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Review Article

Unlocking microalgae's dynamic interactions with other microbes while understanding their roles in the sustainability of the ecosystem

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Abstract

An ecosystem is a complex and interrelated network of living organisms that includes different species interacting with their physical environment and one another. In addition to physical contact, these interactions involve intricate connections that gradually alter the ecosystem’s functioning. In this framework, organisms play a diverse role in energy flow and nutrient cycling. Microalgae have become a renewable and sustainable option for bioenergy production while serving as efficient agents for pollutant removal from wastewater. Microalgae interact with other microbes, especially bacteria and fungi, and exhibit various economic and environmental advantages. This review focuses on the dynamic interactions of microalgae with other microbes within the ecosystem, which holds significant promise for fostering a sustainable ecosystem. It provides insights for developing sustainable solutions for ecosystem management and environmental degradation mitigation through harnessing the synergies between microalgae and other microbes. Understanding and harnessing these microbial interactions can lead to innovative biotechnological applications, such as bioremediation, biofuel production, and aquaculture management. However, still there is a gap that we need to understand more about how these interactions work at the molecular level. Using advanced technologies like genomics, proteomics, and metabolomics to elucidate the specific pathways through which microalgae and microbes affect each other's growth and functions.

Keywords: Ecosystem management, Microbial consortium, Environmental degradation, Microalgae, Biotechnological applications

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1. Introduction

An ecosystem is an interconnected and dynamic community of organisms that come into contact with each other and their physical environment. It is surrounded by living organisms such as plants, animals, and microorganisms and their relationship with non-living components like water, soil, air, and climate. Ecosystems exhibit several characteristics, such as nutrient cycling, biodiversity, and energy flow, contributing to their resilience and stability. Ecosystems can be found in a wide range of habitats, from terrestrial forests to aquatic ecosystems like lakes, rivers, and oceans (Assessment, 2005). Ecosystems provide various important ecological services for the planet's functioning and human welfare. Like releasing oxygen through photosynthesis, regulating the climate by absorbing carbon dioxide, and governing weather patterns. Additionally, ecosystems support biodiversity, and biodiversity contributes to the regulation of the ecosystem, such as nutrient cycling, pest control, and pollination, which eventually benefit human societies (Costanza et al., 1997). Different human activities, such as pollution, habitat destruction, excessive use of resources, and climate change, pose significant threats to ecosystems. Various factors are involved in ecosystem degradation, such as water pollution, soil erosion, loss of biodiversity, and ecological imbalances (Folke et al., 2004). Ecosystem degradation not only affects the survival of numerous species but also threatens the natural systems that support human life. The loss of biodiversity leads to the ecosystem becoming more susceptible to environmental changes and unable to perform basic functions such as water purification, pollination, and carbon sequestration (Elisha and Felix, 2020).

Microalgae are broadly distributed, and it is shown that more than 20,000 species exist in nature. Microalgae contain most freshwater and marine plankton and are responsible for 40-50% of the total photosynthetic production of marine algae. With time, microalgae have adapted to live in rivers, oceans, and lakes and can even survive in harsh environments such as high salinity, high temperature, and wastewater (Zhou et al., 2022). Microalgae interact with other microbes and these interactions play a crucial role in the stability and development of various ecosystems. These interactions involve the complex relationships between microalgae, which are photosynthetic organisms, and the multiple arrays of microorganisms that coexist within their environment. The exchange of chemical compounds is a significant key to the interactions of microalgae with other microorganisms (Hom et al., 2015b). Microalgae are present in lively microbial communities with a multitude of interactions. Understanding the complex mechanisms of these interactions is important for unraveling the complicated web of life and unlocking the potential of microorganisms in various biotechnological applications ranging from environmental remediation to biofuel production. The most studied interactions are those between microalgae-microalgae, microalgae-bacteria, and microalgae-fungi (Lauritano and Galasso, 2023).

These interactions are helpful in ecosystem development, and protection and create a positive impact on the ecosystem. Different ways are involved in their interactions such as symbiotic/mutualistic, parasitic, and competitive (Amin et al., 2022). Nutrient exchange comprises the basis for mutualistic relationships (Zhang et al., 2020b). These interactions contribute to the functioning or formation of complex ecosystems such as freshwater, oceans, lakes, rivers, and even in artificial systems like wastewater treatment plants (Mu et al., 2021). This review highlights the interaction between microalgae and other microbes that can potentially help to maintain the ecosystem. By understanding and exploring the dynamic interactions within microbial consortia particularly the role of microalgae, we can develop innovative solutions for environmental sustainability, energy production, waste management, carbon fixation, animal feed, and ecosystem development, making it highly valuable for both society and industry.

2. Ecosystem Development

An ecosystem is developed when interacting organisms physically associate with their environment to shape biological communities. Similarly, the microalgae ecosystem is not only about microalgae but also about its interaction with other microbes and the physical environment that provides microalgae-microbial interaction and the suitable growth conditions for developing a complete microbial ecosystem (Ashraf et al., 2022, Amin et al., 2022). However, the microalgae-microbial ecosystem is of various types depending upon the interacting microbes and the proliferating environment.

A variety of changes to ecosystem services are leading to the introduction or removal of organisms in ecosystems that disturb or modify ecological processes and biotic interactions (Elisha and Felix, 2020). The physical factors behind the interactive ecosystem of microalgae are temperature, pH, light, air, and most importantly, the environment, either moist or dry, as well as the biological factors that involve the impact of other microalgae and microbes, like bacteria and fungi. Hence, all the factors maintain the interaction of microalgae with microbes and the environment to successfully develop an ecosystem (Zhang et al., 2020b). For the detailed study of the interactive ecosystem of microalgae, it is essential to know the microbes with which microalgae interact, the mechanism of their interaction, and the types of environments in which they give rise to microbial communities (Ashraf et al., 2022).

2.1. Ecosystem development by microalgae-microbial interactions

In microalgae-microbial ecosystem development, it is important to understand the factors that give the final shape to the interactive behavior of microalgae with microalgae and other microbes. Developing an ecosystem via microalgae-microbial interactions involves the symbiotic relationship between microalgae and various microorganisms (Wu et al., 2021). Microalgae are photosynthetic microorganisms that convert sunlight and carbon dioxide into organic compounds through photosynthesis. They are the primary producers in aquatic ecosystems and are crucial in nutrient cycling and oxygen production (Amin et al., 2015).

