



## Review

# Epiphytic biofilms in freshwater and interactions with macrophytes: Current understanding and future directions

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## ABSTRACT

Epiphytic biofilm is an important component in freshwater ecosystems and is one of the main primary producers in shallow freshwater ecosystems. The epiphytic biofilm is comprised of an autotrophic community made up of diatoms, green algae, and cyanobacteria, and a heterotrophic community consisting of bacteria, protozoa, fungi, and other microorganisms. Macrophytes are the host domain for epiphytic biofilm, providing substrate and influencing epiphytic biofilm via structural characteristics. Strong competitive, mutualistic, and commensalistic relationships between epiphytic biofilm and macrophytes have resulted from interactions for resources (e.g., light and nutrients) and trophic and allelopathic dynamics. Even though these interactions have wider implications on ecosystem structure, function, and integrity, the current understanding of epiphytic biofilm-macrophyte interactions is limited. In this review, we highlight the current understanding of epiphytic biofilms in freshwater ecosystems and synthesize their different interactions with macrophytes by providing illustrative examples. Furthermore, we identify key areas where research is currently lacking and provide directions for future research in this field, which will allow for better integrated aquatic ecosystem management and conservation strategies.

## 1. Introduction

Biofilms are complex microbial assemblages with a pronounced three-dimensional architecture that attach to solid surfaces and are surrounded by a self-produced matrix composed of extracellular polymeric substance (EPS) (Castiblanco and Sundin, 2016). Periphyton are biofilms attached to any submerged surfaces (Gubelit and Grossart, 2020), whereas ‘epiphytic biofilm’ occurs on aboveground surfaces of macrophytes. Macrophytes are macroscopic autotrophs growing as submerged, emergent, and floating forms in aquatic ecosystems (Chambers et al., 2007).

Epiphytic biofilm plays multiple roles in aquatic ecosystems (Fig. 1) and is important for maintaining ecosystem structure, specifically community composition and diversity (Jones and Thorner, 2010) and

functions, such as primary production and respiration (Allen, 1971; Alnoe et al., 2016; Cattaneo and Kalff, 1979; Sand-Jensen et al., 1989; Shamsudin and Sleight, 1995; Squires et al., 2009; Vadeboncoeur and Steinman, 2002), trophic interactions (Brönmark, 1985; Jones and Sayer, 2003; Vadeboncoeur and Steinman, 2002), nutrient uptake and cycling (Levi et al., 2015, 2017; Sudo et al., 1978; Vadeboncoeur and Steinman, 2002), decomposition (Rybakova, 2010; Sudo et al., 1978), pollutant removal (Lindell et al., 2016; Phillips et al., 2010), and microbial gene pool preservation (Levi et al., 2017; Rusznyák et al., 2008). Macrophytes are ‘ecosystem engineers’ as they shape the physical properties of aquatic ecosystems; they alter hydraulics by resisting water flow, aid in sediment particle settlement, and influence light availability by shading and maintaining clear water status (Polvi and Sarneel, 2018). Furthermore, macrophytes regulate water chemistry (e.g., dissolved

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oxygen, carbon, and nutrients) and support other aquatic biota and biological processes such as primary production and grazing (Lacoul and Freedman, 2006; O'Hare et al., 2018; Thomaz and Cunha, 2010). In addition, macrophytes are ideal substrates for microbial growth forming macrophyte-biofilm platforms which display unique, complex, and interdependent biological interactions (Eriksson, 2001). The broader periphyton structure and function has been previously reviewed (Gubelit and Grossart, 2020; Larned, 2010; Sand-Jensen and Borum, 1991; Vadeboncoeur and Steinman, 2002), but here we focus on the epiphytic biofilm on freshwater macrophytes. Despite the importance of macrophytes and their biofilms in freshwater systems, there are no comprehensive reviews on their interactions.

Epiphytic biofilms on live macrophytes are different and unique in both structure and function compared to the other periphytic biofilms in inert freshwater habitats (e.g., sand: epipsammon, stone/rock: epilithon, and sediment: epipelton) (Levi et al., 2017). Autotrophic communities in epiphytic biofilm are usually dominated by diatoms, green algae, cyanobacteria, and euglenoids (Costică et al., 2018; Shamsudin and Sleight, 1995; Xia et al., 2020), and dominant algal groups may differ with season and grazing pressure (Jones and Sayer, 2003; Roberts et al., 2003). The heterotrophic community comprises bacteria, protozoa, fungi, and other microorganisms, whereas the bacterial community of epiphytic biofilm is typically dominated by Bacteroidetes, Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria, and a low abundance of Actinobacteria and Planctomycetes (Hempel et al., 2008, 2009; Levi et al., 2017; Xia et al., 2020). Some studies have shown that the epiphytic biofilm has a higher species diversity and presence of unique species than epilithon and epipsammon (Bojorge-García et al., 2014; Levi et al., 2017). In addition, some studies have emphasized that the epiphytic biofilm has lower algal biomass and carbon to nitrogen to phosphorous (C:N:P) ratios compared to epilithon in both lentic (Kahlert and Pettersson, 2002; Wolters et al., 2019) and lotic ecosystems (Belyaeva, 2017). However, the significance of these differences of epiphytic biofilms compared to biofilms on inert substrates in eutrophic freshwater ecosystems is still being debated (Eminson and Moss, 1980; Kahlert and Pettersson, 2002). With regard to reach-scale metabolism in streams, macrophyte habitats (i.e., consisting of both macrophyte and epiphytic biofilm) have shown considerably higher metabolic rates than inert habitats, such as epipsammon and epilithon (Alnoe et al., 2016). Furthermore, a comparative assessment of biomass-specific summertime nutrient uptake rates in streams has shown that epiphytic biofilm is

more efficient in  $\text{NH}_4\text{-N}$  and  $\text{PO}_4\text{-P}$  uptake than benthic biofilms (Levi et al., 2015; Wijewardene et al., unpublished data). Epiphytic biofilm also plays an active role in the nitrification/denitrification processes (Eriksson, 2001; Eriksson and Weisner, 1999) where nitrate assimilation is lower in epiphytic biofilms compared to epipelton in summer stream biofilms (Kreiling et al., 2011).

