Toward Improved Models of Riverine Macrophytes

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ABSTRACT

Aquatic plant communities both affect and are affected by their physical, chemical, and biological environments. Understanding tightly coupled plant and flow processes is especially important in rivers, in which management actions such as water withdrawals, reservoir operations, or in-channel structures can cause strong and rapid feedback cycles. Numerical models provide an important mechanism for understanding and forecasting these dynamics in complex environments. Here, we describe the need for improved models of aquatic macrophytes in rivers. First, we review the role of river macrophytes through the lenses of their ecological roles (e.g., habitat cover), riverine functions (e.g., nutrient processing, hydraulic roughness), and conservation needs (e.g., imperiled species management). Second, we review existing models of riverine macrophytes and put forth a conceptual framework for developing new models. Third, we develop a conceptual model of a common macrophyte as a means to understand the broader functions of aquatic plants. Specifically, we focus on the effects of water management on hornleaf riverweed (*Podostemum ceratophyllum* Michx.) in the Middle Oconee River in Georgia, incorporating relevant predictors of macrophyte growth as well as the potential for feedback between macrophyte growth, hydraulic flow, and nutrient spiraling.

INTRODUCTION

Aquatic macrophytes are plants that grow submerged, emergent, or floating in bodies of water for a significant portion of their life cycle. Existing taxonomic definitions of macrophytes vary in the literature. Some authors consider macrophytes to include all multicellular primary producers (Brundu 2015), while others use the term macrophyte only for vascular plants and consider algae, cyanobacteria, and bryophytes as separate categories (Bowden et al. 2017). Here, we will use the term aquatic macrophytes to refer to aquatic species that are true plants (bryophytes, pteridophytes, gymnosperms, and angiosperms), excluding algae and cyanobacteria.

Macrophytes play foundational roles in the ecology of rivers, many of which are considered to be positive. Macrophytes commonly provide habitat and food for fish and invertebrates (Nelson and Scott 1962, Argentina et al. 2010a), including species of conservation concern (Phillips et al. 2011, Vardakas et al. 2017). They shape biogeochemical cycles of carbon and nutrients, including fixing carbon (Conde-Álvarez et al. 2011, Hyldgaard and Brix 2011) and absorbing excess nutrients, slowing their movement downstream and counteracting eutrophication (Clarke 2002, Mebane et al. 2014). However, excessive macrophyte growth, particularly in the case of invasive species, can have adverse effects on aquatic ecosystems such as reducing light and oxygen in the water column (Pinero-Rodríguez et al. 2021) or competing with native species (Pulzatto et al. 2019, Pinero-Rodríguez et al. 2021).

Macrophytes' numerous roles in ecosystems make them highly relevant to river management as well. Macrophytes influence hydraulic processes such as exerting friction on flow (Dodds and Biggs 2002, Kang et al. 2018) while locally creating microhabitats with diverse flow conditions which may support biodiversity (Sand-Jensen and Mebus 1996). Attempts to model or manage hydraulic flows (Marcinkowski et al. 2018, Bhattacharjee et al. 2019) depend on accurately estimating the hydraulic roughness of the river channel, which is strongly influenced by macrophyte abundance and growth forms (McKay and Fischenich 2011). Macrophytes' effects on dissolved gases, nutrients, and sediments (e.g. Clarke 2002), make them a crucial component of managing systems for water quality or nutrient fluxes, to the point that some researchers have used them as indicators of ecosystem properties such as water quality and anthropogenic activities (Søndergaard et al. 2010, Han and Cui 2016). On the other hand, human use of rivers for water extraction (Campana et al. 2012, McKay 2015), navigation, recreation (Chambers et al. 1999), or hydropower generation (Gómez et al. 2014), may depend on relatively low macrophyte abundance and be hindered by high growth.

