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Review Article

Bacteria and microalgae associations in periphyton—mechanisms and biotechnological opportunities

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Abstract

Phototrophic and heterotrophic microorganisms coexist in complex and dynamic structures called periphyton. These structures shape the biogeochemistry and biodiversity of aquatic ecosystems. In particular, microalgae–bacteria interactions are a prominent focus of study by microbial ecologists and can provide biotechnological opportunities for numerous applications (i.e. microalgal bloom control, aquaculture, biorefinery, and wastewater bioremediation). In this review, we analyze the species dynamics (i.e. periphyton formation and factors determining the prevalence of one species over another), coexisting communities, exchange of resources, and communication mechanisms of periphytic microalgae and bacteria. We extend periphyton mathematical modelling as a tool to comprehend complex interactions. This review is expected to boost the applicability of microalgae–bacteria consortia, by drawing out knowledge from natural periphyton.

Keywords: biofilm, biotechnological applications, ecological interactions, microalgae–bacteria consortia, periphyton

Introduction

All water-immersed surfaces (natural or artificial) are swiftly colonized by a diversity of microorganisms forming biofouling or biofilm (Fig. 1A and B) (Mieszkin et al. 2013, Mantzorou and Ververidis 2019). Thus, in aquatic environments, the majority of microorganisms live attached to surfaces as biofilm in complex and heterogeneous sessile communities (Battin et al. 2016). Common substrata for biofilm formation include submerged macrophytes, sediments, and rocks (Saikia et al. 2013, Gulzar et al. 2017). Biofilm formation is advantageous as it helps in the heterologous adhesion and interaction between microorganisms, and provides a protective environment from a variety of harsh conditions (e.g. exposure to UV irradiation, shear stress, nutrients limitation, toxic metals, and antimicrobial agents), thus providing an edge over cells in the planktonic state (Hall-Stoodley et al. 2004, Battin et al. 2016, Gómez-Ramírez et al. 2019). In these dynamic microbial assemblies, bacteria are usually the primary colonizers, establishing the first layers of a biofilm (Goecke et al. 2013, Mieszkin et al. 2013). The bacterial biofilms moderate the recruitment of algae, fungi, protozoa, and invertebrates, mainly through the production of extracellular polymeric substances (EPS) (Hall-Stoodley et al. 2004, Celler et al. 2014, Battin et al. 2016, Yong et al. 2021). The inherent dynamic character and high complexity are driven by the heterogeneous microbial composition and exposure to a diversity of environmental conditions, such as temperature, nutrients, shear stress, irradiation, and anthropogenic impacts (Murakami et al. 2009, Baba et al. 2011, Ferragut and de Campos Bicudo 2012). Such complex sessile communities have been labelled as periphyton, phototrophic biofilm, epiphytic biofilms, microfouling, stream biofilm, marine biofilm, or microalgal biofilm (Hall-Stoodley et al. 2004, Salta et al. 2013, Battin et al. 2016, Mantzorou et al. 2018, Lamprecht et al. 2022).

As part of the periphyton community, microalgae and bacteria cohabit in a mutually reliant arrangement that provides space and resources for both to thrive (Carr et al. 2005). Besides, both groups of microorganisms have an important role in the aquatic ecosystem and are prominent planktonic microorganisms of aquatic systems (Pushpakumara et al. 2022). Microalgae form the basis of marine and freshwater food webs, as primary producers, play an important role in the remediation of aquatic pollutants and contribute to minimizing the effects of global warming, either within the periphyton or as plankton (Vadeboncoeur et al. 2014, Battin et al. 2016, Zhou et al. 2016, Gómez-Ramírez et al. 2019). Moreover, microalgae have a diversity of biotechnological applications, from wastewater treatment, CO_2 sequestration, biofuel production, and the synthesis of valuable bioproducts (Gómez-Ramírez et al. 2019, Zhang et al. 2020, Yong et al. 2021). In this review, eukaryotic microalgae, diatoms, and prokaryotic microalgae (cyanobacteria) are all included under the term 'microalgae', since they are all photosynthetic. The term 'algae' includes

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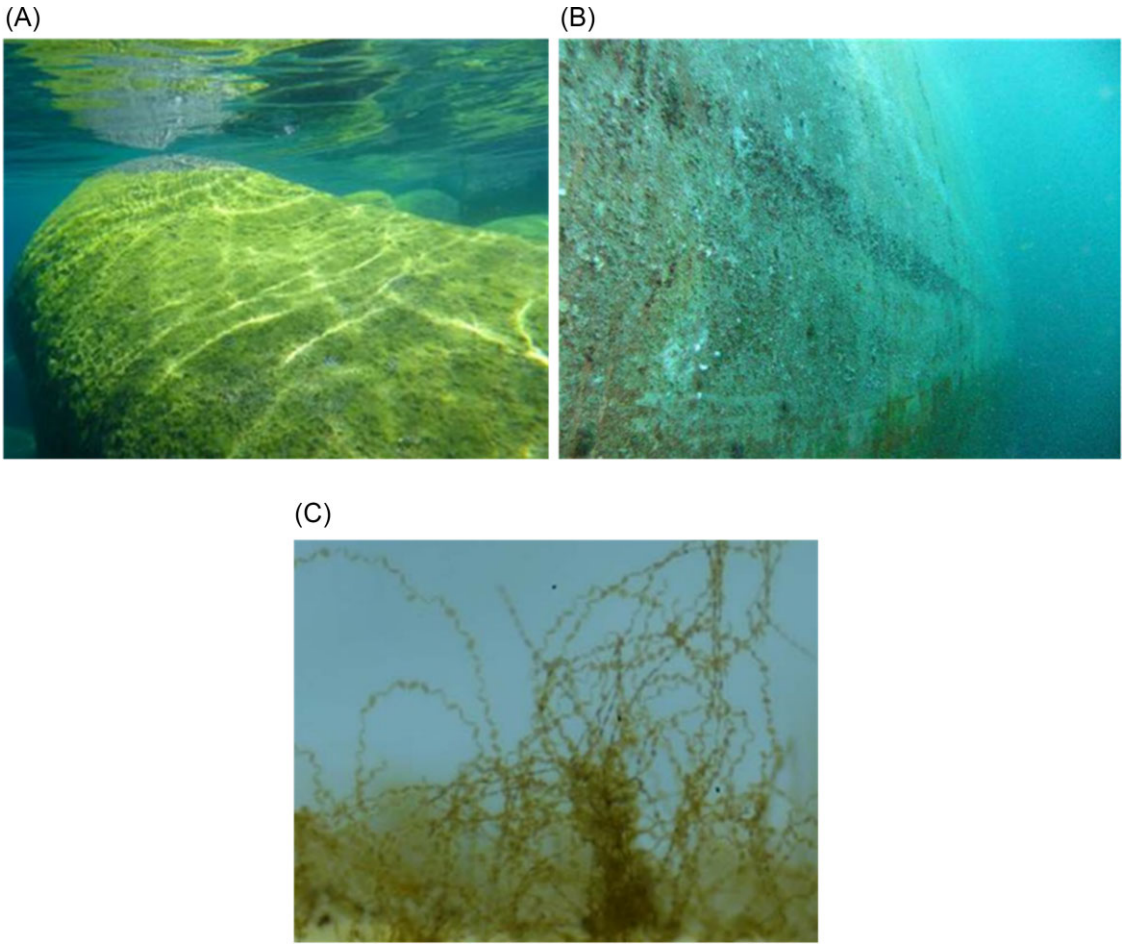

Figure 1. Periphyton development. **(A)** Periphyton growth on rocks (natural surface) in a freshwater environment. Image reprinted with permission from Atkins et al. (2021); **(B)** Periphyton growth on a ship hull (artificial surface) in a marine environment—until recently biofilms have been considered an obstacle since the development of a biofilm in ships hinders the hydrodynamic performance, increasing fuel consumption (Salta et al. 2013, Mantzorou and Ververidis 2019). Image reprinted with permission from Chen et al. (2020); **(C)** *Diatoma* spp. as entangled zigzagging chains that can serve as a scaffold for bacterial growth. Image reprinted with permission from Celler et al. (2014).

macroalgae. When considered pertinent the terms 'diatoms' and 'cyanobacteria' are specified.

Bacteria are unavoidably present in microalgal-biofilm systems (whether from wastewater or airborne bacteria) and interact with microalgae (Hu et al. 2021). In recent years, consideration of the presence of bacteria in these processes has evolved from a 'contamination' to an opportunity to enhance the biotechnological applications of microalgae (Ramanan et al. 2016). The ecological interactions established between these two types of microorganisms cover a wide range of relationships, from mutualism to competition (Ramanan et al. 2016, Zhang et al. 2020). Xia et al. (2020) analysed the community composition and correlations between bacteria and microalgae within periphyton on submerged macrophytes. These authors observed that while positive correlations dominate (68%) the periphyton. The production of allelochemicals, the competition for substrate, and the changes in pH due to microalgae respiration promoted negative correlations.

Bacteria can grow on microalgae surfaces, in a phycosphere (Fig. 2) (Bell and Mitchell 1972). This microenvironment around a unicellular alga serves as an interface for tight relationships and provides a beneficial habitat for bacterial growth, improving the consumption of nutrients, response to fluctuations in environmental conditions, resistance to toxic compounds, and protection from unwanted microbial invasion (Goecke et al. 2013, Mieszkin et al. 2013, Zhang et al. 2020). Additionally, the presence of bacteria improves the remediation of contaminants and bioflocculation. Wastewater treatment may benefit from the use of consortia formed by bacteria and microalgae, increasing the removal of emerging contaminants (Sousa et al. 2023) or helping in sludge removal through bioflocculation (Sátiro et al. 2022). This cooperative interaction between phototrophic and heterotrophic microorganisms is coherent with the Black Queen hypothesis (BQH) (Gubelit and Grossart 2020). The BQH suggests that cooperation between organisms results from coevolution and loss of gene mutations. It is postulated that coadaptation between algae and their microbiomes, with reciprocal adaptive interactions, produces high levels of specific interactions. These relationships are strengthened by horizontal gene transfer (HGT), which certainly determined many of the available evolutionary traits (Amin et al. 2012).

Microbial studies of aquatic systems are typically focused on phytoplankton (Zhou et al. 2016, Martin et al. 2021). Nevertheless, as a shelter for phototrophic and heterotrophic microorganisms, periphyton is an important player in biogeochemical cycles and primary production. Periphyton creates a zone of intense enzymatic and metabolic activity in aquatic systems, have a key role in water quality by removing pollutants, and are important indicators of ecosystems health (Wetzel 1963, Evans 2000, Saikia et al. 2013, Battin et al. 2016, Ma et al. 2018, Atkins et al. 2021).

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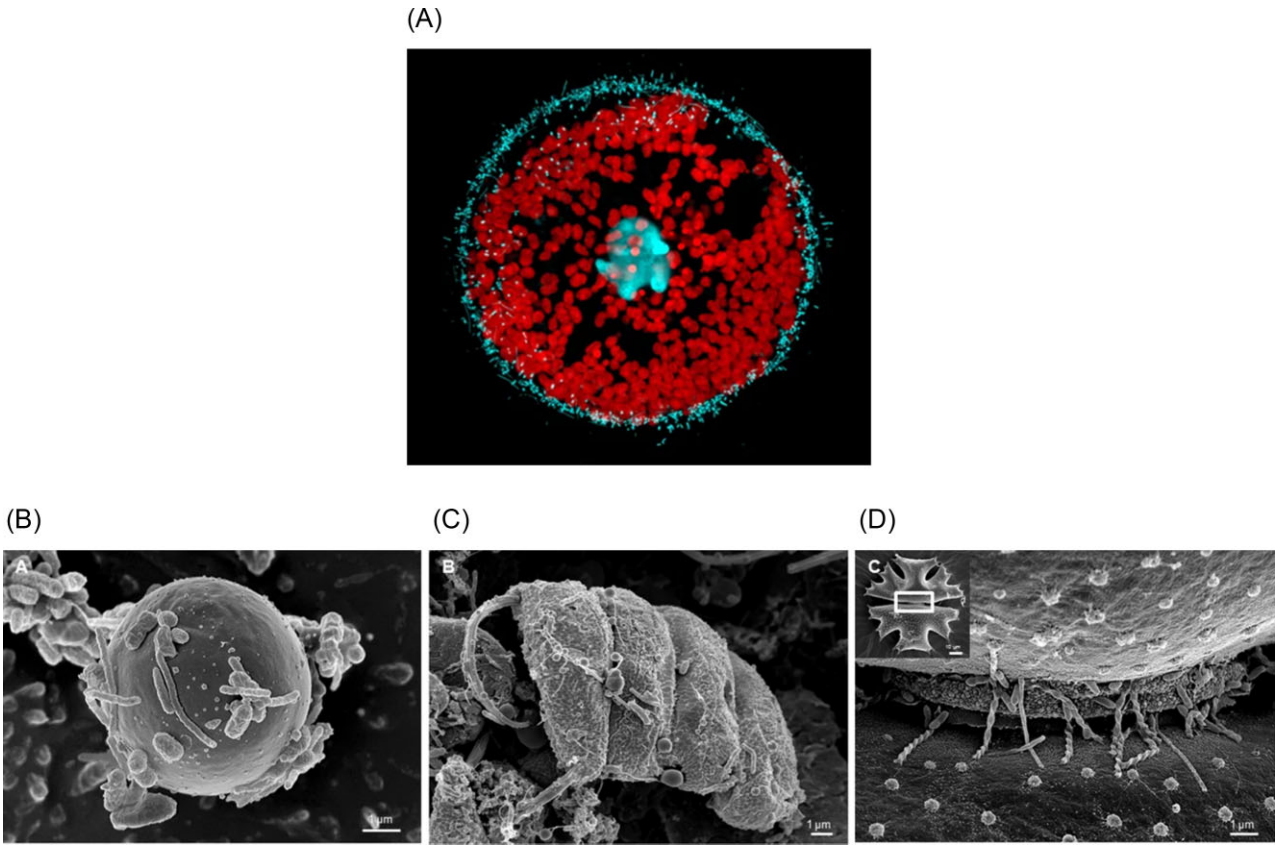

Figure 2. Microscopic observations of the interactions between microalgae and bacteria (phycosphere). **(A)** Confocal microscope observation of the surrounding phycosphere of the diatom *Coscinodiscus* (red, 90 μm across). DNA of the bacteria and microalgae is dyed in blue (British Phycological Society 2020). Image by Davis Laundon and The Marine Biological Association of the UK; **(B)**–**(D)** SEM observation of the microalgae *C. saccharophila*, *S. quadricauda*, and *M. cruxmelitensis*, respectively, with the associated bacteria community. Images reprinted with permission from Krohn-Molt et al. (2017).