Although epiphyton on terrestrial plants have been studied for several centuries, surveys on aquatic epiphyton only came into prominence at the beginning of the 20th century. Fritsch (1907a, 1907b) studied epiphytic communities on aquatic plants in the former British colonial island of Ceylon. Since then, investigations on aquatic epiphytes have expanded rapidly (Fig. S1). Epiphytic structural-functional characteristics are correlated with environmental variables, such as water level, flow velocity, light intensity, temperature, pH, conductivity, dissolved oxygen, turbidity, nutrients, and chloride concentrations (Adam et al., 2017; Eriksson, 2001; Hempel et al., 2009; Lévesque et al., 2017; Morin and Kimball, 1983; Phiri et al., 2007). Environmental variables can affect epiphytic biofilm directly and indirectly via changes to the macrophyte vegetation (O'Hare et al., 2018; Sultana et al., 2010). Some studies suggest that epiphytic biofilm is less sensitive to ambient environmental variables and more dependent on the interactions between macrophyte and biofilm (Lv et al., 2019; Morin and Kimball, 1983). There is still little understanding on epiphytic biofilm-macrophyte specific relationships.

Epiphytic biofilms are understudied compared to other periphytic biofilms in freshwater ecosystems. This is surprising as epiphytic biofilm-macrophyte specific interactions interfere with important ecosystem processes and these interactions are highly complex. To understand the dynamics of macrophyte-dominated ecosystems under continuous anthropogenic influences, we need to gain a better understanding of biofilm-macrophyte interactions, their link with environmental variables, and ecosystem scale implications. Lack of understanding of these interactions may underestimate the importance of macrophyte habitats in freshwater ecosystems due to ignorance of the role macrophytes play as a substrate for microbial biofilm. Therefore, our objectives in this review are (i) to describe the present understanding of the epiphytic biofilm and their interactions with macrophytes. This includes how freshwater macrophytes influence their epiphytic biofilms, how the biofilms are influenced by environmental variables, and how biofilm-macrophyte interactions are impacted by different types of resources. Objective (ii) is to highlight knowledge gaps

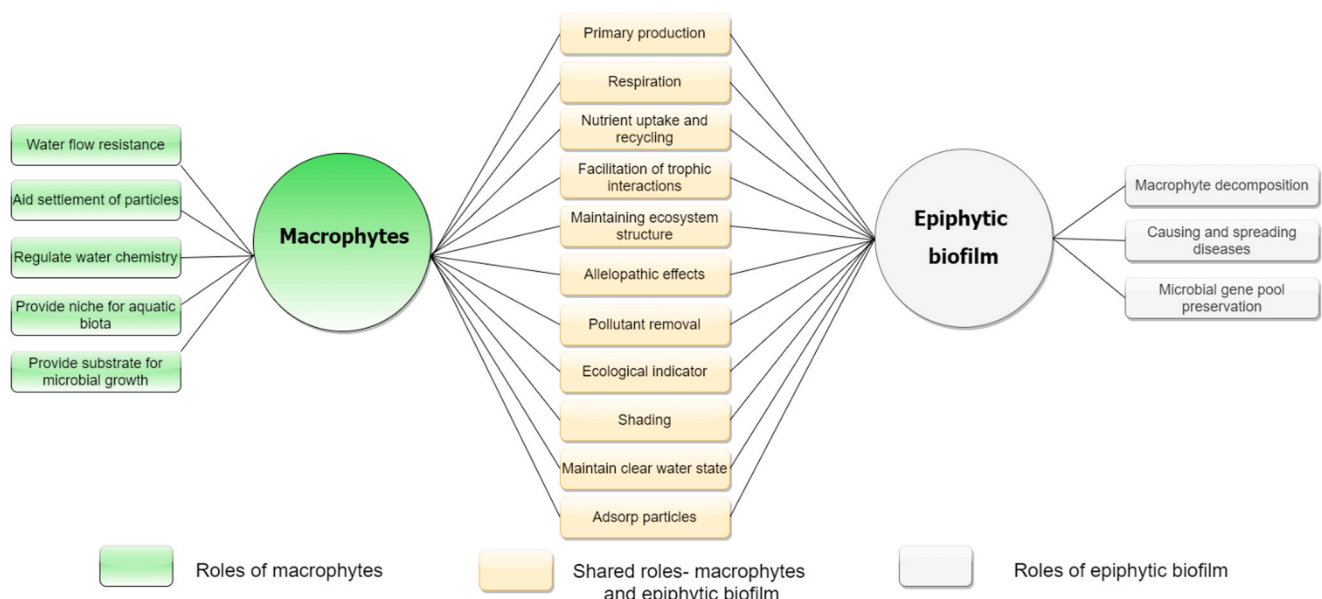


Fig. 1. Separate and combined roles of epiphytic biofilm and macrophytes in aquatic ecosystems.

on this subject and provide directions on future research.

## 2. Methods

Literature was searched on Web of Science (Thomson Reuters) using keywords “macrophyte” and “biofilm” and other relevant keywords in the titles of articles published from 1955 to 2020. The search query was built as below: TI = (macrophyte OR aquatic plant OR hydrophyte OR plant OR macrophytic OR macroalgae OR higher aquatic plant OR aquatic macrophyte OR emergent plant OR submerged plant OR submerged plant OR submerged vegetation OR floating-leaved plant OR free-floating plant OR aquatic autotrophs OR aquatic vascular plants) AND TI = (biofilm OR microbial community OR autotrophic biofilm community OR heterotrophic biofilm community OR epiphytic algae OR epiphytic diatom OR algae OR algal OR diatom OR cyanobacteria OR epiphyte OR epiphyton OR periphyton OR attached alga OR microalgae OR epiphytic flora OR ephiphytism OR bacterial community OR bacterioplankton OR biofilm metacommunity). 3425 references were initially extracted based on keywords defined. We supplied 28 older references (1900–1954) by using the same keywords in the advanced search query on Google Scholar™. By carefully reading titles, abstracts, and the papers (main text), we identified 810 relevant marine and freshwater ecosystem references. We focused on only the 251 freshwater references in this overview, which included studies in artificial freshwater systems such as mesocosms and theoretical modeling studies. We emphasize that this is not an exhaustive review, but rather an overview of the subject matter.