Microbes, including bacteria and fungi, interact with microalgae in several ways, forming complex relationships that contribute to ecosystem development as shown in **Fig. 1.**

2.2. An aquatic ecosystem with variable interactive patterns of microbes

Microalgae interact with microbes and form microbial communities via specific mechanisms; however, outcomes of microalgal interactions can vary depending on the species involved, the environmental conditions, and the availability of resources (Amin et al., 2015, Ramanan et al., 2016). For instance, microalgae sometimes interact with microbes mutually to benefit both parties, form biofilms to provide a habitat for other organisms, and some microbes competitively interact with microalgae to suppress harmful algal blooms (Fuentes et al., 2016, Fuentes Cordero et al., 2016).

Other than freshwater bodies, microbes grow and interact with each other in wastewater as it is the nutrient-enriched medium for their growth and is considered an emerging research area because the growth of interacting microbes significantly acts as bioremediates as they remove pollutants from wastewater and the environment. Like freshwater bodies, wastewater also contains different microbial communities due to inter and intra-species interaction. Some bacteria primarily interact with microalgae symbiotically, enhancing algal biomass production but later releasing some toxins that inhibit microalgal cells. At the same time, the cell-to-cell interaction of fungi and microalgae protects algal cells from these toxins, hence developing an ecosystem with different interactive patterns (Krespach et al., 2020). However, naturally, all microbes exist as consortia in all water bodies, making different microbial communities that finally lead to biological communities and make the ecosystem stable and healthy with various interactions.

3. Microalgae-Microalgae interactions

Interactions between microalgal strains can be highly complex, involving multiple mechanisms simultaneously or changing dynamically over time (Steinrücken et al., 2021). In the case of microalgae-microalgae interaction, various kinds of signaling are involved that help microalgae to detect other microalgal strains present in their environment and let them communicate, in this way making a biological community and then finally an ecosystem (Dow, 2021). Most microbes interact via quorum sensing with them or other microbes; however, other than quorum sensing, microalgae also use chemical, physical, or light signaling to interact with other microalgal strains (Chi et al., 2017, Fallahi et al., 2021b). These interactions occur when different microalgal strains meet each other in their natural environment, aquatic ecosystems.

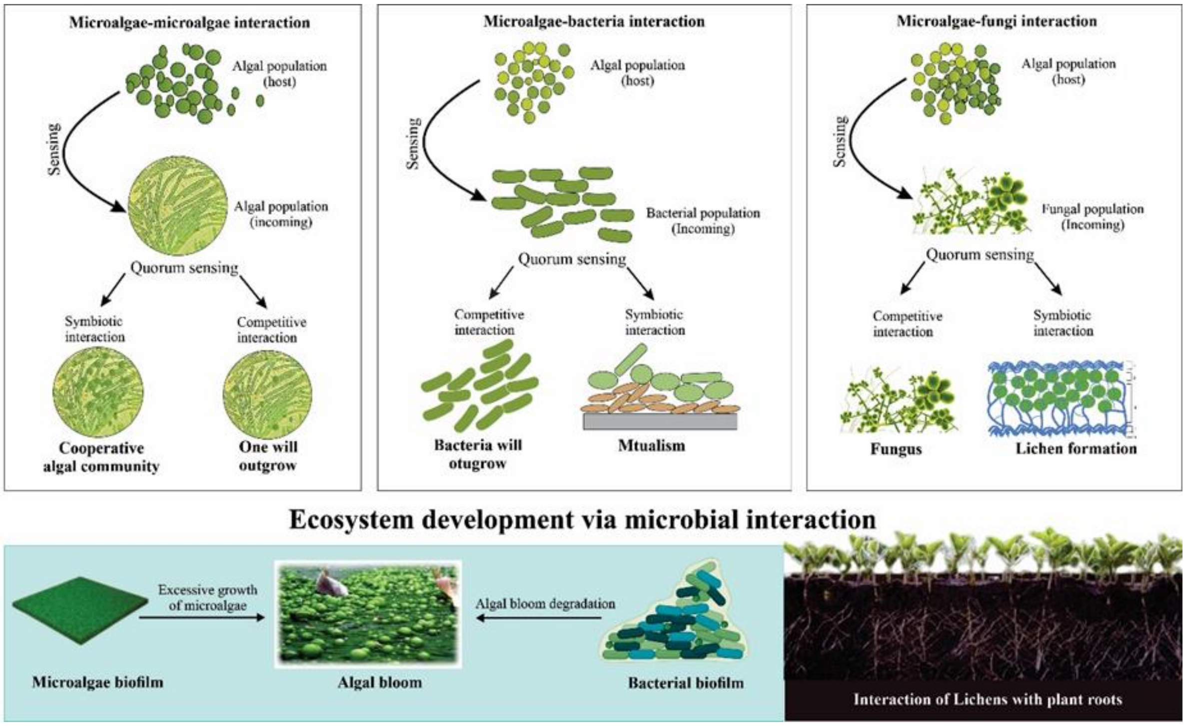

Fig 1. Different interactive patterns of microalgae with other microbes and with microalgae also for the development of a sustainable environment.

3.1. Mechanisms of interaction and their respective growth patterns

Microalgae interact with microalgae in different interactive patterns in their natural ecosystem (aquatic) to form microbial communities and maintain a proper ecosystem according to the availability of nutrients and behavior of interacting species (Santos and Reis, 2014). Interactive patterns such as mutualistic, competitive, predatory, cooperative, and allelopathy are the major possibilities for microalgae-microalgae interaction.

3.1.1 Quorum sensing via chemical signaling

When microalgae sense another microalga in their vicinity, they release some chemicals such as secondary metabolites, pheromones, and allelochemicals to detect that microalga and influence the growth, behavior, and physiological responses of the neighboring microalgae either to interact or repel the detected one (Borowitzka, 2016, Stallforth et al., 2022). In this way, microalgae form a cooperative or competitive ecosystem.

On the other hand, algae, and other microbes, use a process called quorum sensing (QS) to communicate with one another and coordinate their actions according to population density. This communication is mediated by the chemical signals known as autoinducers that allow microalgae to sense the presence and density of other microalgal cells in their surroundings. Algal cells have receptors that detect the concentration of autoinducers (Das et al., 2019). When the concentration of autoinducers reaches the limit, the final ecosystem starts generating by the cooperation of microalgae in a mutualistic pattern (Zhao et al., 2023). Hence, there will be no competition within the microalgae for food and living, making the ecosystem stable and maintained.

