Ecological Dimensions and Potential Facets of Freshwater Cyanobacterial Diversity

Pooja Soudawat*, Ragini Gothalwal

Department of Biotechnology, Barkatullah University, Bhopal-462026

***Corresponding Author**

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ABSTRACT

Freshwater cyanobacteria stand at a critical intersection of ecological stability and industrial innovation. Beyond their fundamental role as primary producers, their vast biodiversity encompasses a spectrum of phenotypic and physiological traits that remain largely untapped. From an ecological perspective, their high photosynthetic efficiency and high biomass production capabilities offer a transformative alternative to synthetic inputs, mitigating the environmental footprint by acting as a powerful and sustainable resource for carbon sequestration, bioremediation, and sustainable agriculture. Furthermore, the ability of specific strains to synthesize bioactive secondary metabolites, ranging from antimicrobial peptides to allelopathic fatty acids, positions them as potent candidates for nature-based bioactive metabolites, biopolymers, bioplastics, biofuels, and biopigments. Due to an extraordinary metabolic plasticity, these organisms thrive in environments unsuitable for traditional crops, such as wastewater or non-arable land, making them ideal drivers for a circular bioeconomy. However, transitioning from laboratory-scale promise to industrial-scale reality necessitates overcoming significant hurdles in scalability, economic feasibility, and regulatory standardization. Also, the potential for rapid proliferation in eutrophic environments allows these organisms to form harmful algal blooms (HABs), which pose a severe threat to aquatic biodiversity, public health, and overall water quality. In this review, we address these challenges through a comprehensive and in-depth bibliographic search, synthesizing current scientific knowledge, compiling existing commercial products, and outlining future research priorities. Thereby highlighting that the systematic documentation and conservation of freshwater cyanobacterial biodiversity are essential not only for ecosystem protection but also for advancing innovative, nature-based solutions in healthcare, energy production, sustainable agriculture, and environmental management.

Keywords: Freshwater cyanobacteria, Circular bioeconomy, Cyanobacterial diversity, Bioremediation, Photoautotrophic chassis, Metabolic engineering, Synthetic biology, Harmful algal blooms (HABs)

INTRODUCTION

Freshwater ecosystems comprising rivers, lakes, wetlands, and aquifers are indispensable to both ecological integrity and human well-being. They provide essential services, including drinking water, food resources, flood regulation, and climate resilience. Despite covering less than 1% of Earth's surface, these habitats support approximately 10% of all known species, underscoring their role as biodiversity hotspots (Haase et al. 2023). However, freshwater ecosystems are facing unprecedented challenges. A recent study indicates that about 24% of global freshwater species are currently threatened with extinction, primarily due to habitat fragmentation, pollution, and overexploitation, highlighting the urgent need for conservation efforts (Sayer et al. 2025).

Beyond biodiversity, freshwater systems play a critical role in climate change mitigation. Recognizing their importance, global initiatives like the 'Freshwater Challenge, 2023' aim to restore 300,000 kilometres of degraded rivers and 350 million hectares of wetlands by 2030, aligning with international biodiversity targets (Wetlands International, 2023). Such efforts are crucial to ensure the sustainability of freshwater ecosystems and the myriad benefits they offer to humanity. The global focus on freshwater quality has increased markedly, driven

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by the high vulnerability of these ecosystems to anthropogenic disturbances, including overexploitation, influxes of pollutants, unmanaged urbanization, and accelerating environmental degradation.

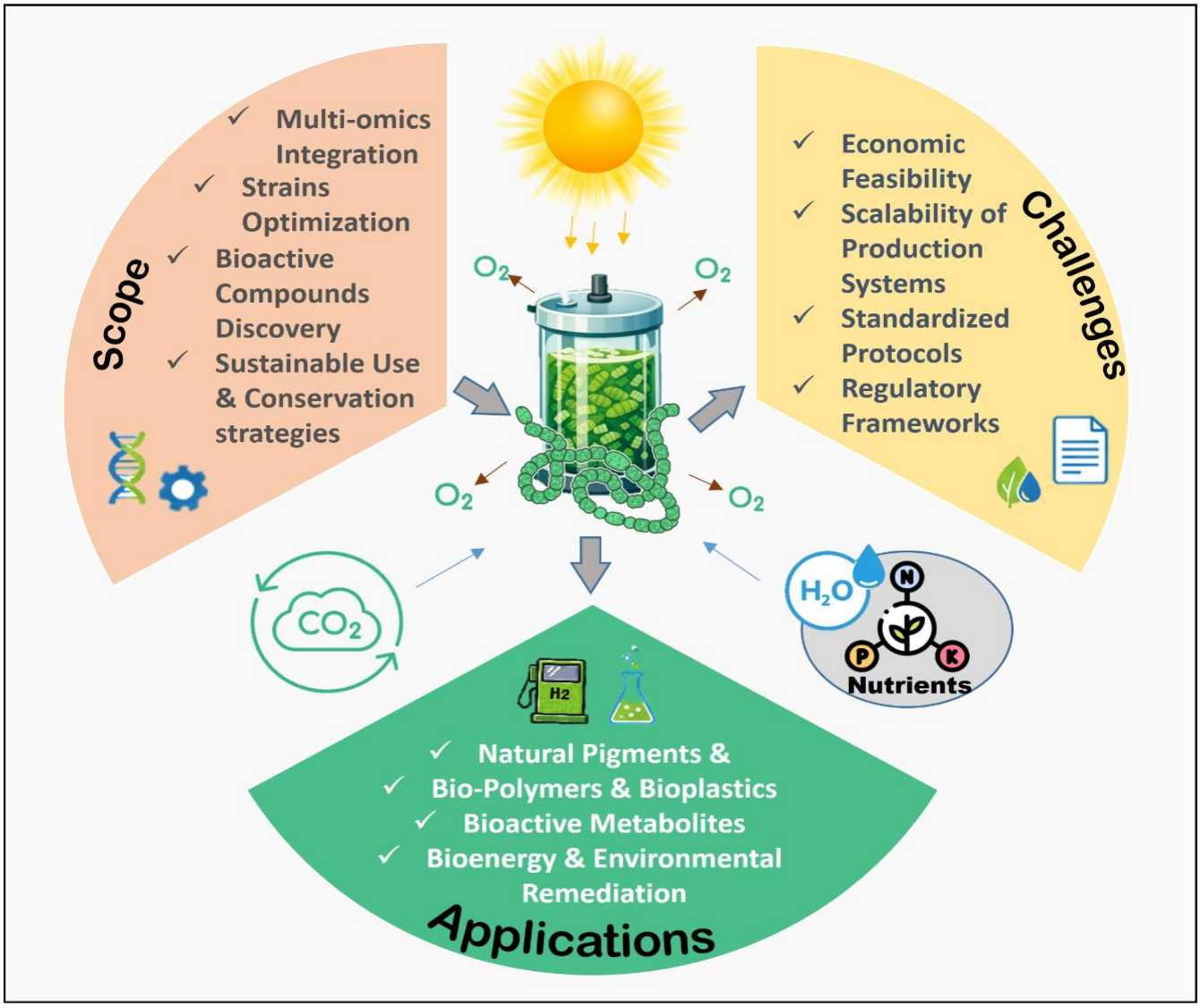

Figure 1: Overview of the present review. The figure illustrates applications of photoautotrophic freshwater cyanobacteria, strategies for yield improvements, and the main research gaps.