Recent advances in OMICS technologies (genomics, metaproteomics, metabolomics, and so on) and new concepts (i.e. phycosphere, interkingdom quorum-sensing—QS, and the BQH) and tools (imaging, modelling, and simulation) are relevant to help to unravel the unknown mechanisms involved in microbial interactions (Zhou et al. 2016, Seymour et al. 2017, Gubelit and Grossart 2020). Tackling the complexity of the interactions between microalgae and bacteria in periphyton is challenging, but once it has been addressed, what knowledge can we withdraw? (Table 1).

In this review, the current knowledge of the associations between microalgae and bacteria in aquatic periphyton is described, with a focus on the development of sessile communities (in the sections 'Periphyton formation' and 'Factors governing species prevalence and the periphyton structure'), microbial biodiversity (in the section 'Functional aspects and biodiversity'), and metabolic exchanges (in the section 'Metabolic exchange and communication'). Furthermore, mathematical models of the microbial interactions established in periphyton (in the section 'Mathematical modelling of periphyton') are described and biotechnological opportunities to be explored from these microbial associations are highlighted (in the section 'Biotechnological applications of periphyton').

Assembly and evolution of a microalgae–bacterial community

A diversity of factors can impact the community assembly and structure, from the species present in the habitat (including their concentration, order of arrival, and competition for resources) to the fluid dynamics (Hall-Stoodley et al. 2004, Lamprecht et al. 2022). The knowledge of species succession is limited, but significant to solve problems associated with some assemblages, such as the presence of undesirable organisms or biofouling (Pollet et al. 2018). To address this problem, some key questions emerge: What are the stages of periphyton formation, and the main species involved? What factors define the prevalence of certain species in the determent of another? What is the structure of such biofilms? This section will address these questions.

Periphyton formation

The first step in periphyton development is the conditioning of the surface by the adsorption of dissolved organic substances (Wu 2016). Axenic microalga biofilms rarely exist in aquatic environments, where bacteria are typical periphyton colonizers (Jordan and Staley 1975, Mantzorou et al. 2018, Moreno Osorio et al. 2021). Hodoki (2005) tested in an outdoor artificial stream and observed that a dense bacterial biofilm promoted the migration of microalgae from the water phase (flowing water above the biofilm) to the periphyton. Several bacteria have been described as primary colonizers. Periphyton starters were found to belong to the *Sphingomonas* genus (e.g. *Sphingomonas elode*, an EPS-producing bacterium) (Battin et al. 2016). *Alteromonas* and *Roseobacter* species were also described as primary colonizers (Salta et al. 2013). Xia et al. (2020) observed that in periphyton development on submerged macrophytes, the most abundant bacteria tolerated environmental stress and produced EPS (i.e. *Exiguobacterium*, *Pseudomonas*, and *Chryseobacterium* species). This initial layer of cells

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Table 1. Potential expertise to be acquired from a complete understanding of periphytic microalgal–bacterial interactions.

Outcomes from microalgal–bacterial interactions	References
Periphyton can alter the dynamics of aquatic environments (e.g. hydrodynamic conditions, chemical gradients, and food chains), so they can help comprehend the energy fluxes and productivity of the aquatic ecosystem	Larned (2010), Battin et al. (2016), Pushpakumara et al. (2022)
Insights into the interactions established in microfouling and macrofouling can help predict and control the settlement and structure of biofouling, which can aid in the development of nonbiocidal antifouling technologies to apply in aquatic infrastructures (i.e. ship hulls)	Evans (2000), Mieszkin et al. (2013), Salta et al. (2013)
Microalgae provide an environment for bacterial growth and therefore can assist in the discovery of new bacterial species	Goecke et al. (2013), Pushpakumara et al. (2022)
Discovering QS inhibitors from algal sources can provide an opportunity to develop agents for the control of sessile bacteria	Mieszkin et al. (2013)
Serve as an ecological indicator and help predict the response of aquatic systems to changes in the environmental conditions, for instance, man-made factors such as global warming and chemical contamination from wastewater treatment plants or agriculture. Nutrient (P and N) enrichment of aquatic bodies is expected to cause excessive periphyton growth in 31% of the discharge areas, which can be linked to eutrophication, reducing the quality of freshwater systems and impairing biodiversity and ecosystems function	Baba et al. (2011), Goecke et al. (2013), McDowell et al. (2020), Lamprecht et al. (2022)
Periphyton is the base of the aquatic food chain. So, understanding the effects of emerging contaminants and metals on these communities (ecotoxicological risk assessment) can help to perceive their impact on a particular threatened ecosystem	Miazek and Brozek-Pluska (2019), Doose et al. (2021)
Insights into the interactions could boost the applicability of the wide range of biotechnological applications of microalgae–bacteria consortia, e.g. environmental remediation and biorefinery (Lamprecht et al. 2022). Bacterial contamination in these systems can be leveraged to promote mutualistic relations	Hu et al. (2021)

allows the subsequent adhesion of phototrophic microorganisms, that further multiply and produce EPS (Lamprecht et al. 2022). However, depending on the irradiation levels, microalgae, mainly diatoms (i.e. *Achnanthidium pyrenaicum)*, can play a primary colonizer role, forming the first layer of cells in periphyton (Battin et al. 2016, Moreno Osorio et al. 2021, Lamprecht et al. 2022). A study of the plastisphere (environment around plastic debris) has shown that diatoms were present in the initial stages of biofilm development (Amaral-Zettler et al. 2020). Nevertheless, a surface with wrinkles and porousness boosts the adhesion of other microalgae due to the higher surface area and protection from hydrodynamic stress (Gómez-Ramírez et al. 2019). The selection of an adequate surface material, starter microbial density, and environmental conditions is fundamental to developing a robust microalgal biofilm for any biotechnological application (Hu et al. 2021).

With enough light irradiation, microalgae will dominate the developing periphyton, particularly green microalgae (*Scenedesmus*, *Characium*, and *Chlorococcum*) or diatoms (*Cocconeis* and *Navicula*) (Vermaat 2005). Diatoms have an important role in the architecture of biofilms, due to their ability to adhere to surfaces and form entangled chains, which allows the establishment of a scaffold/physical structure for growth (Fig. 1C) (Battin et al. 2016). The chains improve nutrient uptake, protect against grazing and reduce sinking, explaining why diatoms have been so successful in colonizing most aquatic ecosystems (Celler et al. 2014). In a later stage, other microorganisms colonize the developing sessile structure, including filamentous and stalked diatoms (*e.g.Achnanthes*, *Gomphonema*, and *Cymbella*), other green microalgae (e.g. *Ulothrix* and *Oedogonium*) and cyanobacteria (e.g. *Lyngbya*, *Oscillatoria*, and *Calothrix*) (Vermaat 2005). This dense layer (centimetres thick) overshadows the inside of the periphyton and, thus, the deeper layers suffer from irradiation limitation and can induce detachment (Asaeda and Son 2000, Vermaat 2005). The biofilm formation culminates with the colonization of macroorganisms (macrofouling), in an epibiotic process, that can be unfavourable due to limiting access to irradiation and resources (Salta et al. 2013). Furthermore, being the basis of food chains, periphyton suffers from grazing by higher trophic level organisms (i.e. gastropods, crustaceans, and fish), influencing the structure of periphyton (Vermaat 2005, Battin et al. 2016). Figure 3 schematizes the steps generally involved in periphyton formation. While some authors describe that a biofilm requires a surface (Schmeisser et al. 2017), a new definition for 'biofilm' has been emerging to include both surface-attached and unattached biofilms, i.e. to include floccules/flocs/aggregates of microorganisms attached by EPS (Kublanovskaya et al. 2020, Moreno Osorio et al. 2021). Sauer et al. (2022) defend that the typical five-step formation model does not necessarily occur in sequence and does not capture the complexity of bacterial biofilms observed in a real scenario such as the variety of structures observed, the continuous exposure to new colonizers, nor considers nonsurface attached biofilms. The authors propose a conceptual open system model with three events: (i) aggregation and attachment: bacteria produce EPS and aggregate to each other, either attached to surfaces or forming floccules; (ii) growth and accumulation: attached biofilms and floccules grow by recruiting cells from the environment; and (iii) disaggregation and detachment: bacteria can transfer from the attached biofilm to the water phase as floccules or single planktonic cells. This is a more dynamic model that considers that new bacteria can colonize the biofilm at any point and that the attached and nonattached pathways interact. Here, we propose that this model can be applied to multispecies biofilm, including periphyton (Fig. 4). Supporting this hypothesis, Kublanovskaya et al. (2020) reported floccules of the microalga *Haematococcus lacustris* in suspension in marine environments and suggested that its incorporation in attached biofilm and/or the release of floccules from the biofilm occurred. Moreover, the authors reported that microalgae can adhere to bacterial floccules, particularly in wastewater

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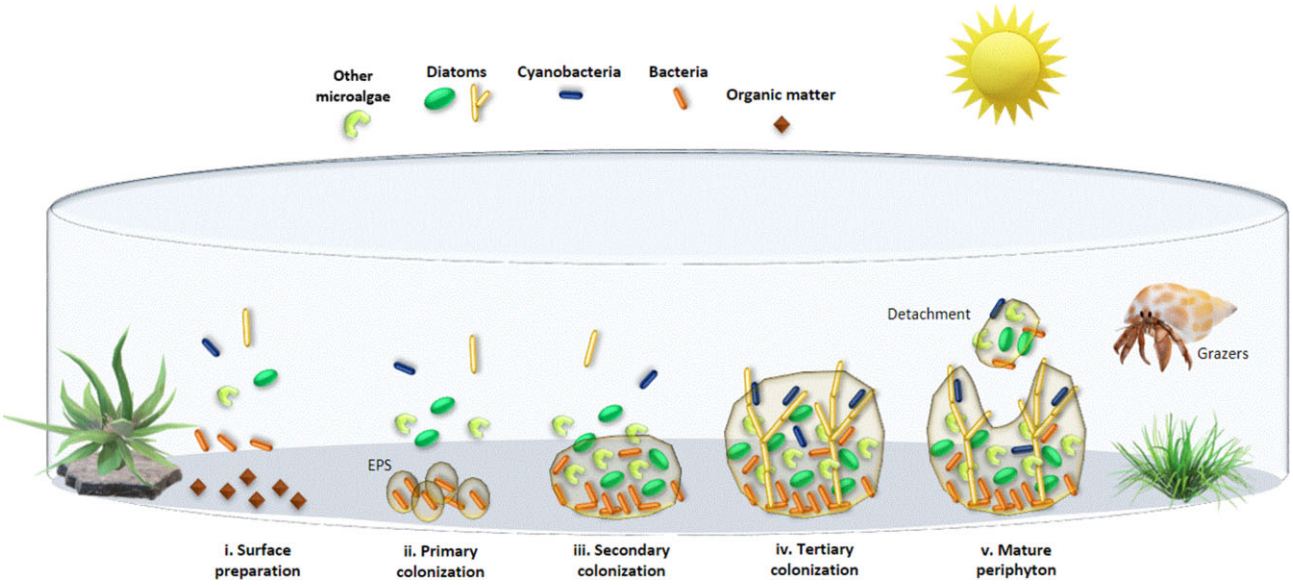

Figure 3. General steps involved in periphyton formation in an aquatic environment: (i) surface conditioning with organic matter; (ii) EPS-producing bacteria are recruited from the environment and binds to the surface; (iii) secondary colonization of microalgae, particularly in environments with high irradiation; (iv) tertiary colonization with filamentous and stalked diatoms forming entangled chains and binding of cyanobacteria; and (v) the mature periphyton suffers from detachment and disturbance by macro organisms (grazers).

