A Producer-Consumer Model With Stoichiometry

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Abstract

Predator-prey systems have been studied for many years in terms of energy flow or mass balance of the system. Loladze, Kuang, and Elser (2000) gave a model using stoichiometry which yielded different dynamics than the predator-prey model without stoichiometry. We generalize their model and give a discussion of the dynamics for several parameter values.

1   Introduction

Population interactions in a food chain have been studied for many years. A specific interaction is the behavior of a predator and its prey. Models of predator-prey systems have mainly focused only on the flow of energy or biomass. However, the ratio of nutrients, such as phosphorus to carbon, in predators is not always the same as the ratio of nutrients in their prey. Because of this, researchers have recently been including stoichiometry, that is the ratio of nutrients, in the models (Loladze, Kuang, and Elser 2000, Sterner and Elser 2002, Kuang, Huisman, and Elser 2004, Andersen, Elser, and Hessen 2004).

Grazers (predators or consumers) typically have a fixed phosphorus to carbon ratio while producers have a range of possible ratios. In a phosphorus limited system, as the population of the producer is allowed to increase, the phosphorus to carbon ratio will decrease. This decreased ratio may not allow the grazer to flourish. To show this behavior, Loladze, Kuang, and Elser (2000) assume the producer and grazer are made of carbon and phosphorus and include stoichiometric terms in the model.

In this paper, we present a model that is an extension of the model by Loladze, Kuang, and Elser (2000). We begin by describing a basic predator-prey model and its dynamics including equilibria and bifurcations. Next, we review the Loladze, Kuang, and Elser model and its dynamics. Finally, we develop our model - a 6-dimensional model that includes producer, consumer and sediment pools where each of these pools is composed of carbon and phosphorus. In each case we vary the producer growth rate as a primary parameter. We construct bifurcation diagrams and look at representative simulations for each region. We then compare and contrast the results with the other models.

2   Dynamical Systems Terminology

Familiarity with the following terms will help in understanding the analysis of the models in this paper. Consider an n-dimensional autonomous system of differential equations, $\dot{\vec{x}} = f(\vec{x})$. An *equilibrium point*, $\vec{p}$, is a point that simultaneously has all of the derivatives in the system equal to zero, that is $\vec{f}(\vec{p}) = \vec{0}$. Because the rate of change of all compartments is zero, solutions starting at an equilibrium point will stay there. Equilibrium points can be stable or unstable. Nearby solutions are attracted to a stable equilibrium point, and most nearby solutions are repelled from an unstable equilibrium point. The stability can usually be determined by looking at the real part of

the eigenvalues of the Jacobian (the matrix of all first-order partial derivatives of the system) evaluated at that point. An equilibrium point is stable if the real parts of all of the eigenvalues are negative and is unstable if the real part of at least one of the eigenvalues is positive. If the largest real part equals zero, there is no conclusion about stability or higher order terms are needed to determine stability (Strogatz 1994).

A bifurcation is a qualitative change in the dynamics of a system as the system parameters are varied. There are many types of bifurcations although only four will be mentioned in this paper.

A *transcritical bifurcation* occurs when two different equilibrium points come together at a bifurcation point and exchange stabilities as they pass through each other. The location of a potential transcritical bifurcation can be identified by determining where an eigenvalue of the Jacobian matrix evaluated at an equilibrium point equals zero (Strogatz 1994).

Equilibrium points with complex eigenvalues cause solutions to spiral. A *supercritcal Hopf bifurcation* occurs when a stable spiral changes to an unstable spiral that is surrounded by a limit cycle. This means before the supercritical Hopf bifurcation solutions spiral in toward the stable equilibrium point, and after the supercritical Hopf bifurcation solutions starting near the equilibrium point spiral out away from the point toward the limit cycle. Solutions starting outside the limit cycle spiral in toward the limit cycle. A *subcritcal Hopf bifurcation* occurs when an unstable limit cycle surrounding a stable equilibrium point shrinks around the equilibrium point making it unstable. Before the subcritical Hopf bifurcation, local solutions spiral in toward the equilibrium point. After the subcritical Hopf bifurcation, local solutions are repelled away from the unstable equilibrium point. The location of a potential Hopf bifurcation can be found by determining where the real part of the eigenvalues of the Jacobian matrix evaluated at the equilibrium point equals zero. More information is needed to determine whether the bifurcation is supercritical or subcritical (Strogatz 1994).

A saddle node bifurcation of equilibrium points occurs when when equilibrium points are created or destroyed. As a parameter is varied, two equilibrium points move toward each other, collide, and annihilate each other. We do not have this bifurcation in our model, but the analogous situation for limit cycles. The saddle node of limit cycles is a global bifurcation. It occurs when an attracting limit cycle and a repelling limit cycle come together, collide, and annihilate each other (Strogatz 1994).

3 Predator-Prey

The models in this paper are based on predator-prey interaction that can be modeled with a variation (Rosenzweig and MacArthur 1963) of the Lotka-Volterra equations:

$$\begin{aligned}
\frac{dx}{dt} &= rx - bx^2 - f(x)y \\
\frac{dy}{dt} &= ef(x)y - dy
\end{aligned} \tag{1}$$

where
phase variables:
x = prey density
y = predator density,

parameters:
r = growth rate of the prey without self limitation
b = coefficient of self limitation of the prey
e = consumption efficiency so $0 \le e < 1$ because the predator is not able to use everything from the prey
d = death rate of the predator
$f(x)$ is a monotonic, non-decreasing function

We will do an analysis of the dynamics of (1) in terms of r using the Monod growth function $f(x) = \frac{kx}{1+k_2x}$, where k and k_2 are constants, $b = 0.05$, $e = 0.8$, $k = 1$, $k_2 = 2$ and $d = 0.25$.

3.1 Equilibria

This system has three equilibra: one at $(x,y) = (0,0)$ where both the prey and the predator do not exist, one at $(20r, 0)$ where there is a prey monoculture (the prey exists but the predator does not), and one at $(\frac{5}{6}, \frac{8}{3}r - \frac{1}{9})$ which is a coexistence equilibrium (both the prey and the predator exist).

3.2 Bifurcations

There are three bifurcations in this system as shown in the bifurcation diagrams of Table 1. When $r < 0$, no life is able to exist so $(0,0)$ is the stable equilbrium. At $r = 0$, there is a transcritical bifurcation where the no life and monoculture equilibria exchange stabilities as they pass through each

Table 1: predator-prey bifurcation diagrams
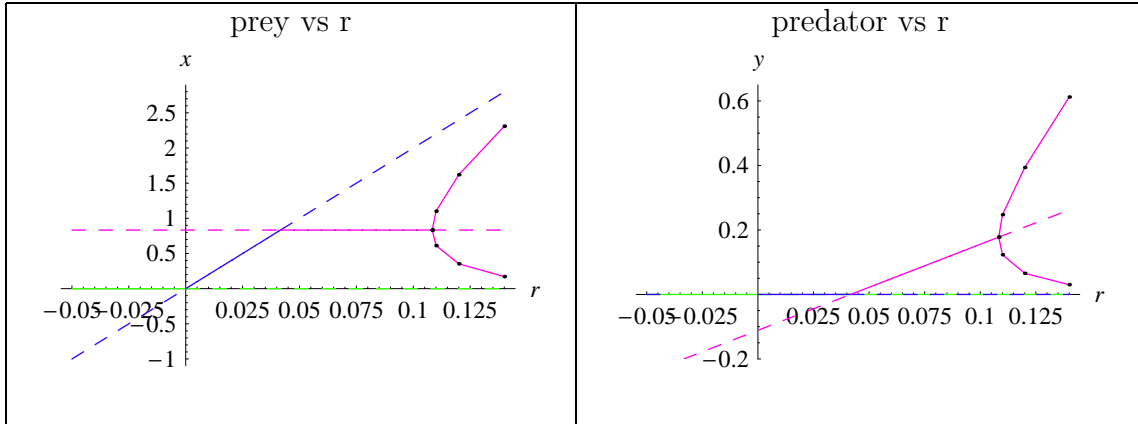
green - no life, blue - prey monoculture, pink - coexistence
solid lines - stable, dashed lines - unstable

other. For $0 < r < 0.04167$, the prey is able to survive, but the predator is not which means the prey monoculture is stable. Near $r = 0.04167$, there is another transcritical bifurcation as the monoculture and coexistence equilibria exchange stabilities. For $r > 0.04167$, both the predator and the prey exist. For $0.04167 < r < 0.1083$, the coexistence equilibrium is stable. Near $r = 0.1083$, there is a supercritical Hopf bifurcation. The coexistence equilibrium becomes unstable and a stable limit cycle emerges. For $r > 0.1083$, the predator and prey populations will oscillate with increasing amplitude a r increases.

Four simulations were done as shown in Table 2 using $x = 1$ and $y = 1$ as initial conditions for all cases. When $r = -0.1$, no life is able to exist so any positive predator or prey population densities decrease to zero. When $r = 0.02$, the predator starves but the prey population density stabilizes. The stable equilibrium point is $x = 0.4$, $y = 0$. When $r = 0.07$, both the predator and prey population densities stabilize. The stable equilibrium point is $x = 0.833$, $y = 0.0756$. When $r = 0.15$, the predator and prey coexist, but now their population densities oscillate around the unstable equilibrium point $x = 0.833$, $y = 0.289$.