Cyanobacteria are a diverse group of oxygenic, photosynthetic prokaryotes found in a wide range of freshwater and terrestrial habitats. These organisms exhibit various morphologies, unicellular, filamentous, or colonial, and many are capable of nitrogen fixation, allowing them to thrive in nutrient-poor environments (Singh et al. 2016). In freshwater systems, cyanobacteria are important primary producers, but they can also form harmful algal blooms (HABs) under nutrient-rich and warm conditions. These blooms often produce cyanotoxins, such as microcystins and anatoxins, which pose significant risks to water quality and public health (Chorus et al. 2021). In addition to their ecological roles, they are recognized for their applications in biofuel production, pharmaceuticals, bioremediation, and agriculture (Duda et al. 2022). Cyanobacterial diversity underpins ecosystem functioning, including primary productivity, nitrogen fixation, and biogeochemical cycling. Their taxonomic richness and adaptive strategies allow them to colonize a broad range of ecological niches, from pristine lakes to polluted waters, making them excellent indicators of environmental change (Komárek et al. 2014).

Freshwater cyanobacteria constitute a significant reservoir of bioactive metabolites, including antimicrobial, antiviral, antioxidant, and anticancer compounds, which have attracted increasing pharmaceutical interest (Mahendran et al. 2021; Dittmann et al. 2015). Their capacity to synthesize biodegradable polymers, natural

pigments, and renewable biofuels further underscores their growing importance in biotechnology, environmental engineering, and sustainable agriculture (Singh et al. 2016; Abed et al. 2020). In addition, several cyanobacterial strains are being actively investigated for carbon sequestration and biofertilizer applications, aligning with global initiatives aimed at mitigating climate change and promoting low-carbon, sustainable technologies (Jurado et al. 2025). Despite these advantages, challenges related to the scalability of production systems, economic feasibility, and regulatory standardization continue to limit broader implementation. In this review, we address these gaps through a comprehensive and in-depth bibliographic search, synthesizing current scientific knowledge, compiling existing commercial products, and outlining future research priorities (**Figure 1**). By doing so, we aim to provide an integrated perspective on the ecological significance, biotechnological potential, and future opportunities associated with freshwater cyanobacterial diversity.

2. TAXONOMIC AND GENETIC DIVERSITY OF FRESHWATER CYANOBACTERIA

Freshwater cyanobacteria are taxonomically diverse and ecologically significant. Many genera are known for forming blooms, producing toxins, or contributing to nutrient cycling. Table 1 consists of some important genera and species of freshwater cyanobacteria, including their features, toxins they secrete, and applications.

Table 1. The most important genera and species of freshwater cyanobacteria.

S.No.	Species	Features	Toxin/ Applications	References
1.	Oscillatoria limnetica	Gliding filamentous forms, benthic or planktonic	Anatoxins, Oxygen depletion	(Halder 2017)
2.	Dolichospermum flos -aquae	Filamentous, nitrogen-fixing, heterocysts	Anatoxin-a, Saxitoxins	(Henao et al. 2020)
3.	Microcystis aeruginosa	Colony-forming, mucilage-covered, common in eutrophic waters	Microcystins (hepatotoxins)	(Huisman et al. 2018)
4.	Planktothrix agardhii	Filamentous, prefers turbid waters	Microcystins, Anatoxins	(Jeong et al. 2020)
5.	Synechococcus elongatus	Unicellular, cosmopolitan, rapid growth	Photosynthesis model, Synthetic biology	(Liu et al. 2024)
6.	Lyngbya wollei	Thick filaments, benthic mats	Lyngbyatoxins, Dermatotoxins	(Sidelev et al. 2020)
7.	Leptolyngbya	Filamentous, benthic, tolerant to diverse habitats	Bioremediation, Nutrient cycling	(Negi et al. 2024)
8.	Aphanizomenonflos-aquae	Gas vesicles form surface blooms	Saxitoxins, Cylindrospermopsin	(Overlinge et al. 2024)
9.	Raphidiopsis raciborskii	Invasive, filamentous, heterocyst-forming	Cylindrospermopsin, Saxitoxins	(Sidelev et al. 2020)
10.	Nostoc commune	Gelatinous colonies, nitrogen-fixing	Biofertilizer, Antioxidant use	(Singh et al. 2016)

The traditional taxonomy of cyanobacteria relied heavily on morphological features such as cell shape, colony formation, and pigmentation. However, these characteristics can be highly variable and influenced by environmental conditions, leading to taxonomic ambiguity. Molecular approaches have revolutionized cyanobacterial taxonomy by providing more accurate, stable, and reproducible classification systems based on genetic data (**Table 2)**.

Table 2. Molecular approaches employed for cyanobacterial characterization.

S.No.	Types of methods	Utility	Resolution Level	Reference
1.	Whole genome sequencing	High precision taxonomy, metabolic traits	Species/strain/genome	(Liyanage et al. 2016)
2.	Metagenomics/ eDNA	Culture-independent identification	Community-level	(Feist et al.2021)
3.	ITS region analysis	Species-level resolution	Species/strain	(Komárek et al. 2020)
4.	16S rRNA sequencing	Basic phylogenetic placement	Genus-level	(Komárek et al. 2020)
5.	MLST/ Phylogenomics	Robust evolutionary relationships	Species/lineage	(Liyanage et al. 2016)

Phylogenetic analyses, primarily based on molecular data (core gene sets and whole genome data), have significantly advanced our understanding of their evolutionary history, diversification, and ecological adaptation. Molecular clock analyses based on 16S rRNA, conserved proteins, and genome-scale datasets support their ancient origin and early divergence among bacterial phyla (Sánchez-Baracaldo et al. 2017). Also, this has led to the reorganization of the traditional cyanobacterial taxonomy into well-supported clades and orders such as Synechococcales, Chroococcales, and Oscillatoriales. (Walter et al. 2017).

