogen or bioethanol. Production of bioethanol from microalgae is a multistep process including pre-treatment for the lysis of cell wall via mechanical, chemical or enzymatic methods, hydrolysis of polysaccharides into oligo or monosaccharides with simultaneous or separate fermentation by *Saccharomyces* or *Zymomonas* and distillation [18]. In a previous work, 3.4 g/L of butanol was produced by *C. vulgaris* by the fermentation of 111 g of acid treated algal biomass [29]. Biobutanol has high energy content amongst all liquid biofuel and it can replace bioethanol in the upcoming future owing to its beneficial characteristics such as lower heat of vaporization and volatility with higher energy density and viscosity [30].

2.3. Production of high-value added compounds (HVACs) using microalgae

Microalgae based biorefineries can contribute to the production of bioactive compounds which have high value and market size. *Chlorella*, *Dunaliella*, *Haematococcus*, *Spirulina* and *Nannochloropsis* are the leading microalgal strains in the market for HVAC production owing to their diverse chemical composition and selective yield enhancement under stress conditions [31]. Microalgae are producers of various carotenoids such as lutein, canthaxanthin, beta-carotene, astaxanthin, zeaxanthin, violaxanthin and many more. Lutein production from *Scenedesmus almeriensis* with yield of 3.2 mg/g of biomass, beta-carotene production from *Dunaliella tertiolecta* with 4.5 mg/L yield and total carotenoids of 11.7 mg/L, and *D. salina* with total carotenoids (102.5 mg/L) and beta-carotene of 10 % of its dry cell weight are a few examples of high carotenoid production in microalgae [32–34]. Beta-carotene, a pigmented carotenoid have been found to be a potent anticancer and antioxidant agent [35]. The most robust natural antioxidant, astaxanthin, is commercially produced by *Haematococcus* (up to 5 % of its dry weight), for its use as a pigmented nutraceutical in food, feed, medicine and cosmetics [36].

Microalgal pigments are approved to be used in food, feed, nutraceuticals, pharmaceuticals and cosmetics among which chlorophyll from *Chlorella*, phycocyanin from *Spirulina*, beta-carotene from *Dunaliella* and astaxanthin from *Haematococcus* are used widely. Chlorophylls are photosynthetic green pigments with antioxidant and antimutagenic properties constituting around 4.5 % of dry weight of *C. vulgaris*. *C. vulgaris* (also known as emerald food) accumulate around 60 % of protein, essential fatty acids, minerals and vitamins along with chlorophyll and trace amounts of other pigments [37]. Phycobiliproteins are protein pigments constituted of allophycocyanin (light-blue pigment), phycocyanin (blue pigment) and phycoerythrin (red pigment). *Spirulina* is known as a prolific producer of phycocyanin (25 % of dry weight) along with chlorophylls, carotenoids, biopeptides, enzymes, phenolic compounds, vitamins (provitamin A, B1, B2, B12 and E), essential fatty acids, and minerals (calcium, chromium, copper, iron, magnesium, phosphorous, sodium and zinc). It is used commercially as a nutraceutical supplement, cosmeceutical, and as food [37]. *Porphyridium* is used for the commercial production of phycoerythrin and was reported to have 55.3 and 66 % of amino acid content, both the essential and non-essential type respectively, under controlled conditions of continuous fluorescent light intensity of 250 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ at 22 °C [38].

It has also been reported that microalgal strains produce substantial quantities of amino acids, and their biomass can be utilized as a food additive [25]. *C. vulgaris* is reported to have 64.1 % of protein content when employed in an integrated system including supercritical water gasification, hydrogen separation, hydrogenation, and a combined cycle [39]. Poly-unsaturated fatty acids (PUFAs) such as omega fatty acids (linoleic and linolenic acids), eicosapentanoic acid (EPA), docosahexaenoic acid (DHA) and arachidonic acid are some of the essential fatty acids produced by *Chlorella*, *Fistulifera* and *Koliella* [18,40]. Accumulation of biopolymers in microalgae is also studied widely when specific conditions are implemented on the strains. *D. salina* demonstrated an extracellular polymeric substances (EPS) yield of 89 % when grown under salt stress and *B. braunii* gave polyhydroxybutyrate (PHB) yield of 16.4 % when grown in sewage wastewater [41,42]. *Chlorella* and *Chlamydomonas*, have also been studied for the production of bioplastics, especially PHB at the laboratory scale [40]. *C. vulgaris* gave a yield of 37.2 % of PHB while incorporation of defatted *Chlorella* biomass with polyurethane lead to an increase in the tensile strength and elongation at break of the composite [43]. Further emphasis, however, is required to seamlessly integrate biotechnological interventions for the synthesis of biopolymers sourced from microalgae biomass cultivated using waste feedstock.

2.4. Bioremediation using microalgae

Through the utilization of pollutants such as nitrates, phosphates, and carbon, microalgae contribute to the bioremediation of effluent by producing lipids, pigments, and other valuable commodities. *Chlorella sorokiniana* when cultivated on wastewater can produce 1.1 mg/L/day biomass, with 15.6 % of lipid content at the lab scale [44]. *C. vulgaris* generated 14–22 % of lipid when cultured in municipal wastewater. Efficient removal of nitrogen and phosphorous by 90 % and decrease in chemical oxygen demand (COD) by 70 % through microalgal cultivation has been reported in different studies [40]. Release of the effluent rich in oxygen has also been reported during the microalgal growth in wastewater, along with removing nitrogen and carbon, thus, reducing the chances for eutrophication in the aquatic systems [45]. In another study, municipal wastewater was treated using oleaginous microalgae with bacterial consortia [46]. Lipid and HVAC's accumulation by microalgal species such as *Spirulina* and *Nannochloropsis*, has been reported when supplemented with waste feedstock such as piggery waste, dairy manure, soy effluent, and others [46]. *Chlorella pyrenoidosa*, when cultivated in starch wastewater with 0.8 % glucose produced 118.4 mg/L/day lipids [47]. Microalgae-based high-rate algal ponds (HRAPs) are being employed to treat urban, agricultural, and industrial wastewaters along with the treatment of water polluted by specific pollutants. *Chlorella*, *Chlamydomonas*, and *Scenedesmus* are among the most studied species for ammonium, phosphorous, carbon, adsorbable organic halogens (AOX), acid mine drainage, hormones, endocrine disrupters and heavy metals absorption from water resources [48]. Many of these strains proved that wastewater can be utilized as a feedstock supplementation source for microalgal cultivation, the production of biofuel and many other metabolites [49,50]. Utilization of wastewater for microalgal cultivation will cut-down the cost of wastewater treatment through conventional treatment while fulfilling freshwater and nutrients requirement for microalgal cultivation giving a win-win situation for microalgal and wastewater treatment industries.

2.5. Bio-electricity generation using microalgae

Microalgal biorefinery concept can also be employed for the production of bio-electricity by setting up an integrated renewable energy park (IREP) which can produce liquid biofuels and electricity while mitigating carbon emissions to zero net amount [51].

Microbial fuel cells (MFCs) work on the principle of transfer of electron from anode, i.e. by the degradation of organic matter (preferably by bacteria through anaerobic respiration) to the cathode, thereby generating a circuit to produce electricity [40]. A photosynthetic alga microbial fuel cell (PAMFC) developed with *C. vulgaris* in cathode and a bacterial consortia as anode, simultaneously generated both electricity and pigments at an enhanced rate [52]. Several other microbial fuel cells operated with *Chlorella*, *Chlamydomonas* and *Spirulina* have also been reported for the generation of bio-electricity with its biomass being used for HVAC production or as a substrate for the growth of bacterial consortia in the opposite compartment [52]. Another study used Tapioca wastewater and microalgae to generate bio-electricity through microalgae-microbial fuel cell technology [53].