The bottom two simulations in Table 2 are plotted parametrically on the xy plane. When $r = 0.07$, the parametric plot shows how the latter part of the solution with initial conditions $x = 1$, $y = 1$ spirals in toward the stable equilibrium point of $x = 0.833$, $y = 0.0756$. Any initial conditions (except
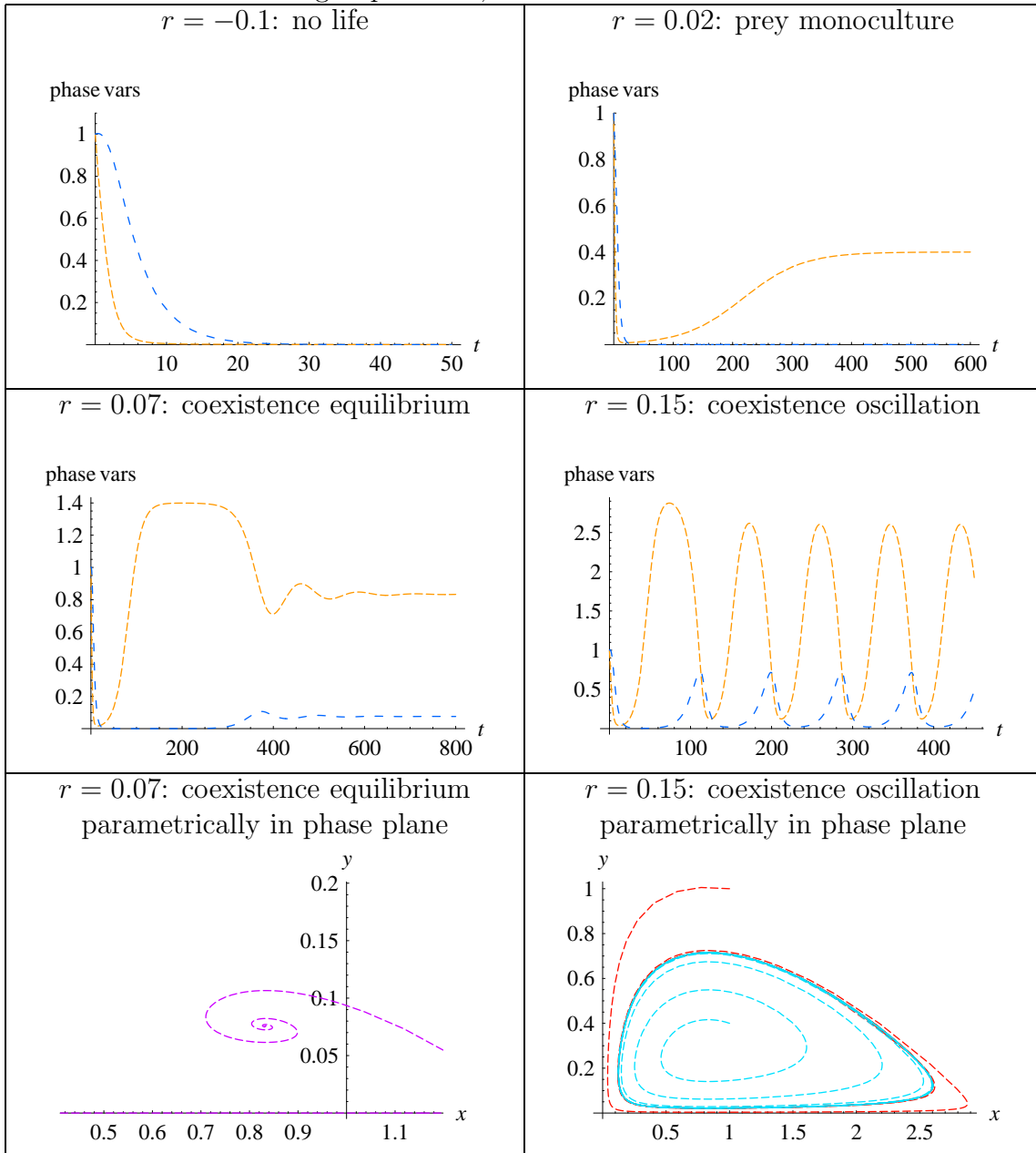
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the equilibrium point) would show the same qualitative behavior. Any r for $0.04167 < r < 0.1083$, would also show this qualitative behavior. When $r = 0.15$, two solution curves with different initial conditions are plotted. The red curve shows how the solution with initial conditions $x = 1$, $y = 1$ spirals in toward a stable limit cycle. The light blue curve shows how the solution with initial conditions $x = 1$, $y = 0.4$ spirals out away from the unstable equilibrium $x = 0.833$, $y = 0.289$ to the stable limit cycle. This shows the qualitative behavior of all solutions for $r > 0.1083$.

3.3   Bifurcation Summary

Therefore, for very small r, the basic predator-prey system cannot support any populations. As r increases, the prey monoculture will exist followed by stable coexistence densities of the predator and prey. As r is further increased, the population densities lose stability and oscillate in a stable cycle.

Table 2: predator-prey simulations

orange - producer, blue - consumer

$r = -0.1$: no life

$r = 0.02$: prey monoculture

$r = 0.07$: coexistence equilibrium

$r = 0.15$: coexistence oscillation

$r = 0.07$: coexistence equilibrium
parametrically in phase plane

$r = 0.15$: coexistence oscillation
parametrically in phase plane

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4   Loladze, Kuang, and Elser (2000) Model

Starting with a variation of Lotka-Volterra equations (compare to equation 1),

$$\frac{dx}{dt} = bx\left(1 - \frac{x}{K}\right) - f(x)y$$
$$\frac{dy}{dt} = ef(x)y - dy \tag{2}$$

Loladze, Kuang, and Elser (2000) modified the carrying capacity of the producer to include nutrient ratios as well as light intensity so the producer density depends on the amount of phosphorus in the system. They also modified the production efficiency to include the quality of the food, so lower quality food gives a lower efficiency. Their model is for a system in water with carbon representing biomass and phosphorus as the only other limiting nutrient.

The assumptions used to create the model are as follows:

1. The total mass of phosphorus in the entire system is fixed, and the system is closed for phosphorus with a total of P.

2. Phosphorus to carbon ratio in the producer varies, but it never falls below a minimum q; the grazer maintains a constant ratio θ.

3. All phosphorus in the system is divided into two pools: phosphorus in the grazer and phosphorus in the consumer.

4. The maximal net growth rate of the grazer is positive.

Their model:

$$\frac{dx}{dt} = bx\left(1 - \frac{x}{\min(K, (P - \theta y)/q)}\right) - f(x)y$$
$$\frac{dy}{dt} = \hat{e}\min\left(1, \frac{(P - \theta y)/x}{\theta}\right)f(x)y - dy \tag{3}$$

where
phase variables:
$x = $ density of producer
$y = $ density of grazer

parameters:

b = intrinsic growth rate of producer

d = specific loss rate of grazer that includes metabolic losses and death

$f(x)$ = grazer's ingestion rate

θ = consumer's phosphorus to carbon ratio

P = total amount of phosphorus in system

q = minimum phosphorus to carbon ratio in producer

K = producer's carrying capacity based on light intensity without regard to stoichiometry

$\hat{e}$ = maximal production efficiency

The system is closed for phosphorus. Since the phosphorus in the grazer is θy, the phosphorus in the producer is $P - \theta y$.

4.1 Bifurcations

For $0 < K < 0.16$, the grazer does not survive because there is not enough food available. From $0.16 < K < 0.98$, grazer density rises while producer density remains the same. At $K = 0.56$ there is a Hopf bifurcation and the equilibrium becomes unstable with a stable limit cycle. The amplitude of the limit cycle increases as K increases. At $K = 0.98$, the limit cycle disappears and a saddle and stable equilibrium appear. As K increases, the producer density also increases while the grazer density decreases. Finally at $K = 1.91$, there is a transcritical bifurcation and the grazer is not able to survive. These bifurcations are shown in Figure 1 (Loladze, Kuang, Elser 2000).

Numerical runs were done, as shown in Figure 2, by increasing K while all other parameters were constants. When $K = 0.25$ (2a), the population densities go toward a stable coexistence equilibrium. When $K = 0.75$ (2b), the population densities oscillate around an unstable equilibrium. When $K = 1.0$ (2c), the oscillations disappear and population densities go toward a different stable coexistence equilibrium with higher population densities. When $K = 2.0$ (2d), the producer monoculture equilibrium is stable (Loladze, Kuang, and Elser 2000).