Evolution of nitrogen fixation, a key trait in many filamentous cyanobacteria (e.g., *Nostoc*, *Anabaena*), is thought to have evolved multiple times. Genes encoding nitrogenase (e.g., nifH, nifD) provide phylogenetic markers to trace this evolution. Evolutionary trends indicate transitions from marine to freshwater environments, with some genera such as *Synechococcus* and *Prochlorococcus* adapting to specific ecological niches. Horizontal gene transfer (HGT), gene loss, and genome reduction have played crucial roles in ecological adaptation (Sánchez-Baracaldo et al. 2017). Molecular dating supports the emergence of cyanobacteria well before the advent of eukaryotic photosynthesis, indicating they were the progenitors of chloroplasts. Studies using fossil calibration and relaxed molecular clocks support their role in shaping early Earth's biosphere (Betts et al. 2018).

3. ECOLOGICAL DISTRIBUTION AND ENVIRONMENTAL DRIVERS

Freshwater cyanobacteria are globally distributed across diverse aquatic habitats, from oligotrophic alpine lakes to eutrophic reservoirs, with their diversity shaped by climate, nutrient availability, light, pH, and hydrological conditions. High-throughput sequencing studies reveal extensive cyanobacterial diversity worldwide, with *Microcystis*, *Dolichospermum*, *Planktothrix*, and *Synechococcus* among the most widespread genera. Bloom-forming and toxin-producing taxa are more prevalent in temperate and tropical regions, likely due to elevated nutrient loading and higher temperatures (Zhang et al. 2022). Phylogenetic evidence indicates strong biogeographic structuring, exemplified by the expansion of *Raphidiopsis raciborskii* from tropical into temperate regions under climate warming (Neilan et al. 2012). Regionally, eutrophic Asian lakes are often dominated by *Microcystis* and *Dolichospermum*, European waters by *Planktothrix* and *Aphanizomenon*, and African systems by *Cylindrospermopsis* and *Microcystis*. In North and South America, bloom dynamics are closely linked to nutrient enrichment and hydroclimatic variability, while Oceania exhibits high cyanobacterial diversity across contrasting climatic zones (Paerl et al. 2020).

3.1. The Environmental Drivers of Diversity

Nutrient concentrations (especially nitrogen and phosphorus), temperature, light availability, and hydrological conditions are the major environmental filters shaping community composition. Anthropogenic impacts, including land-use changes, agricultural runoff, and dam construction, contribute to regional variability in diversity and bloom occurrence (Le Moal et al. 2021). Physicochemical parameters, including nutrient concentrations, pH, temperature, light, and hydrological dynamics, strongly influence the distribution,

composition, and bloom formation of freshwater cyanobacteria (**Table 3**). These factors act as ecological filters, selecting for specific cyanobacterial taxa adapted to the prevailing conditions.

Table 3. Effects of physicochemical factors on cyanobacteria.

S.No.	Factors	Influence on Cyanobacteria	References
1.	pH	Alkaline conditions favor bloom-forming taxa	(Hao et al. 2024)
2.	Hydrology	Stable water columns enhance bloom potential.	
3.	Nutrients	Drive biomass and taxonomic dominance; N_2-fixers vs. non-N_2-fixers	(Le Moal et al. 2021)
4.	Light	Controls vertical stratification and pigment adaptations	(Meng et al. 2021)
5.	Temperature	Enhances growth rates; alters species distribution	(Paerl and Paul, 2020)

Freshwater cyanobacteria play a pivotal role in aquatic food webs and ecosystem processes, acting as both primary producers and modulators of ecological interactions (**Table 4**). Their ecological functions influence nutrient cycling, energy flow, and the structure of aquatic communities.

Table 4. Cyanobacterial roles in aquatic ecosystems.

S.No.	Activity	Ecological Role	References
1.	Nitrogen Fixation	Enriches nitrogen in oligotrophic systems	(Zhang et al. 2022)
2.	Trophic Impact	Low palatability; affects zooplankton feeding and food web efficiency	(Ger et al. 2016)
3.	Ecosystem Disruption (HABs)	Cyanotoxins and hypoxia impact aquatic biodiversity and ecosystem services	(Huisman et al. 2018)
4.	Habitat Modification	Alters light, oxygen, and substrate conditions	(Paerl et al. 2020)
5.	Primary Production	Base of the food web; major contributor to carbon fixation	(Zhang et al. 2022)

4. FRESHWATER CYANOBACTERIA AND WATER QUALITY

4.1. Causes and Consequences of Cyanobacterial Blooms

Cyanobacterial blooms in aquatic systems are frequent and severe worldwide. These blooms pose ecological, public health, and economic challenges (**Table 5**). Thus, understanding the causative factors and their impacts is crucial for effective management. An integrated, ecosystem-based management approach is essential for the sustainable control of cyanobacterial blooms in freshwater systems (Chorus et al. 2021; Xu et al. 2024).

Table 5. Causative factors and consequences of cyanobacterial blooms.

S. No.	Causative Factors	Impact	References
1.	Ecological Impacts	Hypoxia, biodiversity loss, and ecosystem disruption	(Visser et al. 2016)
2.	Toxins	Microcystins, Saxitoxins and others pose health risks to humans and wildlife.	(Chorus et al. 2021)
3.	Economic Effects	Losses in water supply, tourism, and aquaculture	(Visser et al. 2016)
4.	Hydrology	Stratification and retention time support bloom stability	(Chorus et al. 2021)

5.	Nutrient Input	Eutrophication from agriculture and sewage drives bloom formation	(Paerl et al. 2020)
6.	Climate Change	Warmer temperatures enhance cyanobacterial growth and bloom persistence	(Visser et al. 2016)

4.2. Cyanotoxins and their Effects

The Cyanobacteria are capable of producing a wide range of cyanotoxins, secondary metabolites that can be harmful to aquatic life, animals, and humans (**Table 6**). These toxins vary in chemical structure, mode of action, and ecological function. The production of cyanotoxins is influenced by environmental factors such as light, nutrients, and temperature, and is often associated with harmful algal blooms (HABs). Cyanotoxins such as microcystins, cylindrospermopsin, and anatoxins threaten drinking water safety, limit recreational activities, and adversely affect fisheries through toxicity, hypoxia, and bioaccumulation, leading to substantial management challenges and economic losses. The presence of cyanotoxins in water bodies has wide-ranging consequences for public health, economic activities, and recreational safety. Based on the documented impacts, cyanotoxin effects are categorized across three primary areas, including drinking water impacts, fisheries and aquaculture, and recreational activities. The primary health risks in the drinking water sector arise from toxins such as microcystins, cylindrospermopsin (CYN), and anatoxins. Exposure to these toxins through drinking water supplies could necessitate the implementation of water bans and costly specialized treatments to ensure safety. Also, cyanotoxins, particularly microcystins, could lead to significant fish mortality and the bioaccumulation of toxins within aquatic organisms. These events often result in substantial economic losses for the aquaculture industries. Furthermore, recreational water use could be severely compromised by the presence of microcystins and anatoxins, which are known to cause skin irritation and respiratory issues in humans. Consequently, these health concerns often lead to restricted access to affected water bodies for swimming and other water-based sports (Chorus et al. 2021).