2.6. Microalgal biorefinery – challenges and progressive routes

Various possible microalgal biorefinery strategies such as the biochemical conversion of microalgae, development of reactor technologies for the cultivation of microalgae, strain improvements for either hyper accumulation of a single value added compound or co-accumulation of multiple compounds, different methods for the conversion of microalgae into biofuel, and environmental, economic aspects and applications of utilizing microalgae based biorefinery have been discussed extensively in the literature [54,55]. Table 1 gives an overview of microalgal strains reported for the production of various products that can be incorporated in an integrated biorefinery. Microalgae has been majorly studied for biofuels production, however, more focus should be now put on growth, extraction, down-streaming and purification optimization for obtaining high yield of HVACs along with biofuels. Incorporation of genetic engineering for strain improvement also needs to be explored in order to obtain higher yields, for example, a 2.4 fold increase in TAGs production by over-expression of acetyl CoA-synthetase (ACS) in *C. reinhardtii* has been reported [56].

One of the major advantage of using microalgae is its flexibility of consuming diverse media along with wastewaters for growth and compound production. It can grow autotrophically with light energy or heterotrophically with organic carbon, however, the biomass yield is very less (<3 g/L) [13]. Mixotrophic cultivation, where the carbon requirements will be supplemented by both organic and inorganic carbon, has been reported to produce compounds through both autotrophic and heterotrophic pathways in the diatom *Phaeodactylum tricornutum* UTEX-640 [63]. Along with the cultivation parameters, lipid yield also depends on the cell disruption and extraction techniques employed through various solvents and methods such as Soxhlet extraction, accelerated solvent extraction, supercritical fluid extraction, Folch's and Bligh and Dyer's protocols for solvent extraction.

Approximately 40 % of a biorefinery's total cost is spent on harvesting. Employing cost-efficient techniques such as flocculation or cell disruption can cut expenses and boost yields [64]. Furthermore, mild and less damaging extraction techniques should be employed to prevent any damage to other commodities to be extracted further. Integrated cell disruption and lipid extraction techniques such as ultrasound-assisted, microwave-assisted, pulsed electric-field assisted or supercritical fluid extraction techniques have also recently paved their way to the commercial market due to the ease in scalability and lesser time [65]. The wet biomass of a high-lipid strain of *C. vulgaris* underwent ultrasonication, followed by in situ transesterification catalyzed by an immobilized lipase. This process yielded a substantial conversion of biodiesel, highlighting the promising potential of this approach [66]. In intensive culture systems, integrating or accumulating compounds with similar characteristics can enhance the biomass yield. However, the extraction techniques play a crucial role in determining the system's output. Sequential or cascade extraction offers a sophisticated approach, selectively recovering multiple products based on compound delicacy, thus, unlocking the full potential of these systems [13].

3. Fungal biorefinery

Fungi are eukaryotic, heterotrophic organisms that derive carbon, nitrogen and oxygen from the media/biomass available to them. They are omnipresent and recognizable by the existence of spores or conidia, septate or aseptate hyphae, and their capacity to inhabit different living organisms such as insects, plants, or animals through varying levels of association, including, symbiotic, opportunistic or parasitic. The concept of fungal biorefinery is regarded as an attractive source for organic acids, bio-oils and lignocellulosic waste valorization [67]. Lignocellulosic biorefinery has spearheaded the bioconversion of the waste into vast range of bio-products such as

Table 1
Potential algal species for integrated biorefinery with the bio-products reported by researchers.

Microorganism	Biodiesel	Alcohol	Bio-hydrogen	Organic acids	Pigments/VAP	Biopolymer	References
<i>Chlamydomonas reinhardtii</i>	10 g/L	172 mg/g	300 mL/L	NP	7.3 mg/g zeaxanthin, 4.2 mg/g lutein, 23.7 mg/g β -carotene	628 mg/L	[28]
<i>Chlorella vulgaris</i>	35 g/L	136 g/L	530 mL/L	NP	5 mg/g carotenoid, 700 mg/g protein	10.4 mg/g	[25]
<i>Dunaliella</i>	450 mg/L	NP	12.6 mL/g	NP	102.5 mg/L total carotenoids (majorly β -carotene)	944 mg/L	[57–59]
<i>Haematococcus pluvialis</i>	89 mg/L	210 mg/g	NP	NP	45.8 mg/g astaxanthin	P (undefined yield)	[60]
<i>Nannochloropsis</i>	9.4 g/L	NP	183.9 mL/g	NP	408 mg/L (chlorophyll a, violaxanthin, canthaxanthin, astaxanthin)	NP	[60]
<i>Scenedesmus</i> sp	2.2 g/L	11.7 g/L	128 mL/L	NP	98 mg/g β -carotene, lutein and astaxanthin	NP	[32,61]
<i>Schizochytrium</i>	30.8 g/L	11.8 g/L	NP	NP	12.2 g/L DHA, 497.6 μ g/g carotenoids	NP	[62]

Abbreviations: P-produced; NP-Not produced; DHA- Docasahexaenoic acid; Alcohols- Ethanol, butanol, butanediol, propanediol; VAP- value added products.

biofuels, organic acids and others. The major fungal classes contributing to the development of lignocellulosic biorefinery are *Mucoromycota*, oleaginous filamentous fungi and yeasts, owing to the production of diverse range of enzymes such as endo-amylases, exo-amylases, endoglucanase, exoglucanase, beta-glucosidase, xylanase, beta-xylosidase, arabinosidase, esterase, laccase, peroxidase, oxidase, and glucuronidase that can aid in biocommodity production [68]. Primarily, the procurement of lignocellulosic biomass originates from agricultural or industrial waste materials such as barley straw, coconut husk, corn stover, empty fruit bunch, rice, sugarcane bagasse, straw, sorghum stalks, wheat, and wood for biorefineries [69].

Along with bio-fuel, organic acids and ethanol are also a few of the majorly targeted compounds from lignocellulosic biorefineries. Citric and gluconic acid are commercially produced by *Aspergillus niger*, itaconic acid by *Aspergillus terreus*, and kojic acid by *Aspergillus oryzae* along with ethanol as the major by-product. *Rhizopus* is an industrial producer of enzymes, organic acids, fermented foods, alcohols, esters, polymers, volatile compounds, and have been used in cancer research [70]. In addition to HVAC compounds including lipids, single cell proteins, carotenoids, and amino acids, pharmaceutical compounds including antibiotics, antioxidants, and anti-inflammatory substances are obtained from different species [71].

