Regime shifts and hysteresis in the pitcher-plant microecosystem

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ARTICLE INFO

ABSTRACT

Changes in environmental conditions can lead to rapid shifts in the state of an ecosystem ("regime shifts"), which, even after the environment has returned to previous conditions, subsequently recovers slowly to the previous state ("hysteresis"). Large spatial and temporal scales of dynamics, and the lack of frameworks linking observations to models, are challenges to understanding and predicting ecosystem responses to perturbations. The naturally-occurring microecosystem inside leaves of the northern pitcher plant (*Sarracenia purpurea*) exhibits oligotrophic and eutrophic states that can be induced by adding insect prey. Here, we further develop a model for simulating these dynamics, parameterize it using data from a prey addition experiment and conduct a sensitivity analysis to identify critical zones within the parameter space. Simulations illustrate that the microecosystem model displays regime shifts and hysteresis. Parallel results were observed in the plant itself after experimental enrichment with prey. Decomposition rate of prey was the main driver of system dynamics, including the time the system remains in an anoxic state and the rate of return to an oxygenated state. Biological oxygen demand influenced the shape of the system's return trajectory. The combination of simulated results, sensitivity analysis and use of empirical results to parameterize the model more precisely demonstrates that the *Sarracenia* microecosystem model displays behaviors qualitatively similar to models of larger ecological systems.

1. Introduction

Regime shifts in ecological systems are defined as rapid changes in the spatial or temporal dynamics of an otherwise resilient system. Ecological regime shifts are caused by slow, directional changes in one or more underlying state variables, such as species abundance, dissolved oxygen content, or nutrients (Scheffer et al., 2001, 2009). Regime shifts are of particular concern when the return rate to a previous (and perhaps more desirable) state is slow or requires a larger input of energy or resources relative to what initiated the state change (i.e., hysteresis). In the last several years, many researchers have suggested that a wide range of ecological systems are poised to "tip" into new regimes (Scheffer et al., 2009; Petraitis and Dudgeon, 2016), or even that we are approaching a planetary tipping point (Barnosky et al., 2012); but see (Brook et al., 2013). Because identifying changes in the underlying state variables of most ecosystems require high frequency, long-term measurements (Wilson et al., 2013), our understanding of the causes and consequences of ecological regime shifts has progressed relatively slowly. More rapid progress could be achieved by working with well-understood systems that can be described mathematically and manipulated experimentally over shorter time scales.

It is rare to find an ecological system in which the occurrence of a regime shift, and its cause-and-effect relationship with one or more underlying environmental drivers, is unambiguous (Bestelmeyer et al., 2011). This is primarily because long time series of observations collected at meaningfully large spatial scales are required to identify the environmental driver(s), its relationship to the response variable of interest, the stability of each state, the breakpoint between them, and hysteresis of the return time to the original state (Petraitis and Dudgeon, 2016; Bestelmeyer et al., 2011). Detailed modeling, and decades of observations, and experiments have led to a thorough understanding of one canonical example of an ecological regime shift: the rapid shift from oligotrophic (low nutrient) to eutrophic (high nutrient) states in lakes (e.g., Carpenter and Brock, 2006; Carpenter et al., 2011). The primary difficulties with using lakes as models for studying alternative states and ecological regime shifts are their large size (which precludes extensive replication: Carpenter, 1996) and the long time scales (decades) required to observe a regime shift, subsequent ecosystem hysteresis, and eventual recovery (Mittlebach et al., 1995; Contamin and Ellison, 2009). Models of lake ecosystems and their food webs, and associated empirical data have revealed that recovery of lakes from a eutrophic to an oligotrophic state can be very slow—on the

order of decades to centuries (Contamin and Ellison, 2009)—and depends not only on slowing or reversing directional changes in underlying state variables but also on the internal feedback dynamics of the system. Other aquatic systems, including fisheries (Biggs et al., 2009), rocky intertidal communities, and coral reefs (Petraitis and Dudgeon, 2016) have provided additional empirical support for these model results in terms of both dynamics and duration (Dakos et al., 2012).

In a previous study, we experimentally demonstrated that organic-matter loading (i.e., the addition of excess insect prey to pitchers) can cause a shift from oligotrophic to eutrophic conditions in a naturally-occurring microecosystem: the water-filled leaves of the northern (or purple) pitcher plant, *Sarracenia purpurea* L. (Sirota et al., 2013). We use the term "microecosystem" here because the pitcher plant and its inquiline food web is a naturally occurring, co-evolved community of organisms, which is not necessarily the case for microcosms (Odum, 1996). In the typically five-trophic level *Sarracenia* microecosystem, bacteria reproduce rapidly and drive the nutrient-cycling dynamics (Butler et al., 2008). Prey additions cause shifts from oligotrophic to eutrophic states in hours or days rather than years or decades. Further, the comparatively small volume of individual pitchers, the ease of growing them in greenhouses and the occurrence of large, experimentally manipulable populations in the field (Srivastava et al., 2004) have allowed for replicated studies of trophic dynamics and regime shifts in a whole ecosystem.

