Regime shifts and alternative states in the *Sarracenia* microecosystem

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Abstract

text - 200 words, 1 paragraph, Using sensitivity analyses we identify model parameters that most strongly control the dynamics of the pitcher plant ecosystem and show that the system can eventually overcome its hysteresis and return to an oligotrophic state once organic-matter input is stopped.

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Introduction

Regime shifts in ecological systems are defined as rapid changes in the spatial or temporal dynamics of a more-or-less stable system caused by slow, directional changes in one or more underlying state variables (Scheffer et al., 2001, 2009). Ecological systems in which the occurrence of regime shifts is unambiguous are uncommon, primarily because long time series of observations are required to identify both stability of each state and a breakpoint between them (Bestelmeyer et al., 2011). Detailed modeling and decades of observations and experiments have led to a thorough understanding of a canonical example of an ecological regime shift: the rapid shift from oligotrophic to eutrophic states in lakes (Carpenter and Brock, 2006; Carpenter et al., 2011).

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

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

In this model, the observed variable x (e.g., nutrient concentration in a lake) is positively correlated with state variable a (e.g., rate of nutrient loading) and negatively correlated with state variable b (e.g., rate of nutrient removal). A positive feedback loop, $rf(x)$ (in the lake model, this is the rate of nutrient recycling between the lake sediments and water column). If $r > 0$ and $\{rf\prime(x)\} > b$, there will be more than one equilibrium point (i.e., stable state); the function $f(x)$ determines the shape of the switch between the states and the degree of hysteresis (Scheffer et al., 2001).

Models of lake ecosystems and their food webs, and associated empirical data also have revealed that returning lakes to the more "desired" oligotrophic state can be very slow—on the order of decades to centuries—(ref: Contamin and Ellison; others from Carpenter group) and depends not only on slowing or reversing the directional changes in underlying state variables but also on the internal feedback dynamics of the system (i.e., the dynamics of $f(x)$ in Equation 1). Other systems, including fisheries (ref: Carpenter PNAS) and ... (ref; XXX et al. PLoS One) have provided some support for these model results (ref: XXX et al. PLoS One), both in terms of dynamics and duration.

In the last several years, many researchers have suggested that a wide range of ecological systems are poised to "tip" into new regimes (refs...), or even that we are approaching a planetary tipping point. (ref: XXX, but see YYY). If, as in lakes, either changes in the underlying state variables causing these regime shifts or the regime shifts themselves span decades, ecological insights into their causes and consequences will accrue relatively slowly. More rapid progress both in understanding the mechanisms driving ecological

regime shifts and in determining how to reverse them requires well-understood model systems that can be experimentally manipulated over much shorter time scales.

Recently, we have shown experimentally that organic-matter loading (i.e., prey addition) can cause a shift from oligotrophic to eutrophic conditions in naturally-occurring microecosystems: the water and bacteria-filled modified leaves of the northern (or purple) pitcher plant, *Sarracenia purpurea* (ref: Sirota). Because bacteria that reproduce rapidly drive the nutrient cycling dynamics of the *Sarracenia* microecosystem (ref: Butler et al. 2008), the system states change in days rather than years or decades. In addition to introducing a new experimental system for regime shifts and alternative states, Sirota et al. (2013) sketched a model that, in extreme cases, could lead to a rapid (regime) shift from oligotrophic to eutrophic conditions in pitcher-plant leaves. Here, we develop fully the model of the *Sarracenia* microecosystem, introduce more realism into the underlying environmental drivers of the model, use sensitivity analysis to identify the parameters that most strongly control the dynamics of the system, and show that the system eventually can overcome its hysteresis and return to an oligotrophic state once organic-matter input is stopped.