Table 6. Major cyanotoxins produced by freshwater cyanobacteria.

S.No.	Toxin Type	Representative Toxins	Producer Genera	Toxicological Effects	Bio synthetic Genes	References
1.	Cytotoxins	Cylindrospermopsin	Cylindrospermopsis, Aphanizomenon, Umezakia	Protein synthesis inhibition, organ damage	Cyr	(Chorus et al. 2021)
2.	Emerging Toxins	Aetokthonotoxin	Aetokthonos hydrillicola	Avian vacuolar myelinopathy (wildlife deaths)	Unknown	(Breinlinger et al. 2021)
3.	Hepatotoxins	Nodularin-R	Nodularia spumigena	Hepatotoxic, similar to microcystins	Nda	(Chorus et al. 2021)
		Microcystin LR, -RR, -YR	Microcystis, Planktothrix, Dolichospermum	Liver damage, tumor promotion	Mcy	(Huisman et al. 2018)
4.	Neurotoxins	Methylamino L-alanine (BMAA)	Nostoc, Leptolyngbya, Oscillatoria	Linked to neurodegenerative diseases	Unknow (ribosomal)	(Metcalf et al. 2020)
		Anatoxin-a, Homoanatoxin-a	Dolichospermum, Oscillatoria, Cuspidothrix	Neuromuscular blockade, respiratory paralysis	Ana	(Plata-Calzado et al. 2024)
		Saxitoxin, Neosaxitoxin	Aphanizomenon, Dolichospermum, Lyngbya	Sodium channel blocker, paralysis (PSP)	Sxt	(Ramos et al. 2021)

Effective monitoring strategies integrate conventional microscopy and physicochemical assessments with advanced analytical, molecular, and remote sensing tools, enabling early detection of blooms and improved toxin risk evaluation (Cao et al. 2023). Long-term mitigation primarily relies on nutrient load reduction through catchment-based management approaches, supported by regulatory frameworks and public health advisories (Paerl et al.2020; Chorus et al. 2021).

5. BIOTECHNOLOGICAL POTENTIAL OF FRESHWATER CYANOBACTERIA

Freshwater cyanobacteria are prolific producers of structurally diverse and biologically active secondary metabolites. These bioactive compounds include peptides, alkaloids, lipopeptides, and polyketides with applications in pharmaceuticals, agriculture, and biotechnology (**Figure 2**). Cyanobacterial compounds are biodegradable, non-toxic, and derived from renewable resources, making them attractive alternatives to synthetic products in food, cosmetics, and textile industries (Sandybayeva et al. 2022).

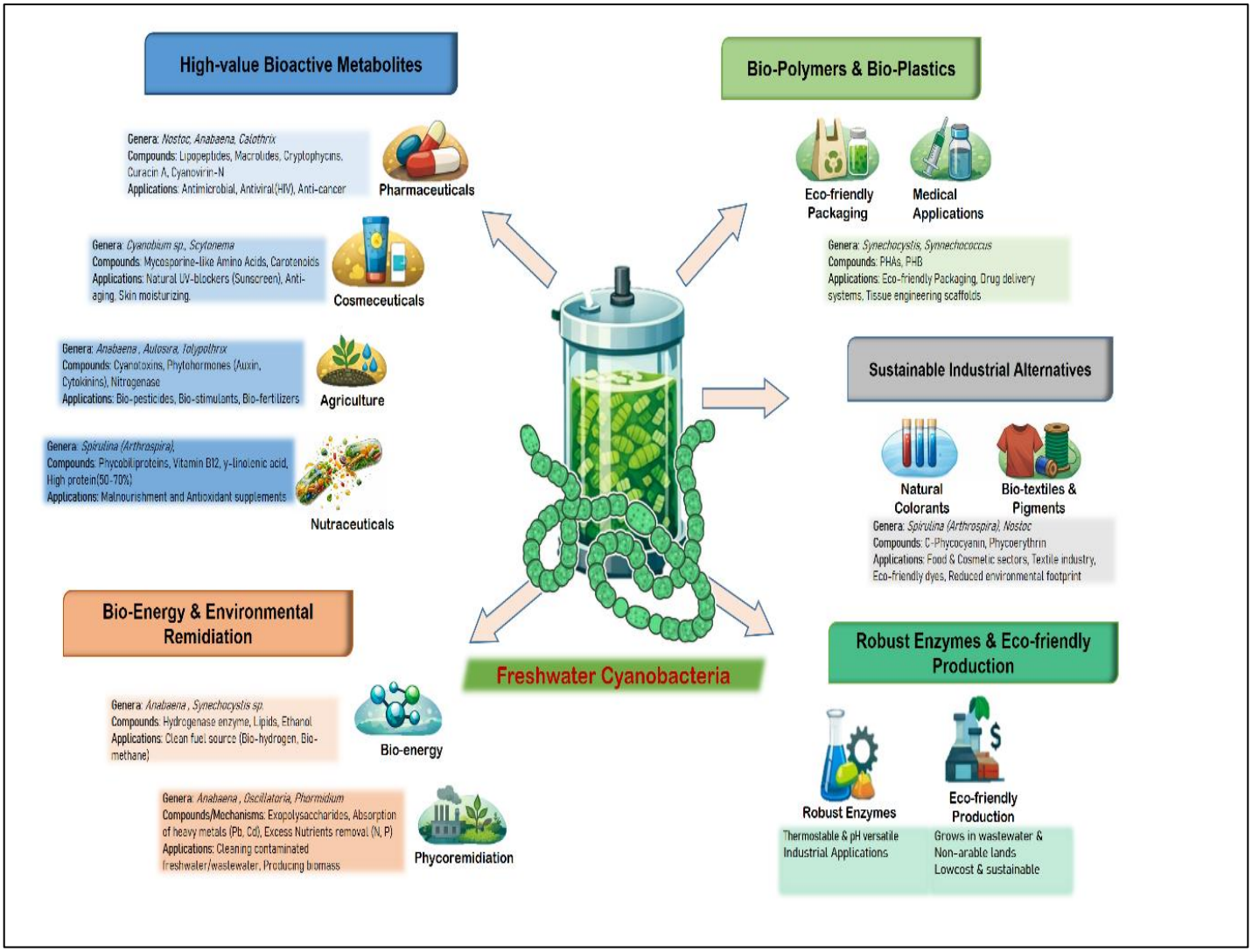

Figure 2: Biotechnological Potential of Freshwater Cyanobacteria

5.1. Bioactive Compounds and Pharmaceuticals

Freshwater cyanobacteria are a promising frontier in drug discovery, producing compounds with anticancer, antiviral, antifungal, and anti-inflammatory properties (**Table 7**) (Mahendran et al. 2021; Dittmann et al. 2015). Recent advances in genomics, metabolomics, and bioengineering have intensified interest in exploiting these organisms for drug discovery (Nandagopal et al. 2021). Continued exploration of their biosynthetic diversity, along with advancements in genomics and synthetic biology, holds immense potential for pharmaceutical innovation.