4.2 Bifurcation Summary

Therefore, for very small K, the producer survives but grazer does not. As K is increased, the population densities go toward a stable equilibrium. Further increases in K cause the population densities to oscillate in a stable cycle, then to stabilize again at a coexistence equilibrium. A final increase causes

Figure 1: Loladze, Kuang, and Elser (2000) bifurcation diagram
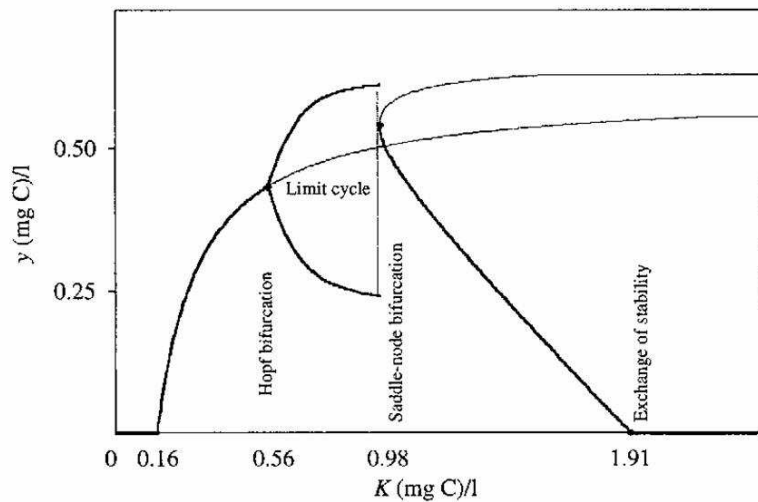
bold - stable, thin - unstable

the grazer population density to decrease to extinction. Thus including sto-
ichiometry into a predator-prey system significantly changed the qualitative
behavior. Both systems go from no life, to a producer monoculture, to stable
coexistence, to a stable oscillation which is the last behavior for the predator-
prey system, but the system with stoichiometry continues with the birth of a
stable coexistence equilibrium in a saddle node bifurcation. Along the stable
branch, the grazer equilibrium population decreases to zero. Finally, high K
results in a producer monoculture (Loladze, Kuang, and Elser 2000).
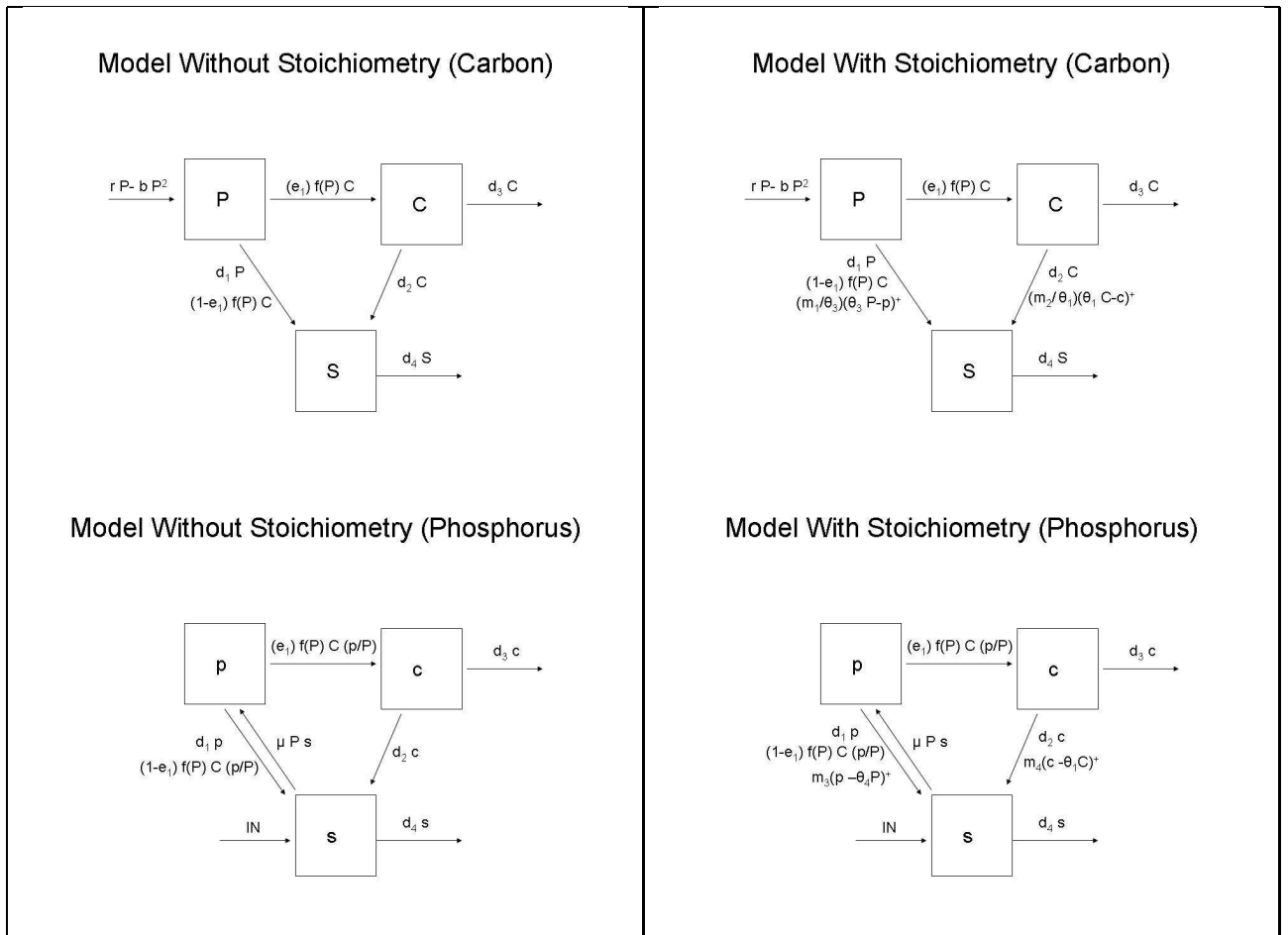
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Figure 2: Loladze, Kuang, and Elser (2000) numerical runs
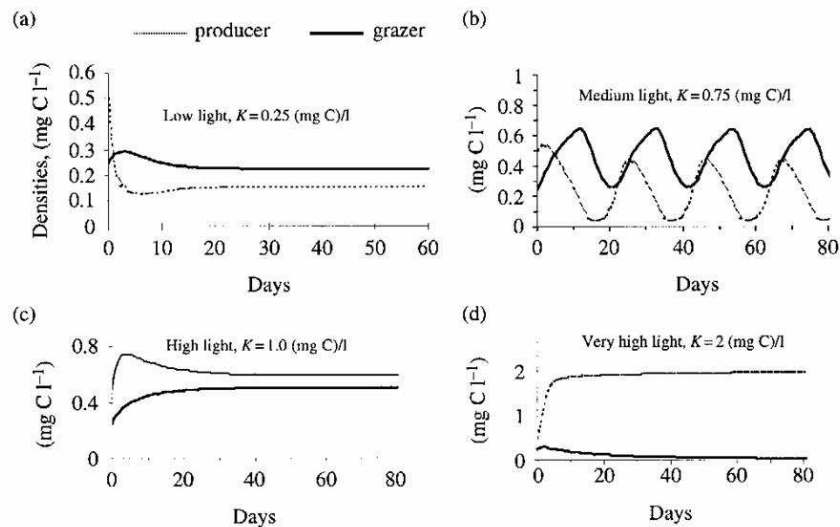
5 Our Model Without Stoichiometry

The model by Loladze, Kuang, and Elser (2000) is for an aquatic system that is closed for phosphorus and does not include nutrient cycling. See, however, Kuang, Huisman, and Elser (2004) for a model including free phosphorus. Their model also uses a fixed ratio of nutrients in the consumer and uses the carrying capacity to represent energy input into the system. We present a more general model that appears to be more realistic for a terrestrial system. It is open for phosphorus, includes a nutrient pool, is driven toward the desired stoichiometric ratios of phosphorus to carbon (rather than fixing the ratios), and uses the producer's growth rate to represent input into the system. We start developing our model by temporarily postponing consideration of stoichiometry. We use producer, consumer, and sediment pools each containing carbon and phosphorus as our phase variables:

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Table 3: Flow chart of our models

Model Without Stoichiometry (Carbon)

$r P - b P^2$ → P → $(e_1) f(P) C$ → C → $d_3 C$

$d_1 P$
$(1-e_1) f(P) C$

$d_2 C$

S → $d_4 S$

Model With Stoichiometry (Carbon)

$r P - b P^2$ → P → $(e_1) f(P) C$ → C → $d_3 C$

$d_1 P$
$(1-e_1) f(P) C$
$(m_1/\theta_3)(\theta_3 P-p)^+$

$d_2 C$
$(m_2/\theta_1)(\theta_1 C-c)^+$

S → $d_4 S$

Model Without Stoichiometry (Phosphorus)

p → $(e_1) f(P) C (p/P)$ → c → $d_3 c$

$d_1 p$
$(1-e_1) f(P) C (p/P)$
$\mu P s$

$d_2 c$

IN → s → $d_4 s$

Model With Stoichiometry (Phosphorus)

p → $(e_1) f(P) C (p/P)$ → c → $d_3 c$

$d_1 p$
$(1-e_1) f(P) C (p/P)$
$m_3(p - \theta_4 P)^+$
$\mu P s$

$d_2 c$
$m_4(c - \theta_1 C)^+$

IN → s → $d_4 s$

P = density of carbon of producer in environment
p = density of phosphorus of producer in environment
C = density of carbon of consumer in environment
c = density of phosphorus of consumer in environment
S = density of carbon in sediment
s = density of phosphorus in sediment