The *Sarracenia* microecosystem

Sketch of the biology of the system

The Model

The detritus-based pitcher-plant food web forms in the small pools of water that accumulate in living and photosynthesizing modified leaves ("pitchers") of *Sarracenia purpurea*. Thus, our model of this food web includes feedbacks between the food web and the plant itself (Bradshaw and Creelman, 1984). The full model is a pair of coupled differential equations:

$$x_{t+1} = \underbrace{a_t A_t}_{\text{Photosynthesis}} - \underbrace{\left\{ m + a_t \left[\frac{w_{t-1}}{K_w + w_{t-1}} \right] \right\}}_{f(w,x,t)} + \underbrace{D_t(x_t)}_{g(x,t)} \tag{2a}$$

$$a_{t+1} = a_t \times \left\{ \frac{a'_{max} - a'_{min}}{1 + \exp(-s \cdot n_t - d)} + a'_{min} \right\} \tag{2b}$$

Table 1: Terms, units, and interpretation for the model of oxygen dynamics in pitcher-plant fluid

Term	Units	Interpretation
a_t	mg/L	Maximum amount of oxygen infused from the plant to the fluid at mid-day
a'_{min}, a'_{max}	mg/L	minimum or maximum possible augmentation of photosynthesis as a result of nutrient fertilization from organic-matter mineralization by the food web
d	mg	inflection point of the sigmoidal curve relating nutrient mineralization to photosynthetic augmentation
D_t	mg/L	Diffusion rate of oxygen from atmosphere into the pitcher fluid
f	$1/t$	constant adjusting sine wave of diurnal PAR for frequency of measurements
K_w	mg/min	half-saturation constant for prey consumption
m	mg/L	amount of oxygen used for basal metabolism (respiration) of bacteria
n_t	mg/L	quantity of nutrients mineralized by decomposition; a function of w_t and x_t
s	dimensionless	steppenss of the sigmoidal curve relating nutrient mineralization to photosynthetic augmentation
t	minutes	time (frequency of model iteration)
w_t	mg	mass of prey remaining at time t
x_t	mg/L	$[O_2]$: concentration of oxygen in the pitcher fluid

In this model, the pitcher-plant fluid is oxygenated by photosynthesis (A_t), with A_{max} augmented by prey mineralization (a_t), as well as some diffusion from the atmosphere ($g(x,t)$). Oxygen is lost from the fluid as prey is decomposed by the food web ($f(w,x,t)$). A full list of model parameters is given in Table 1.

Photosynthesis

In the absence of the foodweb, baseline oxygen concentration $[O_2]$ in the pitcher water, is determined by diurnal photosynthesis: pitchers take up CO_2 from the air or water and release O_2 back into it (Cameron et al., 1977; Bradshaw and Creelman, 1984; Sirota et al., 2013). Photosynthesis is first modeled as $A = A_{max}[1-\exp(-A_{qe}[\mathrm{PAR}-\mathrm{LCP}])]$ (after Peek et al. 2002), where PAR is photosynthetically active radiation, which normally ranges from 0 - 2500 $\mu\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$ and which is modeled as a truncated dirunal sine-wave (PAR = 0 at night, a sine-wave during the day: 1); A is photosynthetic rate (in $\mu\mathrm{mol\,CO_2}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$); A_{max} is the maximum photosynthetic rate of an pitcher plant that has not captured or processed any prey ($\bar{x}\approx 4\,\mu\mathrm{mol\,CO_2}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$; Small 1972; Farnsworth and Ellison 2008); A_{qe} is the quantum yield (≈ 0.3: the initial slope, at low light, of the A vs. PAR curve); and LCP is the light compensation point: the x-intercept when A = 0, $\approx 20\,\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$.

Since we are interested in oxygen dynamics in volumes of water, we convert A from $\mu\mathrm{mol\,CO_2}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$

Figure 1: Four-part figure. (a) truncated sine wave of PAR; (b) observed PAR; (c) A as a function of PAR w/o food web; (d) A as a function of PAR with mineralization augmentation

to mg O_2 / L by noting that there is a 1:1 relationship between μmol CO_2 and μmol O_2 in phothosynthesis; that 1 μmol O_2= 32 μg O_2 $\cdot$ m^{-2} $\cdot$ s^{-1}; and that the specific leaf area of *S. purpurea* $\approx$ 70 cm^2/g (Farnsworth and Ellison, 2008). Thus, O_2 production $\approx$ 0.21 $\mu g\, O_2 \cdot g\, leaf^{-1} \cdot s^{-1}$. The average 5-ml leaf has a surface area of 40 cm^2 and weighs 0.5 g, and a 1-L leaf would weigh 10g. Thus, O_2 production from photosynthesis $\approx$ 2.1 $mg\, O_2 \cdot L^{-1} \cdot s^{-1}$.