In algae, QS can influence sexual reproduction, spore formation, and toxin production. QS insights can improve bioremediation practices by optimizing the conditions for algal growth and pollutant degradation. Algal quorum sensing plays a role in the maintenance and development of biofilms, which are complex structures of cells embedded in EPS (Extracellular Polymeric Substances) (Neu and Lawrence, 2010). Quorum sensing enables cooperation among algal cells to synchronize activities such as the production of extracellular enzymes for nutrient consumption. Manipulating algal quorum sensing can improve the productivity and health of aquaculture systems by stimulating the growth of beneficial algae and limiting the dominance of harmful species. It also mediates competitive interactions, such as the production of allelopathic compounds. Chemicals inhibit the growth of competitive microalgal strains, and this interaction is called allelopathy, which is beneficial to keep the ecosystem stable and healthy (Zuo et al., 2015). One of the interactive patterns that microalgae generate, is suppressing the competitors from the community by releasing chemicals. However, the specific signaling mechanisms and cues involved in microalgal interactions can vary depending on the species, environmental conditions, and the nature of the interaction (e.g., competition, and cooperation) (Coyte and Rakoff-Nahoum, 2019).

3.1.2 Mutualistic interaction

Mutualism is the perfect interactive pattern for developing a stable ecosystem, as the interaction involves the beneficial cooperation of microalgal strains to exchange nutrients and metabolites (Hom et al., 2015a). Another type of mutualism is symbiotic mutualism, in which one algal strain with excessive resources facilitates the other strains and gives rise to biofilms that further facilitate other microbes by providing them with a habitat (Saravanan et al., 2021). When limited resources such as nutrients, space, and light exist, microalgae compete to fit into the environment. In this situation, microalgae with high and rapid growth rates will outgrow and dominate in that environment; however, the competition may be direct or indirect (Fallahi et al., 2021b). In direct competition, one strain inhibits the growth of another strain by releasing chemicals like allelopathy (Zuo et al., 2015), while in indirect competition, the outgrowing strain will alter the environmental conditions that influence the growth and physiology of the neighboring microalgae, not supporting its survival in the competitive ecosystem and hence suppressing algal blooms (Yang et al., 2015).

However, other than freshwater bodies, microalgae-microalgae associations are specifically generated artificially in synthetic medium or, most abundantly, in wastewater to improve algal biomass production, carbon sequestration, and wastewater treatment. For example, *Chlorella* sp. is highly capable of removing pollutants like nitrogen, phosphorous, COD, and BOD from wastewater, and *Scenedesmus* has significant tolerance against high salinity so both can be co-cultured in piggery wastewater to get high biomass and pollutant removal efficiency (Wang et al., 2016).

Also, some studies use binary cultures of microalgae for upraising biomass productivity, lipid productivity, and, most importantly, carbon dioxide fixation rate, such as the symbiotic association of a cyanobacterium, *Leptolyngbya tenuis* with a microalgal strain, *Chlorella ellipsoidea* was studied, and the results encourage the symbiosis as there was approximately three times increase in biomass, 1.5 times in carbon fixation rate, and two times increase in lipid production while comparing it to the mono-cultures of all batches (Satpati and Pal, 2021).

3.1.3 Physical interaction

Physical interaction not only entangled microalgae cells with each other but is significantly involved in exchanging nutrients, metabolites, and signals, which influence the growth, physiology, and behavior of the interacting microbes (microalgae) (Cheah and Chan, 2021). Microalgae interact with microalgae to assist each other in growth by nutrient recycling and exchanging metabolites, increasing their productivity (Fuentes et al., 2016). This cooperative pattern of interaction lets microalgae grow mutually, which is beneficial for all the microalgal strains of that community as mutualism stimulates their growth by making the nutrients more available (Lutzu and Dunford, 2018).

3.1.4 Inter-species interaction

Microalgae use light signaling for inter-species interaction, which causes variations in the physiology, growth, and response behavior of neighboring cells and lets them adopt a mutualistic or competitive interaction pattern for ecosystem development (Gorter et al., 2020). For instance, if there is a severe type of competition within the microalgae community that leads towards predation, in which microalgae start feeding up on their neighboring bacterial or fungal community, it alters the overall structure and stability of the ecosystem (Kaitala et al., 2020).

4. Microalgae-bacterial interactions

In addition to inter-species interaction, microalgae can form stable interactions with other microbes, such as bacteria, to form microbial communities that further interact with other microorganisms in their natural environment (aquatic) to develop a healthier ecosystem (Zhang et al., 2020a). For instance, the complex association of microalgae and bacteria in the photic zone of oceans and lakes gives rise to phytoplankton communities via mutual interaction by nutrient exchange, mutual assistance of growth factors, chemical signaling by quorum sensing, and killing of interactive partners by exchanging pathogens, are all kind of mechanisms behind microalgae-bacteria interaction (Cirri and Pohnert, 2019).

4.1. Mechanisms of interaction and their respective growth patterns

The interactive mechanisms of the bacterial community, either mutualistic or competitive or any other, are specific to the microalgae depending upon the environmental conditions, the behavior of microalgae, and temperature (Nagarajan et al., 2022).

4.1.1 Symbiotic/mutualistic interaction

Like microalgae-microalgae interaction, microalgae and bacteria also form stable ecosystems by creating symbiotic or mutualistic interactions in aquatic environments (Kublanovskaya et al., 2020). The mechanism behind this interaction is mostly the exchange of nutrients between microbes; for instance, microalgae produce oxygen by photosynthesis that facilitates the growth of bacteria and bacteria side by side degrade organic matter and fix nitrogen to provide microalgae with phosphorous and nitrogen, respectively (Kouzuma and Watanabe, 2015). This interaction benefits both species; hence, there is a formation of a stable community that then equally utilizes the available nutrients and is less affected by environmental factors.

However, the most interesting thing about their mutualistic interaction is, in the microalgae-bacteria association, microalgae act as bacterial hosts by providing bacteria an adhering cellular surface of extra polymeric substance (EPS) that named phycosphere and bacteria, in return, reside on that surface as algal commensals (Ramanan et al., 2016).