Efforts to manage and restore riverine ecosystems depend on a strong, predictive understanding of river ecology, including the central roles of aquatic macrophytes. Models represent a crucial component of testing, refining, and communicating our understanding of ecological systems (Rykiel 1996). Conceptual models allow us to synthesize what we know and have yet to learn about these systems, in a format that can be effective for both aggregating insights from diverse sources and communicating those insights widely and clearly (Fischenich 2008). Numerical models, in turn, allow us to evaluate and refine our understanding by testing hypothesized mechanisms against observed data, and to predict the ecological effects of environmental changes or management strategies (Grimm and Railsback 2012, Wang et al. 2018). While some models have been used to investigate effects of environmental conditions on riverine macrophytes (Wright and McDonnell 1987, Carr et al. 1997, Best and Boyd 2007), models of riverine macrophyte growth are relatively scarce compared to models of vegetation growth in other habitats (Charbonneau et al. *in prep*). Furthermore, few models of aquatic vegetation growth take into account feedback mechanisms that result from plants both shaping and responding to environmental conditions, including those altered by management actions.

In this paper, we describe the need for improved models of aquatic macrophytes in rivers. First, we review the role of river macrophytes through the lenses of their physical and chemical roles (e.g. nutrient processing, hydraulic roughness), ecological roles (e.g. habitat cover), and conservation needs (e.g. imperiled species management). Second, we propose a framework for a new model incorporating feedbacks between macrophyte growth, hydraulic processes, and nutrient spiraling. Third, we develop a conceptual model of a common macrophyte as a means to understand the broader functions of aquatic plants with a specific focus on hornleaf riverweed (*Podostemum ceratophyllum* Michx.) in the Middle Oconee River in Georgia.

PHYSICAL AND CHEMICAL ROLES OF MACROPHYTES

Macrophytes directly and indirectly influence a variety of physical and chemical processes in rivers. Here we review three outcomes that are particularly relevant to water resources engineering: effects on hydrodynamics, transport processes, and biogeochemical processes (i.e., water quality).

Macrophytes and other forms of vegetation (e.g., wetlands, riparian zones) have long been acknowledged as important sources of friction and flow resistance. A variety of qualitative and quantitative methods are available for predicting hydraulic roughness from vegetation through parameters such as Manning's *n* (McKay and Fischenich 2011). Notably, flow resistance from vegetation is notoriously challenging to capture due to seasonal senescence, stem bending, washout, and other taxon-specific effects (e.g., Stone et al. 2013). Effects on friction then have indirect effects on other relevant engineering outcomes such as flood stage, flood attenuation, and basin routing.

Multifaceted hydrodynamic effects of macrophytes induce similar complexities in transport processes. Aquatic vegetation beds alter turbulence profiles with subsequent changes in sediment recruitment and settling (Jones et al. 2012). Macrophyte beds can also affect bed stability and river substrate mobilization (Fritz and Feminella 2003). Likewise, effects on transport processes can extend beyond sediment to organic matter and other particulate matter in rivers (Koetsier and McArthur 2000). Notably, trapping and retention of fine materials could be temporary as particles may be resuspended in large flow events (Kleeberg et al. 2010).

Biogeochemical cycling is also affected by macrophyte growth and dynamics. In particular, these processes have been well-studied in the context of constructed wetlands for water quality improvement (Gumbricht 1993). Although less is known in riverine settings, macrophytes take up nutrients directly in biomass and have been shown to play significant roles in nutrient processes such as denitrification, particularly in large-river environments (Pinardi et al. 2009, Houser and Richardson 2010, Forshay and Dodson 2011, Kreiling et al. 2011). Aquatic vegetation can also play roles in uptake and cycling of other constituents such as metals and contaminants (Adams et al. 1973, Heisey and Damman 1982, Wood and Freeman 2017).

As shown, macrophytes play significant roles in modifying the physical and chemical environment of streams and rivers. Effects of riverine environments also exert fundamental controls on aquatic plants, and tight feedback processes exist between macrophyte systems and their environment. Jones et al. (2012) suggest that in some contexts, macrophytes may even serve as "ecosystem engineers" that fundamentally change system function and associated ecological outcomes. The next section examines the ecological importance of macrophytes in this broader sense.

ECOLOGICAL ROLES OF MACROPHYTES

Macrophytes engage in complex interactions with both abiotic and biotic components of their habitats. Here we consider what resources macrophytes need from their habitats, how their growth may affect habitat conditions, and how they interact with other organisms.