3.1. Role of fungi in lignocellulosic biorefineries

Fungal biorefinery can operate by utilizing cheaper lignocellulosic feedstock (comprising lignin, celluloses, hemicelluloses and sometimes, pectin) from agricultural, food and dairy industries, as well as the waste generated from them. Lignocellulosic biorefinery majorly produces biofuel as the main product with electricity and bio-chemicals as co-products. The trajectory of bio-commodity synthesis initiates with the pre-treatment of biomass, followed by the enzymatic breakdown of polysaccharides, subsequent microbial fermentation of sugars, and then, the extraction of the target products [72]. The majorly reported genera from oleaginous fungi which are used as a source of enzymes and bio-products are *Mortierella*, *Aspergillus*, *Penicillium*, *Cunninghamella*, *Mucor*, *Trichoderma*, and *Rhizopus* [73]. While all microorganisms possess the ability to ferment six-carbon sugars, it is the filamentous fungi that stand out for their exceptional aptitude in harnessing five-carbon sugars such as xylose and arabinose [68]. Fungal species such as *Aspergillus* and *Trichoderma* emerge as the prominent industrial enzyme producers for biomass conversion along with organic acids [70]. This selection is rooted in their exceptional enzyme yield, surpassing that of yeast and bacteria counterparts. Notably, their enzymes exhibit high activity under neutral pH conditions and demonstrate remarkable thermal resilience. Even recalcitrant materials such as wood, notorious for its resistance to breakdown, can be effectively degraded by enzymes produced by *Trichoderma reesei* and *Phanerochaete chrysosporium*. Introducing fungal species for the production of biofuels to accelerate the process of enzymatic degradation and modify the chemical composition of biomass has been reported with certain fungal species. For example *Trichoderma atroviride*, *Penicillium pinophilum*, *Periconia* sp., *Humicola insolens*, and *A. niger* are responsible in turning cellulose into bioethanol [74].

T. reesei is known for the production of biofuel without any pretreatment processes using lignocellulosic biomass [75]. With the help of genetic modifications, enzymatic saccharification has been augmented in strains such as *Pichia pastoris*, *T. reesei*, and *Penicillium oxalicum*, for the conversion of celluloses into glucose (value added chemical) and biofuel [76]. *A. terreus* produced 54.4 % of its biomass as lipids with 3 g/L (lipid yield) when cultured on glucose as a source of feedstock [67]. *Penicillium brevicompactum* generated 57.6 % of lipids with an overall yield of 8 g/L when being utilized on sunflower oil cake [77]. *Cryptococcus curvatus* (renamed as *Cutaneotrichosporon curvatus*) produced 41.2 % lipid content when subjected to VFAs from waste paper with 1.8 g/L lipids yield [78].

Production of bioethanol from reducing sugars by fungi depends upon vigorous fermentation process. White rot fungus, *Trametes hirsuta*, had shown capability to directly produce ethanol without any enzymatic hydrolysis by fermenting rice straw, starch and wheat bran in a media and obtaining the yield of 20 g/L [79]. *Fusarium oxysporum*, a mesophilic fungus when cultivated on brewer's spent grain showed enhanced enzyme yields and generated 109 g ethanol/kg of feedstock [80]. Yeast species such as *Wickerhamomyces chambardii* and *Saccharomyces diastaticus* turned corn straw into 26.1 g/L and 32 g/L of ethanol [81]. 74.5–78.4 % yield of ethanol was obtained when *Candida shehatae* was introduced to sugarcane bagasse and rice straw in a continuous batch whereas this yield increased up to 96–98 % when recycled batch mode was followed in the bioconversion process [82]. Lignocellulosic feedstock of wheat bran was utilized for the production of bioethanol with 80 % efficiency when *T. reesei* and *A. niger* were used [83]. Production of bioethanol was also reported by the two fungal strains, *Mucor indicus* and *R. oryzae*, using free sugars from citrus waste [84]. A previous study reported the use of more than one fungus for the production of bioethanol in a stirred tank bioreactor with strains such as *Trichoderma harzianum*, *Phanerochaete chrysosporium*, *Mucor hiemalis*, and *S. cerevisiae*, achieving high yield (31.6 g/L) using palm oil mill effluent (POME) as the substrate [85]. Yeast species are capable of growing in hydrophobic as well as hydrophilic cellulolytic substrates, for example, lipid productivity of 18.2 g/L was reported by *Rhodospiridiobolus fluvialis* when introduced on sugarcane [86].

3.2. Production of biogas and electricity using fungi

Biogas production involves various enzymatic reactions which help in breaking up complex substrate and the conversion of organic acids into methane and CO₂. Majorly, the production of biogas by anaerobic fungi such as *Neocallimastix* has been reported along with anaerobic bacteria and methanogens, with only a few studies reporting the fungi being the sole methane and CO₂ producers. The eight saprophytic fungal strains of *Basidiomycetes* were found to have a tendency of producing methane and CO₂ [87]. Methane and CO₂ were also reported by fungal strains such as *Sporotrichum*, *Aspergillus*, and *Fusarium* [88]. Acetate, formate, CO₂ and hydrogen were obtained by utilizing municipal solid waste, animal waste and lignocelluloses rich substrate with the help of the phylum *Neocallimastigomycota* [89].

Fungal strains act as biocatalyst in the cathode and anode to generate electricity due to the redox-active enzymes present in them. *Saccharomyces*, *Candida*, *Hansenula*, and *Kluyveromyces* have been studied as anodic biocatalyst, while *Trametes*, *Ganoderma*, *Rhizopus*,

Aspergillus and *Penicillium* have been reported as cathodes. *Trametes versicolor*, *Rhizopus* sp., and *Aspergillus* sp. utilize glucose as substrate and are capable of generating 320, 317.3 and 438.2 mW/m³ electricity, respectively [90]. Fungi derived microbial fuel cells can be applied as bio-batteries where low voltage is required to recharge gadgets [91].

3.3. Production of organic acids and lipids using fungi

Rhizopus has been extensively explored for the production of ethanol, lactic, fumaric, malic and succinic acid while utilizing waste substrates such as corn stover, sugarcane bagasse and cassava pulp [70]. *R. oryzae* has been reported to produce 0.9 g of lactic acid per g of glucose, fumaric acid as 0.9 g/g of glucose and ethanol as 0.5 g/g of glucose [92]. *Aspergillus*, on the other hand, has been investigated for the commercial production of citric acid, gluconic acid, itaconic acid, kojic acid and malic acid [68]. *A. niger* is the commercial producer of citric acid (883 g of citric acid per kg of apple pomace with 4 % methanol) and gluconic acid (685 g/kg of dry fig) [68]. A patent filled by Pfizer has reported *A. terreus* to produce itaconic acid on beet molasses with 70 % yield [93]. *A. oryzae* also gave a kojic acid recovery yield of 70–90 % and malic acid yield of 113 g/L, while *A. flavus* gave a maximum kojic acid yield of 889 g/L of the substrate and 154 g/L for malic acid [94–97].

Several fungal genera belonging to *Mucoromycota* tend to accumulate 20–80 % of their biomass as lipids with *Mucor circinelloides* being the first one to be commercially used for the same since 1985 [98]. *Mortierella isabellina* consists of 86 % of its dry weight biomass as oil and *Trichosporon fermentans* was reported to produce 62.4 % of total lipid content with a biomass of 28.1 g/L [99,100]. Recently, few species of fungi are reported as alternative source of producing oil by converting raw material into lipids and the final product biofuel. Higher PUFA were attained in the biodiesel from *M. circinelloides* and *A. terreus*, 22.5 % (C18:3) and 9 % (C15:4, C17:4, C32:3 and C33:4), respectively [101,102]. *A. niger* was reported to have generated 21 mg/g of lipid during the bioconversion of glucose, while *M. isabellina*, *M. circinelloides* and *R. oryzae* gave a yield of 195 mg/g, 57 mg/g and 45 mg/g of lipid, respectively [103–105]. Various strains of yeasts such as *Yarrowia*, *Rhodotrula*, *Cryptococcus*, *Candida*, *Rhodospiridium*, and *Trichosporon* are known to have 70 % lipids in them and suitable for lipid production [106]. *Rhodospiridium toruloides*, when cultivated on sucrose and ammonium nitrate, produced lipids as 65 % of biomass with a yield of 8.2 g/L [107]. Industrial scale production of biofuels and biodiesel using fungi is currently in its early stages of development, with biofuel production still limited to laboratory settings.