Other than freshwater bodies, the symbiotic interaction of microalgae and bacteria is also witnessed in wastewater, considered a nutrient-enriched medium, where they treat wastewater, enhance biomass productivity, and suppress global warming by fixing carbon dioxide. For instance, a microalgal strain, *Auxenochlorella protothecoides,* proliferates while exchanging nutrients with the bacteria as they produce thiamine metabolites to promote its growth in winery wastewater (Higgins et al., 2018).

The mutualistic interaction of microalgae and bacteria always maintains the stability of the ecosystem, as bacteria have the natural mineralization ability, so they degrade organic carbon present in wastewater and provide carbon dioxide to their interactive partner. This assists microalgae in improving their biomass production and pollutant removal efficiency with other beneficial applications (Johnson et al., 2020), such as a study that revealed some biosynthetic pathways by analyzing the exometabolomics of mutualistic interaction of microalgae and bacteria via quorum sensing that finally produce vitamins, methyl acetic acids, and amino acids (Wienhausen et al., 2017).

4.1.2 Physical interaction

Another optimized and, most importantly, structured interaction between microalgae and bacteria again via the mechanism of nutrient exchange is biofilm formation. In an aquatic ecosystem, when bacteria need to be attached to a surface, they mutually interact with microalgae to generate a definite structure in the form of biofilm and get attached to a surface (Kublanovskaya et al., 2020, Cooper and Smith, 2015). In a biofilm, both species exchange nutrients, communicate via chemical signaling, and together, can effectively tackle harsh environmental conditions. The communication and signaling among microalgae and bacteria in a biofilm facilitate them to further interact or repel the detected microbes in their vicinity.

4.1.3 Chemical communication (quorum sensing)

Microalgae and bacteria also interact through quorum sensing, communicating through chemical signaling (Zhou et al., 2016). Chemical signaling lets microalgae detect bacterial communities or cells and then interact or repel them according to their responding behavior (Zhou et al., 2016, Dow, 2021). Sometimes, when there is excessive growth of microalgae, the ecosystem gets polluted because of the formation of harmful algal blooms; in this situation, bacterial communities compete with them and suppress their growth, changing the physiology, behavior, and structure of the ecosystem (Zhu et al., 2022, Ndlela, 2019).

4.1.4 Disease dynamic interactive pattern

Interestingly, one of the interaction mechanisms between microalgae and bacteria is the exchange of pathogens from bacteria to microalgae, which creates disease dynamic interactive pattern (Egan et al., 2014). Unlike microalgae-microalgae interaction, after a few days of the mutualistic association between microalgae and bacteria, bacteria start dying, and the dead cells release toxic chemicals that inhibit the growth of microalgae or compete in a way that transform some pathogenic compounds to the microalgal cells and microalgae get diseased (Ramanan et al., 2016, Fuentes et al., 2016). In this way, interaction shifts from competitive to predatory and changes the whole structure of the ecosystem.

5. Microalgae-fungi interactions

Microalgae-fungi interaction, specifically mycophycobioses, plays a significant role in the marine ecosystem as a producer in the microbial food chain and regulates biogeochemical cycles. Microalgae and fungi form symbiotic, saprophytic, parasitic, pathogenic, and competitive interactions with each other and other microbial communities to develop a stable ecosystem (Lauritano and Galasso, 2023).

5.1. Mechanisms of interaction and their respective growth patterns

5.1.1 Symbiotic interaction

Interspecific interaction is similar to microalgae-bacteria interaction, in which microalgae form a symbiotic association with fungi, which is called lichenization (Cernava et al., 2017). In this interaction, both species benefit each other as fungi absorb water and nutrients from their surroundings, providing a protective and nutrient-enriched environment to microalgae and microalgae, producing oxygen by photosynthesis that fungi lack (Lauritano and Galasso, 2023). This way, microalgae and fungi become interdependent in lichenization and develop a stable ecosystem.

Additionally, lichenization gives rise to distinct biological structures named lichens that colonize many of the substrates simultaneously, such as rocks, trees, and soil, by attaching to their surface and making the interacting species able to survive in extreme environmental conditions such as high altitude regions and deserts (Asplund and Wardle, 2017).

In addition to lichens, another biological structure formed by the interaction of microalgae with fungi and bacteria is called a photobiont or phycobiont. The phycobiont refers specifically to the algal component of the lichen, emphasizing the diverse role of algae in this symbiotic relationship. It involves the symbiotic association of microbes by physical interaction in which microalgal cells reside on the fungal hyphae, and bacteria act as the core microbiome (Xu et al., 2022).

The mutualistic interaction of microalgae and fungi is beneficial in terms of maintaining the stability and development of the ecosystem; that's why they are abundantly used in treating wastewater, improving harvesting efficiency of microalgae and other fermentation applications by cultivating them in wastewater such as a study analyzed the interactive pattern of conidia with microalgae to assist microalgal biomass harvesting via algal-fungal co-cultivation. They studied more than one mechanism of attraction between microalgae and fungi, trapping, attachment of mycelia, and EPS secretion; among them, EPS secretion proved to be the best for symbiosis because EPS secreted from the fungal side has a specific ability of adsorption. Hence, their attachment facilitates the final harvesting process (Wang et al., 2023).

5.1.2 Parasitic interaction

In freshwater and marine ecosystems, one of the groups of fungi named chytridomycota is among the most prominent groups of parasites as they get to benefit from micro and macro-organisms present in their vicinity and alter the overall structure of the food chain only for the sake of nutrients (Kagami et al., 2014). For instance, a study observed their life cycle that showed their parasitic behavior both with Phyto and zooplankton at the zoosporic stage of life; at that stage, their spores move with the flowing water in search of a new host, and after getting the suitable host they make symbiotic association first. Then, at the mature sporangia stage, they become parasitic to produce zoospores again (Laundon et al., 2022).

5.1.3 Competitive interaction

Sometimes, when there are limited resources such as nutrients, physical or chemical factors, and most importantly, space, this is the moment when the co-existing species shift to competition for the sake of survival and similar to the microalgae-fungi interaction (Gutiérrez et al., 2016). It was studied that in marine ecosystems, microalgae or fungi, from their symbiotic association, start a competition for the limited available resources, and interestingly, fungi (chytridomycota) alter or reshape the physiology and structure of the microalgae community by increasing or decreasing the concentration of zoospores (Gutiérrez et al., 2016, Anabalón et al., 2007, Lauritano and Galasso, 2023).