It follows that our functions of PAR and A, taking into account LCP, are:

$$\mathrm{PAR} = c\sin(2\pi f t) \tag{3a}$$

$$A = \begin{cases} a \cdot A_{max}[1 - \exp(-0.3[\mathrm{PAR} - 20])] & : \mathrm{PAR} \geq 20 \\ 0 & : \mathrm{PAR} < 20 \end{cases} \tag{3b}$$

In Eq. 3a, the amplitude c is maximum PAR at mid-day; the constant f adusts for the frequency of measurements. Since our model updates every minute, $f = 1/1440$ (the reciprocal of the number of minutes per day). Without loss of generality, our model runs start at sunrise ($t = 1$), day-length = 12 hours = 720 minutes, and PAR(t) is trunctated = 0 for $t \in \{721, 1440\}$. In Eq. 3b, a is the amount that photosynthetic rate can be increased as a result of nutrients provided to the plant as prey is mineralized by the food web (1).

Respiration

Biological oxygen demand (BOD) of bacteria as they decompose prey rapidly depletes [O_2] in the pitcher fluid. Although different [O_2] may favor different numbers of either aerobic or anaerobic bacteria in the pitcher fluid, the efficiency of organic-matter decomposition by either type of bacteria is roughly equal (Murphy and Condon, 1984), so we assume sufficient numbers of bacteria to decompose prey at a fixed, negative exponential rate:

$$w(t) = ae^{-b[w_0 t]} \tag{4}$$

Biologically, we take this to mean that easily digested parts of insect prey, such as fat bodies, are processed quickly, whereas the more recalcitrant proteins and chitins break down more slowly (Baiser et al., 2011). Field observations have shown that the soft parts of a single $75 - \mu g$ wasp can be comsumed completely over a 48-hour period in a pitcher with 5 ml of fluid. Thus, the baseline parameters for Equation 4 were set

at $a = 20$ mg and $b = 4\,\text{mg} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$. Because we fix the decomposition rate of given mass of prey, to maintain a 48-hour decomposition time of a single $75 - \mu g$ wasp while varying a and b in Equation 4, it is necessary to fix $\frac{a}{b} = 5$. Finally, because *S. purpurea* produces digestive enzymes such as proteases and chitinases only for a short period of time early in leaf growth (Gallie and Chang, 1997), we ignore their effects here.

Oxygen used up by the bacteria in prey consumption (= 1 - BOD) was modeled as a saturating function of the remaining prey. The proportion of the prey remaining = 1 – the amount of prey decomposed, which is a function of the maximum amount of oxygen at mid-day (a in Equation 2a, iteratively augmented by $a'$from Equation 2b and as detailed below in Equations 6, 7a); the mass of prey (w); a half-saturation constant defining the prey-consumption curve (K_w) that determines how much prey is left over each "day" of the iterated model; and the amount of oxygen needed by the bacteria for basal metabolism. Hence:

$$\text{O}_2 \text{ lost}(t) = f(w, x, t) = m + a\left[\frac{w(t-1)}{K_w + w(t-1)}\right] \tag{5}$$

In the sensitivity analysis, m in Equation 5 was fixed = 1, whereas K_w varied.

Diffusion and oxygenation

$[O_2]$ increases in the pitcher fluid in three ways. Some oxygen diffiuses from the atmosphere into the pitcher fluid, but because this happens only at the surface of the pitcher fluid, and the "mouth" of the pitcher is at least an order of magnitude smaller than the surface area of the pitcher itself (Ellison and Gotelli, 2002); we ignore this term and focus on re-oxygenation through baseline oxgyen production and prey-augmented photosynthesis (Equation 3b). The latter results from a positive feedback loop in Equation 2b that links prey mineralization to the uptake of mineralized nutrients by the plant, and the subsequent usage of these nutrients to increase photosynthetic rate of the pitcher (Farnsworth and Ellison, 2008). Ants and wasps, the most common insect prey of pitcher plants (Ellison and Gotelli, 2009), are ≈50% C, have a C:N ratio of 6:1, and N:P:K ratios of ≈12:1.5:0.9 (Sirota et al., 2013). As the prey are mineralized, the nutrients that are released, especially NH_4(Bradshaw and Creelman, 1984) and P (as ^{32}P: Plummer and Kethley 1964), are absorbed rapidly by the pitcher. Photosynthesis by *Sarracenia* is limited by both N and P (and stoichometrically by N: (Ellison, 2006; Wakefield et al., 2005)), and photosynthetic rates of pitcher plants significantly increase following N additions (Ellison and Gotelli, 2002). We model these two processes – nutrient release and augmentation of photosynthesis – with a pair of equations.