Like all plants, aquatic macrophytes have habitat requirements that constrain where they are able to grow. The primary constraints on plant metabolism are light, carbon and nutrient availability. As a crucial component of photosynthesis, light is essential for macrophyte growth. Macrophytes vary, however, in their habitat preferences with regard to light availability. Many species prefer full sun, while others may grow best at lower or intermediate light levels, with growth inhibited above a certain light level. For example, biomass of the endangered macrophyte Texas wild rice (*Zizania texana*) peaked at about 80% of ambient light and declined slightly at greater light levels (Crawford et al. 2020). Some species require consistently high light, to the extent that shading by other macrophytes (He et al. 2019) or by adding dyes or sediments to water (Durán et al. 2010) have been proposed as measures to control unwanted macrophytes.

Other species are able to tolerate periods of high turbidity, partial overgrowth by epiphytes and algae (Wetzel and Neckles 1986) and even temporary burial under shifting sediments (Pahl 2009). Carbon is another crucial component of photosynthesis. Macrophytes use primarily CO_2 and/or HCO_3^- as carbon sources, and effects of factors such as hydraulic flow and pH on their availability can strongly affect where a given macrophyte can grow (Power and Doyle 2004).

Nutrients such as nitrogen and phosphorus are essential for macrophyte growth as well, but again it would be an oversimplification to consider these to be strictly positively related to macrophyte growth. Excessively high levels of nutrients can be toxic to plants (Marschner 1995), but even before nutrient concentrations reach toxic levels, they can harm aquatic macrophytes by increasing the growth and decomposition of unwanted primary producers, thereby reducing light and oxygen availability (Pinero-Rodríguez et al. 2021).

River substrate and hydraulic flow also commonly constrain macrophyte growth. Rooted species tend to prefer finer sediments (Power 1996, Poole and Bowles 1999, Fritz et al. 2004), whereas species that adhere directly to solid surfaces may prefer larger, more stable substrates such as rocks or logs (Argentina et al. 2010b). Hydraulic flow is also an important component of macrophyte habitat, for which species may have distinct preferences. Slow flows rarely pose direct challenges to macrophyte growth, although they can be associated with decreases in dissolved CO_2 that macrophytes need for photosynthesis (Power and Doyle 2004), but may be associated with increased competition from other macrophytes and primary producers (Bowden et al. 2017), and increased susceptibility to herbivory (Wood et al. 2019). In contrast, macrophytes able to tolerate higher flow rates may experience release from the pressures of competition and herbivory (Wood et al. 2019). It is worth keeping in mind that extremely high flows can cause scour, severely damaging any macrophyte community (Nelson and Scott 1962).

Just as macrophytes respond to the characteristics of their environments, so too do they exert effects on their environments. Principal among these is photosynthesis, or primary productivity. Through their metabolism and growth, macrophytes remove CO_2 from the atmosphere and convert it into oxygen and biomass. Much of this biomass passes through food webs and eventually back to the atmosphere, but some of it can be sequestered in soils or sediments for longer time scales (Nelson and Scott 1962). By providing increased physical structure, riverine macrophytes can also trap incoming organic matter such as leaf litter, from upstream and/or terrestrial sources, thereby facilitating local accumulation of carbon and nutrients and delaying their transport downstream (Clarke 2002).

Macrophytes frequently play foundational roles in the ecosystems in which they occur. At one time or another in their life cycles, they may be consumed by herbivores or detritivores, providing carbon, nutrients, and energy to higher trophic levels (Nelson and Scott 1962, Grubaugh and Wallace 1995). While some of this transfer of materials and energy can occur through fully aquatic channels, it can also enter terrestrial channels (Baxter et al. 2005, Takafumi et al. 2015), thus, the presence of macrophytes may increase the opportunity for biogeochemical exchange between terrestrial and aquatic components of a landscape. Macrophytes can also provide habitat for numerous other organisms, from epiphytic algae and microbes to aquatic fish and invertebrates (Phillips et al. 2011, Wilson et al. 2011, Marshall et al. 2015, Vardakas et al. 2017), which may be of conservation concern and can have large effects on food web dynamics.