3.4. Production of high value-added compounds (HVACs) using fungi

Fungal strains are prolific producers of carotenes, azaphilones, polyketides and melanin when grown on waste biomass [108]. *Monascus* is one of the thoroughly investigated and oldest known genus for the production of azaphilone pigments in food such as *koji* rice, with approximately 50 pigments derived from it [109,110]. Filamentous fungi isolated from marine, soil, wood and endophytic environments produce a wide array of hues such as melanins, carotenoids, flavins, monascins, and indigo which can be reproduced when grown on agricultural waste material [111,112]. Around 200 fungal species such as *Mucor*, *Blakeslea*, *Phycomyces*, *Rhodospiridium*, *Ustilago*, *Aspergillus*, *Cercospora*, and *Penicillium* are known for the carotene production [109,113]. Beta-carotene from *Blakslea trispora* and *M. circinelloides* and polyketide pigments such as ankaflavin, rubropunctatin, monascorubramine from *Monascus*

Table 2
Potential fungal species for integrated biorefinery with the bio-products reported by researchers.

Microorganism	Biodiesel	Alcohol	Bio-hydrogen	Organic acids	Pigments/VAP	Biopolymer	References
<i>Aspergillus</i>	210 mg/L	NP	NP	154 g/L malic acid, 200 g/L itaconic acid, 7.7 g/L lactic acid, 100 g/L kojic acid, 72 g/L gluconic acid, 5 g/L citric acid, 16 g/L succinic acid	12.4 g/L yellow pigment, 1.3 mg/g carotenoids, 7.2 g/L pectinase, 13.8 g/L glucoamylase, 28.9 g/L mannanase, 8.2 g/L lipase	26.1 g/L EPS, 2.9 g/L chitosan	[67,68]
<i>Monascus</i>	NP	NP	NP	175 g/L lactic acid, 40.9 mg/L succinic acid	80.7 units/mL of pigments, 2 g/L monacolin K	NP	[127,128]
<i>Mortierella</i>	7 g/L	NP	NP	NP	NP	1.5 g/L EPS	[125,126]
<i>Mucor</i>	4.9 g/L	30.7 g/L	NP	NP	698.4 ± 3.7 µg/g carotenoids, 200 µg/g canthaxanthin	2.4 g/L chitosan	[129,130]
<i>Penicillium</i>	4.4 g/L	NP	NP	240 g/L gluconic acid, 100 mmol/L citric acid	2.5 g/L red pigment, 1.4 g/L yellow pigment, 292.8 ± 0.3 units/mg endoglucanase, 111.72 ± 0.45 units/mg xylanase	138 mg/g chitosan	[127]
<i>Rhizopus</i>	NP	NP	5.4 mmol/g	22.8 g/L fumaric acid, 106.3 g/L lactic acid	100 U/g α-amylase, 2400 U/g protease, 145.5 U/g β-glucosidase, 214 U/g xylanase	210 mg/g chitosan, 5.6 g/L unknown biopolymer	[68]
<i>Rhodotrula</i>	47 g/L	3.7 g/L	NP	NP	210.4 mg/L β-carotene	NP	[131,132]
<i>Trichoderma</i>	9.6 g/L	NP	NP	235.8 g/L malic acid, 138.9 µg/mL acetic acid, 209.1 mmol oxalic acid	40 g/L cellulase	NP	[68]

Abbreviations: P-produced; NP-Not produced; EPS- Extracellular Polymeric Substances; Alcohols- Ethanol, butanol, butanediol, propanediol; VAP-value added products.

sp. are produced at a commercial scale in food, cosmetics and nutraceutical industries [114,115]. Along with imparting alluring shades to the commodities, these pigments also possess therapeutic properties such as antimicrobial, antioxidant and anticancer [108].

Fungal strains such as *F. oxysporum* and *Fusarium moniliforme* are found to be consisting of 30 % more protein than *A. niger* which contains 25.3 mmol per 100 mg of its dry weight [116]. *Conidiobolus coronatus*, an entomopathogenic fungus was reported to produce amino acids glycine (0.7 %), leucine (2.7 %), and proline (6.2 %) of its total weight [117]. Biomass derived from *M. indicus* and *R. oryzae* cultivated on wet distiller's grains from corn were employed as an enriched constituent of monogastric animal feed formulations, while cultivation of *A. oryzae*, *Neurospora intermedia* and *R. oryzae* on vinasse material could yield a protein rich fish feed [118,119].

In addition to its recognition for the synthesis of extracellular enzymes and organic acids, utility as a model organism in scientific research, *A. terreus* has gained prominence for its role in the production of lovastatin, renowned for its cholesterol-reducing properties, harnessed by Merck into a drug named Mevacor [120]. Fungal cell walls are composed of chitin and its deacetylated form, chitosan (two of the most abundant polysaccharides on earth) along with beta-glucan and mannan. Commercially, chitosan is procured from crustaceans, while chitin is obtained from marine sources; however, due to year-long availability, consistent physicochemical properties, controlled growth and ethical issues, fungal species such as *Mucor rauxii*, *A. niger*, *R. oryzae* and *T. reesei* are being studied to jettison marine organisms [121,122].

3.5. Fungal biorefinery – challenges and progressive routes

Presently, biorefineries centered on fungi encounter challenges in attaining optimal sustainability and economic feasibility, particularly those focused on single product outputs. Enhancing efficiency, decreasing procedural steps, temporal requirements, and expenses can be achieved by exploring the untapped capabilities of fungi through the implementation of co-production strategies, judicious utilization of cheaper substrates, and waste materials [70]. In regards with this, *M. indicus* has been explored for utilizing waste material such as rice-straw hydrolysates for the co-production of lipids and bio-polymers; lipids and polyphosphate; lipids and pigments and lipids, chitosan and ethanol [84,98,123,124]. Table 2 gives an overview of fungal strains reported for the production of various products that can be incorporated in an integrated biorefinery. Optimization of growth parameters such as substrate source and concentration, fermentation parameters, and down streaming procedures can also enhance the production of target compounds such as changing the nitrogen source to urea enhanced lipid yield with high biomass in *Mortierella alpina* [125]. Overexpression of beta-isopropylmalate dehydrogenase increased the lipid content by 20 % in *M. alpina* and 70 % in *M. circinnelloides* [126].

Another area that has escalated fascination is investigating the co-cultivation of oleaginous fungi and microalgae as an innovative carbon-neutral approach aimed at producing high lipid yielding biomass. The biomass and lipid yield of microalga *Scenedesmus obliquus* has been augmented by 2.2 and 1.5 folds, by agglomerating its cells with the fungus *Cunninghamella echinulata* [133]. Along with increasing lipid yield in synthetic media simulating wastewater from intensive aquaculture, microalga *C. vulgaris* and fungus *M. indicus* exhibited full elimination of total ammonia (TAN), phosphorus, and nitrogen up to a concentration of 10 mg/mL TAN [134].

Primary limitations of biological pre-treatment strategies for lignocellulosic feedstocks stem from their time-intensive nature and the relatively elevated cost of pure enzymes. A recently emergent approach, termed white biotechnology, entails exclusive reliance on enzymes or biological entities throughout the procedure, proving to be notably efficient. This methodology was adopted for succinic acid production and a life cycle analysis unveiled a 50% reduction in greenhouse gas emissions compared to conventional chemical production [135].