Temporal trends of the publications are illustrated in Fig. S1. Both the annual number of publications and their proportion to the total scientific articles of the databases showed a linear increase over time. Geographical distribution of selected articles for this study are represented in Fig. S2. Most of the studies were performed in lakes, whereas

the structural diversity and functional capabilities of the epiphytic biofilm in stream ecosystems has received less attention, even though they are the main sites for solute cycling in the landscape. In addition, when describing the epiphytic community structure, most studies have solely paid attention to either autotrophic or heterotrophic communities. Of these two, the autotrophic community of the epiphytic biofilm has been more comprehensively studied compared to the heterotrophic community, and community-wide investigations covering both autotrophs and heterotrophs are rare (but see: Gubelit and Grossart, 2020; Levi et al., 2017). The main interactions were identified as the provision of substrate, interactions with resources (light and nutrients), trophic interactions, allelopathy and other interactions on flow, diseases, and pollutants.

## 3. Interactions between epiphytic biofilm and macrophytes

Epiphytic biofilm and macrophytes form a highly interactive unit with the provision of substrate, competition for resources (e.g., light and nutrients), trophic interactions (e.g., herbivory and carnivory), allelopathic interactions, interactions related to flow, diseases, and pollutants – all of which can be categorized into competitive (-/-), mutualistic (+/+), and commensalistic (+/0) interactions under different scenarios (Figs. 2 and 3).

### 3.1. Provision of substrate

Direct interaction between macrophyte and epiphytic biofilm are the result of the provision of substrate for attachment (Fig. 2). Most of the reviewed studies indicate host-plant species specificity on structure and function of the epiphytic biofilm (Adam et al., 2017; Calheiros et al., 2010; Ferreira et al., 2013; Hempel et al., 2008; Lalonde and Downing, 1991; Prowse, 1959; Toporowska et al., 2008; Tóth, 2013; Tunca et al.,

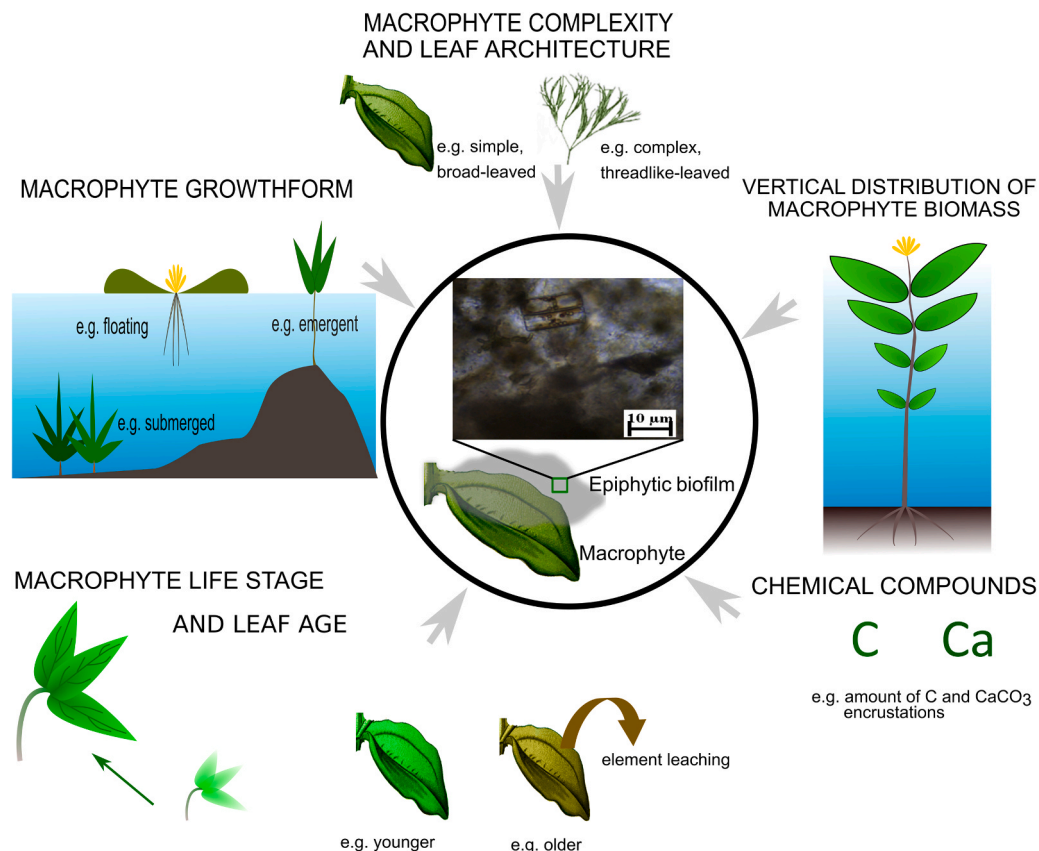
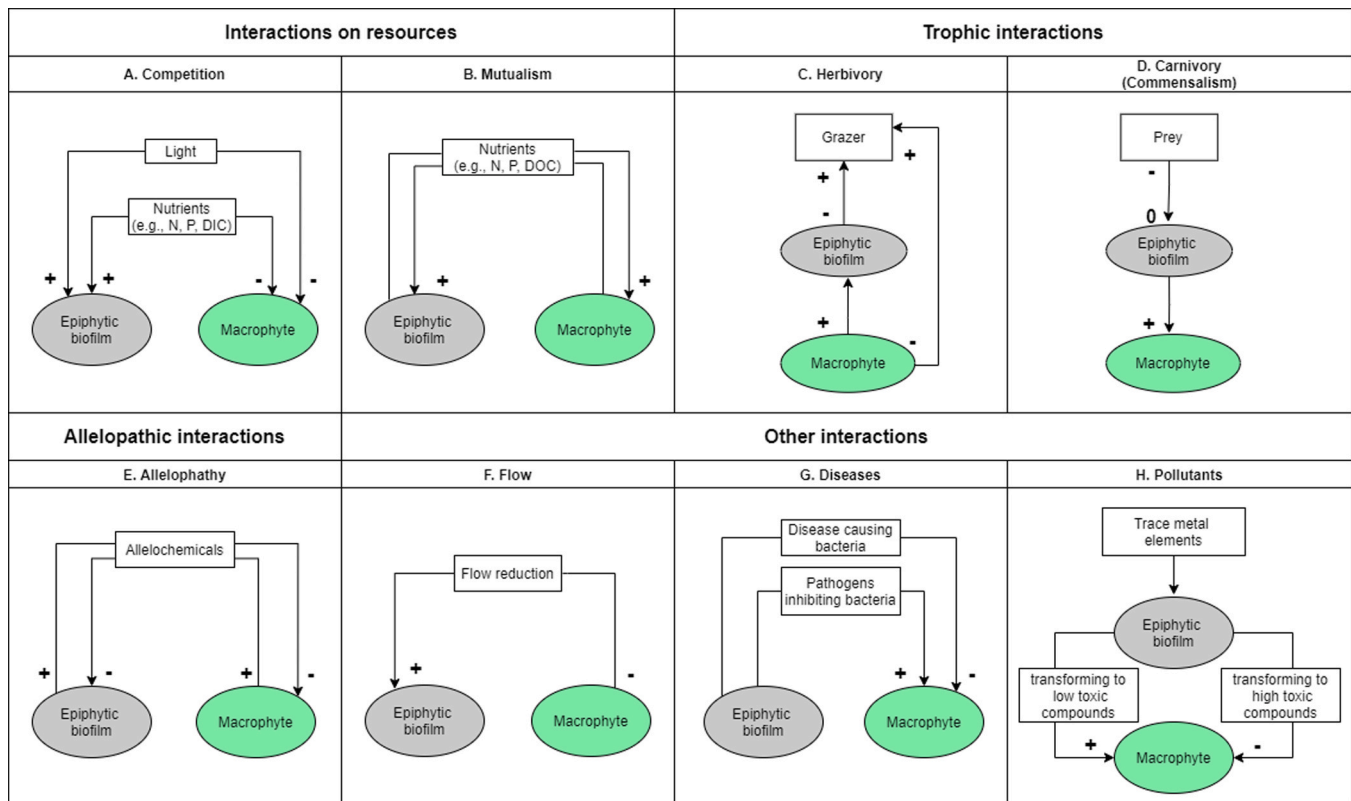