Here, we build on the original mathematical model of the *Sarracenia* microecosystem (Sirota et al., 2013), estimating parameter values using new empirical data and introducing more realism into the underlying environmental drivers of the model. We then use sensitivity analysis to identify the model parameters that most strongly control the dynamics of the system. We illustrate that once organic-matter input is stopped, the *Sarracenia* microecosystem—like large lakes—can eventually overcome the hysteresis in the system and return to an oligotrophic state. We conclude that the mathematical model illustrates dynamic behaviors that are qualitatively similar to models of regime shifts in lakes and other ecosystems, and we suggest that the *Sarracenia* microecosystem is useful model for studying ecological regime shifts in real time.

2. Methods

2.1. The pitcher-plant microecosystem

The eastern North American pitcher plants (*Sarracenia* spp.) are perennial carnivorous plants that grow in bogs, low nutrient ("poor") fens, seepage swamps, and sandy out-wash plains (Schnell, 2002). Their leaves are modified into "pitchers" (Arber, 1941), tubular structures that attract and capture arthropods, and occasionally small vertebrate prey (e.g., Ellison and Gotelli, 2009; Butler et al., 2005). In the pitchers, prey are shredded by obligate pitcher-inhabiting arthropods, including histiostomatid *Sarraceniopus* mites, and larvae of sarcophagid

(*Fletcherimyia fletcheri*) and chironomid flies (*Metrocnemius knabi*) (Jones, 1923; Addicott, 1974; Heard, 1994). The shredded organic matter is further decomposed and mineralized by a diverse assemblage of microbes, including protozoa (Cochran-Stafira and von Ende, 1998), yeasts (Boynton, 2012), and bacteria (Peterson et al., 2008).

Unlike other species of *Sarracenia* that also secrete and use digestive enzymes to extract nutrients from their captured prey, *S. purpurea* pitchers secrete digestive enzymes for only a fraction of their lifespan (Gallie and Chang, 1997). Instead, *S. purpurea* relies on its aquatic food web to decompose the prey and mineralize their nutrients (Butler and Ellison, 2007). As a result, the rainwater-filled pitchers of *S. purpurea* are best considered a detrital-based, "brown" ecosystems in which bacterially-mediated nutrient cycling determines whether it is in an oligotrophic or eutrophic state (Sirota et al., 2013; Butler et al., 2008; Bradshaw and Creelman, 1984).

2.2. Oxygen dynamics in lakes and pitchers

Oxygen dynamics, in both lakes and *Sarracenia* pitchers, can be described using a simple model that yields alternative oligotrophic and eutrophic states and hysteresis in the shift between them (Scheffer et al., 2001):

$$\frac{dx}{dt} = a - bx + rf(x) \qquad (1)$$

In this model, the observed variable x (e.g., oxygen concentration) is positively correlated with state variable a (e.g., rate of nutrient input or photosynthesis), and negatively correlated with state variable b (e.g., rate of nutrient removal or respiration). The function $rf(x)$ defines a positive feedback that increases x (e.g., the rate of nutrient recycling between the sediment in lakes or mineralization-immobilization by bacteria of shredded prey in a water-filled *Sarracenia* pitcher). If $r > 0$ and the maximum of $\{rf(x)\} > b$, there will be more than one equilibrium point (i.e., stable state) (Scheffer et al., 2001); the function $f(x)$ determines the shape of the switch between the states and the degree of hysteresis.

Following (Scheffer et al., 2001), we used a Hill function for $f(x)$:

$$f(x) = \frac{x^p}{x^p + h^p} \qquad (2)$$

The Hill function provides a simple model that can produce threshold behaviors. The dynamics of the state variable x is determined by parameters p and h, which determine the rate of change and the inflection point of the curve, respectively (Fig. 1A). If p is set such that more than one possible state exists for the system, h determines the threshold for the transition between these states. When viewed in phase-space (Fig. 1B), the transition between states can be seen as a path traversed by the system between distinct regions (i.e., phases). In part because of this threshold property, the Hill function has been applied to systems ranging from biochemistry and microbiology to
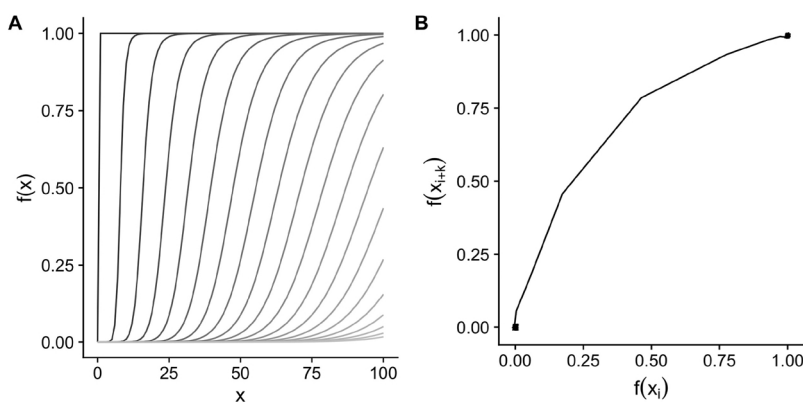

Fig. 1. The threshold dynamics of the Hill function are determined in part by the inflection parameter h. (A) Plotted output of the Hill function for different values of h (different lines shaded darker for lower values), ranging from 0.1 to 150 with $p = 10$. (B) Lagged ($k = 1$ lag term) phase plot of the Hill function with $h = 71.11$, showing the state transition (lower-left to upper-right). A small amount of random variation was introduced to the series to reveal overlapping points within the two states.