Our model without stoichiometry, shown in Table 3 is given here.

$$\frac{dP}{dt} = rP - bP^2 - f(P)C - d_1P$$

$$\frac{dC}{dt} = e_1f(P)C - d_3C - d_2C$$

$$\frac{dS}{dt} = d_1P + d_2C - d_4S + (1 - e_1)f(P)C$$

$$\frac{dp}{dt} = \mu Ps - d_1p - f(P)C\frac{p}{P}$$

$$\frac{dc}{dt} = e_1f(P)C\frac{p}{P} - d_3c - d_2c$$

$$\frac{ds}{dt} = d_2c + d_1p + IN - d_4s - \mu Ps + (1 - e_1)f(P)C\frac{p}{P} \qquad (4)$$

parameters:
r = growth rate coefficient of the producer without self limitation
b = coefficient of self limitation of the producer
$f(P)$ = the consumer's variable ingestion rate multiplier, typically kP or $\frac{kP}{1+k_2P}$
d_1 = coefficient of the rate the producer is going to sediment
e_1 = consumption efficiency
d_3 = coefficient of the rate the consumer is leaving the system
d_2 = coefficient of the rate the consumer is going to sediment
d_4 = coefficient of the rate the sediment is leaving the system
μ = coefficient of the rate phosphorus is taken from the sediment to the producer
IN = rate of phosphorus input into the system via the sediment

terms:

- $rP - bP^2$ is the logistic growth rate of the producer on its own

- $f(P)C$ is the rate of food taken from producer by the consumer

- d_1P is the death rate for the producer

- $e_1f(P)C$ is the rate that the consumer converts food into biomass

- d_3C is the rate of the consumer leaving the system

- d_2C is the death rate for the consumer

- d_4S is the rate of sediment leaving the system

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- μPs is the uptake rate of phosphorus from the sediment by the producer

- $d_1 p$ is the rate of phosphorus going into the sediment due to death of the producer

- $\frac{p}{P} f(P)C$ is the rate of phosphorus taken from the producer by the consumer

- $e_1 f(P)C\frac{p}{P}$ is the rate the consumer takes in phosphorus from the producer

- $d_3 c$ is the rate of consumer phosphorus leaving the system

- $d_2 c$ is the rate of phosphorus going to the sediment due to consumer death

- $d_4 s$ is the rate of sediment phosphorus leaving the system

- $(1 - e_1) f(P)C$ is the rate at which food is taken up by the consumer but not ingested

- $(1 - e_1) f(P)C\frac{p}{P}$ is the rate at which phosphorus is taken up by the consumer but not ingested

Looking at the equations, the three carbon equations decouple from the phosphorus equations because none of the carbon equations depend on the phosphorus phase variables. Furthermore, the producer and consumer carbon equations decouple from the sediment carbon equation because neither depend on the carbon in the sediment. We will first look at the dynamics of the 2-dimensional decoupled system given below.

$$
\begin{aligned}
\frac{dP}{dt} &= rP - bP^2 - f(P)C - d_1 P \\
\frac{dC}{dt} &= e_1 f(P)C - d_3 C - d_2 C
\end{aligned}
\tag{5}
$$

This system turns out to be the same as the basic predator-prey model. We can combine terms in this 2-dimensional model to get it to look like the predator-prey model as shown in Table 4. We can see that the r values of the bifurcations are shifted by d_1 because r in the predator-prey system corresponds to $r - d_1$ in the 2-dimensional decoupled system. For example, in the predator-prey system, the first transcritical bifurcation is at $r = 0$ while the 2-dimensional decoupled system with $d_1 = 0.1$ has its first transcritical bifurcation at $r = 0.1$.

predator-prey term	corresponding 2D model term(s)
x	P
y	C
r	$r - d_1$
b	b
k	k
k_2	k_2
e	e_1
d	$d_2 + d_3$

Using the following values for the variables: $b = 0.05$, $d_1 = 0.1$, $e_1 = 0.8$, $k = 1$, $k_2 = 2$, $d_3 = 0.1$, $d_2 = 0.15$, and $f(P) = \frac{(kP)}{(1+k_2P)}$, we will find the equilibrium points and bifurcations in terms of r, the growth rate of the producer.

5.1 Equilibria

There are three equilibrium points for this system: one where no life exists so P and C are both zero, one where there is a producer monoculture so C is zero and P is nonzero, and one where the producer and consumer coexist so P and C are both nonzero.

5.2 Bifurcations

There are three bifurcations: at $r = 0.1$, near $r = 0.14167$, and near $r = 0.2083$. For $r < 0.1$, no life exists, so the no life equilibrium is stable. At $r = 0.1$, there is a transcritical bifurcation, so for $0.1 < r < 0.14167$, the producer monoculture is stable. Near $r = 0.14167$, there is another transcritical bifurcation so for $0.14167 < r < 0.2083$, the coexistence equilibrium is stable. Near $r = 0.2083$, there is a supercritical Hopf bifurcation, so for $r > 0.2083$ the coexistence equilibrium is unstable and solutions spiral out to a stable limit cycle.

Next we added in the sediment carbon equation and the three phosphorus equations. Because the 2-dimensional decoupled system is the same as the predator-prey system, the 2-dimensional solutions $P(t)$ and $C(t)$ are driving coefficients for the remaining 4-dimensional system.

Plotting a solution using the following parameter values: $r = 0.25$, $b =$

0.05, $d_1 = 0.1$, $e_1 = 0.8$, $k = 1$, $k_2 = 2$, $d_3 = 0.1$, $d_2 = 0.15$, $d_4 = 0.3$, $\mu = 0.2$, and $IN = 0.1$ will show the same solutions as the predator-prey system with $r = 0.15$, shown in Table 2, for the producer's carbon and consumer's carbon as well as solutions for the other four phase variables as shown in Figure 3. The population densities oscillate around the unstable equilibrium $P = 0.833$, $C = 0.289$, $S = 0.482$, $p = 0.244$, $c = 0.0846$, $s = 0.305$.
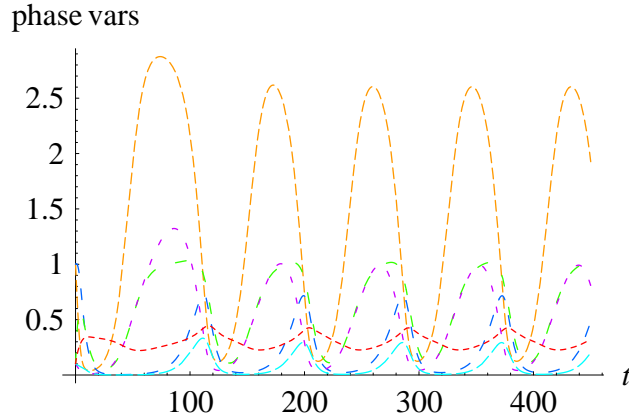

Figure 3: P - orange, C - blue, S - green, p - purple, c - teal, s - red

6   Our model with stoichiometry

We now modify the system without stoichiometry to include the effect of phosphorus and carbon together, rather than just carbon. To add stoichiometry into the model, we will use the following assumptions:

1. We intend that consumers tend toward a fixed phosphorus to carbon ratio, θ_1, and producers tend toward a range of possible phosphorus to carbon ratios, $\theta_3 < p : P < \theta_4$.

2. If consumers have $c : C > \theta_1$, they excrete only phosphorus. If consumers have $c : C < \theta_1$, they excrete only carbon. The rate of excretion is proportional to the distance from the current ratio to the optimal ratio.

3. If producers have $p : P > \theta_4$, they excrete only phosphorus at a rate proportional to the distance from the current ratio to θ_4. If producers have $p : P < \theta_3$, they excrete only carbon at a rate proportional to the distance from the current ratio to θ_3.