Fig. 2. Macrophyte characteristics affecting the epiphytic biofilm.



**Fig. 3.** Interactions between epiphytic biofilm and macrophytes. N, P, DIC and DOC indicate the nitrogen, phosphorous, dissolved inorganic carbon and dissolved organic carbon, respectively. In interactions: +, - and 0 signs imply the positive, negative, and neutral effects, respectively.

2014). Toporowska et al. (2008) found that species composition of epiphytic algae was different according to the host macrophyte (i.e., *Stratiotes aloides*, *Potamogeton lucens*, *Ceratophyllum demersum*, and *Chara* spp). In contrast, some other studies claimed macrophytes to be a neutral substrate for epiphytes (Cattaneo and Kalff, 1979; Frankova et al., 2017; Millie and Lowe, 1983; Shamsudin and Sleight, 1995). Cattaneo and Kalff (1979) studied epiphyton biomass and primary production on natural *Potamogeton richardsonii* plants and morphologically equivalent plastic plants and found no difference in studied parameters between natural and artificial plants. Host-species specificity is high in oligotrophic waters compared to eutrophic waters (Eminson and Moss, 1980; Lalonde and Downing, 1991), which emphasizes that the environmental variables are a potential cause for the lack of host-species specificity.

Structural characteristics of macrophytes (e.g., complexity, growth form, life stage, vertical distribution of biomass, leaf architecture, and leaf age) directly influence the epiphytic biofilm structure (Ferreiro et al., 2013; Lalonde and Downing, 1991; Laugaste and Reunanen, 2005; Pettit et al., 2016; Tóth, 2013) (Fig. 2). Higher morphological complexity of macrophytes (e.g., high perimeter to surface area ratio, high fractal dimension, high species complexity index) supports high epiphytic biofilm biomass and diversity due to enhanced niche diversity (Ferreiro et al., 2013; Hinojosa-Garro et al., 2010; Levi et al., 2017; Pettit et al., 2016). Levi et al. (2017) found that the least complex macrophyte, *Sparganium emersum*, had lower richness and evenness compared to the more morphologically complex macrophyte, *Callitriche* spp. However, Casartelli and Ferragut (2018) have highlighted that these differences in epiphyte density or diversity related to macrophyte complexity may highly depend on the colonization time (e.g., early colonization vs. mature biofilm). Depending on the growth form of macrophytes, submerged plants tend to possess the highest epiphyte abundance, chlorophyll-*a*, biomass, and diversity compared to other growth forms of the aquatic macrophytes since they grow just below the water surface,

which allows higher light penetration and provides a complex and large surface area for epiphyte development (Laugaste and Reunanen, 2005; Pettit et al., 2016). Leaf architecture (e.g., size, shape, flexibility) may affect epiphytic biofilm biomass, abundance, and diversity. For example, ribbon like flexible leaves (e.g., *Vallisneria americana*) had lower epiphytic algal biomass compared to broad-leaved (e.g., *Elodea canadensis*) or whorled leaved macrophytes (e.g., *Myriophyllum spicatum*) (Lalonde and Downing, 1991). The number of bacterial cells per plant area was higher in *Myriophyllum spicatum* than in *Potamogeton perfoliatus* due to a higher surface to volume ratio and whorl-like structure (Hempel et al., 2009).

In addition to plant and leaf complexity, the abundance and diversity of epiphytic algae and bacteria also increases with age of the macrophyte leaves and some of the primary and secondary colonizers even stay present after the death of the host leaves (Rogers and Breen, 1981). These senescing macrophytes are important nutrient reserves for the epiphytic biofilm (Borrego-Ramos et al., 2019; Brönmark, 1989; Carpenter and Lodge, 1986; Xia et al., 2020). Borrego-Ramos et al. (2019) observed higher diatom richness on dead macrophyte stems compared to live macrophytes. Vertical biomass distribution of aquatic macrophytes also tends to influence the mean epiphyton abundance, biomass, cell size, and rate of species succession (Romo and Galanti, 1998), in particular, due to changes in light availability from the edge to the bottom of a macrophyte bed. Apart from macrophyte structural characteristics, the chemical composition of macrophytes, such as the content of carbon, calcium carbonate ( $\text{CaCO}_3$ ) encrustations, and total phenolic compounds, affect biofilm community composition (Hempel et al., 2008, 2009; Wolters et al., 2019). In the study of Wolters et al. (2019), the density of epiphytic bacteria negatively correlates with biofilm  $\text{CaCO}_3$  content from macrophytes. They reasoned that  $\text{CaCO}_3$  encrustations may adsorb free dissolved organic carbon (DOC), amino and fatty acids, and then limit them for use by the bacterial community. The links between the characteristics of macrophyte species and the



epiphytic biofilm structure means that macrophyte richness and coverage will affect the epiphytic algal abundance and taxonomic composition on the ecosystem scale (Casartelli and Ferragut, 2015; de Souza et al., 2015).