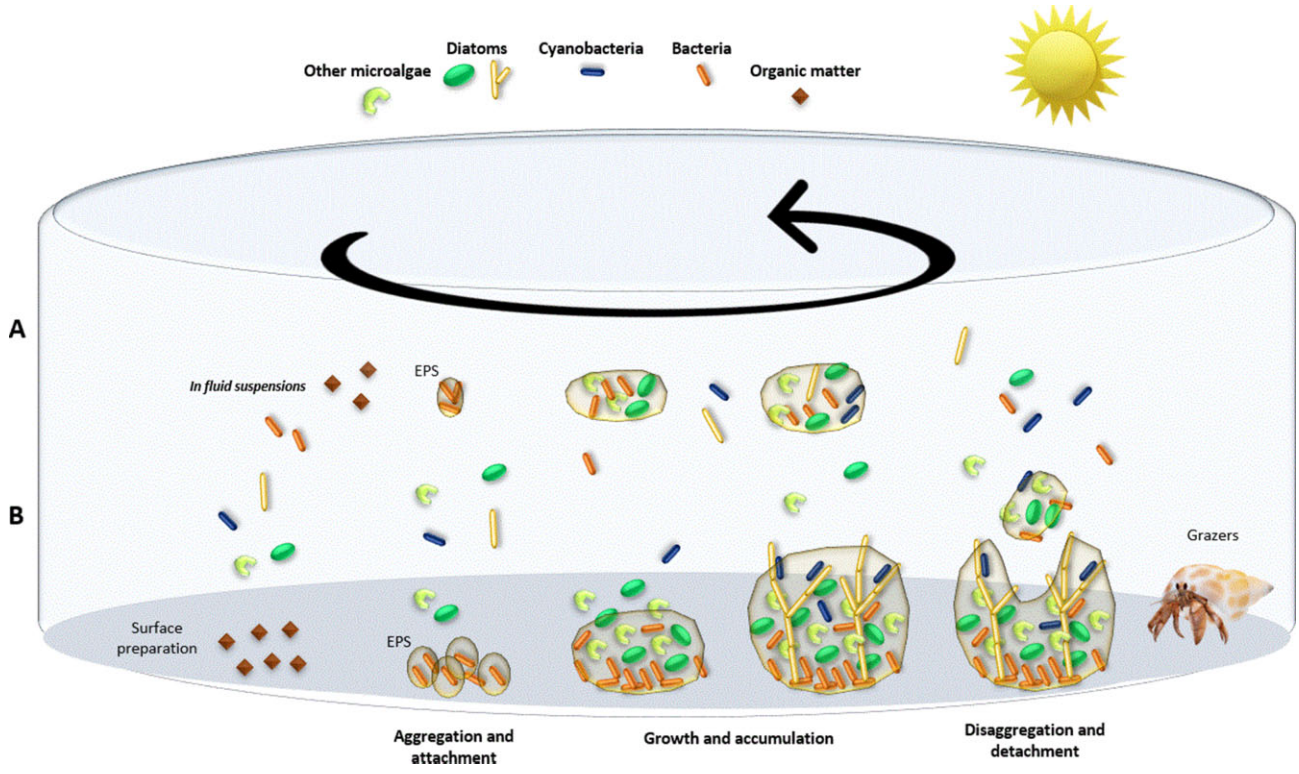

Figure 4. New conceptual model for biofilm formation. General events involved in periphyton formation in an aquatic environment, inspired by the conceptual model proposed by Sauer et al. (2022), are: (i) aggregation and attachment of bacteria cells to each other in floccules (A) or in surface-attached biofilm (B), through EPS production; (ii) growth and accumulation of floccules and surface-attached biofilm through the recruitment of bacteria and microalgal cells from the environment; and (iii) disaggregation and detachment as floccules or planktonic cells.

treatment systems (Arcila and Buitrón 2016, Sales et al. 2022, Wang et al. 2022).

Studies with laboratory-grown periphyton are valuable as they allow monitoring of the species dynamics over time and the influence of environmental parameters in a controlled environment. For instance, Lamprecht et al. (2022) developed a workflow for reproducible synthetic periphyton development by 26 phototrophic species, inoculated in sequence (three groups), after surface colonization with an EPS-producing bacteria: (i) the first group consisted of *A. pyrenaicum* and *Cyclotella meneghiniana*, two diatoms,

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with the first being a known periphyton starter and the second a common low-profile diatom in natural periphyton; (ii) the second group was formed by filamentous and chain-forming diatoms; and (iii) green microalgae, cyanobacteria, and motile diatoms (from the genera *Navicula*, *Nitzschia*, and *Sellaphora*) and also *C. meneghiniana* composed the third group. The first group was grown for 4 days, the second for 14 and the last for 22, developing mature periphyton after 30 days (typical period for natural periphyton). In the mature biofilm, the most abundant species (75% of the population) were *C. meneghiniana*, *A. pyrenaicum*, *Scenedesmus acuminatus*, and *S. vacuolatus* (Lamprecht et al. 2022). Furthermore, all cyanobacteria introduced were detected at the final time, with *Chamaesiphon polonicus* and *Merismopedia glauca*, being dominant. On the contrary, *Tabellaria* sp. and *Melosira* sp. (second group), and *N. vermicularis* (third group) were not found in the mature biofilm. Therefore, the following question naturally arises: What factors define the prevalence of certain species, while inhibiting others?

Factors governing species prevalence and the periphyton structure

Specific environmental conditions can select microorganisms with particular characteristics. For instance, the presence of SiO_2 in water, essential for the frustule formation, and the easy thrive in cold temperatures explains the dominance of Bacillariophyceae in these environments (Baba et al. 2011). Xia et al. (2020) found that the microalgae dynamics in periphyton developed on the surface of macrophytes were influenced by environmental factors (e.g. temperature, P and NH_4^+ content), but also by biotic parameters such as the presence of Proteobacteria and Actinobacteria. Generally, larger filamentous/entangled forms have benefits in the access to irradiation, resources, and space competition, whereas smaller species have an advantage in environments with less irradiation input, due to the higher effectiveness of the pigments (Dunck et al. 2019). Light harvesting by small cells is typically higher since the pigments are more effective as unit size descreases (Dunck et al. 2019). Furthermore, due to their rapid growth (higher surface area/volume, which benefits nutrient consumption), unicellular forms are found in environments associated with sudden changes and disturbances (Dunck et al. 2019). Moreover, the community is influenced by the presence of other macro-organisms (e.g. grazers) and environmental factors (Koedooder et al. 2019). The most important environmental variables are found to be irradiation and water level oscillations: if enough irradiation is available, microalgae will dominate (particularly diatoms) (Evans 2000, Battin et al. 2016); a flood disturbance can 'clean' the substrate, reducing the density and increasing the variability, by allowing other species to colonize (Cantonati et al. 2009, Carapunarla et al. 2014, Vadeboncoeur et al. 2014). Usually, green microalgae are more abundant in the summer, whereas diatoms dominate in the remaining period (under reduced temperatures and increased turbulence) unless eutrophic conditions make cyanobacteria dominant (Baba et al. 2011, Borduqui and Ferragut 2012).

Space and temporal variability affect the structure and functions of the periphyton with different impact from the variations in temperature, irradiation, nutrients type and availability, hydrodynamics, and biotic parameters (e.g. grazing) and substratum (Borduqui et al. 2008, Cantonati and Lowe 2014, Carapunarla et al. 2014, Vadeboncoeur et al. 2014). Periphyton colonizers can change significantly with space (vertical variability) (Vadeboncoeur et al. 2014). Shallow periphyton is affected by fluctuations in the water level, irradiation exposure, changes in temperature, and wave action (Cantonati and Lowe 2014). Microalgae depth-distribution studies (considering densities, biovolumes, photosynthetic efficiency, and community structure and physiology) have found that one of the most important environmental variables is water level oscillations, which are predicted to get worse as a result of climate change (Cantonati et al. 2009, Vadeboncoeur et al. 2014). Higher depths are more stable (fewer disturbances, including grazing) but have lower irradiation penetration (from depth or eutrophication) (Cantonati et al. 2009, Cantonati and Lowe 2014, Vadeboncoeur et al. 2014). In studies of the spatial structure of microalgae along the depth, three zones were described: shallow (commonly affected by disturbances), mid-depth (more stable zone with favourable conditions), and deep (stable but with severely low irradiation penetration) (Cantonati et al. 2009, Cantonati and Lowe 2014). The shallow zone is associated with non-native and invasive algae (e.g. *Jaoa bullata* and *Bangia atropurpurea*, as found in a stydy of benthic algae present in Lake Garda) (Cantonati and Lowe 2014). It is crucial to comprehend and control these recruiting trends to prevent harmful algae blooms. The work by Cantonati et al. (2009) found that the epilithic (growth on stones) diatoms that dominated in the shallow zone (e.g. *Delicata delicatula* and *Denticula tenuis*) were more tolerant to sporadic air exposure. In the mid-depth zone, endangered diatom species (e.g. *Brachysira calcicola*, *Brachysira styriaca*, and *Achnanthes trinodis*) were found, due to the higher diversity resulting from the favourable environmental conditions. In the deeper zone, the irradiation limitation leads to enhanced photosynthetic capacity and a significant rise in the content of fucoxanthin (pigment of brown algae). In that deeper zone, Cantonati et al. (2009, 2014) found *Chlorogloea purpurea*, the alga *Hildenbrandia rivularis*, and *Platessa montana* (shade-tolerant) and dark-brown diatoms. Furthermore, the increase of silicon with the depth leads to the presence of diatoms with highly silicified valves (e.g. *Epithemia*, *Eunotia*, and *Diploneis*) (Cantonati et al. 2009, Baba et al. 2011). Taking into account that the two most important parameters have opposite influences on periphyton growth—irradiation drives growth and wave disturbances hinder it—Vadeboncoeur et al. (2014) reported the ideal settings for periphyton growth in lakes to occur is below 1 m, where disturbance is low but there is abundant irradiation.

With the increasing trend of the world population and associated anthropogenic activity, eutrophication is becoming more relevant (McDowell et al. 2020). Furthermore, due to anthropogenic-based pollution, harmful algal blooms are likely to occur (e.g. *Didymosphenia clavaherculis* on Lake Hövsgö) (Cantonati and Lowe 2014). A study by Borduqui and Ferragut (2012) evaluated the temporal (seasonal) variability of periphytic microalgae succession in a tropical hypereutrophic reservoir, with cyanobacterial blooms, at two climatic periods. The intensity of a cyanobacteria bloom determines the availability of resources and, thus, the performance of individual species, determining their succession and diversity. The trigger for the intensity of a cyanobacterial bloom is the season: in a rainy period there is an intense bloom and, on contrary, a dry period is more prone to periphyton growth. The succession of species found for a rainy period was as follows: in the early and middle phases, cyanobacteria dominated (mainly *Synechocystis aquatilis*, *M. glauca*, and *Cylindrospermopsis raciborskii*, due to their efficient nutrient assimilation and tolerance to low irradiation). In a more advance phase, Bacillariophyceae (class of diatoms) began to dominate (*Gomphonema gracile* and *Achnanthidium minutissimum*, associated with hypereutrophic environments). Therefore, phytoplankton (cyanobacterial bloom) growth negatively impacted diatom growth in early phases, due to better assimilation of resources by cyanobacteria. But, adaptative strategies al-

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lowed the outgrowing of Bacillariophyceae in the latter phase (Borduqui and Ferragut 2012). In the dry period, Bacillariophyceae was dominant, due to lower competition for nutrients. Similarly, a study of the periphytic microalgae community of Patos Lake, over 11 years, observed a higher density during cooler climatic conditions (August/September) due to the prevalence of Bacillariophyceae (Carapunarla et al. 2014). Cyanophyceae (cyanobacteria) were the second most common class, higher in February/March, linked to their ability to store P, fix atmospheric N_2 and absorbed more CO_2 than other microalgae. Furthermore, Hillebrand and Sommer (2000) observed the microalgae assembly on an artificial substratum (1.5 m depth) in a marine environment with artificial eutrophication. They found a lower microalgae evenness with higher nutrient enrichment (artificial eutrophication), which translated into the dominance of some species. Functional homogenization (species with similar roles) was also suggested to be linked to eutrophication by periphyton in an urban swamp, highlighting the negative effects of anthropogenic activities on environmental microbial biodiversity (Hillebrand and Sommer 2000).

Fluid dynamics remarkably impact biofilm development (Hall-Stoodley et al. 2004). In a laboratory study by Cardinale (2011) with eight of the most common species of microalgae found in streams in North America (five Bacillariophyceae and three Chlorophyceae), recirculating streams were set up to emulate natural environmental flow. The author found that distinct species dominated under different conditions. In high flow/shear stress conditions, single-celled diatoms have grown prostrated to a surface, as an adaptation mechanism (e.g. *A. minutissimum* and *Synedra ulna)*, and large filamentous microalgae (more susceptible to drag by shear) prevailed in habitats with low flow (e.g. *Stigeoclonium* sp. and *Melosira varians*). In habitats that had experienced recent disturbance, diatoms with a high-growth rate were dominant (e.g. *A. minutissimum* and *Nitzschia palea*), followed by their replacement by slow-growing species in less often disturbed settings (*Spirogyra* sp., *Stigeoclonium* sp., and *S. ulna)*. Another effect of fluid dynamics is the increasing availability of nutrients from the environment under higher flow regimes. Rusanov et al. (2009) observed the response of lab-grown periphyton (composed by diatoms *A. minutissima* and *Nitzschia* spp. and green microalgae *Scenedesmus* spp. and *Monoraphidium minutum*) to different hydrodynamic conditions under high and low irradiance. Prostrate/motile diatoms (*Nitzschia* spp.) dominated under poor irradiance, while green microalgae and adnate diatoms (*A. minutissima*) were most representative at high irradiance, due to the higher light requirements of green microalgae. As for higher flowing flow velocities, diatoms increased and green microalgae were reduced. Overall, a higher flow decreased the microalgae abundance under high irradiance (from the decrease in green microalgae due to detachment) and increased the relative abundance of diatoms (more resistant to detachment) under shaded conditions. Regarding bacteria, their abundance increased under lower hydrodynamic conditions with high irradiance, and under higher hydrodynamic conditions with low irradiance. Therefore, under high irradiance, bacteria and microalgae growth were correlated, but not under lower irradiance (using a multiple regression module and Pearson's correlation, $P < .05$). The correlation was attributed to the bacterial consumption of microalgae-released compounds (dissolved organic carbon) resulting from the increased photosynthetic activity. In contrast, when microalgae growth decreased, the microalgae exudates did not determine bacterial growth, which combined with the enhanced bacterial growth under high flow highlights the importance of the water-dissolved nutrients for microbial growth (Rusanov et al. 2009).