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These assumptions give six possible cases:

1. $\frac{c}{C} > \theta_1$ and $\theta_3 < \frac{p}{P} < \theta_4$

2. $\frac{c}{C} > \theta_1$ and $\frac{p}{P} < \theta_3$

3. $\frac{c}{C} > \theta_1$ and $\frac{p}{P} \geq \theta_4$

4. $\frac{c}{C} \leq \theta_1$ and $\theta_3 < \frac{p}{P} < \theta_4$

5. $\frac{c}{C} \leq \theta_1$ and $\frac{p}{P} < \theta_3$

6. $\frac{c}{C} \leq \theta_1$ and $\frac{p}{P} \geq \theta_4$

For convenience, we will use the following notation in the model:

$$(x)^+ = \begin{cases} x & \text{if } x \geq 0 \\ 0 & \text{if } x < 0 \end{cases}$$

Our model with stoichiometry is given here and shown as a flow chart in Table 3.

$$\frac{dP}{dt} = rP - bP^2 - f(P)C - d_1 P - \frac{m_1}{\theta_3}(\theta_3 P - p)^+$$

$$\frac{dC}{dt} = e_1 f(P)C - d_3 C - d_2 C - \frac{m_2}{\theta_1}(\theta_1 C - c)^+$$

$$\frac{dS}{dt} = d_1 P + d_2 C - d_4 S + (1 - e_1)f(P)C + \frac{m_1}{\theta_3}(\theta_3 P - p)^+ + \frac{m_2}{\theta_1}(\theta_1 C - c)^+$$

$$\frac{dp}{dt} = \mu P s - d_1 p - \frac{p}{P}f(P)C - m_3(p - \theta_4 P)^+$$

$$\frac{dc}{dt} = e_1 f(P)C\frac{p}{P} - d_3 c - d_2 c - m_4(c - \theta_1 C)^+$$

$$\frac{ds}{dt} = d_2 c + d_1 p + IN - d_4 s - \mu P s + (1 - e_1)f(P)C\frac{p}{P} + m_3(p - \theta_4 P)^+$$
$$+ m_4(c - \theta_1 C)^+ \tag{6}$$

where
parameters:
$\theta_1 = $ target $c : C$ in consumer
$\theta_3 = $ minimum target $p : P$ in producer
$\theta_4 = $ maximum target $p : P$ in producer
$m_1 = $ coefficient of the excretion rate when $p : P$ is too low
$m_2 = $ coefficient of the excretion rate when $c : C$ is too low
$m_3 = $ coefficient of the excretion rate when $p : P$ is too high
$m_4 = $ coefficient of the excretion rate when $c : C$ is too high

terms:

- $\frac{m_1}{\theta_3}(\theta_3 P - p)^+$ is the excretion rate when $p : P$ is too low

- $\frac{m_2}{\theta_1}(\theta_1 C - c)^+$ is the excretion rate when $c : C$ is too low

- $m_3(p - \theta_4 P)^+$ is the excretion rate when $p : P$ is too high

- $m_4(c - \theta_1 C)^+$ is the excretion rate when $c : C$ is too high

Before analyzing this system, we can decompose it to first solve a 5-dimensional system with $P, C, p, c,$ and s, then use those solutions to solve the 1-dimensional non-autonomous system with S because none of the other five equations depend on S. Because the amount of carbon in the sediment does not affect the behavior of the producer or consumer, from here on we will only deal with the 5-dimensional system.

When determining the behavior of a system, one of the first tasks is to find the equilibrium points and their stability. This turned out to be very challenging in this case. Please see the appendix for more details on how they were found.

In general there are three equilibrium points. However, all three points are not always physically relevant as the parameters are varied. Our primary parameter being varied is r. Because r is the producer growth rate, varying r should affect the phosphorus to carbon ratio in the producer which determines if it is high or low quality food for the producer. Our secondary parameter being varied is IN. We choose three values for IN and look for equilibrium points and bifurcations in terms of r in each case. The other parameters are fixed as follows: $b = 0.05$, $d_1 = 0.1$, $e_1 = 0.8$, $k = 1$, $k_2 = 2$, $d_3 = 0.1$, $d_2 = 0.15$, $d_4 = 0.3$, $\mu = 0.2$, $m_1 = m_2 = m_3 = m_4 = 1$, $\theta_1 = 0.031$, $\theta_3 = 0.0038$, $\theta_4 = 0.05$, and $f(P) = \frac{kP}{1+k_2P}$.

6.1 Low Phosphorus Input: IN=0.001

6.1.1 Equilibria

When $IN = 0.001$, there are two equilibrium points: one where all of the variables are zero except the phosphorus in the sediment (no life), and one where the consumer's carbon and sediment are zero and all other variables are nonzero (producer monoculture). The coexistence equilibrium is not physically relevant because the consumer carbon and consumer phosphorus are negative as well as the producer phosphorus for some values of r.

6.1.2 Bifurcations

There is one transcritical bifurcation at $r = 0.1$, shown in Table 5. For $r < 0.1$, the no life equilibrium is stable. At $r = 0.1$ the no life and producer monoculture come together and switch stabilities as they pass through each other, so for $r > 0.1$ the producer monoculture equilibrium point is stable.

Table 5: IN=0.001 bifurcation diagrams
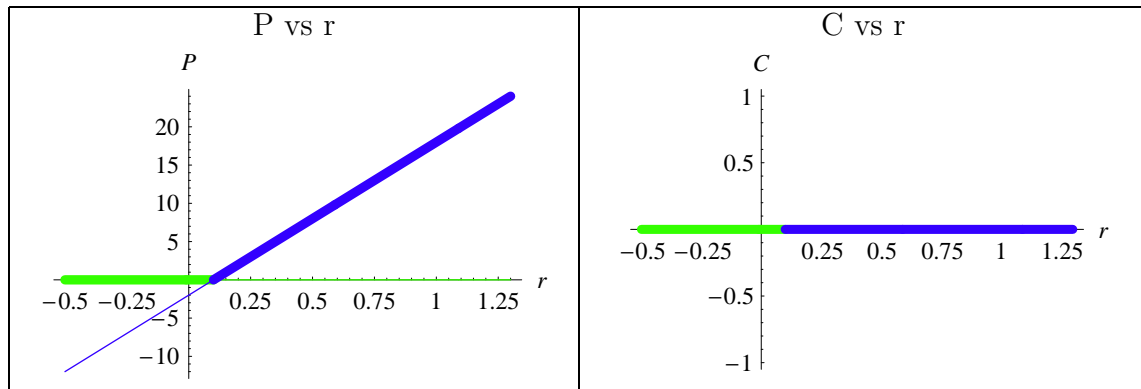
green - no life, blue - producer monoculture
bold lines - stable, thin lines - unstable

Two simulations were done as shown in Table 6 using the initial conditions $P = 0.5$, $C = 0.25$, $p = 2$, $s = 2$, and $c = 2$. When $r = 0.07$, no life is able to exist so any positive producer or consumer population densities will decrease to zero. The only positive phase variable is the phosphorus in the sediment. The stable equilibrium is $P = 0$, $C = 0$, $p = 0$, $c = 0$, $s = 0.0033$. When $r = 0.11$, the producer density stabilizes while the consumer density approaches zero. The stable equilibrium is $P = 0.2$, $C = 0$, $p = 0.00133$, $c = 0$, $s = 0.0033$.

6.1.3 Bifurcation Summary

In this case, the input of phosphorus into the system is very low. The consumer is unable to survive, so when IN=0.001, the system has only the first bifurcation that the system without stoichiometry has and no other behavior. First no life is able to exist, but as the growth rate increases, the producer monoculture is able to exist.

Table 6: IN=0.001 simulations
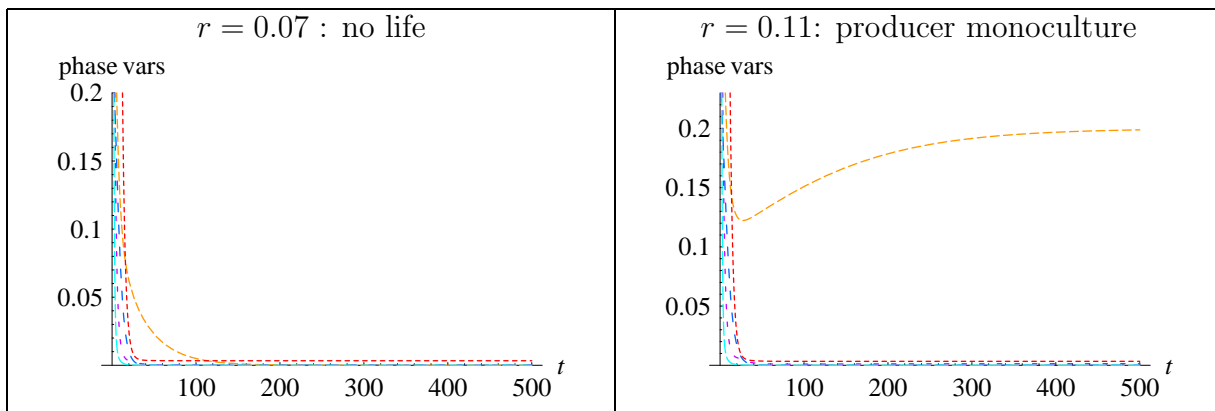

6.2 Intermediate Phosphorus Input: IN=0.01

6.2.1 Equilibria

Now when $IN = 0.01$, there are three physically relevant equilibrium points: one where all of the variables are zero except the phosphorus in the sediment (no life), one where the consumer's carbon and sediment are zero and all other variables are nonzero (producer monoculture), and one where all variables are nonzero (coexistence).