Table 7. Pharmaceutical applications of bioactive compounds.

S.No.	Compound/ Class	Cyanobacterial Source	Pharmaceutical Activity	Mechanism/ Target	References
1.	Cryptophycin52	Nostoc sp.	Anticancer	Microtubule destabilization, apoptosis induction	(Baunach et al. 2024
2.	Curacin A	Lyngbya majuscula	Anticancer	Inhibits tubulin polymerization	
3.	Cyanovirin-N	Nostoc ellipsosporum	Antiviral (HIV, Ebola)	Binds viral envelope glycoproteins	(Gademann and Portmann, 2008)
4.	Scytophycin	Scytonema spp.	Antimitotic, Cytotoxic	Inhibits actin polymerization	
5.	Lyngbyabellins	Lyngbya spp.	Antiprotozoal, Antifungal	Disrupt cytoskeletal elements	(Zahra et al. 2020; Verma et al. 2023)
6.	Aeruginosin 98A	Microcystis aeruginosa	Anticoagulant, anti-inflammatory	Inhibits serine proteases like thrombin	(Xu et al. 2024)
7.	Micropeptins	Microcystis, Planktothrix	Antiinflammatory	Inhibits elastase and trypsin	
8.	Tolytoxin	Tolypothrix spp.	Antifungal, Antitumor	Actin filament inhibition	(Zahra et al. 2020)
9.	Hassallidins	Hassallia spp.	Antifungal	Targets fungal membranes (membrane permeabilizer)	

5.2. Biofertilizers and Bioremediation Agents

Freshwater cyanobacteria are gaining attention as eco-friendly alternatives to chemical fertilizers and as effective agents for environmental remediation. Their ability to fix atmospheric nitrogen, heavy metals removal, and degrade organic pollutants makes them valuable in sustainable agriculture and pollution control.

5.2.1. Biofertilizers

Freshwater cyanobacteria function as effective biofertilizers due to their capacity for biological nitrogen fixation and enhancement of soil fertility (**Table 9**). These microorganisms possess heterocysts that enable atmospheric nitrogen conversion, contributing to nitrogen availability in agricultural soils. Beyond nitrogen input, cyanobacteria improve soil structure by increasing organic carbon content, secreting extracellular polysaccharides, and promoting beneficial microbial activity. They also produce plant growth-promoting metabolites that support crop development and productivity. Commercial use of cyanobacterial biofertilizers has demonstrated reduced dependence on synthetic nitrogen fertilizers while maintaining soil health. Their biodegradability, cost-effectiveness, and sustainability underscore the potential of freshwater cyanobacteria in environmentally sound agricultural systems (Jing et al. 2025).

5.2.2. Bioremediation Agents

Cyanobacteria function as effective bioremediation agents by removing or transforming environmental pollutants through multiple mechanisms (**Table 8**). They exhibit strong biosorption capacity for toxic heavy metals such as Cd^{2+}, Pb^{2+}, and Cr^{3+} from aqueous environment via cell wall components and extracellular polysaccharides. Species of *Nostoc* and *Anabaena* have been reported to accumulate cadmium and chromium from contaminated waters. Cyanobacteria also contribute to the biodegradation of organic pollutants, including pesticides, dyes, and hydrocarbons such as n-octadecane, pristane, naphthalene, phenanthrene, and pyrene.

Additionally, they facilitate nitrate and phosphate removal from wastewater, reducing eutrophication (Dudeja et al. 2025).

Table 8. Pollutants removed by cyanobacteria (Dudeja et al. 2025).

S.No.	Pollutant Type	Removed By	Mechanism	Environment
1.	Heavy metals (e.g., Cd, Pb)	Spirulina, Anabaena, Oscillatoria	Biosorption, bioaccumulation	Industrial effluents
2.	Nitrate, Phosphate	Nostoc, Microcystis	Uptake and assimilation	Wastewater treatment
3.	Methylparathion, chlorpyrifos, anthracene, phenol	Phormidium, Lyngbya	Biodegradation	Contaminated soils
4.	Dyes (e.g., methylene blue)	Anabaena, Oscillatoria	Enzymatic degradation	Textile effluents

5.3. Integrated Applications in Agroecology

Cyanobacterial biofertilizers improve crop yield, soil organic carbon, and microbial biodiversity. In combination with other microbes (e.g., Rhizobium, Azospirillum), they form consortia enhancing both plant growth and pollutant degradation (Chittoraa et al. 2020). Freshwater cyanobacteria hold significant promise as biofertilizers and bioremediation agents (e.g., A*nabaena variabilis*, *Tolypothrix tenuis*, *Calothrix, Oscillatoria salina, Oscillatoria brevis, Microcystis aeruginosa, Lyngbya majuscula*), offering a dual benefit of sustainable agriculture and environmental clean-up (Singh et al. 2016; Dudeja et al. 2025). Advances in biotechnology, strain improvement, and field application strategies are expected to further enhance their utility in integrated ecological management.

5.4. Biofuels and Energy Production

Freshwater cyanobacteria are emerging as a sustainable source of biofuels due to their ability to fix atmospheric CO_2, grow on non-arable land, and accumulate energy-rich compounds like lipids, carbohydrates, and hydrogen. They offer promising avenues for the production of energy-dense fuels such as biodiesel, bioethanol, biogas, and biohydrogen as alternatives to fossil fuels (**Table 9**) (Dutta et al. 2005; Nozzi et al. 2013). Cyanobacteria offer a highly efficient and versatile platform for sustainable biofuel production and carbon-neutral energy systems due to their high photosynthetic efficiency, rapid biomass accumulation, and direct CO_2 fixation via the Calvin–Benson–Bassham cycle. Their ability to grow on non-arable land using saline, brackish, or wastewater resources reduces competition with food and freshwater supplies, enhancing sustainability (Mund et al. 2022; Pandey et al. 2025).