The spatial structure of periphyton gives valuable information on microenvironments where specific species interact (Lamprecht et al. 2022). However, periphyton is inherently complex, making it difficult to identify the organizational elements (Pollet et al. 2018). Natural mature periphyton has a layered structure (Gulzar et al. 2017). The bottom layers are characterized by low-profile and prostate microalgae and the middle layers by upright or stalked taxa, whereas the top layer is dominated by filamentous microalgae that grow upwards to take advantage of the irradiation and nutrient content, and compete for surface area (Asaeda and Son 2000, Gulzar et al. 2017). Furthermore, the top layer protects the deeper layers from detachment and serves as a surface for colonization, essentially composed of bacteria and fungi (Asaeda and Son 2000, Wu et al. 2018). Furthermore, the structure is influenced by environmental factors where irradiation is one of the most important (Asaeda and Son 2000, Hall-Stoodley et al. 2004). Light-stratified communities are commonly formed, with microalgae and cyanobacteria in the top layers, limiting the penetration of irradiation to the deeper layers (Battin et al. 2016, Mantzorou and Ververidis 2019). Then, gradually, as irradiation decreases, heterotrophs and anaerobic bacterial communities prevail (bacteria and archaea) (Battin et al. 2016, Mantzorou and Ververidis 2019). Schnurr and Allen (2015) reported that microalgae present in deeper layers had a heterotrophic metabolism. Kublanovskaya et al. (2020) studied *H. lacustris* biofilms in rock ponds and found three types of physiology: single layer, unattached flocs, and microbial mats. In microbial mats, i.e. multilayered coloured mineralized biofilms, microalgae *H. lacustris* and cyanobacteria were present exclusively on top layers (photoautotrophic layer) and heterotrophs in the deeper layers. Moreover, in microbial mats chemical gradients induced differential gene expression, metabolism and species stratification (Jo et al. 2022). Cyanobacteria are typically presented on the top layer, fixating CO_2 and creating an O_2 gradient. Below are the aerobic chemoheterotrophs that consume O_2, followed by anoxygenic phototrophs (consume sulfide and produce sulfate), and then chemotrophic sulfate-reducing bacteria. The study by Lamprecht et al. (2022) of lab-developed periphyton for 30 days showed that the distribution (3D spatial structure) of species in the mature community was reproducible (Fig. 5). The high-profile diatoms that were inserted in the second group, i.e. filamentous and chain-forming diatoms, contributed the most to the structure due to advantages in resource exploitation. Following the growth of the second group (filamentous and chain-forming diatoms), there was a decrease in the thickness and an increase in roughness and porosity (more heterogeneous structure). The mature periphyton was thicker and denser, and less porous, to which contributed the smaller microalgae from the last group that filled the porous space.

Functional aspects and biodiversity

Typically, the most numerous and diversified periphyton constituents are microalgae (Borduqui and Ferragut 2012) and bacteria, but other microorganisms (e.g. fungi, grazing protozoa, flagellates, and micrometazoa) are also present (Evans 2000). A study on the development of a periphyton community in plastic submerged in a marine environment showed an abundance of 3.5×10^4 cells cm^{-2} prokaryotes and 5.7×10^2 autotrophs (including *Synechococcus*, picoeukaryotes, and nanoautotrophs) during the first day and 20 000 and 9000-fold increase were achieved, respectively, after 75 days (Pollet et al. 2018). However, the metaproteomic analysis showed more proteins of eukaryotic origin, suggesting that

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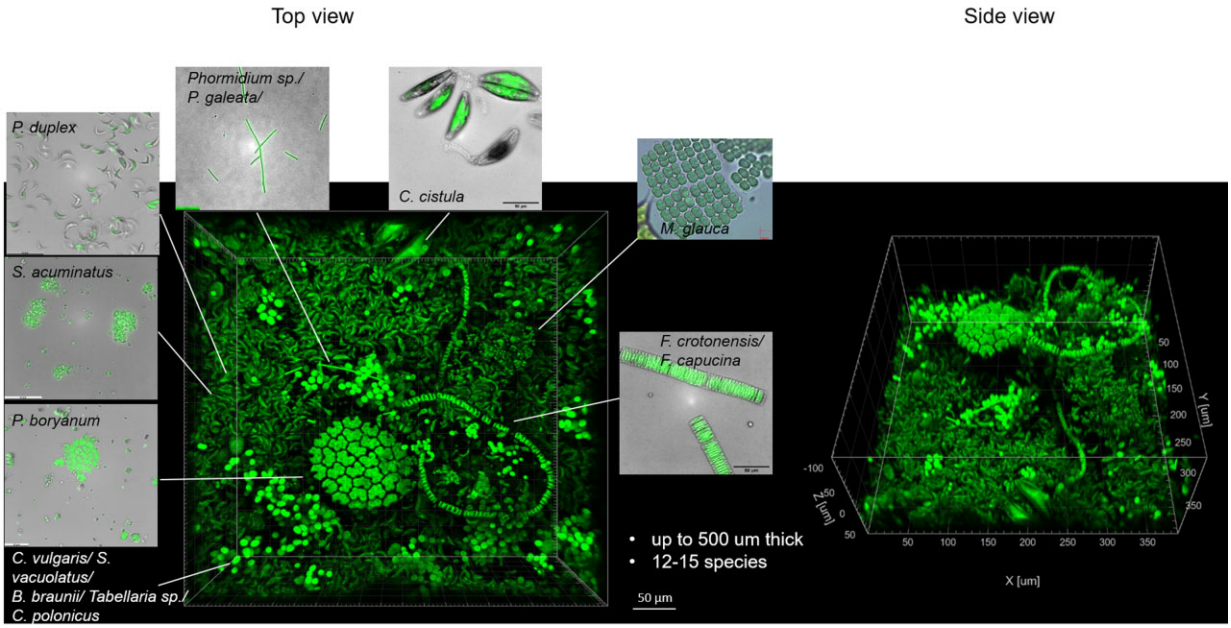

Figure 5. Confocal laser scanning microscopy images of a 30-days-old periphyton with the present species and structural arrangement. Images reprinted with permission from Lamprecht et al. (2022).

productivity is dominated by eukaryotes (Leary et al. 2014). Communities with high biodiversity have shown to be more successful in the uptake of resources from water bodies. For example, microalgal species in periphyton take advantage of niche opportunities and increase the growth and removal of nitrate, a pollutant causing eutrophication (Cardinale 2011). It is still unclear, which factors determine the diversity of the colonizing community and if the bacterial/microalgal associations are species-specific (Krohn-Molt et al. 2017). This section intends to give a description of the most abundant microalgae and bacterial species found in periphyton and unravel the known fundamentals behind the associations.

The bacterial community in the phycosphere is specific as it is phylogenetically different from the one present in the surrounding water (Burke et al. 2011a,b, Salta et al. 2013, Leary et al. 2014, Krohn-Molt et al. 2017, Kimbrel et al. 2019). This pool of bacteria may not be adapted to live planktonically, explaining the differences observed (Burke et al. 2011a). Moreover, the higher concentration of nutrients on the microalgae surfaces compared to the water and the protection from environmental stress may explain the preference for a surface-attached lifestyle (Burke et al. 2011b). The specificity between bacterial strains and microalgae may also be linked to the algal ability to synthesise a wide range of active molecules (e.g. antibiotics and enzymes) that control their phycosphere (Kimbrel et al. 2019, Gubelit and Grossart 2020). Furthermore, microalgae may be influenced by the activity of bacteria, particularly the degradation of polysaccharides, production of antibiotics, allelochemicals, and so on (Goecke et al. 2013).

The proposed theories for the fundamentals behind community assembly are deterministic, stochastic (random neutral hypothesis) or a combination of both (Burke et al. 2011a, Kimbrel et al. 2019, Stock et al. 2022). Diverse studies suggest that associations between microalgae and bacteria are specific (Burke et al. 2011a, Goecke et al. 2013, Gubelit and Grossart 2020, Pushpakumara et al. 2022). Contributing to this theory, different bacterial communities are found in different microalgae from the same habitats, using microalgae as surface for adhesion, and, in the same microalgae species similar communities are found regardless of the habitats (Goecke et al. 2013, Zhou et al. 2016, Koedooder et al. 2019). Kimbrel et al. (2019), in the study of the phycosphere of the microalgae *Phaeodactylum tricornutum* and *Microchloropsis salina* cultivated under similar conditions, found distinct bacterial genera, implying deterministic processes related to microalgal hosts. Lottery-like assembly models suggest neutral colonization, proportional to species abundance (Stock et al. 2022). Stock et al. (2022) reported both deterministic and stochastic processes in the bacterial community associated with the diatom *Cylindrotheca closterium* isolated from marine environments, but in the laboratory environment. The *in situ* precolonization was the main factor responsible for community establishment, but the host-related selection also played a role, even in closely related diatoms. The lottery hypothesis was first applied in coral reef fishes (Sale 1976, Burke et al. 2011a) and proposes that colonization occurs randomly by any suitable microorganism that first encounters the surface, from a pool of suitable species (functional redundancy) (Burke et al. 2011b). According to this model, the species found in periphyton have a common core of functional genes, regardless of the taxonomy (Burke et al. 2011b). With the lottery hypothesis in mind, there is a pool of bacteria, i.e. adapted to colonize microalgae, and which species encounters the surface first (stochastic) will form the community (Burke et al. 2011a,b). Therefore, a specific bacterial group, i.e. repeatedly detected in association with a microalgae host may have developed adaptations (e.g. metabolic pathways and mutualistic interactions) that allow a specific association (Goecke et al. 2013). These characteristics are dispersed among several species, demonstrating functional redundancy among taxa (Burke et al. 2011a). The competitive lottery model predictions are supported by this combination of functional and random processes. Burke et al. (2011a) studied the bacterial composition of samples of the macroalga *Ulva australis* and high variability was found in terms of taxa among different samples (15% similarity), but a common set of functional genes was found in all (70%). This observation implies that rather

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than species, genes/functional similarity might be a determinant factor.

Common features are found within bacterial species that colonize microalgae, particularly the use of the substrates synthesized by these microorganisms and genes characteristic of the surface-associated lifestyle. But, many others were reported (Burke et al. 2011a, Goecke et al. 2013). Hence, the study of functional aspects is essential to comprehend the periphyton species pattern (Dunck et al. 2019). Sanli et al. (2015) studied the periphyton community developed on glass in a marine environment through metagenomics. The periphyton was dominated by bacteria and eukaryotic macroinvertebrates. Phototrophic organisms were present, mainly cyanobacteria, followed by micro and macroalgae, as well as archaea. Regarding the metabolic pathways (functional genes and pathways) specific for an attached lifestyle functional genes coding for a variety of metabolic strategies were found, from carbon fixation pathways, methane, N and sulphur metabolism to photosynthesis. Also, enzymes for the degradation of EPS, such as starch and glycogen, and chitin, are excreted by arthropods. Moreover, genes coding for membrane transport (related to EPS production and tolerance to biocides), cell motility and communication (attachment), and transport and catabolism (microbial interactions). Work by Pushpakumara et al. (2022) analyzed single marker gene-based co-occurrence networks of microalgae and bacteria and underlined the driving factors for the bacteria involved. These include microalgal polysaccharide degradation (e.g. Bacteroidetes and *Verrucomicrobia*) and vitamin B12 (VB_{12}) synthesis (e.g. *Rhizobiales* and *Rhodobacterales*). However, across environments, these bacteria may be different at lower taxonomic levels. Furthermore, Goecke et al. (2013) found that 1/3 of the bacteria isolated from algae were able to degrade structural polysaccharides found on the cell wall. Bacteria isolated from *Chlorophyta*, *Ochrophyta*, and *Rhodophyta* phyla were able to degrade agar, alginate, carrageenan, fucan, laminaran, and ulvan, making it possible for the bacteria to use these polymers as a source of carbon and energy, gaining a competitive advantage when colonizing the host surface. Another example is the glycolate produced by diatoms, which regulates the bacterial community by the response of glycolate-consuming bacteria (Zhou et al. 2016). Therefore, bacteria that have genes for the consumption of this compound increase their density through QS mechanisms (Zhou et al. 2016). In Burke et al. (2011a), the core functions associated with *U. australis* are chemotaxis and motility (allowing the migration to the algae surfaces), proteins involved in the formation of the biofilm matrix and proteins that allow a response to the environment (changes in the algae host)—protection against osmotic stress, O_2 reactive species, and heavy metals (Burke et al. 2011a). The presence of lateral transfer genes was also observed, which is associated with a biofilm-related lifestyle, allowing a fast adaptation (Burke et al. 2011b). Besides, defence proteins were found (e.g. toxins production) that allow a competitive advantage to the *U. australis* community. Furthermore, Krohn-Molt et al. (2013) described the bacteria associated with *C. vulgaris* and *S. obliquus* in a photobioreactor. These bacteria were identified as primary heterotrophs, metabolizing a diverse spectrum of carbon and energy sources produced by the microalgae, such as polysaccharides, proteins, lipids, fatty acids, cellulose, and aromatic compounds. Also, cell motility genes and genes essential for biofilm formation were among the key features observed (Krohn-Molt et al. 2013). Krohn-Molt et al. (2017) analysed the microbiome associated with *C. saccharophila*, *S. quadricauda*, and *Micrasterias cruxmelitensis* and found important features of the metagenome, such as degradation of a variety of carbon and energy sources, aerobic metabolism, N pathways, bacterial photosynthesis and production of vitamins and cofactors. A total of 867 common genes among these three species microbiome were observed. Nonetheless, each microalga-associated microbiome expressed a unique collection of particular genes: 214, 192, and 362 for *C. saccharophil*, *M. cruxmelitensis*, and *S. quadricauda* microbiomes, respectively. The most transcribed genes (24%–35%) were associated with transcription and translation, followed by others presented in Fig. 6A (5%–9% each). However, when studying individual species from each community, different gene expression was found for each (Fig. 6B), highlighting that individual members contribute to the overall function of the community.

