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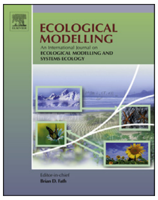

Evidence of alternative states in freshwater lakes: A spatially-explicit model of submerged and floating plants

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ABSTRACT

Freshwater systems provide iconic examples of ecological tipping points. In some lakes and ponds, changes to nutrient levels can drive sudden shifts between primary producer communities dominated by either submerged or floating plants. Several models, ranging in complexity, have been developed to understand the interaction between these primary producer groups. Previous field studies suggest that spatial (e.g., water body size) and temporal (e.g., seasonality) processes are important for the dynamics of this system in nature, but these processes cannot be included in most models without a significant increase in model complexity. Therefore, I developed a spatially- and temporally-explicit model of this system with moderate model complexity that extends a previous model, in which alternative states are known to occur. I found that under low (approximately ≤ 2 mg total nitrogen L^{-1}) or high (approximately ≥ 6 mg total nitrogen L^{-1}) nutrient levels, either submerged or floating plants dominated, respectively. At intermediate nutrient levels, simulations resulted in different final plant states, depending on the initial cover of floating and submerged plants, providing evidence for alternative states. Under most conditions, stable intermediate states were uncommon. Water body size had a large effect on the dynamics of the system, as observed in the field, but only if wind strengths increased with water body size and there was a prevailing wind direction. Surprisingly, species composition and trait diversity did not appear to have major effects on the final plant states. This model allows the integration of processes on multiple scales of biological organization, from species traits and composition, to climate and seasonality or ecosystem-level properties, and it complements the growing realization that spatial context has significant impacts on the dynamics of alternative states in nature.

1. Introduction

Many complex systems including climate, economies, societies, and ecological systems experience tipping points, where a subtle change in conditions can cause a dramatic response in the overall system. In nature, sudden changes between drastically different community and ecosystem states are well known (Folke et al., 2004). Coral reefs (Knowlton, 1992), semi-arid savanna (Walker et al., 1981), temperate forests (Holling, 1978), and many other habitats are often found in discrete states, with rare intermediates, and shifts between the states can occur abruptly. Although many relationships between the conditions and the state of the system (e.g., linear, nonlinear) may underlie these shifts (Lees et al., 2006), these dynamics may indicate the presence of alternative states, where more than one equilibrium state can exist for a given set of conditions (Scheffer et al., 2001).

Freshwater systems provide iconic examples of ecological tipping points. Typically, changes to nutrient levels can drive sudden shifts between very different primary producer communities and ecosystem states (Scheffer, 1990; Blindow et al., 1993). Changes to the trophic structure (e.g., removal of top predators) can also be responsible for such shifts (Carpenter, 2003). Although the original conception focused on clear water (dominated by submerged vegetation) and turbid water states (dominated by phytoplankton), this image has been expanded to include other system states (Scheffer and van Nes, 2007; Meerhoff and Jeppesen, 2009; de Tezanos Pinto and OíFarrell, 2014). At high nutrient levels, rather than phytoplankton dominance replacing submerged vegetation, free-floating plants can become the dominant primary producer in agricultural ditches (de Groot et al., 1987; Janse and Van Puijenbroek, 1998; Scheffer et al., 2003), small temperate wetlands (Smith, 2012, 2014) and ponds (McCann *unpublished data*), shallow urban lakes (Morris et al., 2003a,b), and large tropical and sub-tropical lakes (Scheffer

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et al., 2003; Schooler et al., 2011). At low nutrient conditions, submerged plants are typically the superior competitors because they can take up scarce nutrients from the sediment via their roots. At high nutrient conditions light is often the limiting factor for plant growth and free-floating plants are the superior competitor because of their position on the water surface (Scheffer et al., 2003).

1.1. *Previous models*

There are several existing models, spanning a range of complexities, of floating plants and their interactions with other primary producer groups. For example, PCDitch is an ecosystem model of nutrient and vegetation dynamics in agricultural drainage ditches (Janse and Van Puijenbroek, 1997, 1998; Janse, 1998). PCDitch tracks the flow of biomass, phosphorus, nitrogen, and oxygen, in sediment, the water column, algae, and six functional groups of aquatic plants including floating and submerged plants. PCDitch requires over 250 parameters and includes detailed physiological processes such as temperature- and light-dependent growth and respiration. This model predicts dominance of submerged plants at low nutrient loading, but a switch to floating plant dominance when nutrient loading is high (Janse, 1998) with the threshold increasing with ditch depth (Janse and Van Puijenbroek, 1998). Although PCDitch tracks the flow of materials between biotic and physical components of the ditch, the model is not spatially explicit.