MACROPHYTES AND CONSERVATION

Many riverine macrophytes are rare and in need of conservation due to factors such as endemism, biological invasions, and habitat alteration. Texas wild rice (*Zizania texana*

Hitchcock) is one example; it is an aquatic grass species known only from a 4-5 km portion of the San Marcos river in Texas, where it prefers growing near other native rather than non-native species in coarse, sandy soils, faster currents, and warmer temperatures (Power 1996, Poole and Bowles 1999, Tolley-Jordan and Power 2007). While many macrophytes can use either CO_2 or HCO_3^- as a carbon source for photosynthesis, *Z. texana* can only use CO_2, potentially constraining it to waters with faster currents and lower pH values (Power and Doyle 2004). Its reproduction appears primarily asexual, but it does produce flowers on emergent culms that appear to be wind pollinated (Hutchinson 2019). Wind pollination may make it especially difficult for this species to maintain genetic diversity because wind pollination is most effective in denser populations (Oxley et al. 2008).

Changes in water availability and flow regimes due to water extraction from rivers and lakes are thought to be a major contributing factor to declines in macrophyte abundance and diversity (Chappuis et al. 2011). Related fragmentation of river habitats can also contribute to macrophyte declines by decreasing population sizes and reducing gene flow between them (Richards et al. 2007, Fan et al. 2019). In Japan, the riverine macrophyte *Ranunculus nipponicus* var. *submersus* has become endangered primarily due to water pollution and habitat degradation, and Takafumi et al. (2015) documented further reductions in this species' abundance due to herbivory and trampling by deer. It is not always known why some macrophytes are rare or getting rarer. For instance, the endangered status of *Luronium natans* in Europe has been hypothesized to be due to low competitive ability, although experimental work suggests it can grow readily in new habitats and has sufficient photosynthetic plasticity to grow efficiently under variable light conditions (Hyldgaard and Brix 2011). Some macrophytes can also thrive in novel habitats: high macrophyte diversity, including several endangered species, were documented in a system of human-made canals in Slovakia (Dorotovičová 2013).

Macrophytes can also be of conservation concern not because they themselves are necessarily rare, but because they support other rare or endangered species. Wilson et al. (2011) describe the importance of macrophyte functional types in creating habitat for the endangered mussel *Margaritifera margaritifera*, and Phillips et al. (2011) do the same for the endangered fish *Ethiostoma fonticola*. Two of the three endangered Greek cyprinid fish studied by Vardakas et al. (2017) demonstrated a strong preference for high macrophyte cover. Similarly, the endangered Australian lungfish *Neoceradotus forsteri* relies on dense beds of the macrophyte *Vallisneria nana* to spawn; both the fish and the macrophyte are vulnerable to large shifts in water level caused by human water management activities upstream (Marshall et al. 2015).

MACROPHYTES AS OBSTACLES TO CONSERVATION

In other situations, macrophytes can function as invasive or pest species and present obstacles to conservation. In the case of endangered Texas wild rice *Z. texana*, invasion of nearly half of its native habitat by *Hygrophila polysperma* and *Hydrilla verticillata* further threaten its survival, although models based on hydraulic flow showed some success in indicating sites where manually replacing the invasive species with *Z. texana* could restore some *Z. texana* cover (Hardy et al. 2016). Invasive *H. verticillata* was associated with changes in fish diets and community composition in a river and a reservoir in Brazil, many of which suggested a reduction in habitat quality (Carniatto et al. 2014, 2020). This species was also shown to support colonization by an invasive mussel (Michelan et al. 2014). Another invasive macrophyte of Brazilian rivers, *Hedychium coronarium*, exudes toxins from its rhizomes that negatively affect the growth of neighboring algae, macrophytes, and invertebrates (Costa et al. 2021). The spatial scale of investigation is likely to be important in understanding the effects of invasive macrophytes on native macrophytes. In a study in a reservoir in a dammed subtropical river, abiotic factors were the strongest predictors of invasive *H. verticillata* abundance at large spatial scales, but biotic factors including the abundance of competing native species were stronger predictors of *H. verticillata* abundance at smaller spatial scales (Pulzatto et al. 2019).

REVIEW OF RIVERINE MACROPHYTE GROWTH MODELS

Previous efforts to model riverine macrophyte growth have used a wide variety of techniques. While the development of any model clearly necessitates decision-making specific to the research and/or applied questions at hand, in this section we review existing efforts to model the growth of riverine macrophytes and synthesize a set of recommendations for future model development.