5.5. Industrial Enzymes and Pigments

Freshwater cyanobacteria produce a wide array of enzymes and pigments with significant industrial applications (**Table 9**). Their natural abundance, ease of cultivation, and potential for genetic enhancement make them ideal bio factories for eco-friendly and sustainable biomolecules. Cyanobacteria secrete several extracellular enzymes with applications in biotechnology, pharmaceuticals, food processing, and environmental remediation (Singh et al. 2016). Also, these microorganisms synthesize several natural pigments that are widely used as food colorants, cosmetics, pharmaceuticals, and fluorescent markers (Pagels et al. 2021; Sandybayeva et al. 2022). Moreover, many cyanobacterial enzymes exhibit high thermostability and broad pH tolerance, supporting their use in harsh industrial processes (Singh et al. 2016; Fusco et al. 2025). In addition, pigments such as phycocyanin and carotenoids have applications in nutraceuticals and pharmaceuticals. Advances in metabolic engineering and synthetic biology are further expanding their production potential, positioning freshwater cyanobacteria as a promising resource for green industrial bioprocessing (Pagels et al. 2021).

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Table 9. Cyanobacterial applications in enzymes, pigments, fertilizers, and fuel production.

S.No.	Product/Function		Sources	Applications / Role	References
1.	Bioenzymes	Laccase	Synechocystis, Anabaena	Bioremediation, dye degradation	(Singh et al. 2016)
2.		Cellulase	Nostoc, Oscillatoria	Bioethanol production, animal feed	
3.		Amylase	Spirulina, Nostoc	Food processing, starch hydrolysis	
4.		Protease	Phormidium, Lyngbya	Detergents, leather industry	
5.		Lipase	Microcystis, Anabaena	Biodiesel production, dairy industry	
6.		Superoxide dismutase (SOD)	Anabaena cylindrica	Antioxidant cosmetics, pharmaceuticals	
7.	Biopigments	Phycocyanin (blue)	Spirulina platensis	Natural food colorant, antioxidant, anti-inflammatory	(Sandybayeva et al. 2022; Sithambaram et al. 2022)
8.		Phycoerythrin (red)	Nostoc, Lyngbya	Fluorescent probes in biotechnology	
9.		Chlorophyll-a	All cyanobacteria	Nutraceuticals, dietary supplements	
10.		β-carotene	Synechococcus, Anabaena	Vitamin A precursor, anti-aging products	
11.		Zeaxanthin	Spirulina, Nostoc	Eye health supplements, UV protection	
12.	Biofertilizers	Nitrogen fixation, Symbiosis with Azolla	Anabaena	Rice paddies, wetlands	(Jing et al. 2025)
13.		Nitrogen fixation, polysaccharide production	Nostoc	Soil amendment, drylands	
14.		Nitrogen fixation in flooded fields	Aulosira	Wetland and rice cultivation	
15.		Nitrogen fixation, biofilm formation	Tolypothrix	Soil fertility improvement	
16.	Biofuels	Biodiesel	Synechococcus, Nostoc, Oscillatoria	Lipid accumulation, transesterification	(Dutta et al. 2005; Nozzi et al. 2013)
17.		Bioethanol	Anabaena, Spirulina	Carbohydrate production and fermentation	
18.		Biogas (Methane)	Mixed cyanobacterial biomass	Anaerobic digestion of biomass	
19.		Biohydrogen	Anabaena, Nostoc, Calothrix	Photobiological water-splitting and nitrogenase activity	

6. CHALLENGES AND LIMITATIONS

Despite growing interest in the ecological and biotechnological potential of freshwater cyanobacteria, several scientific and practical challenges persist. These gaps limit both our understanding of cyanobacterial diversity and the safe, scalable application of their bioactive compounds.

6.1. Limitations in Species Identification and Culturing

Accurate identification of cyanobacteria is challenged by high morphological plasticity, limited culture ability, and strong species similarity, which constrain classical taxonomy and strain-level resolution (Komárek et al. 2020). Many taxa remain non-culturable or grow poorly under laboratory conditions, leading to biased biodiversity assessments and restricted physiological characterization (Rai et al. 2022). Additionally, remote and extreme freshwater ecosystems remain underexplored, with metagenomic studies revealing substantial uncultured diversity absent from existing collections (Monchamp et al. 2016). The biotechnological use of cyanobacteria is further constrained by biosafety concerns related to toxin production and by evolving, region-specific regulatory frameworks. Finally, incomplete genomic resources and limited integration of multi-omics approaches hinder a comprehensive understanding of cyanobacterial metabolic potential and stress responses (Bibi et al. 2024).

6.2. Underexplored Ecosystems and Cryptic Diversity

Freshwater cyanobacterial diversity remains substantially underestimated due to limited exploration of remote ecosystems and the prevalence of cryptic species. Tropical wetlands, alpine and glacial lakes, subterranean waters, hot springs, and saline inland systems are poorly studied, despite hosting unique cyanobacterial communities adapted to extreme conditions and possessing novel metabolic traits (Freitas et al. 2024). Traditional morphology-based taxonomy fails to resolve many taxa because genetically distinct lineages often display minimal phenotypic variation. Molecular approaches, including 16S rRNA, ITS, and whole-genome analyses, reveal extensive cryptic speciation with functional differences in toxicity, nitrogen fixation, and ecological tolerance (Pecundo et al. 2023). Comprehensive sampling combined with integrative molecular tools is essential to accurately assess cyanobacterial biodiversity and unlock their ecological and biotechnological potential.

6.3. Biosafety and Regulatory Challenges

Despite their significant biotechnological potential, the application of cyanobacteria raises important biosafety and regulatory challenges. Several taxa produce potent cyanotoxins, including microcystins, anatoxins, cylindrospermopsins, and saxitoxins, which pose risks to food supplements, aquaculture, drinking water, and agricultural applications, necessitating rigorous monitoring and quality control (Papadimitriou et al. 2021). Regulatory frameworks for cyanobacteria-based products, particularly genetically modified strains, remain fragmented and inconsistent across regions, with limited consensus on toxin thresholds, product labeling, and environmental release guidelines (Bibi et al. 2024). Moreover, open-environment applications introduce risks related to horizontal gene transfer, unintended bloom formation, and ecosystem disruption, underscoring the need for robust risk assessment and containment strategies (Chittora et al. 2020). Harmonized international regulations, standardized safety protocols, and interdisciplinary governance are essential to enable safe and responsible advancement of cyanobacterial biotechnology.