Yarrowia lipolytica can be utilized as one of the strains for a wide spectrum of white biotechnology applications owing to its generally regarded as safe (GRAS) status, i.e. for the removal of pollutants such as heavy metals and oil spillage from marine environments, being engineered to bio-factories for the production of proteins and lipids, to producing succinic acid, erythritol and citric acid from crude glycerol [136,137]. Consolidated bioprocessing for biofuel production from lignocellulosic biomass, combining pre-treatment techniques, hydrolysis and fermentation of biomass in a single solid state fermentation step with either a single strain such as *T. reesei* or co-culturing several strains of *Rhizopus*, *Trichoderma*, *Aspergillus* or *Thermoascus* can also decrease the cost, time and infrastructure investments [68].

4. Bacterial biorefinery

Bacteria are unicellular prokaryotic organisms and the target of bioengineering interventions for modified genetic makeup that can utilize waste material to produce value added metabolites and enzymes. Till now, the outstanding example of utilizing genetically engineered *Escherichia coli* for producing FAs with the yield of 14 mg/L h of glucose which were converted into bio-diesel (C₁₂–C₁₈) is still very well-known [138]. Bacteria contribute to the production of economical industrial chemicals using different biological processes, however, the concept of bacterial biorefinery for the production of biofuels and bioethanol is only limited to the feedstock conversion. Major chemical moieties utilized from bacterial contributors are extremozymes, organic acids and PHAs. Several conventionally used enzymes often fall short of meeting the stringent industrial demands such as robust resilience against a range of pH, temperature and aeration levels. Extremozymes have garnered heightened attraction as viable solution to the harsh requirements of biorefineries such as high temperatures, pH, salinity, pressure, nutrient deficiency, and water deficient conditions for optimum commodity production [139]. The enzymatic hydrolysate derived from halotolerant *Haloarcula* LLSG7 was employed as the substrate for *S. cerevisiae* fermentation which yielded 10.7 g/L of bioethanol, surpassing the yields observed with previously documented cellulases [140].

As a case in point, employing thermostable enzymes obtained from thermophile bacteria such as α -amylase from *Geobacillus* spp.

(isolated from thermal springs) gave better conversion efficiency and solubility with a decreased contamination threat at the temperature range of 90–140° C [141,142]. Anoxygenic purple photosynthetic bacteria, such as freshwater *Rhodobacter sphaeroides*, *Rhodospirillum rubrum*, *Rhodopseudomonas palustris*, and the marine *Rhodovulum sulfidophilum*, have substantiated their utility as bioproduction platforms for a range of HVACs. A remarkable aspect of their role is their capacity to harness both CO₂ and carbon monoxide (CO) from synthetic gas produced in the biorefinery as an adept carbon source for the synthesis of valuable molecules [143]. These extremophiles, thus, offer a compelling opportunity for the exploitation and genetic manipulation of cells within the realm of biorefineries, particularly in scenarios demanding the presence of extreme environmental conditions.

4.1. Production of biofuels using bacteria

Bacteria are not known for the accumulation of FAs in huge amount, for example, some of the bacterial strains such as *Dietzia maris*, *Stappia* sp., and *Micrococcus* sp. comprises of 0.3–4 % FAs of their total dry weight [144]. For the cost effective production of biofuels, it is essential to identify and isolate oleaginous bacterial strains for the efficient conversion of cheaper substrate into biofuels. For example, *Rhodococcus opacus* PD630 along with lignolytic enzymes present in cellular compartment produced FAME 400–460 mg/g of dry weight [145].

Thermophiles are responsible for the bioconversion of feedstock (lignocellulolytic) into bioethanol due to the presence of extremozymes such as cellulose and xylanase. 0.4–0.5 g ethanol/g glucose was obtained by the fermentation of *S. cerevisiae* with the help of enzyme produced from the thermophilic species *Geobacillus* spp. R7 [146]. Production of bioethanol by *Caldicellulosiruptor bescii* and *Clostridium thermocellum* was reported with the use of cellulose, hemp and lignocellulosic biomass [147]. 2.7 g/L and 1.3 g/L ethanol was produced by *Clostridium cellulolyticum* p1217 when 10 g/L avicel cellulose and pretreated switchgrass with acid were used as substrate, respectively [148]. *C. thermocellum* when introduced on paper pulp sludge generated 14.1 g/L ethanol in just 240 h [149]. Bioethanol production by thermophile *Thermoanaerobacterium thermosaccharolyticum* on cellulose and xylan has also been reported and *T. thermosaccharolyticum* on hardwood substrate produced 7.4 g/L of ethanol [150,151]. By modifying the bacterial strains genetically, production of biofuels can be increased, as recombinant *E. coli* FBR5 yielded 28.9 g/L ethanol when subjected on corn stover hydrolysate [152].

Psychrotolerant *Pseudomonas putida* is one of the bacterial strains capable of tolerating butanol and assimilates butanol with the help of enzymes [153]. Sugarcane bagasse, rice straw and microalgal hydrolysate were utilized by *Clostridium acetobutylicum* ATCC824 for the production of butanol with 8.4–13.8 g/L yield [154]. ABE (acetone-butanol-ethanol) fermentation is an industrial concept, originating in 1912, for the production of acetone-butanol-ethanol from starch by anaerobic *Clostridium* fermentation [155]. In Russian production plants with *C. acetobutylicum*, the insoluble sludge generated after separation of the solvents was either utilized for producing methane by thermophiles or fed into a yeast-protein fodder plant. Vitamin B12 was also extracted from the archaeobacteria used for methane production and CO₂ and hydrogen produced during fermentation were sold as dry ice, liquid CO₂ and hydrogen. However, for utilizing the vastly available lignocellulosic biomass, extracellular hydrolysis or pre-treatment of biomass is required for *Clostridium* to ferment it to solvents. Furthermore, lack of a continuous fermentation process is still a major drawback of ABE fermentation owing to the acidogenic phase of bacteria leading to "acid crash" inactivation of the culture, bacteriophage and lactic acid bacterial infection, among others [156]. *Lactococcus lactis* produced 2, 3-butanediol when introduced to waste generated from the plastic industry [157].

4.2. Production of biogas using bacteria

Microbial conversions of complex organic substrate are carried out in anaerobic environment, where a group of bacteria degrade the mixture of substrates into methane, CO₂ and hydrogen [158]. Hyperthermophilic and thermophilic bacteria such as *Caldicellulosiruptor saccharolyticus*, *Thermoanaerobacter tengcongensis*, *Thermotoga maritima* and *Pyrococcus furiosus* have been reported to generate hydrogen [159]. Hydrogen producing bacteria (HPB) are a group of obligate anaerobic bacteria used for the production of hydrogen, for example, *Clostridium* sp. yielded 1.5–3 mol of hydrogen per mol hexose as substrate [160]. *Clostridium* spp. is also known to produce CO₂ and hydrogen during ABE fermentation [156]. Bio-hydrogen is also produced by aerobic *Geobacillus* sp. WSUCF1 and anaerobic thermophilic consortium on prairie cordgrass with a yield of 3.7 mmol of hydrogen per g of substrate [161]. Thermophilic *Moorella thermoacetica* and *Carboxidothermus hydrogenoformans* are known to generate energy in the form of CO₂ and hydrogen [162, 163]. *C. hydrogenoformans* is a well-known anaerobic hydrogenogen that utilizes CO and water to produce hydrogen with 82–95 % yield [164].