Many models operate primarily through plant physiology in varying levels of detail. For example, Wright and McDonnell (1986) model changes in biomass as gains due to photosynthesis minus losses due to respiration, death, and advective loss, with species-specific parameterization of photosynthetic rates and a complex sub-model to characterize seasonal and daily variation in light intensity. Davis and McDonnell (1997) expanded on this approach by incorporating phenology, allowing macrophytes to transition between four life stages (growth, maturation, senescence, and dormancy) in which photosynthesis and respiration function differently. They found that model performance was highly sensitive to the rates of photosynthesis and respiration, and the timing but not rates of biomass transfers among growth stages (Davis and McDonnell 1997).

A subsequent series of studies focusing on modeling invasive macrophyte growth used a still more detailed approach, considering light availability to macrophytes as limited by reflectance off of the water surface as well as attenuation by water, epiphytes, community leaf area, and dissolved or suspended organic matter (Best et al. 2001, Best and Boyd 2003, 2007). Photosynthesis was further constrained by available CO_2 and species-specific physiology. These models considered multiple macrophyte biomass pools and metabolism corresponding to different plant organs (leaves, shoots, roots, tubers), which could translocate carbohydrates among each other, with energy requirements, biomass allocation, and carbohydrate translocation dynamics varying among life stages. Transitions between life stages were determined using a degree-days approach. These models were initially developed for invasive macrophytes in lakes (Best et al. 2001, Best and Boyd 2003), but later adapted to include simple effects of current velocity and epiphyte competition on macrophyte photosynthesis (Best and Boyd 2007).

While these models incorporate the biology of the focal macrophyte species in increasing levels of detail, they omit a number of other factors that may shape macrophyte growth and ecology. In particular, among the many possible relationships between macrophyte growth, nutrient availability, and hydraulic flow, they consider only some simple effects of flow on macrophytes (advective loss and/or decreases in photosynthetic rate), but they do not consider nutrient dynamics or effects of macrophytes on hydraulic flow at all.

Another set of models of macrophyte growth take very different approaches to address questions focused on flow and nutrients. A model based in a sharp curve in a Korean river divides its study macrophyte into two groups, permanent and growing, and lets growth vary only with time, focusing instead on using detailed geomorphological information to predict the effects of vegetation and hydraulic flow on riverbed morphology (Kang et al. 2018). Another model, applied to an impounded portion of a river in New Jersey, USA, does not consider macrophyte species or biomass, but treats the macrophyte community as time-variable oxygen equivalents to address questions of oxygen, nitrogen, and phosphorus biogeochemistry (Park and Uchrin 1997).

Other models strike intermediate positions between physiological detail and ecosystem processes. A study in the Rhône River in France used a multi-step stochastic process to model nine macrophyte species' abilities to recolonize quadrats that had been cleared of vegetation, and had significant success reproducing patterns in recolonization based on dispersal strategy (Chiarello and Barrat-Segretain 1997). Another study in the Sorraia River in Portugal used empirical findings of three macrophyte species' habitat preferences in terms of velocity, depth, and substrate to investigate their habitat suitability under different river discharge regimes, and found that targeted management of river discharge could shape habitat availability so as to favor growth of the native versus invasive study species (Ochs et al. 2018). Finally, a model based in a river in Oregon, USA sought to characterize water quality effects on macrophyte growth, which would in turn affect hydraulic flow (Berger and Wells 2008). This model incorporated effects of light, temperature, nutrients, carbon availability, respiration, and mortality on macrophyte growth, and then used vegetation density to calculate hydraulic roughness, and was notably successful at simulating both water quality effects on macrophyte growth, and macrophyte effects on hydraulic flow (Berger and Wells 2008).

TOWARD IMPROVED MODELS OF RIVERINE MACROPHYTES

Using insights from our review of existing efforts to model macrophyte growth in rivers, we now put forth a framework for developing new models. Our goal here is not to prescribe a single model formulation, as different questions necessitate different model structures. Rather, we suggest a framework for choosing and identifying relevant terms and processes to include.