6.2.2 Bifurcations

There are five bifurcations in this case, shown in the bifurcation diagram in Table 7. Note that the first three bifurcations are the same as the predator-prey system, shown in Table 1. The first transcritical bifurcation is shifted 0.1 to the right. When $r = 0$, no life exists. The only nonzero value is the phosphorus in the sediment. The system continues to have the no life equilibrium stable until the first bifurcation which occurs at $r = 0.1$. This is a transcritical bifurcation. The no life and monoculture equilibria come together here. As they pass through, the no life equilibrium goes from stable to unstable, and the monoculture equilibrium goes from unstable to stable. Near $r = 0.14167$, there is another transcritical bifurcation. The monoculture equilibrium goes from stable to unstable and the coexistence equilibrium point becomes stable. Near $r = 0.2083$ there is a supercritical Hopf bifurcation. The coexistence equilibrium point becomes unstable and nearby solutions spiral out to a stable limit cycle. Near $r = 0.4757$, there is a subcritical

Table 7: IN=0.01 bifurcation diagrams

green - no life, blue - producer monoculture, pink - coexistence
bold lines - stable, thin lines - unstable
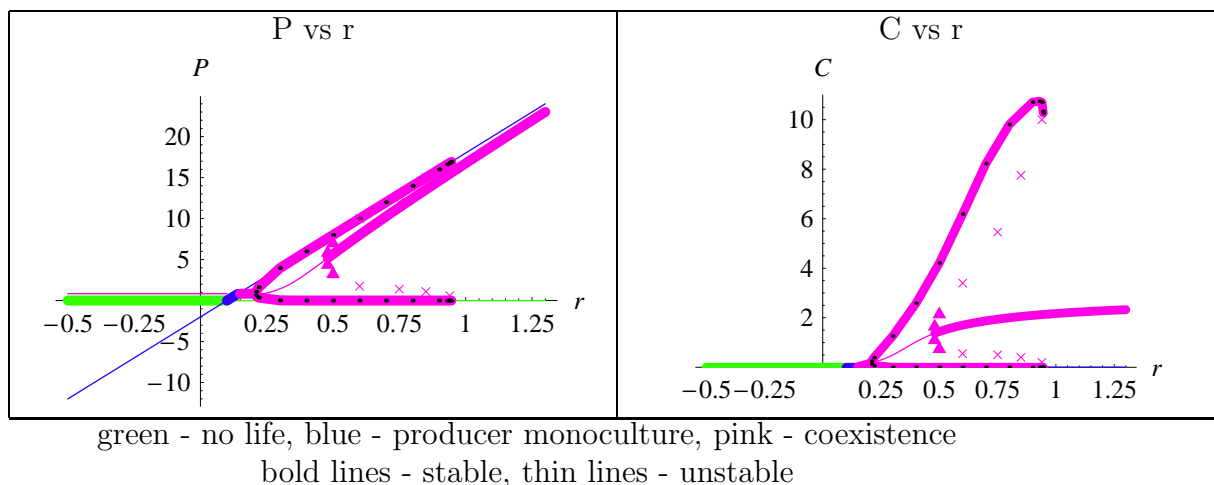
Hopf bifurcation moving from larger r to smaller r, resulting in bistability, with two coexisting attractors. Solutions starting near the equilibrium point have oscillations that damp out and go to that point. Solutions starting "farther" away from the stable equilibrium will go to the stable limit cycle. The last bifurcation occurs near $r = 0.946$. Our conjecture is that there is an unstable limit cycle between the equilibrium point and the stable limit cycle, and the two limit cycles come together and disappear in a saddle-node bifurcation of limit cycles. As r is increased past 0.946, the solutions go toward a stable coexistence equilibrium for all initial conditions. Some initial conditions allow solutions to reach the stable equilibrium very quickly. However, solutions with initial conditions near the ghost of the now disappeared pair of limit cycles move slower as they seem to be weakly repelled away from the disappeared pair of limit cycles until they reach the stable equilibrium point.

In Table 7, the branches representing the stable limit cycles were plotted by connecting the black data points. The points were found by determining the maximum and minimum values of the carbon in the producer and the carbon in the consumer from simulations done in *Mathematica*. For the unstable limit cycle, we were only able to get two maximum and two minimum values for both the carbon in the producer and the carbon in the consumer from simulations. These points are represented by pink triangles. The pink x's are conjectured points for the unstable limit cycle.

Seven simulations were done as shown in Table 8. The first four were done with the initial conditions $P = 0.5$, $C = 0.25$, $p = 1$, $c = 1$, $s = 1$.

When $r = 0.05$, no life is able to exist so any positive amounts of carbon or phosphorus in the producer and consumer go to zero while the phosphorus in the sediment stabilizes. The stable equilibrium is $P = 0$, $C = 0$, $p = 0$, $c = 0$, $s = 0.033$. When $r = 0.11$, the producer's carbon and phosphorus stabilize as well as the sediment's phosphorus. The carbon and phosphorus in the consumer go to zero. The stable equilibrium is $P = 0.2$, $C = 0$, $p = 0.0103$, $c = 0$, $s = 0.033$. When $r = 0.16$, all phase variables stabilize as they approach the stable equilibrium $P = 0.833$, $C = 0.0489$, $p = 0.0421$, $c = 0.0017$, $s = 0.0328$. When $r = 0.215$, all phase variables oscillate in a stable cycle around the unstable equilibrium of $P = 0.833$, $C = 0.1956$, $p = 0.03004$, $c = 0.00626$, $s = 0.0312$.

When $r = 0.5$, two sets of initial conditions were used that resulted in two very different behaviors. Initial conditions set 1 is $P = 12$, $C = 1.3$, $p = 0.1$, $s = 0.05$, $c = 0.05$. For this set, all phase variables oscillate with increasing amplitude until a stable limit cycle is reached. Initial condition set 2 is $P = 5$, $C = 1$, $p = 0.1$, $s = 0.02$, $c = 0.04$. For this set, all phase variables have oscillations that damp out and go to a stable coexistence equilibrium of $P = 5.66$, $C = 1.44$, $p = 0.1053$, $c = 0.0394$, $s = 0.0202$.

When $r = 1$, the initial conditions of $P = 0.5$, $C = 0.25$, $p = 1$, $c = 1$, $s = 1$ were used. All phase variables oscillate, then go to a stable equilibrium of $P = 16.741$, $C = 2.171$, $p = 0.2878$, $c = 0.05798$, $s = 0.014$. Other initial conditions at this r value may go to the stable equilibrium very quickly without oscillating.

In Table 9, two simulations with $r = 0.5$ are shown as projections in the PC plane. The solution curves do not cross themselves in the full 5-dimensional phase space, but they may appear to in the plots because the curves in five dimensions are being projected onto two dimensional planes. The first plot has initial conditions of $P = 5$, $C = 1.6$, $p = 0.1$, $c = 0.05$, $s = 0.05$. The solutions appear to get attracted to a 2-dimensional surface. Once the solutions reach this surface, they spirals out to a stable limit cycle. The second plot has initial conditions of $P = 5$, $C = 1.5$, $p = 0.1$, $c = 0.05$, $s = 0.05$. In this case, once the solution reaches the attracting surface, it spiral in toward a stable equilibrium point. The initial conditions for both plots are very close to each other. The only difference is the first plot has $C = 1.6$ and the second plot has $C = 1.5$. In the plot of the two solutions together, we see that both solutions appear to reach an attracting surface near the same place, but one solution goes to a stable cycle while the other goes toward a stable equilibrium point.