Methanogenic bacteria is a class of bacteria which has the potential to produce methane by consuming hydrogen, CO₂, formate and acetate. *Clostridium*, *Methanosarcina*, *Methanospirillum*, and *Petrimonas* were reported to produce maximum methane yield of 65.8 % from co-digestion of POME hydrolysate and oil palm trunk [165]. The introduction of Consortium TC-5 into digested sludge exhibited 36.6 % methane production under thermophilic conditions [166]. A consortium of *Clostridium*, *Bacteroides*, *Ruminococcus* and *Methanosarcina* applied on particulated rice straw gave a maximum yield of 275 mol of hydrogen per g of substrate [167]. Members of anaerobic *Clostridiales* class were also able to produce methane from wheat straw, swine manure and corn stover [168,169].

4.3. Production of high value-added compounds (HVACs) using bacteria

Lactic acid production is reported from lactic acid bacteria (LAB) comprising *Carnobacterium*, *Enterococcus*, *Lactobacillus*, *Lactococcus*, *Pediococcus*, *Streptococcus*, and *Weissella*, which are GRAS (except pathogenic *Streptococcus*), have acid tolerance, are known to be probiotics and produce antimicrobials, food aromas and flavors, vitamins, texturing agents, sweeteners, nutraceuticals, and

biopolymers along with ethanol [170]. They require pre-treated substrate to act on monosaccharides for producing lactic acid as starch-degrading *Lactobacillus* strains have low yield/enantioselectivity [171]. Engineered *Lactobacillus plantarum* was successfully able to degrade raw corn starch and it showed 85 % lactic acid yield [172]. *Lactobacillus helveticus* strain milano has achieved a maximum lactic acid yield of 9.7 g/L/h with whey-yeast permeate medium [173]. *Enterococcus faecalis* RKY1 gave a lactic acid yield of 95.7 g/L with molasses-yeast extract substrate [174]. Succinic acid is one of the important chemicals produced by the bacterial strain *Actinobacillus succinogenes*, with a yield of 35.6 g/L and *E. coli* with a yield of 58.3 g/L in aerobic fermentation [175,176].

In the integrated biorefinery approach, frees sugars, essential oils and phenols are separated from orange peel extract followed by pectin separation. The remaining extract was hydrolyzed to harbor *Komagataeibacter sucrofermentans* for the production of bacterial cellulose with a yield of 11.6 g/L [177]. Similarly, 1 kg of winery waste was used to generate 42.6 g bacterial cellulose, 624.8 g tannins, 80.2 g ethanol, antioxidants, 20.3 g tartaric acid, 24.3 g grape-seed oil, 40.3 g phenolic-rich extract and 157.8 g of succinic acid by *A. succinogenes* [178]. *Paracoccus zeaxanthinifaciens*, *Bradyrhizobium* sp. and *Streptomyces* sp. contributed to carotene production, however, bacterial carotenoid production is still limited to the research and development stage [115,179,180].

4.4. Production of polyhydroxyalkanoates (PHAs) using bacteria

Biopolymers are produced by many microorganisms in an integrated biorefinery system by utilizing waste feedstock or produced as a by-product. Bacterial strains such as *Cupriavidus necator* (*Ralstonia eutropha*) and *Burkholderia sacchari* are known for the production of PHBs from glucose and glycerol obtained from bioethanol and sugar waste based biorefineries [181]. An advantage of employing bacterial strains lies in their extensively researched metabolic pathways, which substantially heighten the potential for enhanced PHA production through genetic manipulations. *C. necator* is a model chemolithoautotroph, known for accumulating PHA up to 70 %, while the engineered strain accumulated 3 g/L of 1, 3-butanediol (precursor for synthetic rubber) or exhibited 93.4 % increase in growth efficiency and 74.7 % increase in PHB accumulation [182,183]. *C. necator* when harbored on plant oils or waste frying oils generated PHB up to 62.5 % and 36.5 %, respectively [184].

B. sacchari contained 62 % of its biomass as PHA when grown on sugarcane bagasse in an integrated biorefinery, while the engineered strain had an augmented yield of 80 % [185]). PHA is also produced by recombinant *E. coli* harboring on molasses and sucrose [186]. *P. putida*, a psychrotolerant extremophile, is reported to be producing PHA from organic acids, while *R. rubrum* produced PHA up to 45 % of the dry cell weight in nitrogen-limiting conditions [187,188]. When grown on insoluble kraft lignin, the mutant *P. putida* strain (A514) utilized it as a sole carbon source for PHA production up to 73 % of dry cell weight [189].

Table 3

Potential bacterial species for integrated biorefinery with the bio-products reported by researchers.

Microorganism	Biodiesel	Alcohol	Bio-hydrogen	Organic acids	Pigments/VAP	Biopolymer	References
<i>Bacillus</i>	3.1 g/L	22.3 g/L	22.6 ± 2.6 mmol H ₂ /L	7.6 g/L acetic acid	103.3 mg/g carotenoids	7.2 g/L PHB	[197,198]
<i>Clostridium</i>	0.4 g/g	97.3 g/L ABE	2.4 L H ₂ /L	33 g/L butyric acid, 15.2 g/L acetic acid	Enzymes (undefined yield)	975 mg/L PHB, 421 mg/L PHA	[199]
<i>Cupriavidus</i>	1 g/L	3 g/L 1,3 butanediol, 3.4 g/L isopropanol	NP	NP	NP	11.4 g/L PHB, 11.7 g/L PHA	[182,183]
<i>Enterobacter</i>	NP	0.8 g/L ABE, 12.3 g/L ethanol, 39.5 g/L acetoin	193.7 mL/g	69 g/L succinic acid, 46.2 g/L lactic acid	NP	8.8 g/L EPS	[200]
<i>Gluconobacter</i>	NP	NP	NP	54.7 g/L glyceric acid, 58.5 g/L xylonic acid	125.8 g/L dihydroxyacetone, 60 g/L miglitol, 23.2 mg/L riboflavin, 30.5 g/L 2-keto-l-gluconic acid	9.1 g/L cellulose	[201]
<i>Klebsiella</i>	NP	6.7 g/L 1,3 propanediol, 9.8 g/L ethanol, 131.5 g/L butanediol	117.8 mmol/L	133 g/L lactic acid, 83.8 g/L 3-hydroxypropionic acid, 28.7 g/L succinic acid	3.7 g/L dihydroxyisovalerate, 38.2 g/L 2-ketogluconic acid	23.8 g/L PHB, 15 g/L EPS	[202]
<i>Lactobacillus</i>	NP	84.5 g/L 1,3-propanediol, 13.4 g/L butanol	NP	210 g/L lactic acid	NP	NP	[203,204]
<i>Paracoccus</i>	P	NP	NP	NP	760 mg/L carotenoids, 480 mg/L astaxanthin	9.5 g/L PHA, 32.1 g/L PHB	[205]
<i>Pseudomonas</i>	NP	NP	NP	78 g/L lactobionic acid, 8.8 g/L gluconic acid, 21 g/L lactic acid, 22 g/L muconic acid	413 mg/L carotenoids, 198.8 mg/L vitamin B12, 51 mg/L zeaxanthin	2.6 g/L PHA, 9.3 g/L PHB, 2.1 g/L alginate	[206]

Abbreviations: P-produced; NP-Not produced; Alcohols- Ethanol, butanol, butanediol, propanediol; ABE- Acetone-Butanol-Ethanol; PHA- Polyhydroxyalkanoate; PHB- polyhydroxybutyrate; VAP- value added products.