Diverse common classes of microorganisms are reported as periphyton colonizers. The dominance of microalgae belonging to the classes Bacillarophycaea, Chlorophycaea, and Cyanophycaea is frequently described (Baba et al. 2011, Borduqui and Ferragut 2012, Gulzar et al. 2017). Baba et al. (2011) focused on the periphytic microalgal community of the river Sindh and found that the population was Bacillariophyceae (87% of the density and 32 taxa) comprised mainly *Amphora ovalis*, *Amphora pediculus*, *Amphora veneta*, *Diatoma mesodon*, *Gomphonema germinatum*, *Gomphonema truncatum*, *Hannaea arcus*, *Navicula* sp. and *Tabellaria* sp., and Chlorophyceae (8.5% and 9 taxa), of which *Zygnema* sp., *Closterium* sp., *Diadesmis* sp., and *Ulothrix zonata* were the most representative. Cyanophyceae comprised 4.5% of the community with seven genera (*Calothrix* sp., *Coelospharum* sp., *Leptolyngbya* sp., *Lyngbya* sp., *Merismopedia* sp., *Oscillatoria* sp., and *Phormidium* sp.) and Xanthophyceae had one genus present—*Vaucheria* sp. Regarding studies on specific substrates, the periphytic microalgae grown on glass in a tropical estuary was mainly composed of diatoms (78%, dominated by *Skeletonema costatum* and *Thalassiosira rotula*) and cyanobacteria (19%, mainly *Synechococcus* sp.) (Salta et al. 2013). In another study using glass surfaces in seawater, the main genera of microalgae were *Navicula*, but the genera *Achnanthes*, *Amphora*, *Cymbella*, *Licmophora*, and *Oscillatoria* were also observed (Gómez-Ramírez et al. 2019). Furthermore, the periphytic microalgae on the surface of the petiole of *Eichhornia azurea* Kunth in a lake observed 39 taxa distributed into 11 classes (from the most representative to the least): Cyanophyceae, Chlorophyceae, Bacillariophyceae, Zygnemaphyceae, Euglenophyceae, Chrysophyceae, Oedogoniophyceae, Xanthophyceae, Cryptophyceae, Rhodophyceae, and Dinophyceae (Carapunarla et al. 2014). Xia et al. (2020) studied the community of different submerged macrophytes. The dominant microalgae phylum was *Chlorophyta*, *Bacillariophyta*, *Cyanophyta*, *Pyrrophyta*, and *Euglenophyta*.

Bacteria found in association with microalgae are mostly aerobic heterotrophic and from the main phyla of Proteobacteria (mainly α- *and* γ-Proteobacteria) and Bacteroidetes (especially Flavobacteriia) (Amin et al. 2012, Goecke et al. 2013, Salta et al. 2013, Krohn-Molt et al. 2017, Pollet et al. 2018, Kimbrel et al. 2019, Stock et al. 2019, Pushpakumara et al. 2022). In these phyla, the genera *Sulfitobacter*, *Roseobacter*, *Alteromonas*, *Ruegeria*, and *Erythrobacte*, as well as *Flavobacterium*, are particularly associated with diatoms (Amin et al. 2012). Pollet et al. (2018) also described that Flavobacteriia is a dominant member, with an important role, often underestimated, in the functional properties of marine biofilms. In other studies, at lower taxonomic levels, *Halobacteria*, *Rhizobiales*, *Cytophagales*, *Rhodobacterales*, *Cellvibrionales*, *Verrucomicrobia*, and *Roseobacter* were also recurrent with microalgae (Ramanan et al. 2016, Zhang et al. 2020, Pushpakumara et al. 2022). Besides, planctomycetes are commonly associated with macroalgae (Pushpakumara et al. 2022). In the study of the microbiome associated with *C. saccharophila*, *S. quadricauda*, and *M. cruxmelitensis*, the most representative bacteria are α-Proteobacteria and Bacteroidetes, with the families Comamonadaceae (dominant

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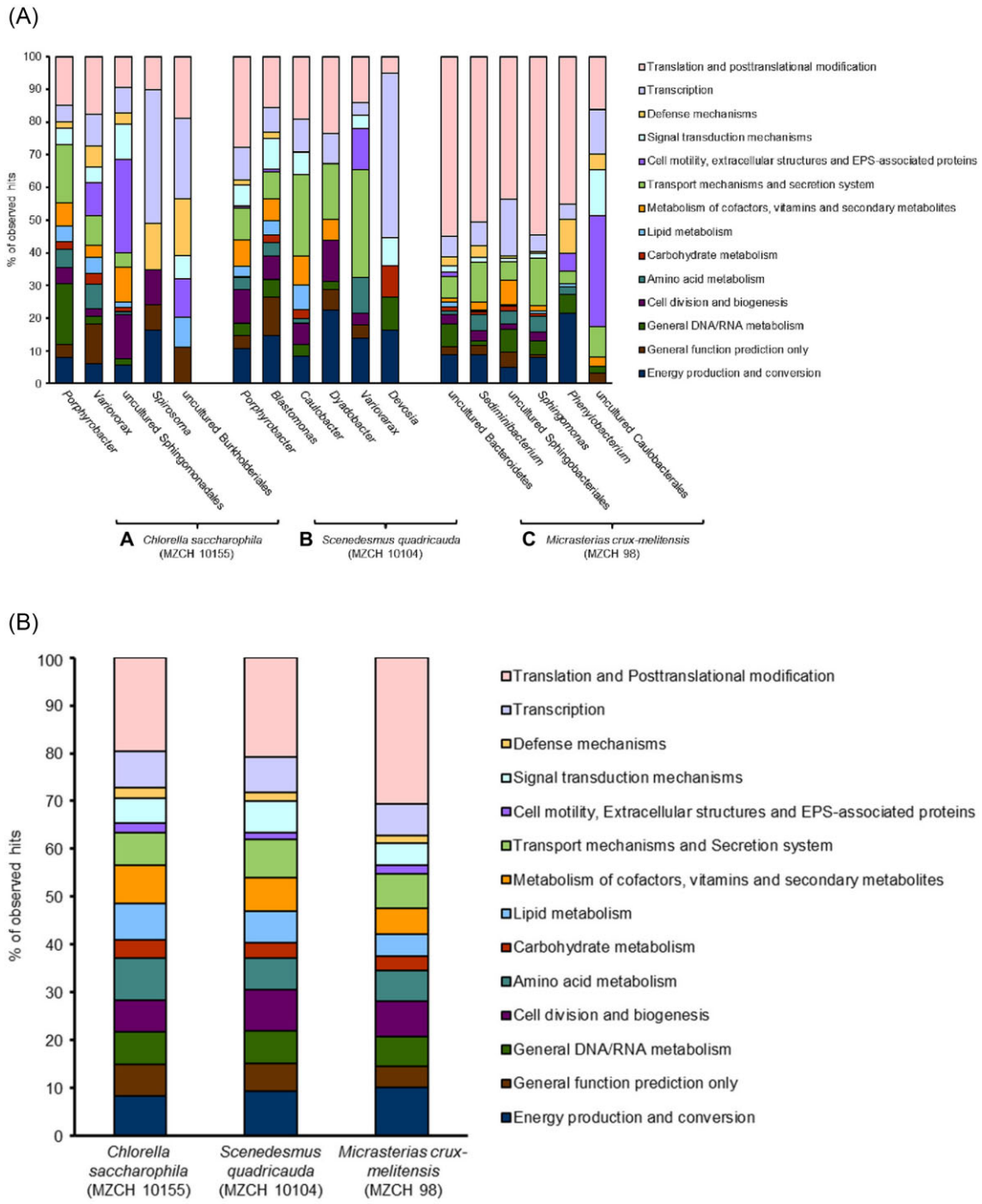

Figure 6. Expressed genes for the bacterial community of *C. saccharophila*, *S. quadricauda*, and *M. cruxmelitensis* **(A)** and each individual bacterial species **(B)**. All three microbiomes show a general expression of common processes, with the most frequently expressed genes being those involved in transcription and translation, energy production and conversion, transport mechanisms and secretion system, and cofactor metabolism. Images reprinted with permission from Krohn-Molt et al. (2017).

for *Scenedesmus*), Caulobacteraceae, Chitinophagaceae, Flexibacteraceae, and Sphingomonadaceae (dominant for *Micrasterias*) and other unclassified bacteria (Krohn-Molt et al. 2017). Using photobioreactors, α-Proteobacteria (genus *Sphinogomonas*) were found associated with *C. vulgaris*, and α-Proteobacteria and γ-Proteobacteria with *Dunaliella tertiolecta* (Lakaniemi et al. 2012). Furthermore, the bacterial phylum associated with *C. vulgaris* and *S. obliquus* in a photobioreactor were mainly Proteobacteria and Bacteroidetes (Sphingomonadaceae, Caulobacteraceae, Rhizobiaceae, Comamonadaceae, Xanthomonadaceae, Sphingobacteriaceae, and Flavobacteriaceae) (Krohn-Molt et al. 2013).

Metabolic exchange and communication

The communication between microorganisms involves the production and release of bioactive molecules (Azam and Malfatti 2007). This chemical ecology-based process is responsible for the underlying mechanisms involved in microbial interactions and

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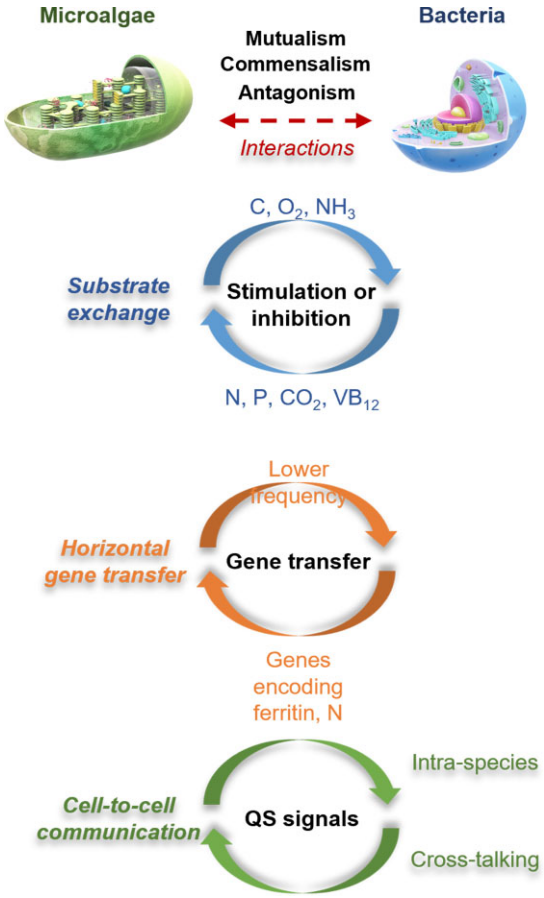

Figure 7. Interactions between microalgae and bacteria in a community. The microbial interactions in ecosystems (i.e. mutualism, commensalism, or antagonism) can be associated with substrate exchange, gene transfer (through HGT), and cell-to-cell communication (through quorum sensing, QS, signals) (adapted from Zhang et al. 2020).

community homeostasis in specific ecosystems (Azam and Malfatti 2007, Hay 2009). The bioactive metabolites produced by microorganisms are structurally and functionally diverse, presenting multiple or simultaneous functions, such as chemical defence (e.g. antipredator and antibacterial compounds, such as polyunsaturated aldehydes, fatty acids, and toxins) and cell-to-cell communication (e.g. amino acids, methylated amines, acyl-homoserine lactones, and dimethylsulfoniopropionate—DMSP) (Ribalet et al. 2007, van Donk et al. 2011).