When seeking to quantitatively model a system, it is helpful to start with a conceptual model. Conceptual models are powerful, versatile tools for synthesizing current understanding of a system, and the process of developing them can accomplish useful goals such as deciding which factors and relationships to consider, and identifying the strengths and weaknesses of our understanding of their interactions (Fischenich 2008). Identifying key areas of uncertainty can be especially important in allowing preparation for the unpredictability these uncertainties may introduce into the modeled system (Casper et al. 2010). Such areas of uncertainty can also provide a fruitful starting point for the next iteration of empirical research in a field.

Although the details of any conceptual or quantitative model of riverine macrophyte growth will necessarily depend on the specific research question(s) involved, we suggest that models of riverine macrophyte growth should consider the following broad factors: specific nature of macrophyte growth, macrophyte requirements for growth, environmental and anthropogenic factors that influence growth, and feedback effects of macrophyte growth on environmental factors. Below, we list a series of variables associated with these factors that merit consideration in the development of macrophyte growth models. This is intended to be a conceptual framework to guide model development, but not a complete or prescriptive list; we expect that most models will omit many of these factors, and others may find it necessary to include factors not on this list.

- Specific nature of macrophyte growth
    - Relevant characteristics of macrophyte growth

  - Variation among plant tissues, life stages, species, or seasons
  - Plant population ecology: recruitment, growth, reproduction, mortality
  - Spatial and temporal scale(s)
- Macrophyte requirements for growth
  - Light availability and plant responses to changes in light
  - Forms and availability of carbon for photosynthesis
  - Nutrient availability, limitation, or toxicity
  - Substrate size or stability
  - Hydraulic flows: stability versus variability of flow, frequency of extreme flows, distribution of periods of flow within study species' preferred ranges
- Environmental and anthropogenic factors affecting growth and survival
  - Water quality: temperature regime, pH, dissolved oxygen, turbidity, pollutants
  - Biotic interactions: competition, herbivory, parasitism, mutualism, facilitation, or pathogenicity
  - Climate: seasonality, year-to-year variation, climate change, probabilities of extreme weather events
  - Anthropogenic impacts: management impacts on flow or water quality, direct manipulation of macrophytes, or land use changes in the surrounding watershed
- Feedback effects of macrophytes on environment
  - Effects of macrophyte growth on environmental factors such as hydraulic flow, water quality, or nutrient spiraling

CONCEPTUAL MODEL CASE STUDY: EFFECTS OF WATER MANAGEMENT ON *PODOSTEMUM CERATOPHYLLUM*

We will consider the macrophyte *Podostemum ceratophyllum* Michx. (hornleaf riverweed) as a case study of the utility of conceptual and numerical modeling for understanding and forecasting the effects of water management on macrophytes and river ecosystems. This species is a flowering plant in the family Podostemaceae with lobed to deeply dissected leaves of highly variable morphology (Wood and Freeman 2017). Its roots do not grow into sediments like those of most plants, but instead attach directly to hard, stable substrates such as large rocks using specialized structures called haptera (Rutishauser et al. 2003). *Podostemum ceratophyllum* grows primarily in shallow, well-lit areas with fast currents such as shoals or waterfalls (Philbrick and Crow 1983, Argentina et al. 2010b). It can tolerate significant levels of turbidity and even temporary burial under shifting sediments (Pahl 2009), but experiences high mortality under low flows due to desiccation and/or herbivory (Pahl 2009, Wood et al. 2019). This species occurs in low to mid elevation streams in the eastern and midwestern United States and Canada, with scattered populations in Central America. Despite its wide geographical range, *P. ceratophyllum* is undergoing widespread population declines (Philbrick and Crow 1983, Wood and Freeman 2017) and is currently listed as vulnerable, imperiled, or critically imperiled in much of its range (USDA Plants Database 2021, NatureServe 2021).