Table 8: IN=0.01 simulations

$r = 0.05$: no life

phase vars

$r = 0.11$: producer monoculture

phase vars

$r = 0.16$: coexistence equilibrium

phase vars

$r = 0.16$ smaller range

phase vars

$r = 0.215$: coexistence small oscillation

phase vars

$r = 0.5$ initial cond set 1:
coexistence large oscillation

phase vars

$r = 0.5$ initial cond set 2:
coexistence equilibrium

phase vars

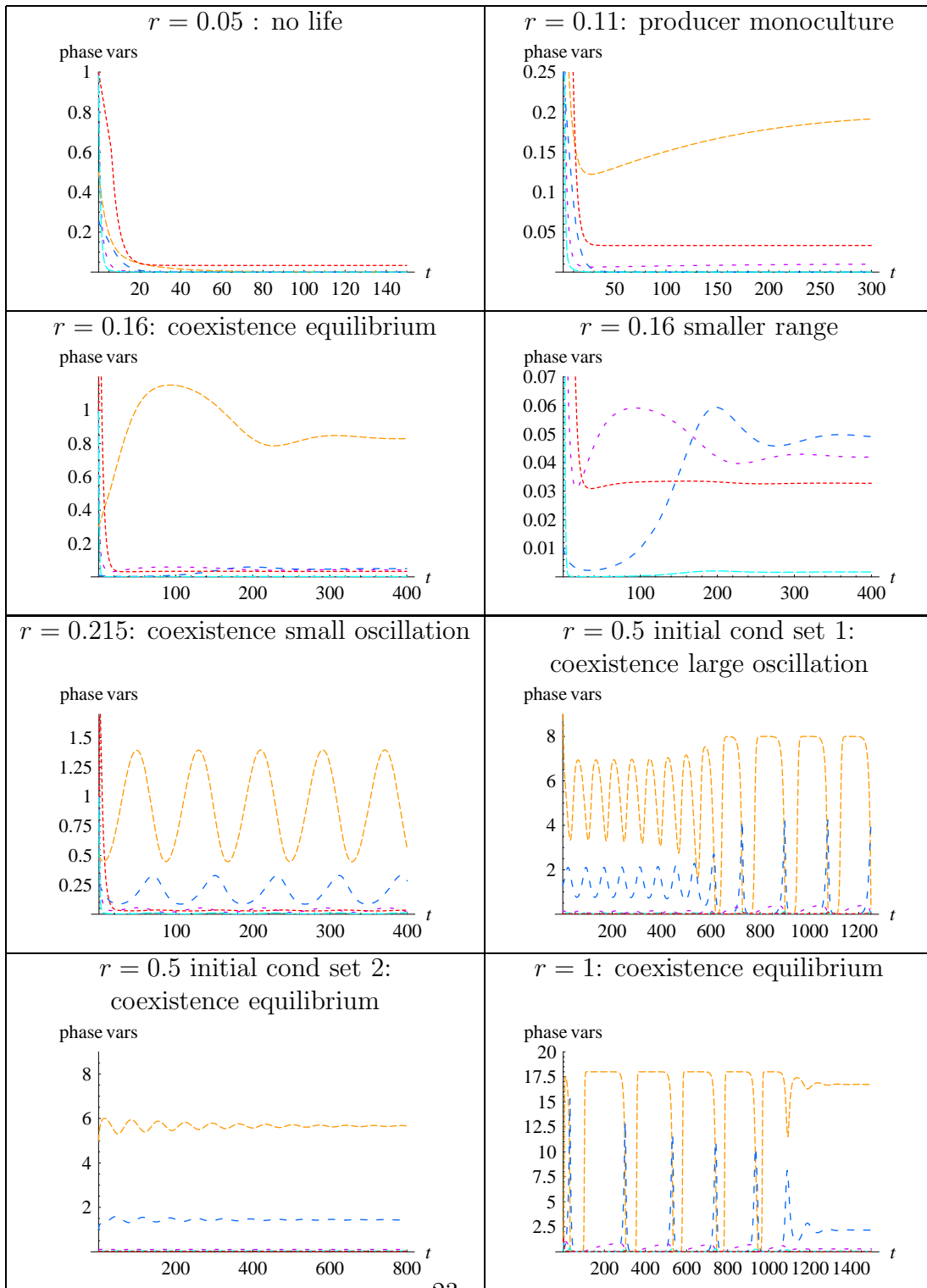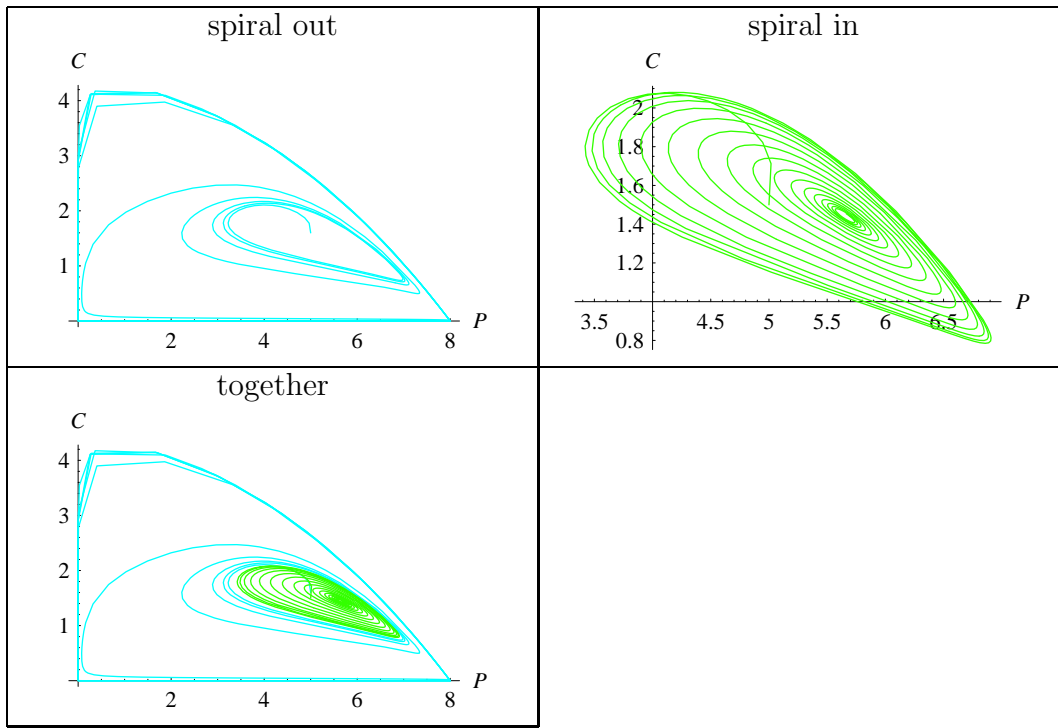$r = 1$: coexistence equilibrium

phase vars

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Table 9: IN=0.01 2D projections of solutions when $r = 0.5$

6.2.3 Bifurcation Summary

With a very low producer growth rate, no life is able to exist. Increasing the growth rate slightly allows the producer to survive. By further increasing the growth rate, the producer and consumer are able to coexist though the way the species coexist may vary. They start by going toward stable equilibrium populations, then to a stable oscillation. Next the producer and consumer population densities have bistability either going to a stable equilibrium or to a stable oscillation. Finally both population densities go only to a stable equilibrium.

6.3　High Phosphorus Input: IN=1

6.3.1　Equilibria

For IN=1, there are three physically relevant equilibrium points: one where all of the variables are zero except the phosphorus in the sediment (no life), one where the consumer's carbon and sediment are zero and all other variables are nonzero (producer monoculture), and one where all variables are nonzero (coexistence).

6.3.2　Bifurcations

There are three bifurcations: a transcritical bifurcation at $r = 0.1$, a transcritical bifurcation near $r = 0.14167$, and a supercritical Hopf bifurcation near $r = 0.2083$.

Table 10: IN=1 bifurcation diagrams
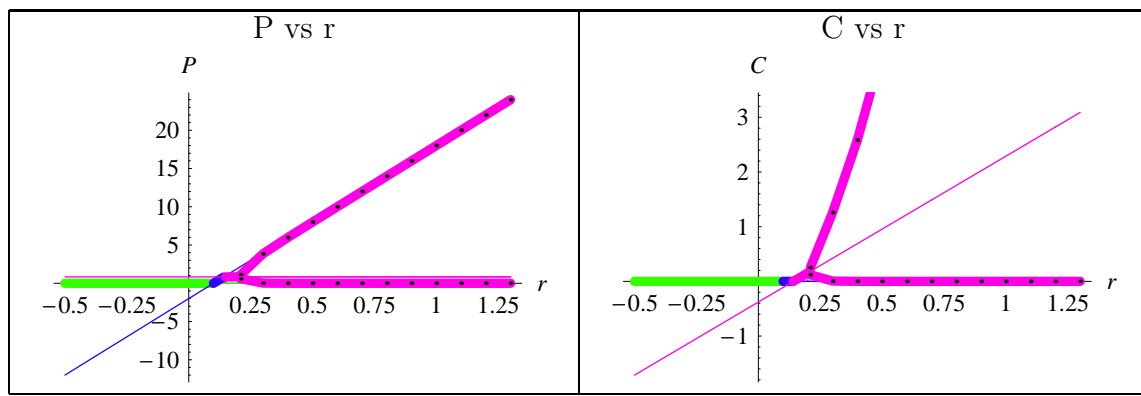
green - no life, blue - producer monoculture, pink - coexistence
bold lines - stable, thin lines - unstable

Four simulations, shown in Table 11, were done using initial conditions of $P = 0.5$, $C = 0.25$, $p = 2$, $c = 2$, $s = 2$. When $r = 0.05$, no life is able to exist so any positive amount of carbon or phosphorus in the producer and consumer go to zero while the phosphorus in the sediment stabilizes. The stable equilibrium is $P = 0$, $C = 0$, $p = 0$, $c = 0$, $s = 3.33$. When $r = 0.12$, the producer's carbon and phosphorus stabilize as well as the sediment's phosphorus. The carbon and phosphorus in the consumer go to zero. The stable equilibrium is $P = 0.4$, $C = 0$, $p = 0.261$, $c = 0$, $s = 3.33$. When