Based on a report by Zhang et al. (2020) the interactions established between microalgae and bacteria (i.e. mutualism, commensalism, or antagonism) can be caused by: (i) substrate exchange; (ii) gene transfer (through HGT); and (iii) cell-to-cell communication (through QS signals) (Fig. 7). The exchange of substrate between these microorganisms can be through sharing micro and/or macronutrients, causing growth inhibition or stimulation (Fig. 7) (Liu et al. 2017). Several micronutrients are described as being the basis of a stimulant interaction between microalgae and bacteria through the following phenomena: (i) photosynthesis—microalgae supply carbon and O_2 for bacterial usage; (ii) respiration—bacteria produce inorganic substances and CO_2 to ensure microalgae growth, and; (iii) bacteria produce and secrete several metabolites to promote microalgae growth and metabolism, such as vitamins (i.e. cobalamin, thiamine, and biotin) (Krohn-Molt et al. 2013, Ramanan et al. 2016, Liu et al. 2017). Microalgae cannot produce these vitamins, as well as phytohormones (e.g. indole-3-acetic acid—IAA, abscisic acid, cytokinins, ethylene, and gibberellins), thiamine derivatives, and siderophores (e.g. vibrioferrin). On the other hand, N-mediated compounds and P-related compounds are regular nutrients exchanged between microalga and bacteria (Kim et al. 2014). Since microalgae do not have a mechanism to fix N, the presence of growth-promoting bacteria that facilitate N assimilation can be advantageous, as a mutualistic interaction (Villa et al. 2014). This positive interaction was observed among *C. vulgaris* in the presence of *Rhizobium* sp. (Kim et al. 2014) and *Neochloris oleoabundans* and *Scenedesmus* sp. in the presence of *Azotobacter vinelandii* (Villa et al. 2014). Additionally, inorganic P can be provided by bacteria to microalgae, as described by Jiang et al. (2007), showing a positive interaction in the maintenance of an appropriate P concentration in *Microcystis aeruginosa* through the transfer of P by *Pseudomonas* sp.

Contrary to positive interactions, the known metabolites produced by microalgae or bacteria as growth inhibitors can be of the following types: (i) antibacterial compounds that inhibit bacterial growth, such as fatty acids (e.g. eicosapentanoic acid and hexadecatrienoic acid), glycosides, chlorellin, terpenes, and chlorophyll derivatives (e.g. pheophytin *a* and chlorophyllide *a*); and (ii) algicidal compounds that promote cellular lysis, death, respiration inhibition, and protein synthesis, such as derivatives of quinolones, chitinases, pyrroles, glucosidases, derivatives of amino acids, peptides, and alkaloids (Liu et al. 2014, Yang et al. 2015, Wang et al. 2016).

In terms of gene transfer, HGT is a key factor for microbial evolution and adaptation within a community (Fig. 7) (Keeling 2009, Song et al. 2021). The relationship between microalgae and bacteria in HGT remains to be understood, however, a few insights were made to perceive the complex interaction mainly among macroalgae (i.e. *Ulva* genus) or cyanobacteria and bacteria (Kouzuma and Watanabe 2015, Wichard 2023). The gene transfer described between macroalgae and bacteria in biofilms is mainly related to the synthesis of vitamins, adhesion to surfaces, biofilm development, polysaccharide assimilation, defence and stress mechanisms, and proteins synthesis (e.g. genes encoding ferritin), nutrient (essentially N) transport, and phlorotannin degradation (Zhang et al. 2020, Song et al. 2021). In particular, the gene involved in the ornithine–urea cycle (that improves the removal of N in wastewater treatment) is believed to be transferred from bacteria (Allen et al. 2011). These authors showed that the exosymbiont-derived ornithine–urea cycle facilitated a fast recovery from prolonged nitrogen limitation. Also, they found that depleted metabolites were formed by ornithine–urea cycle intermediates empowered by the products of genes laterally acquired from bacteria. In addition, gene transfer between the cyanobacterium *Synechococcus elongatus* and the bacterium *Escherichia coli* allowed a higher bacterial resistance to different antibiotics (e.g. ampicillin and kanamycin) (Lee 2019). Moreover, considering microalgae and bacteria HGT, genes earlier produced only in microalgae and associated with protein production (i.e. actin and profilin) were found in the cyanobacterium *M. aeruginosa* and the bacterium *Prosthecobacter tubulins*, suggesting HGT between these species (Guljamow et al. 2007). Overall, HGT between microalgae and bacteria occurs at a low frequency and is mainly from bacteria to microalgae (Keeling and Palmer 2008). This arises since bacteria have enormous gene pools, allowing the putative acquisition of new functions by microalgae (Keeling and Palmer 2008, Qixin et al. 2022).

QS is a communication machinery between microorganisms through the release, 'sensing of' and response to signal molecules (Fig. 7) (Ribeiro et al. 2022). In the phycosphere, QS-mediated

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communications extensively impact the symbiotic relationships among microalgae and bacteria (Geng and Belas 2010). Cell-to-cell communication in the phycosphere includes (Geng and Belas 2010, Zhou et al. 2016): (i) interbacterial communication; (ii) intermicroalgal communication, and; (iii) interkingdom signalling (cross-talking) (Fig. 7). Bacterial interactions are primarily regulated through the exchange of autoinducers (i.e. *N*-acyl homoserine lactones—AHLs and furanosyl borate diester) and autoinducing peptides, being responsible for increases in cell density and specific phenotypes and cell functions (Zhang et al. 2018a). AHLs contribute to the regulation of biofilm development in the earlier stages, boosting microalgal cell attachment into the biofilm, and extracellular hydrolytic alkaline phosphatase activity, responsible for particulate organic carbon degradation (Jatt et al. 2015). On the other hand, a different cellular response can be observed when microalgae are in contact with bacterial QS signals, such as: (i) the degradation of chlorophyll levels in *Chlorella* and *Scenedesmus* spp. (an algicidal effect) by AHLs released by bacteria (Natrah et al. 2014); (ii) a boosted ability to aggregate, forming bioflocs, by microalgae *Chlorophyta* sp. (Zhou et al. 2017); and (iii) a spore-release trigger in the red algae *Acrochaetium* sp. by the presence of the QS molecule *N*-butyl-homoserine-lactone (Weinberger et al. 2007). Moreover, the signalling molecule DMSP stimulates chemotaxis in bacteria and regulates metabolism (Cirri and Pohnert 2019). Several signalling molecules are used by microalgae for different cellular and interspecies processes, such as allelochemicals (e.g. synomones), phospholipids, flavonoids, and QS signals (Zhou et al. 2016). In cell-to-cell communication between microalgae cells, the signalling allelochemicals and QS molecules are the most commonly used to regulate their behaviour (Zhou et al. 2016). As secondary metabolites, allelochemicals are responsible for microalgal survival, reproduction, and growth in a community (Graneli and Pavia 2006). Furthermore, these allelopathic molecules present a key role in the regulation of levels of target species, microalgal cell defence, and metabolism (Inderjit et al. 2011). On the other side, these allelopathic molecules can also regulate the production and release of microbial toxins (e.g. saxitoxin) by some microalgae (e.g. *Alexandrium* spp. and *Prymnesium* spp.), enhancing their growth in the community (Weissbach et al. 2011). Regarding the microalgal QS, several molecules were already described: amino acids (e.g. tryptophan), organic acids (e.g. *p*-coumaric acid), nitric oxide, and 5,6-membered ring molecules (e.g. laurenciones, malyngamides, and honaucins) (Vardi et al. 2008, Gerwick et al. 2013). Besides the regular function of these QS signals, they can be responsible for the recruitment of microalgal cells to improve their antioxidant or anti-inflammatory responses against oxidative stress that can cause cellular damage (Vardi et al. 2008, Gerwick et al. 2013). Moreover, diverse studies reported the regulation of bacterial behaviour (such competition for space and metabolism) through the secretion of diverse microalgal molecules: (i) vitamin derivates (e.g. lumichrome) can mimic the AHL signals, occupying the binding sites and reducing bacterial biofilm development and/or population density; and (ii) AHL-inactivating enzymes (e.g. lactonases, acylases, and oxidases) cause the hydrolysis of the homoserine lactone ring (crucial for AHLs synthesis), quenching the QS mechanism (Dong and Zhang 2005, Rajamani et al. 2008, Butler and Sandy 2009, Rajamani et al. 2011).

The mechanisms involved in cross-talking among microalgae and bacteria species are still unknown in periphyton. However, a few insights regarding microalgae–bateria interactions have been found and a similar behaviour is expected in a periphyton. This cross-talking can regulate several sets of ecological processes in periphyton, such as biofilm development, community distribution, and acquisition of nutrients and cofactors (e.g. N, P, and iron) (Fig. 7) (Raina et al. 2009, Dickschat 2010, Inderjit et al. 2011). It is described that the interkingdom signalling between macro or microalgae and bacteria occurs mainly by three different molecules and/or mechanisms, namely lipid-based molecules, structurally conserved molecules (e.g. helix–turn–helix-containing proteins) and bacterial molecules (e.g. methylamine, Roseobacticide B, and IAA) (Vannini et al. 2002, Decho et al. 2011). Amin et al. (2015) described the importance of the production and release of IAA by *Sulfitobacter* species to promote cell growth of diatoms and to support a positive relationship among the community. Contrary, Mitsutani et al. (2019) reported a negative relationship between the diatom *S. costatum* and the bacterium *Pseudoalteromonas* sp. through the production of an algicidal that promoted *S. costatum* lysis. Furthermore, microalgae can also sense QS molecules produced by bacteria, responding positively or negatively to these external signals, as described above. Therefore, QS signals can be employed to promote biofilm formation for wastewater treatment or other biotechnological applications (Qixin et al. 2022). Overall, a regulated and operative mechanism is essential to have a sustainable relationship in these multifaceted ecological communities among microalgae and bacteria.

Mathematical modelling of periphyton

Conventional periphyton biomass evaluation through field monitoring, although precise, is relatively costly and time-consuming (Vollmer et al. 2016). Thus, to understand the population dynamics and biomass development under different conditions present in the environment, mathematical modelling has been used with great success in dealing with nonlinear interactions in complex systems (Huang et al. 2021). The use of predictive mathematical models can offer the necessary information to identify the principles inherent to the relationships established in microalgae–bacteria communities and their habitat, as well as provide the required knowledge to engineer them (Song et al. 2014). For clarification, the models here described were divided into two groups: (i) habitat-related models, which are based on external factors present in the environment (i.e. nutrient availability, stream velocity and grazing phenomena); and (ii) interspecies interaction models (i.e. related to interactions between microalgae and bacteria present in the periphyton communities).

Habitat-related models

There are a few abiotic factors that can influence primary production in aquatic ecosystems: irradiation and nutrient availability, temperature, water flow, depth, and salinity are the main ones (Buzzelli et al. 2000, Larned 2010). Therefore, the application of models is based on several key factors that influence periphyton growth (Table 2). An interesting conceptual model was developed by Biggs et al. (1998a) for unshaded temperate streams, based on three main parameters. These three parameters—periphyton stability, nutrient supply, and invertebrate grazing—are closely intertwined, which means that any disturbance in the habitat matrix can affect nutrient availability and the grazing community, and in turn, change the dynamics of the periphyton population, and *vice versa*. Through the assessment of periphyton biomass and division of functional groups concerning its strengths and weaknesses, this model can predict which periphyton communities will strive under certain stream conditions, proven in a realistic situation (Biggs et al. 1998b). The shortcomings of the Biggs model

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Table 2. Mathematical models for the description of periphyton growth considering the influencing factors.