### 3.2. Interactions on resources: light

The autotrophic community in the epiphytic biofilm shows a rapid response to light. Epiphytic algal density and biomass show a positive relationship with light intensity up to a saturation level or until another limiting factor for photosynthesis emerges (Lévesque et al., 2017; Sultana et al., 2004). Sultana et al. (2004) investigated colonization and growth of epiphytic algae under two light regimes, i.e., low:  $80 \mu\text{mol m}^{-2} \text{s}^{-1}$  and high:  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ . While the species composition of the most abundant epiphytic algae did not change under the two light regimes, a subset of unique rare species had developed under each light regime. Furthermore, vertical distribution of the epiphytic algae under both light levels showed that the basal part of macrophytes were inhabited by a homogenous community of the epiphytic algae while the apical plant parts were occupied with a mosaic community.

Asaeda et al. (2004) and Tóth (2013) showed a 60–80% reduction in macrophyte production due to direct competition for light between epiphytic biofilm and macrophytes (Fig. 3A). A large part of the light reaching the leaf surface of macrophytes is attenuated by the epiphytic biofilm, which can be > 80% under high nutrient conditions (Raeder et al., 2010; Sand-Jensen and Søndergaard, 1981). In eutrophic freshwater ecosystems, shading by the epiphytic biofilm has been identified as a main cause for drastic reduction of submerged vegetation in late summer (Min et al., 2017; O'Hare et al., 2018; Phillips et al., 1978; Song et al., 2017a). Additionally, the shading effect of epiphytic biofilm becomes crucial for macrophytes in shaded or light-limited environments (Köhler et al., 2010; Sand-Jensen and Revsbech, 1987). Contrary to the well-known negative effect of epiphytic biofilm on macrophyte light availability, epiphyton has been identified as a protective cover for macrophytes from desiccation and harmful short-wave radiation such as UV (Gaiser et al., 2011; Klančnik et al., 2015). Klančnik et al. (2015) studied the effects of epiphyton on the quality and quantity of radiation transmitted through the leaf tissue of submerged macrophytes. They have found that removal of epiphyton significantly increased the transmittance of short-wave radiation and have emphasized the role of the epiphyton dominated by diatoms for the prevention of potential harmful effects of short-wave radiation.

Compared to studies on the shading effects of epiphytic biofilm on macrophytes, investigations into the macrophyte shading effect on epiphytes are limited. However, where macrophyte biomass is dense, epiphytic production is strongly constrained by macrophyte shading (Morin and Kimball, 1983; Squires et al., 2009). Alteration of light penetration from macrophytes is identified as major determinant of the epiphytic biomass, while macrophyte biomass and their epiphyton were inversely correlated (Cattaneo et al., 1998; Gosselain et al., 2005; Pettit et al., 2016). This tends to also affect the functional role of epiphytes, for example, strong vertical gradients in metabolism (Vis et al., 2006) and nutrient uptake (T. Riis, unpublished data). Generally, macrophytes show morphological (e.g., average number of leaves, total shoot length, number of newly recruited shoots, and stem diameter) and physiological (e.g., expansion or contraction of leaf area) adaptations to optimize light availability (Asaeda et al., 2004; Riis et al., 2012; Sultana et al., 2010). Although macrophytes shaded by epiphytic algae do not show significant adaptations to overcome the light limitation (Asaeda et al., 2004), long-term colonization of epiphyton and its shading effect can induce morphological changes in aquatic macrophytes (Sultana et al., 2010). Recent studies on light competition between epiphytic biofilm and macrophytes, focus on modeling approaches to tackle this complex relationship (Zhang et al., 2015, 2018).

### 3.3. Interactions on resources: nutrients

Elevated chlorophyll-*a* content, biomass, primary production, and a shift in species composition or decreased diversity are the initial responses of the epiphytic biofilm to nutrient enrichment in the surrounding water (Bécares et al., 2008; Mei and Zhang, 2015; Min et al., 2017; Romo et al., 2007; Song et al., 2017a). In mesocosm experiments, the increment of epiphytic biomass and chlorophyll-*a* were higher in the combined N and P nutrient treatments compared to individual N or P nutrient treatments (Ray et al., 2014). Nevertheless, P is considered a key nutrient in most studies, as it plays a major role in freshwater systems. Romo et al. (2007) stated that levels above  $0.1\text{--}0.2 \text{ mg L}^{-1}$  P prevent the coexistence of macrophyte, epiphytic biofilm, and phytoplankton resulting in a reduction of submerged macrophyte biomass. According to Lalonde and Downing (1991), a weak and non-linear relationship was found between total P (TP) and epiphytic biomass, where epiphytic biomass increased until  $0.039 \text{ mg L}^{-1}$  TP but decreased at higher levels in their study conducted in 11 lakes in Canada based on macrophytes such as *Elodea canadensis*, *Myriophyllum spicatum*, *Vallisneria americana*, and *Potamogeton* spp. However, in Romo et al. (2007), epiphytic biomass increased linearly with increased TP up to  $0.35 \text{ mg L}^{-1}$  TP in their mesocosms study conducted in a Mediterranean lake dominated with *Chara* spp. and *Phragmites australis*. In addition, different epiphytic algae show differences in P source dependency. For example, filamentous *Mougeotia* and long-stalked *Gomphonema* depend on external water for P while small adnate forms like *Acanthes* depend on macrophytes for 20–60% of their P requirement (Moeller et al., 1988).

The direct interaction between epiphytic biofilm and macrophytes for nutrients is difficult to isolate since the consequences are shared with different compartments of the environment, such as the epiphytic biofilm, macrophytes, phytoplankton in surrounding water, and sediments. Rooted macrophytes may exclusively depend on sediment nutrients, while epiphytic biofilms have limited access to sediment nutrients and mostly depend on nutrients in the water column, nutrient release from macrophytes or internal nutrient sources (Allen, 1971; Moeller et al., 1988; Périllon and Hilt, 2019). There is overwhelming evidence to support the hypothesis that epiphytic biofilm and macrophytes are competitors for nutrients (e.g., O'Hare et al., 2018; Périllon and Hilt, 2019; Romo et al., 2007; Xie et al., 2013) (Fig. 3A). Mechanisms underlying the suppression of aquatic vegetation through a rapid increase of epiphyte biomass and its shading effect under mesotrophic and eutrophic scenarios are well-studied (e.g., Bécares et al., 2008; Phillips et al., 1978) and were revised recently by adding the roles of competitive and non-competitive macrophytes (O'Hare et al., 2018). Initially, abundance, density, and biomass of both epiphytic algae and macrophytes increase with nutrient enrichment, but with increasing eutrophication macrophytes lose the competition due to light limitation by epiphytic shading. Moreover, recent studies suggest that physiological changes occur in macrophytes (e.g., increased antioxidant enzyme activities, reduced chlorophyll content, and promoted peroxidation of membrane lipids) due to nutrient enrichments, which further enhances these deleterious effects (Min et al., 2017; Song et al., 2017a). In addition to N and P, the epiphytic biofilm and macrophytes are also competing for dissolved inorganic carbon (DIC) (Jones et al., 2002; Wolters et al., 2019; Xie et al., 2013). Epiphytic algae and macrophyte density were negatively correlated and the steepness of the slope decreased with increasing DIC concentrations, emphasizing competition for DIC between them (Jones et al., 2002).