Charisma is a model of submerged plants, and although it does not explicitly consider floating plants, it is relevant because it is a spatially explicit agent-based model (van Nes et al., 2003). With moderate complexity (i.e., 85 parameters and aggregation of individuals into super-individuals), Charisma has been used to model competition dynamics between two submerged species, *Chara aspera* and *Potamogeton pectinatus*, and the alternative states that they can produce (van Nes et al., 2003). Bicarbonate limitation (rather than inorganic nutrients) is the main competitive mechanism in this model. Typically, nitrogen or phosphorous and not bicarbonate are considered to be the major limiting resource driving competition between floating and submerged plants (Scheffer et al., 2003).

There are also models that only describe the dynamics of floating plants. These models are usually based on differential equations of biomass growth dependent on factors such as temperature, light, nutrients, and crowding (Peeters et al., 2013; Driever et al., 2005). These models predict the biomass of floating plants as a function of conditions through time, but are not used to describe spatial patterns and are not explicitly dependent on interactions with other primary producer groups.

Finally, differential equation models of floating plant growth like those described above can be linked with similar growth models for submerged plants (Scheffer et al., 2003; van Gerven et al., 2015). In these models interactions between the functional groups occur through competition for nutrients, light, and space. The Scheffer et al. (2003) model require relatively few parameters (13) and is solved for equilibrium conditions without explicitly considering space or time. Depending on the parameterization, this model can produce either nonlinear dynamics with a single equilibrium community at a given nutrient level or nonlinear dynamics with more than one equilibrium plant state under some nutrient levels. The van Gerven et al. (2015) model allows for the added complexity of nutrient fluxes and light limitation in a vertical water column, although it assumes that both plant groups compete for nutrients in the water column, despite the fact that submerged plants are known to acquire much of their nutrients directly from the sediment (Barko et al., 1991). Although the model can produce alternative states under certain conditions, the authors conclude that floating plant dominance is unlikely to be an alternative state based on parameterizations that are expected in the field (van Gerven et al., 2015).

1.2. *Goals and questions*

Although the models described above have utility for both management decisions (e.g., Janse and Van Puijenbroek, 1998) and developing ecological theory (e.g., Scheffer et al., 2003), many of these models do not consider temporal or spatial dynamics. If they do, then it comes with the consequence of significant increases in model complexity.

The goal of this study was to develop a model of floating- and submerged-plant interactions with explicit inclusion of spatial and temporal dynamics, while maintaining moderate model complexity. Such a model would allow me to address questions motivated by previous field observations and lab experiments (Scheffer et al., 2003; McCann, 2016, McCann *unpublished data*). In particular, I asked three questions: (1) Do water body size and shape and wind disturbance affect the presence of alternative states? (2) What is the effect of growing season length on the presence of alternative states? and (3) What is the effect of floating plant species composition and trait diversity on the presence of alternative states? These questions are well-suited to exploration with a spatially- and temporally-explicit simulation model because of their complex nature and the difficulty with addressing them in a natural setting. For example, the whole-lake manipulations that could address some of these questions are labor- and resource-intensive, so a modelling framework is advantageous.

1.3. *Expectations*

Although alternative states have been shown to exist in non-spatial and non-temporal models of freshwater lakes and ponds (Scheffer et al., 2003), I also expect that alternative states would exist when space and time are included in the model. Like previous models, this model will have asymmetric competition, where submerged plants are superior competitors at low nutrients, and floating plants are superior competitors for light when nutrients are high. This type of competition will provide the mechanism for positive feedbacks, which can contribute to the occurrence of alternative states. If my new model produces alternative states, then this would support field evidence suggesting that alternative states between floating and submerged plants exist in spatially expansive systems (i.e., water bodies larger than agricultural ditches, Smith, 2012, McCann *unpublished data*).

Spatially-explicit models of this system would also allow me to understand why larger water bodies are rarely dominated by floating plants, as observed in the field (McCann *unpublished data*). This pattern may be due to the fact that larger water bodies have a greater fetch and that greater wind disturbance could prevent floating plants from covering the entire water body (Scheffer et al., 2003). If wind increases with water body size, then submerged plant states would be more likely than floating plant states in larger water bodies (Question 1). I also expect that water bodies with irregular shapes, including protected bays where floating plants can accumulate, would have greater floating plant cover than similar water bodies with less complex shapes (Question 1). Water bodies that experience a prevailing wind direction should also have less floating plant cover than water bodies without a prevailing wind (Question 1). Alternatively, larger water bodies in seasonal environments may be more difficult for floating plants to dominate because most of the floating plant biomass dies off each winter and there are a limited number of days each growing season for floating plants to spread across the water surface. Therefore, floating plants may to be able to dominate in larger water bodies if the growing season is