First, nutrient release following bacterial mineralzation is a function of prey mass (w) and available

oxygen (x) used by bacteria to break down and mineralize the prey:

$$n(t) = \frac{w(t)x(t)}{c} \tag{6}$$

where c is a scaling constant (we set $c = 100$).

Nutrients absorbed by pitchers and not stored for future use (Butler and Ellison, 2007) could be used to make additional enzymes for photosynthesis (Givnish et al., 1984), and we model uptake as a signmoidal (saturating) relationship betwen additional nutrients absorbed and augmentation of the peak rate of photosynthesis (a in Equation 2a):

$$a' = \frac{a'_{max} - a'_{min}}{1 + exp(-[sn(t) - d])} + a'_{min} \tag{7a}$$

$$a(t+1) = a(t) \times a'(t) \tag{7b}$$

In Equation 7a, a'_{min} is the minimum possible augmentation of photosynthesis, which we set = 0; $a'_{max}$is the maximum possible augmentation, which we set = 2; s is the steepness of the increase (set = 10); and d is the inflection point of the curve (= 0.5). Augmentation evolves as the day's leftover prey (i.e., that not completely broken down in a given day) accumulates (within the $n(t)$ term), and is mineralized on subsequent days. We note that modeling this as discrete day-to-day carry-over is an artefact of iterations in computer models. In real pitchers, decomposition is more continuous. Similarly, the model updates the value of $a\prime$ once each "day" using Equation 7b because conversion of nutrients to new photosynthetic enzymes is assumed to occur slowly relatively to bacterial decomposition itself.

Sensitivity analysis

Five paramters were varied over a wide range of values to explore the sensitivity of the model to prey input (mass added each day); the decomposition rate (a and b in Equation 4), the half-saturation constant for prey consumption (K_w in Equation 5) and the inflection point d for augmentation of photosynthesis in Equation 7a. The range of values for each of these parameters is given in Table 2.

Models were run for each of the possible combinations of $\{w_0, a, b\, K_w\, d\}$—note that the joint set of a and b includes only 4 combinations: {(5,1), (10,2), (20,4), (40,8)}—for a total of 180 model runs.

Table 2: Values of parameters used in the sensitivity analyses. Note that the values of a and b must change in concert to maintain a constant ratio of 5 so that prey decomposition is complete within 48 hours

Variable	values
Prey added (w_0)	0, 1, 5 mg/day
a	5, 10, 20, 40 mg
b	1, 2, 4, 8 mg $\cdot$ mg^{-1} $\cdot$ d^{-1}
K_w	0.001, 0.01, 0.1 mg/min
d	-1, -2, -3, -4, -5 mg

Results

Model dynamics

Illustrative examples (?spark charts or some subset of them) illustrating the range of possible outcomes - controls, intermediate dynamics, collapse, recovery.

This should include time-series plots as well as phase-space plots. Examples in Sirota et al. PNAS supplement, but I think we can do better/differently here.

- Different state = change in O2 production where the non-transient maximum values are different from control

Sensitivity analysis

Which parameters drive the dynamics? Multivariate plots, additional analyses, ...

- Transient = returning to the maximum
- Prey: increases crashes
- D: transient when D = -1, stable or crashing otherwise
- K: increases the buffering of the system, increases return rates, increases the number of stable states
- ab: alters transient return rates, alters stable point

Discussion

1. Why we need model systems for regime shifts and alternative states

2. Similarities and differences between pitcher plants, lakes, and other ecological systems in which regime shifts have been identified and explored

3. Insights from pitcher plant system and model that could be applied to other systems

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