Like many macrophytes, *P. ceratophyllum* functions in many ways as a foundation species in the rivers it inhabits. Its physical structure reduces water velocity, intercepts sediment and organic debris, and thereby provides habitat, energy, and nutrition to much of the river food web, from a complex invertebrate community (Nelson and Scott 1962, Grubaugh and Wallace 1995) to diverse fish assemblages (Argentina et al. 2010a, Katz and Freeman 2015). These mechanisms likely also affect nutrient dynamics, in particular retaining nutrients locally and reducing their translocation downstream (Newbold et al. 1981). Because of its foundational role in the rivers it inhabits and its sensitivity to hydraulic flow conditions, *P. ceratophyllum* is likely useful as an indicator of the ecological health of river ecosystems and a target for river management strategies such as the timing and extent of water withdrawals for municipal use (Campana et al. 2012, Bhattacharjee et al. 2019).

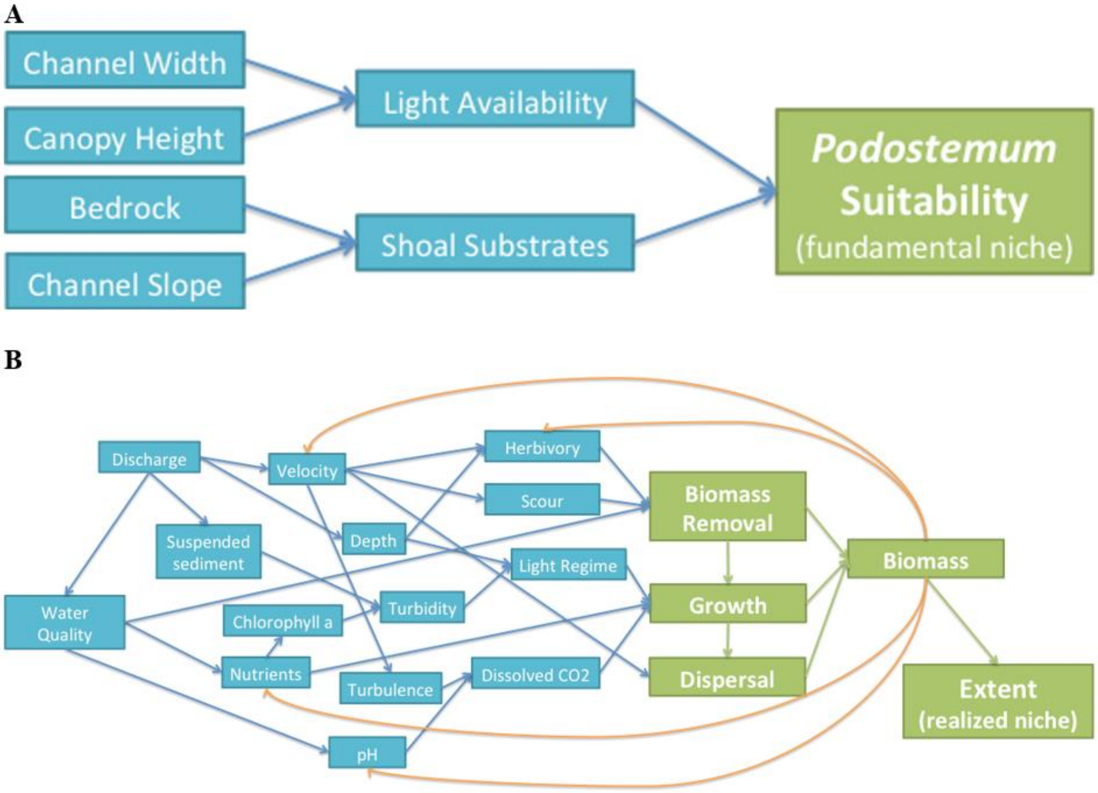

Figure 1. Conceptual model of the distribution and growth of the macrophyte *Podostemum ceratophyllum*. (A) Habitat suitability model designed to address the question of where *P. ceratophyllum* could potentially grow. (B) Local growth model designed to explore mechanisms governing the growth of *P. ceratophyllum* in specific habitats identified by the model in (A). Blue boxes and arrows represent environmental predictor variables, green boxes and arrows represent *P. ceratophyllum* response variables, and orange arrows represent feedback effects of *P. ceratophyllum* growth on environmental predictor variables.