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Table 11: IN=1 simulations
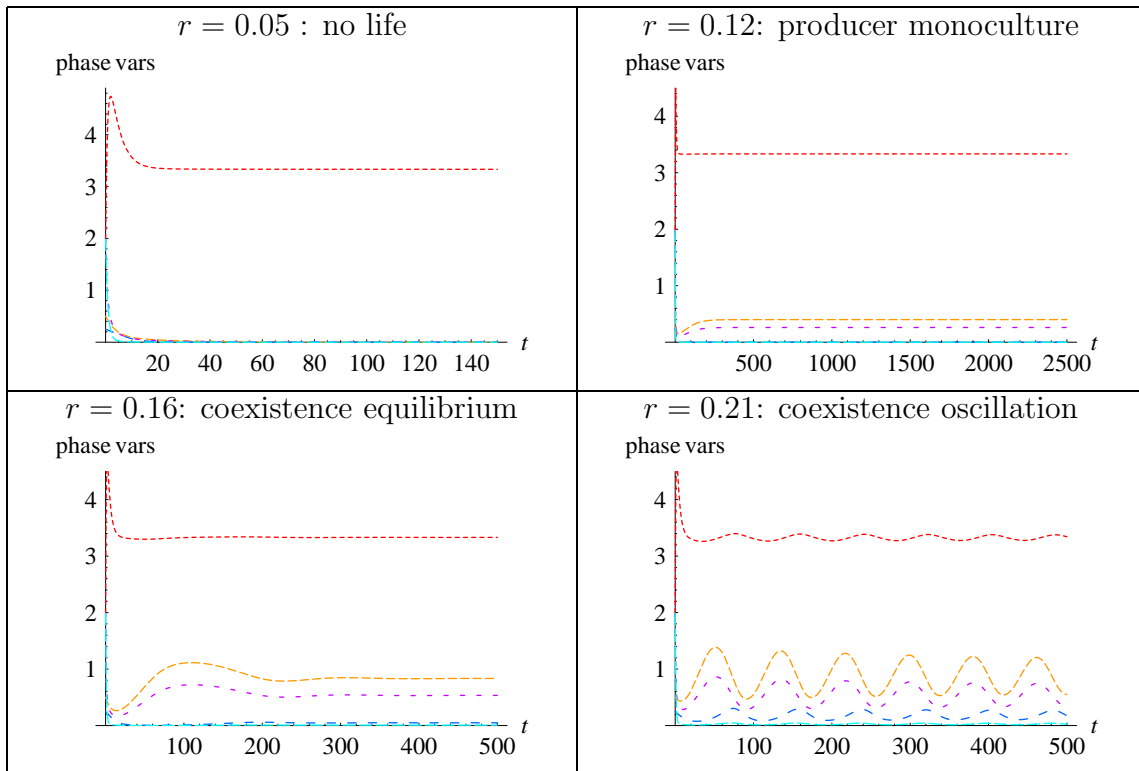
$r = 0.16$, all phase variables stabilize as they approach the stable equilibrium $P = 0.833$, $C = 0.0489$, $p = 0.534$, $c = 0.00747$, $s = 3.331$. When $r = 0.22$, all phase variables oscillate in a stable cycle around the unstable equilibrium of $P = 0.833$, $C = 0.182$, $p = 0.51$, $c = 0.0268$, $s = 3.32$.

6.3.3 Bifurcation Summary

Since phosphorus is abundant, this system has the same behavior as the predator-prey system. Stoichiometry has no effect. With a very low growth rate no life is able to exist. Increasing the growth rate allows the producer to exist. As the growth rate is increased further, the producer and consumer coexist by first going to a stable equilibrium then to a stable oscillation.

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7 Summary

Several models have been presented in this paper: predator-prey, Loladze, Kuang, and Elser (2000), our model without stoichiometry (6-dimensional and 2-dimensional decoupled), and our 5-dimensional with stoichiometry considering three cases. In all of the models, the dynamics were investigated using one parameter cuts as the producer growth was varied. There are many similarities and differences in the behavior of these models.

The model with stoichiometry for $IN = 0.001$ is like all the other models because it has a transcritical bifurcation separating no life stability and producer monoculture stability. This model is different from all the other models because it is the only bifurcation in the system and the other models have additional bifurcations. In this model the amount of phosphorus in the system is too low to have a coexistence equilibrium.

The predator-prey model, our model without stoichiometry and our model with stoichiometry for $IN = 1$ have the same qualitative behavior. They all have two transcritical bifurcations and one supercritical Hopf bifurcation which yields stability in the progression of no life, producer monoculture, coexistence equilibrium, and coexistence oscillation. It was shown earlier that the predator-prey model and our model without stoichiometry are equivalent for the producer/prey and consumer/predator. The model with stoichiometry for $IN = 1$ is like the other two because amount of phosphorus in the system is so high. This gives us a system with essentially unlimited phosphorus. This means stoichiometry did not need to be considered, which is exactly the case for the predator-prey model and the model without stoichiometry.

The model by Loladze, Kuang, and Elser (2000) and our model with stoichiometry for $IN = 0.01$ give the most interesting behavior of the models presented here. In both of these models, there are two transcritical bifurcations followed by a supercritical Hopf bifurcation giving stability in the order of no life, producer monoculture, coexistence equilibrium, and coexistence oscillation. After this point the dynamics of the two model differ. The model by Loladze, Kuang, and Elser (2000) next has a saddle-node bifurcation making the coexistence equilibrium stable followed by a transcritical bifurcation where the monoculture equilibrium becomes stable. In our model, we next have a subcritical Hopf bifurcation so population densities either go toward a stable coexistence equilibrium point or a stable limit cycle followed by a conjectured saddle-node of cycles bifurcation after which all population densities go toward the stable coexistence equilibrium.

Both the model by Loladze, Kuang, and Elser (2000) and our model with stoichiometry with $IN = 0.01$ show that including stoichiometry in the model when phosphorus is limited (but not too limited) give qualitatively different

results than the models without stoichiometry or with unlimited phosphorus although the qualitative results the the two models are quite different.

8   Discussion, Model Limitations and Future Work

Although our model is fairly complicated as it stands, there are significant modeling assumptions that could be addressed. One behavior of the Loladze, Kuang, and Elser (2000) model which is not present in our model is high quantity, low quality food for the consumer. Consequently, in our model, although the producer's ratio of phosphorus to carbon is sometimes lower than the consumer's ratio, our consumer population density never decreases with increased producer population. It is possible that this behavior is present for parameter combinations which we did not investigate. A more complete investigation of the parameter space might also yield additional behaviors.

An interesting observation is that the prescribed target ratio (θ_1) of phosphorus to carbon in the consumer is not typically achieved, even when the system is at equilibrium. The forces driving the system toward the prescribed ratio are balanced by the other dynamics in the system. A similar comment applies to the producer. It is likely that the rate at which a consumer is driven toward its target ratio is much larger than the rate at which a producer is driven toward its target ratio. This might explain the wider range of observed phosphorus to carbon ratios in producers versus consumers.

Several of the terms in our model could be replaced by altering our assumptions. For example, because we have $rP - bP^2$ as the self-limited birth rate term, we could use $\mu(rP - bP^2)s$ instead of μPs. In addition, the s could also be modified to be $f(s)$, so we could use $\mu(rP - bP^2)f(s)$ for the uptake of phosphorus from the sediment by the producer. Using an $f(s)$ function could allow the uptake to be linear at first and level off as time goes on, similar to the $f(P)$ function used in the models in this paper. Another possibility could be to use $\frac{s}{S}$ instead of s to have $\mu(rP - bP^2)\frac{s}{S}$ as the uptake term. This way the uptake rate would depend on the ratio of phosphorus to carbon in the sediment. In this case, all six equations would be needed.

An alternate interpretation could be used for the bP^2 term. It can be considered as a reduction in the birth rate or an increase in the death rate. We considered it as a reduction in the birth rate so $rP - bP^2$ is the self-limited birth rate. However if it is considered as an increase in the death rate, we would need to include corresponding terms in the sediment carbon

and phosphorus equations.

Other possible future work could include trying to use limiting values to get our 5-dimensional model with stoichiometry to reduce to the model by Loladze, Kuang, and Elser. Within our system, possibilities include making it closed for phosphorus (i.e. set $IN = d_4 = d_3 = 0$), trying different values for each m, using different $f(P)$ functions, or trying to find bifurcations in terms of another variable, such as IN or μ, instead of r.

9   Appendix

Our equations use the Unit Step expression to include stoichiometry in the model. The software *Mathematica* could not solve for the equilibrium points of the full 5D system in terms of a single parameter when all remaining parameters were fixed. Because of this, we considered the following six cases.

1. $\frac{c}{C} > \theta_1$ and $\theta_3 < \frac{p}{P} < \theta_4$

2. $\frac{c}{C} > \theta_1$ and $\frac{p}{P} < \theta_3$

3. $\frac{c}{C} > \theta_1$ and $\frac{p}{P} \geq \theta_4$

4. $\frac{c}{C} \leq \theta_1$ and $\theta_3 < \frac{p}{P} < \theta_4$

5. $\frac{c}{C} \leq \theta_1$ and $\frac{p}{P} < \theta_3$

6. $\frac{c}{C} \leq \theta_1$ and $\frac{p}{P} \geq \theta_4$

In each case a loop was used to give a value for r and then find the corresponding equilibria and eigenvalues for the equilibria. Next the ratio of $p : P$ and $c : C$ had to be checked to see if the conditions were satisfied for the case to determine whether or not the equilibria given were feasible. Finally, we looked at the eigenvalues of the feasible equilibria in each case to find potential bifurcations.

Although we used the Unit Step expression to include stoichiometry, there are several possible expressions that could have been used for the stoichiometry terms including $if - then$ or $arctan$. However, for these expressions, *Mathematica* was not able to solve for equilibrium points in terms of a single parameter when all other parameters were fixed. The software also had difficulty solving for equilibrium points when all parameters were fixed.

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