Overall, the interactions between microalgae and fungi create diverse and resilient ecosystems that contribute to the functioning and stability of various habitats. Also, among all the interactions, microalgae-fungi interaction, specifically the mycospheres, is the best microbial association for ecosystem development.

Table 2 Algal-microbial interactions and their impact on growth and biochemical composition.

Algal Species	Microbial partner	Biomass production (g/L/d)	Protein (%)	Carbohydrate (%)	Lipid (%)	Reference
***Scenedesmus* sp.**	*Chlorella* sp.	0.12	--	--	--	(Hasan et al., 2021)
***Chlorella* sp. and *Scenedesmus* sp.**	*Azospirillum brasilense*	0.11 and 0.09	30.6 and 33.4	25.6 and 30.1	--	(Choix et al., 2023)
Chlorella vulgaris	*Ganoderma lucidum*	0.167	--	--	--	(Xu et al., 2021)
***Scenedesmus obliquus* .**	*Cunninghamella echinulata*	0.199	--	--	40.86	(Srinuanpan et al., 2018b)
C. vulgaris	*R. sphaeroides*	--	64	17	06	(You et al., 2021)
C. vulgaris	*Aspergillus* sp.	0.8	38.6	26.2	35.2	(Yang et al., 2019)

6. Factors affecting microalgae-microbial interactions

Several factors can influence the interaction between microalgae and other microbes. These factors significantly affect the nature and outcome of their interaction. Additionally, specific interactions can vary depending on the microalgae and microbial species involved and the environmental context in which they exist.

6.1. Nutrients availability

The available nutrients in the interactive environment of microbes significantly influence the microalgae-microbial interaction; for instance, if the nutrients are equally available to the microbes, there will be a mutualistic association, but if the nutrients are limited automatically, there will be competition between interacting species. The abundance and availability of these nutrients in the environment can shape the dynamics of their interaction. For example, a study reported that sudden changes in temperature and pH change the distribution of nutrients between co-existing species by increasing the growth of predators in the environment (Pleissner et al., 2020).

6.2. pH and Temperature

pH and temperature are the significant abiotic factors that influence the proliferation of microbes in their growth medium. Microalgae and other microbes are temperature and pH-specific; that's why their intra and inter-specific interactions vary or shift from cooperative to competitive or vice versa (Pleissner et al., 2020). Microalgae-microbial interaction either in their natural environment or cultivated by choice in wastewater or other growth media cannot be temperature or pH controlled; however, in rare conditions such as in indoor cultivation, these parameters can be controlled, and they significantly affect the pollutants up taking potential of microbes (Su et al., 2022).

6.3. Light intensity and quality

Microalgae, as photosynthetic microorganisms, demand an appropriate amount of light for their growth and energy production. Similarly, light intensity and quality play significant roles in microalgae-microbial interaction. If microalgae do not have sufficient light to produce oxygen, the interacting microbe will automatically outgrow by competing with microalgae. This will further affect the composition of the overall microbial community. (Sharma et al., 2022).

6.4. Oxygen level

Another environmental factor that greatly affects the association of microbes, especially with microalgae, is the level of oxygen, some microbes are anaerobic, so they depend on their interacting host for oxygen. At the same time, some are aerobic and hence negatively affected by the excess amount of oxygen in their environment. This is how oxygen levels alter the physiology and composition of the microbial community by either facilitating or inhibiting the interacting microbes. For instance, a study evaluates the positive impact of oxygen levels on microalgae-based microbial fuel cells and wastewater treatment by microalgae-microbial interaction, as microbial oxygen facilitates cathodic reactions in the daytime (Arun et al., 2020).

6.5. Environmental stressors

Environmental stressors such as salinity changes, temperature fluctuations, intense light, toxins, and pollutants greatly affect the microalgae-microbial interaction directly and indirectly. They have a direct impact on the survival of microorganisms and an indirect impact on their interacting mechanisms, as sudden changes in temperature and salinity with the release of toxins from other microbial communities in the environment will inhibit their growth because only a few microbes can be adapted to these fluctuations hence there will be a great change in the interacting ecosystem (Nagarajan et al., 2022).

6.6. Co-existence and competition

Microalgae-microbial interaction is stable only when they cooperate by equally distributing the available resources and contributing to the stability of their ecosystem. However, suppose they start the competition for the available nutrients, space, carbon dioxide, and organic matter. In that case, there must be one species that can thrive or outgrow and alter that community's overall structure and co-existing potential.

6.7. Genetic diversity of species

Genetic diversity is another factor that influences the interaction of microbes as different species have different traits and potential, so they have varying adaptability; some are cooperative but have a low potential of adaptation in a harsh environment, while some are competitive as they have high adaptability potential hence outgrow and change the composition and structure of the microbial community (Ayre et al., 2021). Genetic diversity helps microbes attract or repel each other and form variable interactive patterns (Zamorano-López et al., 2019).

7. Protection of the ecosystem by microalgae-microbial interaction

These interactions play a significant role in the bioremediation of wastewater, heavy metals removal, CO_2 sequestration, and biofuel and biofilm formation, providing a protective environment to the microorganisms that increase their ability to attach to the surface and colonize.

7.1. Bioremediation of wastewater

Due to increasing anthropogenic activities such as industrial wastes, urbanization, and agricultural activities, serious health and environmental issues are posed. One of the significant threats this scenario is posing to the environment is eutrophication leading to algal blooms, oxygen depletion, and destruction of aquatic life and the freshwater ecosystem (Renuka et al., 2013). Conventional wastewater treatment methods are not effective and several studies reported the potential of microalgae-microbial interactions and their applications in the industry (Wang et al., 2016). Microalgae-microbial interaction plays a significant role in the bioremediation of wastewater, especially in high-rate algal ponds, as it addresses issues of contamination and degradation of complex compounds and naturally occurring naturally in the environment.

7.1.1 Role of microalgae-bacterial Interaction

Microalgal-bacterial interactions are helpful in bioremediation and pollutant removal of wastewater **(Table 2)**. Literature has reported the potential of the symbiotic interaction of bacteria and microalgae. The symbiotic relationship works as bacteria use organic compounds as carbon sources released by photosynthetic microalgae. In return, bacteria release carbon dioxide, which the microalgae use for photosynthesis, as shown in **Fig. 2**. This cooperative interaction is more complex than nutrient removal as both synergistically improve growth by releasing extracellular polymeric substances such as siderophores and vitamins (Subashchandrabose et al., 2011).