Following the approach outlined above, we present a conceptual model of the growth and occurrence of *P. ceratophyllum* (Fig. 1). Briefly, we propose a two-step hierarchical nested approach based on the concept of fundamental versus realized niches (Connell 1961). First, we use relatively simple drivers of substrate, channel slope, and light availability to identify habitats potentially suitable for *P. ceratophyllum* growth (i.e. its fundamental niche). We next use a more comprehensive set of variables to examine ways in which elements of water quality, river discharge, and biotic interactions affect the fate of *P. ceratophyllum* in potentially suitable habitats. We focus on abiotic drivers due to a combination of data availability and the present understanding of *P. ceratophyllum*'s ecology, however, we do include competition from algae in the form of water turbidity, as well as herbivory, which is negatively related to water velocity (Wood et al. 2019). These factors can affect *P. ceratophyllum* by increasing or decreasing growth, biomass removal, and dispersal, which together determine biomass in a site. To represent effects of *P. ceratophyllum* growth on its environment, *P. ceratophyllum* biomass is allowed to affect local velocity, herbivory, nutrient availability, and pH. Sites with sustained nonzero biomass then represent the realized niche of *P. ceratophyllum* in a given river system.

We notably do not include a number of factors for which sufficient information is not available. Little is known about the relative biomass, chemical composition, photosynthetic capacity, or phenology of stems, leaves, and other tissues in this species, so we consider just a single biomass pool. Similarly, we have found minimal information about potential effects of environmental toxins, pathogens, symbionts, or facilitation on *P. ceratophyllum,* so those factors are also absent from our conceptual model even though they may meaningfully affect its growth. Environmental toxins such as heavy metals or other pollutants may be especially important in limiting *P. ceratophyllum* growth or occurrence (Adams et al. 1973, Heisey and Damman 1982, Wood and Freeman 2017), but we lack consistent quantitative information about toxin concentrations in rivers and how *P. ceratophyllum* may respond to them. Similarly, *P. ceratophyllum* has been shown to have seasonally variable competitive interactions with the alga *Lemanea australise* (Everitt and Burkholder 1991), but we lack sufficient information about the strength of these interactions, or the abundance of *L. australise,* to include them in the model.

CONCLUSIONS

In efforts to manage rivers, whether we seek to control flow regimes, support biodiversity, shape nutrient dynamics, or provide opportunities for transportation or recreation, it is necessary to consider how management activities will interact with riverine macrophyte communities. Macrophytes fulfill many essential functions in rivers, including moderating environmental flows by hydraulic friction, providing food and habitat for riverine food webs, and slowing the downstream transport of sediment, nutrients and other material. Thus, in order for management actions to be successful, it is crucial to understand their effects on macrophytes, as well as subsequent macrophyte-mediated effects on river ecosystems.

Conceptual and numerical modeling are powerful tools for testing and refining our understanding of biological systems, and for making predictions about their future behavior. In our review of existing quantitative models of riverine macrophytes, we identified a trend of increasing complexity in simulations of light availability and macrophyte physiology, and also noted a wide variety of ways of modeling macrophyte growth depending on the research question at hand. In light of this review, we proposed a conceptual framework to aid in the development of models of riverine macrophyte growth by compiling and organizing a list of potentially relevant factors to include. We emphasize that this conceptual framework is a tool for organizing ideas, and not a set of instructions for model development. We then applied this framework to the macrophyte *Podostemum ceratophyllum* as a case study and developed a two-part nested conceptual model that first aims to predict the species' habitat distribution, and then to simulate its growth over time.

Moving forward, we aim to use this conceptual model as the foundation for a numerical model of the distribution and growth of *Podostemum ceratophyllum*. We will start in a reach of the Middle Oconee River in Georgia, USA for which abundant data is available on the occurrence and habitat associations of *P. ceratophyllum* (Nelson and Scott 1962, Grubaugh and

Wallace 1995, Pahl 2009, Argentina et al. 2010b) and the geomorphological structure of the river (Bhattacharjee et al. 2019). We will then use a vegetation growth modeling framework (Charbonneau et al. *in prep*.) to simulate the growth of *P. ceratophyllum* over time in this system, comparing against measured values (Conn et al. *in prep*.), and then seek to expand this modeling framework to other rivers in the region. Broadly, we aim to use this modeling approach to assess and refine our understanding of this species' ecology, and predict how it may respond to different environmental conditions and management actions.

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