	Model	Equation	Parameters	References
Habitat-related periphyton models	Simple model for periphyton nutrient uptake and recycling	$Q_2 * C_2 = Q_1 * C_1 - A_{bed} * R + I$	$Q1$ and $Q2$ are the flows at the upstream and downstream sites ($m^3\ s^{-1}$), $C1$ and $C2$ are the concentrations ($g\ m^{-3}$) at the upstream and downstream sites, R is the net areal uptake rate ($g\ m^{-2}\ s^{-1}$), A_{bed} is the area of a stream bed between sites (m^2), I is the mass inflow between sites ($g\ s^{-1}$)	Rutherford et al. (2020)
	Simple model to evaluate the impact of nutrients on shallow periphyton-dominated streams	$P, N = P, N_0 - \frac{r_{pa} * k_{gn} * a}{U * H} * x$	P,N is the available phosphorus or nitrogen concentration ($\mu g\ l^{-1}$), P, N_0 is the available phosphorus or nitrogen concentration at the mixing point ($\mu g\ l^{-1}$), r_{pa} is the periphyton phosphorus-to-chlorophyll a ratio ($\mu gP\ \mu gA^{-1}$), k_{gn} is the net periphyton first-order growth rate (day^{-1}), a is the periphyton biomass expressed as chlorophyll a ($mgA\ m^{-2}$), U is the stream velocity ($m\ day^{-1}$), H is the stream depth (m), x is the distance downstream (m)	Chapra et al. (2014)
	Periphyton growth model to assess phosphorus dynamics	$GPP = \left[C_{peri} * \left(P_{max} * O^{(T_W - T_{ref})}\right) * \left(\frac{PAR_0}{I_k + PAR_0}\right) * \left(\frac{TP_w}{K_{TP} + TP_w}\right) * \left(1 - \frac{C_{peri}}{C_{max}}\right)\right]$	GPP is the gross primary production ($g\ C\ m^{-2}\ d^{-1}$), C_{peri} Is the average daily periphyton biomass ($g\ C\ m^{-2}$), $Pmax$ is the maximum photosynthetic rated (d^{-1}), O is the Arrhenius constant, T_w is the water temperature (°C), T_{ref} is the reference temperature for metabolism (°C), PAR_0 is the photosynthetically active radiation ($\mu moles\ m^{-2}\ s^{-1}$), I_k is the half-saturation value for irradiance, K_{TP} is the half-saturation value of phosphorus uptake, C_{max} is the maximum periphyton biomass ($g\ C\ m^{-2}$)	Buzzelli et al. (2000)
	Model constructed to study the interaction between phosphorus and periphyton dynamics	$\frac{F(A,P)}{A} = \mu_{max} * \left(\frac{P}{(K_\mu + P)}\right) * \left(\frac{1 - A}{A_{max}(P)}\right) - m$	A is the amount of phosphorus bound to periphyton per unit volume, P is the available phosphorus per unit volume in water, μ_{max} is the maximum growth rate of periphyton ($g\ g^{-1}\ d^{-1}$), $A_{max}(P)$ is the maximum standing crop of periphyton ($g\ m^{-3}$), K_μ is the half-saturation coefficient for growth rate of periphyton as a function of P ($g\ m^{-3}$), m is the mortality ($g\ g^{-1}\ d^{-1}$)	Dong et al. (2002)
	Model to estimate the spatiotemporal distribution by calculating periphyton biomass thought inorganic phosphorus influence, adapted from Uehlinger et al. (1996)	$\frac{dX}{dt} = \mu_{max} * X * \frac{1}{1 + K_{x,inv} * X} * \frac{I}{I + K_I} * exp\{\beta(T - T_0)\} * \frac{N}{N + K_N} - C_{det} * Q(X - X_0) - K_{flood}(X - X_0)$	X is the periphyton biomass ($mg\ m^{-2}$) and t is time (days), dX/dt is the daily increase or decrease in periphyton biomass, Q is the daily mean discharge, N is the nutrient concentration, T is the daily mean water temperature, $K_{x,inv}$ is the half saturation constant for periphyton ($mg\ m^{-2}$), K_I half saturation constant for the daily integrated irradiation intensity ($E\ m^{-2}$), β is the temperature dependence of growth ($°C^{-1}$), K_N is the half saturation constant for the nutrient concentration ($mg\ m^{-3}$), C_{det} is the detachment of periphyton t ($s^{-1}\ m^{-3}\ day^{-1}$), K_{flood} is the catastrophic detachment of periphyton (day^{-1}), μ_{max} is the maximum specific growth rate	Kazama and Watanabe (2018)
	Ecological model for vertical accumulation under irradiation attenuation	For nonfilamentous subcommunity: $\frac{dC}{dt} = C * [q^{T-20} * G_{div} * R - G_{mortal} - G_{detach}]$	C is the development of the nonfilamentous community, t is time, q is the temperature constant, T is the water temperature (°C), G_{div} is the reproduction rate (day^{-1}), R is the light Index, G_{mortal} is the mortality rate (day^{-1}), G_{detach} is the detachment rate (day^{-1}), L is the length of the filaments ($cell\ filament^{-1}$)	Asaeda and Son (2000)

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Table 2. Continued

Model	Equation	Parameters	References
	For filamentous subcommunity: $\frac{dL}{dt} = L * q^{T-20} * G_{div} * R$		
Coupling of a periphyton model influence by nutrient and irradiation to a nutrient transport model	$\frac{dEN_S}{dt} = \frac{K_v}{D_s} * (EN - EN_s) + \frac{K_{conv}}{D_s} * [q^{T-20} * G_{decomp} * D * IN - UN_{max} {}^{*}q^{T-20} * \frac{IN_{max}-IN}{IN_{max}-IN_{min}} * \frac{EN_s}{K_N+EN_s} * C]$	EN_S is the nutrient concentration ($\mu g\ l^{-1}$), t is time (day), K_v is the exchange coefficient between two zones (m day^{-1}), D_s is the thickness of stationary zone (mm), K_{conv} is the conversion factor (10^{-6} $mm^3\ l^{-1}$), EN is the external nutrient concentration, G_{decomp} is the decomposition rate (day^{-1}), q is the Arrhenius constant, T is the water temperature (°C), D is the detritus as dead cells (cell mm^{-2}), IN_{max} IN_{min} are the maximum and minimum internal nutrient concentration (μg $cell^{-1}$), IN is the internal nutrient concentration, $K_N$is the half-saturation nutrient concentration for uptake process, C is the time rate of change of the population of any algal species (cell mm^{-2})	Son and Fujino (2003)
Model of periphyton detachment that integrates the hydrodynamic factor, using the biomass losses in the detachment term (f_{lim})	$G(t) = \mu_0 * \frac{I(t)}{I_{opt}} * e^{-k_{ext}(\frac{I(t)}{I_{opt}} * \theta^{T(t)-T_{opt}}} * \min \frac{N_i(t)}{N_i(t)+K_{Ni}} * B(t) * f_{lim}(B(t))$	f_{lim} is the limitation term due to biomass accumulation, G is the biomass production rate (kg Ash Free Dry Mass (AFDM) $m^{-1} day^{-1}$), μ_0 periphyton maximal growth rate (day^{-1}), I is the irradiation intensity (W m^{-2}), I_{opt} is the optimal irradiation intensity (W m^{-2}), K_{ext} is the irradiation extinction coefficient, θ is the temperature coefficient, T is the water temperature (°C), T_{opt} is the optimal water temperature(°C), nutrient i concentration (kg m^{-3}), K_{ni} is the half-saturation coefficient for the nutrient i, B is the periphyton biomass (kg AFDM m^{-1})	Fovet et al. (2010)
Model for periphyton biomass-dependent growth rate, a detachment rate directly proportional to discharge and biomass, and a catastrophic loss rate	$\frac{dX}{dt} = \mu_{max} * X * \frac{1}{1+K_{x,inv}*X} * \frac{I}{I+K_I} * exp\{\beta(T-T_o)\} - C_{det} * Q(X-X_0) - K_{flood}(X-X_0)$	X is the periphyton biomass (mg m^{-2}) and t is time (days), Q is the daily mean discharge, T is the daily mean water temperature, $K_{x,inv}$ is the half saturation constant for periphyton (mg m^{-2}), K_I half saturation constant for the daily integrated irradiation intensity (E m^{-2}), β is the temperature dependence of growth ($°C^{-1}$), C_{det} is the detachment of periphyton t (s^{-1} m^{-3} day^{-1}), K_{flood} is the catastrophic detachment of periphyton (day^{-1}), μ_{max} is the maximum specific growth rate	Uehlinger et al. (1996)
Model for epilithic biofilm biomass dynamics based on grazing and local hydrodynamic	$\frac{dB}{dt} = \mu_{max} * B * \frac{1}{1+K_{inv}*B} * \exp(\beta(T-T_0)) * \frac{I}{I+k_I} - C_{det} * u(B-B_0) - K_{flood} * u(B-B_0 - C_{auto} * B_b(B-B_0) - TNF_{Gr}$	μ_{max} is the maximum specific growth rate at the reference temperature T_0 (day^{-1}), B is the epilithic biofilm biomass (g AFDM m^{-2}), t is the time (days), T is the mean daily temperature (°C), T_0 is the reference temperature biomass (20°C), I is the daily integrated irradiation intensity (E m^{-2}), B_0 is the minimal biomass that allows the epilithic biofilm community to recover, k_{inv} is the inverse half-saturation coefficient (m^2 g^{-1}), β is the coefficient of temperature dependence ($°C^{-1}$), K_I is the irradiation half-saturation coefficient (E m^{-2}), C_{det} which is an empirical detachment coefficient, u and B ($s\ m^{-1}$ day^{-1}), K_{flood} is the empirical coefficient for massive biofilm detachment ($s\ m^{-1}$ day^{-1}), C_{auto} is the detachment coefficient ($cells^{-1}$ m^2), the B_b is the active bacterial density (cells m^{-2})	Graba et al. (2014)

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Table 2. Continued

	Model	Equation	Parameters	References
	Least squares-support vector machine model	Artificial Intelligence model normalized through: $yi = \frac{\lvert Xi - Ximin\rvert}{Ximax - Ximin} * 0.8 + b$, where yi is the normalized data, xi is the input data, $xmin$ and $xmax$ are the minimum and maximum of the input data, and b is the bias value ($b = 0.1$)	Water temperature, irradiation intensity, total nitrogen, total phosphorus, discharge, and chlorophyll *a*	Huang et al. (2021)
Interspecies relationship-focused models	Interpretation of several models and the influence of spatial structure on microbe dynamics	'Mean-field' model: $\frac{1}{\overline{N_j}(t)} * \frac{d\overline{N_j}(t)}{dt} = b_j * f_j(\bar{R}) * \bar{E} - \delta$ 'Shaken' model: $\frac{1}{\overline{N_j}(t)} * \frac{d\overline{N_j}(t)}{dt} \approx b_j * f_j((1 - \frac{1}{\max(A_{mic}, A_{res})} * \bar{R}) - L_j) * \bar{E} - \delta$ 'Full spatially explicit' model population dynamics simulation through computer simulation.	$\overline{N_j}(t)$ is the fraction of all sites occupied by microbe j, b_j is the maximum birth rate of microbe j, $f_j(R)$ is the amount that reproduction is reduced for microbe j by resource limitation in site x, $\bar{E}$ is the fraction of sites near x that are not occupied, δ is the microbe death rate, L_j is the amount of excess resource limitation that microbe j experiences because of variation in resources, A_{res} is the number of sites over which resources diffuse, A_{mic} is the number of sites over which propagules disperse	Stump et al. (2018)
	A model created to assess the impact of 'leaky' resources on the community and the microorganism itself	$\frac{dN_j}{dt} = [g_j(1 - \frac{\sum_{k=1}^{S} N_k}{X}) - d_j] * N_j$	N_j is the microbe j's density, g_j is the growth rate, X is the shared carrying capacity, d_j is the microbe j's death rate, and $\sum_{k=1}^{S}$ is the summation over the S species of microbes, N_k is the resource produced by microbe k	Estrela et al. (2016)
	Model to study localized interactions in cross-feeding	$\frac{dN_j}{dt} = [g_j(1 - \frac{\sum_{k=1}^{S} N_k}{X})] * N_j$	N_j is the microbe j's density, g_j is the growth rate, $\sum_{k=1}^{S}$ isthe summation over the S species of microbes, N_k is the resource produced by microbe k, X is the shared carrying capacity given by $X = X_{min} + X_{max}(\prod_{i=1}^{n} \frac{\sum_{k=1}^{S} a_{i,k} N_k}{\sum_{k=1}^{S} N_k})$, χ_{min} and χ_{max} were the minimum and maximum carrying capacities, the product is over n traits, and $a_{i,k}$if a microbe performs a certain function i	Oliveira et al. (2014)

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are related to the exclusion of smaller-scale parameters from the overall evaluation to the detriment of large-scale patterns. Nevertheless, it is a good starting point to perceive the numerous interactions that are present in these grouped communities.

Other studies have focused on developing models evaluating nutrient assessment (Hillebrand and Kahlert 2001, Son and Fujino 2003). A relatively straightforward model was developed by Chapra et al. (2014) to perceive the relationship between nutrient uptake on shallow streams dominated by periphyton and, although simple, it can be used to determine nutrient loading to control periphyton biomass levels. Others have created nutrient-related models capable of quantifying the uptake and recycling of P and N (Rutherford et al. 2020). After field observations, the authors concluded that the model was oversimplified and could be improved by the introduction of other parameters. Moreover, P is described as a limiting factor in microalgae development, and Buzzelli et al. (2000) focused precisely on the simulation of the P dynamics through its influence on the periphyton biomass. Other authors shared the same focus on the environmental disturbance caused by P enrichment, using this nutrient as the foundation for modelling periphyton growth (Dong et al. 2002, Kazama and Watanabe 2018). The reason for more focused modelling research on nutrient availability is the practicability in resolving the harmful algae bloom-related problems, i.e. not much can be done in controlling irradiation, flow rates and temperature in streams and rivers and thus, the problem must be solved by aiming to control the nutrient discharge present in many aquatic ecosystems (McDowell et al. 2020). In contrast, Asaeda and Son (2000) disregarded the influence of nutrient uptake and focused on the vertical distribution of a periphyton community. In this case, by considering that nutrients were sufficiently provided, irradiation was a defining factor for biomass growth and cell resistance against forces caused by stream flow, as well as morphological differences in filamentous and nonfilamentous microalgae for microbial mats formation, and flow velocity for the detachment process.