7. FUTURE PERSPECTIVES AND APPLICATIONS

Cyanobacteria represent a remarkably diverse phylum, characterized by a vast spectrum of phenotypic and physiological adaptations. Traditionally, cyanobacteria are categorized based on their structural forms and reproductive strategies, and hence, they often fail to capture the high gene content variation present even among closely related strains. However, the advent of molecular phylogenetics, specifically 16S rRNA sequencing and whole-genome analysis, has revolutionized this classification system. These genetic insights reveal that traditional morphological categories do not always align with true evolutionary lineages. Modern taxonomy now recognizes multiple distinct clades (Shestakov and Karbysheva 2017; Jung et al. 2024). This phenotypic diversity

is a direct result of genetic clusters that, despite their proximity in a phylogenetic tree, have evolved cohesive and distinct environmental associations. Ultimately, this transition to genome-based phylogeny provides a more informative and reproducible toolset. It allows for the reconstruction of evolutionary histories that accurately mirror environmental adaptations, bridging the gap between clinical microbiology and field-based ecology. Emphasizing open access and the continuous comparison of unique gene sequences against genomic frameworks is now essential for a robust, modern classification system (Walter et al. 2017). This refined understanding of cyanobacterial phylogeny underscores the biological complexity and evolutionary significance of these ancient organisms as they continue to be reclassified in light of new genomic data.

An extraordinary metabolic and genomic plasticity allows cyanobacteria to execute rapid genetic and physiological shifts, enabling them to thrive in environments unsuitable for traditional crops, such as wastewater or non-arable land, making them ideal drivers for a circular bioeconomy. Such insights into their intricate genetic architecture are vital for both understanding their ecological roles and harnessing their versatility for biotechnological applications. However, the potential for rapid proliferation in eutrophic environments allows these organisms to form harmful algal blooms (HABs), which pose a severe threat to aquatic biodiversity, public health, and overall water quality. Ecologically, these blooms trigger devastating shifts in food webs and induce hypoxia, leading to quantified biodiversity loss and the contamination of drinking water through cyanotoxin production. While emerging technologies like AI-driven models and satellite-based remote sensing of pigments like phycocyanin show immense promise, they require further refinement for widespread application. Management of cyanobacterial blooms is fundamentally hampered by their spatial and temporal unpredictability, which renders traditional, time-consuming water sampling methods inadequate for real-time dynamics. These challenges are exacerbated by climate change, specifically rising temperatures, water column stratification, and the persistent difficulty of regulating dispersed nutrient loads like agricultural runoff. Direct interventions include the cautious use of algaecides such as hydrogen peroxide or the exploration of biological agents like cyanophages and grazing zooplankton, though these require rigorous safety validation before large-scale deployment (Saleem et al. 2025).

While frequently associated with the deleterious effects of toxic HABs, these microorganisms simultaneously offer a transformative platform for sustainable biotechnology. Their innate capacity for oxygenic photosynthesis allows for the direct conversion of solar energy and atmospheric CO_2 into high-value carbohydrates and complex metabolites. Despite decades of foundational research aimed at harnessing cyanobacterial chassis, several systemic bottlenecks persist that hinder commercial viability. When compared to traditional heterotrophic hosts like *Escherichia coli*, cyanobacterial platforms consistently struggle with sub-optimal product titers and biological instability in large-scale photobioreactors. A primary hurdle in closing this yield gap is our limited understanding of cyanobacterial regulatory networks (Lindberg et al. 2023). Currently, our understanding of carbon-to-electron flow, complex protein regulation, and circadian-driven gene expression lacks the depth available for established industrial microbes (Chen et al. 2023). To move forward, the field must prioritize the development of advanced synthetic biology toolkits, including precise promoters, CRISPR-based regulation, and predictable riboswitches to achieve the same level of modularity seen in *E. coli* (Opel et al. 2023). Also, a significant knowledge gap persists regarding systems-level integration. We lack a comprehensive blueprint of the regulatory circuits that dictate the stoichiometry and cellular abundance of photosynthetic complexes. In industrial settings, the inability to synchronize light-harvesting efficiency with biomass accumulation often leads to metabolic waste in the form of heat or fluorescence. The process of oxygenic photosynthesis is driven by intricate bioenergetic mechanisms consisting of interconnected photosynthetic and respiratory electron transport chains. The ultimate goal of characterizing these mechanisms is to move beyond observational biology toward predictive metabolic engineering. By optimizing the synchronization between energy input (light) and metabolic output (biomass/products), we can engineer strains that maintain high photosynthetic efficiency even under the fluctuating conditions of industrial-scale photobioreactors. Mapping these regulatory networks is the prerequisite for tuning cyanobacterial chassis to bypass natural bottlenecks (Burnap 2023). Overcoming these metabolic constraints is not merely a technical challenge but a prerequisite for a circular bioeconomy.

For decades, genetic engineering was largely confined to a few workhorse strains: *Synechocystis* sp. PCC 6803, *Synechococcus elongatus* PCC 7492, and *Anabaena* sp. PCC 7120. However, the discovery of faster-growing, more robust freshwater cyanobacteria species, such as *Synechococcus elongatus* PCC 11801, is redefining the

upper limits of cyanobacterial productivity. These newer strains offer high thermotolerance and salinity tolerance necessary for large-scale outdoor cultivation, though they often require the adaptation of established genetic tools. Despite the expansion of the molecular toolset, cyanobacterial engineering remains less predictable. Recent advancements have focused on molecular tools for gene expression regulation, such as transcriptional and post-transcriptional fine-tuning to control the rate of translation. In addition, the CRISPR revolution has moved the field toward markerless selection and multiplexed gene knockdown, allowing rapid reconfiguration of cyanobacterial cell factories. Furthermore, the integration of potential DNA assembly strategies, like the modular cloning technique with these diverse regulatory layers, might replace conventional time-consuming testing on a handful of mutants in the future (Jaiswal et al. 2018; Opel et al. 2023).

Moreover, the landscape of freshwater cyanobacterial synthetic biology is rapidly evolving, transitioning from basic genetic modification to context-specific solutions by integrating multi-layered regulatory circuits. Regulatory elements often lose precision or strength when placed within the unique physiological environment of a phototroph. Past studies suggest light-dependent regulation for enhanced protein stability and utilizing small effector proteins to fine-tune metabolic flux without the metabolic burden of heavy protein overexpression, which is critical for maintaining stable production titers. While rational engineering provides precision, adaptive laboratory evolution (ALE) offers a powerful alternative for developing robust industrial phenotypes. By subjecting cultures to serial environmental stress, stable and high-yield mutants optimized for a unique physiological environment can be achieved. This also provides regulatory advantages as ALE-derived strains are often classified as non-GMO in specific jurisdictions, significantly lowering the barrier for industrial licensing and public acceptance. Integrating modular cloning strategies and laboratory automation technologies allows for the rapid assembly and screening of vast mutant libraries, effectively shortening the development timeline from years to months (Portnoy et al. 2011; Mavrommati et al. 2022; Opel et al. 2023).