However, studies have suggested mutualistic interactions also for nutrients between epiphytic biofilm and macrophytes (Fig. 3B). The epiphytic biofilm benefits from living macrophyte nutrient exudates (Kahlert and Pettersson, 2002; Wolters et al., 2019) resulting in effects on epiphytic biofilm biomass and nutritional value (e.g., lower C:N:P molar ratio). According to Burkholder and Wetzel (1990), the main source of P for epiphytes is the host macrophyte during the growing

season, but Carignan and Kalff (1982) and Moeller et al. (1988) found that living macrophytes release very little P for epiphytes (e.g., ca. 3.4–9%; Carignan and Kalff, 1982 and ca. 2%; Moeller et al., 1988). Wolters et al. (2019) stated that nutrient release (e.g., N, P, and DOC) of both living and senescing macrophytes may affect associated epiphytic biofilm. DOC exudations of both living and senescing macrophytes may support the heterotrophic community of the epiphytic biofilm (Demarty and Prairie, 2009; Xia et al., 2020). In this mutualistic interaction, macrophytes can benefit from N fixation (Srivastava et al., 2017) occurring in epiphytic biofilm community. Hempel et al. (2008) listed the positive effects of epiphytic biofilm on macrophytes linked with nutrient interactions as (i) providing organic compounds and carbon dioxide and (ii) enhancing nutrient recycling.

### 3.4. Trophic interactions

Epiphytic biofilm is important for primary production in freshwater systems and as a site of trophic interactions benefitting both macrophytes and the epiphytic biofilm. Fast growth and high nutrition value of epiphytic algae make it an important food source for secondary producers in shallow aquatic ecosystems (Jaschinski et al., 2011; Jones et al., 1999). The epiphytic algae initiate a crucial food web that include lower trophic level invertebrates (e.g., micrograzers, meiofauna, herbivore macroinvertebrates) and higher trophic level organisms, such as fish (Brönmark and Vermaat, 1998; Jones and Sayer, 2003). Invertebrates show differential preference toward various epiphytic algae types: stalked and tubular diatoms are usually preferred by nematodes, rotifers induce grazing pressure on prostrate diatoms, while both rotifers and ciliates show a preference for *Cocconeis*-type diatoms (Albay and Aykulu, 2002).

Macrophytes are susceptible for direct herbivory by grazers. However, macrophytes and grazers have a mutualistic relationship driven by epiphyte-dependent trophic interactions (Jones et al., 1999; Underwood et al., 1992) (Fig. 3C). Macrophytes benefit from grazers (e.g., by increased survival, growth, and biomass) since they can release the macrophytes from epiphytes that compete for resources and provide nutrients to the macrophytes from their excretory by-products (Brönmark, 1985, 1989; Jones et al., 1999; Underwood et al., 1992). In return, macrophytes support macroinvertebrate grazers “by providing a large surface area for colonization by epiphytic algae and bacteria, by improving biofilm stoichiometry and by stimulating bacterial growth” (quote: Wolters et al., 2019). The epiphytic biofilm acts as a protective cover that shields macrophytes from grazer-induced damages (Dudley, 1992). Further, carnivorous macrophytes (e.g., *Utricularia* spp.) use the epiphytic biofilm to facilitate prey utilization resulting in a commensalistic trophic relationship (Caravieri et al., 2014; Diaz-Olarte and Duque, 2009; Diaz-Olarte et al., 2007; Pitsch et al., 2017; Šimek et al., 2017) (Fig. 3D). Epiphytes also benefit from grazers as the physical disturbance created by grazers allows fast regeneration of epiphytic biofilm while shedding off the thick, old, and dead biofilm (Rodrigues and Bicudo, 2001). The aforementioned trophic interactions are usually considered as an adaptive evolutionary advantage for macrophytes, given that dissolved organic matter released by macrophytes can attract grazers, which can feed on epiphytes (Brönmark, 1985). However, some studies rejected this hypothesis, while stating that chemical signals (e.g., organic compounds) released by certain species of algae in the epiphytic biofilm can attract invertebrates. For example, the epiphytic algae of *Egeria najas* attract the snail, *Hebetancylus moricandi* (Mormul et al., 2010).

### 3.5. Allelopathic interactions

Allelopathy, the secretion of chemical compounds to inhibit growth of other organisms, is another direct interaction between specific macrophytes and epiphytic biofilm for the benefit of their competitive interactions (Fig. 3E) (see Gross, 2003; Mohamed, 2017 for detailed

reviews). Macrophytes, such as *Myriophyllum*, *Ceratophyllum*, *Elodea*, *Najas*, *Stratiotes*, and *Chara* genera, are identified as allelopathic active macrophytes which are able to secrete toxic compounds (e.g., polyphenolic compounds, sulfur compounds) to inhibit the formation, growth, and establishment of epiphytic biofilms (Gross et al., 2003; Hilt, 2006; Hilt and Gross, 2008; Mulderij et al., 2009) and reduce species richness and diversity of epiphytic biofilms (Hai-ting et al., 2013). Among different epiphytic algal groups, diatoms and cyanobacteria show a higher sensitivity to macrophyte allelopathic substances compared to green algae (Erhard and Gross, 2006; Hilt, 2006; Hilt and Gross, 2008). Epiphytic bacterial community composition may differ due to the macrophyte allelopathic compounds and some of these bacterial communities are capable of degrading allelopathic substances (Hempel et al., 2009). Conversely, the epiphytic biofilm might release compounds that are toxic to macrophytes and mainly cyanobacterial species of epiphytic biofilm express this allelopathic interactions (Mohamed, 2017).