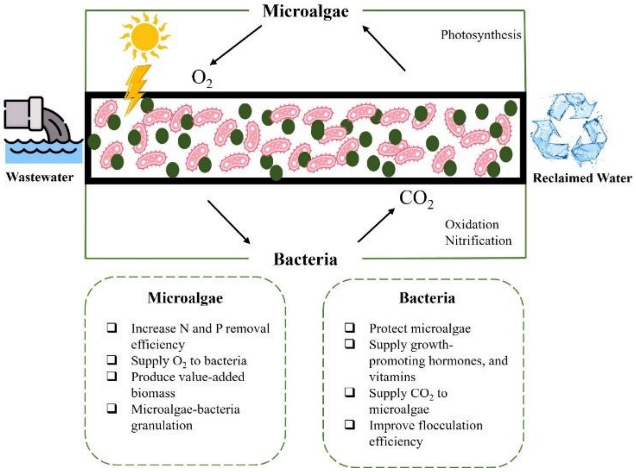

Fig. 2. Microalgae-bacterial interaction helps each other for growth and wastewater treatment.

A study reported that the co-cultivation of the microalgae species *Chlorella vulgaris C. sorokiniana* and *Azospirillum brasilense* efficiently remove the nutrients from the wastewater as well as enhances biomass production, and reduces the cost of aeration and greenhouse effect became negligible as the system carbon neutral as microalgae utilize the carbon dioxide released by the bacteria (De Godos et al., 2009). Apart from the advantages, some limitations are still observed in high-rate algal ponds, including light penetration, which disturbs the bacterial respiration and oxygen production by microalgae and the harvesting of microalgae. Therefore, the literature suggested the cultivation of consortiums in closed photobioreactors for municipal wastewater treatment.

Few studies reported the application of these consortiums in immobilized growth systems. They reported using a biofilm reactor to treat primary treated wastewater using the native microalgal-bacterium consortium isolated from the centrate wastewater. The removal efficiency of TN, TP, and TOC was 70, 85, and 90% respectively (Posadas et al., 2013).

A major problem related to microalgae cultivation is the harvesting of microalgal cells which increases the cost of the system. Keeping in view some studies employed the use of microalgal-bacterial flocs composed of native bacteria and *Chlorella* sp., *Pediastrum* sp., *Phormidium* sp., and *Scenedesmus* sp. consortium to treat primary treated municipal wastewater. The results suggested that these microalgal-bacterial flocs removed 61.2% and 56.8% of TN and PO4-P (Posadas et al., 2013, Van Den Hende et al., 2011).

Table 2. Microalgal-bacterial interaction for bioremediation and pollutant removal from wastewater.

Microorganism	Wastewater	Operation Mode	COD (%)	TN (%)	TP (%)	References
C. vulgaris & endophytic bacteria	Biogas slurry	Batch mode	88.29	88.31	88.21	(Xu et al., 2020)
Scenedesmus obliquus & *Acinetobacter pittii*	Synthetic wastewater	Batch mode	--	85.90	91.50	(Russel et al., 2020)
C. vulgaris & activated sludge bacteria	Dairy digestate	Airlift PBR	85	86.12	--	(Feng et al., 2020)
Pantanalinema sp. & wastewater-borne bacteria	Synthetic wastewater	Glass reactor	--	--	86	(Ji et al., 2020)
Chlorella with granule sludge bacteria	Synthetic domestic wastewater	Column-type PBR	95	80-84	79.1	(Zhang et al., 2022)
Chlorella sp. with activated sludge bacteria	Synthetic wastewater	Membrane aeration system	--	90	80	(Zhang et al., 2020c)
Chlorella sp. with activated sludge	Simulated wastewater	Sequencing batch reactor	100	53.85	85.13	(Huang et al., 2023)
C. vulgaris with *R. sphaeroides*	Piggery and Starch wastewater	--	97	95	96	(You et al., 2021)
Microalgal consortium & activated sludge	Synthetic wastewater	Membrane reactors	95	34.3	32.6	(Sun et al., 2020)

Microalgae-bacterial interaction also promotes the extent of nitrification by cultivation of microalgae consortium with nitrifying bacteria communities (Bankston et al., 2020). A study demonstrated the impact of microalgae cultivation on the bacterial treatment of poultry anaerobic digestate, and results suggested that the co-cultivation of activated sludge with *Chlorella sorokiniana* improves the nitrates production by nitrification 2.7 times greater than monoculture of activated sludge microbial community. Moreover, the results suggested that there was no nitrite in the co-culture, indicating the complete nitrification occurring in the system, and the study hypothesized that the microalgae produce the dissolved oxygen above saturation that supports the nitrification reaction (Bankston et al., 2020).

Ammonium concentration is an important factor in microbial interaction as under low ammonium microalgae could negatively impact the nitrifying bacteria (Tiron et al., 2017). Ecological literature reported that it is one of the major factors causing the negative interaction. On the other hand, numerous ecological studies reported the positive interaction of nitrifying bacteria and microalgae in an adequate amount of ammonium (Su et al., 2012).

7.1.2 Role of microalgae-fungal interaction

Microalgae and fungi formed all kinds of symbiotic interactions that are recognized in nature, such as parasitism, commensalism, and mutualism (Ashraf et al., 2022). However, few studies have reported that the chemical ecology that regulates the microalgae-fungi interaction and their synergistic interaction can play a significant role in the bioremediation of wastewater **(Table 2)**. Photosynthetic microalgae utilize the CO_2 produced by the fungi through respiration and symbiotically degrade the complex organic compound into simpler compounds **(Fig. 3)**.

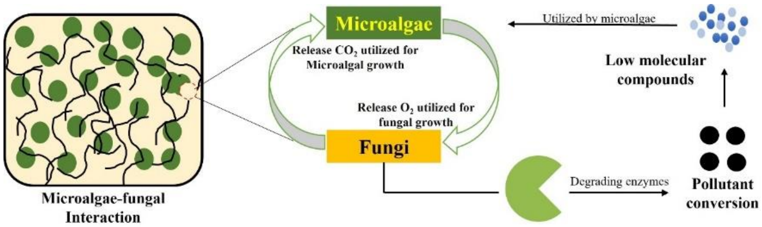

Figure 3. Microalgae-fungal interaction plays a significant role in the bioremediation of wastewater.