Despite the importance of developing models focused on the crucial parameters for specific purposes, most are certainly inadequate in the process of representing a realistic scenario, where several parameters influence periphyton growth (Holomuzki et al. 2010, Larned 2010). Multifaceted models are focused on more parameters for an accurate representation of periphyton development. Graba et al. (2014) focused on variables present in the environment that could affect epilithic periphyton: invertebrate grazing, local hydrodynamics, and evaluation of biomass dynamics. The model accurately predicted the data obtained, establishing an intricated cycle of biofilm growth and detachment more effectively than parameterization using a single set of empirical parameters. A comparable model was proposed by Uehlinger et al. (1996), assessing periphyton dynamics by applying several parameters (i.e. biomass levels, irradiation, water temperature, and discharge). Through these parameters and measured data, a model was developed involving a biomass-dependent growth rate, a catastrophic loss rate and a detachment rate directly proportional to discharge and biomass, proving the significance of flow-related factors. Other cases used a least squares-support vector machine model and evaluated the correlation between irradiation, discharge, total P, total N, temperature, and chlorophyll *a*, to control downstream periphyton communities through dams discharge control (Huang et al. 2021). Nevertheless, as the authors pointed out, the ecological interactions were not evaluated in the model, which is an important modelling component for periphyton characterization. Therefore, the following section will give a deeper look at models considering diverse types of interspecies relationships.

Interspecies relationships and the BQH modelling

It is rather unusual for a microbe to be completely self-sufficient, instead relying on other microorganisms to produce resources necessary for critical functions (Morris 2015). This dependence on others can lead to the loss of function of certain genes through drift or selection (McCutcheon and Moran 2012). The BQH proposes that a selective force occurs when a certain function is vital and 'leaky' for the community, creating mutants with deactivated genes that are costly and undesirable, known as 'beneficiaries', while some maintain that function for the greater good, named 'helpers' (Morris et al. 2012, Morris 2015). Under the BQH framework, we can include the development of the biofilm matrix, particularly the role of heterotrophic bacteria in the development of phototrophic biofilms. The documented research indicates an advantage when bacteria are present as opposed to bacteria-free biofilm, promoting faster and stronger biofilm development (Roeselers et al. 2007, Lubarsky et al. 2010). According to Morris (2015), the dependence on bacteria for microalgae to survive and persist in harsh environments is in line with the evolutionary philosophy of the BQH, since a function is performed to provide 'leaky' products necessary for the whole community and not only for the 'helper'. In contrast, Stump et al. (2018) challenged this hypothesis, assessing its viability and using a spatial model to alter the expectations of the BQH. Under no spatial effects, there is a prevalence of 'beneficiaries' and 'helpers' to the detriment of mutualistic behaviour, but the effects of neighbour uncertainties under a spatial parameter can explain the persistence of mutualistic microorganisms in the natural environment (Boyle et al. 2012, Oliveira et al. 2014). Therefore, the presence of a spatial variable gives a new approach to the BQH. Through its analysis of the spatial parameter, Stump et al. (2018) focused on three specific cases presented in Table 2: (i) a 'mean-field' model for a baseline belief of what occurs without the presence of spatial parameter; (ii) a 'shaken' model with interactions over a short distance creating neighbour uncertainty without spatial structure; and (iii) a 'full spatially explicit' model that incorporates both the spatial structure and neighbour uncertainty, improved from a previous model. In the 'full spatially explicit' model, nonproducers or 'beneficiaries' are affected due to the shortage of one resource and abundance of the other, while mutualist microorganisms and obligate microorganisms will be equally distributed. This 'spatially explicit' model could very well represent periphyton due to the physical network and resource exchange, as communities with more structure distribution appear to favour mutualistic interactions (Tolker-Nielsen and Molin 2000). Other authors were also concerned with the assessment of microbe dynamics through the applications of relevant models for resource interactions. Estrela et al. (2016) represented growth with a Lotka–Volterra-type model to understand how 'leaky' resources with individual and communal benefits influence mutual interdependency. Their results suggest that obligate exploitation is a rare occurrence and mutual interdependency dominates for a loss of microbial dependency. In comparison to the Stump et al. (2018) model, the Estrela et al. (2016) model indicates a lack of spatial structure, as well as perceiving the resources as having a multiplicative effect and not limited by the rarer resource. Oliveira et al. (2014) focused on localized interactions between different strains and species, indicating that the BQH and its expectations will not always occur. In this

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case, it may be advantageous for a certain microbe to produce all the resources it needs, depending on the level of genetic mixing. As such, low mixing will tend to favour genotypes that produce all the resources needed in the community, whereas high mixing will generally favour nonproducer genotypes. The model also presented a scenario where nonproducers becoming dominant would not lead to community collapse, which contrasts with the spatial model developed by Stump et al. (2018). Additionally, there are other ways to approach the modelling of a microbial community, and an effective way to assess it could be through metabolic network modelling. Henry et al. (2016) tested a metabolic network model for predicting interspecies interactions related to metabolic exchange for circumstances where the axenic information is not available, using a phototroph–heterotroph consortium to validate the results obtained. Ravikrishnan et al. (2020) built a metabolic index to exhibit the advantages that each microorganism brings in a coculture, implementing metabolic exchange prediction by computer analysis and practical verification of the model through experimentation. For a better understanding of microbiome interaction, Levy and Borenstein (2013) integrated genome-scale metabolic modelling with metagenomic data for the computational framework of a mechanistic model for the prediction of microorganism communication in cocultures. Many other studies pay special attention to the metabolic side of microbial interactions, revealing important modelling steps for comprehending complex interfaces that can be applied in periphyton-type communities (Christian et al. 2007, Levy et al. 2015, Ravikrishnan and Raman 2018).

Biotechnological applications of periphyton

In recent years, the biotechnological applications of microalgae have attracted remarkable interest, as comprehensively reviewed by several authors (Mata et al. 2010, Rizwan et al. 2018, Wollmann et al. 2019, Singh et al. 2020, Gonçalves 2021, Sousa et al. 2022). Applications generally include phycoremediation and biomass production for several applications, such as pharmaceuticals, cosmetics, feed, food additives, bioenergy, and so on (Ramanan et al. 2016, Vale et al. 2022). However, the bottlenecks of microalgae-suspended culturing systems limit their applicability (Mantzorou and Ververidis 2019).

Limitations in microalgae cultures can potentially be tackled by understanding their interactions with co-occurring species, thereby facilitating the growth of microalgal biomass (see the section 'Assembly and evolution of a microalgae–bacterial community') and the production of desired compounds (see the section 'Metabolic exchange and communication'). The limitations in microalgal cultures could potentially be addressed by understanding their interactions with co-occuring species, and thus facilitating microalgal biomass growth (see the section 'Assembly and evolution of a microalgae–bacterial community') and the production of desired compounds (see the section 'Metabolic exchange and communication'). In particular, the low biomass production rates and harvesting costs can be overcome by the use of microalgal biofilms (Ramanan et al. 2016, Mantzorou and Ververidis 2019, Moreno Osorio et al. 2021, Qixin et al. 2022), where the presence of bacteria, whether from inevitable environmental contamination (deriving from photobioreactors or wastewater) or the exogenous addition of a particular species, is becoming of biotechnological interest (Ramanan et al. 2016, Gonçalves et al. 2017). Biorefineries, i.e. a biotechnological process of sustainably converting biological material into multiple products, can be expected to contribute to the bioeconomy transition. Mutualistic interactions with bacteria will reflect an increase in microalgae biomass productivity and the production of bio-based valuable products, bioenergy, and new sources of functional food (Ramanan et al. 2016). In Zhang et al. (2018b), the influence of the bacteria naturally present in wastewater was assessed on the potential for biofuel production by microalgae. The authors found that QS molecules upregulated the enzymes involved in fatty acid synthesis, resulting in an 88% increase in lipid productivity by *Chlorophyta* sp. Furthermore, biomass harvest, which accounts for most of the costs associated with microalgae production, benefits from the presence of bacteria since several species have shown to induce sedimentation/bioflocculation (Li et al. 2019, Nguyen et al. 2019). Nguyen et al. (2019) found 92% *C. vulgaris* settling efficiency by bioflocculation with bacteria from wastewater. Zhou et al. (2017) reported that the formation of bioflocs was related to QS mechanisms as 41% settling efficiency of *Chlorophyta* sp. was achieved in response to QS molecules produced by sludge bacteria. Finally, in the extraction of microalgae components, algicidal bacteria can be used to facilitate the disruption of microalgal walls, with lower costs than conventional methods (Lenneman et al. 2014, Demuez et al. 2015, Wang et al. 2020). Ren et al. (2010) found that *P. aeruginosa* exhibited algicidal activity against *M. aeruginos*a, a species associated with cyanobacterial blooms, through the release of algicidal compounds (e.g. hydroxyphenazin and oxychlororaphine). Furthermore, several works have shown the advantages of mixed cultures in the bioremediation of wastewater, to remove specific nutrients (Gonçalves et al. 2016, Sun et al. 2018, Makut et al. 2019), metals (Batool et al. 2019, Yang et al. 2020), and emerging contaminants (Eio et al. 2015, Ismail et al. 2016, da Silva Rodrigues et al. 2020, Kahla et al. 2021).

Associations of microalgae and bacteria in biofilm have also been studied for several applications, particularly for wastewater treatment. Microbial immobilized systems are particularly interesting for wastewater treatment due to the simpler biomass harvesting, higher biomass density, resilience to toxic conditions, and lower operating costs (Ramanan et al. 2016, Sousa et al. 2022). Several reports already addressed wastewater treatment with periphyton. Sutherland and Craggs (2017) reviewed the use of periphyton-based nutrient removal systems (e.g. algal turf scrubbers, periphyton-based storm-water treatment areas, periphyton filters, and filamentous algae pond systems) to reduce nutrient loads to waterways, highlighting its economic advantage, lower land requirements, and recovery of secondary products. Zhao et al. (2022) employed a periphyton grown on basalt fibre to efficiently remove N and P from water, achieving 90% and 97% removal, respectively. Similarly, Kebede-Westhead et al. (2003) employed periphyton to treat dairy manure wastewater and found removal rates of 70 and 13 mg (g dry weight m^2 $d)^{-1}$, for N and P, respectively. Regarding the removal of chemical contaminants, Kang et al. (2018) studied the removal of pharmaceuticals and personal care products by periphyton grown on glass plates and found efficient removals for the contaminants bisphenol A, hydrochlorothiazide and ibuprofen. Similarly, Feng et al. (2017) developed a hybrid adsorption-periphyton reactor that removed 99.95% of methylene blue from wastewater. Furthermore, Lu et al. (2018) showed that periphyton can grow on salt-affected surfaces, reducing its salt content, and, as an organic fertilizer, can improve soil nutrient content. Wu et al. (2010, 2011) applied periphyton to control harmful algal blooms. The decrease in the water content on P and the release of allelochemicals by the periphyton helped control cyanobacterial blooms (Wu et al. 2010, 2011).

The periphyton biomass has potential biotechnological applications. de Souza et al. (2020) found that lipids, carbohydrates,

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antioxidants, proteins, and pigments were present in the periphyton biomass after bioremediation with an algal turf scrubber. Proteins can be used for feed, carbohydrates for biofuels (bioethanol, biohydrogen, and biogas), antioxidants in the pharmaceutical industry, and pigments in cosmetics and food (de Souza et al. 2020). Furthermore, periphytic biomass also has the potential for biodiesel production from lipids (de Souza et al. 2020). However, the contamination of biomass by metals may limit its value (de Souza et al. 2020). Another well-described application of periphyton is in aquaculture, where the composition of the feed is important to determine the quality of the fish (Fuentes et al. 2016). Savonitto et al. (2021) used periphyton from marine biofilters as feed and reported higher protein content in fed fish, meanwhile reducing aquaculture production costs and contributing to a circular economy. Toi et al. (2014) found that feeding *Artemia* with both microalgae and bacteria improved N assimilation. Similarly, Guttman (2019) applied periphyton to remove N from an aquaculture effluent and later applied the biomass to feed the fish.

Concluding remarks

Periphyton is a key player in aquatic ecosystems, dominated by complex interkingdom interactions. Microalgae, specifically Bacillarophycaea, Chlorophycaea, and Cyanophycaea, are known to be the main constituents of periphyton. Bacteria, mainly Proteobacteria and Bacteroidetes, are commonly associated with microalgae, earning from a stimulating environment to grow. The main environmental parameters that influence periphyton are irradiation and fluid dynamics, determining the dominance of diatoms under low temperature, high turbulence and irradiation conditions, and the dominance of phototrophs at the top and heterotrophs at the bottom side of periphyton. Furthermore, cyanobacteria dominance is linked to eutrophication and loss of biodiversity, negatively impacting ecosystems. Besides, rather than species-specific interactions, functional genes were found to govern the interactions. In this review, we have further summarized the important functional aspects of microalgae-associated bacteria. The broad metabolic exchanges between species, ranging from cooperative to competitive, are gaining understanding through recent concepts such as substrate exchange, gene transfer and cell-cell communication. Furthermore, mathematical models help unravel population dynamics and metabolic interactions, contributing to understanding the impact of human-made disturbances on aquatic ecosystems and the control of harmful algae blooms. Therefore, recent advances help to unravel the biodiversity of the communities, as well as functional aspects. However, the links between the variety of species found in biofilms and their functions remain to be understood. Interactions in periphyton can be exploited for diverse biotechnological applications. The growth benefits from microalgae cultivation in the presence of bacteria provide an approach of potential impact for biorefinery industries and aquaculture. Likewise, an enhancement of water bioremediation is achieved by these microbial communities. On the other side, algicidal bacteria in periphyton are of interest to control harmful algae blooms. In general, the use of consortia of microorganisms rather than single species, drawing inspiration from natural periphyton, has the potential to boost the kinetics and metabolic yield of biotechnological processes.

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