Freshwater cyanobacteria stand at the forefront of the bio-economy as unique photoautotrophic chassis capable of direct CO_2 valorization. These are promising microbial cell factories for the production of biochemicals and biofuels from CO_2 (Chen et al. 2023). Also, the transition from plant-based lipids, such as palm and coconut oils, to cyanobacterial fatty acids represents a critical shift toward a more sustainable bio-economy. Recent laboratory advancements have demonstrated the feasibility of producing a diverse array of high-value derivatives beyond simple fatty acids, including fatty alcohols (household detergents), fatty aldehydes (rubber, plastics, and cosmetics), hydrocarbons (biofuels and lubricants), hydroxy fatty acids (pharmaceuticals and polymers), etc. Utilizing cyanobacteria as photoautotrophic platforms, further ecological degradation associated with tropical monoculture could be avoided. Despite several technical milestones, achieving cost-competitiveness remains a challenge. Although the theoretical sustainability of cyanobacterial products manufacturing is undisputed, the future of the field depends on our ability to harmonize high-flux metabolic engineering with a commercial license to operate. The technical success of a cyanobacterial platform is often secondary to the public and regulatory perception of genetically modified organisms (GMOs) (Sattayawat et al. 2023). As illustrated by the Ecover case study, even products with clear environmental benefits can face significant market withdrawal due to activist pressure and consumer skepticism regarding precision-engineered biology. The experience of Ecover demonstrates how divergent consumer opinions can impede the progress of GMO-based technologies. In 2014, Ecover launched a new line of commercial laundry detergents formulated with algae-derived oil as a sustainable alternative to palm oil. However, shortly thereafter, the activist group “ETC” raised concerns regarding the use of ingredients produced through precision-engineered organisms. In response to the ensuing public attention and debate, Ecover decided to discontinue the use of algal oil in its products (Asveld et al. 2016). This case highlights that, despite the potential environmental advantages offered by synthetic biology-driven chemical production, such approaches remain sensitive and sometimes controversial in the public domain. Only by bridging this gap could unsustainable tropical agriculture be replaced with solar-powered biomanufacturing.

The industrial demand for natural pigments is undergoing a significant shift as sectors move away from synthetic dyes in favor of sustainable, bio-based alternatives. Cyanobacteria, with their immense biodiversity and photoautotrophic efficiency, offer a unique ability to produce a spectrum of high-value colorants. Rather than treating pigments as a secondary by-product, modern strategies favor a biorefinery approach. This involves the simultaneous extraction of multiple components, such as chlorophylls, carotenoids, and phycobiliproteins, from a single biomass source to maximize economic feasibility. While laboratory yields are promising, the bench-to-

market transition faces several distinct hurdles, such as the stability of pigments under food-processing conditions (high temperature and varying pH). Also, crude extracts often carry earthy off-flavors that can impact consumer acceptance. Advancements in encapsulation and refined purification techniques are necessary to ensure that pigments function effectively as additives without altering the taste profile of the final product. By optimizing the cultivation-to-formulation pipeline and utilizing non-arable land and saline water, a sustainable, scalable source of pigments that meet both nutritional and aesthetic industrial standards could be achieved (Deepika et al. 2023).

Freshwater cyanobacteria offer a unique biological route to hydrogen production by leveraging their native metabolic pathways. Unlike conventional thermochemical processes, cyanobacterial H_2 production is less energy-intensive and could be integrated into a circular bio-economy. Some key mechanisms include direct photolysis, fermentative metabolism, and nitrogenase-mediated production (Tiwari and Pandey 2012). Despite the theoretical potential, biological H_2 yields are currently hindered by the activity of uptake hydrogenase, which recaptures a significant portion of the generated gas, thereby reducing the net yield. Also, both hydrogenase and nitrogenase enzymes are highly sensitive to molecular oxygen, an inherent byproduct of photosynthesis that acts as a potent inhibitor. While heterocystous strains, for example, *Anabaena sp*. PCC 7120 is generally more efficient for this process, but they introduce further complexities such as high energy requirements and the simultaneous production of oxygen and hydrogen gas separation costs. The future of the biohydrogen sector is not merely a biological challenge but a multidisciplinary one, including metabolic optimization with bioprocess scaling and the need for precise genetic regulation of heterocyst frequency through factors like the HetR protein. Strategies to mitigate these challenges involve sophisticated interventions, including the use of nanotechnology for oxygen-ejection membranes, the application of sulfur stress to induce anaerobic conditions, and the genetic engineering of oxygen-tolerant hydrogenase variants (Dutta et al. 2005). Moreover, the integration of cyanobacterial H_2 production with wastewater treatment or CO_2 sequestration could provide the economic lift needed for market entry.

Unlocking the full ecological and biotechnological potential of freshwater cyanobacteria requires targeted, multidisciplinary research efforts. Integrative approaches combining genomics, transcriptomics, metabolomics, and ecological modelling are essential for refining phylogenetic classification, improving environmental monitoring, bioprocess development, and identifying novel bioactive compounds. Advances in synthetic biology and metabolic engineering further enable the development of optimized cyanobacterial strains with enhanced metabolite yields, reduced toxicity, and improved stress tolerance for applications in biofuels, pharmaceuticals, and carbon capture. Equally important are sustainable use and conservation strategies that protect cyanobacterial diversity, particularly in underexplored freshwater ecosystems, through ecosystem-based management, ethical bioprospecting, and robust regulatory frameworks. Overall, coordinated efforts integrating molecular science, ecology, biotechnology, and regulatory policy will be critical for advancing safe innovation and maximizing the societal benefits of cyanobacterial resources.

8. CONCLUSION

Freshwater cyanobacteria are fundamental components of aquatic ecosystems, contributing to primary productivity, biological nitrogen fixation, and food-web structure. However, under favourable environmental conditions, certain taxa can proliferate excessively, forming blooms that alter ecosystem functioning and degrade water quality, with consequences for aquatic biota and ecosystem services. Advancements in molecular tools, phylogenetic analyses, and omics technologies have greatly enhanced our understanding of cyanobacterial taxonomy, evolution, and ecological interactions. Nevertheless, challenges such as taxonomic uncertainty, underexplored habitats, safety concerns, and inadequate regulatory frameworks remain. Future research must prioritize the intricacies of cyanobacterial ecology, focusing on stress responses and multi-trophic interactions within freshwater ecosystems. Integrating advanced genetic and metabolic engineering will be essential for realizing the sustainable potential of these organisms in bioremediation and biofuel production.

Concurrently, a deeper understanding of the triggers behind harmful algal blooms (HABs) is necessary to develop robust management strategies and protect public health. Finally, addressing the impacts of climate change and anthropogenic activity on freshwater cyanobacterial biogeography is vital for preserving biodiversity and the essential ecosystem services it provides. By synergizing ecological, biotechnological, and conservation

frameworks, we can harness the multifaceted benefits of cyanobacteria while mitigating their environmental risks.

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Ethical Approval

This is a review article; therefore, no ethical clearance is required for this study.

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