R. sulfidophilum accumulated 33 % of its dry biomass as PHA when grown in salinity environment, while engineered *R. sphaeroides* gave a PHB production yield of 79 % of its biomass under nitrogen-limiting conditions [190,191]. In lignocellulosic or starch waste based biorefineries, simple sugars are present in wastewater and hydrolysates, which can be utilized by strains such as *C. necator*, *P. putida*, or *Methylobacterium organophilum* to produce PHB [184]. Furthermore, methanotrophic bacteria (bacteria utilizing methane as a carbon source) such as *Methylobacterium* and *Methylosinus* have also been explored to produce ectoine, PHB, and lipids with 80 % PHB recovery efficiency in a two-stage bioreactor [192]. In a recent study, it was reported that the bacteria *Magnetospirillum gryphiswaldense* MSR-1 (Mgryph) can produce magnetic nanoparticles. These nanoparticles make up around 4% of the total cell mass, and the downstream processing of the Mgryph biomass also yielded proteins and polyhydroxyalkanoates (PHAs), which have additional value [193]. These analyses anticipate that manipulating the genetic makeup of extremophilic bacterial species holds great potential as a viable pathway for synthesizing PHA within a biorefinery setting.

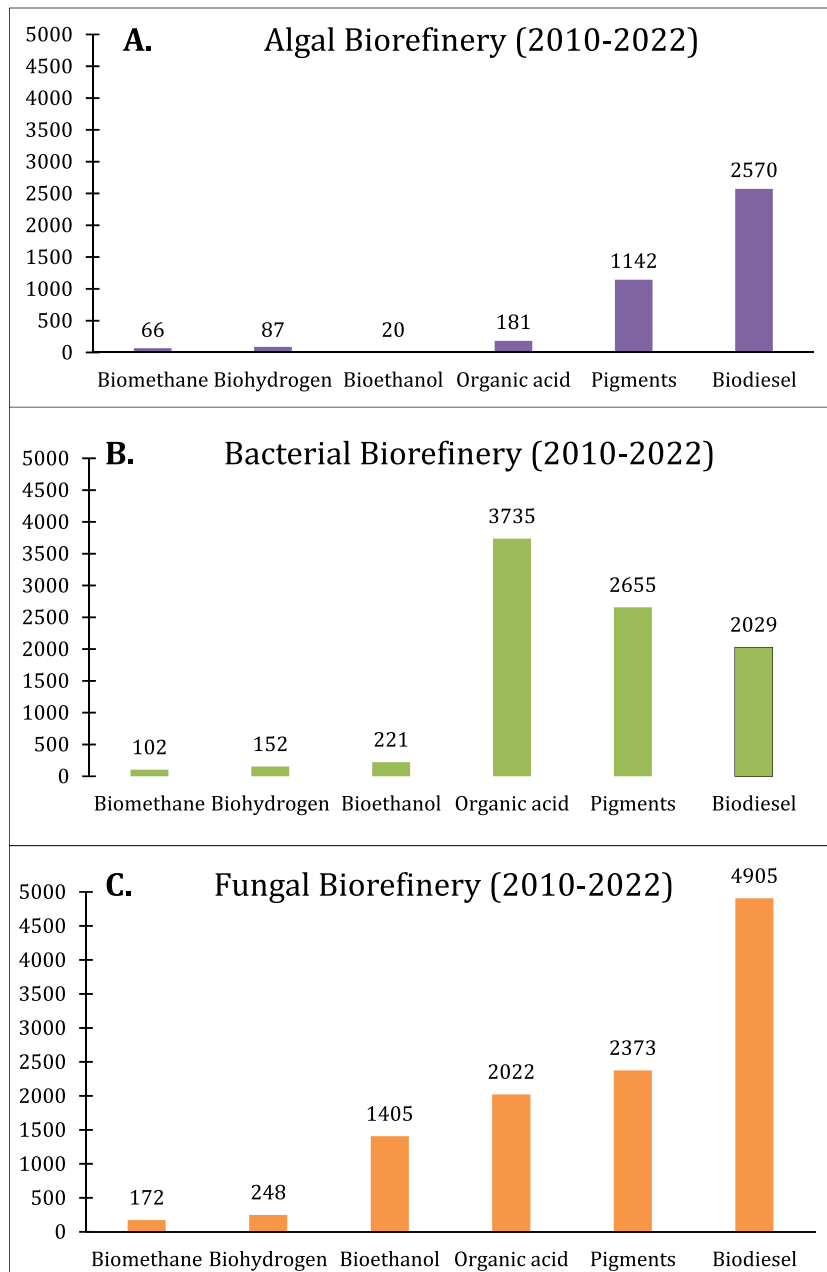


Fig. 3. Illustration based on the analysis of publications in PubMed, demonstrating the trend of an increase in concepts developed for A-Algal, B-Bacterial and C-Fungal biorefineries. The data shown was retrieved using PubMed (<https://www.ncbi.nlm.nih.gov/pubmed>) on March 21, 2022 and it covers the time period 2010–2022.

4.5. Bacterial biorefinery – challenges and progressive routes

Similar to fungal biorefinery, bacterial biorefineries have also started to incorporate the beneficial concepts of co-culturing and consolidated bioprocessing. Co-culturing of bacterial strain such as *Rhodococcus* or *Botryococcus* autotrophic microbes such as microalgae (*Chlamydomonas* or *Nannochloropsis*) is also reported for commercial production of biogas and bio-hydrogen [194,195]. The consolidated bioprocessing has produced 20 % more ethanol by saccharification and fermenting in a single step process using strain *C. thermocellum*, with the help of cellulose as the substrate [196]. Table 3 provides an overview of different bacterial strains reported for the production of various products that can be incorporated in an integrated biorefinery.

Even though extremophiles can be the driving force of bacterial biorefineries, their upscaling is challenging owing to the rigorous conditions necessary for their cultivation. Requirement of highly saline media can add to the monetary investments for maintenance, extraction and treatment of wastewater in PHA production. However, to combat these issues, new materials such as polyether ether ketone were formulated to prevent the corrosion of stainless-steel parts by highly saline media in bioreactors and autoclavable materials [207].

Additional obstacle is the establishment of a comprehensive enzymatic framework with a biorefinery context. A single thermostable enzyme induces synergistic response that can disrupt the functionality of the enzyme assembly within the biorefineries. Construction of an entire enzymatic system of thermostable enzymes can be a future trajectory to combat this. However, the primary hurdle related to it will be the development of chassis cells for the incorporation of extremophile-derived enzymes to harness their maximal industrial efficiency. These next-generation extremozymes producing cell factories can be a breakthrough for the production of platform chemicals from substrates such as lignin, while playing a crucial role in consolidated bioprocessing [208].

5. Trends in microbial biorefinery

Microbial biorefinery is not a new term, but the trends in the research being carried out on the products obtained from the refineries based on algae, fungi and bacteria shows that these concepts are still being developed for some bio-products. The research focus for different biorefineries (algal, fungal and bacterial) is expanding owing to the increasing demand for sustainable and eco-friendly solutions. As shown in Fig. 3, biodiesel is particularly notable in the realm of fungal and algal biorefineries and has been extensively studied. Organic acids and pigments are the primary commodities derived under bacterial and fungal biorefineries, while algae have been the targeted resource for carotenoids and FAs production during the last decade. In addition, it is clear from the biorefinery based publications analyses that there is a need to push the research towards the biofuels other than the biodiesel, i.e., bioethanol, biomethane and bio-hydrogen, as these have been of least interest in the last decade as compared to the other commodities in order to have a circular economy from these sustainable resources [209].