Hilt (2006) tested the hypothesis that “epiphyton has higher vulnerability to macrophyte allelopathy than phytoplankton”, but the results indicated low vulnerability of epiphyton to macrophyte (*Myriophyllum spicatum*) allelopathy, showing no impact on epiphytic algal species (i.e., the green algae *Stigeoclonium tenue* and diatom *Gomphonema parvulum*) and even showed increased growth of an epiphytic cyanobacterium (*Oscillatoria limosa*). Similarly, Mohamed and Al Shehri (2010) highlighted that allelopathic compounds of *Stratiotes aloides* supported growth and toxic production of epiphytic cyanobacteria such as *Merismopedia tenuissima* and *Leptolyngbya boryana*. Epiphyton may develop resistance to the allelopathic substances of macrophytes and the mechanism behind this is still being debated as co-evolution and local adaptation (Gross, 2003; Reigosa et al., 1999) or only an algal strain-specific response (Eigemann et al., 2013). Despite numerous studies on allelopathic interaction of macrophytes on epiphytic biofilm and vice versa, the results are often contradictory and differ among macrophyte species and their epiphytes. These differences may be due to differences in (i) scale of experiments (e.g., laboratory studies, mesocosm studies, and studies conducted in natural ecosystems), (ii) extraction methods of allelopathic compounds from the macrophytes, and (iii) source of epiphytic species (e.g., single species or mixed communities).

### 3.6. Interactions with flow velocity

The water flow is crucial to freshwater macrophytes and epiphytic biofilm and derives direct interactions. Macrophytes cause resistance to the water flow and low water velocity aids the colonization and growth of epiphytic biofilm (Fig. 3F). On the other hand, high velocities are beneficial to macrophyte growth as the result of reduced resource competition by sloughing of the epiphytic biofilm (Špoljar et al., 2017). Furthermore, epiphytic biofilm-macrophyte interactions with regards to metabolism of dissolved oxygen / inorganic carbon, nitrification, and denitrification processes may be altered by flow velocities. This is manifested by the flow-induced variations of diffusion rates to and from epiphytic biofilms and by alterations of metabolic rates within the epiphytic community (Eriksson, 2001). Eriksson (2001) studied the macrophyte-epiphytic biofilm complex of *Potamogeton pectinatus* at flow velocities of 0, 0.03, and 9 cm s<sup>-1</sup> and noted a progressive increase of photosynthesis and respiration rates with the flow velocity. Further, flow velocity significantly affected denitrification in epiphytic biofilms. High flow velocities facilitate efficient transport of organic matter to and from epiphytic biofilm-macrophyte interfaces and stagnant water conditions support the bacterial community within the epiphytic biofilm aiding to internal metabolic processes.

### 3.7. Interactions regarding diseases

Diseases can be another direct interaction between epiphytic biofilm

and macrophytes (Fig. 3G). Some evidence suggests that heterotrophic communities in the epiphytic biofilm may cause disease or malformations in macrophytes. Extensive inward swelling, disorganization of the epidermal walls, and degradation of epidermis and mesophyll cell walls were observed following an increase in density and diversity of epiphytic bacteria with macrophyte leaf age (Rogers and Breen, 1981). Contrary to the general negative impact of epiphytic biofilm causing a disease in macrophytes, some bacterial genera (e.g., *Pseudomonas*) in epiphytic biofilm may prevent disease in macrophytes by suppressing pathogenic microorganisms in the biofilm and promote macrophyte growth (Zhao et al., 2017). Xia et al. (2020) observed the presence of bacterial genera such as *Exiguobacterium*, *Pseudomonas*, and *Chryseobacterium* in epiphytic biofilms, which have the potential to inhibit phytopathogenic fungi.

### 3.8. Interactions with water pollutants

Trace metal elements, pesticides, and other pollutants in aquatic ecosystems may adversely affect the structure and function of the epiphytic community in aquatic ecosystems (Mingchao et al., 2013; Wendt-Rasch et al., 2004). This has led to the use of epiphytic communities as an indicator to assess aquatic pollution and biomonitoring of aquatic ecosystems (Kiss et al., 2003; Mingchao et al., 2013; Phiri et al., 2007). There is a direct interaction between a macrophyte and its epiphytic biofilm not only for macroelements like C, N, and P, but also for trace metal elements (Fig. 3H). The trace metal transformation pathway from sediment to macrophyte to epiphytes was traced by Jackson et al. (1994) experimenting on *Myriophyllum spicatum*; they found that  $^{60}\text{Co}$  and  $^{54}\text{Mn}$  of the epiphytes were mostly derived from their host macrophytes.

Moreover, interactions between epiphytic biofilms and macrophytes can cause an increase or decrease in the toxicity of trace metal elements to macrophytes, particularly by the heterotrophic community in the epiphytic biofilm, which contributes to trace metal accumulation and biomagnification through food chains. Epiphytic bacteria tend to accumulate mercury (Hg) and produce methylmercury (MeHg), the latter being much more toxic than the former (Coelho-Souza et al., 2011; Dranguet et al., 2017; Gentes et al., 2017). Beauvais-Flück et al. (2018) found negative impacts of MeHg on the macrophyte, *Elodea nuttallii*, in which antioxidant responses were induced. In contrast, epiphytic bacteria have shown the ability to oxidize trace metal elements and these oxidized compounds are less toxic to the macrophytes than their original state. The production of biogenic Mn oxides in epiphytic biofilms composed of bacterial strains, such as *Acidovorax*, *Comamonas*, *Pseudomonas*, and *Rhizobium*, was reported on the leaf surfaces of *Egeria densa* (Tsuji et al., 2017). Furthermore, to make practical use of their accumulation ability, the use of epiphytic biofilms have been tested and recommended as part of remedial treatment of water polluted with trace metal elements and organic compounds (e.g., *Salvinia minima* recommended to treat coal pile runoff: Lindell et al., 2016; *Typha latifolia* recommended to treat naphthenic acids: Phillips et al., 2010). According to Zhang et al. (2014), macrophyte species may play a more significant role in the removal of pollutants than the epiphytic bacterial community. The specific roles of epiphytic biofilms on the removal of pollutants have been highlighted in recent studies. Further, macrophyte-epiphytic biofilm interactions towards breaking down complex compounds to simple nutrients, metal ion mobilization and inducing uptake of pollutants by macrophytes are also recognized (Srivastava et al., 2017).