A study reported that the co-cultivation of microalgae and yeast significantly increases biomass production and value-added compounds. Microalgae utilize the CO_2 produced by yeast and produce O_2 that helps to facilitate heterotrophic metabolism (Lutzu and Dunford, 2018). Several studies have reported that this interaction communicates through quorum sensing, but more information is still needed. Co-cultivation of microalgae and fungi works more efficiently for nutrient recovery of organic and inorganic compounds from the wastewater than monoculture A study reported that co-cultivating *Chlorella vulgaris* and *Aspergillus* sp. in a photobioreactor system significantly removed 70.34% in COD, 44.68% in TN, and 84.79% in TP from swine wastewater (Zhou et al., 2012).

Harvesting microalgae cells is a severe challenge in algal cultivation due to small particle size, and to solve this problem, fungal-assisted flocculation can be applied. Numerous fungal species have been reported for efficient algal harvesting named as *Rhizopus* sp., *Penicillium* sp., *Aspergillus* sp., *Trichoderma reesei*, *Cladosporium cladosporoides*, and *Ganoderma sp*., and interestingly, these strains form biomass pellets at a particular phase of their growth (Singh et al., 2022).

Table 3. Microalgae-fungi interaction in bioremediation of wastewater and pollutant removal.

Microorganism	Wastewater	Operation Mode	COD (%)	TN (%)	TP (%)	Reference
Scenedesmus sp. & *Trichoderma reesei*	Secondary effluent	PBR	74	44	93	(Srinuanpan et al., 2018a)
C. vulgaris & *Ganoderma lucidum*	Biogas slurry	PBR	81.06	82.32	82.98	(Yang et al., 2022)

C. vulgaris & *Aspergillus sp.*	Swine manure	PBR	70.34	44.68	84.70	(Zhou et al., 2012)
C. pyrenoidosa & *Aspergillus oryzae*	Starch wastewater	PBR	92.08	83.56	96.58	(Wang et al., 2022)
C. variabilis & *Ganoderma lucidum*	Synthetic wastewater	PBR	75.5	76.7%	74.7	(Jiang et al., 2019)

8. The positive impact of microalgal-microbial interaction on the ecosystem

These interactions have been studied in different environmental, industrial, and agricultural applications.

8.1. Environmental applications of microalgal-microbial interaction

8.1.1 Wastewater treatment

Water is the basic need for survival and a crucial earth resource. The world faces water scarcity due to unplanned population growth and urbanization. The continuous discharge of wastewater containing a heavy number of emerging contaminants or pollutants makes the availability of freshwater a future global challenge. Integrating microalgal systems within wastewater treatment plants is an efficient technology.

Microalgae were found to reduce the concentration of inorganic compounds, heavy metals, and emerging contaminants from industrial wastewater (Sforza et al., 2020). Microalgae have the potential to utilize these nutrients from the wastewater for their growth. Microalgal systems use three major pathways to bioremediate pollutants: biosorption, biodegradation, and bioadsorption. The main advantage of using microalgal systems for bioremediation is the ability to recover the resources for reuse through biorefinery of algal biomass for value-added products such as animal feed, fertilizer, biofuel, and bioplastics (Sutherland and Ralph, 2019).

Monocultures are helpful in wastewater treatment, but polycultures (microalgae-microalgae consortium) have been reported as more useful due to their high nutrient utilization efficiency along with high biomass production. Additionally, the symbiotic relationship between the microalgal-bacterial consortium and microalgal-fungal consortium is considered a promising strategy for wastewater treatment because it utilizes nutrients more efficiently and quickly.

8.1.2 Carbon sequestration

The application of microalgal systems in carbon fixation along with wastewater treatment has been considered a promising technique. The atmospheric carbon is increasing day by day due to human activities. So, there is a need to fix more and more carbon through biological systems. Microalgal systems fix the inorganic carbon from the atmosphere into organic compounds that store chemical energy. Microalgal culture is a viable technology for CO_2 capture from the environment due to its photosynthetic potential (Kong et al., 2021).

8.1.3 Ecosystem stability and habitat formation

Microalgal systems provide a habitat for aquatic microorganisms; they support their growth and survival, which can affect the marine ecosystem. Studies showed that algal systems or communities have a significant impact on the food web and ecosystem. When microalgae consortium works together, it forms colonies, biofilms, and mat-like structures, which provide sites for attachment or shelter for various organisms. These structures are helpful to enhance the diversity of the ecosystem and develop microhabitats. These microhabitats support the reproduction and survival of various organisms such as fish, microbes, invertebrates, and zooplankton (Nava and Leoni, 2021).

8.2. Industrial applications of microalgae-microbial interaction

8.2.1 Biofuel production

It has been reported that microalgae can utilize solar energy and fix CO_2 at a frequency 10-50 times higher than plants. Higher levels of carbon dioxide can stimulate the growth of microalgae, it accounts for almost half of the dry weight of algal biomass.

Biomass can also attain high productivity of organic compositions which can be converted into biofuel or high-value chemicals. Based on different biomass transformation methods like pyrolysis, gasification, fermentation, and solvent extraction, microalgae can be converted into various sustainable biofuels such as biohydrogen, biogas, biodiesel, and biocrude (He et al., 2023). The biochemical composition of microalgal biomass makes it suitable for future applications—a high concentration of lipid content in biomass results in high biofuel yield.

8.2.2 Pharmaceuticals

Algal biomass produced from different algal-microbial systems is used for pharmaceutical applications like antibiotics, anti-inflammatory agents, and anticancer drugs. Algae contain bioactive compounds such as pigments, proteins, and polysaccharides, which have specific therapeutic properties (Jacob et al., 2021). The presence of bioactive compounds in algae is to be expected due to the cooccurrence of these organisms in natural aquatic communities, where an inhibitory interaction occurs between competitors and producers within the same habitat. Various strains of cyanobacteria and microalgae produce extracellular and intracellular metabolites with multiple biological activities such as antiviral, antifungal, antialgal, and antibacterial. (Priyadarshani and Rath, 2012).