The economic assessment of an integrated biorefinery that employs microalgae and *Jatropha* biomass to synthesize biofuels and biochemicals has unveiled a striking return on capital, accomplishing full recuperation of initial investment outlay in a mere span of 3.3 years. Within the biorefinery's operational ambit, the final products include biodiesel, a glycerol fraction, de-oiled biomass for biogas generation, and residual biomass utilized for animal feed. Notably, the amalgamation of biomass generation with the facilitation of nutrient phytoremediation has yielded substantial benefits of approximately 172.4 US dollars for each metric tonne of produced biomass [210]. Green Biologics Company has developed a technology of producing bio butanol using corn raw materials by thermophilic *Clostridium* strains [211].

Globally, the countries which are operating microbial biorefineries from pilot scale to commercial plants are Australia, Austria, Denmark, Germany, Ireland, Italy, The Netherlands, Sweden, China, South Korea, and USA. According to IEA Bioenergy Global Biorefinery report 2022, 42 countries are enlisted where the pilot and commercial scale plants have been established [15]. The major stakeholders in these countries are universities, industries, and joint partnerships among both. An industry named Sarina Biorefinery Mackay (Queensland, Australia) has set up a commercial plant which converts molasses (feedstock) into bioethanol, at a capacity of 60 million liters per year. In Germany, BIEWERT majorly focuses on the bioconversion of grass into biogas and Agrifer^{BW} (biofertilizer) at commercial level [15]. In India, the scenario of biorefinery is different from the aforementioned countries. The Department of Biotechnology has set up five major bioenergy centers across India, for the development of methods in research and translational activities related to commercially viable sustainable biofuel produced from agricultural residue and municipal waste along with the development of an economically cost efficient system for algal production, bio-hydrogen and biorefinery system [212].

6. Challenges and future prospects

One of the major hurdles that has prevented the incorporation of microbial biorefineries in the commercial market is the high energy and monetary investments required for their set-up and co-production of commodities, as compared to the chemical based production [213]. As studied by Ref. [214], the net energy consumption of conventional production routes (petroleum and ethane-based) were 60–150% lesser than the biomass and microbes based routes. However, investing in the waste feedstock such as lignocellulosic biomass along with re-utilization of by-products such as glycerin or spent biomass have the potential of enhancing the profit margins by 60 %, while reducing the GHG emissions [215]. For example, the utilization of waste glycerol from biodiesel production to produce propionic acid reduced the GHG emission by 60 %, while the environmental impact of the biomass based route in the terms of CO₂ emissions was 50 % lesser than the conventional routes [213,214].

Another limitation in microbial biorefineries is posed by the specific growth requirements of these microorganisms. For example, microalgae are capable of generating the biofuel/products independently without any substrate involved, whereas bacteria and fungi

requires different feedstock as a substrate or either fermentation processes to be able to produce biofuel or side products. The integration of the substrate from one microorganism to another microorganism is still to be instigated and studied thoroughly. Further, many common potential microbes do not meet the industrial requirements, such as being able to be functional under variable temperature ranges and inhibitors. Here, extremophiles providing novel metabolic pathways and catalytically stable/robust enzymes which are able to act as biocatalysts under harsh and extreme industrial conditions on their own would be the demand in biorefineries. The insights furnished by genomics, proteomics, and transcriptome methodologies offer a valuable resource for the identification of novel targets and strains with the implementation of metabolic engineering strategies within the biorefinery sector. Through the application of multi-omics techniques, intricate metabolic regulations and pathways can be comprehensively elucidated, thus facilitating the refinement of strain performance and productivity. A case in point involves the utilization of the *S. cerevisiae* INVSc1 strain, which has been augmented with a synthetic genetic circuit encompassing heat shock protein sourced from *Thermus thermophilus* HB8, and superoxide dismutase derived from *Thermoanaerobacter tengcongensis* MB4. This engineered strain exhibits robust growth at elevated temperatures (42 °C), outperforming its wild-type counterpart by significantly boosting ethanol production levels [216].

Processes involving the potential strains which are highly specific, efficient and can tolerate the extreme conditions are needed for the commercialization and points out the necessity of accelerating the commercialization of biorefinery based processes. For example, the host cells sourced from extremophilic organisms underwent modification through synthetic biological modalities. The identification of exceedingly potent extremophiles was accomplished utilizing histochemical techniques and novel metabolic routes. Leveraging the annotation and genomic data of *Comamonas* sp. 35, in conjunction with metabolic assessments employing Gas Chromatography-Mass Spectrometry (GC-MS), the intricate pathways responsible for lignin degradation were elucidated. This comprehensive study led to the identification of five distinct metabolic pathways governing lignin breakdown. This path can be chosen to achieve genetic modifications of the chassis cells for utilizing the vast potentials of lignin to the fullest [217].

Remedial approaches such as the utilization of continuous and immobilized bioreactors with cell recycling, development of genetically engineered strains and co-culturing consortia could also improve the yields in the process. Moreover, utilizing only one kind of feedstock would lead to shortage and disregularity in microbial activity depending upon the seasons and type. Thus, emerging technologies that are equipped with tools to regulate multiple types of feedstocks are also a dire need. For example, CRISPR-Cas methodologies have proven to be effective in facilitating genetic modification in *Clostridium* strains. The employment of the *Streptococcus pyogenes* Type II CRISPR-Cas9 system has facilitated genome manipulation in *C. acetobutylicum* DSM792T, resulting in the degradation of both glucose and xylose substrates [218].

A breakthrough in screening, pathway optimization, production technology and reducing the technological gap between enzymes produced in laboratory conditions and obtaining the final commercial product may support the acceptance of these microorganisms and in shifting the laboratory research towards industrial applications. However, thanks to the advancements in nanotechnology, artificial intelligence, data mining, and machine learning, the possibilities for research, innovation, and product development in microbial biorefineries are endless.

7. Conclusions

Biorefineries associated with microorganisms are essential and bear the potential for the production of sustainable value-added products. However, multiple value-added products could be derived from the microbial resources (algae, bacteria and fungi), but most of the studies have targeted towards a single product or are limited to the production of two products. In this review, these independent approaches have been reviewed and the study indicated that these microorganisms bear immense potential for the production of biofuels (bio-hydrogen, biofuel, and biogas) and other commodities. The research trend clearly demonstrates the continued interest in utilizing different microbial systems to create bio-based products with potential applications in various industries. Improvement of strains using metabolic engineering, synthetic biology tools, whole genome sequencing technology, multi-omics approaches, bioinformatics, algorithms based in-situ mutagenesis and gene shuffling to improve the stability of protein may lead to highly efficient microbial-based green biorefinery processes. Therefore, it is essential to carefully choose the most promising, versatile and resilient microbes and economically viable strategies to fully harness their potential in future biorefineries.

Ethics statement

Review and/or approval by an ethics committee was not needed for this study as it did not utilize any animal or human based experiments/case studies.

Data availability statement

Data will be made available on request.

CRedit authorship contribution statement

Suchitra Gaur: Writing – original draft, Investigation. **Mehak Kaur:** Writing – original draft, Validation, Investigation. **Rishu Kalra:** Figure conceptualization. **Eldon R. Rene:** Writing – review & editing, Validation. **Mayurika Goel:** Writing – review & editing, Validation, Supervision, Resources, Conceptualization.

Declaration of competing interest

Authors declare no conflict of interest.

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