### 4. Knowledge gaps and future research directions

Although environmental variables are important drivers of structural and functional properties of epiphytic biofilm, interrelationships among these environmental variables and the effects of combined environmental variables on epiphytic biofilm need more attention in future studies (Flynn et al., 2002). Rather than considering environmental

variables individually, experiments should be designed to observe their combined influence on the epiphytic biofilm, such as shown for epilithon by Guo et al. (2020). In addition, seasonal dynamics of the epiphytic biofilm have only been addressed in a few studies (e.g., Toporowska et al., 2008; Tunca et al., 2014). Most seasonal studies focused on summer months or were largely restricted to four samplings representing the four seasons of the year. Therefore, correlations of environmental variables with structural and functional properties of the epiphytic biofilm should be studied at a high temporal resolution (e.g., Wijewardene et al., unpublished data). Studies on biofilm community trait composition and functional features, such as functional diversity and redundancy, have been performed in epilithic biofilm in order to understand environmental drivers and processes structuring the community (Guo et al., 2020; Wu et al., 2019), but studies related to trait composition of epiphytic biofilm are still rare (e.g., Ács et al., 2019). Including functional traits in future research would greatly expand our current understanding of environmental drivers and processes governing the functionality of epiphytic communities.

Host plant-species specificity and influences of macrophyte characteristics on the epiphytic biofilm are still to be determined. Current studies are restricted to few main genera of macrophytes, such as *Myriophyllum*, *Potamogeton*, *Ceratophyllum*, *Vallisneria*, *Phragmites*, and *Nymphaea*, and investigations are needed to focus on other important macrophyte species to formulate a comprehensive view on the epiphytic biofilm. Furthermore, studies on the reverse scenario, the effect of the epiphytic biofilm structure on macrophyte morphology and other characteristics is greatly lacking (but see, Sultana et al., 2010).

Interactions within the epiphytic biofilm-macrophyte complex for nutrients have received little attention. For example, the use and dependency of macrophytes on nutrients derived from epiphytic biofilm and the use and dependency of epiphytic biofilm on leaching nutrients from macrophytes still need more research. More investigations should be designed to isolate nutrient relationships within this unique platform under various ambient environmental settings, e.g., using advanced tracer experiments of stable isotopes ( $^{15}\text{N}$ ,  $^{32}\text{P}$ , and  $^{13}\text{C}$ ) coupling with nutrient uptake kinetic models (e.g., differentiate abiotic uptake by adsorbing and biotic uptake) (e.g., Scinto and Reddy, 2003; Song et al., 2017b). The importance of the epiphytic biofilm in trophic interactions and its involvement in trophic cascades are emphasized in many studies, but the hypotheses regarding underlying mechanisms of these trophic interactions are usually contradictory, e.g., whether grazers are attracted by macrophytes or epiphytic biofilm (Brönmark, 1985; Mormul et al., 2010). Therefore, more research is needed to clarify the triggering factor of these trophic interactions. The availability of increased imaging technology, molecular markers, and using stable isotopes as tracers to track C, N, and P in the complex food chains will aid in the exploration of trophic interactions (Bakker et al., 2016).

Allelopathic effects of macrophytes on phytoplankton and bacterioplankton are well-studied, but studies on epiphytic biofilm are limited. The responses of epiphytic heterotrophs to macrophyte allelopathic compounds are unknown. In terms of the epiphytic biofilm, only cyanobacteria are usually highlighted as candidates capable of inducing allelopathic reactions in the plant (Mohamed, 2017). More studies are needed to test the allelopathic potential of other groups of the epiphytic biofilm such as green algae, diatoms, and bacteria. Moreover, since the results of allelopathy experiments are often depending on the specific epiphyte-macrophyte combination under investigation, there is a need to investigate the allelopathic activity through a wide range of epiphyte-macrophyte combinations. Most of the allelopathic studies have been conducted in the laboratory using extracts from macrophytes and cultures of certain species of the epiphytic biofilm (Erhard and Gross, 2006; Mohamed and Al Shehri, 2010), but whether these observations are consistent with those in their natural habitats (e.g., Mulderij et al., 2009) is not yet fully known. Therefore, more field studies based on metacommunity ecology (i.e., not on individual species but the community) should be conducted to understand allelopathic



relationships under natural conditions and scale-up effects on ecosystem level. Rather than growth, effects of allelopathy at the molecular and genetic level also should be studied. Other interactions discussed in this review, i.e., flow, diseases, and pollutants, have great potential for improving applications of epiphytic biofilm-macrophyte interactions in wastewater treatment and managing freshwater aquatic ecosystems under anthropogenic pressures such as pollution.

## 5. Concluding remarks

Epiphytic biofilms play a key role in shallow aquatic ecosystems by contributing to ecosystem structure, function, and integrity. The structure and function of the epiphytic biofilm is largely related to its host (e.g., macrophyte species, morphology, and characteristics). Consequently, a myriad of interactions between the epiphytic biofilm and host macrophytes have been documented, such as interactions on resources, trophic interactions, and allelopathic interactions. These interactions can often be complex in natural habitats, manifested through competitive, mutualistic, and commensalistic relationships. Despite these findings, there are several key areas where research is currently lacking. This overview not only attempts to identify such knowledge gaps, but also acts as a basis for designing future studies – with a particular emphasis on including epiphytic biofilm to understand, maintain, and improve freshwater ecosystem health and integrity (Adam et al., 2017; Costică et al., 2018; Lorch and Ottow, 1986; Phiri et al., 2007). Improved knowledge of the biofilm-macrophyte relationship can be used to enhance our understanding of the costs and benefits of current management practices, such as removing of natural vegetation and re-oligotrophication (Baatrup-Pedersen et al., 2002; Geist and Hawkins, 2016). This can also lead to incorporation of epiphytic biofilm-macrophyte interactions in modeling approaches to predict future dynamics in aquatic ecosystems and guiding conservation strategies (Wade et al., 2002; Ward et al., 2016; Zhang et al., 2018).

## CRedit authorship contribution statement

**Lishani Wijewardene:** Conceptualization, Data curation, Writing – original draft, Writing – review & editing. **Naicheng Wu:** Supervision, Writing – review & editing. **Nicola Fohrer:** Supervision, Writing – review & editing. **Tenna Riis:** Conceptualization, Supervision, Writing – review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.aquabot.2021.103467](https://doi.org/10.1016/j.aquabot.2021.103467).

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