8.2.3 Aquaculture feed

Aquaculture is a speedily growing chain in the food industry that is being directed by increased human consumption as increasing demand for fish meat has risen in the last ten years (Štěrbová et al., 2023). Algae can provide a food source for fish, while bacteria and fungi can help maintain the waste and water quality. Algal-fungal interactions can produce novel food products with high nutritional and functional properties. Fungi can also help to increase algae's protein content and digestibility, and algae can provide a source of minerals, vitamins, and antioxidants. Algal biomass produced from different algal systems can be used as feed for aquatic animals. It is mainly useful at the larvae and juvenile finfish stages and for raising the zooplankton required for juvenile animals. Mostly *Chlorella, Tetraselmis*, *Chaetoceros, Thalassiosira,* and *Spirulina* are used as feed for fish, poultry, and ornamental birds. Usually, *Tetraselmis* and *Thalassiosira* are used as feed for larvae. Several companies produce aquaculture feeds by using *Chlorella* and *Spirulina*. Over the last four decades, several microalgal species have been tested as food, but presumably, less than 20 have gained widespread use in aquaculture (Priyadarshani and Rath, 2012).

8.3. Agricultural applications of microalgae-microbial interaction

8.3.1 Biofertilizer

Algal biomass is utilized as a fertilizer, improving plant growth and nutrient uptake. The microalgae assimilate the nitrogen and phosphorus in biomass, which is used as a biofertilizer, and minimize mineral fertilizers and sewage disposal. The availability of nutrients such as nitrogen, phosphorus, and potassium directly influence agricultural efficiency. The algal biomass obtained after phycoremediation can replace mineral fertilizers and improve soil quality and crop productivity (Sharma et al., 2021). Biofertilizers also help secrete plant growth hormones and alleviate the adverse effects of synthetic fertilizers. The microalgae have been reported to comprise several plant-growth-promoting substances such as polysaccharides, proteins, phytohormones, and lipids (Silambarasan et al., 2021).

8.3.2 Disease suppression and plant protection

The bioactive compounds in the biomass have some unique antimicrobial properties that can help combat plant pathogens. The symbiotic interactions between algae and other microbes provide an eco-friendly approach to disease suppression and reduce the dependency on chemical pesticides. Microalgae are regarded as valuable resources for plant improvement due to the presence of mineral substances such as amino acids, pigments, vitamins, and plant growth regulators.

8.3.3 Water management and irrigation efficiency

Phycoremediation of wastewater and its judicious utilization as a source of irrigation is the need of today to meet the demand for water sustainability and resource-efficient agricultural system. Microalgal systems can be employed in water management strategies in agriculture. Bacteria and fungi associated with algae assist in excessive nutrient utilization like nitrogen and phosphorus, present in irrigation water, thereby mitigating water pollution and eutrophication (Sharma et al., 2021) .

Table 3. The positive impact of microalgal-microbial interaction on the ecosystem.

Impact on ecosystem	Algae-microbial interactions	Strains in consortium	Applications	References
Environmental	Algae-algae	*Scenedesmus* sp. and *Chlorella* sp.	Bioremediation, wastewater treatment, carbon fixation, ecosystem establishment	(Lin et al., 2022, Amin et al., 2022, Hasan et al., 2021)
	Algae-bacteria	*Beijerinckia fluminensis,* and *Chlorella* sp.		
	Algae-fungi	*Chlorella* sp. and *Aspergillus niger*.		
Industrial	Algae-algae	*Selenastrum minutum* and *Scenedesmus dimorphus*	Used as feed, biofuel production, pharmaceuticals	(Amin et al., 2022, Liu et al., 2018, Wu et al., 2023)
	Algae-bacteria	Algae-bacteria granular consortium		
	Algae-fungi	*C. vulgaris* and *Yarrowia lipolytica*		
Agricultural	Algae-algae	Consortia of *Nostoc* and two *Anabaena* strains	Rice crop, biofertilizer, enhanced crop yields, and soil fertility	(Renuka et al., 2018, Fallahi et al., 2021a, Lin et al., 2022)
	Algae-bacteria	*Pseudomonas putida* and *C. vulgaris*		
	Algae-fungi	*Trichoderma reesei* and *Scenedesmus* sp.		

9. Challenges and future directions

Despite all of this, our knowledge of the specific mechanisms and pathways through which microalgae and microbes interact is still limited. The complexity of these interactions at the molecular level remains unclear, being unable to utilize these interactions or relationships for practical applications. As well as issues related to large-scale applications such as maintaining stable microbial consortia and ensuring consistent performance need to be addressed. As reported, the economic feasibility of using microalgae-microbial consortium in the industrial sector is currently unknown. Specifically, the interaction of microalgae with bacteria and fungi is still not fully understood. Particularly due to many heterotrophic bacteria, fungi, and photosynthetic microalgae are yet uncultured. Consequently, it is challenging to comprehensively demonstrate their roles in ecosystem-wide processes such as metabolic pathways and nutrient cycling.

Accordingly, the advent of omics technologies (metabolomics, proteomics, and genomics) can help us to understand the molecular mechanisms of interactions. By identifying important pathways and regulatory networks, this knowledge could help to optimize microbial consortia for specific applications. Also implementing pilot scale studies can help bridge the gap between lab-scale studies and real-world applications. This can provide valuable data on economic viability, stability, and performance. Explore other microalgae microbial species that will help uncover novel interactions and synergies, potentially leading to adaptable and robust biotechnological applications.

10. Conclusion

Ecosystem development depends on the interaction of living organisms with each other and their environment. However, interactions may vary depending upon the acceptability of the host and incoming population or community. The same applies to an ecosystem where microalgae symbiotically interact with other microalgae or bacteria, giving rise to a biofilm via cell-to-cell interaction. Still, sometimes, when microalgae outgrowth destabilizes the ecosystem, bacteria compete with algal cells to protect it and maintain its sustainability, such as degradation of algal blooms. Similarly, a symbiotic interaction between microalgae and fungi also leads towards lichenization, and this is how a stable ecosystem develops through different microbial interactions. Furthermore, microbial consortia can enhance the efficiency of wastewater treatment processes by synergistically degrading organic pollutants and reducing nutrient loads. This holistic approach advances our understanding of microbial ecology and offers practical pathways toward long-term environmental sustainability.

Conflict of Interest

The authors have no conflicts of interest to declare.

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